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Morphometric analyses of cave bear mandibles (Carnivora, Ursidae)

Gennady F. BARYSHNIKOV[1*], Andrei Yu. PUZACHENKO[2] & Svetlana V. BARYSHNIKOVA[1]

1 *Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, 199034 Saint Petersburg, Russia*
2 *Institute of Geography, Russian Academy of Sciences, Staromonetnyi per. 29, 109017 Moscow, Russia*
* *Corresponding author: E-mail: g_baryshnikov@mail.ru*

Abstract
Morphometric variability of cave and brown bears and their ancestors (*Ursus minimus* and *U. etruscus*) is examined using multivariate statistics based on measurements of 679 mandibles from 90 localities in Northern Eurasia. The variability is dependent on sexual dimorphism in size: it is well seen in big cave bears (*U. spelaeus*, *U. kanivetz = ingressus, U. kudarensis*), whose males are nearly 25% larger than females. In the morphological space, we identified two main types of mandibles: the "arctoid" type [*U. minimus*, *U. etruscus, U. arctos, U. rodei* (?)], and the "spelaeoid" type (*U. spelaeus spelaeus*, *U. s. eremus, U. kanivetz*, *U. kudarensis*). The intermediate "deningeroid" type includes *U. deningeri*, *U. savini*, *U. rossicus* (males), and *U. spelaeus ladinicus*. An additional unit is formed by female sample of *U. rossicus*. The mandible bones are less informative for understanding of cave bear evolution, because in comparison to crania, they have a rather simple shape.

Keywords
Ursus, cave bears, morphometrics, variations, mandible, evolution, adaptation, Pleistocene.

Résumé
Analyse morphométrique de la mandibule chez les ours des cavernes. - La variabilité morphométrique des ours des cavernes, des ours bruns et de leurs ancêtres (*Ursus minimus* et *U. etruscus*) est étudiée à partir des mesures de 679 mandibules de 90 sites d'Eurasie du nord, à l'aide des méthodes d'analyses statistiques multivariées. La variabilité dépend du dimorphisme sexuel pour la taille, plus important chez les grands ours des cavernes (*U. spelaeus, U. kanivetz = ingressus, U. kudarensis*), dont les mâles ont une taille de 25 % supérieure à celle des femelles. Pour la morphologie, nous distinguons deux principaux types de mandibule: le type « arctoïde » [*U. minimus, U. etruscus, U. arctos, U. rodei* (?)] et le type « spéléen » (*U. s. spelaeus, U. spelaeus eremus, U. kanivetz, U. kudarensis*). Le type « deningeroïde », intermédiaire entre les deux, inclut *U. deningeri, U. savini, U. rossicus* (mâles) et *U. ladinicus*. Un type secondaire est représenté par le groupe *U. rossicus* femelle. En raison de leur forme relativement simple, les informations apportées par les mandibules paraissent moins riches d'enseignements que les crânes pour apprécier l'évolution des ours des cavernes.

Mots-clés
Ursus, ours des cavernes, morphométrie, variations, mandibule, évolution, adaptation, Pléistocène.

1. INTRODUCTION

Fossil remains of cave bears (subgenus *Spelearctos* of the genus *Ursus*) are known from numerous Pleistocene localities of Europe, the Caucasus, as well as from Siberia and the Tien Shan (Baryshnikov, 2007). These big animals inhabited forest, forest-steppe, and steppe landscapes, occurring in mountains up to the Alpine belt. Recent studies show significant genetic diversity of cave bears. Analyses of ancient mtDNA revealed three evolutionary lineages for the Late Pleistocene, which are frequently regarded as separate species (Rabeder *et al.*, 2008; Knapp *et al.*, 2009; Rabeder *et al*., 2010; Stiller *et al*., 2014): *Ursus spelaeus* Rosenmüller, 1794 (Western Europe and Western Siberia), including subspecies *U. s. eremus* Rabeder, Hofreiter, Nagel & Withalm, 2004 (Alps and Altai Mountains) and *U. s. ladinicus* Rabeder *et al*., 2004 (highlands in Alps), *U. ingressus* Rabeder *et al*., 2004 (Eastern Europe and Ural), and *U. kudarensis* Baryshnikov, 1985 including subspecies *U. k. praekudarensis* (Baryshnikov, 1998) (Caucasus and, probably, Northern Siberia).

Examination of the recent *U. arctos* L., 1758 from Hokkaido Island demonstrated morphometric differences between three genetic clades (Baryshnikov *et al*., 2004; Baryshnikov & Puzachenko, 2011). Previously, we used

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metric variability of skulls (Baryshnikov & Puzachenko, 2011) and metapodial bones (Baryshnikov & Puzachenko, 2017) to elucidate differences between the mitochondrial clades of cave bears. This paper presents the results of the morphometric analysis of mandible bones.

2. MATERIALS AND METHODS

The current study is based on 679 mandible bones and samples from more than 90 localities (Fig. 1, and Table 1) : *U. k. kudarensis* (n=26), *U. k. praekudarensis* (n=11), *U. d. deningeri* von Reichenau, 1904 (n=84), *U. spelaeus spelaeus* (n=118), *U. s. eremus* (n=29), *U. s. ladinicus* (n=6), *U. ingressus* (n=97), *U. kanivetz* Vereshchagin, 1973 (n=40), *U. rossicus* Borissiak, 1930 (n=28), and *U. savini* Andrews, 1922 (n=13). We also analysed several other fossil ursids to compare with cave bears: *U. minimus* Devèze de Chabriol & Bouillet, 1827 (n=10), *U. etruscus* G. Cuvier, 1823 (n=10), *U. rodei* Musil, 2001 (n=1) and fossil and recent *U. arctos* L., 1758 (n=206).
U. ingressus was found to genetically group with *Ursus spelaeus kanivetz* Vereshchagin, 1973 from Medvezhiya Cave (type locality of the last taxon) in Northern Urals (Baca *et al*., 2012; Stiller *et al*., 2014). The cave bears from other localities of Urals geographical region, Bol'shoy Glukhoy Grotto and Serpievskaya Cave, also belong to the "*ingressus*" haplogroup (Stiller *et al*., 2010). Therefore, according to rules of International Code of Zoological Nomenclature, cave bears belonging to "*ingressus"* haplogroup should be denominated by *Ursus kanivetz* (= *ingressus*). A craniometrical difference was detected between the populations from Eastern Europe and Urals (Baryshnikov & Puzachenko, 2011); hence, in the present study we analyze two separate geographical samples: *U. kanivetz* (Urals) and *U. ingressus* (Eastern Europe up to Volga River).
The authors have examined collections of the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg, Russia), Borissiak Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia), National Museum of Natural History of National Academy of Sciences (Kiev, Ukraine), Finnish Museum of Natural History (Helsinki, Finland), Natural History Museum (London, UK), Staatliches Museum für Naturkunde (Stuttgart, Germany), Niedersächsischen Landesmuseum (Hannover, Germany), Muséum National d'Histoire Naturelle (Paris, France), Centre de Conservation et d'Etude des Collections du Musée des Confluences (Lyon, France), Institut für Paläontologie (Vienna, Austria), Moravské Museum (Brno, Czech Republic), Institute of Systematics and Evolution of Animals (Krakow, Poland), Dipartimento di Scienze della Terra, Sapienza Università di Roma (Roma, Italy).
Characteristics of cheek teeth wear show that the specimens belong to the adult age group (Baryshnikov,

