Cave Bears from the Paleolithic of the Greater Caucasus

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ABSTRACT.–I studied a series of skulls, mandibles, and molars of cave bears, *Spelearctos* (Carnivora, Ursidae), from multilayered Paleolithic faunal assemblages from the Kudaro 1 and Kudaro 3 caves in Transcaucasia (Georgia). Morphometric and morphotypical analyses of variation of molars have been made and a new technique for revealing morphotypes of teeth is proposed. A comparison of tooth morphotypes from different layers of the Kudaro caves demonstrates their usefulness for biostratigraphic subdivision of Quaternary cave deposits. The remains of bear from the Acheulean layer 5c in Kudaro 1 are placed in a new subspecies *Spelearctos deningeri praekudarensis* subsp. nov. The bear from the Mousterian fauna of Kudaro 3 (layers 3 - 4) belonged to the subspecies *Spelearctos deningeri kudarensis.* Cave bears of the Greater Caucasus had a slower rate of evolution than cave bears from Central and Eastern Europe. In the Late Pleistocene the cheek teeth retained an archaic structure. I traced evolutionary pathways of cave bear dentition in the course of their specialization for plant foods and these pathways are reported.

ПЕЩЕРНЫЕ МЕДВЕДИ ИЗ ПАЛЕОЛИТА БОЛЬШОГО КАВКАЗА

Г. Ф. Барышников

АБСТРАКТ.–Изучена серия черепов, нижних челюстей и коренных зубов пещерного медведя из многослойных палеолитических стоянок в пещерах Кударо 1 и Кударо 3 в Закавказье (Грузия). Проведен морфометрический и морфотипический анализ изменчивости коренных зубов, предложена новая методика выделения морфотипов. Сравнение морфотипов зубов из разных слоев Кударских пещер показал возможность использования их для биостратиграфического расчленения четвертчных пещерных отложений. Остатки медведя из ашельского слоя 5с в пещере Кударо 1 отнесены к новому подвиду *Spelearctos deningeri praekudarensis* subsp. nov. Ьедведь из мустьерской фауны пещеры Кударо 3 (слои 3-4) принадлежал к подвиду *Spelearctos deningeri*

Quaternary Paleozoology in the Northern Hemisphere. J. J. Saunders, B. W. Styles, and G. F. Baryshnikov (Editors). 1998. Illinois State Museum Scientific Papers, Vol. XXVII. Springfield.

kudarensis. Кавказские пещерные медведи эволюционировали более медленными темпами по сравнению с пещерными медведями из средней и восточной Европы. В позднем плейстоцене они сохраняли архаичное строение коренных зуюов. Прослежены закономерности эволюции зубного аппарата пещерных медведей при специализации их к питанию растительными кормами.

INTRODUCTION

Cave bears, *Spelearctos* (Carnivora, Ursidae), inhabited Western and Eastern Europe during the Middle and Late Pleistocene. Their fossil remains have been reported in this region from Great Britain and Spain in the west to the Urals in the east. They also have been reported from Transcaucasia, Kazakhstan, and Southern Siberia (to Transbaikalia in the east; Vereshchagin and Tikhonov 1994) and, in recent years, from the Middle Pleistocene of Western (Israel) and Central (Kirghizia) Asia (Baryshnikov 1995; Batyrov 1994; Tsoukala 1994). Early Pleistocene *Ursus etruscus* G. Cuvier, 1823 is considered to be the ancestor of cave bears, which had a Palearctic distribution (Kurtén 1968).

Cave bears are characterized by a high skull with a thick sagittal crest, a steep flexure of the frontal profile, short nasal bones, and a large nasal opening. In dentition we observe the absence of anterior premolars and a complex molar structure with numerous additional cusps. Hindlimbs are strongly shortened in comparison with fore ones. Metapodial bones have a small notch on the posterior keel of the distal trochlea (Birula 1930). The main evolutionary pathway of cave bears led to strengthening of the herbivorous adaptation, which resulted in an increased masticatory surface of molars and increased molar rugosity.

The morphological distinctiveness of cave bears is so great that they are normally regarded as a separate subgenus, *Spelearctos* Geoffrey, 1833, within the genus *Ursus*. However, they should be placed in a separate genus based on criteria used in the systematics of recent mammals (Gromova 1965:120). The genus *Spelearctos* includes two species of large bears bound by the "ancestor-descendant" relationship: *S. deningeri* (Reichenau, 1904) and *S. spelaeus* (Rosenmüller, 1794), and one species of small steppe bear, *S. rossicus* (Borissiak, 1930), whose relationship to these species remains obscure.

In the Greater Caucasus, cave bears have bee reported from nearly all the Paleolithic sites. I Transcaucasia, accumulations containing man thousands of fossil remains have been reported fron caves, for example Kudaro 1, Kudaro 3, Tsona, an Akhshtyrskaya. In the Northern Caucasus, cave bear occurred less abundantly.

Scientists studying the Caucasian Pleistocene faun identified the cave bear from the Caucasus as *Ursu spelaeus* (Burchak-Abramovich 1960, 1961; Gromov 1948; Vereshchagin 1967). However no detaile description of the cave bear from the Caucasus has bee made.

This paper reports the detailed study of fossi remains of cave bears from Acheulean and Mousteria layers of the Paleolithic sites Kudaro 1 and Kudaro 3 i Transcaucasia.

Preliminary morphological study of bear remain from the Mousterian layers of Kudaro 3 in South Osseti has already shown the distinctiveness of the Caucasia form (Baryshnikov and Dedkova 1978). Later, it wa placed in a separate subspecies *"Ursus" spelaeu kudarensis* Baryshnikov, 1985, and later, on the basis c molar structure, included in the species *"Ursus deningeri* (Baryshnikov 1987; Liubin et al. 1985) Furthermore, the morphological characterization of th cave bear from the Acheulean has not been completed

KUDARO CAVES

Geographic position

The Kudaro 1 and Kudaro 3 caves are located nea the village Kvaisa in South Ossetia in the valley of th Dzhodzhori River. They are situated in the Rioni Rive basin on the southern slope of the Central Caucasus They represent gallery-type caves and lie on immediately beneath the other. They are situated at a elevation of 1,600 m above sea level. The sites wer discovered and were excavated regularly since 1956 b archaeologist Dr. V. Liubin (St. Petersburg).

Stratigraphy

Loamy clay deposits in both caves contain archaeological artifacts of Acheulean, Mousterian, and more recent periods. In Kudaro 1, the thickness of sediments fluctuates from 1.5 to 4.5 m. Five lithological layers are distinguished, of which layer 5 (with subdivisions 5a, 5b, 5c) is Acheulean and layers 3 and 4 are Mousterian (Liubin et al. 1985). Absolute dates have been obtained for the site. Two of them have been obtained by thermoluminiscent dating: layer 5c–360,000±90,000 years B.P. (RTL-379) and layer 5a-b–350,000±70,000 years B.P. (RTL-373) (Liubin and Kulikov 1991). There is also a radiocarbon date obtained for bone from layer 3a–44,150±2,400/1,850 years B.P. (Gr-6079) (Liubin 1989). The age of the site, according to the Alpine geochronological scale, is Mindel (oxygen isotope stage 10 - 11) for layer 5c and Early and Middle Würm (oxygen isotope stage 3 - 4) for layers 4 and 3 (Liubin et al. 1985).

Kudaro 3 has approximately the same cycles of sediment accumulation as Kudaro 1. However, thickness of its deposits, particularly for the Mousterian, is much greater, and attains 6 - 7 m. Eight lithological layers have been recognized; layers 5 - 8 are Acheulean and layers 3 - 4 are Mousterian (Liubin 1989). The upper Acheulean layer, layer 5, contains a thermophilous mammalian fauna with an interglacial affinity (Baryshnikov 1987) and may be dated to the warm stage within the latest Middle Pleistocene (Riss, oxygen isotope stage 7). Palynological data obtained by Dr. G. Levkovskaya for layer 5 demonstrate a change from mesophytic subalpine herbaceous vegetation to the development of West-Kolhid spruce forest. Lithological and biostratigraphical attributes of layers 3 and 4 are similar to those of Kudaro 1 and permit correlating the time of their formation to the first half of the Würm (Liubin 1989, 1993), except for the lowermost horizon that has thermophilous species of mammals and may be dated to Riss-Würm (oxygen isotope stage 5e).

