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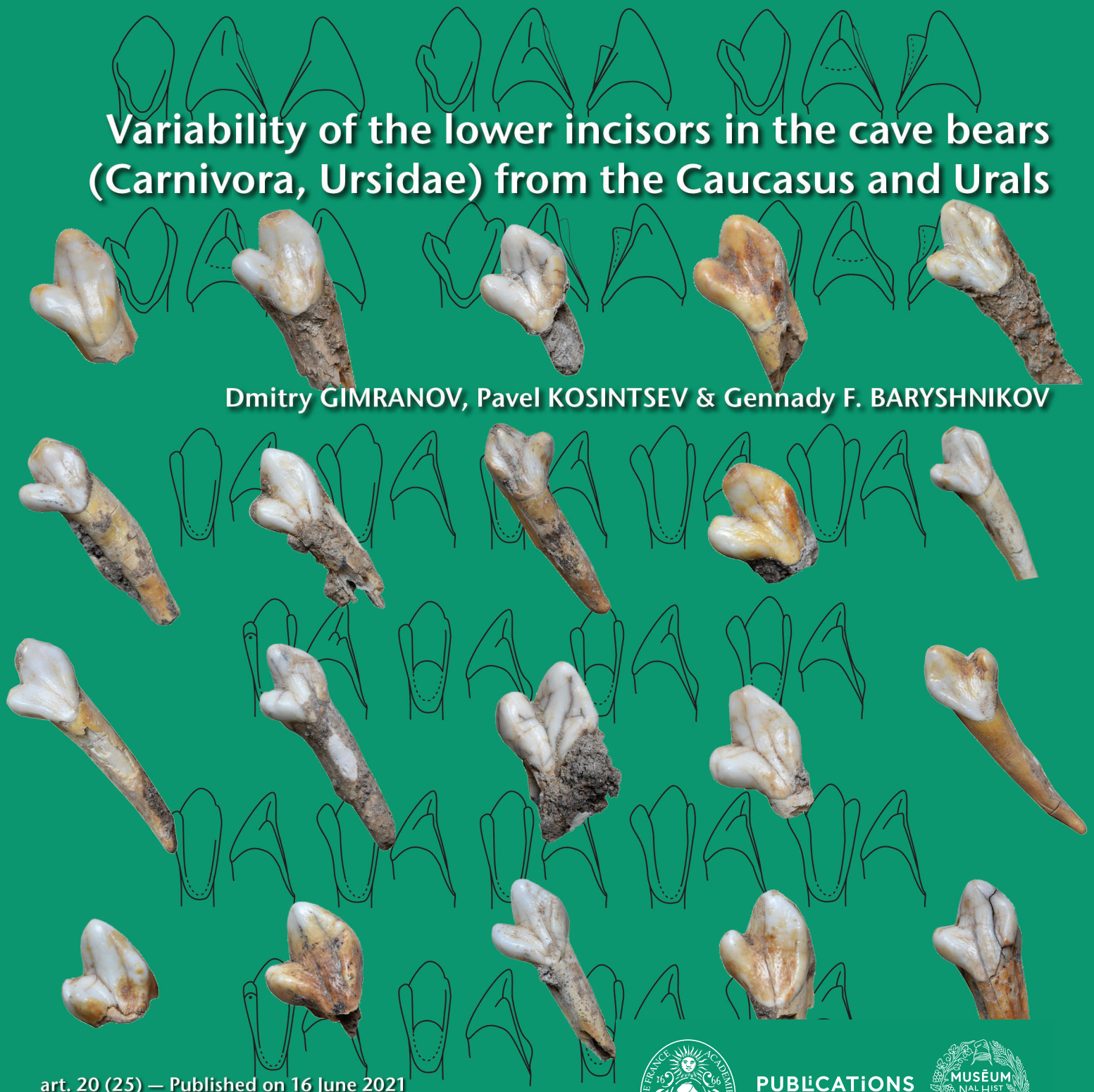

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Variability of the lower incisors in the cave bears (Carnivora, Ursidae) from the Caucasus and Urals

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ABSTRACT
Morphometric and morphotypic variability of the cave bear lower incisors from two different geographic regions (Caucasus and Urals), different stratigraphic periods (Middle and Late Pleistocene), and bearing different mitochondrial haplogroups (*kudarensis* (Baryshnikov, 1985) and *ingressus* Rabeder, Hofreiter & Withalm, 2004) was studied. Urals *Ursus kanivetz* Vereshchagin, 1973 is clearly distinguished from Caucasian *U. kudarensis* by morphology of the upper and lower incisors. The Urals cave bear exhibits more derived features compared to the Caucasian cave bears. *Ursus kanivetz* exhibits the largest average size of the lower incisors. The lower incisors of *U. kanivetz* are clearly distinct from those in *U. kudarensis*. Also, *U. kudarensis* specimens display a clear separation from all other groups of cave bears. Morphology of the incisors of the cave bears is clearly different from that of Early Pleistocene *U. etruscus* G. Cuvier, 1823, as well as from that of recent *U. arctos* L., 1758 (Rabeder, 1999) and *U. maritimus* Phipps, 1774. Our results suggest that the incisors of the cave bears are similar to each other and demonstrate a hypocarnivorous adaptation as a major evolution trend in the lineage of *Spelearctos* group. These adaptation features were perhaps developed in parallel in different lineages of the cave bears (*U. spelaeus* Rosenmüller, 1794 and *U. kanivetz* on the one hand and *U. kudarensis* on the other hand) in the Late Pleistocene.

KEY WORDS
Carnivora,
Ursidae,
Pleistocene,
Caucasus,
Ural,
cave bears,
morphotypes,
size,
variations,
lower incisor.

RÉSUMÉ
Variabilité des incisives inférieures chez les ours des cavernes (Carnivora, Ursidae) du Caucase et de l'Oural.
La variabilité morphométrique et morphotypique des incisives inférieures de l'ours des cavernes de deux régions géographiques différentes (Caucase et Oural), de différentes périodes stratigraphiques (Pléistocène moyen et tardif) et portant différents haplogroupes mitochondriaux (*kudarensis* (Baryshnikov, 1985) et *ingressus* Rabeder, Hofreiter & Withalm, 2004) a été étudiée. *Ursus kanivetz* Vereshchagin, 1973 se distingue clairement de *U. kudarensis* par la morphologie des incisives supérieures et inférieures. L'ours des cavernes ouralien présente des caractéristiques plus dérivées que les ours des cavernes caucasiens. *Ursus kanivetz* présente la plus grande taille moyenne des incisives inférieures. Les incisives inférieures de *U. kanivetz* sont clairement distinctes de celles de *U. kudarensis*. De plus, les spécimens d'*U. kudarensis* présentent une nette séparation par rapport à tous les autres groupes d'ours des cavernes. La morphologie des incisives des ours des cavernes est clairement différente de celle de l'ancien *U. etruscus* G. Cuvier, 1823, ainsi que de celle des modernes *U. arctos* L., 1758 (Rabeder, 1999) et *U. maritimus* Phipps, 1774. Nos résultats suggèrent que les incisives des ours des cavernes sont similaires les unes aux autres et démontrent une adaptation hypocarnivore comme tendance majeure dans l'évolution de la lignée du groupe *Spelearctos*. Ces caractéristiques d'adaptation ont peut-être été développées parallèlement dans différentes lignées d'ours des cavernes (*U. spelaeus* Rosenmüller, 1794, *U. kanivetz* et *U. kudarensis*) au Pléistocène tardif.

MOTS CLÉS
Carnivora,
Ursidae,
Pléistocène,
Caucase,
Oural,
ours des cavernes,
morphotypes,
taille,
variations,
incisive inférieure.

INTRODUCTION

Cave bear remains are often found in abundance in the Middle to Upper Pleistocene levels of cave deposits. The cave bear (*Ursus spelaeus* Rosenmüller, 1794) is one of the best studied European Pleistocene faunal representatives (Kurtén 1955, 1976; Musil 1980). Cave bear's cheek teeth, skulls, mandibles and post-cranial elements are usually described applying a morphological approach (Rode 1935; Erdbrindk 1953; Rabeder 1999; Baryshnikov 2007; Rossi & Santi 2011; Wagner & Cernak 2012; Jiangzuo *et al.* 2018; Heteren *et al.* 2019). The number of publications about the cave bear has increased markedly over the past 20 years (e.g. Figueirido & Heteren 2019). However, insufficient attention was paid to the incisors, although they that are also of great interest since these teeth play an important role in bear foraging. Though the cave bears are believed to be herbivorous animals eating mainly hard vegetable food (Bocherens *et al.* 1994; Bocherens 2015; Krajcarz *et al.* 2016), there are alternative points of view (Robu *et al.* 2013, 2018; Bocherens 2019).

Cave bear incisors are larger and have a more complex morphology compared to the incisors of recent brown bear, *Ursus arctos* L., 1758 (Rabeder, 1999). The incisors of the cave bears from western Europe were described by several authors (Grandal d'Anglade 1993; Rabeder 1999; Rabeder *et al.* 2005, 2016; Tsoukala *et al.* 2006; Frischauf 2014; Frischauf *et al.* 2017; Knaus *et al.* 2018). But there are almost no data on the structure of the cave bear incisors from the Caucasus and Urals in the literature, excepting a single publication on the upper incisors (Baryshnikov *et al.* 2019). The present arcticle, which deals with the lower incisors, sets out to continue the study, started in this previous publication.