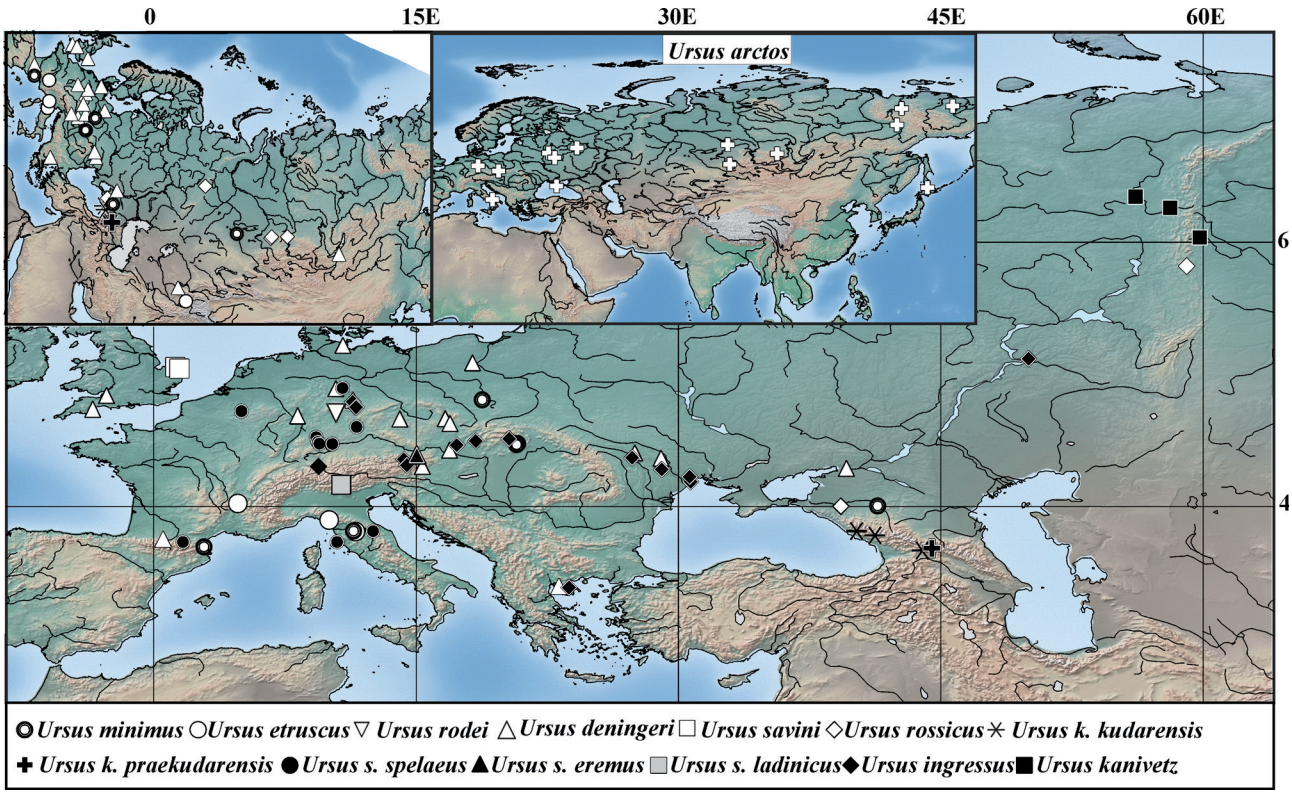

Fig. 1: Map of the fossil bear samples which were used in the present study.
Fig. 1: Carte de répartition des spécimens d'ours fossiles auxquels il est fait référence dans ce travail.

Table 1: The bears samples of mandible bones. Partition into males (M) and females (F) based on *a priori* determination and on results of discriminant analysis.

Species	Subspecies	Sample size, N		Total	Localities
		M	F		
U. kudarensis	*U. k. kudarensis*	10	16	26	Dagomys (Russia), Pskhu, Kudaro 1, Kudaro 3 (Georgia)
	U. k. praekudarensis	6	5	11	Kudaro 1 (Georgia)
U. spelaeus	*U. s. spelaeus*	48	70	118	Goyet, B5, B4 (Belgium), L'Herm (France), Zoolithen, Rübeland, Hohlenstein-Stadel, Charlottenhöhle, Sibyllenhöhle, Steinheim an der Murr, Baden-Württemberg (Germany), Buca delle Fate, Piobbico (Italy)
	U. s. eremus	14	15	29	Ramesch, Schwabenreith-Höhle, Drachenhöhle (Austria)
	U. s. ladinicus	2	4	6	Conturines (Italy)
U. kanivetz	*U. ingressus*	57	40	97	Gamssulzen, Taubach-Ehringsdorf, Burg Ranis (Germany), Stratenská jaskyňa = Psie diery, Tmavá skala, Medvedia (Slovakia), Styria (Austria), Wildkirchli (Switzerland), Shiriaevo 1, Mokhovoi (Russia), Il'inka, Odessa (Ukraine), Ikel R., Buteshty (Moldova), Petralona (Greece)
	U. kanivetz	11	29	40	Medvezh'ya Cave, Secrets (Russia)
U. rossicus		8	20	28	Krasnodar, Kizel, Bachatsk, Mokhovo, Berezhekovo (Russia)
U. deningeri	*U. d. deningeri*	28	54	82	Overstrand, Kent's cavern, Westbury-Sub-Mendip Quarry (UK), Mosbach, Holstein, Deutsch-Altenburg, Sussenborn, Hunes, Einhorn-Höhle (Germany), Czarnowo (Poland), Repolusthöhle (Austria), Gargas (France), Koneprusy, Chlum 1, Za Hájovnou Cave (Czech Republic), Azov Region, Tologoi (Russia), Petralona (Greece), Vykhvatintsy, Starye Duruitory (Moldova)
	U. d. batyrovi	2	-	2	Sel'-Ungur (Kyrgyzstan)
U. savini	*U. s. savini*	8	2	10	Forest Bed, E. Runton, Mundesley, Sidestrand (UK)
	U. s. nordostensis	1	2	3	Ulakhan-Sullar, Chersky, Duvanny Yar (Russia)
U. etruscus		6	4	10	Val Darno (Uppe Valdarno Basin), Olivola (Italy), Saint-Vallier (France), Kuruksai (Tadjikistan)
U. minimus		4	6	10	Gaville (Italy), Perpignan (France), Węże (Poland), Kosyakino (Russia), Moiseevka (Kazakhstan), Včeláre 2 (Slovakia), Osztramos 7 (Hungary)
U. dolinensis		1	-	1	Untermassfeld (Germany)
U. arctos		150	56	206	Taubach-Ehringsdorf (Germany), Monte-Verde (Italy), Predmosti (Czech Republic), Eliseevichi, Sungir, Buran-Kaya, Nizhneudinskaya Cave, Krasny Yar, Razboinichya Cave, Duvanny Yar, Kura Sullar, Mamontovaya Gora, Smolensk, Voiny, Karakalinskaya, "European part of Russia", Kamchatka Peninsula, Kuril Islands (Russia), Kudaro 3 (Gergia), Odessa (Ukraine), Hokkaido (Japan)
Total		356	323	679	

2010). The scheme of measurements is in Fig. 2: GL – total length of mandible, Hd – height of the mandible in diastema, Hm1 – height of mandible behind m1, Hc – height of the vertical ramus, c1L and c1W – length and width of lower canines along the lower margin of enamel, c1_m3L – length of tooth row between c1 and m3, p4_m3L – length of tooth row between p4 and m3.

For the damaged fossil bones with incomplete sets of measurements, we use the expectation-maximization (EM) algorithm (Dempster *et al*., 1977) to estimate the missing values. The missing data were estimated for males and females separately, except for small samples of *U. spelaeus ladinicus, U. savini, U. etruscus*, *U. rodei* which were combined with samples *U. spelaeus eremus*, *U. rossicus*, and *U. arctos,* respectively. In all cases, the hypothesis that "values in a data set are missing

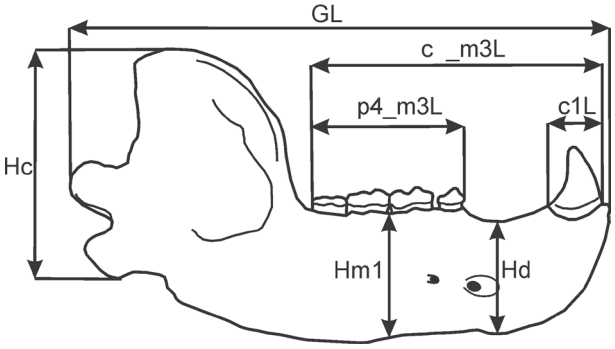

Fig. 2: Scheme of mandibular measurements in bears.
Fig. 2: Schéma de mensurations des mandibules d'ours.

completely at random" was accepted. EM estimates the mean, covariance matrix, and correlation of measures with missing values, using an iterative process. Statistical differences between the measures (average, variance) were tested by comparing the initial data set to the data set filled in by the EM method.

Sexual size dimorphism (*SSD*) in the *Ursus* lineage is primarily expressed through differences in total size of the canine teeth and some other features of the skull. A high degree of sexual size dimorphism in skull and canines has been observed for cave bears as well (Kurtén, 1955; Andrews & Turner, 1992; Baryshnikov & Puzachenko, 2011). Preliminary assessment of fossil bones belonging to one of the sexes has been done using the size of the lower canine (c1L, c1W). We checked SSD for different samples using the discriminant analysis. We then used these results to estimate missing values for measures of the mandible.