Three dates have been obtained for the lowermost deposits in Kudaro 3 with the radiothermoluminiscent method. Two of them, 245,000±49,000 years B.P. (RTL-534) and 252,000±51,000 years B.P. (RTL-511), were obtained at the obscure contact between layers 4f and 5. One date, 560,000±112,000 years B.P. (RTL-512), was obtained for the lowermost cultural layer 8a (Liubin 1993).

MATERIALS AND METHODS

Materials

I have studied eight skulls found in Kudaro 1: five specimens from Mousterian layer 4 and three specimens from Acheulean layer 5c. Ten large fragments of the lower jaw have been measured. There are large series of molars from both caves. Molars were distributed among three samples: 1) Kudaro 1, layer 5c, Acheulean (Mindel)–123 specimens, 2) Kudaro 3, layer 5, Acheulean (Riss)–101 specimens, 3) Kudaro 3 , layers 4 and 3, Mousterian (Riss-Würm and Early and Middle Würm)–147 specimens. The collection examined has been deposited at the History of Faunas Department of the Zoological Institute of the Russian Academy of Sciences (ZIRAS) in St. Petersburg.

For comparison I used the following materials of *S. spelaeus*: from the collections of the ZIRAS, 2 skulls from Austria (Nos. 10282, 10273, Steiermark, Graz), 1 skull from the Northern Urals (No. 30354, Medvezhya Cave), 114 isolated molars from the Ukraine (Nos. 10292 - 10296, 10317 - 10319, 10415, 10425, 10427, "Sued-Russland," A. Nordmann; 10384 - 10395, Nerobai near Odessa, J. F. Brandt); from the collections of the Zoological Museum, University of Helsinki, Finland, 1 skull from the Alps, 5 fragments of skull (Nos. P-82, P-86, P-87, P-714, P-716) and 160 molars from Odessa (collections of A. Nordmann); as well as a small collection of *S. deningeri* from the Institute of Systematics and Evolution of Animals in Krakow, Poland (54 isolated molars from the Middle Pleistocene locality Kozi-Grzbiet in central Poland).

Methods

I have taken up to 27 measurements of skulls and up to nine measurements of mandibles, according to the measurement scheme provided by Driesch (1976). Locations of measurements for molars are shown in Figure 1. Numbers of measurements are presented in Tables 1 - 11 in parentheses. I calculated limits, i.e., minimum and maximum (min, max) values and mean (M) values, and also sample standard deviations (SD). Significance of differences between compared samples was determined by a Students *t* test with different levels of significance indicated by a "+" (0.05>P>0.01) or "++" (P< 0.01) (see Tables 7, 12). I also performed a principal components analysis of the molars using SYSTAT.

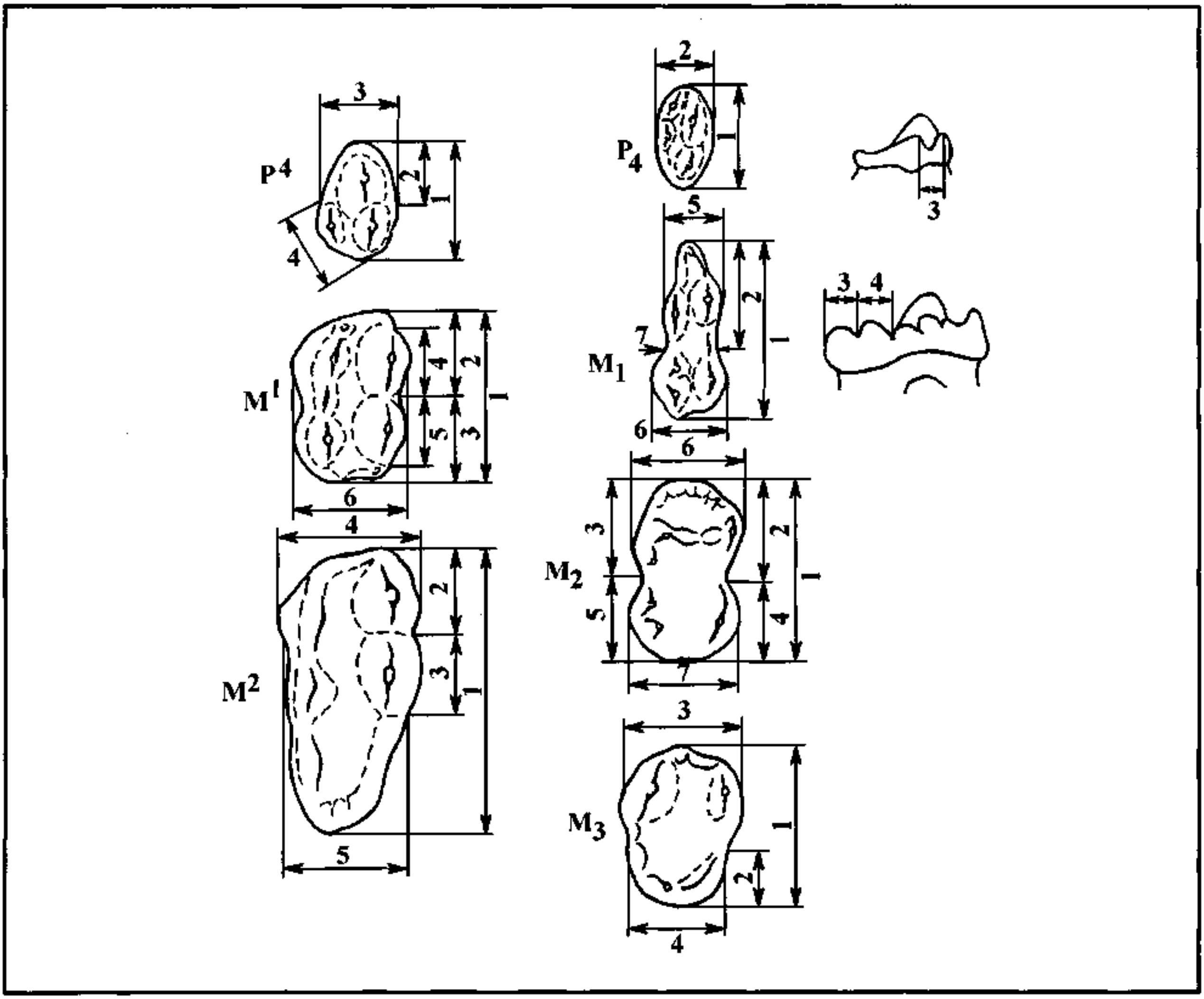

Figure 1. Measurements of cheek teeth (maxillary teeth on left, mandibular teeth on right). The names of the variates are given in the tables reporting tooth measurements.

The study of molar morphotypes follows Rabeder (1983) and Paunovic (1988). However, I used a different method for distinguishing morphotypes. The main characters (a, b, c, d) and levels of their change (from 1 to 6) were determined for each tooth. Directed change of characters is shown by the tendency toward increasingly complicated masticatory surfaces of molars in *Spelearctos*. Each morphotype represents a combination of characters according to the level of their advancement, e.g., A1 = a1, b2, c1. For the sake of convenience, rare combinations were combined with more common ones, although for other samples they can be regarded as separate morphotypes.

