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Late Pleistocene cave bear (*Ursus deningeri kudarensis*) from the Akhstyrskaya Cave in the Caucasus (Russia)

by

Gennady BARYSHNIKOV *)

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Abstract

Study of bones and teeth of cave bear from the Palaeolithic layers in Akhstyrskaya Cave near Sochi City shows that it was inhabited by larger bears belonging to the subspecies *Ursus deningeri kudarensis*, with more archaic morphology than that of *Ursus spelaeus*. Analysis of the bone material indicated the natural mortality of animals in the cave.

1. Introduction

First mentions about the cave bear in the Caucasus belong to the end of the of XIX century (ANUTSCHIN 1887), but numerous bone material was obtained only with the beginning of excavations in Akhstyrskaya Cave. GROMOVA (1948) noted the large size of animals and almost full absence of any pathological signs. This bear has been identified as the European species *Ursus spelaeus* Rosenmüller (GROMOVA, 1948; VERESHCHAGIN, 1959).

It was shown later that structure of the cheek teeth in the Caucasian cave bear were more archaic than in the *U. spelaeus* and similar to the *U. deningeri* von Reichenau from Middle Pleistocene (BARYSHNIKOV & DEDKOVA, 1978). Two chronosubspecies has been described from Kudaro Caves in Transcaucasia: *U. deningeri palaeokudarensis* (Acheulean layers) and *U. d. kudarensis* (Mousterian layers) (see BARYSHNIKOV, 1998). Taxonomical state of the bear from the latest Pleistocene retained undetermined. Since Akhstyrskaya Cave contains both Mousterian and Upper Palaeolithic layers, it allows to elucidate the problem.

Akhstyrskaya Cave is situated on the right bank of Mzymta River in 15 km from coast of Black Sea near Adler (Sochi Region), Northwestern Transcaucasia. It lies at height of 100 m above the river and 300 m a.s.l. Archaeological works were conducted here by S. Zamiatnin (1937-1938), M. Panichkina and E. Vekilova (1961), E. Vekilova (1962-1963, 1965, 1978) and S. Kulakov (1998-1999), the greatest area (90 square meters in the entrance part of the cave) being taken by the excavations of S. Zamiatnin (VEKILOVA et al., 1978). Thickness of cave sediments reaches 4-5 m. Seven lithological layers were distinguished grouping in 3 levels (VEKILOVA et al., 1978). Lowest level (layers 6-7) - multicolored loam with river pebbles in the base, middle level (layers 3-5) - dark-grey light loam with heavily weathered detritus, upper level (layers 1-2) - dark-brown loam with numerous angular fragments of limestone. Lower layers 6-7 probably had been formed before opening of the cave cavity by Mzymta River, and do not contain palaeozoological and archaeozoological finds. Layers 3-5 include Mousterian stone tools, and plenty of large mammals bone remains; layer 2 bears Upper Palaeolithic industries.

Layer 3a was dated by U/Th from stalactites - 35 000 ± 2 000, layer 2b by radiocarbon dating 19 000 ± 500 (VEKILOVA et al., 1978). Later O. Kulikov (Moscow) obtained two thermoluminiscent dates: 306 000 ± 61 000 (RTR-926) for layer 7 and 112 000 ± 22 000 (RTR-927) for lower part of layer 5.

More than 4 thousand bones of large mammals were elevated from Akhstyrskaya Cave, most of which belonging to the cave bear (near 96%). Accompanying fauna includes following species (GROMOVA, 1948, VEKILOVA et al., 1978, my data): *Vulpes vulpes, Canis lupus, Ursus arctos, Martes* sp., *Mustela nivalis, Panthera spelaea, Lynx lynx, Felis sylvestris, Sus scropha, Capreolus capreolus, Cervus elaphus, Megaloceros giganteus* (one bone in layer 5), *Alces alces* (only layer 2), *Bison* sp., *Capra caucasica/ibex*, cf. *Ovis orientalis*.

In 1999, as a result of washing of cave sediments new data on the micromammals fauna were obtained (determined by me, and Dr. M. Zaitsev for Insectivora): *Sorex satunini, S. volnuchini, Cricetus cricetus,*

*) Dr. Gennady Baryshnikov, Zoological Institute, Russian Academy of Sciences, 199034 Saint Petersburg, Russia.