The sexual size dimorphism (*SSD*) ratio is calculated as $SSD=100 \times (M_{male}-M_{female}) / (M_{male}+M_{female})$, where M_{male}, M_{female} are means for males and females correspondingly. Average sexual size dimorphism (*ASSD*) was calculated according to expression:

$$ASSD = 1 / n \sum_{i=1}^{n} SSD_i,$$

where *n* is the number of mandible measurements (8).

The pipeline for multivariate analysis is described in detail in prior publications (Baryshnikov & Puzachenko, 2011; Puzachenko *et al*., 2017). Standardized measures are used to calculate square Euclidean distances matrix and a similarity matrix of Kendall's tau-*b* (corrected for ties), a measure describing association among all pairs of mandibles for males and females jointly and separately. Nonmetric Multidimensional Scaling (NMDS) technique (Davison & Jones, 1983) was used to construct two types of the multivariate models (morphological space or morphospace). The Euclidean metric integrally describes the variability of mandible size, while the Kendall's coefficient is the difference between the probabilities that the observed rank data describes the coordination of variation between different measurements of two specimens. As a result, we have a multidimensional model of morphospace, which reproduces the size diversity (SZM model), and a morphospace that reproduces variation in mandible proportions (shape) (SHM model). The dimensions of SZM and SHM models are marked as E1, E2… and K1, K2…, respectively.

The statistical analysis was carried out using STATISTICA v. 8.0 (StatSoft, Tulsa, OK, USA), PAST v. 3.12 (Hammer *et al*., 2001), NCSS 2007 (Hintze, 2007).

3. RESULTS

3.1 Canines

3.1.1 Sexual size dimorphism

The relative variance components (in %) that were explained by *SSD* were 35 – 40.5 (GL – Hd), 66.5 (c1L), and 59.8 (c1W). Therefore, the canines showed the greatest degree of sexual size dimorphism. Among cave bears (Table 2), the highest degree of sexual dimorphism was found in *U. s. spelaeus* where differences between males and females on average are 21.8% (c1L, *SSD*=12.3) and 25.5% (c1W, *SSD*=14.6). Small cave bear, *U. rossicus*, shows the lowest *SSD* (5.8, 3.5 for c1L and c1W, respectively). Among potential ancestors of cave and brown bears, the highest values of *SSD* were found in *U. minimus* (Table 2), but this result is probably incidental, since the sample size was very small. In the modern *U. a. arctos*, *SSD* of low canines is high (10.5, 12.2) and it is comparable to the result derived from cave bears. *U. etruscus* showed the lowest level of *SSD* (4.1, 8.9) within the last group.

We found a positive correlation between the size of male mandibles (GL) and *SSD* indexes in "spelaeoid" bears. The Coefficients of correlation were very high for spelaeoid bears – 0.92 for c1L and 0.88 for c1W. Correlations in females were lower (0.69, 0.65) and not statistically reliable. Therefore, we assume that the *SSD* of canines in cave bears is, first, a specific feature of male postnatal growth, and secondly, is related to general size allometry. There is no correlation between mandible size (measure Hc) and *SSD* in *U. minimus*, *U. etruscus*, and *U. arctos*.

3.1.2. Variation in size and shape of canines among taxa

The relative variance in components of c1L and c1W associated with taxa on the background of *SSD* is not high – 11.8 and 23.0 percent. Therefore, under such conditions, it is appropriate to analyze males and females separately (Fig. 3). In addition to two measures of canine, we use an "elongation factor" (EF) calculated as 100*(c1L/c1W).

According to the results shown in Fig. 3, taking into account the difference between males and females, there are three variants of the crown base length and width ratio.

Table 2: Measures of mandible (GL – CW) in males (M) and females (F) and sexual size dimorphism indexes (*SSD*, *ASSD)* in the different taxa of bears

	GL	c_m3	p4_m3	Hc	Hm1	Hd	cL	cW	*ASSD*
U. k. kudarensis									
M	309.7±6.08	182.3±1.99	100.8±0.87	143.1±3.53	70.2±1.41	63.8±1.38	27.4±0.53	20.2±0.51	
F	294.6±7.82	170.2±2.20	94.4±0.66	134.2±3.36	66.3±1.58	58.7±0.96	23.4±0.64	17.7±0.30	
SSD	2.5	3.4	3.3	3.2	2.8	4.2	7.8	6.6	4.2
U. deningeri									
M	301.0±6.09	180.0±2.28	100.6±1.10	133.6±4.45	63.4±1.35	57.4±1.19	24.3±0.40	18.0±0.30	
F	272.8±4.03	164.5±1.35	91.9±0.68	119.7±2.04	57.1±0.73	52.2±0.71	20.4±0.33	15.1±0.15	
SSD	4.9	4.5	4.5	5.5	5.3	4.8	8.6	8.0	5.8
U. s. spelaeus									
M	329.3±3.28	196.7±1.34	106.1±0.56	150.2±2.17	71.4±0.81	68.0±0.68	28.7±0.50	22.2±0.22	
F	289.9±2.52	176.2±1.08	98.2±.55	131.0±1.80	60.5±0.55	56.7±0.53	22.5±0.30	16.54±0.16	
SSD	6.4	5.5	3.9	6.8	8.3	9.1	12.3	14.6	8.4
U. s. eremus									
M	313.8±2.99	190.5±2.28	103.2±0.83	143.0±1.86	69.1±0.93	63.0±0.64	27.3±0.29	20.6±0.42	
F	291.6±4.84	179.2±1.76	99.1±1.45	128.5±2.92	62.1±1.43	58.3±1.16	22.6±0.46	16.9±0.51	
SSD	3.7	3.1	2.0	5.3	5.4	3.9	9.3	9.8	5.3
U. ingressus									
M	330.2±2.57	195.1±1.27	107.6±0.59	150.1±1.78	69.8±0.83	65.0±0.60	27.8±0.45	21.1±0.21	
F	294.4±2.57	174.5±1.30	99.3±0.66	128.0±1.41	57.5±0.66	54.8±0.47	22.0±0.64	16.9±0.32	
SSD	5.7	5.6	4.0	8.0	9.7	8.5	11.6	10.9	8.0
U. kanivetz									
M	314.9±2.43	191.3±2.05	109.1±1.70	142.0±1.03	69.7±1.75	66.2±1.84	30.1	-	
F	284.6±2.43	173.2±2.29	101.9±0.63	-	60.0±0.81	56.1±0.76	20.6	-	
SSD	5.1	5.0	3.4	-	7.5	8.2	-	-	-
U. rossicus									
M	262.4±3.46	161.3±3.68	92.7±1.05	121.5±0.50	54.7±1.98	51.0±1.46	23.8±0.87	17.0±0.33	
F	257.8±3.21	150.4±1.33	86.7±0.97	120.6±2.06	54.0±0.93	51.6±0.77	21.2±1.11	15.9±0.79	
SSD	0.9	3.5	3.4	n.s.	n.s.	n.s.	5.8	3.5	2.2
U. minimus									
M	-	129.9±2.75	72.7±2.42	93.9±10.70	39.7±2.95	42.4	24.6±0.68	14.3±0.34	
F	-	107.7±1.30	64.9±1.30	78.7	34.0±2.13	34.6±0.60	18.2±0.55	10.9±0.45	
SSD	-	9.3	5.7	-	7.7	-	14.9	13.7	-
U. etruscus									
M	242.0±16.50	148.5±2.94	79.8±2.23	96.9±2.67	43.2±0.79	44.8±0.96	23.5±0.99	15.7±0.65	
F	212.5±3.50	123.2±3.96	71.8±3.08	86.3	40.4±1.93	38.8±1.74	21.6±0.87	13.2±0.75	
SSD	6.5	9.3	5.3	-	3.4	7.2	4.1	8.9	-
U. arctos (all subspecies)									
M	250.5±1.47	149.8±0.70	83.8±0.44	110.9±0.75	47.8±0.43	46.0±0.38	24.4±0.52	17.4±0.33	
F	220.5±2.06	135.6±1.26	78.7±0.84	94.1±1.02	40.2±0.55	40.7±0.53	19.7±0.40	13.7±0.28	
SSD	6.4	5.0	3.1	8.2	8.7	6.1	10.6	11.7	7.5
U. a. arctos									
M	243.9±2.24	147.9±1.36	84.1±1.12	105.1±1.40	46.2±0.81	45.0±0.79	24.3±0.53	17.4±0.36	
F	219.6±3.64	135.1±2.15	78.5±1.36	93.8±1.63	40.1±0.88	40.7±0.82	19.7±0.50	13.6±0.36	
SSD	5.3	4.5	3.4	5.7	7.1	5.1	10.5	12.2	8.7

