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MORPHOMETRICAL VARIABILITY OF CHEEK TEETH IN CAVE BEARS

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Abstract: As a result of the morphometric study, tooth samples examined in 17 sites of Western and Eastern Europe and the Caucasus were distributed into two groups. The first group is formed by teeth from localities of the Middle Pleistocene and from the Late Pleistocene layers 3-4 of Kudaro 3 Cave, which were identified as *Ursus deningeri*. The second group united specimens from the Late Pleistocene localities attributed to *U. spelaeus*. The sample from Furtins Cave in France was shown to occupy a transitional position. The teeth from Bacton Forest Bed in England and from Kizel Cave in the Ural Mountains resemble those in the first group, revealing, nevertheless, some difference; despite the produced analysis allows no confidence in the establishment of their species attribution, these may be tentatively referred to *U. savini*.

Key words: Cave bear, *Ursus,* teeth, variability, Pleistocene.

INTRODUCTION

It is generally known that cheek teeth provide reliable characters for the purposes of diagnostics and taxonomy of Ursidae. The study of the tooth morphometry and morphology has usually led to dividing cave bears into 2 species: *Ursus deningeri* VON REICHENAU and *U. spelaeus* ROSENMÜLLER (Kurtén, 1968; Rabeder, 1999). Other studies of the dental characters, on the contrary, suggest uniting the cave bears into a single species, *U. spelaeus* (Grandal d'Anglade & López-Gonzáles, 2004).

In the cave bears, cheek teeth demonstrate progressive modification of the occlusal surface during the Pleistocene, the temps of such changes growing toward the finish of this epoch (Rabeder & Tsoukala, 1990; Rabeder, 1999). It has been also revealed that the sites of equal age were geographically grouped with regards to the cave bear dental measurements; this phenomenon may be explained by regional peculiarities in the bear diet (Baryshnikov *et al.,* 2003).

The aim of the present study is to give morphometrical analysis of the tooth samples from the European and Caucasian sites of different geological ages and geographical positions in order to elucidate stratigraphic and geographic variability of teeth in the cave bears.

MATERIAL AND METHODS

The work embraces tooth collection from 17 sites of the Western and Eastern Europe and the Caucasus, which are dated at the Middle and Late Pleistocene.

The Middle Pleistocene sites are Westbury-sub-Mendip Fissure in England, Jagsthausen Cave, Mosbach (terra typica for *U. deningeri*) and Einhorn Cave in Germany, Kudaro 1 Cave (layer 5) in Georgia. The examined collection from Einhorn comes from the early excavations having no stratigraphic division; however, later excavations have exhibited the presence of several stratigraphic levels in the cave, with the oldest one dated more that 100 thousands years (Nielbock, 1987).

The Late Pleistocene sites comprise Eiros in Spain, Arcy-sur-Cure in France, Zoolithen Cave (terra typica for *U. spelaeus*) and Rübeland in Germany, Nietoperzowa Cave in Poland, Odessa in Ukraine, Kudaro 3 Cave (layer 3-4) in Georgia, Secrets Cave and Medvezhiya Cave in Russia (the Ural Mountains) (fig. 1). Their geological dates correspond to the time of the late glacial. In Arcy-sur-Cure, the teeth originating from the layers of the Middle and Late Paleolithic reveal no reliable difference in size (Baryshnikov & David, 2000), being, therefore, examined together.

The age of deposits in the Furtins Cave in France is somewhat elder. It is estimated as beginning of the Late

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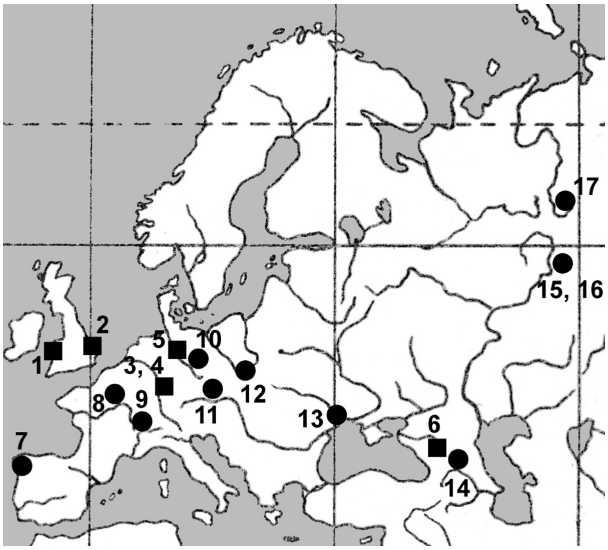

Figure 1. Distribution of examined localities from the Middle Pleistocene (quadrate) and Late Pleistocene (circle). 1 - Wesrtbury; 2 - Bacton Forest Bed; 3 - Jagsthausen; 4 - Mosbach; 5 - Einhorn Cave; 6 - Kudaro 1 Cave; 7 - Eiros; 8 - Arcy-sur-Cure; 9 - Furtins Cave; 10 - Rübeland; 11 - Zoolithen Cave; 12 - Nietoperzowa Cave; 13 - Odessa; 14 - Kudaro 3 Cave; 15 - Kizel Cave; 16 - Secrets Cave; 17 - Medvezhiya Cave.

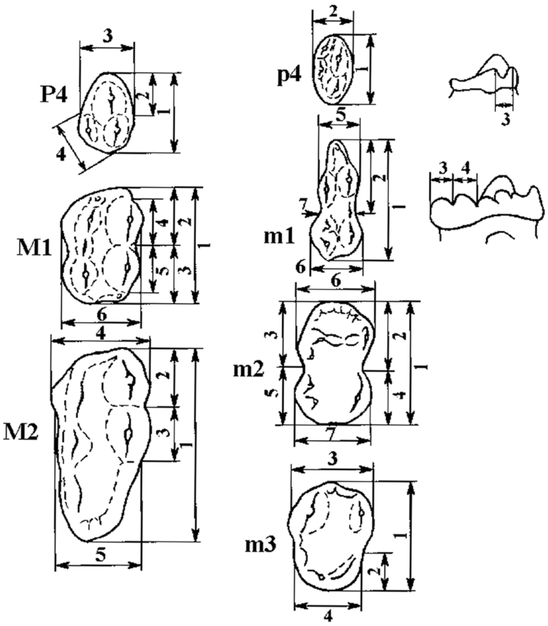

Figure 2. Scheme of measurements of upper (P4-M2) and lower (P4-m3) cheek teeth. Designations of measurements are shown in tab. 1-14.

Pleistocene (late interglacial or early late glacial) (Argant, 1991).

In addition, two small tooth collections have been examined. One of them originates from Bacton Forest Bed in England, which is dated at the early Middle Pleistocene (Sutcliffe, Kowalski, 1976). This collection represents the type material of *U. savini* (Andrews, 1922) whose status of being a separate species is not always accepted (Kurtén, 1968). The other one was collected in the Late Pleistocene sediments of Kizel Cave in the Ural Mountains (Russia). This material was described as *U. uralensis* Vereshchagin, but later the taxon has been referred to *U. rossicus* BORISSIAK as a subspecies (Vereshchagin & Baryshnikov, 2000).

Since the examined samples predominantly consisted of the isolated teeth, their comparison was carried out separately for each cheek tooth. The specimens, which are retained in the jaws, were also used. In total, more than 1750 upper teeth and more than 2350 lower teeth have been measured.

Each sample (with rare exceptions) includes as many as 10 specimens. Teeth were measured by calipers with accuracy 0.05 mm according to the scheme given in fig. 2. The metric data are summarized in tables 1-14.

For processing the obtained data, the Dicriminant Analysis and Cluster Analysis from STATISTICA 6.0 were used. The examined samples were classified basing on the means of the standardized variables. In the Discriminat Analysis, the forward stepwise method was applied. The dendrograms of similarity were built according to Squared Mahalanobis Distances.

RESULTS

Sexual dimorphism. For the analysis, the cheek teeth were not sexed, as sexual dimorphism in the tooth size of cave bears seems to be weakly developed (Kurtén, 1955). At the same time, morphometric study of teeth in the recent brown bear (*U. arctos* L.) from Hokkaido Island revealed that males and females differ in the upper (P4) and lower (m1) average carnassial length (Baryshnikov *et al.*, 2005).

In order to elucidate whether sexual dimorphism in the cave bears is pronounced in the size of cheek teeth, the upper and lower jaws where cheek teeth were associated with the upper or lower canine were used, since males of cave bears are differ reliably from females in the canine width (Kurtén, 1955).

