

Pleistocene small cave bear (*Ursus rossicus*) from the South Siberia, Russia

Un pequeño Oso de las Cavernas (*Ursus rossicus*) del Sur de Siberia, Rusia

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ABSTRACT

The skull, mandibles and cheek teeth of *U. rossicus* from four localities of the South Siberia are examined. This species inhabited the steppe regions in early Middle and Late Pleistocene. By odontological characters it is more close to *U. r. rossicus* from Krasnodar, than to *U. rossicus uralensis* from Kizel Cave in Ural. Discriminant analysis, based on measurements of lower cheek teeth of the cave bears from seven sites of Europe and Siberia, demonstrated that *U. rossicus* most resembles morphometrically *U. savini*. As a result of cladistic analysis employed 17 characters of skull, limb bones, and dentition, the phylogenetic tree has been obtained for 7 species of the genus *Ursus*. A four species of the cave bears are included in the subgenus *Spelearctos*: *U. savini*, *U. rossicus*, *U. deningeri* and *U. spelaeus*.

Key words: cave bears, *Ursus*, Siberia, Pleistocene, evolution

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INTRODUCTION

Small cave bear *Ursus rossicus* Borissiak, 1930 has been widely distributed in Northern Eurasia in the Middle and Late Pleistocene. In East Europe this species was found in the south of Ukraine, Northern Caucasus, Lower Volga River, Bolshoi Irgiz River basin, Ural River and in foothills of Ural Mountains (BORISSIAK, 1932, VERESHCHAGIN 1959, 1982, KUZMINA, 1975, BARYSHNIKOV *et al.*, 1991). It is also known from the plain areas of Kazakhstan (KOJAMKULOVA, 1969). Two subspecies were distinguished: *U. r. rossicus* from Northern Caucasus (Krasnodar), Lower Volga (Kopanovka) and adjacent plains, and *U. r. uralensis* Vereshchagin, 1973 from Kizel Cave and other cave localities of Middle and South Ural. The geography of fossil findings points out that the small cave bear was mainly a dweller of open herbaceous areas including the steppe ones. It did not evidently penetrate to West Europe where its remains are not recorded.

In Siberia, N. Vereshchagin first identified *U. rossicus* by os penis from Strashnaya Cave in Altai (OKLADNIKOV *et al.*, 1973). It was elucidated later that small cave bear was distributed over the whole of South Siberia. It was recorded at Irtysh River (Omsk Region), Ob River (Krasnyi Yar), Altai Mountains (Strashnaya Cave, Denisova Cave), Kuznetsk Basin (Bachatsk and Mochovsky quarries), Yenisei River (Kurtak) and in Transbaikalia (Tologoi on Selenga River) (ALEXEEVA, 1980; FORONOVA, 1982, 1999;

VERESHCHAGIN & TIKHONOV, 1994; BARYSHNIKOV, 1995). These findings are also associated with the zones of spreading of the Pleistocene grass communities.

ALEXEEVA (1980), who gave brief characteristics of *U. rossicus* from Krasnyi Yar, came to the conclusion that the Siberian bear had been more specialized to consume plants than other geographic races. In the later paper she (ALEXEEVA, 1996) proposed a new subspecies name *U. rossicus* obensis, but did not give a diagnosis and did not designate the type, which makes this name not acceptable according to the Code of Zoological nomenclature. Vereshchagin & Tikhonov (1994) gave the map of findings of the small cave bear in Siberia. FORONOVA (1999, in press) published the photographs and brief morphological description of mandibles of *U. rossicus* from Kuzbass localities. The complete morphological analysis of the Siberian material is still absent.

This paper presents the first detailed description of skull fragments and teeth of the small cave bear from the collection of Zoological Institute Russian Academy of Sciences in Saint Petersburg (ZIN) and Institute of Geology (IG), and Institute of Archaeology and Ethnography (IAE), Siberian Branch of Russian Academy of Sciences in Novosibirsk.

MATERIAL AND METHODS

The material studied contains the skull fragment (ZIN 32748) and the right mandible (ZIN 35075) from Krasnyi Yar in Tomsk Province, the right mandible (IG 328) from Bachatsk quarry (figure 1) and

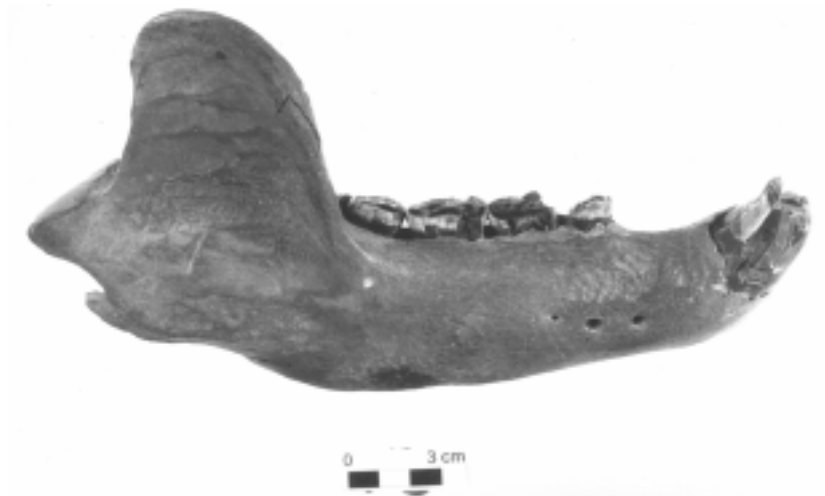


Figure 1. Right mandible of *Ursus rossicus* from Bachatsk quarry, IG 328. Lateral view.

the left mandible (IG 10128) from Mokhovo quarry (figure 2) in Kemerovo Province, 19 mandible fragments (IAE 36, 63, 81, 88, 89, 93, 122, 171, 235, 330, 331, 455 *et al.*) from Berezhekovo, Kurtak archeological region, Krasnoyarsk Territory (figure 3, 4), and also several isolated cheek teeth and limb bones from these localities. We have also used the photograph of the skull from Kurtak, kindly provided by Dr. Nikolai Ovodov (Novosibirsk).

The material examined was compared with the collections of *Ursus savini* Andrews from Bacton Forest Bed and *U. deningeri* von Reichenau from Westbury Quarry Cave, England (Natural History Museum, London) and Kudaro 1 Cave, Caucasus (ZIN), *U. rossicus uralensis* from Kizel Cave, Ural (ZIN), *U. spelaeus* Rosemüller from Arcy-sur-Cure, France (Laboratoire d'Éthnologie préhistorique, Nanterre), from Odessa, Ukraine (ZIN

and University of Helsinki), and from the Secrets Cave, Ural Mountain (our data).

For the cranial characters analysis, we examined also skulls of recent *U. arctos* L. and *U. maritimus* Phipps from ZIN collection. We used the information on *U. etruscus* G.Cuvier published by MAZZA & RUSTIONI (1992). Additional data on cave bear was obtained from Andrews (1922), BORISSIAK (1932), RABEDER (1922), RABEDER & TSOUKALA (1983), RABEDER & TSOUKALA (1990), MAZZA *et al.* (1995), Baryshnikov (1998), VERESHCHAGIN & BARYSHNIKOV (in press).

In the mode of measurements for skull and mandible we follow von den DRIESCH (1976). Cheek teeth were measured following BARYSHNIKOV (1998). Dimensions were taken with dial calipers with accuracy up to 0.1 mm. The data were processed by Factor Analysis, Cluster Analysis and Discriminant Analysis from STATISTICA, 6.0. In



Figure 2. Left mandible of *Ursus rossicus* from Mokhovo quarry, IG 10128. Lateral view.



Figure 3. Fragment of right mandible *Ursus rossicus* from Berezhekovo 4, IAE 171. Occlusal view.