The data obtained previously revealed the presence of several major clades of the cave bears, which can correspond to separate species (Knapp *et al.* 2009; Rabeder *et al.* 2009; Baca *et al.* 2012; Stiller *et al.* 2014). Analyses of mitochondrial DNA have shown that cave bears from the Caucasus comprise a group genetically distinct from those found in Europe (Knapp *et al.* 2009; Stiller *et al.* 2009; Dabney *et al.* 2013). The Caucasian cave bear *U. kudarensis* (Baryshnikov, 1985) has intensified this interest at the present time. *Ursus kudarensis* became isolated earlier than the Middle Pleistocene bear *U. deningeri* von Reichenau, 1904 from Europe. Deninger's bear is considered to be the ancestor of the Late Pleistocene European species *U. spelaeus* and *U. kanivetz* Vereshchagin, 1973, for which we accept two separate geographical subspecies, *U. k. kanivetz* (Urals) and *U. k. ingressus* Rabeder, Hofreiter & Withalm, 2004 (Eastern Europe up to Volga River). The species name *kanivetz* has priority over *ingressus* due to earlier publication date (Baryshnikov & Puzachenko 2017, 2019a, b; Baryshnikov *et al.* 2018).

Incisors of *U. kudarensis* from two localities in the southern Caucasus (the Kudaro 1 Cave and Kudaro 3 Cave) and the incisors of *U. kanivetz kanivetz* from three localities in the Urals (the Secrets Cave (Tain Cave), the Ignatievskaya Cave and the Zapovednaya Cave) (Fig. 1) were studied. The remains of Ural cave bears belong to the *ingressus* haplogroup discovered in Central and Eastern Europe (Baca *et al.* 2012; Stiller *et al.* 2014).

Remains of *U. kudarensis* from the Kudaro 1 Cave and Kudaro 3 Cave localities belong to two chronosubspecies, namely *U. k. praekudarensis* (Baryshnikov, 1998) (Middle Pleistocene) and *U. k. kudarensis* Baryshnikov, 1985 (Late Pleistocene) (Baryshnikov, 1998). In our previous publication (Baryshnikov *et al.* 2019) we did not define the subspecies status of *U. kudarensis* from the Middle Pleistocene deposites of the Kudaro 3 Cave (layers 5-8) because specimens were early classified as transitional between the two subspecies (Baryshnikov 1998).

TABLE 1. — Data on geography and geological age of the studied samples of the cave bear incisors.

Taxon	Cave name	Location	Data	Age	References
U. k. praekudarensis (Baryshnikov, 1998)	Kudaro 1 (layer 5)	42°31'N, 43°38'E (Southern Ossetia)	360.000 ± 90.000 BP(RTL-379); 350.000 ± 70.000 BP (RTL-373)	Middle Pleistocene	Lioubine 1998
U. kudarensis (Baryshnikov, 1985)	Kudaro 3 (layers 5-8)		252.000 ± 51.000 BP; 245.000 ± 49.000 BP	Middle Pleistocene	
U. k. kudarensis Baryshnikov, 1985	Kudaro 1 & 3 (layers 3-4)		44.150 ± 2.400/1.850 BP (Gr-6079); >41.600 BP (OxA-19611); 47.900 ± 2.500 BP (OxA-19612); 47.700 ± 1.800 BP (OxA-19613)	Late Pleistocene	Lioubine 1998; Baryshnikov 2011, 2016
U. kanivetz Vereshchagin, 1973	Zapovednaya Cave	54°33'N, 57°16'E (Southern Urals)	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)	Late Pleistocene	Kosintsev *et al.* 2013
	Ignatievskaya Cave	54°54'N, 57°47'E (Southern Urals)	41.900 ± 1.200 BP (OxA-10887); >27.620 BP (IPAE-59); >27.500 BP (IEMEG-723); >27.500 BP (IPAE-21)	Late Pleistocene	Smirnov *et al.* 1990; Kosinsev *et al.* 2016
	Secrets Cave	59°25'N, 57°46'E (Middle Urals)	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)	Late Pleistocene	Baryshnikov 2007; Pacher & Stuart 2009

The aims of this paper were to: 1) study evolution of the cave bear lower incisors from different stratigraphic levels of the Kudaro caves; and 2) trace changes in morphology of the cave bear lower incisors from different genetic lineages and geographically remote areas.

MATERIAL AND METHODS

GEOGRAPHY AND GEOLOGICAL AGE

Data on geography and geological age of the studied samples are presented in Table 1. A detailed description of the samples is provided in our previous work (Baryshnikov *et al.* 2019).

Material of the Caucasian cave bear (*U. kudarensis*) is housed in ZIN RAS (Zoological Institute of Russian Academy of Sciences in Saint Petersburg). Material of the Urals cave bear (*U. kanivetz*) is housed in IPAE RAS (location numbers: nos 639, 253, 810). The studied incisors were assigned to six sets: *U. k. praekudarensis* (the Kudaro 1 Cave, layer 5), *U. k. kudarensis* (the Kudaro1 Cave and Kudaro 3 Cave, layers 3-4), *U. kudarensis* (the Kudaro 3, layers 5-8), and three sets of *U. kanivetz* from the Urals (the Secrets Cave, the Zapovednaya Cave and the Ignatievskaya Cave). Hereinafter the set of *U. kudarensis* (the Kudaro 3, layers 5-8) is specified as *U. kud.* (K3, 5-8). A description of the entire sample is provided in Table 2.

The measurements were taken according to Rode (1935) and to Baryshnikov (2007): L, greatest length; W, greatest width. Measurements were taken with calipers to the nearest 0.1 mm. All measurements are in mm. The measurements were not taken off the worn teeth. Dental size differences between the groups of cave bear 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. Dental nomenclature follows those of Rabeder (1999). The morphodynamic index (MI) (Rabeder 1999) was calculated on the basis of the identified morphotypes.

ABBREVIATIONS

CA correspondence analysis;
L lenght;
MI morphodynamic index;
PCA principal component analysis;
W width.

DESCRIPTION OF TEETH MORPHOTYPES

The i1 morphotypes

The i1 morphotypes differentiate by the degree of development of the cingulum and the number of cusps (Fig. 2):

A1 distoconid (Dd) present;
A2 distoconid and cingulum around the lingual side (mesial (mC) + distal (dC) cingulum) are present;
A3 mesioconid (Msd) present, mesioconid is smaller than distoconid.

The i2 morphotypes

The i2 morphotypes are characterized by the presence, number and degree of development of the cusps (Fig. 2):

A1 distoconid present;
A2 distoconid very large;
A3 mesioconid present, distoconid is not large;
A4 mesioconid present, distoconid very large;
A5 mesioconid and distoconid very large;
B mesioconid present and double distoconid present too;
C1 distoconid and lingual cusp are present;
C2 mesioconid, distoconid and lingual cusp are present;
C3 mesioconid, lingual cusp and distoconid very large are present.

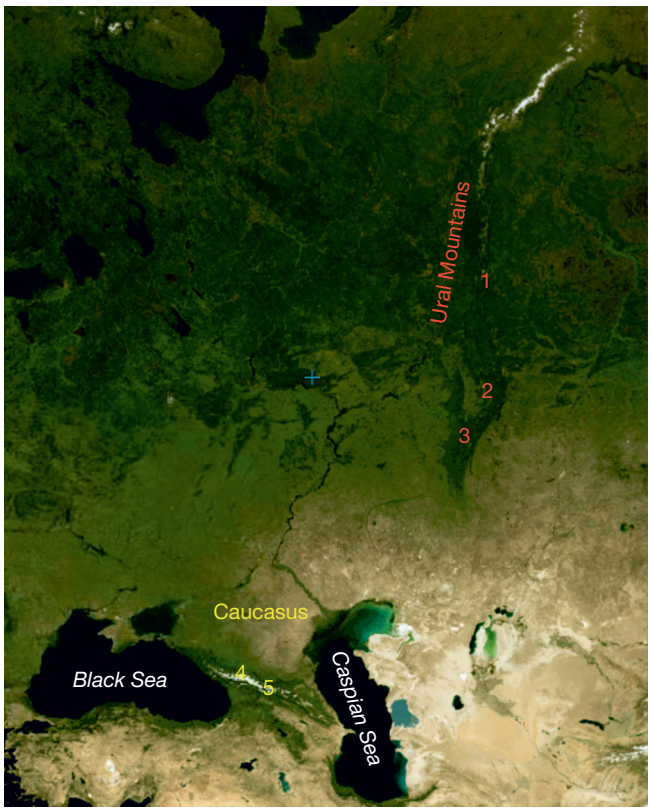

Fig. 1. — Map of the cave bear localities. *Ursus kanivetz* Vereshchagin, 1973: **1**, Secrets Cave; **2**, Ignatievskaya Cave; **3**, Zapovednaya Cave. *Ursus kudarensis* (Baryshnikov, 1985): **4**, Kudaro 1 Cave; **5**, Kudaro 3 Cave.

The i3 morphotypes

The i3 morphotypes differ in the morphology by the presence, number and degree of development of the cusps (Fig. 3):

A1	without distoconid;
A2	distoconid is small;
A3	distoconid is large;
A4	mesioconid present;
A5	mesioconid is large;
B	distoconid is normal size and lingual cusp are present;
C1	distal additional cusp smaller then distoconid;
C2	distal additional cusp well development then distoconid;
D1	double mesioconid present;
D2	double mesioconid and double distoconid are present, distal additional cusp smaller then distoconid.

RESULTS

Morphotypic analysis

The i1 morphotype frequencies for the cave bears are given in Table 3. The *U. kanivetz* reveals the dominating morphotypes A1 and A2 (40.0 and 54.5%). The *U. kudarensis* has dominating morphotype A1 (68.1%); whereas the morphotype A2 is less common (26.4%). *Ursus k. kudarensis* and *U. k. praekudarensis* are close by the frequency of morphotypes, being distinguishable by a predominance of types A1 and A3 in *U. k. praekudarensis* (69.7 and 4.9%) unlike those in *U. k. kudarensis* (65.5 and 1.2%). Rare morphotype A3 is more often recorded in *U. kanivetz* and *U. k. praekudarensis*.

Table 2. — Samples of the cave bear incisors employed in this study.