In the material from Mosbach, the upper canine width was 20.5-17.3 mm in males (n=8) and 16.7-13.3 mm in females (n=10); whereas the lower canine width varied from 18.9-16.7 mm in males (n=5) to 16.0-13.9 mm in females (n=7). In the material from Zoolithen, these dimensions were correspondingly 25.5-20.5 mm (n=6) and 17.9-15.4 mm (n=11) for the upper canine and 23.7-18.7 mm (n=11) and 17.2-14.6 mm (n=17) for the lower canine. These measurements reflect that *U. spelaeus* possessed more robust canines in comparison with *U. deningeri*, the sexual dimorphism in the canine size in *U. spelaeus* being more developed, as KURTÉN (1969) noted.

After the material has been examined on sexing, it was found out that in the sample from Mosbach the length of the upper tooth row P4-M2 represents 80.4-101.5, M=89.65 mm (n=6) in males and 79.6-89.7, M=83.87 mm (n=12) in females; whereas in the sample from Zoolithen it is measured as 89.7-101.5, M=96.70 mm (n=10) in males and 82.5-91.2, M=87.15 mm (n=22) in females. The length of the lower tooth row p4-m3 from Mosbach represents 97.0-106.8, M=100.71 mm (n=7) in males and 86.0-98.7, M=92.21 mm (n=8) in females; in the sample from Zoolithen it is 98.6-110.5, M=103.95 mm (n=11) in males and 92.9-99.8, M=96.84 mm (n=10) in females. In the both sites, in the means of length of the tooth row males were larger than females, though in the overlapping of the sample extremes occurred. Therefore, unsexed tooth samples may demonstrate difference in the average size with regard of the ratio of male and female teeth, as has been already hypothesized (GRANDAL D'ANGLADE, 2001; BARYSHNIKOV *et al.*, 2003).

Size. The comparison of the samples, which have been sexed by the length of the upper teeth P4-M2 and lower teeth p4-m3, revealed that both the males and females from the Middle Pleistocene on average demonstrate longer tooth rows than those from the Late Pleistocene, i.e. the Late Pleistocene cave bears possessed more robust teeth than the Middle Pleistocene bears. At the same time, in the length of P4-M2 (88.4-95.5, M=90.72 mm, n=5) and the length of p4-m3 (98.1-103.4, M=101.07 mm, n=6), males from the Late Pleistocene site of Kudaro 3 (layers 3-4) in Caucasus resemble males from the Middle Pleistocene site of Mosbach in Europe.

It should be, however, noted that in the material from Kizel Cave, where males were not separated from females, the length of P4-M2 (74.0-82.0, M=77.29 mm, n=8) and that of p4-m3 (85.9-91.6, M=88.23 mm, n=6) were markedly smaller than those dimensions even in the females from the Middle Pleistocene sites. Similar dimensions were recorded in the unsexed sample from Bacton (76.4, 81.5 mm, n=2 and 78.3-91.3, M=87.09 mm, n=7, correspondingly).

Relative size. I failed to find any reliable difference between relative length of the cheek teeth in the cave bears from the Middle and Late Pleistocene.

In the upper tooth row P4-M2, the length of each tooth constitutes: 21.2-21.9% (P4), 29.4-30.7% (M1) and 47.8-49.6% (M2). The sample of *U. savini* from Bacton represents an exception, demonstrating robust upper carnassial tooth P4 (22.8%) and small last lower molar m3 (45.2%). By these indices, *U. savini* seems to be more archaic as compared not only to other cave bears examined from the Middle and Late Pleistocene, but even in comparison with *U. rodei* from the locality of Untermassfeld in Germany, which is dated by the late Early Pleistocene (MUSIL, 2001).

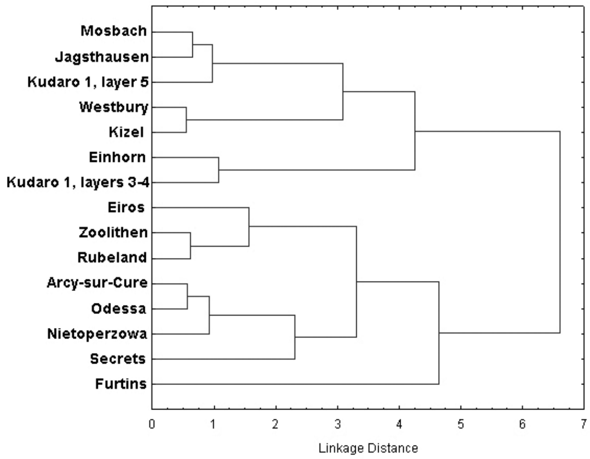

Figure 3. Hierarchical tree plot for P4 of cave bear.

In the lower tooth row p4-m3, each tooth occupies 14.6-15.9% (p4), 28.5-29.7% (m1), 29.2-30.2% (m2) and 25.6-26.5% (m3) of the tooth row total length. Similar proportion has been found in the cave bear from Kizel Cave (15.1-28.8-29.7-26.3%) as well as in *U. rodei* from Untermassfeld (15.5-29.4-30.3-24.8%), despite that the latter species possesses shorter m3 (MUSIL, 2001). On the contrary, the sample from Bacton (16.1-28.8-28.2-26.9%) is characterized by the combination of primitive characters (robust p4, m1 longer than m2) with derivative one (enlarged m3).

Variability of the upper cheek teeth. In the measurements of the upper carnassial tooth P4, the examined samples were united into two groups predominantly divided by the paracone length (fig. 3). The first group incorporates all the specimens from the Middle Pleistocene as well as from Kudaro 3 and Kizel Cave. The teeth from localities of Kudaro 3 and Einhorn occupied the isolated position within this group, characterizing in the pronounced distance between the anterior margin of protocone and posterior margin of the tooth crown. The second group comprises the samples from the Late Pleistocene localities, including Furtins. The material from

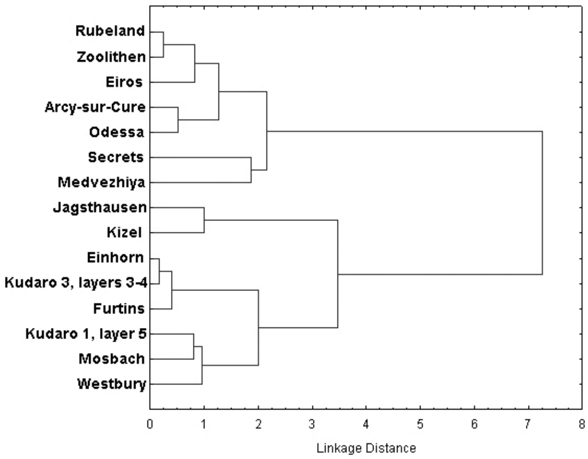

Figure 4. Hierarchical tree plot for M1 of cave bear.

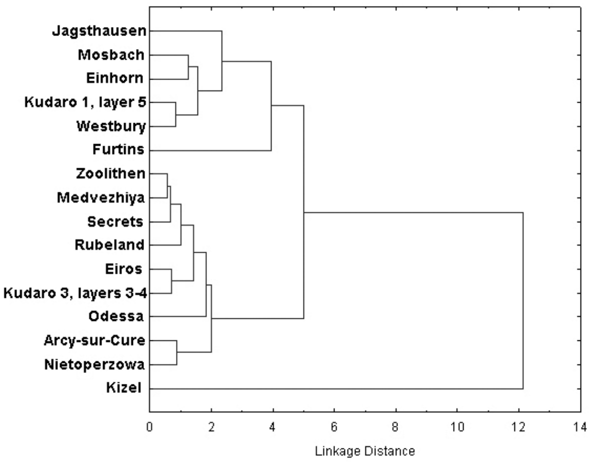

Figure 5. Hierarchical tree plot for M2 of cave bear.

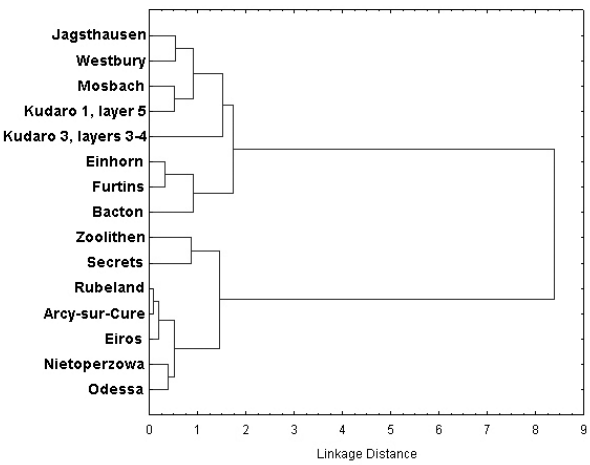

Figure 6. Hierarchical tree plot for p4 of cave bear.

the latter locality forms an isolated subgroup, since P4 from Furtins demonstrate marked shift of the protocone backwards.