Prometheomys schaposchnikovi, Apodemus cf. *uralensis, Arvicola terrestris, Chionomys roberti, Terricola majori, Microtus arvalis.*

Presence of the *Prometheomys schaposchnikovi* in the middle part of layer 2 is very interesting. This vole inhabits now the alpine zone at height more than 1400 m, and its record in Akhstyrskaya Cave indicates decrease of altitude belts in the Western Caucasus during the coldest climate phase of the Latest Glacial to 1000 m.

The material keeps in the Zoological Institute, Russian Academy of Sciences in St. Petersburg (ZIN). Cave bear collection from 1937-1938 (ZIN 21600-21604), 1961-1963 and 1965 excavation and one skull from 1978 excavation (ZIN 32134) have been used for the present study.

2. Results

All skeletal elements of cave bear were found in Akhstyrskaya Cave: fragments of skull, vertebrae, ribs, sternum, long and sort limb bones, bakula and hyoid (Table 1). Bones are broken on the large pieces, or kept intact. Such taphonomy testifies that bone assemblage was formed as a result of death of animals inside the cave. Only several bones were gnawed by predators, and we did not see any traces of gnawing by large rodents.

2.1. Description.

The only complete skull (ZIN 32134) has been found in the Upper Mousterian level. Judging by the condylobasal length (454 mm) and heavily worn teeth it belonged to an old male. According to the size it is slightly smaller than largest males of *Ursus spelaeus* from the Secrets Cave in the Ural Mountains (Table 2) and from the Drachenhöhle in the Alps (Marinelli, 1931). Frontal profile is abruptly arched, first premolars being absent.

Factor analysis for 21 measurements demonstrated that the skull from Akhstyrskaya Cave is placed closer to the *U. deningeri kudarensis* from Kudaro 3 Cave, than to the *U. spelaeus* from Austria, Germany and Ural Mountains (Fig. 1). The neurocranium of Caucasian cave bear is comparatively more broad and high.

The size of cheek teeth is rather permanent in different layers (Table 3). Reliable distinctions are observed only in p4 width ($t = 2.27$, $0.02 < P < 0.05$) and m2 length ($t = 2.47$, $0.01 < P < 0.02$) between the samples from the layers 4-5 and from the layer 3.

By the greatest length, cheek teeth quite exceed those of the *U. deningeri kudarensis* from the Mousterian layers of Kudaro 3 Cave in Central Transcaucasia (Baryshnikov, 1998), and only p4 ($t = 3.69$) and m2 ($t = 3.43$) are reliably longer. Most teeth (P4, M1, m1, m2, m3) seem to be undoubted shorter that the samples of the *U. spelaeus* from Wierzchowska Gorna in Poland (coll. Institute of systematics and evolution of animals, Krakow), (Table 4).

By the greatest width of cheek teeth, the samples from Akhstyrskaya Cave and Kudaro 3 Cave show more significant differences. Greatest width of M3 ($t = 3.36$), p4 ($t = 7.15$), m2 ($t = 7.89$) and m3 ($t = 3.01$) in Akhstyrskaya Cave reliably larger. The teeth from the cave studied according to this measurement are very similar to ones of the *U. spelaeus* from Wierzchowska Gorna, except of m2 which occurred wider ($t = 4.58$) in investigated sample.

Thus, the data from Akhstyrskaya Cave indicate that teeth of the Caucasian cave bear were relatively wider than those of the *U. spelaeus*. Comparison with previous sample from Kudaro 3 Cave allows to suggest that the width of crown in the Caucasian bears increased during the Late Pleistocene.

Evolution of the *U. spelaeus* demonstrates the increase of occlusal surface of cheek teeth and development of additional structures on them. Such changes testify the transition from omnivorous diet to preferably vegetable one (Kurtén, 1976) that is confirmed by the data of isotope analysis of fossil remains (Bocherens et al., 1997). The same tendency was observed in the Caucasian cave bear, however transformation of its dental system were less considerable.

Cave bears are characterised by the "molarization" of premolars which morphologically and functionally resemble molars strengthening the chewing zone of dental row. For example, lower p4 in the *U. spelaeus* extends, additional tubercles are developed on the lingual side of the main cone and on the "talonid" (Rabeder, 1983). In specimens from Akhstyrskaya Cave, average size of p4 nearly equal to those in the *U. spelaeus*, but this tooth is more simple in structure, mostly without additional formations. Its roots in the teeth examined are fused (Fig. 2), meanwhile these usually divided in the *U. spelaeus*. Such fusion of roots may strengthen the base structure of tooth under the increase of pressure on the crown.