RESULTS

Skulls

Skulls vary notably in size, completeness, and degree of wear of molars. All specimens lack an associated mandible. In some specimens (Nos. 31890, 31892) the sagittal crest was gnawed by porcupines (genus *Hystrix)* in ancient times. Two skulls (Nos. 31893, 31260) have oval polished areas (12 x 40 mm in diameter) on the anterior surface of the upper canines. Initially these polished areas were attributed to traces of human ritual activities (Vereshchagin and Baryshnikov 1980). However, they are in all probability the result of natural causes. Similar vertical wear of the anterior surface of upper canines is observed for recent *U. arctos*, e.g., on skulls of old individuals from Kamchatka in collections of the ZIRAS. It is the result of friction between crowns of upper and lower canines during their occlusion.

Most skulls are large in size (Table 1), with a long and strong sagittal crest and thick zygomatic arches set widely apart (if the latter are preserved). Molars are worn to different degrees. Total length of skulls exceeds 450 mm; condylobasal length exceeds 416 mm; basal length exceeds 390 mm. These specimens may be regarded as males. Measurements conform to the variation of those in supposed males of *S. spelaeus* from Belgian sites (Cordy 1972). Upper canines in Kudaro specimens are also large. Their length at the base of the crown is 24.7 to 29.7 mm; width at this position is 18.5 to 24.2 mm. These measurements are quite typical of male cave bear canines (Kurtén 1955).

A skull (No. 31894) from layer 5c in Kudaro 1 is of much smaller size. Its total length is 420 mm, its basal length equals 372 mm. This specimen is characterized by a steeper position of the frons and by a weak and long sagittal ridge. The skull possesses worn molars and belonged to an adult animal. The left frontal bone has a large funnel-shaped hollow of pathological origin that joins the brain cavity, which could have formed as a result of osteomyelitis. The small size of the skull suggests that it was a female. It is unlikely that the small size of the skull could be attributed to degenerative development of the animal. Measurements of canines, e.g., length = 22.6, width = 19.3 mm, are also typical of females.

In layer 4 of Kudaro 3, a small skull (No. 31890) also has been found, but its teeth are not worn, the frons is sloping, the sagittal crest is short, and skull sutures are distinct. These characters are typical of a young individual. The total length of the skull is 415 mm. The length of the canine is 22.8 mm amd the width is 19.3 mm.

Therefore, although we have found in Kudaro 1 and 3, skulls of both males (2 specimens in Kudaro 1, 4 specimens in Kudaro 3) and females (1 specimen), the number of males is much greater. An additional skull belongs to a semiadult animal, the sex of which cannot be determined. A different ratio of males to females, i.e., 2 skulls of males and 3 skulls of females, is observed in bears from Tain (= Secret) Cave in the Middle Urals (collection of ZIRAS).

Skulls of adult bears from the Kudaro caves have steep frons, relatively large nasal openings dilated downwards, short nasal bones, and other characters typical of the genus *Spelearctos*. Three anterior premolars are naturally absent and a diastema occurs between the canine and P^4. Among eight skulls, one has a single-rooted P^3. It is a simple tooth with one apex, weakly compressed laterally. Its length is 8.4 mm and its width is 7.1 mm.

Scant material and the varying degree of completeness of skulls make it difficult to determine significant diagnostic characters of the Kudaro bears. Specimens from Acheulean layer 5c in Kudaro 1 (Nos. 31894, 31896, 33161) are fragmentary and belong to individuals of different ages and sex (Figs. 2, 3). In their proportions they are similar to skulls of *S. deningeri kudarensis* (Table 1), but their molars have a more archaic structure.

Males of *S. deningeri kudarensis* from Mousterian layers of Kudaro 3 (holotype No. 31260, layer 4, horizon 4; Figs. 4, 5) are characterized by somewhat smaller linear measurements of the skull, than males of *S. spelaeus spelaeus* (Table 2). Their zygomatic arches are set more widely apart and their neurocrania are relatively wider. Supraorbital processes are well-developed and deflected downwards. Skull measurements of a male *S. spelaeus kanivetz* (Vereshchagin, 1973) from Medvezhya Cave (lectotype No. 30354) as well as measurements of other specimens from caves in the Urals in the ZIRAS collections are smaller than those of the Kudaro bear. A comparison of *S. deningeri kudarensis* with cave bears from the Middle Pleistocene of Europe shows that males of *S. deningeri romeviensis* (Prat et Thibault, 1976) from Nauterie in France have somewhat smaller average values of such measurements as basal length, facial length, and breadth of the neurocranium (Prat and Thibault 1976). In addition, Kudaro skulls are relatively wider in the region of the canines and between the supraorbital processes.

Mandibles

Mandibles are represented by isolated halves. They are moderately long with a high horizontal ramus and tall ascending ramus and they possess deep masseteric fossa (Fig. 6). The anterior premolars are normally lacking and a diastema is situated behind the canine. Alveoli for single-rooted P_{1-2} or for P_{2-3} are present on two of the 12 specimens that have been examined.

Table 1. Size of skulls in *Spelearctos deningeri* from the Kudaro caves.

	S. d. praekudarensis ssp. nov. Kudaro 1, layer 5c, Acheulean			*S. d. kudarensis* Kudaro 3, layers 3-4, Mousterian				
Measurements, mm	33161 sen. ♂	31896 ad. ♂	31894 ad. ♀	31260 sen. ♂	31892 ad. ♂	31891 ad. ♂	31893 ad. ♂	31890 subad.
Total length (1)	451		420	478	452	483	476	415
Condylobasal length (2)	416		394	443	420	451	450	
Basal length (3)	390		372	415	395	426	424	
Upper neurocranium length (7)			236	274	257		355	210
Facial length (9)			219	242	232		247	227
Greatest length of the nasals (10)							105	
"Snout" length (12)			158	188	165	182	179	155
Medial palatal length (13)	ca 230		218.5	235	237	249	240	
Length of C^1-M^2	155	179	158	167	162	167	164	153
Length of P^4-M^2	87	95.1	81.5	90.9	88.4	95.5	89.4	90.6
Length of M^1-M^2 (16)	70.2	76.4	64.6	73.5	71.6	74.8	71.4	70.6
Greatest mastoid breadth (23)	212		189	242	243	243	249	169
Greatest breadth of the occipital condyles (25)	93.5		83.5	81	88	91	83	
Greatest neurocranium breadth (29)	130		110	119	121	117	120	115
Zygomatic breadth (30)			237	290	312	305	293	
Least breadth of skull (31)			80.5	97.5	93	87	85	86
Frontal breadth (32)			132	170	162		153	129.5
Least breadth between the orbits (33)			80	114	111	110		93
Greatest palatal breadth (34)	110	108.5	102	110	115.5	119	108	98
Least palatal breadth (35)	84	80	80	89	79	90	83.5	72
Breadth at the canine (36)	120	100	100	116	105	120	110	95
Greatest inner height of the orbit (37)			55	75	68	63	67	67
Skull height (38)	134		110	147	ca 122	149	135	