The morphometric analysis of the first upper molar M1 has grouped all Middle Pleistocene samples together with teeth from Kudaro 3, Furtins and Kizel Cave (fig. 4). M1 from Kizel Cave and Jagsthausen are similar to each other in the greatest width of the tooth crown. The second group is formed by remaining samples from the Late Pleistocene localities. Both groups are diverged in the greatest length M1 and the length of the posterior portion of its crown.

In the measurements of the second upper molar M2, the analyzed samples form three groups (fig. 5). The first group contains teeth from the Middle Pleistocene sites and Furtins. The second one consists of the samples from the localities of the Late Pleistocene, including Kudaro 3. Both groups are divided due to the anterior width and posterior width of the tooth. The third group is formed by the teeth from Kizel Cave, which possess shortened metacone.

Variability of the lower cheek teeth. The analysis of measurements of the forth lower premolar p4 provided distribution of the samples examined into two groups, within each of which no reliable difference has been established between teeth from various localities (fig. 6). The first group incorporates samples from the Middle Pleistocene localities as well as from Furtins and Kudaro 3. The second group unites remaining Late Pleistocene samples. The difference between groups is pronounced in the greatest width of p4. The analyzed teeth from Bacton Forest Bed can be grouped together with those from the Middle Pleistocene sites.

The examined samples of the lower carnassial tooth m1 (with the exception of measurements 3 and 4) similarly form two groups diverging in the tooth greatest length (fig. 7). The first group unites the samples from the Middle Pleistocene localities as well as Bacton, Kizel Cave, Kudaro 3 and Furtins. Within this group, the isolating position is revealed for the samples from the localities of younger geological age (Einhorn, Furtins), and Kudaro 1, where teeth are larger and comparatively more narrow across trigonid. The second group comprises samples from other Late Pleistocene sites, which show no noticeable difference.

The analysis of measurements of the second lower molar m2 has demonstrated somewhat different distribution of the samples. These are united into three groups, diverging in the greatest length m2 and width of its trigonid. The first group consists of the teeth from the localities of the Middle Pleistocene and specimens from Kizel Cave and Kudaro 3 as well as teeth from Zoolithen and Medvezhiya Cave that is unusual (fig. 8). Within this group, the teeth from Kizel Cave form an isolated subgroup which is distinguished by the greatest length and lingual length of talonid. The second group involves all remaining samples from the Late Pleistocene sites. Lastly, the third group consists of the teeth from Bacton, which are, on the average, smallest.

The samples of the third lower molar m3 are split into two groups according to the length and width of talonid, differences between groups being inconspicuous (fig. 9). The first group contains specimens from the localities of the Middle Pleistocene, including Bacton and Kudaro 3 as well as Medvezhiya Cave. The second group involves specimens from other localities of the Late Pleistocene, including Furtins.

DISCUSSION

As a result of the analysis, a clear tendency in the time distribution of the examined samples was revealed, which is observed for each cheek tooth. The samples form two well-isolated clusters. The first cluster contains samples from the Middle Pleistocene sites, whereas the second one consists of specimens from the Late Pleistocene sites. However several samples do not fall into groups that correspond to their geological age.

Within the Middle Pleistocene group, the specimens from Jagsthausen and Mosbach are grouped together. According to the P4/p4-index, the sample from Jagsthausen seems to be the most archaic in Europe (Rabeder & Tsoukala, 1990). This is according to the shape of the lower carnassial tooth m1 whose entoconid looks like large, inconspicuously divided cusp (fig. 10). The most distanced from this cluster is the sample from Einhorn, which is, in several cases, united with the samples of a later geological age (with Kudaro 3 for P4 and Furtins for p4 and m1).

The sample from layers 3-4 of Kudaro 3 is most often placed by the morphometric analysis within the Middle Pleistocene group, in spite of these cave layers dated by the Late Pleistocene. Only by the metric characteristics of M2 does this site belong to the second group. This result is consistent with the opinion on the preservation of the archaic dentition in the Caucasian cave bears as late as almost the finish of the Pleistocene (Baryshnikov, 1998). The entoconid portion of the lower carnassial tooth m1 from layers 3-4 in Kudaro 3 is divided into three cusps successively becoming higher posteriorly, as in *U. deningeri* (fig. 11, *3-5*).

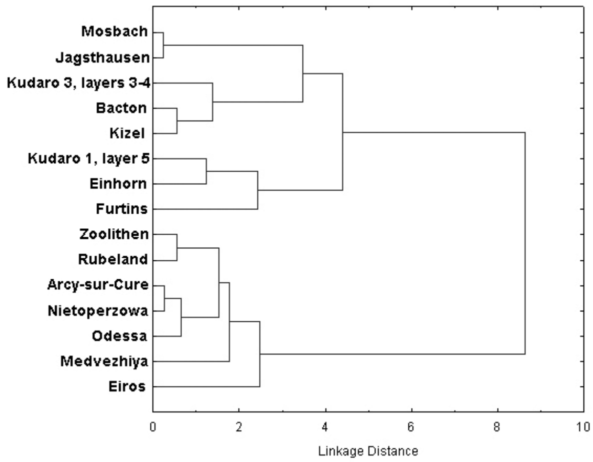

Figure 7. Hierarchical tree plot for m1 of cave bear.

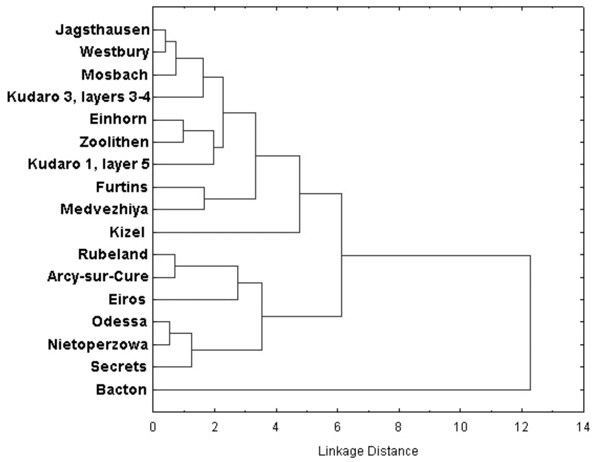

Figure 8. Hierarchical tree plot for m2 of cave bear.

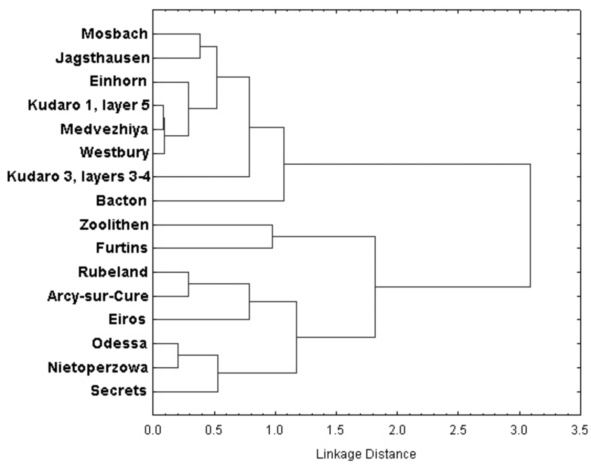

Figure 9. Hierarchical tree plot for m3 of cave bear.

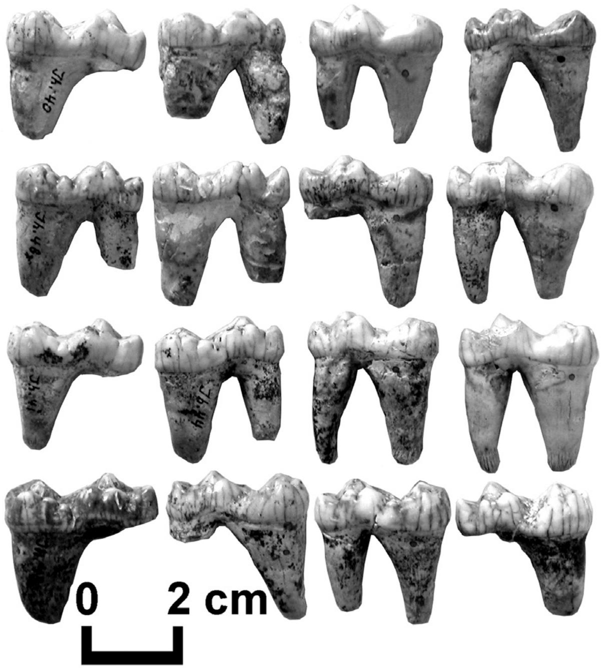

Figure 10. *Ursus deningeri*, lower carnassial tooth m1 from Jagsthausen (SMNS 31101, Staatlichen Museum für Naturkunde, Stuttgart). Lingual view.