Taxa	Locality	Tooth i1	i2	i3	Total
U. k. praekudarensis (Baryshnikov, 1998)	Kudaro 1 (layer 5)	144	144	148	436
U. kudarensis (Baryshnikov, 1985)	Kudaro 3 (layers 5-8)	39	46	52	137
U. k. kudarensis Baryshnikov, 1985	Kudaro 1 & 3 (layers 3-4)	84	87	103	274
U. kudarensis	All layers	267	277	303	847
U. kanivetz Vereshchagin, 1973	Zapovednaya Cave	14	30	129	173
	Ignatievskaya Cave	33	50	58	141
	Secrets Cave	10	17	22	49
	All sites	57	97	209	363
Total		324	374	512	1210

Table 3. — Frequency of the i1 morphotypes for the Caucasian and Ural cave bears.

Taxa		A1	A2	A3	Total
U. kanivetz Vereshchagin, 1973	n	22	30	3	55
	%	40.0	54.5	5.5	100
U. k. kudarensis (Baryshnikov, 1998)	n	55	28	1	84
	%	65.5	33.3	1.2	100
U. k. praekudarensis (Baryshnikov, 1998)	n	99	36	7	142
	%	69.7	25.4	4.9	100
U. kud. (K3, 5-8)	n	27	8	4	39
	%	69.2	20.5	10.3	100

The i1 morphotype frequenci of *U. kud.* (K3, 5-8) is similar to that of *U. k. praekudarensis*. The values of MI are high in *U. kanivetz* and are the lowest in *U. kudarensis* (Table 6).

The i2 morphotype frequencies are given in Table 4. The *U. kanivetz* is dominated by morphotype A3 (65.9%), co-dominant is morphotype A1 (22.4%). In *U. kudarensis* morphotype A3 is also dominant (81.9%), morphotype A1 is rarer (7.6%). *Ursus k. kudarensis* differs from *U. k. praekudarensis*, because the number of morphotypes encountered is much higher for the latter. Morphotypic diversity in *U.k. kudarensis* is low. The morphotype frequencies observed in *U. kud.* (K3, 5-8) are similar to both subspecies of the Caucasian cave bear, but differ in the frequent presence of morphotype A5 (10.8%). This is the reason that the MI values are high in the group of *U. kud.* (K3, 5-8). MI are high in *U. kudarensis* and are the lowest in *U. kanivetz* (Table 6).

The i3 morphotype frequencies are given in Table 5. Morphotypes A3 in all are dominant. The *U. kanivetz* and *U. kud.* (K3, 5-8) are similar and differ from other Caucasian cave bears in frequency of occurrence of morphotypes A3 (65.9 and 53.2%) and C1 (27.5 and 23.4%). *Ursus k. kudarensis* and *U. k. praekudarensis* are quite similar and differ in that the latter has many rare morphotypes (A1, A2, A5 and D1). These morphotypes have not been found in *U. k. kudarensis*. MI values are very high in *U. kud.* (K3, 5-8). MI in *U. kanivetz* is not as high, but higher than in *U. k. kudarensis* and *U. k. praekudarensis* (Table 6).

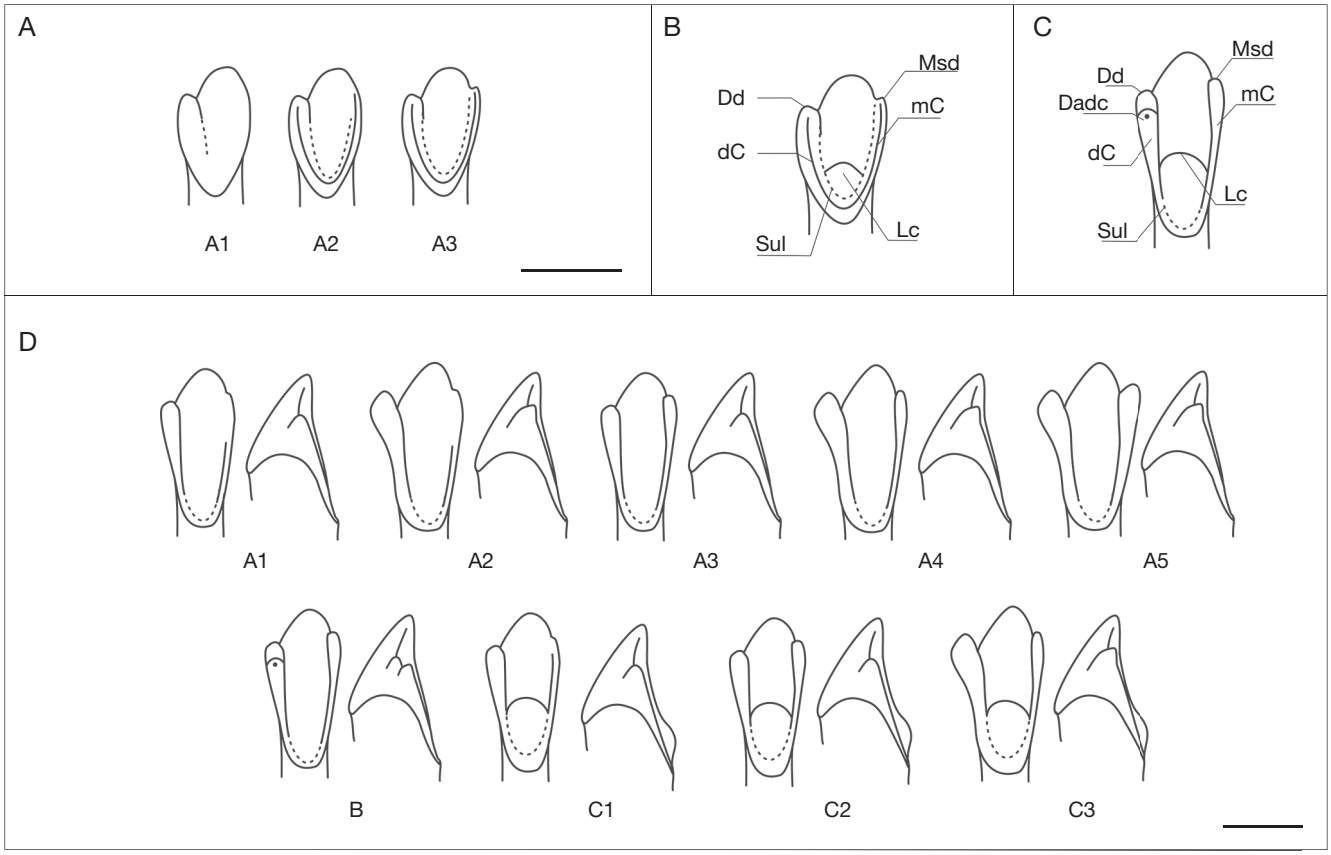

FIG. 2. — The i1 (**A**, **B**) and i2 (**C**, **D**) morphotypes of the cave bears; lingual and distal views. To identify the elements of the tooth crown we follow Rabeder (1999) and his terms with some modifications. Abbreviations: **Dadc**, distal additional cusp; **Dd**, distoconid; **dC**, distal cingulum; **Lc**, lingual cusp; **mC**, mesial cingulum; **Msd**, mesioconid; **Sul**, sulcus or groov. Scale bars: A, D, 10 mm.

TABLE 4. — Frequency of the i2 morphotypes for the Caucasian and Ural cave bears.

Taxa		A1	A2	A3	A4	A5	*B*	C1	C2	C3	Total
U. kanivetz Vereshchagin, 1973	*n*	19	3	56	3	0	1	2	1	0	85
	%	22.4	3.5	65.9	3.5	0.0	1.2	2.4	1.2	0.0	100.0
U. k. kudarensis (Baryshnikov, 1998)	*n*	6	0	83	2	0	0	0	0	0	91
	%	6.6	0.0	91.2	2.2	0.0	0.0	0.0	0.0	0.0	100.0
U. k. praekudarensis (Baryshnikov, 1998)	*n*	18	1	99	3	6	0	0	6	1	134
	%	13.4	0.7	73.9	2.2	4.5	0.0	0.0	4.5	0.7	100.0
U. kud. (K3, 5-8)	*n*	1	2	30	0	4	0	0	0	0	37
	%	2.7	5.4	81.1	0.0	10.8	0.0	0.0	0.0	0.0	100.0

TABLE 5. — Frequency of the i3 morphotypes forthe Caucasian and Ural cave bears.

Taxa		*A1*	*A2*	*A3*	*A4*	*A5*	B	*C1*	*C2*	*D1*	D2	Total
U. kanivetz Vereshchagin, 1973	*n*	0	0	59	3	0	1	25	0	2	1	91
	%	0.0	0.0	64.8	3.3	0.0	1.1	27.5	0.0	2.2	1.1	100.0
U. k. kudarensis (Baryshnikov, 1998)	*n*	0	0	102	3	0	0	3	5	0	0	113
	%	0.0	0.0	90.3	2.7	0.0	0.0	2.7	4.4	0.0	0.0	100.0
U. k. praekudarensis (Baryshnikov, 1998)	*n*	1	2	98	13	1	0	9	0	3	0	127
	%	0.8	1.6	77.2	10.2	0.8	0.0	7.1	0.0	2.4	0.0	100.0
U. kud. (K3, 5-8)	*n*	0	0	25	3	0	0	11	0	3	5	47
	%	0.0	0.0	53.2	6.4	0.0	0.0	23.4	0.0	6.4	10.6	100.0

TABLE 6. — Morphodynamic index in the cave bears groups: **1***, *U. kanivetz* Vereshchagin, 1973; **2**, *U. k. kudarensis* (Baryshnikov, 1998); **3**, *U. k. praekudarensis* (Baryshnikov, 1998); **4**, *U. kud*. (K3, 5-8).