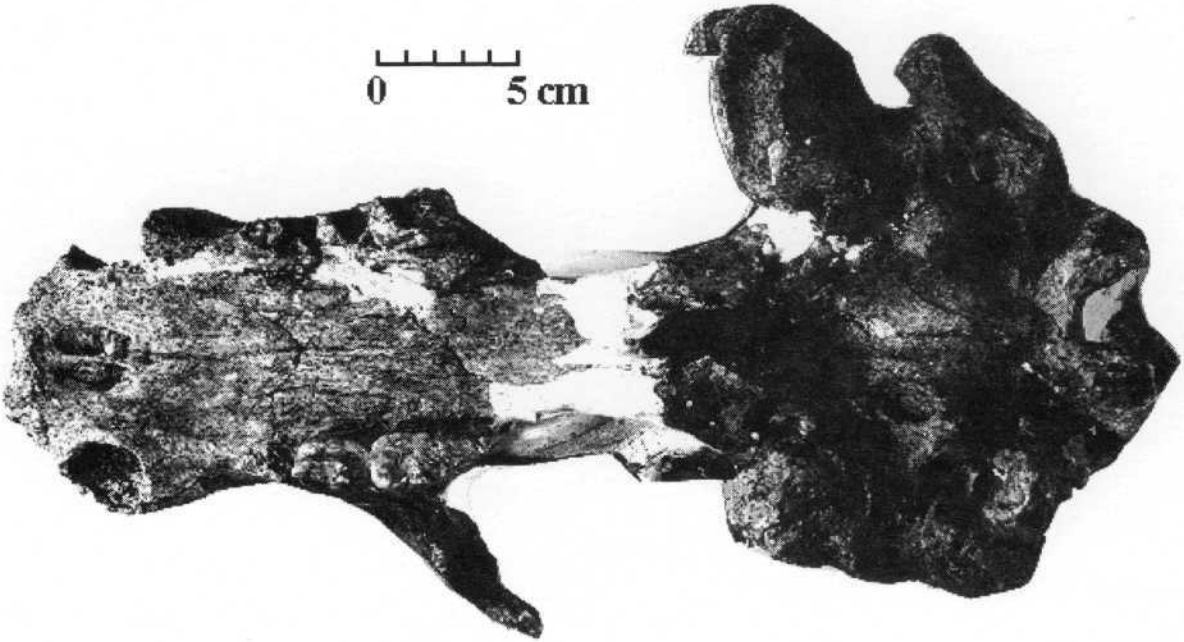

Figure 2. Skull of *Spelearctos deningeri praekudarensis*, subsp. nov. (No. 33161, holotype), male. Kudaro Cave 1, stratum 5c. Palatal view.

In the total length of the mandible and particularly in the length of the lower row of molars, *S. deningeri kudarensis* from layers 3 - 4 in Kudaro 3 was smaller than the European *S. spelaeus* (Table 3). However, both forms are similar in the height of the horizontal ramus and the height of the ascending ramus. Kudaro specimens differ in being less massive and in having less expressed convexity of the lower border of the horizontal branch below the posterior molars. The processus articularis in Kudaro specimens is less elevated above the level of the dental row than in *S. spelaeus* from the Alps and Odessa.

The jaw of the subadult bear from layer 5c in Kudaro 1 (No. 33162) is notably smaller than specimens of *S. deningeri kudarensis*. Its total length is 265 mm; the length of C_1 - M_3 is 231 mm; and the length of P_4 - M_3 is 95.7 mm.

Dentition

Upper molars. The presence of complete skulls from individuals of different ontogenetic age in the Kudaro caves allowed me to trace the main stages of wear of upper molars. The parts that begin wearing first are the apices of the lingual cusps on M^1, then erosion is spread to the protocone of P^4, then to the labial cusps of M^1, and eventually traces of wear appear on the masticatory surface of M^2.

One can distinguish five stages of wear (Fig. 7) as follows: I – wear facets are situated close to the apex of the protocone of P^4 and the apices of the lingual cusps on M^1, but wear facets are lacking on M^2; II – on P^4 the protocone is worn up to one half of its height; on M^1 erosion covers the paracone and the metacone, and the lingual row of cusps form a single zone of wear; on M^2 there are abrasive spots along the lingual edge of the crown on the paracone and on the talon; III – P^4 metacone begins wearing off; on M^1 the erosional zones of the metacone and lingual row of cusps fuse; and on M^2 wear facets extend to the apices of the paracone and metacone; IV – the P^4 metacone continues to wear off; a single worn area appears on M^1 that includes all of the main cusps, and erosional facets of the labial and lingual rows partly coalesce on M^2; V – molars are strongly worn over their entire masticatory surface and M^2 sometimes have open pulp cavities.

In general the degree of wear of tooth crowns in cave bears is correlated with the age of the animal. In some cases, however, individual deviations related to the peculiarities of occlusion or abrasive qualities of the food, or diseases are observed. Thus, for instance, in the

Figure 3. Skull of *Spelearctos deningeri praekudarensis*, subsp. nov. (No. 31894, paratype), female. Kudaro Cave 1, stratum 5c. Lateral view.

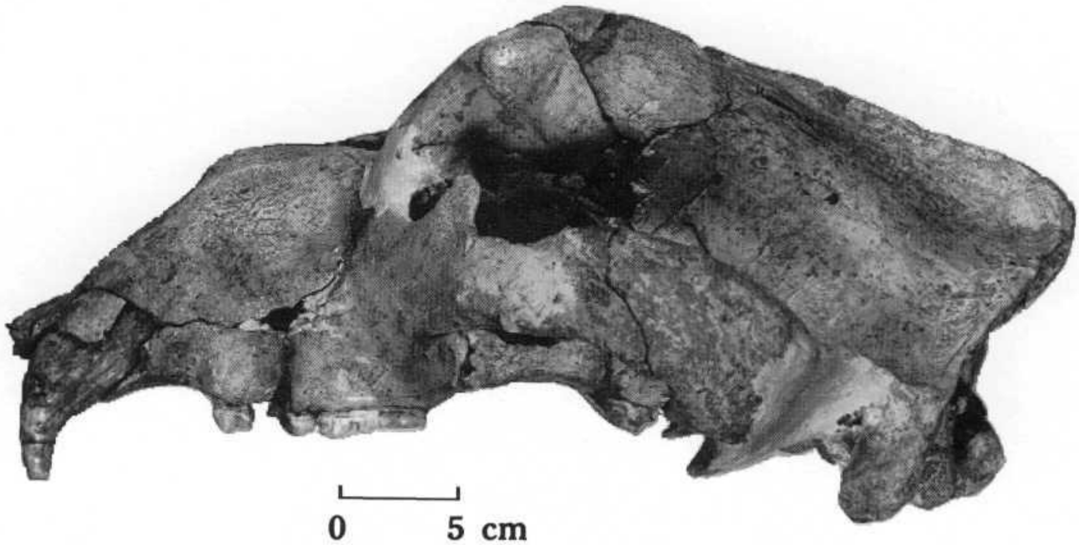

Figure 4. Skull of *Spelearctos deningeri kudarensis* (No. 31260, holotype), male. Kudaro Cave 3, stratum 4. Lateral view.

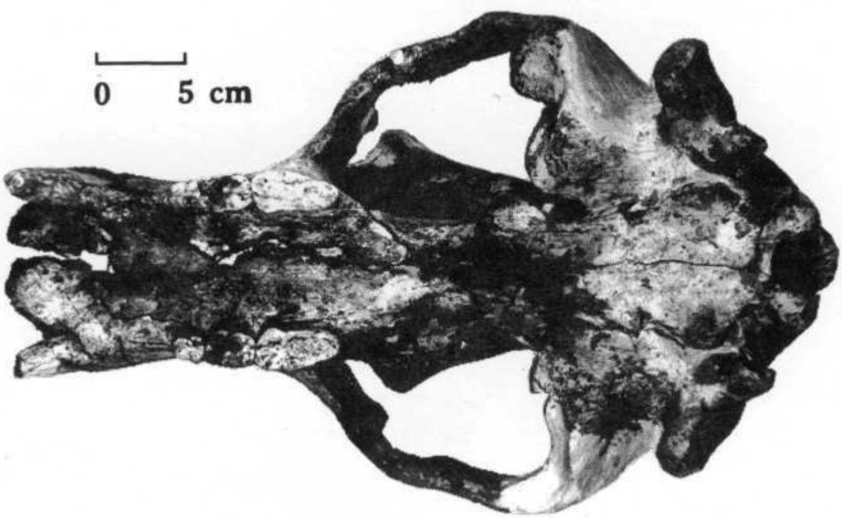

Figure 5. Skull of *Spelearctos deningeri kudarensis* (No. 31260, holotype), male. Kudaro Cave 3, stratum 4. Palatal view.

Table 2. Comparison of skulls of males in the genus *Spelearctos*.