Discriminant Analysis, we used the forward stepwise method. PAUP computer program (version 3.1.1) was applied for the phylogenetic analysis.

GEOLOGICAL SETTING AND STRATIGRAPHY

The studied material is originated from the famous localities of the

Pleistocene mammal fauna in the south of Western and Middle Siberia: Kuznetsk Basin, Krasnyi Yar at the Ob River, and Kurtak archaeological region.

The Kuznetsk Basin is situated in the southeast of the Western Siberia. It was formed in the Late Cenozoic as an enormous intermountain depression, restricted by the Kuznetsk Alatau, Gornaya Shoriya, and Salair Ridge. This region is one of the



Figure 4. Left mandible of juvenal *Ursus rossicus* from Berezhekovo, IAE 268. Occlusal view.

most biostratigraphically important in the non-glacial zone of Northern Asia. Thick Quaternary sediments (seven alternated sub aerial and sub aquatic formations) with a great number of fossil bone remains uncovered in opencast coalmines. More than 60 taxa of the carnivores, proboscides, perissodactyls and artiodactyls of various geological age were recorded here, allowing reconstruction of the faunal history in the south of Western Siberia from the Early Pleistocene to Holocene, to trace phylogenetic lines in basic mammalian groups, and also to elucidate the successive stages of their evolution (FORONOVA, 1982, 1986, 1998, 1999, in press).

The bear remains (mandibles and postcranial elements) have been recorded in the Kuznetsk Basin *in situ* at different stratigraphical levels. The mandible IG 328 of *Ursus rossicus* was found in Latyshovo levels of Kedrovka Formation in Bachatsk quarry. Kedrovka Formation represents bluish-gray loam and clay, plastic, flaky, with wood debris, basal shingle

and hydromorphic fossil soils. These deposits mainly have lacustrine-alluvial genesis, fill the pits in lower layers and reach the thickness of 45 m. In Kuznetsk Basin, Kedrovka Formation is associated with the most of Pleistocene large mammals remains. In the morphology and ecological peculiarities, recorded species from lower and upper levels of this formation belong to the different faunistic complexes.

In the basal part, represented by the Krasnogorsk Member, the fossil remains contain *Gulo* cf. *schlosseri*, *Mammuthus trogontherii* (corresponding in its morphometrical data to those of this species from Süßenborn locality in Germany), *Equus mosbachensis*, *Rangifer* sp., and a very large bison, *Bison* aff. *priscus*. This fauna is correlated with the Tiraspolian and Viatkian faunas in East Europe and West Siberia and the Cromerian faunas of Western Europe.

The overlying Latyshevo Member contains *Ursus rossicus*, *Panthera spelaea*, *Mammuthus* aff. *chosaricus*, *Equus* aff. *tauba* -

densis, *E. ex gr. mosbachensis-germanicus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Megaloceros giganteus*, *Bison priscus*. The teeth of *M. aff. dosariicus*, in comparison with its ancestor *M. trogontherii*, differ in less enamel thickness, the length of plates and larger plate frequency. Generally, the species composition and evolutionary level of the fauna representatives correspond to the Holstein, which conform to Tobol interglacial in Western Siberia.

The mandible IG 10128 was found in the sediments of Krasnobrodsk Formation in Mokhovo quarry. These are lacustrine-alluvial loam with ferruginous shingle at its base and cryoturbations and frost-wedge casts in its upper part. Accompanied fauna is represented by remains of *Vulpes vulpes*, *Panthera spelaea*, *Equus przewalskii*, *Equus ex gr. gallicus*, *Equus aff. hydruntinus*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Megaloceros giganteus*, *Aloes aloes*, *Rangifer tarandus*, *Bison priscus*, *Saiga* sp., and *Mammuthus primigenius*. Both thin and thick-enamel variations of mammoth teeth can be distinguished. The first group may correspond to the beginning of the Weichselian, while the second one having the radiocarbon dates 39.1, 31.9 and 28.9 thousand years belongs to the Middle Weichselian (Karginsk) warming. Creating of these formations finishes apparently in the Late Weichselian cooling, as evidenced by cryoturbation features in the uppermost part of the sequence.

The locality Krasnyi Yar that is the place of finding the skull ZIN 32748 and mandible ZIN 35075, is situated 0 t Ob River in Tomsk Province. A lot of bones have been gathered over several years on

the riverbank. These were not associated with geological layers, but mainly originated from the Middle and Late Pleistocene levels. The degree of conservation of the bones allows suggesting that the main part of the bone assemblage had been formed in the Later Pleistocene. *Castor fiber*, *Canis cf. lupus*, *Ursus cf. deningeri* (large form), *Crocota spelaea*, *Panthera spelaea*, *Equus caballus* subsp., *E. cf. przewalskii*, *E. hemionus*, *Dicerorehinus kirchbergensis*, *Coelodonta antiquitatis*, *Megaloceros giganteus*, *Cervus elaphus*, *Aloes aloes*, *Bison priscus*, *Saiga borealis* were recorded here (ALEXEEVA, 1980).

Kurtak archaeological region is situated in the south of Middle Siberia, in the Northern Minusinsk Basin. The sites were discovered after the flooding of the Yenisei River valley and forming of Krasnoyarsk Reservoir. The thickest Quaternary sediments of various origins are exposed in the left riverbank, at Berezhekovo sites. There are opened here the ancient alluvial deposits of high Yenisei terraces, colluvial formations (filling of the former ravines cutting through terraces), and covering, mainly eolian loess-like loams and sandy loams, containing several paleosol horizons. At the present time these sections have been examined geologically, archaeologically, and paleontologically, and thermoluminescent and radiocarbon data have been obtained (DROZDOV, *et al.* 1990a, 1992; DROZDOV, *et al.* 1990b). The bear remains described in this study, have been found at the Berezhekovo 2,3 and 4 sites in the Middle and Late Quaternary eroded brown loams, in the basement of section, and on the river beach. There were found remains (determined by

I. Foronova) of Canidae gen. indet., *Homotherium* sp., *Panthera spelaea*, *Mammuthus primigenius*, *Mammuthus* sp., *Equus* sp. (large form), *Equus* aff. *hydruntinus*, *Equus* cf. *przewalskii*, *Coelodonta antiquitatis*, *Cervus elaphus*, *Megaloceros giganteus*, *Alces alces*, *Rangifer tarandus*, *Capreolus capreolus*, *Ovis* cf. *ammon*, *Bos* sp., *Bison priscaus*. The mandible IAE 36 was recorded in Berezhekovo 2, IAE 1681 in Berezhekovo 4, IAE 93, 330, 331, 455 in Berezhekovo 3-4. These localities are also associated with the Middle and Late Pleistocene small mammals fauna (KRUKOVER & CHEKHA, 1999).

DESCRIPTION

Skull

The skull of the bear from Krasnyi Yar (ZIN 32748) has only the facial portion. Cheek teeth are heavily worn. Their occlusal surface nearly lost enamel, demonstrating the patches of dentine. Small size and slender canines (length at enamel border 16.3 mm, width 12.7 mm) indicate this specimen as an old female.

Frontal bones are convex, abruptly raised over the nasal bones. The postorbital process is short but broad and blunt. Orbits are placed closer than minimum breadth between orbits in the nominative subspecies from Krasnodar (BORISSIAK, 1932). The orbit is comparatively large (greatest diameter 52 mm) and directed in its upper portion more anterior than in *U. arctos* (ALEXEEVA, 1980). There are two lacrimal foramina approximately equal in size. The anterior root of the zygomatic

arch is thickened; its height equal to 40 mm. The infraorbital foramen is small, situated over the posterior part of 1. Nasal bones are short, narrow, in anterior half being parallel to the palate. Their anterior end is finished at the level of 4. Nasal aperture is large, nearly as high as broad. The palate is comparatively broad. Its breadth increases greatly in front of the anterior border of 4 (68.3 mm) to the canine alveoli (89 mm). The distance between medial margins of the latter exceeds that between 2, resembling in this feature the specimens from Krasnodar (BORISSIAK, 1932). The length of incisors row is 62.4 mm. The anterior premolars P1-3 are absent; ALEXEEVA (1980) mistakenly considered the alveolus of P3 as an anterior alveolus of P4. The length of post canine diastema is 38.5 mm. The distance from the level of P4 anterior margin to I1 alveolus is somewhat shorter than the length of P4-M2.