			Taxa			
Incisors	**Morphotypes**	**Factor**	**1***	**2**	**3**	**4**
i1	A1	1	40.0	65.5	69.7	69.2
	A2	2	109.1	66.7	50.7	41.0
	A3	3	16.4	3.6	14.8	30.8
	Total		165.5	135.7	135.2	141.0
i2	A1	1	22.4	6.6	13.4	2.7
	A2	1.5	5.3	0.0	1.1	8.1
	A3	2	131.8	182.4	147.8	162.2
	A4	2.5	8.8	5.5	5.6	0.0
	A5	3	0.0	0.0	13.4	32.4
	B	3	3.5	0.0	0.0	0.0
	C1	2	4.7	0.0	0.0	0.0
	C2	3	3.5	0.0	13.4	0.0
	C3	3.5	0.0	0.0	2.6	0.0
	Total		180.0	194.5	197.4	205.4
i3	A1	1	0.0	0.0	0.8	0.0
	A2	2	0.0	0.0	3.1	0.0
	A3	2.5	162.1	225.7	192.9	133.0
	A4	3.5	11.5	9.3	35.8	22.3
	A5	4	0.0	0.0	3.1	0.0
	B	3.5	3.8	0.0	0.0	0.0
	C1	3.5	96.2	9.3	24.8	81.9
	C2	3.5	0.0	15.5	0.0	0.0
	D1	4.5	9.9	0.0	10.6	28.7
	D2	5.5	6.0	0.0	0.0	58.5
	Total		289.6	259.7	271.3	324.5
i1-i3	Total		635.0	590.0	603.9	670.9

MORPHOMETRIC ANALYSIS

As in the previous study (Baryshnikov *et al.* 2019), we cannot ignore the sexual dimorphism in the size of the incisors. 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 lower incisors (as well as of the upper incisors in Baryshnikov *et al.* 2019) is not pronounced in the examined groups of the cave bears.

The dimensions of the cave bear incisors are given in Table 7 and Figures 4-6. The size of the incisors *U. kanivetz* differs from that in *U. kudarensis*, it is observed in i1, i2 and i3 (Figs 4-6). The scatters of the i1 are the least overlapping, whereas the more overlap is observed in the i2 dimensions and largest overlap is observed in the i3 dimensions. The Caucasian cave bears form rather compact plots in the morphospace in terms of size of the i3 (Fig. 6). In terms of size i1 and i2 samples *U. kud.* (K3, 5-8) is slightly different from both samples *U. k. kudarensis* and *U. k. praekudarensis*. *Ursus kud.* (K3, 5-8) has larger first incisor i1. *Ursus k. kudarensis* and *U. k. praekudarensis* are very similar in size to the lower incisors (Table 7). *Ursus k. praekudarensis* has longer length (L) and width (W) variability limits (Table 7). The interspecific differences *U. kanivetz-U. kudarensis* are primarily observed in the tooth length.

DISCUSSION

MORPHOTYPIC ANALYSIS

U. kanivetz is quite isolated from other groups with regard to the i1 morphology (Fig. 7A). Other groups are located separately. *Ursus k. praekudarensis* and *U. kud.* (K3, 5-8) are close, as opposed to *U. k. kudarensis*. The PC1 experience the highest loadings from morphotypes A1 and A2, whereas for the PC2 – from morphotype A3 (Table 8). Loads are such because the frequencies of dominant morphotypes A1 and A2 are close in Caucasian cave bears (Table 3). The frequencies of dominant morphotype A1 are most similar in *U. k. praekudarensis* and *U. kud.* (K3, 5-8). The position of *U. kud.* (K3, 5-8) is plotted closer to *U. k. praekudarensis*.

As well as in the morphology of i1 *U. kanivetz* quite differs from other cave bears in the morphology of i2 (Fig. 7B). *Ursus k. kudarensis*, *U. k. praekudarensis* and *U. kud.* (K3, 5-8) are equidistant from each other. The position of *U. kud.* (K3, 5-8) is plotted closer to *U. k. kudarensis*. The PC1 experience the highest loadings from morphotypes A1, B and C1, whereas for the PC2 from morphotype C2 and C3 (Table 8). Loads occur because the *U. kanivetz* has a high frequency of sub-dominant morphotype A1 and not a high frequency of dominant morphotype A3, which is different from Caucasian cave bears. There are also loads because only *U. kanivetz* has morphotypes B and C1 and high frequency morphotypes A4. *Ursus k. praekudarensis* is located more isolated from *U. k. kudarensis* and *U. kud.* (K3, 5-8) because it has morphotypes C2 and C3, which are loaded by PC2.

Ursus kanivetz is quite isolated from other groups on with regard to the i3 morphology (Fig. 7C). The same situation is observed in morphology i1 and i2. Caucasian cave bears form a more compact group: *U. k. praekudarensis* and *U. k. kudarensis* closer to each other than a *U. kud.* (K3, 5-8). The PC1 experience the highest loadings from morphotypes A1, A2, A5 and C1, whereas for the PC2 from morphotyp C2 and D1 (Table 8). Only *U. k. praekudarensis* has morphotypes A1, A2 and A5 which explains the high loads on the PC1. *Ursus k. kudarensis* has no morphotype D1 and only *U. k. kudarensis* has morphotype C2. That explains the high loads on the PC2.

As the PCA results show, the position of *U. kanivetz* relative to Caucasian cave bears is more certain. In terms of the i1, i2 and i3 morphology *U. kanivetz* occupies an isolated position (Fig. 7). *Ursus k. praekudarensis* and *U. k. kudarensis* are less different from each other than the Ural cave bear. The position of *U. kud.* (K3, 5-8) varies between different of the incisors. Morphology i1 and i3 brings the *U. kud.* (K3, 5-8) centroid closer to *U. k. praekudarensis*, while based on the i3 morphology it is closer to *U. k. kudarensis* (Fig. 7). This result can reflect the transitional nature of this sample (transition from *U. k. praekudarensis* to *U. k. kudarensis*). We obtained the same conclusions from the study of upper incisors morphotypes in Caucasian and Ural cave bears (Baryshnikov *et al.* 2019). Previously, our studies have shown that the species and subspecies of cave bears are not clearly differentiated by using the PCA analysis of the upper incisors (Baryshnikov *et al.* 2019). It should be noted that despite the fact that the results of the

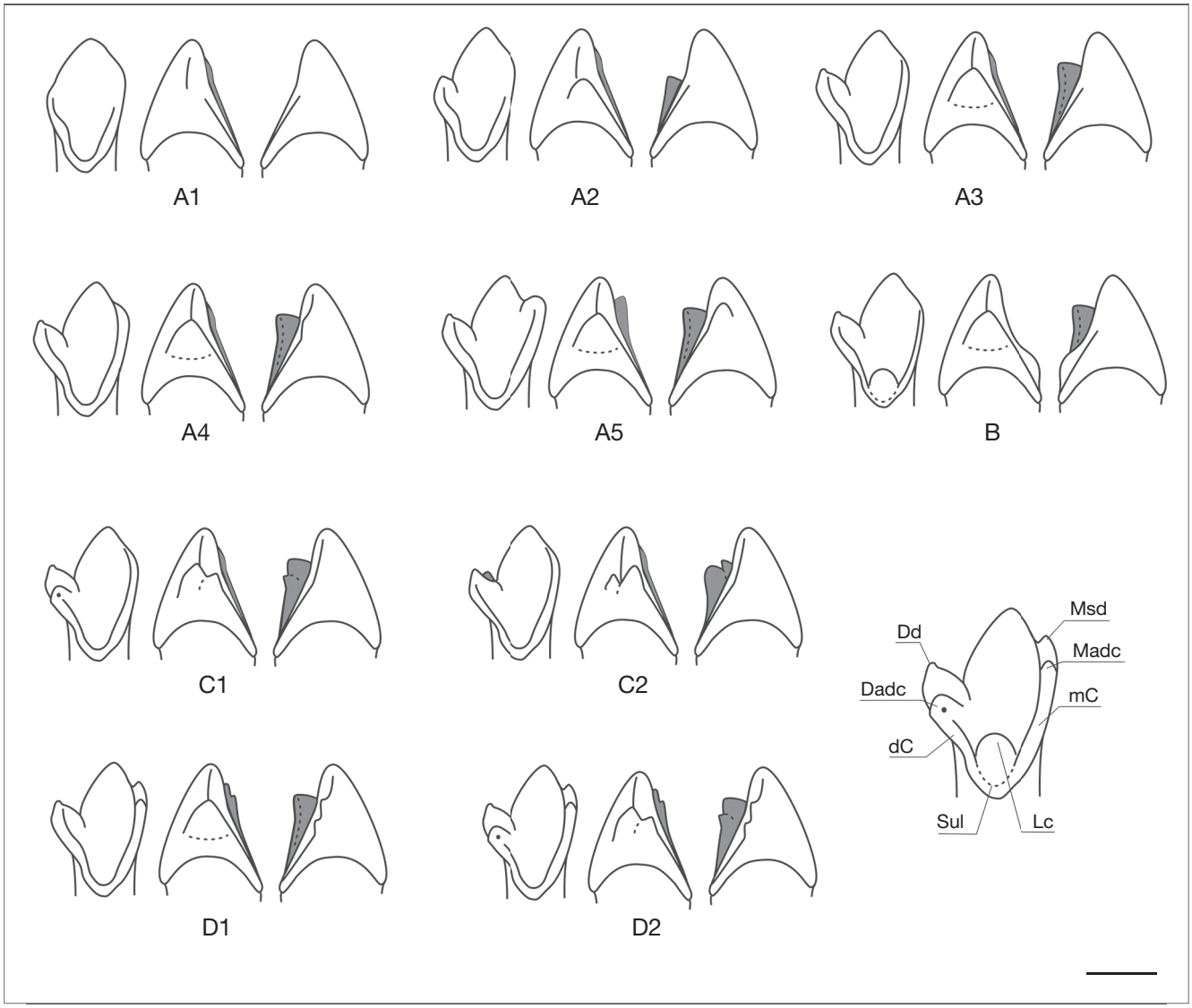

FIG. 3. — The i3 morphotypes of the cave bears; lingual, mesial and distal views. To identify the elements of the tooth crown we follow Rabeder (1999) and his terms with some modifications. Abbreviations: **Dadc**, distal additional cusp; **Dd**, distoconid; **dC**, distal cingulum; **Lc**, lingual cusp; **mC**, mesial cingulum; **Madc**, mesial additional cusp; **Msd**, mesioconid; **Sul**, sulcus or groov. Scale bar: 10 mm.