Measurements, mm	*S. deningeri kudarensis* Kudaro 3, Caucasus					*S. spelaeus spelaeus* Alps and Odessa					*S. spelaeus kanivetz* Medvezh'ya Cave, Northern Urals
	n	min	max	M	SD	n	min	max	M	SD	n = 1
Total length (1)	4	452	483	472.2	13.8	3	462	528	494.3	-	440
Condylobasal length (2)	4	420	451	441.0	14.4	2	443	470	-	-	430
Basal length (3)	4	395	426	415.0	14.2	2	417	441	-	-	410
Upper neurocranium length (7)	3	255	274	262.0	-	2	260	266.5	-	-	219
Facial length (9)	3	232	247	240.3	-	2	260	263	-	-	241
"Snout" length (12)	4	165	188	178.5	9.7	2	191	199	-	-	172
Median palatal length (13)	4	235	249	240.2	6.2	4	217	261	241.7	15.8	239
Length of C^1-M^2	4	162	167	165.0	2.4	5	163	192	174.7	10.8	177
Length of P^4-M^2	4	88	95	91.0	3.1	4	92	109	99.0	6.8	84.9
Length of molar row M^1-M^2 (16)	4	71	74	72.8	1.6	5	72	83	77.5	4.2	68
Greatest mastoid breadth (23)	4	242	249	244.2	3.2	3	222	233	228.5	-	214
Greatest breadth of the occipital condyles (25)	4	81	91	85.7	4.6	5	78	102	88.8	8.5	83
Greatest neurocranium breadth (29)	4	117	121	119.2	1.7	5	107	115	111.4	2.7	117
Zygomatic breadth (30)	4	290	312	300.0	10.3	2	288	290	-	-	265
Lest breadth of skull (31)	4	85	97	90.6	5.7	4	78	90	83.6	4.3	81
Frontal breadth (32)	3	153	170	161.7	-	3	123	148	135.6	-	116
Least breadth between the orbits (33)	3	110	114	111.7	-	2	103	110	-	-	92
Greatest palatal breadth (34)	4	108	119	113.1	5.0	4	113	120	116.4	2.7	105
Least palatal breadth (35)	4	79	90	85.4	5.1	4	79	87	82.7	3.3	77
Breadth at the canine (36)	4	105	120	112.7	6.6	3	103	118	109.2	-	101
Greatest inner height of the orbit (37)	4	63	75	68.2	5.0	2	63	64	-	-	69
Skull height (38)	4	122	149	138.2	12.5	4	119	145	136.7	10.3	126

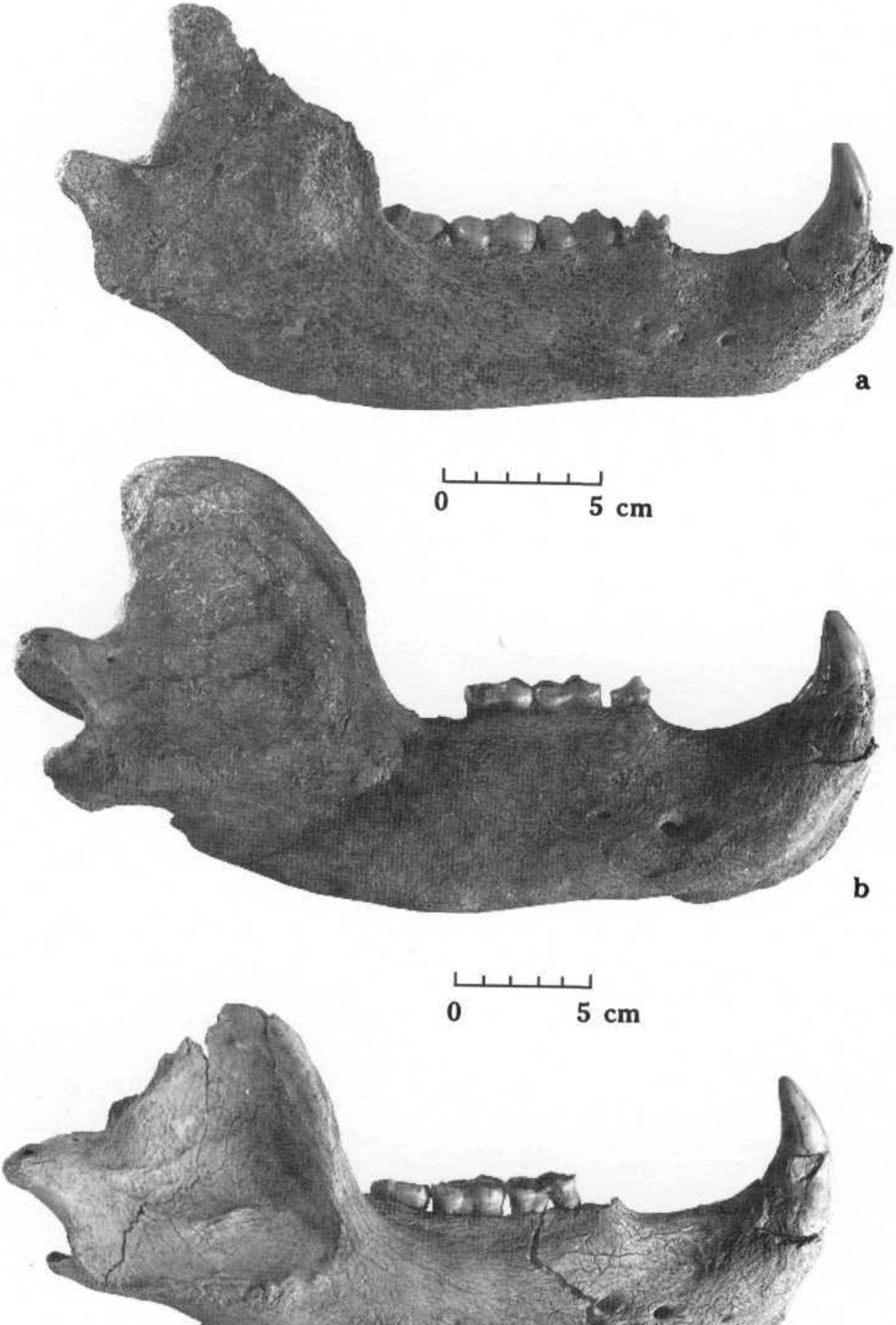

Figure 6. Lower jaws of *Spelearctos deningeri praekudarensis*, subsp. nov., Kudaro Cave 1, stratum 5c (a) and *S. deningeri kudarensis*, Kudaro Cave 3 (b–stratum 4, c–stratum 3). Labial views. a–No. 33162, subad., paratype; b–No. 34254, ad.; c–No. 342533, sen.

Table 3. Size of mandibles in the genus *Spelearctos*.

Measurements, mm	*S. deningeri kudarensis* Kudaro 3, Caucasus					*S. spelaeus* Alps and Odessa				
	n	min	max	M	SD	n	min	max	M	SD
Total length (1)	3	318	323	320.7	-	4	317	348	330.9	13.1
Length: angular processes-Infradentale (2)	3	310	324	318.3	-	4	316	348	328.4	13.7
Length: caudal indentation-Infradentale (3)	3	299	302	300.0	-	4	302	329	310.6	12.4
Length: condyle process-aboral border of canine (4)	7	264	286	278.1	7.3	7	274	308	288.1	12.4
Length P_4-M_3	7	95	102	99.2	2.8	16	97	114	106.5	4.6
Length of molar row M_1-M_3 (10)	8	78	86	81.7	2.5	17	82	96	89.7	4.5
Height of the vertical ramus (18)	4	145	155	149.4	4.0	6	120	168	147.0	16.1
Height of the mandible behind M_1 (19)	9	65	76	69.9	3.6	17	56	82	68.3	9.2
Height of the mandible in diastema (20)	8	61	71	64.9	3.7	17	53	73	63.7	6.7

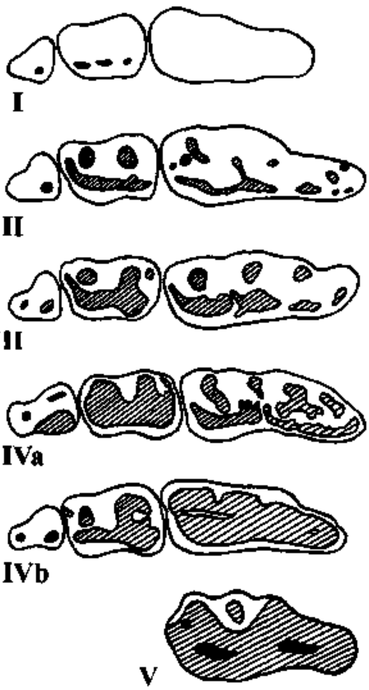

Figure 7. Stage of wear I - V in upper cheek teeth. Marks of wear (dentin facets) are shaded. The open pulpar cavity (in stage V) is black.

skull from Austria (No. 10282) the right M^2 has weakly worn lingual cusps while on the left M^2 these cusps are unworn.