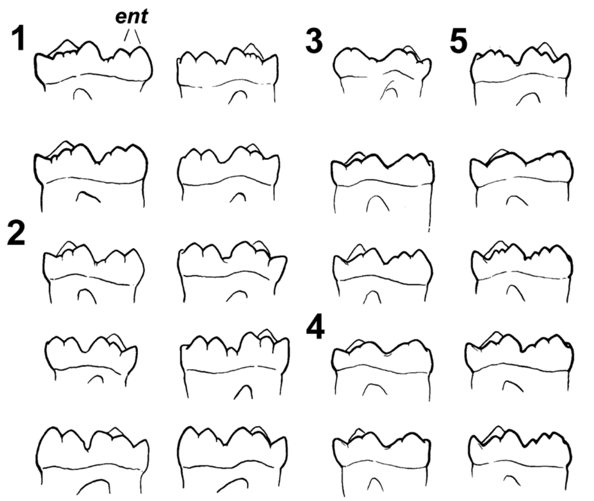

Figure 11. Structure of entoconid (*ent*) of lower carnassial tooth m1 of *Ursus spelaeus* (1, 2) and *U. deningeri* (3-5) (coll. Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZIN). 1 - Medvezhiya Cave; 2 - Odessa; 3 - Kudaro 3 Cave, layer 3; 4 - Kudaro 3 Cave, layer 4 (horizons 1-4); 5 - Kudaro 3 Cave, layer 4 (horizons 5-6).

Within the second group, which is formed by the samples from localities of the Late Pleistocene, no units associated with the age or geographic position of the sites were revealed. It should be mentioned that in the characters of several teeth the samples from the Ural Mountains (Secrets Cave and Medvezhiya Cave, by measurements of M1) as well as the samples from Germany (Zoolithen and Rübeland, by measurements of P4, M1 and m1) form distinct groups; however, all these sites are closely placed according to M2 dimensions. The specimens from Medvezhiya Cave and Odessa possess entoconid of m1 consisting of two distanced cusps that is typical of *U. spelaeus* (fig. 11, *1-2*).

The sample from Furtins Cave either falls into the Middle Pleistocene teeth (on the basis of metric characters of M1, M2, p4 and m1) or groups together with the Late Pleistocene teeth (by measurements of P4, m2 and m3). Such variability indicates a transitional position of this sample and agrees with the geological age of the cave. The dental morphometry in specimens from Furtins indicates the transition from the Middle Pleistocene cave bears to the Late Pleistocene animals.

Two other Late Pleistocene samples, by measurements of m2 (Zoolithen, Medvezhiya) and m3 (Medvezhiya), are associated with the Middle Pleistocene group, whereas the Middle Pleistocene sample (Kudaro 1) by metric characters of m2 is placed within specimens from the localities of the Late Pleistocene. The obtained data disagree with the age of the localities as well as with dimensions of other teeth. This contradiction may be explained by the inaccuracy in the teeth measuring or tooth composition in a sample (the ratio between the isolated teeth and teeth fixed in jaws, presence of the tooth crowns without roots belonging to young bears, etc.).

The average values of measurements markedly vary in the different samples, which is obviously substantiated by the ratio between male and female teeth within each sample. The lower means of tooth dimensions in Secrets Cave and Medvezhiya Cave implies the predominance of females, whereas higher means of tooth measurements in Arcy-sur-Cure indicate prevalence of male teeth.

In the average, the teeth from Kudaro 1 (layer 5) are found to be smaller than those from Kudaro 3, the first site containing, however, the largest individual specimens. Most likely, predominantly males perished in Kudaro 3, whereas mainly females died in Kudaro 1. This hypothesis is confirmed by findings of numerous milk teeth in layer 5 of Kudaro 1 (Baryshnikov, 1999). Therefore this cave was used by bears as a den.

In spite of the predominance of male mortality being hypothesized for the Arcy-sur-Cure site, numerous milk teeth have been found there (Baryshnikov & David, 2000). Most probably, in different times of bears exploiting this cave, it was a winter shelter of males or den for females with cubs. Similarly, it had been found that the Goyet site in Belgium that it was occupied by males in the colder stages of the Pleistocene and by females in the warmer stages (Germonpré, 2004).

Rather small samples of the cheek teeth from Bacton Forest Bed (*U. savini*) and Kizel Cave (*U. rossicus uralensis*) are distributed into the Middle Pleistocene group or, with regard to M2 for Kizel Cave and m2 for Bacton, form a distinct group. In the structure of lower carnassial tooth m1 whose entoconid is divided into two or, more seldom, three crowded cusps, the cave bear from Kizel Cave exhibits resemblance with *U. deningeri* (fig. 12). In the metric characteristics of m1, the samples from Bacton and Kizel Cave are distributed close to each other, occurring in the different groups by the measurements of m2. Therefore, the conducted analysis gives no clear reply to the degree of similarity of these samples. At the same time, these samples are well distanced from other groups.

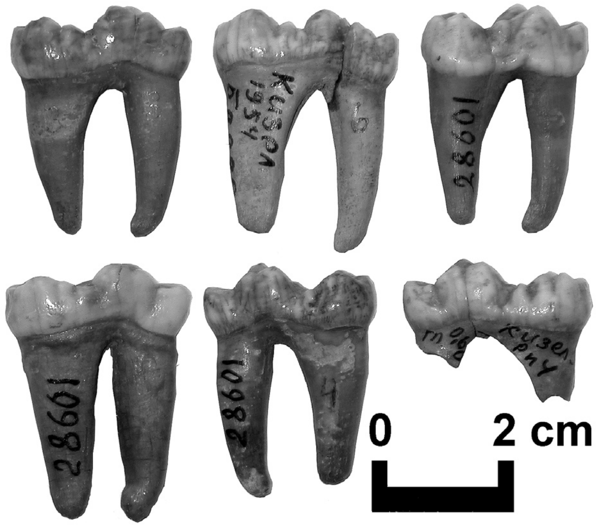

Figure 12. *Ursus savini uralensis*, lower carnassial tooth m1 from Kizel Cave (ZIN 28601). Lingual view.

CONCLUSION

Thus the peculiarities of grouping of the examined tooth samples resulting from the morphometric analysis substantiate the difference in the dentition between cave bears from the Middle and Late Pleistocene. A group of samples from Mosbach, Jagsthausen, Westbury, Einhorn, Kudaro 1 (layer 5), and Kudaro 3 (layers 3-4) belongs to *U. deningeri*, whereas other group (Zoolithen, Rübeland, Arcy-sur-Cure, Eiros, Nietoperzowa, Odessa, Secrets, Medvezhiya) is attributed to *U. spelaeus*. In addition, the sample with characters transitional between teeth of these species (Furtins) has been revealed.

U. spelaeus stratigraphically replaces *U. deningeri*, the boundary between these species roughly coinciding in Europe with the boundary between the Middle and Late Pleistocene, as has been already stated (Musil, 1981; Rabeder *et al.,* 2000; Petronio *et al.,* 2003). However, in the Caucasus, cave bears with the tooth characters similar to those in *U. deningeri* survived till the Late Pleistocene.

The systematic position of *U. savini* and *U. rossicus* remains unclear. Both species share a model of dental transformation (combination of the modified p4 and archaic m1) that is unusual for other cave bears. In addition, *U. rossicus* differs from *U. deningeri* and *U. spelaeus* by a smaller cranial size and structure of baculum (Vereshchagin & Baryshnikov, 2000). *U. savini* and *U. rossicus* are placed closely to each other in the phylogenetic scheme of the genus *Ursus* (Baryshnikov & Foronova, 2001), being, probably, a single species.

Meanwhile it should be noted that such an interpretation of the cave bear taxonomy is based mainly on the dental characters. No reliable cranial features distinguishing *U. deningeri* from *U. spelaeus* as well as from *U. savini/rossicus* is known. The smaller size of *U. rossicus* may be of adaptive nature (adaptation to steppe environmental conditions). It is not excluded that all cave bears could belong to a polytypical species, *U. spelaeus*, which is characterized in the pronounced stratigraphic and geographic variability.