TABLE 7. — Measurements of the lower incisors in the cave bears from the Caucasus and the Urals (mm).

			i1		i2		i3	
Taxa	**Locality**	**Measure-ments**	**Lim (min-max)**	**Mean**	**Lim (min-max)**	**Mean**	**Lim (min-max)**	**Mean**
U. kanivetz Vereshchagin, 1973	Zapovednaya Cave	L	5.4-6.8	6.8	8.3-10.5	9.4	10.6-14.9	13.0
		W	7.6-9.8	9.2	9.4-13.6	11.6	10.7-14.5	12.5
	Secrets Cave	L	6.5-8.4	7.3	8.7-11.4	10.3	11.4-15.3	13.3
		W	8.4-10.7	9.6	9.5-12.7	11.1	10.5-14.3	12.4
	Ignatievskaya Cave	L	5.4-8.4	7.1	8.9-12.3	10.4	11.5-15.1	13.4
		W	7.5-10.7	9.2	9.3-13.1	11.0	9.9-15.3	12.2
All sites		L	5.4-8.4	7.1	8.3-12.3	10.1	10.6-15.3	13.2
		W	7.5-10.7	9.3	9.3-13.6	11.2	9.9-15.3	12.4
U. k. kudarensis (Baryshnikov, 1998)	Kudaro 1 & 3 (layers 3-4)	L	4.7-7.2	5.8	7.2-10.1	8.4	9.6-12.6	11.0
		W	6.5-9.8	8.3	8.1-11.4	9.9	8.8-12.7	10.8
U. k. praekudarensis (Baryshnikov, 1998)	Kudaro 1 (layer 5)	L	4.5-7.4	5.8	6.9-10.6	7.1	8.0-13.6	11.0
		W	6.8-9.9	8.3	7.1-12.5	10.0	8.8-13.1	10.8
U. kudarensis (Baryshnikov, 1985)	Kudaro 3 (layers 5-8)	L	4.8-7.2	6.0	7.0-10.9	8.6	9.5-12.3	11.0
		W	7.7-9.5	8.5	8.8-12.6	10.4	9.3-11.9	10.6
All sites		L	4.5-8.9	5.9	6.9-10.9	8.1	8.0-13.6	11.0
		W	6.5-9.9	8.4	7.1-12.6	10.1	8.8-13.1	10.7

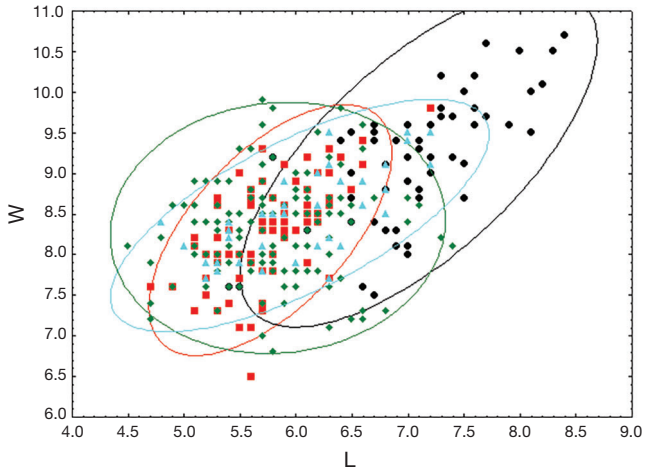

Fig. 4. — Length (**L**) and width (**W**) of the i1 in the cave bears. **Black circles**, *U. kanivetz* Vereshchagin, 1973; **red square**, *U. kudarensis kudarensis* (Baryshnikov, 1998); **green rhombus**, *U. k. praekudarensis* (Baryshnikov, 1998); **blue triangle**, *U. kud.* (K3, 5-8); ellipses delineate 95% of the empirical range.

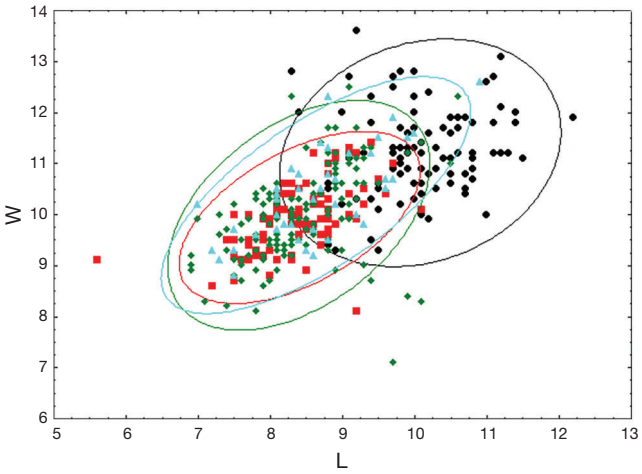

Fig. 5. — Length (**L**) and width (**W**) of the i2 in the cave bears. **Black circles**, *U. kanivetz* Vereshchagin, 1973; **red square**, *U. kudarensis kudarensis* (Baryshnikov, 1998); **green rhombus**, *U. k. praekudarensis* (Baryshnikov, 1998); **blue triangle**, *U. kud.* (K3, 5-8); ellipses delineate 95% of the empirical range.

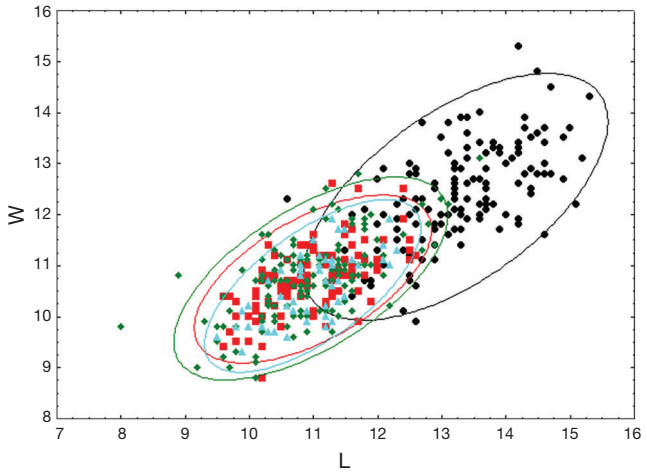

Fig. 6. — Length (**L**) and width (**W**) of the i3 in the cave bears. **Black circles**, *U. kanivetz* Vereshchagin, 1973; **red square**, *U. kudarensis kudarensis* (Baryshnikov, 1998); **green rhombus**, *U. k. praekudarensis* (Baryshnikov, 1998); **blue triangle**, *U. kud.* (K3, 5-8); ellipses delineate 95% of the empirical range.

lower incisors are more distinct, PCA analysis is not suitable for such studies.

Thus our next step is to apply CA to study the similarities and differences in morphotypes frequencies in the examined groups of the cave bears (Fig. 8A-D). The CA is typically used when analyzing the frequencies of qualitative features. The PCA is often used to analyze metric data.

In the cases of i1 and i2 position *U. kanivetz* seems clear. *Ursus kanivetz* is well distanced from Caucasian cave bears (Fig. 8A-B). But in the case of i3 such a situation is not observed. In the i3 structure is the furthest from the other cave bears *U. k. praekudarensis* (Fig. 8C). So in terms of the morphotype frequency of all lower incisors *U. kanivetz* is not very distant from other cave bears. In all cases i1-i3 separated look like *U. k. praekudarensis* (Fig. 8D).

The position of *U. kud.* (K3, 5-8) is less certain. In terms of the frequencies of the i1 morphotypes, this sample is closer to *U. k. praekudarensis* (Fig. 8A), while in terms of the frequencies of the i3 morphotypes – to *U. kanivetz* (Fig. 8C). In terms of the frequencies of the i2 morphotypes of *U. kud.* (K3, 5-8) equidistant from all groups (Fig. 8B), while in terms of the frequencies of the all teeth morphotypes closer to *U. k. kudarensis* (Fig. 8D). We can conclude that this reflects a transitional position of *U. kud.* (K3, 5-8). Previously based on CA results reported *U. kud.* (K3, 5-8) closer *U. k. kudarensis* in terms of the frequencies of the upper teeth morphotypes (Baryshnikov *et al.* 2019). The lower incisors do not exactly confirm these results. *Ursus kanivetz* is clearly distinguished from the *U. kudarensis* subspecies by morphotypes of the upper incisors (Baryshnikov *et al.* 2019). This result is confirmed in the case of i1 and i2. In the case of i3 *U. kanivetz* is no different from other cave bears.

MI values for Caucasian and Ural cave bears are presented in Table 6 and Figure 9. There is a strong similarity in the MI value of the i1-i3 in *U. k. kudarensis* and *U. k. praekudarensis*. The MI value of the i1 and i2 *U. k. kud.* (K3, 5-8) are quite similar to other samples from the Caucasus. Only i3 *U. kud.* (K3, 5-8) is more complicated. *Ursus kanivetz* differs from *U. k. kudarensis* and *U. k. praekudarensis* on MI values. i1 and i3 in *U. kanivetz* are more complex, while i2 has a simplified morphology. Data on MI values of the upper incisors more clearly show the evolutionary relationships within Caucasian cave bears (Baryshnikov *et al.* 2019).