I have observed the following pattern in the distribution of skulls based on wear stages of their teeth: Kudaro 1, Acheulean: stage I (2 specimens), stage III (1 specimen); Kudaro 3, Mousterian: stage I (1 specimen), stage II (2 specimens), stage III (1 specimen), stage IV (1 specimen). All age groups are represented, from young to old individuals. In other karst regions of Transcaucasia we have found the skulls of very old animals, e.g., in Akhshtyrskaya Cave (ZIRAS No. 32134) and Ablaskir Cave where they have strongly worn last molars.

S. spelaeus kanivetz skulls from Tain Cave in the Urals, to judge by tooth wear, can be assigned to juveniles (2 specimens), an adult (1 specimen), and old animals (2 specimens). The skull from Medvezhya Cave in the Northern Urals belonged to an adult individual. For *S. rossicus* from Kizel Cave in the Middle Urals (ZIRAS Collections) remains of four age groups have been found: stage I (1 specimen), stage II (1 specimen), stage III (2 specimens), stage IV (1 specimen). Therefore bears in caves in different geographic regions show a similar pattern of age composition. The deaths of these bears probably resulted from natural causes, e.g., disease, senility, starvation, or drowning in spring floods that inundated karst cavities (Vereshchagin 1982).

P^4 (Fig. 8). Four measurements of P^4 were taken (Fig. 1). In the length of the crown the Kudaro bears are significantly smaller than European *S. spelaeus* (Tables 4, 5). A principal components analysis yields three factors. The percentage of total variance explained is 81.8 for Factor 1, 13.7 for Factor 2, and 2.8 for Factor 3. Factor score coefficients for standardized variables indicate which variables are important in segregating groups of P^4 (Table 6). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 2 (Fig. 9). The distinction for Factor 2 is related to a more posterior position of the protocone in the Odessa teeth (measurement 4). Metric indices of *S. deningeri* from Kozi-Grzbiet are similar to those of the Caucasian form. Size differences between samples from different layers in the Kudaro caves are slight, but there is a progressive increase in the maximal width of the crown through time.

Morphotypes of P^4 (morphotype group "A") have been distinguished on the basis of the structure of the protocone, the presence of the metastyle, and the lingual cingulum, and also on the degree of development of the accessory cusp on the lingual wall of the metacone (Fig. 10). This accessory cusp is characteristic of the genus *Spelearctos.* Rabeder (1983) called the accessory cusp a metaconule, although it probably did not develop on the postprotocrista, but on the wall of the metacone, i.e., it is not homologous to the metaconule. Changes of this cusp are unidirectional. It may be lacking (a1), may appear as a small convexity or swelling of enamel (a2), have the form of a small cusp (a3), or attain a relatively

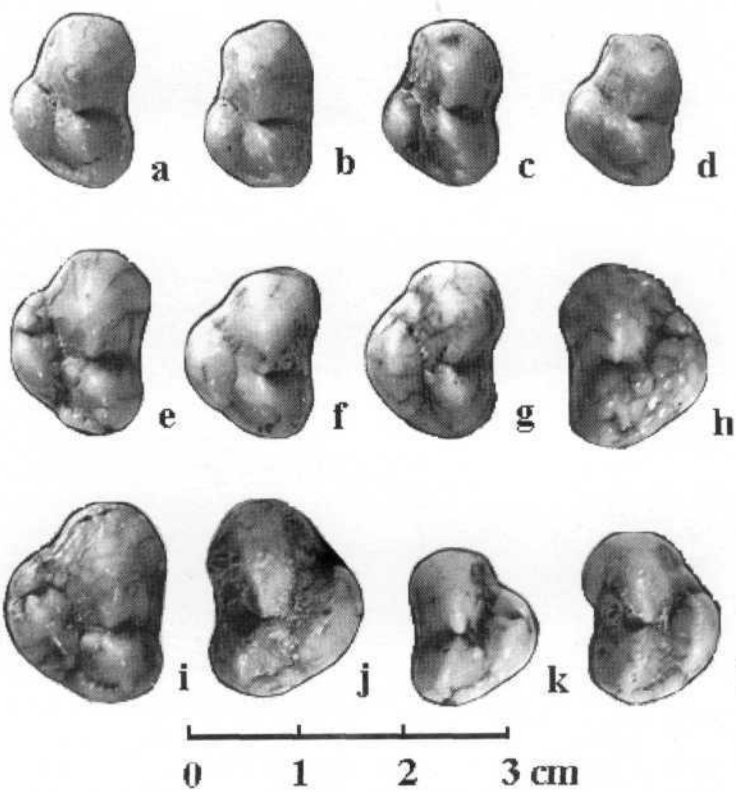

Figure 8. The fourth upper premolar, P^4, occlusal view. a - d–Kudaro Cave 1, stratum 5c; e - h–Kudaro Cave 3, stratum 5 i - l–Kudaro Cave 3, strata 3 - 4.

Table 4. Measurements (in mm) of upper premolar P^4 in the genus *Spelearctos*.

Locality		Maximum length (1)	Length of paracone (2)	Maximum breadth (3)	Least distance between frontal ridge of protocone and caudal side of crown (4)
S. deningeri					
Kudaro 1,	n	20	20	20	20
layer 5c	min	16.6	10.2	11.7	12.9
	max	23.7	14.8	16.9	18.8
	M	19.56	12.27	13.65	15.32
	SD	1.71	1.20	1.49	1.80
Kudaro 3,	n	18	18	18	18
layer 5	min	16.8	10.4	12.4	13.2
	max	21.3	14.2	16.6	18.3
	M	19.18	11.99	14.22	15.92
	SD	1.28	0.80	1.11	1.37
Kudaro 3,	n	13	14	14	13
layer 4	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
S. spelaeus					
Odessa	n	30	30	30	30
	min	18.8	11.8	12.8	13.1
	max	24.0	15.3	17.1	17.4
	M	21.61	13.80	15.07	15.19
	SD	1.46	1.08	1.08	1.32

Table 5. Significance test to differentiate the means of the upper teeth in the genus *Spelearctos*.

+ = P<0.05, ++ = P<0.01			
Upper premolar P^4			
Maximum length			
	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Maximum breadth			
Kudaro 1, layer 5c	-	+	++
Kudaro 3, layer 5		-	+
Kudaro 3, layer 4			-
Upper molar M^1			
Maximum length			
	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4		-	++
Maximum breadth			
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Upper molar M^2			
Maximum length			
	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Breadth of frontal			
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++

Table 6. Factor score coefficients for standardized variables in principal components analysis of specimens of upper premolar P^4.