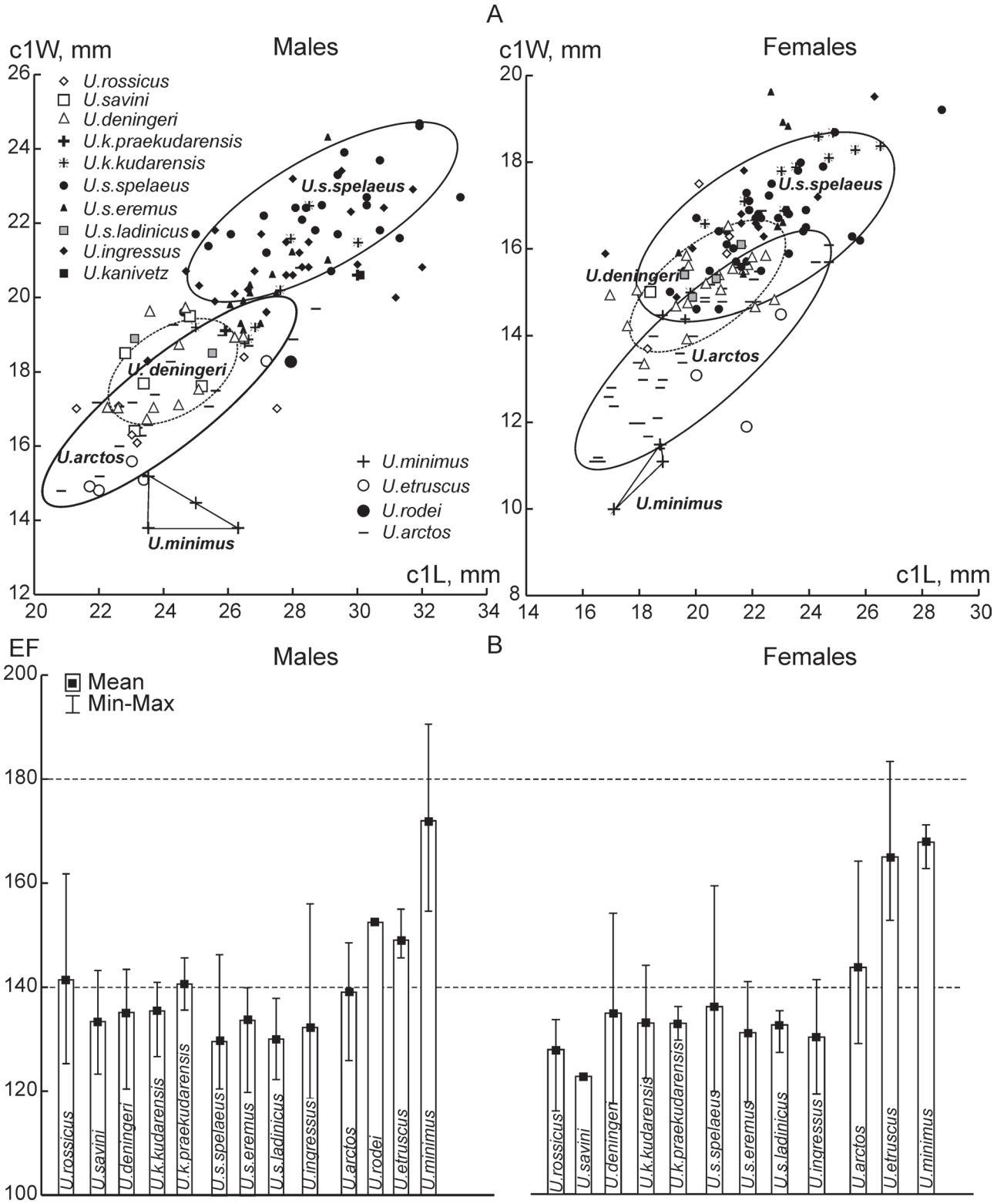

Fig. 3: Scatterplots of measurements of canines (c1L and c1W) in males and females (A), and "elongation factor" (EF) of canines in different bear taxa (B).

Fig. 3: Diagrammes de répartition des mesures des canines (c1L et c1W) des mâles et des femelles (A), et « facteur d'allongement » (EF) des canines des différentes espèces d'ours (B).

The first variant is associated with *U. minimus*: a small canine with an oblong base of crown; width of crown is about 52-65% of its length, "elongation factor" – 154-190. Etruscan bear, brown bear, and, possibly, *U. rodei* belong to the second variant: canines vary widely in size but have a more orbicular crown base – about 55-79% of the length with EF – 128-183. The last variant is found in typical "spelaeoid" bears (*U. s. spelaeus*, *U. ingressus*, *U. k. kudarensis,* and others). It is characterized by a large of canine size and a more or less orbicular shape of the crown base. The width of the crown is about 62-95% of the length and EF is 105-160. Intermediate positions on the described trend between *U. minimus* and *U. spelaeus* are occupied by *U. deningeri, U. savini, U. rossicus, U. k. praekudarensis* with canines of intermediate size. The width of crown in these taxa is about 62-88% of crown length, EF is about 114-160.

The dimensions of the lower canine in bears strongly depend on sex, and so have little significance in phylogenetic studies. Most pairwise differentiations (Table 3; Mann-Whitney U test used) observed on c1W. *U. deningeri* differ from that on *U. kudarensis*, *U. spelaeus*, *U. minimus,* and *U. etruscus*, but are close to small cave and brown bears in the size and shape of the crown. Etruscan and brown bears with *U. minimus* significantly differ from the group of cave bears in dimensions of crown as well as by EF.

3.2 Mandible

3.2.1 Sexual size dimorphism

SSD indexes of measures describing general size of mandible (GL, Hc, Hm1, Hd, Table 2) vary within a wide range, from 0-0.9 in small cave bear (sexual dimorphism is statistically dubious or absent) to 8-12 in *U. s. spelaeus*, *U. ingressus*, and subspecies of brown bear, *U. arctos piscator* Pucheran, 1855. On this background, *SSD* measures that describe tooth row and diastema length (c1_m3L, p4_m3L) are lower on average, except c1_m3L in *U. minimus* (Table 2). A relatively low level of *ASSD* index was observed in *U. rossicus, U. k. kudarensis*, and the highest – in *U. s. spelaeus*, *U. ingressus, U. a. piscator* (Fig. 4).

3.2.2 SZM and SHM morphological spaces

In order to eliminate the impact of sexual dimorphism on the results, models were constructed for males and females separately. All measures of the mandible are well correlated with each other in both males and females (r varies 0.62-0.97), so we could anticipate, a low dimensionality in SZM models. Indeed, in all cases, only two dimensions are enough to describe the variability in all measurements of the mandible. The dimensionalities of SHM morphospaces are equal to one in both sexes. The biological sense of morphospace coordinates are recovered from their correlations with the initial measurements of the mandible and several derivative indexes (EF, 100*(Hm1/GL) and 100*(p4_m3L/c1_m3L) (Table 4).

Very high correlations with measures of the mandible (Table 4) testify that the first dimension of SZM morphospace (E1) describes the "general size" of mandible and all variability that is associated with it. In males and females dimensions E1 correlate well with the ratio of Hm1 and GL (r=0.75; 0.69). As it would be possible to assume in advance, EF negatively correlates with the "general size" of mandible. In females, EF also negatively correlates with the second coordinate of space. Variation of canine length (c1L) in males and females has two independent linear components. The first component positively correlates with the "general size" of the mandible and the second one – negatively correlates with the second dimension of SZM morphospace (E2) (Table 4). Hence, dimensionality of both types of models is linked only with the variability of c1L.

Contrary to the biological contents of SHM spaces which are alike in males and females, one-dimensional "spaces" that describe shape variability of mandibles show some specifics related to gender. In males, the K dimension strongly correlates (Table 4) with the "general size" of the bone. This result demonstrates predominance of allometry. Thus, isometry is the leading factor in variation of shape of the female mandible, because variation in single dimension of the SHM morphological space (K) is independent or shows low correlation with the initial measures. Thus K does not depend or weakly depends on the size variation of mandible. The dimension K in males correlates with the ratio of Hm1 and GL (r = 0.66, Table 4). Thus, K describes the relative height of the mandible body. In females, K correlates with the index 100*(p4_m3L/c1_m3L) (r=-0.54, Table 4) and roughly describes the ratio between the length of the tooth row and the length of the diastema.