Morphology of the cave bear lower incisors from numerous West European localities has been studied, but so far data on representative samples were only available for some caves in Austria (Rabeder 1999). In that study, Rabeder (Ibid.) described five morphotypes for the i1: A, B, C, C/D and D. Of these, morphotype A of Rabeder corresponds to morphotype A1 in the classification put forward in the present study. Rabeder's morphotypes C and C/D correspond to

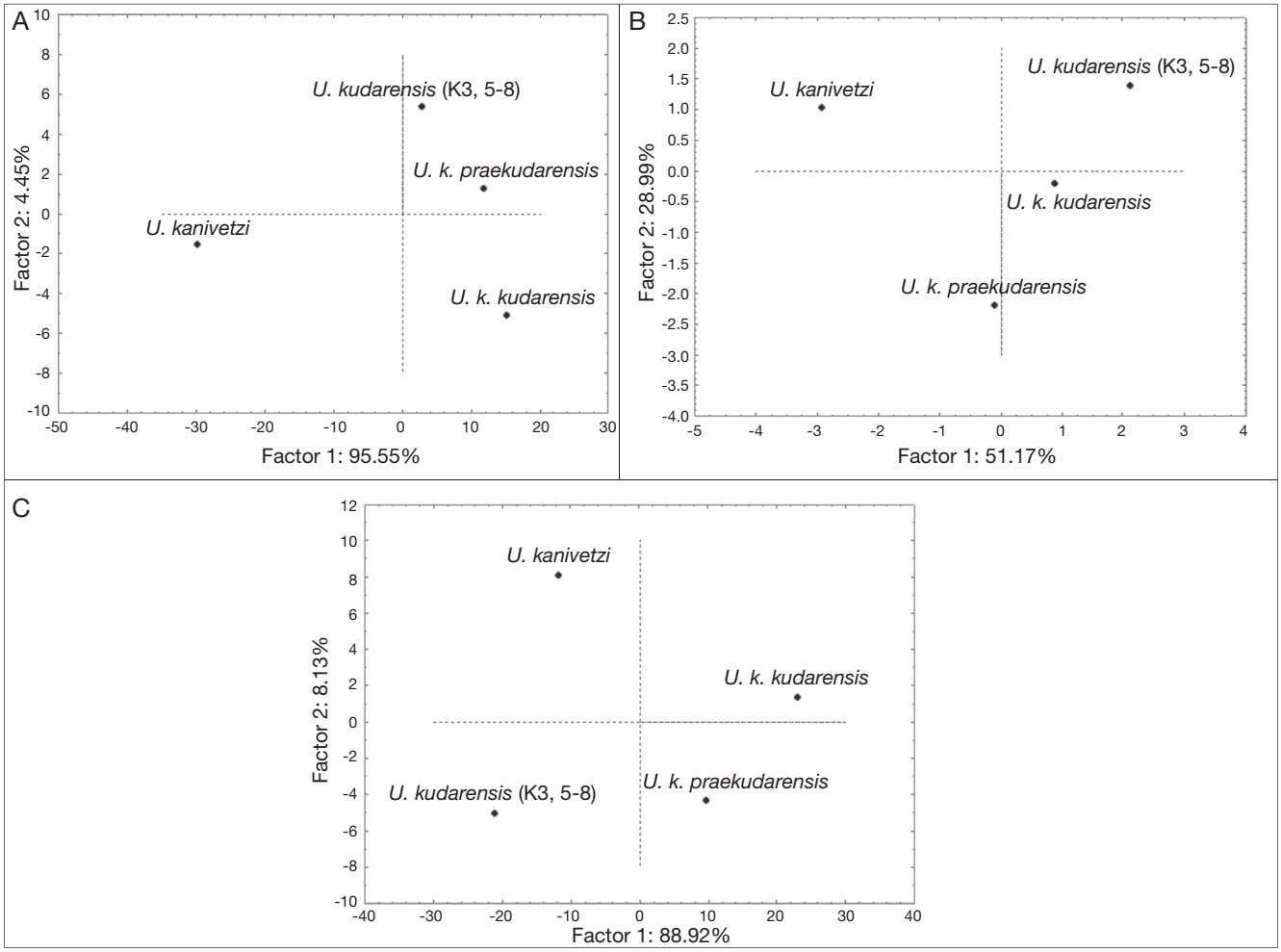

Fig. 7. — Principal component analysis based on the i1 (**A**), i2 (**B**), i3 (**C**) morphotype frequencies.

morphotypes A2 in our scheme, while morphotype D corresponds to A3, respectively. Rabeder's morphotype B has not been observed in the samples employed in the present study. According to Rabeder, in the samples from the Gamssulzenhöhle, Herdengelhöhle and Schwabenreith-Höhle caves belonging to *U. kanivetz ingressus* and *U. spelaeus eremus*, simple morphotypes A and B are predominant while the frequency of morphotype C is also relatively high (about 40%). In the Conturineshöhle (*U. s. ladinicus*), the frequency of A and B is as high as 84% while in the *U. deningeroides* Mottl, 1964 samples from the Repolust Cave these morphotypes were observed in 92% of specimens. According to the ratio of morphotypes A1 and A2 (our research), *U. k. kanivetz* is more similar to *U. k. ingressus* and *U. spelaeus eremus* Rabeder, Hofreiter & Withalm, 2004 while *U. kudarensis* is closer to *U. s. ladinicus* Rabeder, Hofreiter & Withalm, 2004 and *U. deningeroides*. A study of the samples from the Križna jama (Frischauf 2014) cave has shown that it is not possible to separate the cave bear species on the basis of the evolutionary level of the i1.

Rabeder (1999) describes three morphotypes of the i2: d ("deningeri"), d/s ("deningeri/spelaeus") and s ("spelaeus").

Table 8. — PC loadings of the morphotypic variables (percentage of morphotypes).

Variable		PC1	PC2
i1	A1	0.94842	0.31702
	A2	-0.99728	-0.07374
	A3	0.41034	-0.91193
i2	A1	-0.98925	-0.10233
	A2	0.07261	0.77814
	A3	0.77765	-0.03520
	A4	-0.90880	-0.24844
	A5	0.68645	0.20556
	B	-0.90491	0.42244
	C1	-0.90491	0.42244
	C2	-0.28419	-0.84184
	C3	-0.03093	-0.90610
i3	A1	0.87441	-0.46587
	A2	0.87441	-0.46587
	A3	0.67428	0.73806
	A4	0.60749	-0.78687
	A5	0.87441	-0.46587
	B	-0.46982	0.08922
	C1	-0.80619	-0.44889
	C2	0.162515	0.90853
	D1	-0.48638	-0.80837
	D2	-0.63437	-0.53857

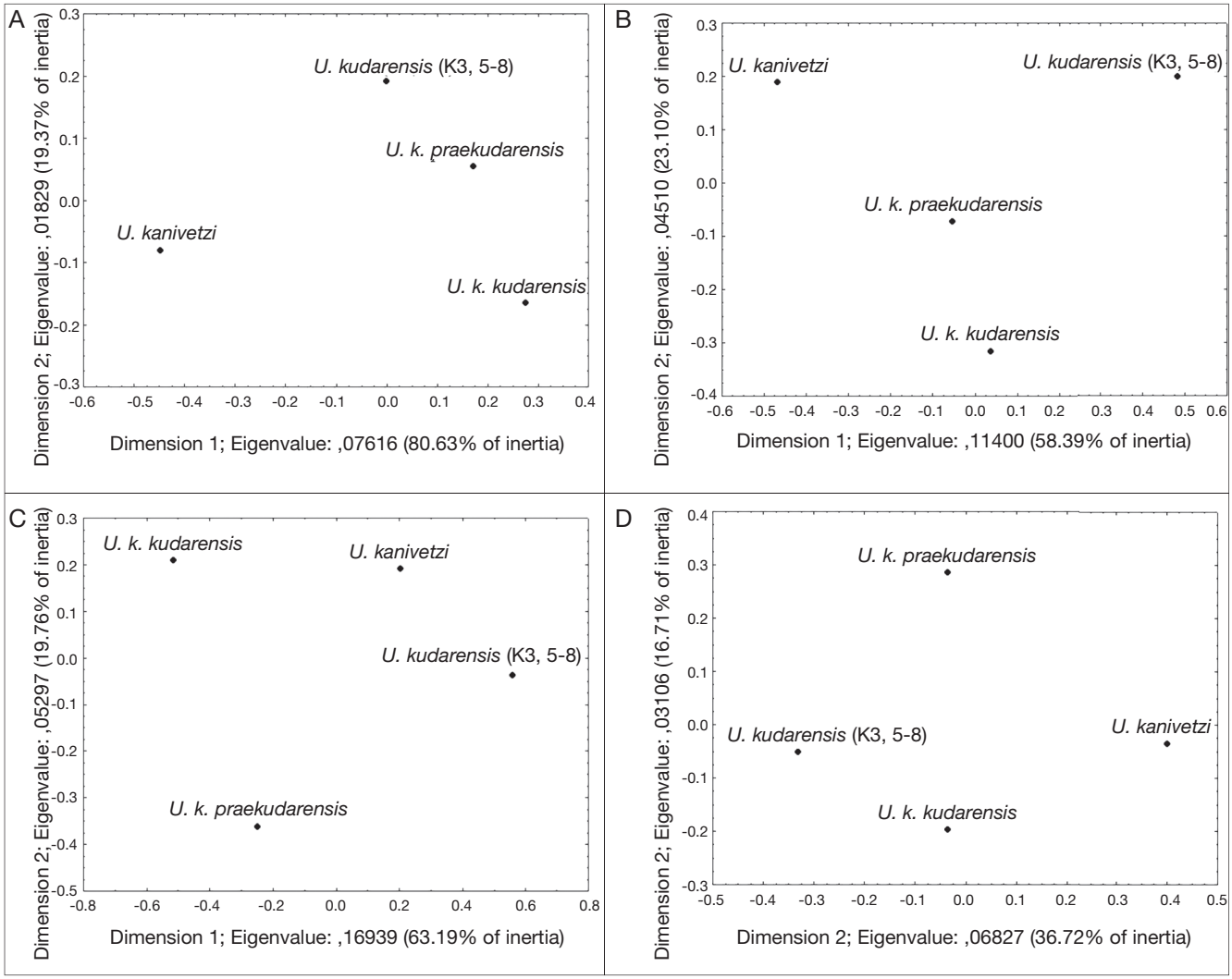

Fig. 8. — Correspondence analysis two-dimensional row plot, based on symmetrical normalization, illustrating the relationships among the four cave bears groups based on the i1 (**A**), i2 (**B**), i3 (**C**), i1-i3 (**D**) morphology.