Measurements	Factor 1	Factor 2	Factor 3
1	0.288	0.484	0.940
2	0.281	0.621	0.608
2	0.292	-0.177	-2.490
3	0.242	-1.802	1.176

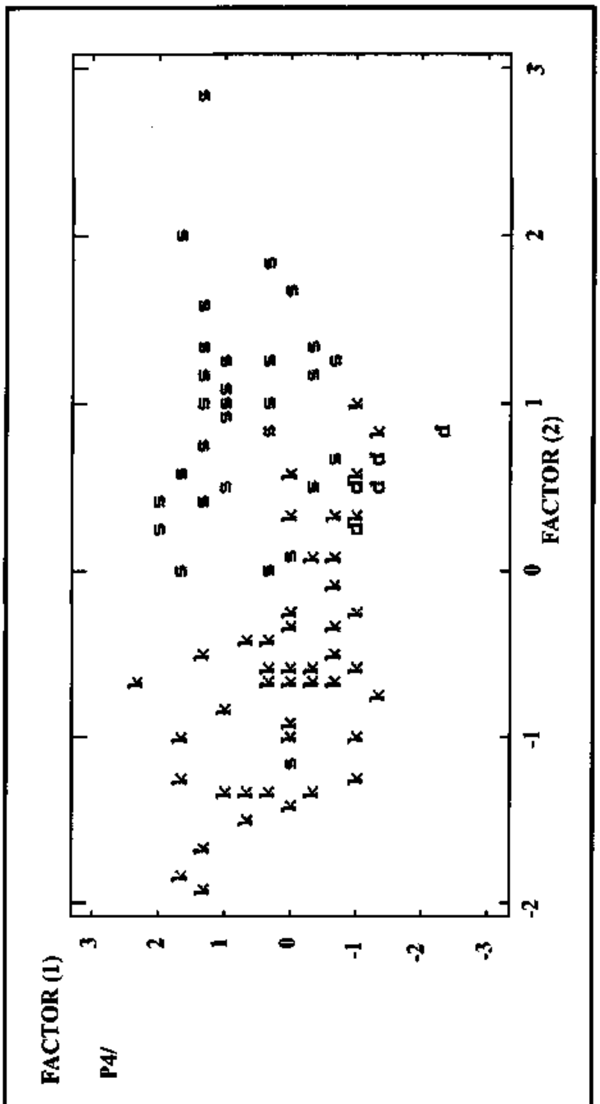

Figure 9. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of upper premolar P^4. d–*Spelearctos deningeri*, Kozi-Grzbiet; k–*S. deningeri*, Kudaro Cave 1 and Kudaro Cave 3; s–*S. spelaeus*, Odessa.

large size and a ridge-shaped appearance (a4). The last level of transformation (a4) is typical of *S. spelaeus* where this ridge-shaped element sometimes joins an analogous formation on the opposite side of the protocone, forming a transverse ridge – metaloph in the interpretation of Rabeder and Tsoukala (1990). The protocone varies from a whole single cusp (b1), to a more complicated form with one anterior or posterior cusp (b2), or with two (b3) accessory cusps. The lingual cingulum is either lacking entirely (c1) or can be traced near the base of the protocone (c2). The metastyle may be either lacking (d1) or present (d2).

Group "A" morphotypes (A1 - A12) are formed by a combination of the characters considered above, as follows: A1 (a1, b1, c1, d1), A2 (a1, b1 - 2, c1, d2), A3 (a2, b1, c1, d1), A4 (a2, b1, c1 - 2, d2), A5 (a2, b2, c2, d1 - 2), A6 (a3, b1, c1, d1), A7 (a3, b1, c1, d2), A8 (a3, b1, c2, d1), A9 (a3, b2, c1 , d2), A10 (a3, b2, c2, d1 - 2), A11 (a4, b1, cl, d2), A12 (a4, bl - 3, cl-2, d2).

The samples compared differ morphotypically (Fig. 11). In Kudaro 1 morphotypes A2 and A3 are predominant in layer 5c (Fig. 11a). They are characterized by a simple structure of P^4, which had a more carnassial and cutting appearance than is observed on samples from geologically more recent levels.

Kudaro 3 layer 5 (Fig. 11b) contains nearly all morphotypes except the most archaic ones, i.e., A1 - A2. In this sample A4 and A6 are more common than others. In Kudaro 3 layers 3 - 4 (Fig. 11c), the proportion of more complicated morphotypes (A10 and A9) increases.

In *S. spelaeus* from Odessa (Fig. 11d) one observes the predominance of morphotype A11, which only rarely occurs in Kudaro samples. Morphotype A11 reflects the increase in the number of tubercles on the masticatory surface of P^4 in the European cave bear.

Comparison of samples shows that there has been a unidirectional change in the structure of P^4. I can trace

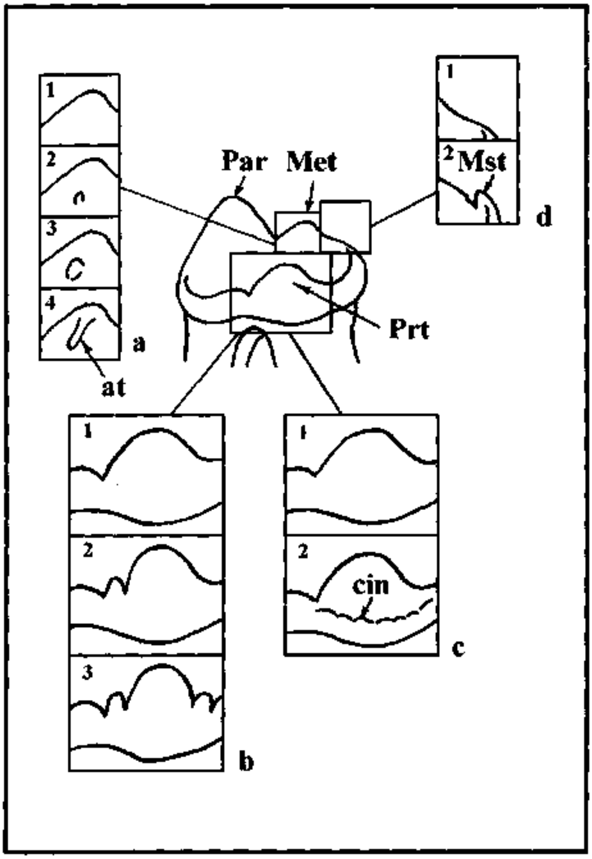

Figure 10. Schematic of fourth upper premolar, P^4, structure, lingual view. The levels of derivation in metacone (a), protocone (b), lingual cingulum (c) and metastyle (d) are demonstrated. at–additional cusp in internal side of metacone, cin–cingulum, Met–metacone, Mst–metastyle, Par–paracone, Prt–protocone.

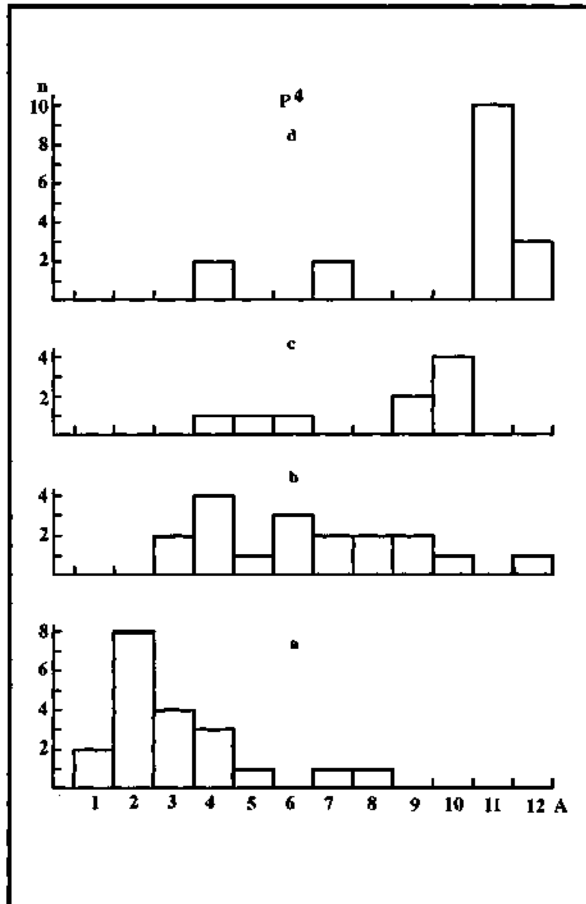

Figure 11. Encountered frequency of morphotypes of group "A". a - c–*Spelearctos deningeri*, d–*S. spelaeus*. a–Kudaro Cave 1, stratum 5c; b–Kudaro Cave 3, stratum 5; c–Kudaro Cave 3, strata 3 - 4, d–Odessa.

a trend towards complication of the crown and the appearance of an increasingly large number of pronounced accessory elements. The crushing and shredding role of the tooth increased. In contrast, the cutting role, characteristic of Pliocene omnivorous and carnivorous ancestors of the genus *Spelearctos*, was reduced. Extension of the area of the crown and increase of the number of accessory cusps on P^4 were responses to the processing of plant foods, and performance of a masticatory function that was not typical of the ancestral adaptation.