This specimen is peculiar in a rather posterior position of incisive foramina, which exceed beyond the level of posterior edges of canines. This is not characteristic for the cave bears and is probably caused by the very old age of the individual.

The skull ZIN 32748 in its size and morphology is similar to those of *U. rossicus* from Krasnodar and Kizel Cave (BORISSIAK, 1932, VERESHCHAGIN & BARYSHNIKOV, in press).

Measurements (mm): "snout" length - 138, length C1-M2 - 137.5, length P4-M2 - 79.6, least breadth between the orbits - 74.6, greatest palatal breadth - 84, breadth at the canine alveoli - 89, breadth between for. infraorbitale - 73.8, greatest breadth of nasal opening - 57.6.

The skull from Berezhekovo is compressed and belongs to the young individual. The palatine between posterior molars is narrow. The anterior premolars are absent.

Mandible

Most specimens have worn to heavily worn cheek teeth. In Berezhekovo, only three of 19 mandible fragments studied may be attributed to young animals. The specimen from Mokhovo quarry also belonged to a young bear.

Males of *U. rossicus* were probably much larger than females (VERESHCHAGIN & BARYSHNIKOV, in press), sexual dimorphism is shown mainly in the canine size. In the material investigated, three mandibles were attributed to males due to their greater total length and width of the lower canine (table 1, 2).

Mandibles demonstrate structure and

size common to *U. rossicus*. Anterior premolars p1-p3 are absent, the length of diastema changes from 34.5 to 46 mm. The body of the mandible is high; the line of its inferior border is curved. The height of the body is considerably decreasing anteriorly, reaching its minimum at the diastema. The angular process rising, the condylar process is situated at the level of articular surface. There are two mental foramina, the posterior one being larger and situating below p4, and sometimes it is divided in several small openings.

By the total size and the length of the dental row, the samples from Siberia are very similar to those of *U. rossicus* from Krasnodar (BORISSIAK, 1932) and from Kizel Cave (table 3). They are somewhat smaller on average than mandibles of *U. savini* from Forest Bed, but this difference is not statistically reliable.

Factor analysis has been carried out for 11 measurements of male mandibles. The results are shown in the figures 5, 6 and in

Measurements, mm ^a	Berezhek.	Berezhekovo	Mokhovo	Krasnoj Yar
	IG 323, juv.	IAE 36, juv.	IG 10123, juv.	ZIN 33075, ad.
Total length (1)	255.5	-	267.0	-
Length from angular process to infraorbital (2)	243.0	272.5	256.0	-
c1-m2 length	152.3	169.5	155.6	153.0
p4-m2 length	24.5	26.3	39.1	39.2
m1-m2 length (10)	79.5	70.2	74.7	75.1
Height of the vertical ramus (13)	121.0	122.0	-	-
Height of the mandible behind m1 (12)	54.5	64.2	54.0	50.3
Height of the mandible in diastema (20)	52.1	57.0	54.7	47.5
Teeth:				
c1 length	26.5	27.5	-	25.0
Width	13.4	17.0	-	16.3
p4 length	15.0	14.4	-	-
Width	9.5	9.9	-	-
m1 length	27.0	25.4	24.7	25.7
Width	13.5	12.1	13.1	12.6
M2 length	23.5	27.3	25.3	25.2
Width	17.0	17.2	17.1	15.5
M3 length	25.5	27.7	25.4	22.2
Width	17.2	19.1	15.1	17.1

^a After von den DRIESCH (1976)

Table 1. Sizes of mandibles in males of *Ursus rossicus* from the South Siberia.

Measurements, mm ⁴	Berezikovo				
	IAE 51, an.	IAE 23, an.	IAE 35, ad.	IAE 39, ad.	IAE 45, an.
Length from angular process to infraorbital c (2)	-	-	-	04245	-
c1-m2 length	-	144.0	147.5	143.0	145.0
p4-m2 length	35.7	31.5	33.5	33.0	36.4
m1-m2 length (10)	71.7	74.2	66.0	65.5	73.0
Height of the mandible behind m1 (19)	59.0	49.9	53.0	60.0	47.5
Height of the mandible in diastema (20)	55.4	43.2	50.0	65.5	47.7
Teeth:					
p4 length	13.9	-	-	-	-
Width	10.1	-	-	-	-
m1 length	34.0	22.6	-	-	-
Width	13.1	13.3	-	-	-
m2 length	24.4	26.3	-	-	-
Width	16.1	16.2	-	-	-
m3 length	22.2	24.6	-	-	23.9
Width	17.7	13.2	-	-	-

⁴ After von den DRIESCH (1976)

Table 2. Sizes of mandibles in females of *Ursus rossicus* from the South Siberia.

Measurements, mm ⁴	South Siberia				Kizel Cave, Ural			
	n	lim	\bar{x}	σ	n	lim	\bar{x}	σ
	Male							
Total length (1)	2	235.5-267.0	-	-	3	261.0-272.0	265.00	-
Length c1-m2	4	133.6-169.5	160.60	6.13	4	143.0-164.0	156.25	6.33
Length p4-m2	4	39.1-46.3	39.45	3.50	5	32.0-41.0	36.00	1.00
Height of the mandible behind m1 (19)	4	54.0-64.2	55.37	5.79	5	53.0-59.0	56.00	1.37
Height of the mandible in diastema (20)	4	47.5-57.0	52.32	4.07	5	43.0-54.0	50.30	2.59
	Female							
Length c1-m2	4	143.0-147.5	144.37	1.33	6	143.0-155.0	150.33	5.48
Length p4-m2	6	33.5-41.5	34.52	4.95	6	35.0-39.0	36.67	1.63
Height of the mandible behind m1 (19)	3	47.5-60.0	53.69	4.73	7	46.0-53.0	53.43	5.47
Height of the mandible in diastema (20)	11	47.7-55.4	49.72	2.13	7	47.0-56.5	51.43	2.30

⁴ After von den DRIESCH (1976)

Table 3. Comparison of mandibles in *Ursus rossicus*.

table 4. In plot of the Factor 1 (c1-m3 length, m2 length, m2 width) and Factor 2 (m1 length), the samples are divided in two groups. The first one comprises *U. savini* from Forest Bed and *U. deningeri* from Kudaro 1 Cave; the second contains *U. rossicus* from Siberia localities and from Kizel Cave (figure 5). In space of the Factor 2 and Factor 3 (p4-m3 length, m1 width), the sample of *U. deningeri* appeared to be separated from others (figure 6). Despite the fact that we dealt with a rather small collection, we can suggest a

morphometrical resemblance not only between the *U. rossicus* from Siberia and from Ural, but also the similarity of this small cave bear with *U. savini*.