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Table 1
Measurements (in mm) of upper premolar P4 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Greatest width (3)	Least distance between frontal ridge of protocone and caudal side of crown (4)
Jagsthausen	n	22	22	21	22
	min	16.6	10.4	10.8	12.2
	max	21.4	13.2	15.0	18.0
	M	18.32	11.35	12.49	14.09
	SD	1.13	0.70	0.99	1.40
Mosbach	n	37	37	36	36
	min	15.6	9.8	10.4	11.8
	max	21.6	14.9	15.4	17.2
	M	18.47	11.70	13.05	14.43
	SD	1.49	1.22	1.29	1.52
Westbury	n	48	48	48	48
	min	16.2	10.1	11.0	11.8
	max	21.4	14.5	15.7	17.6
	M	18.54	12.28	13.20	14.65
	SD	1.18	1.04	1.03	1.30
Kudaro 1, layer 5	n	77	77	80	80
	min	16.5	9.7	11.3	12.8
	max	23.7	14.8	16.9	18.8
	M	19.25	11.84	13.54	15.13
	SD	1.33	0.97	1.09	1.34
Einhorn	n	52	52	52	52
	min	17.0	10.4	11.4	12.8
	max	22.2	13.9	17.3	19.9
	M	19.12	12.04	14.10	15.66
	SD	1.23	0.84	1.09	1.40
Furtins	n	16	16	16	15
	min	16.8	10.4	11.1	11.2
	max	20.1	12.8	15.0	15.3
	M	18.74	11.67	13.47	13.25
	SD	1.10	0.72	0.91	1.04

Table 2
Measurements (in mm) of upper premolar P4 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Greatest width (3)	Least distance between frontal ridge of protocone and caudal side of crown (4)
Zoolithen	n	62	62	62	62
	min	17.7	11.5	11.6	12.4
	max	22.1	14.7	15.8	17.4
	M	20.04	13.23	13.71	14.81
	SD	1.16	0.74	0.93	1.17
Rübeland	n	37	37	37	37
	min	16.7	10.2	12.4	13.3
	max	23.8	15.7	16.5	17.7
	M	20.25	13.20	14.28	15.35
	SD	1.49	1.07	0.93	1.10
Arcy-sur-Cure	n	31	31	31	31
	min	18.9	11.6	12.7	13.3
	max	23.4	15.3	16.9	17.3
	M	21.08	13.50	14.95	15.28
	SD	1.26	0.91	1.03	1.26
Eirós	n	17	17	17	17
	min	18.1	10.9	12.5	13.8
	max	21.8	14.2	16.0	17.9
	M	20.41	12.87	14.38	15.84
	SD	1.20	0.87	1.10	1.29
Nietoperzowa	n	30	30	30	31
	min	18.1	12.0	12.6	12.2
	max	23.5	15.0	16.3	18.0
	M	20.83	13.45	14.31	14.89
	SD	1.43	0.98	0.98	1.38
Odessa	n	50	50	50	50
	min	18.2	10.3	12.8	9.9
	max	24.0	16.4	17.1	18.5
	M	21.30	13.66	14.83	14.80
	SD	1.49	1.18	1.07	1.64
Secrets Cave	n	19	19	19	18
	min	17.3	10.7	12.0	10.3
	max	22.7	14.8	17.6	16.3
	M	19.70	13.01	14.09	13.84
	SD	1.60	1.10	1.62	1.84
Kudaro 3, layer 3-4	n	13	14	14	13
	min	17.2	10.0	12.5	13.8
	max	21.8	13.9	16.8	18.7
	M	19.47	12.19	14.80	16.09
	SD	1.47	1.05	1.21	1.47
Kizel	n	21	21	22	21
	min	15.5	10.0	10.9	11.1
	max	19.5	13.8	14.3	15.8
	M	17.82	11.95	12.55	13.71
	SD	1.13	0.93	0.83	1.11

Table 3
Measurements (in mm) of upper molar M1 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of frontal part (2)	Length of caudal part (3)	Length of paracone (4)	Length of metacone (5)	Greatest width (6)
Jagsthausen	n	14	14	14	14	14	14
	min	22.7	11.1	10.9	7.9	7.6	15.4
	max	27.2	13.3	13.7	10.5	10.4	20.0
	M	24.91	12.19	12.43	9.22	8.52	17.30
	SD	1.01	0.60	0.84	0.75	0.77	1.13
Mosbach	n	47	47	47	47	47	47
	min	21.2	9.7	10.5	7.7	6.9	15.4
	max	28.9	13.7	14.9	11.3	10.4	22.3
	M	23.38	12.04	12.90	9.20	8.74	18.35
	SD	1.89	0.89	1.08	0.83	0.86	1.46
Westbury	n	34	34	34	34	34	34
	min	23.7	11.0	11.6	7.5	7.5	16.6
	max	28.4	15.4	15.1	10.4	11.1	21.0
	M	25.70	12.43	13.38	9.27	9.00	18.85
	SD	1.19	0.84	0.90	0.58	0.76	1.08
Kudaro 1, layer 5	n	75	67	71	67	69	83
	min	22.2	10.5	10.9	8.1	7.5	16.8
	max	29.7	15.9	15.8	11.5	11.7	22.5
	M	26.02	12.61	13.36	9.75	8.77	18.91
	SD	1.53	0.80	0.94	0.69	0.76	1.27
Einhorn	n	55	55	55	55	55	55
	min	23.4	11.7	11.1	8.4	7.9	16.5
	max	29.6	14.7	15.3	11.7	10.5	22.3
	M	26.74	13.09	13.27	9.89	9.16	19.35
	SD	1.44	0.66	0.94	0.67	0.57	1.26
Furtins	n	38	38	38	38	38	38
	min	23.7	11.7	10.7	8.2	7.8	16.8
	max	31.5	15.2	15.7	11.5	12.0	21.5
	M	26.85	13.17	13.24	10.14	9.61	19.37
	SD	1.65	0.74	1.04	0.75	0.83	1.18

Table 4
Measurements (in mm) of upper molar M1 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of frontal part (2)	Length of caudal part (3)	Length of paracone (4)	Length of metacone (5)	Greatest width (6)
Zoolithen	n	62	62	62	62	62	62
	min	25.3	11.6	12.7	8.3	8.0	18.1
	max	31.8	15.6	17.7	11.9	11.6	23.2
	M	28.61	13.75	14.63	10.51	9.59	19.74
	SD	1.45	0.82	1.04	0.76	0.71	1.14
Rübeland	n	45	45	45	45	45	45
	min	25.3	12.3	12.7	9.2	8.5	17.4
	max	32.4	15.4	16.9	11.7	11.0	23.0
	M	29.05	13.87	14.91	10.45	9.72	19.93
	SD	1.57	0.72	0.95	0.65	0.61	1.28
Arcy-sur-Cure	n	31	31	31	31	30	31
	min	24.9	11.5	13.1	8.6	8.5	18.3
	max	32.0	15.3	17.1	12.0	11.7	22.9
	M	29.09	13.79	15.22	10.63	10.17	20.38
	SD	1.89	0.93	1.28	0.84	0.78	1.38
Eirós	n	26	26	26	26	26	26
	min	26.0	12.0	13.1	9.0	8.6	16.9
	max	30.8	14.6	16.4	11.4	10.7	21.7
	M	28.43	13.56	14.72	10.06	9.58	19.85
	SD	1.32	0.69	0.86	0.53	0.57	1.23
Odessa	n	53	53	53	53	53	52
	min	27.6	13.1	13.9	9.9	9.2	18.5
	max	33.4	16.0	18.0	12.4	11.8	23.6
	M	29.82	14.14	15.59	11.08	10.37	20.83
	SD	1.35	0.69	0.91	0.60	0.50	1.11
Secrets Cave	n	20	20	20	20	20	20
	min	25.7	12.5	13.1	9.0	8.5	17.2
	max	30.7	14.9	17.4	11.5	11.4	22.1
	M	27.91	13.61	14.97	10.13	9.74	19.24
	SD	1.56	0.67	1.12	0.67	0.71	1.37
Medvezhiya Cave	n	22	22	22	22	22	22
	min	26.4	12.5	12.9	9.3	8.6	18.2
	max	32.6	17.5	17.7	11.4	10.7	22.0
	M	29.31	14.23	15.25	10.22	9.85	20.16
	SD	1.54	0.98	1.20	0.59	0.56	0.98
Kudaro 3, layer 3-4	n	20	20	19	18	17	20
	min	23.7	11.6	12.0	8.6	7.7	17.6
	max	28.5	13.9	14.9	10.7	10.1	21.1
	M	26.50	12.76	13.19	9.67	8.83	19.13
	SD	1.16	0.64	0.76	0.58	0.59	0.89
Kizel	n	29	27	28	27	28	29
	min	22.2	10.8	9.8	7.8	6.9	15.2
	max	29.0	12.7	13.8	9.4	10.0	19.4
	M	24.44	11.89	12.11	8.61	7.98	17.10
	SD	1.21	0.52	0.85	0.41	0.60	1.05