Cluster analysis carried our for two measurements of cheek teeth from various localities of Europe and Caucasus indicated that the samples were divided on two groups (Fig. 3). First group comprises *U. spelaeus* samples, the second one includes *U. deningeri* samples. Akhstyrskaya Cave and Kudaro 3 Cave occurred among the sites with *U. deningeri* teeth, the sample from the first cave being more distinguished. Dentition of cave bear from Transcaucasia even to the end of the Pleistocene morphometrically did not reach dental parameters of the *U. spelaeus*.

Long bones in the material studied were broken because of sediment press. Two tibia, retained complete, have large size (greatest length is 344 and 345.5 mm). Metacarpals and metatarsals only slightly shorter those of *U. spelaeus* (Table 5-6). Index of the

correlation between the breadth of diaphysis in the middle part and the greatest length of metacarpus 2 (SD/GL) in Akhstyrskaya Cave nearly the same in males and females (Table 5). It exceeds in average that of *U. deningeri praekudarensis* from Kudaro 1 Cave (20.0%, n = 23) but considerably less the index of *U. spelaeus* from Secret Cave in Ural (23.1%, n = 15). Therefore, metacarpals and metatarsals are more slim those of *U. spelaeus*.

2.2. Sexual and age composition

Sexual dimorphism in cave bear expresses in the canine size, and correlation between manes and females in the different localities may be determined by the frequency distributions for canines according width at the base of the enamel (KURTÉN, 1955). Strong bimodal distribution was obtained from the samples from Drachenhöhle in Austria and Odessa in Ukraine (KURTÉN, 1955), and my calculation for Kudaro 1 Cave. In Akhstyrskaya Cave, measurements of 56 canines (upper and lower) did not demonstrate so clear sexual division. I have attributed to males those specimens that have size peculiar to the males from Drachenhöhle. In this case, more than a half of specimens from Akhstyrskaya Cave (59%) belonged to males. Sexual ratio differs in various layers of the cave: in layers 4-5, and in layer 2 it is equal, in layer 3 males twice exceed females.

Frequency distributions for greatest length of metacarpals and metatarsals also allow to evaluate sexual composition of the sample. It is generally bimodal, but sometimes it may be different, graphically with the only top (for Mtc 1, Mtc 5, Mtt 1 and Mtt2). In the latter variant, attribution of bones to sex has been made conventionally.

Several very short bones from this cave were preliminary attributed to females in Table 5-6. These might belong to immature animals, or to small adults, which were not able to reach normal size. These specimens did not include to the following calculation. Studied metacarpals (n = 156) and metatarsals (n = 168) demonstrated that a number of males in Akhstyrskaya Cave were less than that of females (44% and 33% correspondingly). In various layers, male portion presents: in layers 4-5 - 21%, in layer 3 - 53%, in layer 2 28%. As in the case with canines, their portion is greater in the upper Mousterian level.

Increase of the female number in the upper and lower parts of section allows to suggest that at that time the cave was used by bears as burning den. Rarity of the milk teeth does not contradict to this opinion being explained by the imperfect technique of former excavations.

There were found two extremely long metacarpal 4 belonging to very huge males. Such males possibly lived separately from females and young males and seldom came to the cave.

Most teeth were worn in a heavy degree. More than a half of examined incisors (n = 66) belongs to those. There are 72% of them among molars (n = 126), while the week worn specimens present only 11%. Especially heavily worn crowns the lower molar m1, with pulpar cavity being often opened (such specimens were not measured). Obtained age profile corresponds to the attritional death assemblage which is typical for the sites forming in the results of death of old animal perishing from diseases and starvation. The age of perished animals does not differ considerably in various layers; there were more young groups in layer 3 (14%).

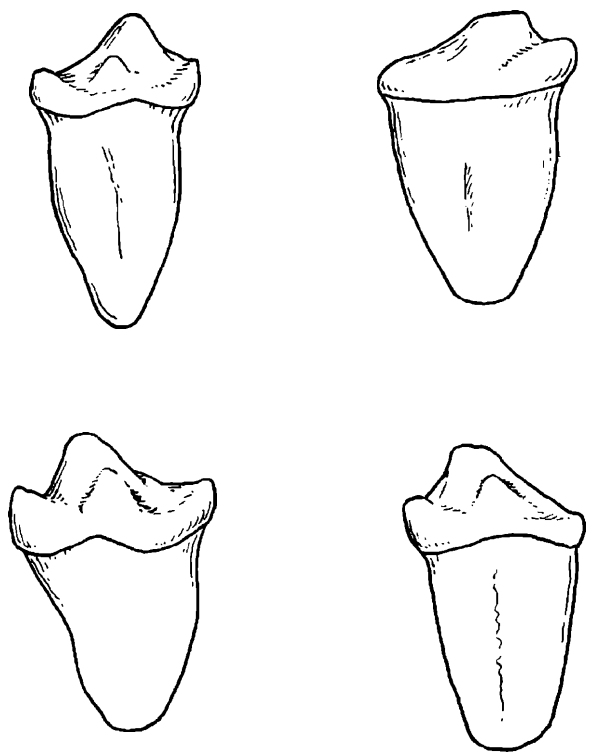

Figure 1: Lower premolar p4 from the Akhstyrskaja cave, lingual view.