3.2.3 Classification

The main effects of a priory taxonomy are observed in the dimensions E1 (see relative variance components in Table 4). Scatterplots of E1, E2, and K (Fig. 5) show that the main partition is observed between the group that includes *U. minimus*, brown bear, Etruscan bear, and small cave bear (*U. rossicus*) and the group that includes big cave bears. Dimension K1 contributes to some differentiation on shape features of the mandible within cave bears. In the configuration described above, the *U. deningeri* occupies an intermediate position, especially in males. In contrast to males, females small cave bears form a separate cluster in the SZM morphospace.

It is shown above, that the studied taxa form a nearly uninterrupted spectrum of mandible size and shape variability within SZM/SHM morphological spaces. The relationships between taxa centroids in these modeled spaces are presented in the neighbor joining classification trees (Fig. 6A and B), where the centroid of *U. minimus* is used as an "outgroup".

Table 3: Mann-Whitney U test z' values (males – above and females – under diagonal) for the measures of canines (c1L, c1W) and elongation factor - 100 (c1W/c1L). The statistical significance values (p<0.05) underlined.

Taxa		1	2	3	4	5	6	7	8	9	10
					c1L						
U. deningeri	1		0.91	-1.68	-3.31	-4.07	-3.79	-3.87	-0.07	1.36	0.30
U. rossicus	2	-0.39		-1.31	-2.54	-3.38	-2.54	-3.19	-1.04	0.08	-0.86
U. k. praekudarensis	3	1.35	0.96		-	-0.34	-	0.09	1.17	1.35	1.73
U. k. kudarensis	4	-3.35	-1.47	-2.07		-1.63	0.35	-0.57	2.39	2.67	2.7
U. s. spelaeus	5	-3.80	-1.41	-2.24	1.45		2.14	1.49	2.59	3.06	4.54
U. s. eremus	6	-3.33	-1.42	-1.83	1.06	-0.56		-0.91	2.74	2.37	3.24
U. ingressus	7	-2.24	-1.16	0.09	1.50	0.43	1.11		2.47	2.90	3.91
U. minimus	8	2.01	1.49	1.18	2.49	2.83	2.46	2.21		1.35	0.45
U. etruscus	9	-1.24	-0.29	-1.44	1.32	0.73	1.02	0.06	-1.74		-0.99
U. arctos	10	1.50	1.22	1.74	3.66	4.66	3.33	2.83	-0.78	1.42	
					c2W						
U. deningeri	1		1.85	-1.79	-2.94	-5.10	-4.00	-5.00	2.89	2.37	1.06
U. rossicus	2	-1.40		-1.84	-3.04	-3.82	-3.38	-3.77	2.47	1.74	-0.78
U. k. praekudarensis	3	1.66	0.69		-0.13	-2.15	-0.59	-1.47	1.64	1.74	1.83
U. k. kudarensis	4	-4.45	-2.21	-2.12		-3.03	-0.69	-1.57	2.64	2.86	3.33
U. s. spelaeus	5	-4.82	-0.78	-2.33	3.26		3.31	3.33	3.19	3.53	6.06
U. s. eremus	6	-3.31	-0.71	-2.04	1.12	-0.32		1.85	2.89	3.16	4.39
U. ingressus	7	-4.47	-1.25	2.16	2.03	-0.89	-0.39		3.19	3.50	5.75
U. minimus	8	2,73	1.94	1.44	2.56	2.83	2.45	2.61		-1.59	-2.99
U. etruscus	9	2.49	1.59	0.59	2.56	2.84	2.45	2.61	-1.74		-2.12
U. arctos	10	3.27	2.26	1.82	4.99	6.35	4.13	5.08	-2.53	-0.69	
					elongation factor						
U. deningeri	1		-1.35	-0.89	0.04	1.66	0.76	1.35	-2.81	-3.06	-1.46
U. rossicus	2	1.60		-0.16	1.36	2.01	1.54	1.81	-2.24	-1.73	0.13
U. k. praekudarensis	3	0.47	-0.23		0.65	1.75	1.19	1.29	-1.62	-1.74	0.18
U. k. kudarensis	4	0.86	-0.59	-0.09		1.78	0.58	1.36	-2.63	-2.85	1.40
U. s. spelaeus	5	-0.05	-1.29	-0.60	-1.08		-1.86	-1.03	-3.11	-3.36	-3.46
U. s. eremus	6	0.76	-0.85	-0.12	0.15	0.84		-1.02	-2.84	-3.11	-2.25
U. ingressus	7	1.45	-0.74	0.25	0.35	1.47	0.53		-3.08	-2.98	-2.72
U. minimus	8	-2.71	-1.94	-1.44	-2.49	-2.82	-2.40	-2.56		2.08	3.04
U. etruscus	9	-2.63	-1.94	-1.44	-2.49	-2.67	-2.40	-2.56	0.43		2.91
U. arctos	10	-3.06	-2.83	0.18	-3.47	-3.60	-2.79	-3.84	2.75	2.42	

"Arctoid" and "deningeroid/spelaeoid" groups form two main morphological groups of bears on neighbor joining trees. Within the first group, Etruscan and brown bears are well differentiated from each other. *U. etruscus* is closest to the "outgroup" which may indicate its close phylogenetic relationship with *U. minimus*. The specimen of *U. rodei* is close to brown bear. However, this conclusion is only preliminary and the samples need further investigation. Small cave bears are a part of the second group, but occupy a separate position within it. In terms of mandible dimensions, *U. rossicus* resembles brown bears.

Big cave bears form a compact group of morphologically close taxa on the neighbor joining tree. There is some *SSD* effect on the position of *U. deningeri*. In males, the Deninger's bear takes the intermediate position between "arctoid" and "spelaeoid" groups, but in females, is closer to the core of the "spelaeoid" group.

Morphologically males and females of *U. savini* and *U. spelaeus ladinicus* are very close to the Deninger's bear. The relationships between taxa within cave bears (*sensu stricto*) are not clearly defined, so that the position on the tree depends on whether it is male or female.

Brown bears and cave bears lived concurrently on the

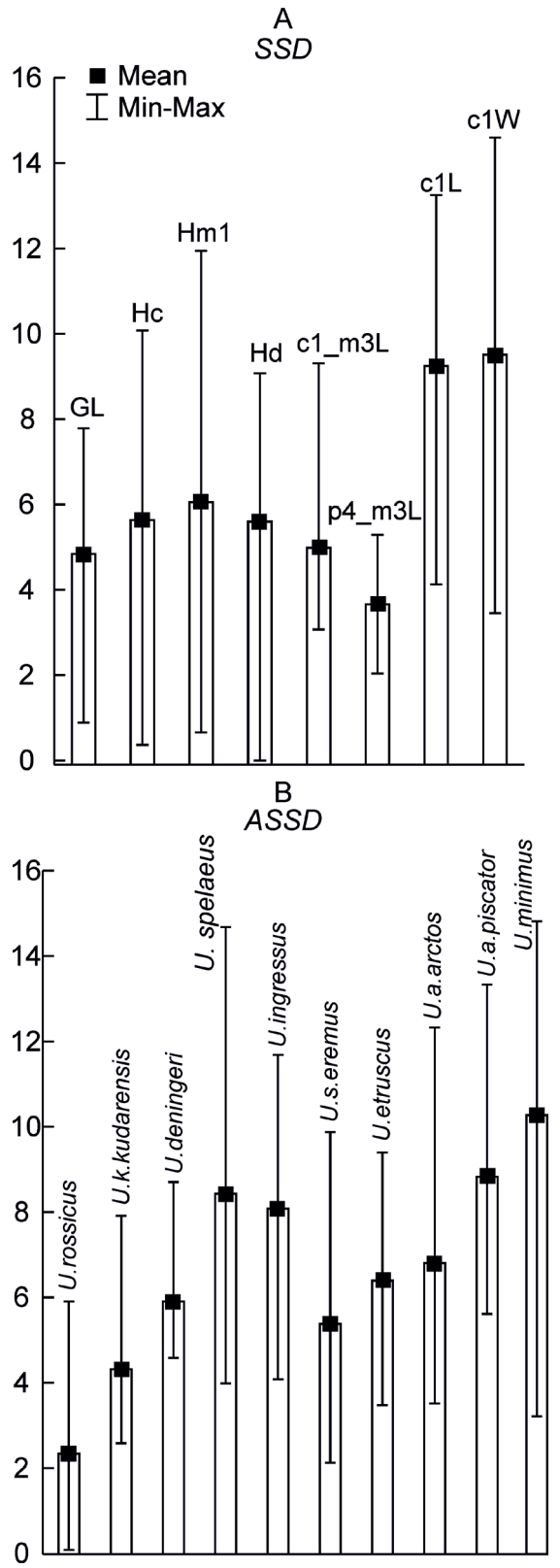

Fig. 4: Sexual dimorphism - *SSD* indexes (mean values) for measurements of mandible (A) and *ASSD* indexes (B) in different bear taxa.