Dentition

Upper teeth. Upper cheek teeth of the skull ZIN 32748 are heavily worn and are not suitable for a morphological analysis. Therefore only M2 has been measured in this specimen. Additionally, three samples of this tooth with obliterated occlusal

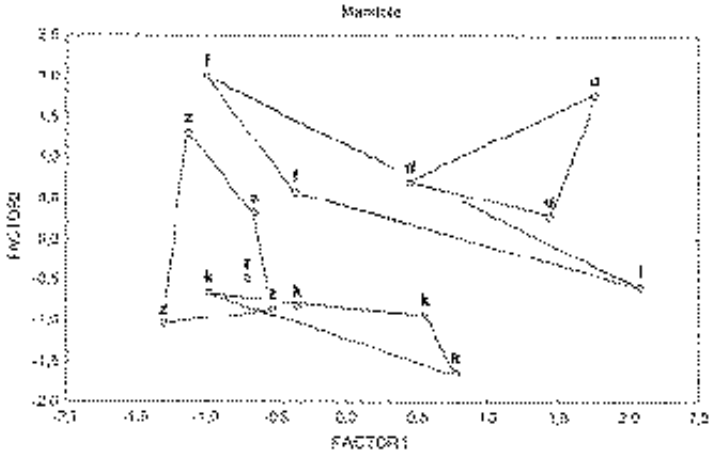


Figure 5. Plot of factor scores of Factor 1 and Factor 2 from principal component analysis of mandibles. d- *Ursus deningeri*, Kudaro 1 Cave; f- *U. savini*, Bacton Forest Bed; k- *U. rossicus*, South Siberia; z- *U. rossicus*, Kizel Cave.

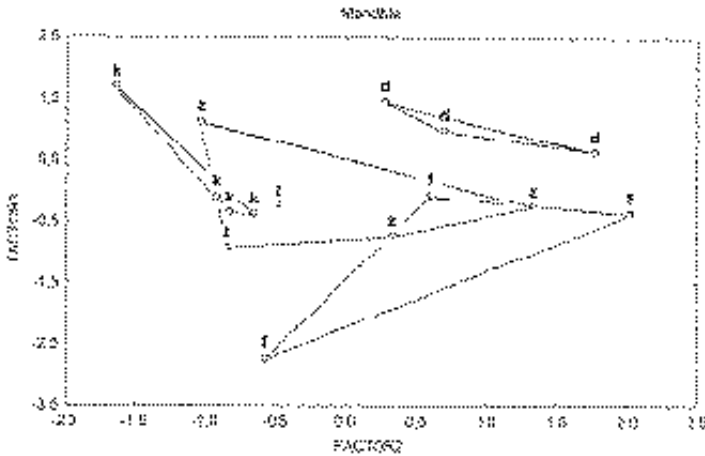


Figure 6. Plot of factor scores of Factor 2 and Factor 3 from principal component analysis of mandibles. The symbols are as in figure 4.

surface were recorded in Berezhekovo. On a Berezhekovo skull, judging from photograph, the upper molars bear numerous additional tubercles.

M2. The greatest length and width of this tooth is correspondent to those in *U. rossicus* from Krasnodar and Kizel Cave

(table 5). The paracone is large, with a blunt top. One specimen demonstrates the lack of the additional tubercle in front of the paracone, which is represented on the teeth from Krasnodar (BORISSIAK, 1932) and is commonly present in *U. spelaeus*. The metacone is undivided, considerable

Measurements	Factor 1	Factor 2	Factor 3
c1-m3 length	0,743	0,352	0,449
pt-m3 length	0,424	0,242	0,711
Height of the mandible in diastema region	0,619	0,639	0,178
pt length	0,691	0,068	-0,342
pt width	0,468	-0,553	-0,291
m 1 length	0,410	0,719	-0,257
m 1 width	0,627	0,151	-0,710
m 2 length	0,713	-0,483	0,094
m 2 width	0,818	-0,087	0,027
m 3 length	0,219	-0,536	0,483
m 3 width	0,622	-0,342	-0,028
Explained variance by components	3,93	2,39	1,75
Percent of total variance explained	36,25	21,72	15,96

Table 4. Correlations of characters with the first three principal components for mandibles.

Measurements, mm	<i>U. rossicus rossicus</i>								<i>U. rossicus waltoni</i>			
	South Siberia				Krasnodar (Borisovsk 1952)				Kizel Cave, Ural			
	n	lim	\bar{x}	σ	n	lim	\bar{x}	σ	n	lim	\bar{x}	σ
	Upper teeth											
M2 length	3	33.2-45.0	40.35	-	7	37.5-45.0	42.21	3.11	24	35.3-42.2	35.73	1.95
M2 Width	3	19.2-21.1	20.53	-	3	13.5-21.0	19.37	0.99	24	17.5-21.3	19.02	1.15
	Lower teeth											
p4 length	5	13.2-15.0	14.50	0.41	3	14.0-17.0	15.53	1.31	16	10.1-15.4	13.29	1.35
p4 Width	5	9.5-10.3	9.94	0.30	3	9.5-10.5	9.91	0.46	10	3.3-10.6	3.29	0.70
m1 length	11	21.6-27.0	24.66	1.49	7	23.5-26.0	24.57	1.09	27	23.3-23.4	23.67	1.22
m1 Width	11	11.0-14.5	12.66	1.02	7	12.5-14.0	13.21	0.49	28	11.6-16.5	12.95	0.91
m2 length	14	23.5-28.2	25.92	1.46	3	24.0-27.0	25.50	1.19	30	21.6-23.1	23.32	1.05
m2 Width	13	14.5-18.2	16.10	1.07	3	15.5-17.0	16.44	0.62	28	14.6-17.2	15.77	0.67
m3 length	11	22.0-27.7	23.91	1.53	3	21.0-26.5	24.69	2.31	20	20.5-25.2	23.13	1.22
m3 Width	9	16.7-19.1	17.72	0.73	3	16.2-20.0	18.31	1.41	19	14.3-13.0	16.33	0.79

Table 5. Comparison of cheek teeth in *Ursus rossicus*.

rably smaller than the paracone, and its apex is moved anteriorly. The row of lingual tubercles in all specimens is heavily worn. In *U. savini*, this tooth is on average somewhat shorter and narrower, and in *U. deningeri* from Westbury, it is, on the contrary, longer and wider, but in both cases the differences are not statistically reliable. It differs more noticeably with that of M2 in *U. spelaeus* from Odessa, where it is apparently larger (BARYSHNIKOV, 1998).

Lower teeth. The lower cheek teeth are more numerous; all of them were retained in mandibles and show the various degrees of crown abrasion. Relative values of the average length for p4, m1, m2 and m3 are 16,3-27,7-29,1-26,9%. For this index, the small cave bear from Siberia is similar to *U. rossicus* from Kizel Cave and Krasnodar, although the former has relatively longer m1 (29,1%). All the cave bears show m1 on average is shorter than m2, with exception for *U. savini*, having

in contrary m1 longer than m2 (a primitive character inherited from *U. etruscus*).

p4. The crown is of the equal width in the anterior and posterior parts. The protoconid is high, blunt-pointed, and without crests. Its base bears two large adjacent cusps on the lingual side (paraconid and metaconid), these sometimes being linked with a small denticle (figure 7, 8). The paraconid commonly extends in front of the protoconid. A slender ridge runs from the metaconid posteriorly. The posterior tooth part is abruptly bent backward, without additional tubercles, which are recorded in the Krasnodar specimens (BORISSIAK, 1932). There are two well-separated roots.

The multiple discriminant function analysis based on three measurements (greatest length, greatest width, and distance between paraconid and metaconid tips) was carried out for six samples: *U. savini* (n=10), *U. deningeri* (n=8), *U. rossi* -

aus, Siberia (n=5), *U. spelaeus* from Arcy-sur-Cure (n=41), from Odessa (n=40), and from Secrets Cave (n=13). The results of this analysis are present in figure 9, which shows the centroid of each group plotted onto the first two canonical variates. A little over 85% of dental variation is explained by the first canonical axis, 13% by the second. The first canonical variate discriminates greatest width, on the second canonical variate including greatest length (table 6). The bivariate plot of centroids clearly shows an ordination into 2 separate groups, with savini/deningeri samples on the one hand and all the other samples on the other. Squared Mahalanobis distances between members of these groups are high (from 5.59 to 14.5). In the second group, which contains *U. rossicus* from Siberia, the distances are lower (less than 3.87). The Siberian sample shows statistically reliable differences only from *U. deningeri* ($p < 0.001$).