3. Conclusion

Studied collection indicated that Akhstyrskaya Cave were a cave bear den. There are no obvious signs of the utilisation of bear bones by ancient men.

Obtained results testified difference of cave bear from the Late Pleistocene of Caucasus and *U. spelaeus* by skull proportion and teeth morphology. Its dentition is more similar to that of the earlier species *U. deningeri*. Although Akhstyrskaya Cave bear demonstrates several advanced characters comparatively to the bear from Kudaro 3 Cave, both may be attributed to the subspecies *U. deningeri kudarensis*.

Bears from the subgenus *Spelearctos* evidently dwelt in the Transcaucasia as early as the beginning of the

Middle Pleistocene, but later Caucasian population had been isolated from the main range. Both isolation and pleasant environmental conditions promoted the reduction of natural selection pressure, so the dental system in Caucasian cave bear evolved slower than in European ones.

Palaeogeographical, taphonomical, and morphological data from various Caucasian localities allow to tentatively reconstruct cave bear palaeoecology. These animals inhabited in various landscape belts: from the see coast to alpine meadows. Most probably, females with cubs and young males lived in small groups, and mature males dwelt alone. Females might lie for hibernation collectively. Bears consumed umbellate and other nutritious herbs, berries, fruits, nuts, bulbs and roots. Their diet might also include rodents, invertebrates, carrion. As material from Kudaro 1 Cave show, bears caught salmons spawning in rivers, in order to store fat for overwintering.

Available zoogeographical data show that Transcaucasia in the Pleistocene had been a refuge where faunal relicts were retained (GUERIN & BARYCHNIKOV, 1987). One of such relicts was of Caucasian cave bear which, as present study indicates, lived here nearly the end of the Pleistocene.

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5. References

ANUTSCHIN, D.,1887. Ueber die Reste des Höhlenbären und des Menschen aus Transcaucasien. — Bull. Soc. Imper. Nat. Moscou, Nr. **1-2**:216-221, 374-377.

BARYSHNIKOV, G.,1998. Cave bears from the Paleolithic of the Greater Caucasus. — in: (SAUNDERS, J.J., STYLES, B.W., and BARYSHNIKOV, G.F., eds.) Quaternary Paleozoology in the Northern Hemisphere. Spring-field, p. 69-118. (Illinois State Museum Scientific Papers, Vol. **XXVII**.)

BARYSHNIKOV, G.F., DEDKOVA, I.I., 1978. Cave bears of the Great Caucasus. —Trudy Zool. Instit. AN SSSR, Vol. **75**:69-77 (in Russian)

BOCHERENS, H., BILLIOU, D., PATOU-MATHIS, M., BONJEAN, D., OTTE, M., MARIOTTI, A., 1997. Paleobiological implications of the isotopic signatures (^{13}C, ^{15}N) of fossil mammal collagen in Scladina Cave (Sclayn, Belgium). — Quarternary Research, **48**:370-380.

GROMOVA, V., 1948. To the history of mammal fauna of the Caucasus. — Izvestia AN SSSR., Ser. biol., **5**:517-538. (in Russian)

GUERIN, C., BARYCHNIKOV G., 1987 Le rhinoceros acheulean de la grotte de Koudaro 1 (Georgie, URSS) et le probleme des éspèces relictes du Pleistocene du Caucase. — Geobios, **20/3**:389-396.

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

KURTÉN, B., 1976. The cave bear story. Life and death of a vanished animal. New York, 163 pp.

MARINELLI, W., 1931. Schädel des Höhlenbären. — In: ABEL O., KYRLE, G. Die Drachenhöhle bei Mixnitz. Speläol. Monogr. 7-9:332-497, Wien.

RABEDER, G., 1983. Neues vom Höhlenbären: Zur Morphogenetik der Backenzähne. — Die Höhle,**34/2**:67-85.