Fig. 4: Dimorphisme sexuel - Indices *SSD* (valeurs moyennes) pour les mesures de mandibules d'ours et Indices *ASSD* pour différentes espèces d'ours.

same territory during the Pleistocene in Eurasia. Their remains are found in the same layers, especially in cave sites, leading to problems in their identification. Other difficulties are associated with the distinction between the Deninger's bear and "true" cave bears (*U. spelaeus, U. ingressus, U. kanivetz*), brown bears, small cave bears and Kudaro cave bears. To test the possibility of distinguishing taxa in mixed samples, we used "structure units" of the mandible that are most often preserved as fossils: the body of mandible (measurements Hd, Hm1) and the tooth row (measurements c1_m3L and p4_m3L). In addition, we tested several ratios of measurements that we mentioned above, but their effectiveness is low and is not discussed here. Pairs of measurements that allow the simplest determination of fossil remains on a scatterplot were selected using results of both parametric ANOVA (Welch's F – test) and nonparametric Mann-Whitney U test (Table 5).

For the pair of "brown bear - large cave bear group" the best differentiation was made using measurements c1_m3L and p4_m3L (Fig. 7). The area of uncertainty ("grey zone") on the scatterplot where it is impossible to distinguish a brown bear from cave bears reliably, is relatively small. In our sample, only 7.8% of cave bears and about 10.4% of brown bears fall into the "gray zone". Note the only specimen of *U. rodei* located beyond the boundaries of the brown and cave bear range of variability. His diastema (estimated as "c1_m3L"-"p4_m3L") is larger than is typical brown bears, but the tooth row is shorter than that of cave bears.

Brown bears and Kudaro cave bears were best distinguished by measuring Hm1 and p4_m3L. The "grey zone" in this case covers five specimens of brown bear (2.5%) and three Kudaro bears (9.2%).

The best result for the pair "*U. arctos – U. deningeri*" was obtained using Hm1 and c1_m3L. However in this case, a fairly large number of specimens (28-34%) fall into the "gray zone" on the scatterplot (Fig. 7), which indicates a less clear morphological differentiation.

Identifying a small cave bear in the sample containing a brown bear and vice versa is difficult. The general dimensions of mandible in Deninger's bear are on average smaller than in the cave bear (*U. s. spelaeus*). The height of the diastema (Hd) and the length of the tooth row (c1_m3L, p4_m3L) marked the greatest differences between them in the studied sample set. However, the distinction between taxa is difficult because of the strong sexual dimorphism of cave bears and an overlap in measurement values.

In our sample set we did not find any metric variables that could satisfactorily distinguish *U. kanivetz = ingressus* from *U. spelaeus, U. spelaeus* from *U. s. eremus*, and *U. s. eremus* from *U. kanivetz = ingressus*.

Table 4: Correlation coefficients among the measures of mandible and indexes with the dimensions of SZM and SHM models (E1, E2, and K); r^2 – coefficients of determination in the linear multiple regression models.

Variables	Males				Females			
	SZM morphospace		SHM morphospace	r^2	SZM morphospace		SHM morphospace	r^2
	E1	E2	K		E1	E2	K	
GL	0.97	0.17	0.70	0.95	0.96	0.06	0.32	0.95
c1_m3	0.97	0.08	0.67	0.95	0.94	0.14	0.40	0.92
p4_m3	0.94	-0.10	0.53	0.89	0.91	-0.03	0.17	0.82
Hc	0.96	0.21	0.70	0.93	0.95	0.11	0.38	0.92
Hm1	0.96	0.20	0.72	0.96	0.92	0.23	0.43	0.91
Hd	0.96	0.12	0.65	0.94	0.94	0.10	0.31	0.89
c1L	0.67	-0.69	0.18	0.77	0.69	-0.61	-0.34	0.86
c1W	0.87	-0.49	0.07	0.87	0.87	-0.26	-0.12	0.86
EF	-0.55	-0.08	-0.29	0.37	-0.43	-0.52	-0.35	0.57
100*(Hm1/GL)	0.75	0.31	0.66	0.63	0.69	0.17	0.33	0.52
100*(p4_m3/c1_m3)	-0.20	-0.48	-0.42	0.29	-0.21	-0.45	-0.54	0.30
	Relative variance components (%) of dimension associated with taxonomical composition							
	88.3	19.9	30.8		81.4	39.9	33.1	

Table 5: Effects of morphological differentiation between bears by the results of parametric ANOVA (Welch's F – test) and nonparametric Mann-Whitney U Test (M-U Z, absolute values). Values corresponding to statistical significance p <0.001 are underlined.

Variable	N	Welch's F - test	M-U Z	N	Welch's F - test	M-U Z
	U. arctos vs. *U. spelaeus, U. ingresus,* and *U. kanivetz*			*U. arctos* vs. *U. kudarensis*		
c1_m3L	425	1166.6	17.6	228	242.5	8.8
p4_m3L	465	1313.9	18.2	236	270.2	8.8
Hm1	478	937.8	18.0	236	465.3	9.1
Hd	471	894.4	17.9	240	337.2	9.2
	U. arctos vs. *U. deningeri*			*U. arctos* vs. *U. rossicus*		
c1_m3L	251	196.1	10.2	220	15.9	3.0
p4_m3L	274	210.6	10.8	233	37.9	5.2
Hm1	277	251.7	11.3	232	80.3	6.3
Hd	273	154.2	9.9	234	79.7	6.1
	U. deningeri vs. *U. s. spelaeus*			*U. spelaeus* vs. *U. ingressus*		
c1_m3L	156	50.3	5.9	182	1.6	1.3
p4_m3L	174	43.8	6.0	197	12.5	3.3
Hm1	187	28.8	5.0	210	0.2	0.4
Hd	180	51.8	6.3	203	0.1	0.2
	U. deningeri vs. *U. kudarensis*			*U. s. eremus* vs. *U. ingressus*		
c1_m3L	89	7.2	2.0	105	0.7	0.91
p4_m3L	102	9.8	1.5	114	6.8	2.25
Hm1	107	46.8	4.8	119	0.4	0.57
Hd	103	31.6	4.6	112	0.1	0.26