Figure 7. Lower premolar p4 of *Ursus rossicus* from Berezhekovo. Occlusal view. **Figure 7.** Plot of centroids for each locality on the plane canonical variate 1 and 2 for p4.

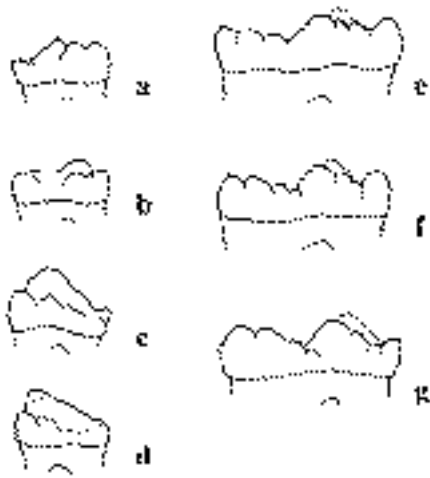


Figure 8. Lower cheek teeth p4 (a-d) and m1 (e-g) of *Ursus rossicus* from South Siberia. Lingual view. a-c, e-f - Berezhekovo, d- Bachatsk, g- Mokhovo.

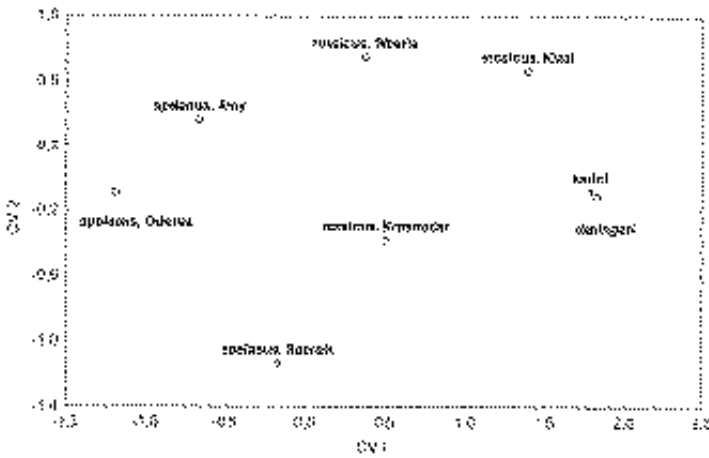


Figure 9. Plot of centroids for each locality on the plane canonical variate 1 and 2 for p4.

Measurements	CV 1	CV 2	CV 3
Greatest width	-0,3804	0,2572	0,3383
Distance between peak of paraconid and peak of metaconid	0,3646	0,3630	0,7417
Greatest length	-0,3741	0,3264	-0,0430

Table 6. Correlations of canonical variate for p4.

Based on the results of this analysis, we may conclude that p4 proportions in *U. rossicus* are similar to those of *U. spelaeus*, being different with those *U. savini*, and more sufficiently from *U. deningeri*.

Among teeth of *U. rossicus* studied, the mean of the greatest length is at a maximum in Krasnodar and minimum in Kizel Cave (table 5), and the differences between them are reliable for this measurement ($p < 0.01$). The greatest crown width in the all samples slightly varies.

U. etruscus and *U. maritimus* exhibit a simple p4 without additional cusps. *U. arctos* sometimes demonstrates a weak paraconid. Cave bears are characterized in the complication of the crown with accessory tubercles ("molarization"). In *U. deningeri*, there is a paraconid and occasionally a small metaconid, these cusps being usual for *U. savini*. Both species show the two cusps well separated. In *U. rossicus*, paraconid and metaconid are larger and more approached together; sometimes additional tubercles are developed near paraconid and metaconid and on the posterior crown side. This trend is continued in *U. spelaeus*, demonstrating the larger tooth size and dilation of the posterior tooth part; the paraconid is slightly moved anteriorly and together with the metaconid is separated from protoconid by a deep groove. Consequently, p4 in *U. rossicus* exhibits an advanced morphology (tooth enlarging, development of the additional crown structures).

m1. Lower carnassial tooth in the Siberian samples is considerably wide. The protoconid is considerably lower than the metaconid. The latter is moved posteriorly and divided in two or three denticles. The

hypoconid is large, with well-developed lingual part. The entoconid is in the form of a longitudinal ridge consisting of two or three closely placed cusps; their length gradually increases backwards (figure 8). At the place of trigonid and talonid contact, there is a weak labial cingulid.

The discriminant analysis based on seven measurements (greatest length, length of trigonid, length of posterior entoconid tubercule, length of anterior entoconid tubercule, width of trigonid, width of talonid and width in the middle part of crown) was carried out for seven samples: *U. savini* (n=7), *U. deningeri* (n=11), *U. rossicus* from Siberia (n=6) and from Kizel Cave (n=12), *U. spelaeus* from Arcy-sur-Cure (n=31), from Odessa (n=29), and from Secrets Cave (n=8). The results of this analysis are present in figure 10. Nearly 86% of dental variation is explained by the first canonical axis, almost 10% by the second. The first canonical variate discriminates greatest length and length of posterior entoconid tubercule, on the second axis length of anterior entoconid tubercule contributes to discrimination (table 7). The plot of centroids demonstrates division into 3 separate groups: 1) *U. savini* and *U. rossicus*, 2) *U. deningeri* and 3) *U. spelaeus*. Squared Mahalanobis distances between the first and the second groups (from 5.73 to 6.42) are noticeably lower than between the second and third ones (from 7.99 to 11.38). In the first group, the both samples of *U. rossicus* are well-separated from one another (Mahalanobis distance 9.17), the Siberian specimens being closer to *U. savini* (1.17). Statistically reliable differences ($p < 0.001$) are observed between all

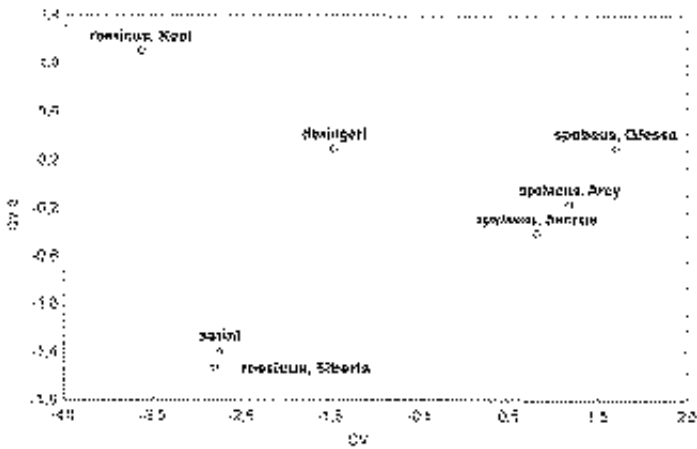


Figure 10. Plot of centroids for each locality on the plane canonical variate 1 and 2 for m1.

Measurements	CV 1	CV 2	CV 3
Greatest length	0,3137	0,3168	-0,1053
Length of anterior entoconid tubercular	0,0822	0,5392	-0,7270
Length of posterior entoconid tubercular	0,5308	-0,4568	-0,6513
Least width in the middle part	0,4168	-0,1233	0,0633

Table 7. Correlations of canonical variate for m1.

samples with the exception of *U. rossicus* from Siberia/*U. savini*. Thus the m1 proportions among *U. rossicus* are rather different, but demonstrate more resemblance with those in *U. savini*, than with other cave bears (in the least degree with *U. spelaeus*).

In the samples of *U. rossicus*, the longest m1 has been recorded in Kizel Cave (table 5), however its differences in this measurement with Siberian and Krasnodar specimens are not statistically reliable.