VEKILOVA, E.A., GRICHUK, V.P., GUBONINA, Z.P., ERMOLOVA, N.M., ZUBOV, A.A., MURATOV, V.M. and FRIDENBERG, E.O., 1978. Akhstyrskaya Cave. — In: Arkheologia i paleogeographia rannego paleolita Kryma i Kavkaza. M., Nauka, p. 37-48 (in Russian).

VERESHCHAGIN, N.K., 1959. Mammals of the Caucasus. History of the evolution of fauna. — Moscow-Leningrad: Izdatelstvo AN SSSR, 802 pp. (in Russian)

DRIESCH, A. von den, 1976. A guide to the measurement of animal bones from archaeological sites. — Peabody Mus. Bull., **1**:1-136, **Town ?**.

Table 1. Representation of skeletal elements for cave bear (*Ursus deningeri kudarensis*) in Akhstyrskaya Cave (S. Zamiatnin, excavation in 1937-1338). Total bones / minimal number of individuals.

Bones	Lower Mousterian	Upper Mousterian	Upper Paleolithic	Mixed layers	Total
Cranium	—	—	—	13	13
Mandible	—	—	—	22	22
Hyoid	—	—	—	27	27
Upper isolated teeth	11/3	48/5	18/2	6/1	83
Lower isolated teeth	61/13	86/10	44/5	10/3	201
Vertebrae	17	44	17	311	389
Ribs	—	2	1	197	200
Sternum	—	6	2	5	13
Scapula	—	—	—	9	9
Humerus	2	6	2	9	19
Ulna	4	11	3	21	39
Radius	7	7	3	9	26
Carpals	63	85	53	87	288
Metacarpals	45/9	50/12	23/6	75/12	193
Pelvis	—	—	—	5	5
Femur	10	14	3	31	58
Patella	7	13	5	41	66
Tibia	2	9	—	3	14
Fibula	5	6	—	31	42
Calcaneus	10/6	8/7	3/3	27/14	48
Astragalus	15/10	15/8	5/4	33/15	68
Tarsals	38/8	43/7	16/7	24/3	121
Metatarsals	49/9	54/9	17/4	98/17	218
Fragments of carpals / tarsals	—	—	—	304	304
Phalanx I	101	176	52	125	454
Phalanx II	41	91	29	20	181
Phalanx III	46	87	27	52	212
Sesamoids	—	—	—	3	3
Os penis	—	—	—	1	1
Total	543/13	861/12	323/7	1599/17	3317

Table 2. Sizes of skulls of cave bear males from the Caucasus and Ural. Measurements taken following Driesch, E. van den (1976: fig. 14)

Measurements, mm	*Ursus (Spelearctos) deningeri kudarensis*	*Ursus (Spelearctos) spelaeus*			
	Akhstyrskaja Cave ZIN 32134, sen.	Secrets Cave & Medvezhiya Cave			
		n	lim	x	SD
Total length (1)	499	5	438–501	472,30	30,58
Condylobasal length (2)	454	4	419–426	437,75	18,30
Basal length (3)	432	4	390–431	411,26	16,69
Upper neurocranium length (7)	298	5	219–261	245,36	19,23
Facial length (9)	249	5	235–261	245,32	9,81
"Snout" length (12)	183	5	172–199	181,36	10,37
Length of C1 – M2	167	5	167–179	173,88	4,51
Length of P4 – M2	98,1	5	84,9–95,9	91,72	4,37
Greatest mastoid breadth (23)	241	5	195–239	222,62	18,08
Greatest breadth of th occipital condyles (25)	88,5	5	83–99,2	93,18	6,44
Greatest neurocranium breadth (29)	164	5	117–126	122,30	3,63
Zygomatic breadth (30)	318	5	240–303	278,20	24,79
Frontal breadth (32)	171	5	112–148	129,50	16,05
Least breadth between the orbits (33)	113,5	5	87,7–115	101,14	11,12
Greatest palatal breadth (34)	133	5	104–120	109,90	6,35
Least palatal breadth (35)	92	4	77–90	84,25	5,44
Breadth at the inner canine alveoli (36)	122	5	101–117	110,16	6,33
Greatest inner height of the orbit (37)	64	4	65–69	67,00	1,63
Skull height (38)	159	5	126–144	134,60	7,70

Table 3. Sizes of cheek teeth in *Ursus deningeri kudarensis* from the Akhstyrskaja Cave.