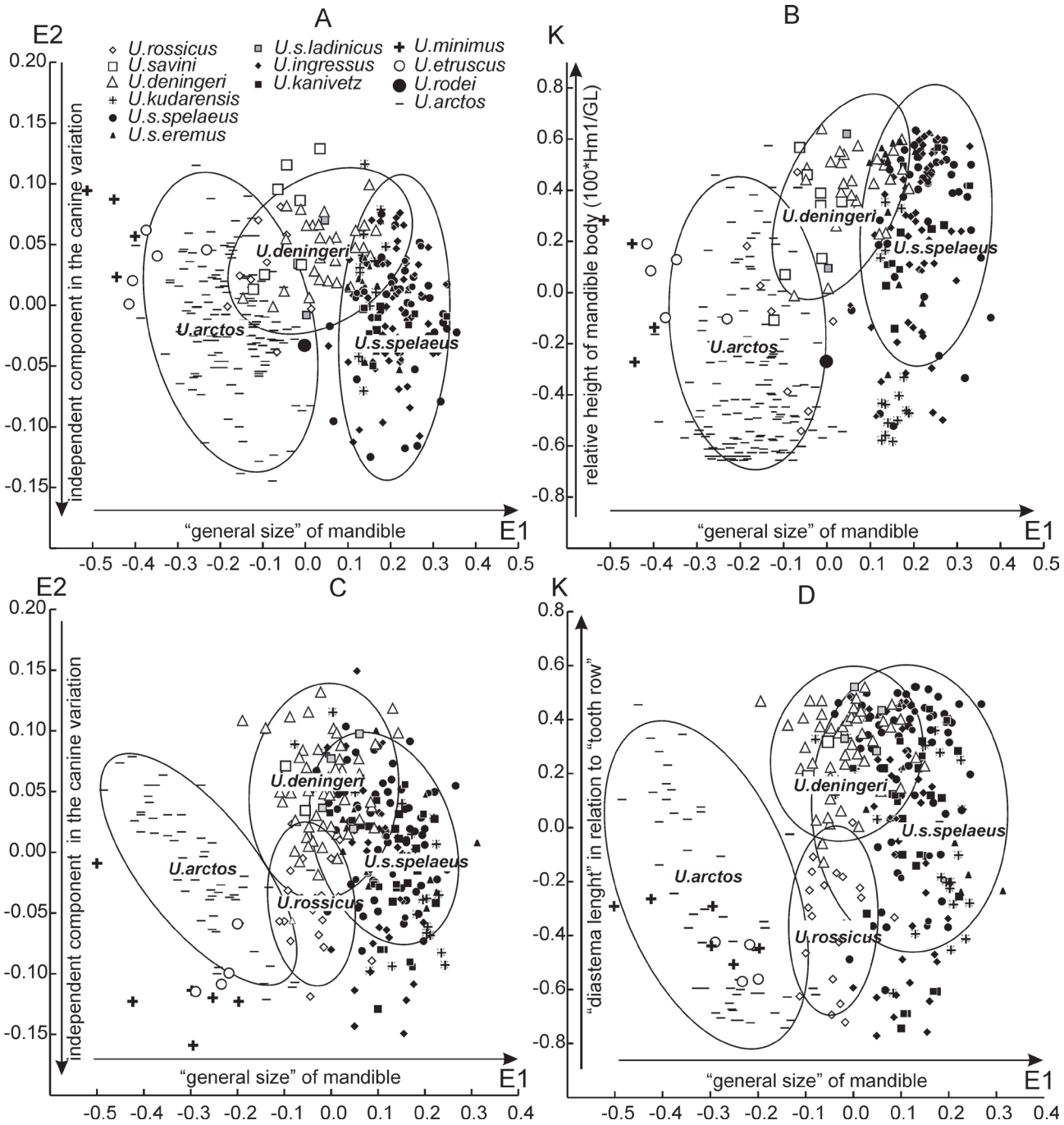

Fig. 5: A, C – SZM morphospaces reproducing size variation of mandible in males (A) and females (C). B, D – combination of first coordinates of the SZM and SHM (shape variation) morphospaces for males (B) and females (D). Ellipses' horizontal and vertical projections onto the axes are equal to the "sample mean" (centroid) ± "the highest value - the lowest value" x 0.95.

Fig. 5: A, C - Catégories morphologiques « SZM » basées sur la variation de taille de la mandibule des mâles (A) et des femelles (C). B, D - Combinaison des premières coordonnées des catégories SZM et SHM (variation de forme) pour les mâles (B) et les femelles (D). Les projections horizontales et verticales des ellipses sur les axes sont égales à : [« moyenne de l'échantillon » (centroïde) ± « la plus haute valeur - la valeur la plus faible » x 0,95].

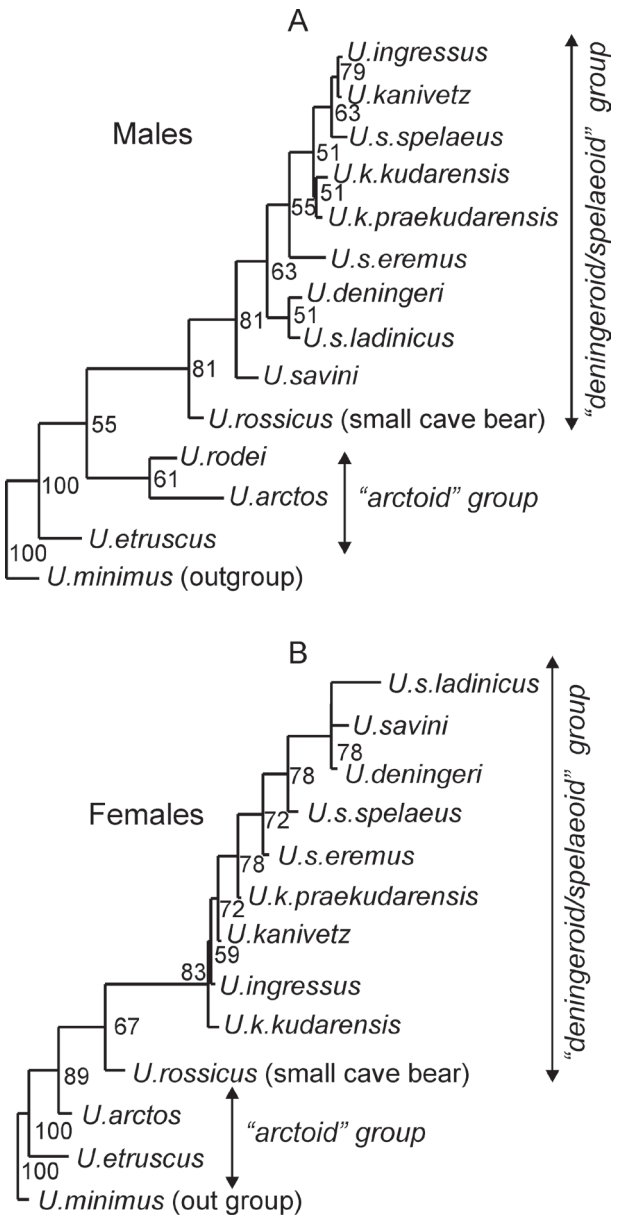

Fig. 6: Neigbor-joining trees of different bear taxa based on their centroids in SZM and SHM models of morphological spaces for males (A) and females (B); numbers near the nodes - bootstrap (1000 repeats) supports >50%.

Fig. 6: Arbres de voisinages phylogénétiques des différents taxons d'ours basés sur leurs centroïdes dans les modèles SZM et SHM des espaces morphologiques pour les mâles (A) et les femelles (B); nombres situés près des nœuds - bootstrap (1000 simulations) supports > 50 %.

4. DISCUSSION

Cave bears demonstrate noticeable sexual dimorphism in their skull size. The intensity of this dimorphism is heightened in big cave bears. In previously published work, we estimated the *ASSD* index (average on 20 measurements) for the cranium of cave bears to vary from 3.5 (*U. rossicus*) to 6.4-6.7 (*U. deningeri – U. spelaeus*) (Baryshnikov & Puzachenko, 2011). This index in brown bears was 4.7 (*U. arctos piscator*) and 7.7 (*U. a. yesonensis* Lidekker, 1897). The sexual size dimorphism of the mandible is greater, and, as has been shown in the present study, it is more pronounced in large cave bears. The dimorphism is even greater for canine size more than any other measurements. In addition, the sexual dimorphism is, on the average, strongly pronounced in the height of the horizontal ramus. This dimorphism, probably, correlates with skull size. In fossil bears, sexual dimorphism of this measurement is most pronounced in large *U. s. spelaeus* and *U. ingressus*, and in modern brown bear – in a large-sized subspecies, *U. a. piscator*. In the last case, *SSD* index is greater than in cave bears. Very high index values were obtained for the proposed common ancestor of brown and cave bear lineages – smallest-sized *U. minimus* (but note that the length of the canine in this species was greater than that of *U. etruscus*, *U. rossicus*, and *U. a. arctos*). The *ASSD* in small-sized Etruscan bear is greater than that in the small cave bear, Deninger's bear, Kudaro cave bear, and *U. s. eremus*. Thus, in studied bears the variability of sexual dimorphism of the mandible, as well as the cranium (Baryshnikov & Puzachenko, 2011), does not contain a phylogenetic signal.

In the SZM morphological space, we identified two main morphological types of mandible (Fig. 5), namely, the "arctoid" type [*U. minimus*, *U. etruscus, U. arctors, U. rodei* (?)], and the "spelaeoid" type (*U. s. spelaeus*, *U. s. eremus, U. kanivetz = ingressus*, *U. kudarensis*). The intermediate between them, "deningeroid" type includes *U. deningeri*, *U. savini*, *U. rossicus* (males), and *U. s. ladinicus*. In female sample, *U. rossicus* forms a separate group.

In comparison to the cranium (Baryshnikov & Puzachenko, 2011: fig. 3), mandibular size disparity between "deningeroid" and "spelaeoid" variants is more pronounced. The shape of the cranium in *U. rossicus* shows specific features that separates this species from large cave bears, and is more similar to brown bears. The morphological variability of (mainly recent) brown bear cranium in Northern Eurasia is comparable to that in the true cave bear taxa, and is significantly higher in comparison with the Deninger's bear. A similar relationship between the "arctoid" and "spelaeoid" lineages was obtained in the case of the mandible. Also, our study confirms the isolated position of the small cave bear (*U. rossicus*).

If we take the Pliocene *U. minimus* as a common ancestor, then the Etruscan bear would be the most similar in morphology to this taxon. The next "step" of morphological differentiation from the putative ancestor is the brown bear. Thus, the last two taxa have opposite characteristics to the group of "deningeroid/spelaeoid" bears on the classification tree (Fig. 6).