Table 5
Measurements (in mm) of upper molar M2 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Length of metacone (3)	Greatest width (4)	Width through hypocone (5)
Jagsthausen	n	11	11	11	11	11
	min	37.4	10.0	8.2	18.4	16.0
	max	46.1	14.3	11.9	22.6	19.9
	M	40.38	11.74	10.26	19.94	18.14
	SD	2.61	1.43	0.97	1.16	1.12
Mosbach	n	52	53	53	53	52
	min	35.2	9.2	7.4	18.0	15.3
	max	50.1	15.8	14.2	24.2	20.5
	M	40.81	12.08	10.57	20.84	17.88
	SD	3.03	1.31	1.40	1.39	1.24
Westbury	n	37	37	37	37	37
	min	35.1	9.3	8.0	19.0	16.4
	max	50.8	15.1	13.8	24.0	23.4
	M	43.42	12.20	11.03	21.32	19.04
	SD	3.44	1.45	1.42	1.30	1.53
Kudaro 1, layer 5	n	47	50	51	57	49
	min	37.7	10.3	7.0	19.3	15.4
	max	49.7	15.9	13.9	25.1	22.6
	M	43.49	12.88	11.44	21.84	18.83
	SD	2.54	1.13	1.40	1.30	1.41
Einhorn	n	54	54	54	54	54
	min	38.5	10.8	8.1	19.7	15.9
	max	49.1	15.8	14.2	24.1	21.8
	M	43.14	12.98	10.69	21.90	18.56
	SD	2.52	0.95	1.21	1.13	1.16
Furtins	n	32	32	32	31	32
	min	34.9	10.2	6.6	19.4	17.4
	max	48.5	14.6	12.7	24.3	20.7
	M	42.79	12.20	9.32	21.97	19.00
	SD	2.82	1.05	1.36	1.32	1.00

Table 6
Measurements (in mm) of upper molar M2 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of paracone (2)	Length of metacone (3)	Greatest width (4)	Width through hypocone (5)
Zoolithen	n	65	65	65	65	65
	min	39.1	10.7	8.9	20.2	17.7
	max	50.4	15.3	13.5	25.9	23.7
	M	44.54	13.07	11.13	22.87	20.28
	SD	2.55	1.03	1.10	1.27	1.16
Rübeland	n	55	55	55	55	55
	min	40.4	11.4	9.7	20.9	18.6
	max	52.1	15.6	14.6	25.5	23.6
	M	45.64	13.79	11.74	23.11	20.81
	SD	2.54	0.99	1.30	1.08	1.16
Arcy-sur-Cure	n	32	32	32	32	32
	min	38.5	11.8	8.3	21.4	19.3
	max	56.4	15.5	14.2	26.7	25.3
	M	46.61	13.41	10.70	23.44	21.61
	SD	3.56	1.03	1.41	1.31	1.34
Eirós	n	25	25	25	25	25
	min	41.4	11.0	7.6	20.3	17.8
	max	47.1	14.7	12.1	25.1	21.6
	M	44.71	12.96	10.22	22.61	20.27
	SD	1.52	0.92	1.05	0.92	0.78
Nietoperzowa	n	31	37	36	39	31
	min	42.0	12.3	8.3	21.0	18.5
	max	51.3	15.1	14.8	27.7	24.4
	M	46.65	13.66	11.33	23.94	21.64
	SD	2.44	0.83	1.40	1.35	1.25
Odessa	n	53	53	53	52	53
	min	36.7	12.0	8.7	19.9	16.0
	max	51.9	15.4	15.0	27.1	23.0
	M	46.32	13.55	11.40	23.73	20.42
	SD	2.87	0.81	1.46	1.61	1.53
Secrets Cave	n	83	75	79	83	82
	min	41.3	10.6	8.4	20.4	18.3
	max	49.4	15.0	13.4	25.8	25.8
	M	44.49	12.54	11.11	22.71	20.68
	SD	1.98	0.81	0.94	1.08	0.99
Medvezhiya Cave	n	21	21	21	21	21
	min	39.1	11.3	10.1	19.9	18.1
	max	52.6	18.4	14.4	27.7	24.5
	M	44.10	13.03	11.71	22.72	20.50
	SD	3.14	1.48	1.07	1.52	1.51
Kudaro 3, layer 3-4	n	24	26	25	25	23
	min	39.0	9.6	7.4	19.2	17.9
	max	47.8	14.9	12.2	24.7	23.5
	M	42.91	12.61	10.46	21.97	19.94
	SD	2.17	1.56	1.15	1.35	1.49
Kizel	n	29	28	28	29	28
	min	35.4	9.3	7.0	17.5	13.7
	max	42.3	13.2	9.8	21.8	18.4
	M	39.24	10.54	8.21	19.13	17.01
	SD	2.08	0.92	0.66	1.12	1.07

Table 7
Measurements (in mm) of lower premolar p4 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Greatest width (2)	Distance between peak of paraconid and peak of metaconid (3)
Jagsthausen	n	21	21	14
	min	12.4	7.6	4.0
	max	15.7	9.9	7.6
	M	14.21	8.81	5.76
	SD	0.98	0.63	1.00
Mosbach	n	20	20	14
	min	13.5	7.7	4.7
	max	17.2	9.9	8.2
	M	14.99	8.80	6.09
	SD	0.92	0.63	1.10
Westbury	n	20	20	8
	min	12.5	6.9	4.5
	max	16.7	10.2	6.6
	M	14.53	8.77	5.45
	SD	1.03	0.87	0.70
Kudaro 1, layer 5	n	68	67	40
	min	11.1	7.7	3.7
	max	17.9	10.6	8.1
	M	15.08	9.09	6.16
	SD	1.26	0.73	1.03
Einhorn	n	28	28	19
	min	11.8	8.1	3.8
	max	16.3	11.3	6.8
	M	14.30	9.43	5.15
	SD	1.07	0.85	0.79
Furtins	n	12	12	9
	min	12.3	8.4	3.4
	max	16.8	12.0	9.0
	M	14.93	9.46	5.11
	SD	1.30	0.94	0.922
Bacton Forest Bed	n	14	14	10
	min	12.7	7.9	6.1
	max	16.8	10.4	10.0
	M	14.53	8.81	4.82
	SD	1.05	0.78	1.03

Table 8
Measurements (in mm) of lower premolar p4 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Greatest width (2)	Distance between peak of paraconid and peak of metaconid (3)
Zoolithen	n	55	55	52
	min	11.9	8.6	3.2
	max	19.7	12.8	6.8
	M	15.61	10.31	4.90
	SD	1.26	0.91	0.95
Rübeland	n	38	38	38
	min	12.5	8.5	2.7
	max	19.0	14.2	5.7
	M	15.49	10.69	4.06
	SD	1.44	1.16	0.75
Arcy-sur-Cure	n	41	41	41
	min	11.5	9.4	2.4
	max	17.6	12.9	5.8
	M	15.47	10.85	4.10
	SD	1.17	0.96	0.79
Eirós	n	17	17	17
	min	11.3	8.9	2.4
	max	17.8	12.4	5.1
	M	15.52	10.64	3.83
	SD	1.63	0.92	0.69
Nietoperzowa	n	34	34	35
	min	14.0	9.4	3.2
	max	18.0	13.3	5.8
	M	16.26	10.88	4.21
	SD	1.02	0.77	0.71
Odessa	n	56	56	52
	min	12.9	9.5	2.1
	max	18.5	13.0	6.3
	M	16.14	11.24	5.00
	SD	1.27	0.83	0.98
Secrets Cave	n	24	24	23
	min	14.8	9.6	3.3
	max	18.5	12.0	6.2
	M	16.51	10.65	4.64
	SD	1.19	0.69	0.80
Kudaro 3, layer 3-4	n	10	11	10
	min	12.6	8.9	3.9
	max	16.2	10.5	9.7
	M	14.62	9.59	6.03
	SD	1.11	0.52	1.60
Kizel	n	17	10	
	min	10.1	7.3	
	max	15.4	10.6	
	M	13.35	9.09	
	SD	1.59	0.97	