Measurements, mm		Lower Mousterian, layers 4–5				Upper Mousterian, layer 3				Upper Palaeolithic, layer 2			
		n	lim	x	SD	n	lim	x	SD	n	lim	x	SD
Upper teeth													
P4	L	3	19,6–19,8	19,68	—	6	17,3–20,5	19,05	1,25	3	20,9–21,2	20,73	—
	W	3	13,9–16,2	14,90	—	6	13,6–16,2	14,87	1,05	3	15,7–17,1	16,62	—
M1	L	2	24,0; 25,3	—	—	6	25,5–28,6	26,87	1,34	2	26,7; 27,0	—	—
	W	2	17,5; 19,6	—	—	6	18,6–20,7	20,00	1,00	2	19,7; 20,0	—	—
M2	L	3	44,0–45,9	45,00	—	9	39,2–47,0	44,07	2,53	1	45,3	—	—
	W	3	22,4–25,3	23,70	—	9	21,0–26,0	23,68	1,85	2	22,1; 23,5	—	—
Lower teeth													
p4	L	5	15,0–16,9	16,00	0,85	18	14,2–17,7	16,08	0,99	5	15,3–17,6	15,93	0,99
	W	5	9,5–11,3	10,47	0,64	18	10,4–12,6	11,20	0,58	5	10,2–12,2	11,07	0,78
m1	L	1	28,2	—	—	3	26,0–28,0	26,82	—	2	27,3; 27,6	—	—
	W	1	15,1	—	—	7	13,6–15,9	14,61	0,87	4	14,4–16,1	15,42	0,74
m2	L	12	27,0–30,5	28,58	0,85	17	27,2–31,9	29,53	1,23	4	28,8–29,9	29,30	0,49
	W	12	18,1–20,6	19,46	0,69	17	17,6–22,0	20,11	1,22	4	18,2–21,1	20,02	1,37
m3	L	19	22,9–28,3	25,43	1,23	19	22,7–29,3	25,42	1,70	6	23,3–26,7	25,23	1,20
	W	19	17,3–20,5	19,25	0,90	17	16,7–23,9	19,68	1,56	6	18,6–20,1	19,43	0,59

Table 4. Sizes of cheek teeth in cave bears from the Caucasus and Poland.

Measurements, mm		*Ursus deningeri kudarensis* Akhstyrskaja Cave				*Ursus spelaeus* Wierzchowska Gorna			
		n	lim	x	SD	n	lim	x	SD
Upper teeth									
P3	L	3	6,3–10,0	8,38	—	—	—	—	—
	W	3	6,5–6,8	6,67	—	—	—	—	—
P4	L	14	18,3–21,2	19,61	1,09	10	19,5–22,9	21,69	1,15
	W	14	13,6–17,1	15,30	1,10	10	12,8–16,7	15,14	1,02
M1	L	12	24,0–28,6	26,61	1,29	28	24,4–32,2	28,75	1,60
	W	12	17,5–21,8	19,86	1,10	26	17,1–22,5	19,99	1,26
M2	L	17	39,2–48,4	44,35	2,19	6	44,2–50,7	47,25	2,76
	W	18	21,0–26,0	23,45	1,43	6	22,4–26,1	23,88	1,62
Lower teeth									
p4	L	30	14,2–17,7	16,04	0,90	3	15,0–16,0	15,63	—
	W	30	9,5–12,6	11,02	0,65	3	10,4–11,0	10,80	—
m1	L	9	26,0–29,0	27,71	0,97	37	26,4–34,4	30,73	1,68
	W	15	13,6–16,1	15,04	0,79	40	12,6–17,4	14,81	1,10
m2	L	35	27,2–31,9	29,13	1,13	39	27,8–35,2	30,95	2,02
	W	35	17,6–22,0	19,92	1,09	40	17,0–22,1	18,72	1,23
m3	L	48	22,7–29,3	25,40	1,43	21	24,9–30,8	27,71	1,65
	W	46	16,7–23,9	19,56	1,21	20	17,5–21,3	19,88	1,07

Table 5. Sizes of metacarpals of cave bear (*Ursus deningeri kudarensis*) from the Akhstyrskaja Cave, abbreviations: GL – greatest length, SD – breadth of diaphysis in the middle part.