In *U. spelaeus*, the crown is most narrow at the trigonid and talonid junction but in *U. rossicus*, *U. savini* and *U.*

deningeri, this place is approximately as wide as trigonid. *U. etruscus*, *U. maritimus* and *U. arctos* show the complicated metaconid and entoconid, the latter consisting of one or two cusps. Cave bears demonstrate a trend toward further development of entoconid portion. In *U. rossicus*, *U. savini* and *U. deningeri*, it is formed by two or three adjacent tubercles, while in *U. spelaeus* the entoconid more often has a shape of two large well-separated tubercles of almost equal height. Thus, *U. rossicus* demonstrates a rather primitive m1 structure.

m2. This tooth is rectangular in shape, with talonid wider than trigonid. The

protoconid is undivided, situating below the metaconid. The latter is divided in two or three nearly equal cusps, the middle one being the longest. This tubercle is not moved medially, which often takes place in *U. spelaeus*. The hypoconid is wider than the entoconid. The latter is longer than hypoconid and consists of two large and well-separated tubercles. Sometimes an additional denticle between the metaconid and the entoconid occurs.

The discriminant analysis based on seven measurements (greatest length, labial length of trigonid, lingual length of trigonid, labial length of talonid, lingual length of talonid, width of trigonid, and width of talonid) was carried out for seven samples: *U. savini* (n=11), *U. deningeri* (n=31), *U. rossicus* from Siberia (n=9) and from Kizel Cave (n=13), *U. spelaeus* from Arcy-sur-Cure (n=43), from Odessa (n=37), and from Secrets Cave (n=8). The results of this analysis are presented in figure 11. More than 76% of dental variation is explained by the first canonical axis, 11% by the second. The first canonical variate discriminates labial length of talonid, greatest length and width of trigonid, on the second axis lingual length of talonid contributes to discrimination (table 8). The plot of centroids demonstrate an ordination into 3 separate groups: 1) *U. savini* and *U. rossicus*, 2) *U. deningeri*, and 3) *U. spelaeus*. Squared Mahalanobis distances between the first and second groups (from 2.95 to 6.74) are approximately the same to those between the second and third ones (from 4.57 to 8.94). In the first group, both samples of *U. rossicus* situate more close with one another (Mahalanobis distance 1.75), than to that

of *U. savini* (5.76, 5.81). Statistically reliable distances ($p < 0.001$) separate all samples, with the exception of the samples from Siberia and Kizel Cave. The results indicate the resemblance of both samples of *U. rossicus* in m2 measurements, but they are well separated from the other collections examined. Among cave bear species, the proportions of m2 in *U. rossicus* are similar to those of *U. savini*, being more remote from *U. deningeri*, and especially from *U. spelaeus*. The morphometrical resemblance of *U. rossicus* and *U. savini* in this character has been already noted by KURTÉN (1959).

Three samples of *U. rossicus* are similar in m2 length (table 5), the collections from Krasnodar and Kizel Cave being significantly distinguished in the greatest width of crown (< 0.02).

The m2 has a complicated metaconid and the large cusp of entoconid in *U. etruscus*, *U. maritimus* and *U. arctos* but the latter is associated anteriorly with two or three small denticles. In contrary, *U. spelaeus* demonstrates two-cusped entoconid complicated by additional enamel folds. There is a cingulid on the crown lingual side, which is only slightly developed in *U. rossicus*.

m3. The m3 crown is somewhat elongated, with straight anterior and round posterior edges. It is shorter than that of m1, and wider than m2 crown. The large talonid bears a clear notch on the labial tooth side. The protoconid is longer than metaconid. The latter is high and divided in two tips. The hypoconid is large, approaching the protoconid. The entoconid is represented by a serrate ridge. The crown area between tubercles is large and rugous.

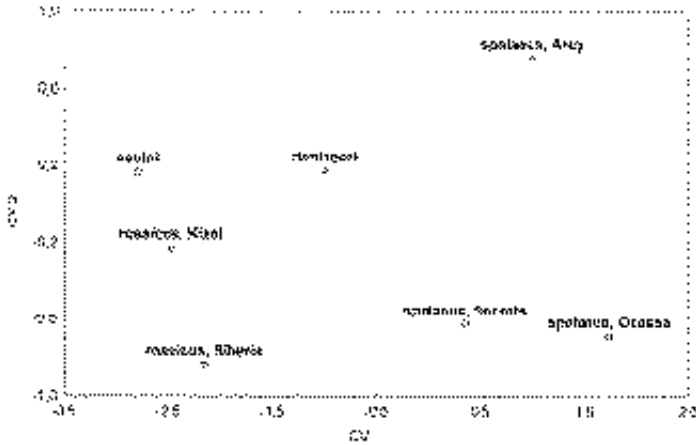


Figure 11. Plot of centroids for each locality on the plane canonical variate 1 and 2 for m2.

Measurements	CV 1	CV 2	CV 3
Labial length of talonid	0,8280	-0,5353	0,0136
Greatest length	0,8589	0,2055	0,1006
Lingual length of talonid	0,4272	-0,6551	0,2029
Width of trigonid	0,7311	0,1069	-0,2338
Labial length of trigonid	0,6370	-0,2608	-0,2150
Width of talonid	0,6279	0,0069	-0,2727

Table 8. Correlations of canonical variate for m2.

The discriminant analysis based on four measurements (greatest length, length of talonid, greatest width, and width of talonid) was carried out for six samples: *U. savini* (n=11), *U. deningeri* (n=47), *U. rossicus*, Siberia (n=6), *U. spe-laus* from Arcy-sur-Cure (n=41), from Odessa (n=42), and from Secrets Cave (n=8). The results of this analysis are presented in figure 12. Nearly 74% of dental variation is explained by the first canonical axis, almost 16% by the second. The first canonical variate discriminates includes all measurements (table 9). The plot of centroids clearly shows an ordination into 2 separate groups, with all samples of *U.*

spelaus on the one hand and all the other examined samples on the other. Squared Mahalanobis distances between samples of these groups are rather low (from 2.59 to 5.06). In the first group, all the samples distribute very close to one another (Mahalanobis distances from 0.16 to 1.65). Differences between the samples of *U. rossicus* and *U. spe-laus* are statistically reliable (p<0.001); there are no consistent differences between the samples of the first group. Based on the results of this analysis we may conclude that by m3 measurements *U. rossicus* is more similar to *U. savini/deningeri*, than to *U. spe-laus*.

Although the Krasnodar collection

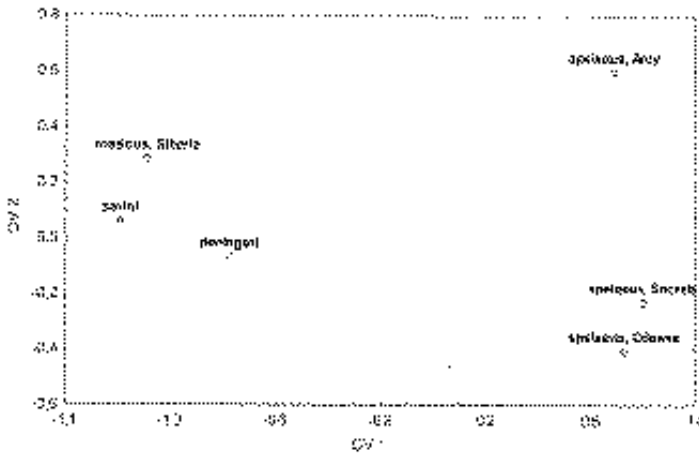


Figure 12. Plot of centroids for each locality on the plane canonical variate 1 and 2 for m3.