Table 9
Measurements (in mm) of lower molar m1 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of trigonid (2)	Length of entoconid 1 (3)	Length of entoconid 2 (4)	Width of trigonid (5)	Width of talonid (6)	Least width in middle part (7)
Jagsthausen	n	27	27	20	20	27	27	27
	min	25.0	15.6	4.6	1.7	9.0	11.6	9.1
	max	30.4	19.8	7.8	6.0	11.3	13.6	11.6
	M	27.20	17.40	5.80	3.51	10.14	12.77	10.21
	SD	1.29	1.05	0.76	1.01	0.59	0.57	0.61
Mosbach	n	20	17	12	12	17	20	17
	min	24.5	16.0	4.1	3.1	9.4	11.7	9.5
	max	31.1	21.0	7.3	5.7	11.2	14.5	11.6
	M	27.34	17.53	5.35	4.05	10.22	13.04	10.39
	SD	1.70	1.23	0.97	0.76	0.57	0.89	0.55
Westbury	n	6	6	4	4	6	6	6
	min	25.8	16.1	3.9	3.8	9.9	11.5	9.6
	max	27.5	18.2	5.8	6.0	11.3	13.6	11.1
	M	26.77	16.88	4.80	4.73	10.5	12.78	10.28
	SD	0.65	0.77	0.80	0.93	0.49	0.95	0.59
Kudaro 1, layer 5	n	88	75	52	52	76	123	104
	min	25.3	15.5	2.3	2.8	8.7	11.6	9.0
	max	32.7	21.2	7.1	7.3	12.6	15.8	12.9
	M	28.51	18.12	4.66	4.82	10.93	13.57	10.91
	SD	1.60	1.32	1.08	0.97	0.76	0.88	0.80
Einhorn	n	42	42	42	42	42	42	42
	min	25.5	15.9	3.2	2.8	9.9	12.3	9.4
	max	33.4	21.4	7.4	5.6	13.6	17.6	13.7
	M	28.82	18.20	5.21	4.17	11.48	14.13	11.43
	SD	1.57	1.11	0.87	0.66	0.73	0.93	0.77
Furtins	n	38	38	38	38	38	38	38
	min	25.6	14.7	2.3	2.7	9.9	12.0	9.7
	max	30.9	19.7	6.2	5.9	13.0	15.4	13.0
	M	28.26	17.43	4.15	4.09	11.65	13.69	11.43
	SD	1.30	1.01	0.70	0.75	0.77	0.92	0.88
Bacton Forest Bed	n	11	11	7	7	11	11	11
	min	24.6	15.6	3.1	3.2	9.7	11.9	9.8
	max	28.1	18.5	6.3	5.0	11.7	15.5	12.8
	M	26.00	16.72	4.69	4.26	10.53	13.12	10.86
	SD	1.29	0.99	0.98	0.62	0.66	0.98	0.87

Table 10
Measurements (in mm) of lower molar m1 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of trigonid (2)	Length of entoconid 1 (3)	Length of entoconid 2 (4)	Width of trigonid (5)	Width of talonid (6)	Least width in middle part (7)
Zoolithen	n	51	51	51	51	51	51	51
	min	26.8	16.8	3.5	4.0	9.8	11.7	9.9
	max	34.3	21.8	7.1	6.9	13.5	17.2	13.3
	M	29.85	18.78	5.53	5.15	11.56	14.20	11.29
	SD	1.76	1.10	0.76	0.68	0.83	1.06	0.80
Rübeland	n	39	39	39	39	39	39	39
	min	28.2	17.5	4.1	3.7	10.3	12.9	9.9
	max	33.7	21.8	7.8	6.6	13.4	16.6	12.8
	M	30.69	19.27	6.10	5.28	11.88	14.80	11.54
	SD	1.43	0.99	0.84	0.66	0.77	0.94	0.71
Arcy-sur-Cure	n	31	31	31	31	31	31	31
	min	27.3	17.2	3.4	3.8	10.7	13.1	10.2
	max	33.4	20.7	6.3	7.1	13.9	16.7	12.9
	M	30.75	19.29	5.31	5.68	12.33	14.98	11.57
	SD	1.43	0.94	0.66	0.75	0.68	0.83	0.60
Eirós	n	25	25	25	25	25	25	25
	min	27.7	17.3	4.3	3.8	10.4	13.4	10.4
	max	34.0	21.1	7.0	7.2	13.1	16.0	12.6
	M	31.32	19.42	5.34	5.36	11.67	14.81	11.19
	SD	1.48	0.94	0.86	0.77	0.69	0.76	0.55
Nietoperzowa	n	18	19	19	20	19	19	20
	min	27.5	17.4	4.0	4.0	10.2	12.0	10.4
	max	33.5	21.4	6.8	6.4	13.3	17.1	13.0
	M	30.53	19.26	5.24	5.20	12.27	14.68	11.54
	SD	1.79	1.05	0.74	0.70	0.87	1.18	0.74
Odessa	n	45	42	40	40	45	45	45
	min	28.0	10.2	4.5	4.2	10.8	13.8	10.9
	max	34.1	26.0	7.5	8.2	14.4	17.2	14.1
	M	31.24	19.72	5.54	5.59	12.60	15.40	11.98
	SD	1.53	2.08	0.68	0.83	0.82	0.77	0.64
Medvezhiya Cave	n	24	24	24	24	24	24	24
	min	26.9	17.3	4.8	4.0	10.8	12.8	9.8
	max	33.9	21.5	9.6	6.4	12.4	16.2	12.0
	M	30.11	19.24	6.04	5.14	11.73	14.36	10.96
	SD	1.68	1.15	1.06	0.63	0.58	0.96	0.60
Kudaro 3, layer 3-4	n	22	22	16	16	23	23	23
	min	24.7	15.0	2.5	2.6	9.5	12.5	9.9
	max	29.7	18.9	5.9	6.9	11.7	14.8	12.4
	M	27.08	17.00	4.56	4.19	10.94	13.74	11.09
	SD	1.30	0.90	1.03	1.22	0.63	0.62	0.62
Kizel	n	14	14	12	13	13	14	13
	min	24.2	15.4	3.9	2.5	9.0	11.6	9.1
	max	27.2	17.4	7.3	3.9	11.7	14.1	11.0
	M	25.48	16.34	5.68	2.99	10.19	12.75	10.36
	SD	0.87	0.69	0.96	0.36	0.75	0.63	0.56

Table 11
Measurements (in mm) of lower molar m2 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Labial length of trigonid (2)	Lingual length of trigonid (3)	Labial length of talonid (4)	Lingual length of talonid (5)	Width of trigonid (6)	Width of talonid (7)
Jagsthausen	n	27	27	27	27	27	27	27
	min	25.2	15.1	13.0	8.6	10.2	14.1	14.8
	max	32.5	19.9	18.0	11.7	15.2	18.3	20.1
	M	28.46	16.91	14.91	10.14	12.31	16.46	17.48
	SD	2.04	1.33	1.49	0.82	1.35	1.06	1.33
Mosbach	n	42	39	39	39	39	40	42
	min	24.6	13.7	11.6	7.8	8.9	13.4	14.1
	max	31.1	18.5	16.1	12.5	13.9	18.5	20.0
	M	27.43	16.19	14.18	9.57	11.48	15.91	17.08
	SD	1.46	1.20	1.10	1.00	1.24	1.04	1.31
Westbury	n	31	31	31	31	31	31	31
	min	23.6	13.8	11.4	9.0	9.3	13.3	14.6
	max	33.0	20.1	18.3	12.2	15.0	19.2	20.0
	M	28.53	17.05	14.78	10.49	12.32	16.36	17.61
	SD	2.17	1.50	1.60	0.77	1.54	1.36	1.46
Kudaro 1, layer 5	n	72	72	72	72	72	72	72
	min	25.1	14.6	13.1	9.9	10.1	14.8	15.3
	max	34.4	21.1	18.2	14.0	16.7	19.8	20.9
	M	29.56	17.63	15.37	11.43	13.37	16.86	18.05
	SD	1.92	1.50	1.11	0.98	1.24	1.20	1.27
Einhorn	n	42	42	42	42	42	42	42
	min	24.2	14.0	13.0	9.0	10.0	13.5	13.5
	max	32.0	19.6	17.4	13.0	15.0	19.2	20.9
	M	29.07	16.79	14.87	10.86	12.27	16.96	17.59
	SD	1.67	1.38	1.03	0.98	1.08	1.21	1.44
Furtins	n	44	43	44	44	44	44	44
	min	25.8	14.1	12.5	9.1	9.0	14.6	14.8
	max	31.0	18.5	19.4	12.0	13.5	19.2	19.3
	M	28.08	16.51	15.48	10.57	11.39	16.65	17.06
	SD	1.39	1.15	1.21	0.73	1.04	0.85	1.00
Bacton Forest Bed	n	10	10	10	10	10	10	10
	min	23.3	14.4	13.2	7.5	9.5	13.8	15.3
	max	28.3	18.1	15.2	9.6	11.2	17.0	18.1
	M	25.38	16.12	13.96	8.72	10.42	15.46	16.39
	SD	1.43	1.20	0.71	0.89	0.64	1.03	0.78

Table 12
Measurements (in mm) of lower molar m2 in of Late Pleistocene cave bears.