Measurements, mm		Males				Females			
		n	lim	x	SD	n	lim	x	SD
Mtc1	GL	12	71,5–73,1	72,80	0,98	23	65,4–71,5	69,10	1,62
	SD	12	14,2–17,5	15,50	1,01	22	12,8–17,0	14,80	1,01
Mtc2	GL	13	86,5–91,8	89,08	1,74	18	81,0–85,5	83,50	1,14
	SD	13	17,7–21,6	19,49	1,02	18	16,8–19,7	18,10	0,76
Mtc3	GL	13	92,0–99,0	94,04	1,78	26	78,0–90,5	86,71	3,14
	SD	13	18,4–21,5	19,71	0,96	25	15,5–21,0	18,60	1,06
Mtc4	GL	15	91,5–106,5	95,82	4,04	9	84,8–89,7	87,87	1,55
	SD	15	18,0–23,0	20,05	1,57	9	17,5–21,7	19,02	1,21
Mtc5	GL	16	92,0–97,4	94,24	1,78	17	83,6–91,8	88,80	2,06
	SD	16	18,8–23,9	20,97	1,36	17	17,4–22,4	20,48	1,10

Table 6. Sizes of metatarsals of cave bear (*Ursus deningeri kudarensis*) from the Akhstyrskaja Cave, abbreviations: GL – greatest length, SD – breadth of diaphysis in the middle part.

Measurements, mm		Males				Females			
		n	lim	x	SD	n	lim	x	SD
Mtt1	GL	16	62,7–68,3	65,27	1,76	38	57,3–62,0	60,10	1,33
	SD	16	13,0–15,5	13,97	0,63	38	12,2–15,0	13,45	0,74
Mtt2	GL	6	79,3–84,9	80,83	2,06	29	67,8–77,8	74,42	2,27
	SD	6	13,8–18,2	16,48	1,62	29	13,0–17,5	15,44	1,01
Mtt3	GL	13	84,7–92,9	87,50	2,35	22	74,6–83,5	80,85	2,09
	SD	13	16,2–21,4	17,82	1,27	22	14,5–17,9	16,33	0,83
Mtt4	GL	13	97,8–108,9	101,11	2,97	18	87,0–95,5	92,72	2,69
	SD	13	17,2–22,4	19,38	1,51	18	16,9–19,6	18,15	0,78
Mtt5	GL	8	97,0–101,8	99,69	1,80	12	80,8–95,8	92,81	3,86
	SD	8	15,4–18,2	17,00	0,97	12	15,0–16,8	15,99	0,53