Measurements	CV 1	CV 2	CV 3
Greatest length	0,8901	0,1854	0,1293
Labiell length of talonid	0,7893	-0,2415	-0,4496
Greatest width	0,7896	0,4254	-0,4365
Width of talonid	0,8835	0,1976	0,0860

Table 9. Correlations of canonical variate for m3.

demonstrates the largest m3 in three samples examined of *U. rossicus* (table 5), only the specimens from Krasnodar and Kizel Cave reliably differ in the greatest crown width ($P < 0.02$).

In *U. etruscus*, *U. maritimus* and *U. arc-tos*, m3 is moderate in size, resembling an elongated triangle or oval in occlusal view. Commonly it is not clearly divided into trigonid and talonid. In contrary, the cave bears and especially *U. spelaicus* and *U. rossicus* are characterized by an increase of tooth size, mainly of its talonid being well separated from trigonid.

General remarks

Comparison of the lower cheek teeth size in *U. rossicus* from Siberia, Krasnodar and Kizel Cave indicates a large metric resemblance of the first two samples. In contrast, there are reliable differences ($p < 0.01$) between the material from Siberia and Kizel Cave by the greatest width of p4, and between samples from Krasnodar and Kizel Cave by the greatest length of p4, width of talonid in m2 and the greatest width of m3. Cluster analysis based on the average length and width of the lower teeth p4, m1, m2 and m3, has also confirmed (figure 13) that the sam-

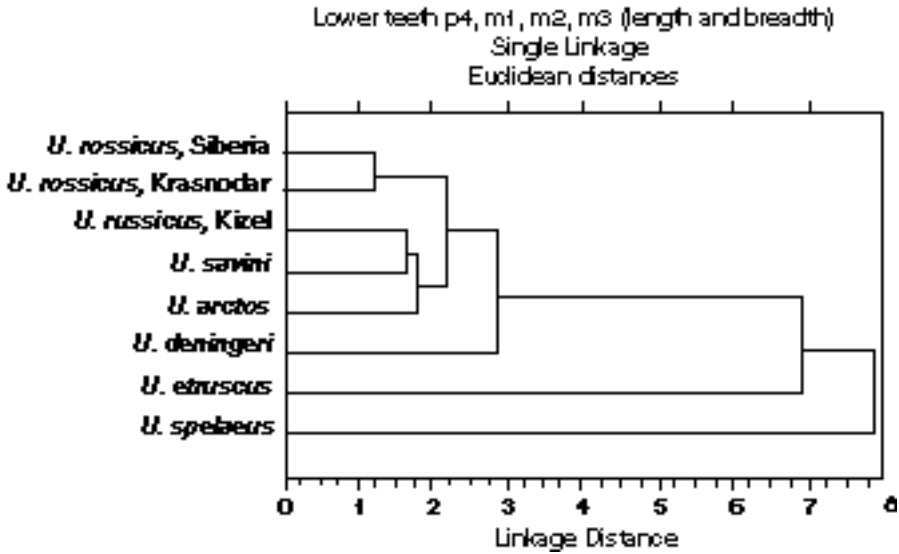


Figure 13. Similarity dendrogram of samples of genus *Ursus* based on length and width means of lower cheek teeth p4, m1, m2 and m3.

ples from Siberia and Krasnodar constitute one cluster, while the sample from Kizel Cave groups with that of *U. savini*.

The obtained results of the discriminant analysis show the resemblance of *U. rossicus* with *U. savini* in proportions of the lower molars m1, m2 and m3. However in proportions of the lower premolar p4, the former species is more close to *U. spelaeus*. The enlargement and complication of p4 may be treated as a specialization of *U. rossicus* to consume rough herbaceous food.

Postcranial skeleton

The isolated limb bones of a small cave bear have been found in Mokhovo quarry and in Berezhekovo. To identify their sex we used the data on the size sex dimorphism in *U. rossicus*, established for the sample from Kizel Cave (see

VERESHCHAGIN & BARYSHNIKOV in press). The specimens examined resemble in size the corresponding bones from Kizel Cave (table 10). The single fourth metacarpal, unlike those from Kizel Cave, does not have the incision on the distal articulate ridge.

CLADISTIC ANALYSIS OF CAVE BEARS

The subgenus *Speleartos* E.Geoffroy, 1833 includes four species: *U. savini* Andrews, 1922 (early Middle Pleistocene), *U. deningeri* von Reichenau, 1904 (Middle and Late Pleistocene), *U. rossicus* Borissiak, 1930 (Middle and Late Pleistocene) and *U. spelaeus* Rosenmüller, 1794 (late Middle and Late Pleistocene). The first and fourth species are found in Europe only, the both others are found in

Bone	Measurements, mm	Males n=12	Females n=1
Humerus	Ep	64.2	58.0
	Dp	74.2	70.0
	SD	-	29.7
Ulna	Bd	-	78.0
	DPA	70.0	62.5
Radius	BPC	47.2	44.7
	GL		
	Ep	42.2, 42.4	39.1
Met+	SD		21.0
	Bd		34.1
	GL		67.3
	Ep		18.2
Talus	SD		15.4
	Bd		21.9
	GL	48.8	41.0
	GB	53.2	50.5

Abbreviations:
 Bd - Breadth of the distal end,
 Ep - Breadth of the proximal end,
 BPC - Breadth across the coronoid process,
 Dp - Depth of the proximal end,
 DPA - Depth across the Procoracoe anconeus,
 GB - Glacial breadth,
 GL - Glacial length,
 SD - smallest breadth of diaphysis (for metacarpal - breadth of diaphysis in middle part).

Table 10. Sizes of limb bones in *Ursus rossicus* from South Siberia.

the many localities of the Northern Eurasia.

We scored seven ursid taxa and 17 characters of skull, cheek teeth, limb bones, and body size (see table 00). We used *U. etruscus* G.Cuvier, 1823 as an outgroup. This species is considered to be ancestral both for the cave bears and the recent species of the genus *Ursus* (*U. arctos* and *U. maritimus*) (ERDBRINK, 1953, KURTÉN, 1968).

Characters. 1. Frontal profile: gentle (0), steep, so the frontal bones are strongly raised over the nasal bones (1).

2. Nasal bones: long, terminating anteriorly over the posterior edge of the upper canine (0), short, the anterior end situated over 4 (1).

3. Condylar process: lies at the level with the occlusal surface of the lower cheek teeth (0), elevated higher than the level of the latter (1).

4. Body of the mandible: relatively low, its inferior border being straight (0), high, and the inferior border is curved, forming a prominence under m2 (1).

5. Entepicondylar foramen of humerus: present (0), absent (1). Among recent bears this foramen is observed in primitive *Ailuropoda* and *Tremarctos*, and is absent in the representatives of all other genera. In *U. etruscus*, this feature varies (MAZZA & RUSTIONI, 1992).

6. Metacarpal and metatarsal bones: short (0), relatively long (1).

7. Ridge of the distal articulate surface on metacarpal and metatarsal bones: round, without incision (0), with small incision on the distal border (1).

8. Premolars P2-3/p2-3: present completely (0), present partly (1), absent (2).

9. Anterior premolars P1/p1: present (0), absent (1).

10. Protocone of P4: simple (0), subdi-

vided or associated with additional tubercles (1).

11. Medial wall of the metacone P4: without tubercle and enamel fold (0), those present (1).

12. Talon of M2: short and relatively narrow (0), long and moderately wide (1), long and very wide, its inner field with large rugae (2). The genus *Ursus* is characterized by the elongation of 2 talon, which is secondary reduced in *U. martimus* (MAZZA, *et al.* 1995).

13. Lower carnassial tooth m1: large, longer than m2 (0), slender, shorter than m2 (1).

14. Lower premolar p4: simple (0), complicated with labial cusps (paraconid and metaconid) (1), complicated with labial cusps and additional tubercles (2).