In general, the differences between taxa reflect size of

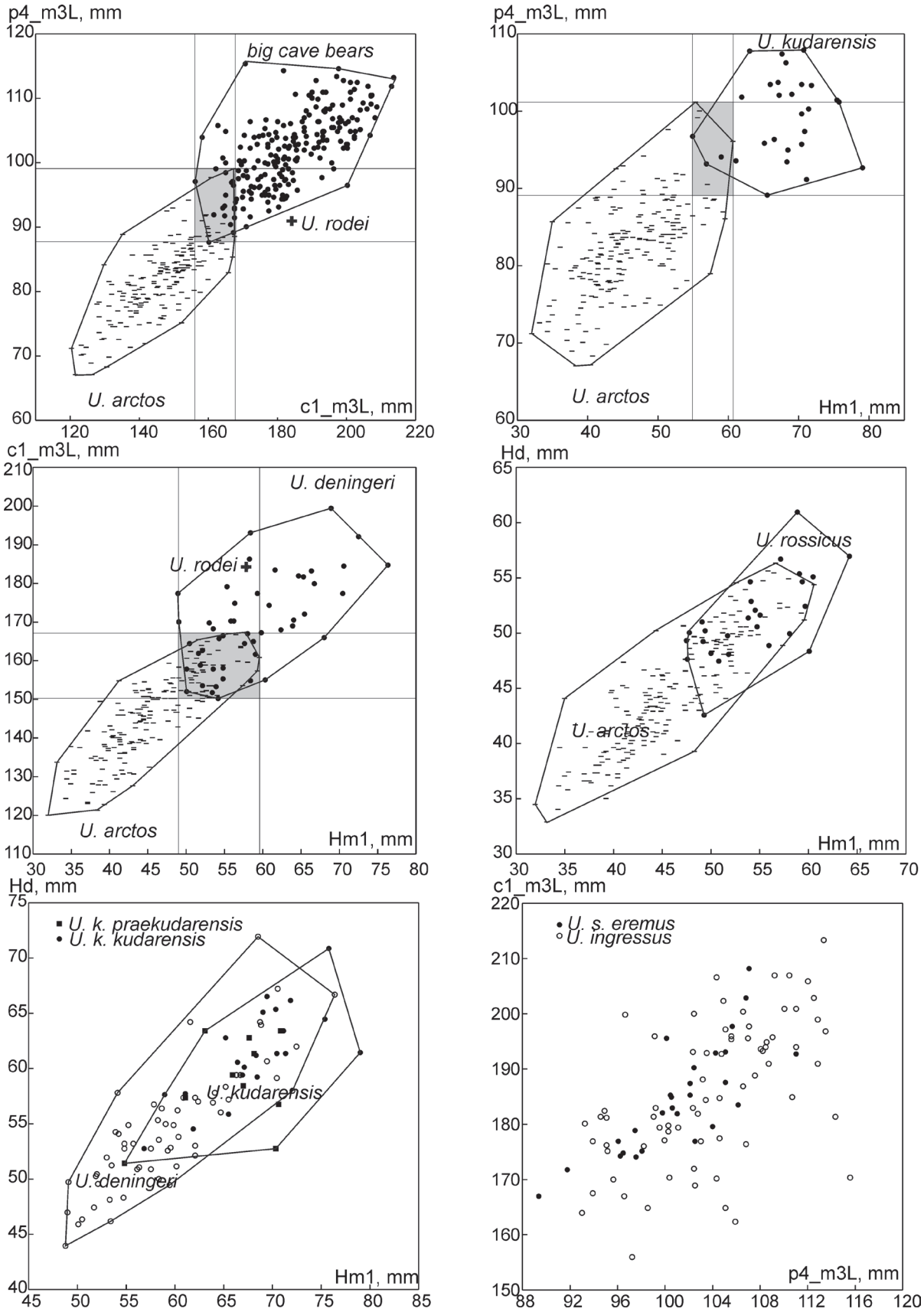

Fig. 7: Estimation of effectiveness in identification of bears in mixed samples using metric features of mandible.

Fig. 7: Evaluation de l'efficacité de l'utilisation des caractères biométriques des mandibules pour la détermination spécifique d'ours parmi des échantillons composites.

mandible, but not its proportions, except the base of canine crown. However, there is a trend from *minimus* to *arctos*, where we could note a decrease in the ratio of the "diastema height/ height of the horizontal ramus of mandible" and the relative length of the diastema with increasing tooth row (at least between *etruscus* and *arctos*). The described sequence of morphological differentiation is found in males and females and does not contradict the hypothesis that the Etruscan bear is an ancestor of the brown bear and cave bear (Rabeder *et al*., 2010).

Rossi & Santi (2011) summarized data on bear mandibles and related the main differences between Etruscan/ brown bear from cave bear with progressive adaptation to plant food nutrition: strengthening of the horizontal ramus of mandible, especially in its middle part, meant specific changes to the shape of the coronary process and the shape of mandibular condyle. The authors supported the opinion of a number of previous researchers on the extreme similarity of the mandible parameters in the Deninger's and big cave bears. According to the results of our morphometric analysis, the height of the coronary process changes in proportion to the general size of mandible (Table 4). In "arctoid" bears, the relative height of the process (median – 43.7% of mandible length) is only slightly less than in the "spelaeoid" ones (45-46 %). Recent studies have shown that the morphological differentiation of the mandible (and skull) in the *Ursus* lineage appears to be more influenced by ecological adaptation to diet than phylogeny (Fuchs *et al*., 2015). The analyses of functional morphology of mandible in cave bears and other members of the family Ursidae (Heteren *et al*., 2016) showed that on a morphospace *U. spelaeus* is closer to extant brown bears, but has some specific features, which make it similar to phyllophagous panda *Ailuropoda melanoleuca* (David, 1869). The proximity of the cave bear to the brown bear in the morphospace represents a phylogenetic signal of their origin from a common ancestor within the genus *Ursus*. On the other hand, cave bear morphological niche is not similar to that of a polar bear' niche (*U. maritimus* Phipps, 1774 is a typical meat-eater). Some proximity to the niche of evolutionarily distant panda reflects the influence of an ecological adaptation to a plant diet. In accordance with the results of the work cited above, about 44% of the morphological variation in mandibles in Ursidae can be explained by diet and 37.5% by phylogeny. The remaining variability is almost completely explained by "phylogenetically structured dietary variation".

The further partition of taxa within "deningeroid/ spelaeoid" lineage is more complicated and allows for different interpretations. According to cranial and mandibular features, the small cave bear (*U. rossicus*) is closer to the brown bear than to the main group of cave bears. This is also possibly due to the ecological similarity of feeding in small cave bears and brown bears. This result was obtained earlier based on studies of the cranium (Baryshnikov & Puzachenko, 2011: fig. 10). The morphometric classification of the "deningeroid/ spelaeoid" bears critically dependents on sex [= sexual size dimorphism and, probably, breeding type variation (Gittleman & Valkenburgh, 1997)].

Comparison of two trees in Fig. 6 allows us to distinguish three taxa, which form independent morphological subgroups: *U. deningeri*, *U. savini*, and *U. spelaeus ladinicus*. The taxa nearest to this group are different: in males it is *U. s. eremus*, and in females – *U. s. spelaeus* and *U. s. eremus*. Further, the pair "*U. kanivetz* – *U. ingressus*" retains closeness in both classification trees that corresponds to their genetic affinity. The position of Kudaro cave bear is uncertain: in males, both subspecies are very close to the *U. s. spelaeus*, in females they are found on different branches of the tree. Note that on the cladogram built using cranial traits, *U. kudarensis* is closer to the Deninger's bear (Baryshnikov & Puzachenko, 2011).

We have three mandibles identified as remains of *U. savini nordostensis* Baryshnikov, 2011 from the North-East Siberia localities – Chersky, Duvanny Yar, and Ulakhan-Sullar (Sher *et al*., 2011; Boeskorov *et al*., 2012). According to their dimensional characteristics the specimens do not differ from *U. savini* from England. At the same time, parameters of these mandibles lay within the variation of both *U. deningeri* and *U. rossicus*. In addition, we note that morphological variability of Savini's bears falls within the range of *U. deningeri*, too (Fig. 5). Thus, mandibles of not large spelaeoid bears known from northeastern Siberia do not differ noticeably from *U. deningeri*.

Based on the obtained results and taking into account similar data about cranial disparity in the studied taxa, we cannot substantiate any specific phylogenetic scheme within the true cave bears group.

Studies of mandibular bones are important, because mandibles are durable and, unlike cranium, often remain intact in a fossil state. At the same time, in comparison to the cranium, mandibles have a more simple arrangement which makes them less informative for the study of evolution.

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