Localities		Greatest length (1)	Labial length of trigonid (2)	Lingual length of trigonid (3)	Labial length of talonid (4)	Lingual length of talonid (5)	Width of trigonid (6)	Width of talonid (7)
Zoolithen	n	57	57	56	57	56	56	57
	min	25.7	14.9	12.3	8.9	9.4	14.9	15.6
	max	36.3	21.7	18.8	16.8	17.1	20.2	21.9
	M	29.70	17.66	15.31	11.36	12.55	17.54	18.44
	SD	2.24	1.51	1.49	1.45	1.53	1.20	1.44
Rübeland	n	39	39	39	39	39	39	39
	min	27.8	14.6	13.5	9.2	10.5	15.9	16.4
	max	34.3	20.1	18.3	13.7	15.0	20.3	22.1
	M	31.18	18.14	16.14	11.73	13.01	18.11	18.43
	SD	1.67	1.18	1.17	0.98	0.97	1.04	1.18
Arcy-sur-Cure	n	44	44	44	44	44	44	44
	min	28.0	16.2	13.2	9.6	10.1	15.8	16.0
	max	34.2	20.6	19.2	14.9	15.3	21.0	21.4
	M	31.29	18.48	16.34	11.84	12.71	18.26	18.89
	SD	1.62	1.00	1.22	1.19	1.23	1.13	1.26
Eirós	n	24	24	24	24	24	24	24
	min	28.3	15.7	14.4	10.3	11.4	15.5	17.1
	max	34.5	19.9	17.7	14.3	16.0	20.5	22.8
	M	31.36	17.56	15.77	12.48	13.33	17.66	19.12
	SD	1.42	1.18	0.84	0.94	1.17	1.04	1.27
Nietoperzowa	n	31	31	31	31	31	31	31
	min	27.0	16.6	13.0	10.0	11.3	16.3	16.0
	max	34.7	21.2	18.7	14.4	17.1	20.5	22.3
	M	31.18	18.84	16.14	12.77	14.46	18.59	19.18
	SD	1.76	1.20	1.37	1.00	1.39	1.00	1.29
Odessa	n	89	89	89	89	89	89	89
	min	27.5	16.4	13.5	9.9	10.8	16.4	17.1
	max	35.7	21.9	19.6	15.2	18.0	20.9	22.1
	M	31.26	18.73	16.44	12.74	13.99	18.44	19.30
	SD	1.64	1.27	1.29	1.21	1.54	1.01	1.09
Secrets Cave	n	62	62	62	62	62	62	62
	min	27.3	14.9	13.6	10.1	11.9	15.0	17.0
	max	37.3	23.4	20.3	18.7	18.8	24.0	26.0
	M	31.61	18.94	16.02	12.44	14.78	18.69	19.75
	SD	2.08	1.91	1.73	1.80	1.88	1.94	1.93
Medvezhiya Cave	n	15	15	15	15	15	15	15
	min	27.4	15.3	14.5	10.0	9.7	15.5	15.6
	max	31.9	18.9	17.2	14.2	15.7	18.6	19.9
	M	29.17	17.02	15.73	11.76	12.60	17.04	17.49
	SD	1.35	0.88	0.79	1.26	1.43	0.89	1.32
Kudaro 3, layer 3-4	n	20	20	20	20	20	20	20
	min	25.3	15.8	12.1	9.4	10.5	14.7	15.7
	max	30.9	18.8	16.6	12.1	14.5	18.2	19.3
	M	28.24	17.23	14.67	10.78	12.21	16.78	17.87
	SD	1.46	0.88	1.08	0.75	0.93	0.83	0.96
Kizel	n	12	12	12	12	12	12	12
	min	24.2	13.9	12.4	8.2	9.2	14.0	15.2
	max	27.5	17.2	14.3	11.1	13.3	16.3	17.2
	M	26.22	15.49	13.37	9.36	11.72	14.90	16.02
	SD	0.98	1.03	0.61	0.79	1.16	0.63	0.75

Table 13
Measurements (in mm) of lower molar m3 of Middle Pleistocene cave bears.

Localities		Greatest length (1)	Length of talonid (2)	Greatest width (3)	Width of talonid (4)
Jagsthausen	n	37	37	37	37
	min	20.9	7.4	15.7	8.0
	max	30.1	14.1	19.9	18.2
	M	24.44	9.86	17.77	15.81
	SD	2.04	1.71	1.10	1.74
Mosbach	n	34	31	32	32
	min	19.8	6.5	15.3	13.0
	max	29.8	14.4	20.8	19.4
	M	24.28	10.20	17.90	15.84
	SD	2.33	2.02	1.26	1.60
Westbury	n	50	47	50	47
	min	18.2	7.2	14.9	11.8
	max	30.0	14.4	21.3	20.2
	M	24.72	10.42	18.24	16.39
	SD	2.49	1.67	1.47	1.97
Kudaro 1, layer 5	n	124	111	131	111
	min	20.7	7.5	15.7	13.0
	max	30.6	14.5	22.0	21.1
	M	25.26	10.84	18.42	16.63
	SD	2.01	1.46	1.18	1.52
Einhorn	n	42	42	42	42
	min	22.3	7.5	15.5	14.1
	max	31.3	13.5	21.6	21.0
	M	25.12	10.41	18.70	17.08
	SD	1.90	1.30	1.34	1.51
Furtins	n	8	8	8	8
	min	22.5	10.5	18.0	16.8
	max	29.9	15.1	21.4	19.8
	M	25.61	11.79	19.25	18.57
	SD	2.66	1.47	1.26	1.20
Bacton Forest Bed	n	10	10	10	10
	min	21.8	7.4	15.4	14.2
	max	27.1	13.5	20.7	18.0
	M	24.20	10.39	17.57	16.19
	SD	1.70	1.75	1.63	1.31

Table 14
Measurements (in mm) of lower molar m3 of Late Pleistocene cave bears.

Localities		Greatest length (1)	Length of talonid (2)	Greatest width (3)	Width of talonid (4)
Zoolithen	n	55	55	55	55
	min	21.4	8.5	16.9	13.8
	max	31.1	16.0	22.4	21.5
	M	25.87	12.63	18.92	18.02
	SD	2.02	1.73	1.12	1.80
Rübeland	n	33	33	33	33
	min	22.2	9.4	16.6	15.3
	max	30.8	16.2	21.5	22.4
	M	26.97	12.11	18.89	17.99
	SD	2.46	1.75	1.27	1.77
Arcy-sur-Cure	n	41	41	41	41
	min	23.8	9.6	17.1	15.6
	max	31.7	15.2	22.2	22.0
	M	27.91	12.68	19.53	18.73
	SD	1.78	1.23	1.18	1.32
Eirós	n	12	12	12	12
	min	25.2	10.6	17.4	14.8
	max	30.1	14.6	21.0	20.3
	M	27.20	12.45	19.32	17.70
	SD	1.78	1.40	1.17	1.65
Nietoperzowa	n	30	31	30	31
	min	24.8	8.4	17.2	16.0
	max	33.0	18.7	23.6	23.6
	M	28.08	13.65	20.08	19.26
	SD	2.21	2.16	1.38	1.83
Odessa	n	100	100	99	99
	min	21.0	8.1	17.5	14.1
	max	31.4	16.7	22.7	22.0
	M	27.33	12.86	19.91	18.79
	SD	2.10	1.45	1.24	1.48
Secrets Cave	n	18	18	18	18
	min	22.9	9.1	16.2	14.6
	max	31.4	15.0	22.4	21.0
	M	27.46	12.40	20.19	18.73
	SD	2.39	1.81	1.48	1.61
Medvezhiya Cave	n	22	22	22	22
	min	21.5	8.8	15.7	13.3
	max	29.7	13.1	21.4	19.5
	M	25.36	10.72	18.59	16.86
	SD	2.14	1.15	1.42	1.69
Kudaro 3, layer 3-4	n	24	24	24	23
	min	20.7	8.3	16.5	13.2
	max	28.1	13.3	21.1	19.3
	M	24.87	10.74	18.68	17.20
	SD	2.08	1.32	1.14	1.54
Kizel	n	19		19	
	min	21.0		14.8	
	max	25.2		18.0	
	M	23.25		16.82	
	SD	1.12		0.81	

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