Rabeder's morphotype d corresponds to morphotypes A1, A2, C1 in the our classification. Morphotype s corresponds to morphotypes A3, A4, A5, B, C2, C3, respectively. But our results cannot be directly compared with Rabeder's data beacuse of a difference in the total number of described morphotypes. As such, values of MI and evolutionary level cannot be compared as well. According to Rabeder (1999), in the *U. k. ingressus*, *U. s. eremus* and *U. s. ladinicus* samples from the Gamssulzenhöhle, Conturineshöhle, Herdengelhöhle and Schwabenreith-Höhle caves only "spelaeus" morphotypes were observed. In the *U. deningeroides* sample from the Repolust Cave, "deningeri" morphotypes are prevalent. In all the cave bear samples employed in this study, "spelaeus" morphotypes are predominant, but it is of note that the frequency of "deningeri" morphotypes in the cave bears from the Urals is also quite high (28.3%). This makes *U. k. kanivetz* more similar to *U. deningeroides* in terms of i2 morphology. Apparently, the cave bear species cannot be distinguished using features of the i2.

For the i3, Rabeder (1999) puts forward five morphotypes: A, B, B/C, C and D. Results of that study are hardly comparable with our own results since Rabeder did not described differences in development of the mesioconid, distoconid and lingual cusp for the samples he studied. Thus, Rabeder's and our morphotypes described in the present study for the i3 are particularly different. The only feature which can be compared is development of the mesial cingulum: it is not developed in morphotype A, weakly developed in morphotypes B and B/C, and well pronounced in morphotypes C and D. In our sample we have not found cases of the absence of the mesial cingulum. A weakly developed cingulum is found in morphotypes A1 and A2 while a strongly pronounced cingulum is typical of morphotypes A3, A4, A5, B, C1, C2, D1 and D2. According to Rabeder (1999), *U. k. ingressus*, *U. s. eremus* and *U. s. ladinicus* display an i3 with a developed mesial cingulum (morphotypes C-D), and only *U. deningeroides* exhibits a large number of i3 with a weakly pronounced mesial cingulum (morphotypes A and B). The cave bears from the Caucasus

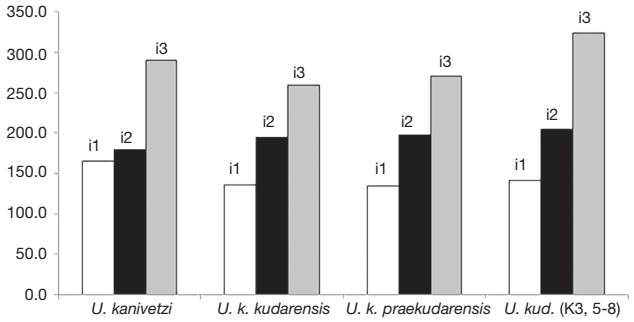

Fig. 9. — Ratio diagrams of the morphodynamic index (MI) of the lower incisors of the cave bears groups (according to (total) Table 6).

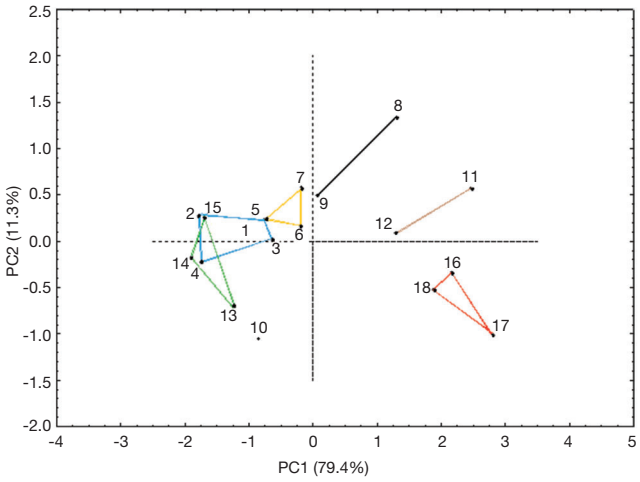

Fig. 10. — Morphological variability based on measurements of the lower incisors of the cave bears of Western Europe, the Caucasus and the Urals (PCA): **1**, Gamssulzenhöhle; **2**, Steigelfadbalm; **3**, Loutra Arideas bear cave; **4**, Križna jama; **5**, Herdengelhöhle; **6**, Schlenkendurchgangshöhle; **7**, Schwabenreith-Höhle; **8**, Conturineshöhle; **9**, Brieglersberghöhle; **10**, Eirós Cave; **11**, Dripstone cave of Flatz; **12**, Repolust; **13**, Zapovednaya Cave; **14**, Secrets Cave; **15**, Ignatievskaya Cave; **16**, Kudaro 1 & 3 (layers 3-4); **17**, Kudaro 1 (layer 5); **18**, Kudaro 3 (layers 5-8). Lines: **red**, *U. kudarensis* (Baryshnikov, 1998) (Caucasus); **green**, *U. kanivetz kanivetz* Vereshchagin, 1973 (Ural); **blue**, *U. kanivetz ingressus* Rabeder, Hofreiter & Withalm, 2004 (Western Europe); **yellow**, *U. spelaeus eremus* Rabeder, Hofreiter & Withalm, 2004 (Western Europe); **black**, *U. s. ladinicus* (Western Europe); **brown**, *U. deningeroides* Mottl, 1964 (Western Europe); **number 10**, *U. spelaeus* ssp. (Western Europe, see Table 9).

and Urals display an i3 with a developed mesial cingulum as well. An exception is *U. k. praekudarensis*: in the sample of this subspecies there were several teeth with a weakly pronounced mesial cingulum observed. These observations can be interpreted as an evidence of a similarity between the Middle Pleistocene *U. deningeroides* and *U. k. praekudarensis*. Many of the complex morphotypes of the i3 have not been ever observed in the West European cave bears (Rabeder 1999). This suggests a higher evolutionary level of i3 morphology in *U. kudarensis* and *U. k. kanivetz*. According to MI value, this level is the highest in *U. k. kanivetz*. But taken together our results demonstrate that morphology of the lower incisors cannot be used for separating the cave bear taxa.

Compared to the upper incisors (see Baryshnikov *et al.* 2019), the lower incisors almost do not exhibit features that are common for the Middle Pleistocene cave bears (i.e., *U. deningeroides* and *U. k. praekudarensis*). The lower incisors of *U. k. kanivetz* are in general more developed than in *U. kudarensis*.

Basic (primitive) morphology of the cave bear incisors is characterized by the absence of any additional elements on the tooth crown, while derived morphology shows development of certain additional elements. Morphotypes A1 are primitive for the i1, whereas morphotype A1 and C1 are primitive for the i2, and morphotypes A2, A3 and B – for the i3.

This gives us an evidence to suggest that *U. k. praekudarensis* retains some archaic features of the first lower incisor while *U. k. kanivetz* retains archaic features of the second lower incisor, and, finally, *U. k. kudarensis* displys such features of the third lower incisor. Regularity is not observed. In general, *U. k. kanivetz* exhibits more derived features than the Caucasian cave bears.

Morphometric analysis

Data on the size of the lower incisors in European cave bears from published works were used to compare (Table 9). Data on the length (L) and width (W) of the teeth were used by PCA (Fig. 10). The analysis included data on the teeth sizes of *U. k. ingressus* from Austria (Gamssulzenhöhle, Herdengelhöhle), Switzerland (Steigelfadbalm), Slovenia (Križna jama) and Greece (Loutra Arideas bear cave) (Rabeder 1999; Tsoukala *et al.* 2006; Frischauf 2014; Frischauf *et al.* 2017). The analysis included data of *U. s. eremus* from Austria (Herdengelhöhle, Schwabenreith-Höhle, Schlenkendurchgangshöhle) (Rabeder 1999; Knaus *et al.* 2018). Also analysis included data of *U. s. ladinicus* from Austria (Conturineshöhle and Brieglersberghöhle) (Rabeder 1999; Rabeder *et al.* 2005) and *U. deningeroides* from Austria (Dripstone cave of Flatz, Repolust) (Rabeder 1999; Rabeder *et al.* 2016). The analysis included data of *U. spelaeus* ssp. from Spain (Eirós Cave) (Grandal d'Anglade 1993).

Position of the samples in Figure 10 mainly shows that the size of the incisors in *U. k. kanivetz* is larger compared to *U. k. ingressus*. The lower incisors of *U. kanivetz* are clearly distinct from those in *U. kudarensis*. Also, *U. kudarensis* specimens display a clear separation from all other groups. The *U. kud.* (K3, 5-8). sample demonstrates similarity to *U. k. kudarensis*. On the contrary, *U. kud.* (K3, 5-8) is distant from *U. k. praekudarensis*.

U. k. praekudarensis displays an isolated position compared to *U. k. kudarensis* and *U. kud.* (K3, 5-8) also in terms of the size of the upper incisors (Baryshnikov *et al.* 2019). Specimens belonging to *U. s. eremus*, *U. s. ladinicus* and *U. deningeroides* are separated. The *U. s. eremus* sample is close to *U. kanivetz* while the *U. deningeroides* sample is found closer to *U. kudarensis*. Such a clear picture is not observed for the upper incisors (Baryshnikov *et al.* 2019). The observed differences in locations of the cave bear samples (Fig. 10) are due to a small size of the lower incisors in *U. kudarensis*. *Ursus s. ladinicus* and *U. deningeroides* also display smaller lengths and widths of the teeth compared to *U. k. kanivetz* and *U. k. ingressus*. *Ursus kanivetz* exhibits the largest average size of the lower incisors (Table 9).

TABLE 9. — Sample means of the lower incisors measurements of the cave bears of Western Europe, the Caucasus and the Urals.