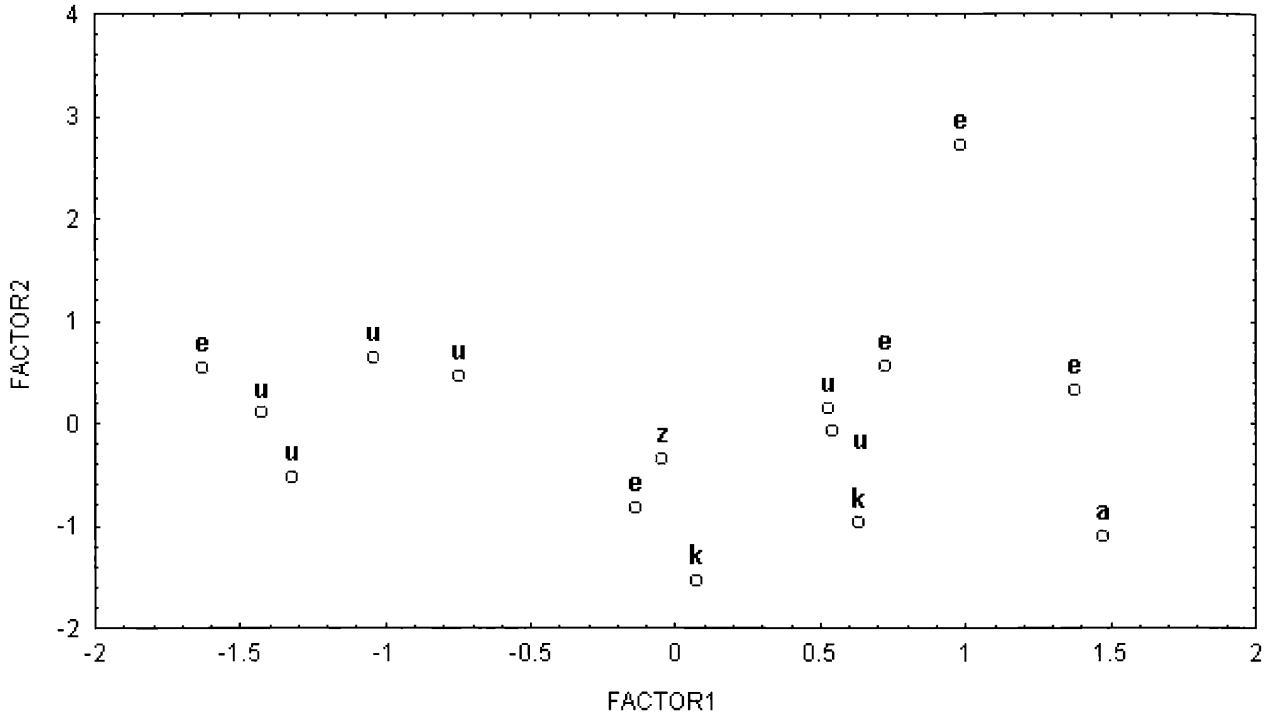

Figure 2: Plot of factor analysis for skulls of cave bear a - Akhstyrskaya Cave, Caucasus, k - Kudaro 3 Cave, Mousterian layers, Caucasus, u - Secrets Cave and Medvezhiya Cave, Ural Mountains, w -West European localities, z - Shiriaevo, Volga River, Russia.

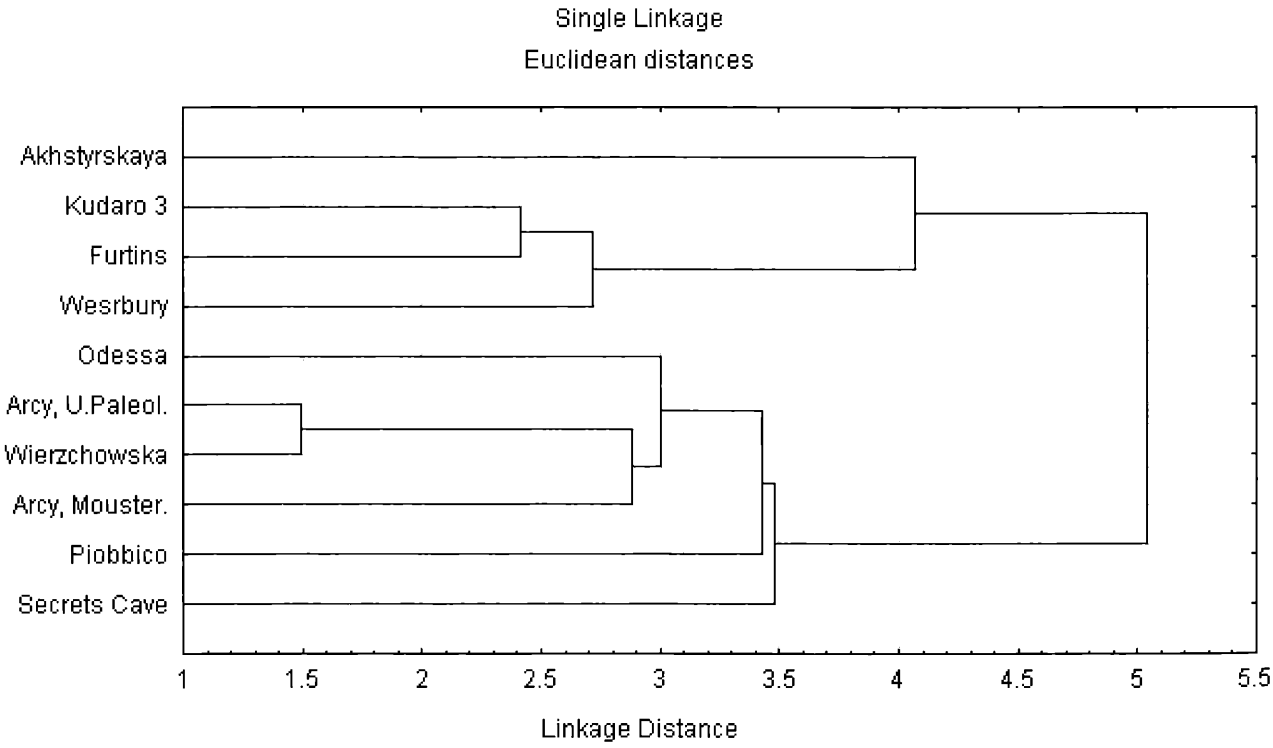

Figure 3: Tree of cluster analysis for cave bear teeth from sites of the Caucasus and Europe. Middle Pleistocene - Europe: Furtins, France; Westbury, England. Late Pleistocene - Caucasus:Akhstyrskaya Cave, Kudaro 3 Cave, Mousterian layers; Europe:Arcy-sur-Cure, France, Mousterian layers and Upper Paleolithic layers; Odessa, Ukraine; Piobbico, Italy; Secrets Cave, Ural, Russia; Wierzchowska Gorna, Poland.