15. Endoconid of m1: usually with a single tip (0), with two tips or comb-shaped (1).

16. Talonid of m3: not developed (0), wide, separated from trigonid (1).

17. Body size: medium or small (0), large (1).

Results. The data matrix was run by heuristic search option of PAUP and one tree was produced (TL=23, CI=0.826, RI=0.852). A parsimony analysis resulted in the phylogenetic hypothesis shown in figure 14.

Among the selected features of the group *Ursus arctos/martimus* plus *Spelearctos* character 5 are here considered equivocal, but character 8(1) is considered an unambiguous synapomorphy. Both peculiarities separate this group from primitive ursids.

Monophyly of the subgenus *Spelearctos* is supported by 12 synapomorphies. These

confirm the distinct taxonomic status of this subgenus. Peculiarity of the cave bears is caused by the high rate of their morphological evolution, and mainly by changes of their masticatory system, provoked by transition from omnivorous to chiefly vegetable diet.

Relationships within *Spelearctos* are determined by two synapomorphies (characters 14(2) and 3). These indicate the further specialization of the cave bears to various plant food.

The obtained phylogenetic tree generally agrees with the data on the sequence of cave bear species appearance in the geological record. *U. spelaeus*, for example, seems to be not only the most advanced but also the youngest among them.

DISCUSSION

Our investigation confirms that *U. rossicus* was widespread in South Siberia in Middle and Late Pleistocene. In proportions of the cheek teeth, the Siberian bear is more similar to the nominative subspecies than to *U. rossicus uralensis*. Therefore, the range of the nominative taxon included the steppe zone from Ukraine to the Northern Caucasus in the west to Kazakhstan and south of Middle Siberia in the east. The specimens from the Middle and Late Pleistocene do not show sufficient differences, possibly the former are somewhat larger.

BORISSIAK (1932: 190) suggested *U. rossicus* was a steppe race of the cave bear, which had more progressive dental structures than in *U. spelaeus* from Europe. However, archaic characters of its dentition allow him to treat these bears as a

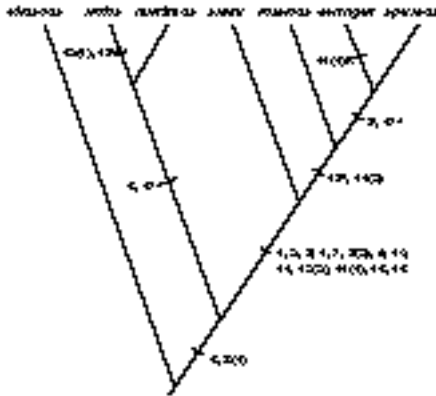


Figure 14. Proposed phylogenetic hypothesis for the genus *Ursus* according to either accelerated (ACCTRAN) optimization (L=23, CI=0.826, RI=0.852). See text for the description of inferred synapomorphies 1-17. Character matrix is in table 11. Symbols: *-parallelism, R- revers.

Taxon	Characters																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>U. arctos</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>U. maritimus</i>	0	0	0	0	1	1	0	1	0	0	0	1	1	0	0	0	1
<i>U. savini</i>	1	1	0	1	1	?	?	2	1	1	1	2	0	1	1	1	0
<i>U. rossicus</i>	1	1	0	1	1	0	1	2	1	1	1	2	1	2	1	1	0
<i>U. deningeri</i>	1	1	1	1	1	0	1	2	1	1	1	2	1	1	1	1	1
<i>U. spelaeus</i>	1	1	1	1	1	0	1	2	1	1	1	2	1	2	1	1	1

Table 11. Character matrix for genus *Ursus*.

parallel branch, originating from the common ancestor.

The obtained results partly support the Borissiak opinion. *U. rossicus* has a specialized lower premolar p4. The trend to complication of this tooth among cave bears is demonstrating by *U. savini* (see ANDREWS, 1922), reaches its greatest development in *U. rossicus* and *U. spelaeus*. *U. deningeri*, in contrast, demonstrates simplification of p4. The morphology of the other lower cheek teeth in *U. rossicus* is rather primitive and consequently, the

level of differentiation of its dentition does not exceed that in *U. savini/deningeri*.

Judging by material examined, published data (BORISSIAK, 1932, VERESHCHAGIN & BARYSHNIKOV, 2000), and distribution, we can imagine that *U. rossicus* was a small bear of 1.5 m in length and 0.8 m in height in scapular area. It seems to have been relatively sluggish and fed mainly on the vegetative parts of plants, roots, berries, fruits, and occasionally invertebrates, smaller vertebrates, and carrion. This bear inhabited the open landscapes of plains and lower

mountains, where its small height allowed it to hide from enemies in grass and relief cavities. For over wintering, it evidently dug earth dens at slopes and ravines, using caves rather seldom.

The phylogenetic analysis carried out, demonstrated the systematic unity of the cave bears. They may be treated either as a subgenus of *Speleartos* within the genus *Ursus*, or as a distinct genus as has been repeatedly proposed by different authors (BORISSIAK, 1932; VERESHCHAGIN, 1973; BARYSHNIKOV, 1998). Such a point of view may be supported by the fact that distinctions, which subdivide the sister species-group (*U. arctos* and *U. maritimus*), are quite often considered to be the generic ones (for example, ELLERMAN & MORRISON-SCOTT, 1966; McKENNA & BELL, 1997).

Our phylogenetic hypothesis (figure 14) is topologically identical with the phylogenetic tree for the genus *Ursus* presented by MAZZA & RUSTIONI (1994). THESE authors interpreted the hypothetical ancestors for (*deningeri* + *spelaeus*) + (*artos* + *maritimus*), and for *artos* + *maritimus* clades as belonging to "*Ursus* gr. *arctos*". The latter was originated, in their opinion, from the early *Ursus* aff. *etruscus*, which was more omnivorous than the later *U. etruscus*. Really, the brown bear retained in dental morphology many features, which are primitive for the cave bears. However, the hypothesis of the origination of the both cave and polar bears from *U. arctos*, is unacceptable in our opinion, because if this a case *U. arctos* would represent the paraphyletic association (see also TALBOT & SHIELDS, 1996).

The evolutionary scenario, which we

reconstruct for the cave bears, suggests their wide distribution in Eurasia and rapid adaptive radiation. We agree that they originated in the end of the Early Pleistocene. Among *Speleartos*, a small *U. savini* seems to be the most ancient, retaining to a considerable degree the omnivorous characters of dentition (the lower carnassial tooth being large; additional tubercles on molars are slightly developed). It was probably a forest species mainly. Its remains are recorded only in Europe (England, Austria), but we believe it may be found also in Asia. To this species, probably, belongs also *U. "etruscus" gombaszoegensis* from Gombaszog, in dentition of which one may recognize the tendency to *U. savini* and in some degree to *U. deningeri* (KRETZOI, 1938).

In the early Middle Pleistocene, *U. ros-sicus* and *U. deningeri* appeared. The former retained a small size and settled the Asiatic steppes. It did not reach the skeleton proportions of *U. spelaeus*, but its cheek teeth were already partly specialized for consuming vegetable food.

U. deningeri, in contrast, was an inhabitant of the forest and forest-steppe landscapes of Europe, Caucasus, Central Asia and south of Siberia. Its size has increased. The crowns of the upper and lower molars became more complicated but even the latest representatives of the species did not reach the level of complication observed in *U. spelaeus*.

In the late Middle Pleistocene, the forms transitional to *U. spelaeus* had appeared in Europe, this species predominating in the Late Pleistocene faunas. These were very large bears, inhabiting various plain and mountain biotopes. In compari-

son with *U. rossicus* and *U. deningeri*, it shows the further strengthening of masticatory structures, which were necessary for more effective fragmentation of plant food. This contributed to the successful competition of *U. spelaeus* with other omnivorous large mammals of the Late Pleistocene and species penetration far to north, up to the Northern Ural (Medvezhiya Cave at 620 N; see Kuzmina 1971).

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