Taxa	Locality	i1 L	i1 W	n	i2 L	i2 W	n	i3 L	i3 W	n
U. kanivetz ingressus Rabeder, Hofreiter & Withalm, 2004	Gamssulzenhöhle	6.6	8.8	40	9.7	10.9	33	13.2	12.5	60
U. k. ingressus	Steigelfadbalm	6.9	9.2	2	11.0	11.3	1	13.0	12.1	2
U. k. ingressus	Loutra Arideas bear cave	6.5	8.8	58	9.9	11.1	113	12.7	11.8	107
U. k. ingressus	Križna jama	6.9	9.4	15	10.0	11.2	5	13.4	12.6	17
U. spelaeus eremus Rabeder, Hofreiter & Withalm, 2004 + *U. k. ingressus*	Herdengelhöhle	6.7	9.2	30	9.7	10.3	26	13.2	11.9	33
U. s. eremus	Schlenkendurchgangshöhle	6.5	8.8	50	9.7	10.7	98	12.6	11.4	111
U. s. eremus	Schwabenreith-Höhle	6.2	8.4	40	9.9	10.4	34	12.7	11.8	30
U. s. ladinicus Rabeder, Hofreiter & Withalm, 2004	Conturineshöhle	5.9	7.5	40	9.5	9.6	40	12.3	10.8	30
U. s. ladinicus	Brieglersberghöhle	6.3	8.5	22	9.6	10.3	40	12.7	11.5	52
U. spelaeus ssp.	Eirós Cave	6.2	9.8	8.0	10.1	11.3	3	11.8	12.4	13
U. deningeroides Mottl, 1964	Dripstone cave of Flatz	5.4	7.5	4	8.6	9.8	3	11.4	10.4	3
U. deningeroides	Repolust	5.8	8.2	30	9.1	10.2	40	11.6	11.2	30
U. kanivetz kanivetz Vereshchagin, 1973	Zapovednaya Cave	6.8	9.2	14	9.4	11.6	29	13.0	12.5	57
U. k. kanivetz	Secrets Cave	7.3	9.6	10	10.3	11.1	17	13.3	12.4	21
U. k. kanivetz	Ignatievskaya Cave	7.1	9.2	33	10.4	11.0	49	13.4	12.2	54
U. kudarensis kudarensis Baryshnikov, 1985	Kudaro 1 & 3 (layers 3-4)	5.8	8.3	81	8.4	9.9	83	11.0	10.8	106
U. k. praekudarensis (Baryshnikov, 1998)	Kudaro 1 (layer 5)	5.8	8.3	143	7.1	10.0	140	11.0	10.8	145
U. kudarensis ssp.	Kudaro 3 (layers 5-8)	6.0	8.5	37	8.6	10.4	39	11.0	10.6	51

It is most likely that the size of the lower incisors confirms the taxonomic differences in the studied taxa of cave bears better compared to the size of the upper incisors. But more data on *U. s. ladinicus* and *U. deningeroides* is required to confirm this conclusion. In terms of the size of both upper and lower incisors, *U. kud.* (K3, 5-8) is closer to the Late Pleistocene *U. k. kudarensis*. Thus, we show that morphology of the incisors of the cave bears contains a taxonomic and phylogenetic information.

Comparison with other species of the genus *Ursus*

Ursus etruscus Cuvier, 1823 is the ancestor of the cave and brown bears, because of that we consider the structure of incisors of this species more precisely. The data on morphology of the lower incisors of Early Pleistocene *U. etruscus* is very scarce. All known *U. etruscus* i1 have following patterns: distoconid is present, lingual cusps are absent, mesioconid is absent (Teilhard de Chardin 1940; Medin *et al.* 2019). General type of structure i1 *U. etruscus* is similar to morphotype A1. *Ursus etruscus* i2 has following patterns: distoconid is present, lingual cusps are absent (Teilhard de Chardin 1940; Medin *et al.* 2019). Mesioconid is absent in *U. etruscus* from Dmanisi (Medin *et al.* 2019), but is present in *U. etruscus* from Choukoutien (Teilhard de Chardin 1940). General type of structure i2 *U. etruscus* is close to morphotypes A1 or A3. *Ursus etruscus* i3 has following epatterns: distoconid is present, lingual cusps are absent (Teilhard de Chardin 1940; Medin *et al.* 2019). General type of structure i3 *U. etruscus* is similar to morphotype A3.

The lower incisors of *U. deningeri* von Reichenau, 1906, the basal representative of the European cave bears, display a similar morphology to *U. etruscus*. All lower incisors of *U. deningeri* are characterized by a massive distoconid without additional cusps (Tchernov & Tsoukala 1997; Rabeder *et al.* 2009). The lower incisors of *U. deningeroides* from Repolust Cave (Rabeder 1999) show a very similar morphology to *U. deningeri*. Another cave bear species, *U. savini* Andrews, 1922, had a more developed morphology of the lower incisors (Borissiak 1932): i1 and i3 had additional lingual surface elements (grooves) of the crown, while i2 displayed a mesoconid. The incisors of *U. spelaeus sensu lato* (inc. *Ursus s. spelaeus*, *U. s. eremus*, *U. s. ladinicus*, and *U. k. ingressus*), like other teeth of the cave bears, are quite specific. Their crowns have a lot of additional elements: lingual cusps, mesioconids and grooves on the lingual surface. The general structure of the *U. spelaeus sensu stricto* lower incisors is similar to *U. kanivetz* and *U. kudarensis*.

From existing literature on the Late Pleistocene brown bear incisors (Pacher 2007; Gimranov & Kosintsev 2017) we know that the lower incisors of *U. arctos priscus* Goldfuss, 1818 are characterized by a distoconid on every tooth and absence of additional elements of the crown (Pacher 2007). The lower incisors of *U. arctos* from Severnaya Cave (Middle Ural) have some additional cusps (Gimranov & Kosintsev 2017). Recent species *U. arctos* and *U. maritimus* Phipps, 1774 display a simplified structure of the lower incisors, while only the polar bear has mesioconid on i2 (Gimranov & Kosintsev 2017).

The results for the lower incisors are consistent with the data obtained for the upper incisors (Baryshnikov *et al.* 2019). The evolutionary lineage from *U. etruscus* to *U. arctos* is thought to be the main in the genus *Ursus* (Baryshnikov, Puzachenko, 2019). In general, the brown bear is similar to the Etruscan bear in terms of morphology of the lower incisors that preserve primitive patterns in morphology of the incisors and other teeth. On the contrary, the cave bears are an independent evolutionary lineage of the phylogenetic tree of the genus *Ursus* (Baryshnikov 2007; Rabeder *et al.* 2009). The cave bear developed a strong hypocarnivorous trend, which manifests

itself in an increased number of additional crush and grind elements on the teeth. These adaptative features were perhaps developed in parallel in different evolutionary lineages of the cave bears (*U. spelaeus*, *U. kanivetz* and *U. kudarensis*) in the Late Pleistocene. Similar data were previously obtained based on the study of the Caucasian bear's cheek teeth size (Baryshnikov & Puzachenko 2019a, b). This is also confirmed by phylogenetic isolation of the Caucasian cave bears.

CONCLUSION

The upper and lower incisors of the cave bears are morphologically similar but have different trends of variability among species. While *U. k. praekudarensis* retains some archaic features of the first lower incisor, *U. k. kanivetz* exhibits archaic elements of the second lower incisor. *Ursus k. kudarensis* displays the very same features of the third lower incisors. A consistent pattern is not found. *Ursus kud.* (K3, 5-8) is closer to *U. k. kudarensis* in terms of the frequencies of the upper teeth morphotypes (Baryshnikov *et al.* 2019). But the lower incisors do not exactly confirm these results. *Ursus kanivetz* is clearly distinguished from *U. kudarensis* by morphology of the upper incisors (Baryshnikov *et al.* 2019). But this result only applies to the i1 and i2. In general, the Urals cave bear exhibits more derived features compared to the Caucasian cave bears.

The size of the lower incisors in *U. k. kanivetz* is larger compared to *U. k. ingressus*. *Ursus kanivetz* exhibits the largest average size of the lower incisors. Nevertheless, the lower incisors of *U. kanivetz* are clearly distinct from those in *U. kudarensis*. Also, *U. kudarensis* specimens display a clear separation from all other groups. In terms of the size of both upper and lower incisors, *U. kud.* (K3, 5-8) is closer to the Late Pleistocene *U. k. kudarensis*. The *U. s. eremus* and *U. s. ladinicus* are close to *U. kanivetz* while the *U. deningeroides* is found closer to *U. kudarensis*. It is most likely that the size of the lower incisors better confirms the taxonomic differences in the studied species of cave bears compared to the size of the upper incisors. Sexual dimorphism of the lower incisors is not pronounced in the examined groups of the cave bears.

Morphology of the incisors of the cave bears is clearly different from that of the recent *U. arctos* and *U. maritimus*, as well as from that of ancient *U. etruscus*. *Ursus deningeri* and *U. deningeroides*: their incisors are more primitive, while the incisors of *U. savini*, *U. kudarensis*, *U. spelaeus sensu lato*, and *U. kanivetz* are more advanced. In general, the incisors of the cave bears are similar to each other and demonstrate a hypocarnivorous adaptation as a major trend in the evolution of the lineage of *Spelearctos* group. Additional elements on the occlusal surface are the adaptation of the cave bears to a specific diet based on hard vegetables. These adaptation features were perhaps developed parallel in different lineages of the cave bears (*U. spelaeus*, *U. kanivetz* and *U. kudarensis*) in the Late Pleistocene. *Ursus kudarensis* was separated from other cave bears in the early Middle Pleistocene and has lived in isolation for a long time. However, *U. kudarensis* developed some similar adaptive teeth features with other cave bears, apparently in parallel.

One more main conclusion of this study coincides with the previously published observation (Baryshnikov *et al.* 2019): incisors morphology is as important and informative in terms of studying cave bear phylogeny, as more commonly used cheek teeth. In this study, we show that morphology of the incisors of the cave bears contains valuable taxonomic and phylogenetic information.

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