M^1 (Fig. 12). Six measurements were taken. In all measurements, teeth from the Caucasus are considerably smaller than those of *S. spelaeus* (Table 7) and have a relatively shorter posterior part of the crown. A principal components analysis yields three factors. The percent of total variance explained is 84.3 for Factor 1, 5.2 for Factor 2, and 4.7 for Factor 3. Factor score coefficients for standardized variables indicate which variables are important in separating groups of M^1 (Table 8). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 2 (Fig. 13). Distinctions are apparent for Factor 1. These include all variables, with the possible exception of length of the metacone. The molars from Kozi-Grzbiet fall within the limits of variation for the Caucasian form. Variation in the sizes of M^1 in different layers of the Kudaro caves are slight.

M^1 morphotypes (Group "B") were determined on the basis of the form of the metaconule (Fig. 14a), the width of the posterior portion of the inner longitudina

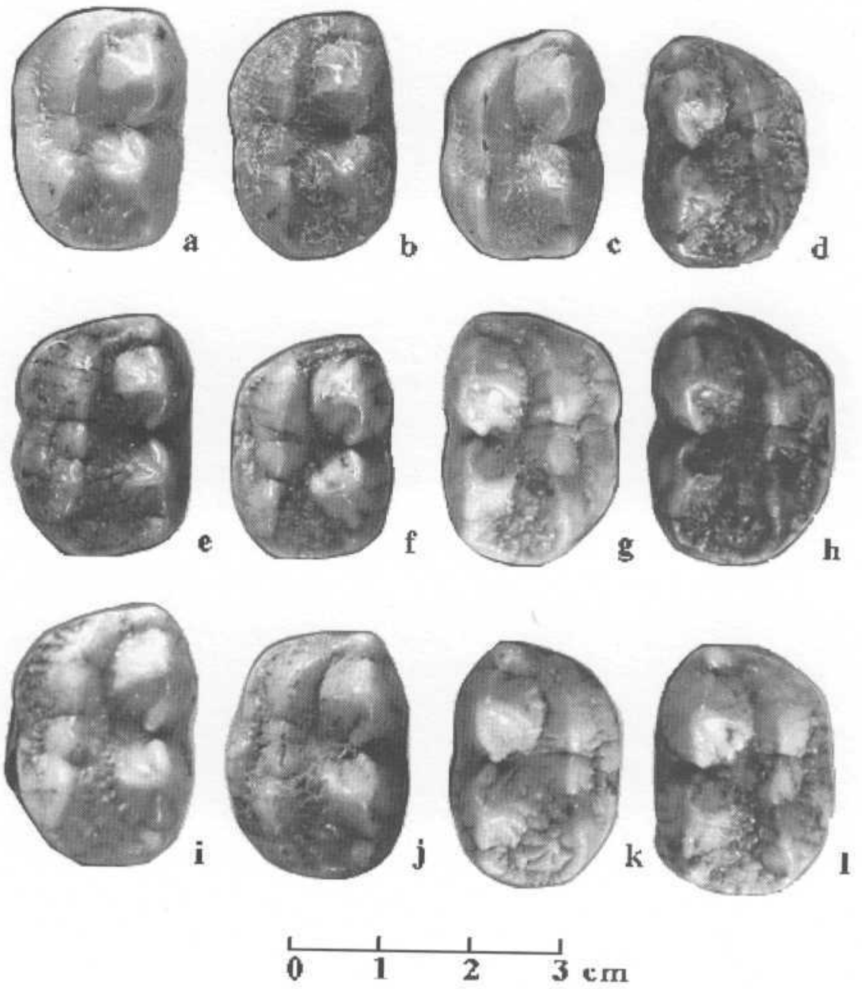

Figure 12. The first upper molar, M^1, occlusal view. The site and level attributions are as Fig.8.

valley separating the internal and external rows of cusps (Fig. 14b), and the length of the lingual cingulum (Fig. 14c). The metaconule may be short and flattened (a1), or have the shape of a cusp with a single (a2) or bifurcated (a3) apex. The medial valley either remains narrow in the posterior direction with joining bases of lingual and labial tubercles (b1), is slightly dilated (b2), or becomes wide and flattened and contains small cusps (b3). The cingulum is situated near the base of the protocone only on the lingual side (c1), or extends also to the anterior wall of the crown (c2).

Ten group "B" morphotypes (B1 - B10) have been distinguished by the following combinations of features discussed above: B1 (a1, b2, c1 - 2), B2 (a2, b1, c1), B3 (a2, b1, c2), B4 (a2, b2, c1), B5 (a2, b2, c2), B6 (a2, b3, c1 - 2), B7 (a3, b2, c1), B8 (a3, b2, c2), B9 (a3, b3, c1), B10 (a3, b3, c3).

Frequency of occurrence of M^1 morphotypes in samples from the Kudaro caves changes from layer to layer. In more recent levels the proportion of teeth with complicated crowns increases.

Table 7. Measurements (in mm) of upper molar M^1 in the genus *Spelearctos*.

Locality		Maximum length (1)	Length of frontal part (2)	Length of caudal part (3)	Length of paracone (4)	Length of metacone (5)	Maximum breadth (6)
S. deningeri							
Kudaro 1,	n	16	16	16	17	14	17
layer 5c	min	22.0	10.5	11.1	8.5	8.0	16.2
	max	29.5	15.9	14.0	11.1	10.4	22.5
	M	26.01	12.50	13.25	9.92	8.79	18.97
	SD	1.54	1.10	0.76	0.71	0.75	1.32
Kudaro 3,	n	17	17	17	17	17	17
layer 5	min	23.2	10.9	11.6	7.9	7.7	16.8
	max	30.0	14.1	15.2	10.5	10.5	22.0
	M	26.19	12.55	12.60	9.58	8.63	18.60
	SD	1.69	0.89	0.92	0.66	0.71	1.34
Kudaro 3,	n	20	20	19	18	17	20
layers 3-4	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	8.89	19.13
	SD	1.16	0.64	0.76	0.58	0.63	0.89
S. spelaeus							
Odessa	n	20	20	20	20	20	20
	min	27.7	13.3	14.4	10.1	9.3	18.5
	max	33.4	16.0	18.0	12.1	11.0	23.6
	M	29.84	14.29	15.79	10.89	10.35	20.99
	SD	1.72	0.81	1.03	0.57	0.45	1.31

Table 8. Factor score coefficients for standardized variables in principal components analysis of specimens of upper molar M^1.

Measurements	Factor 1	Factor 2	Factor 3
1	0.192	0.372	0.316
2	0.187	-0.199	0.678
3	0.175	1.123	-0.819
4	0.178	-0.710	0.752
5	0.172	-1.052	-1.302
6	0.184	0.413	0.248

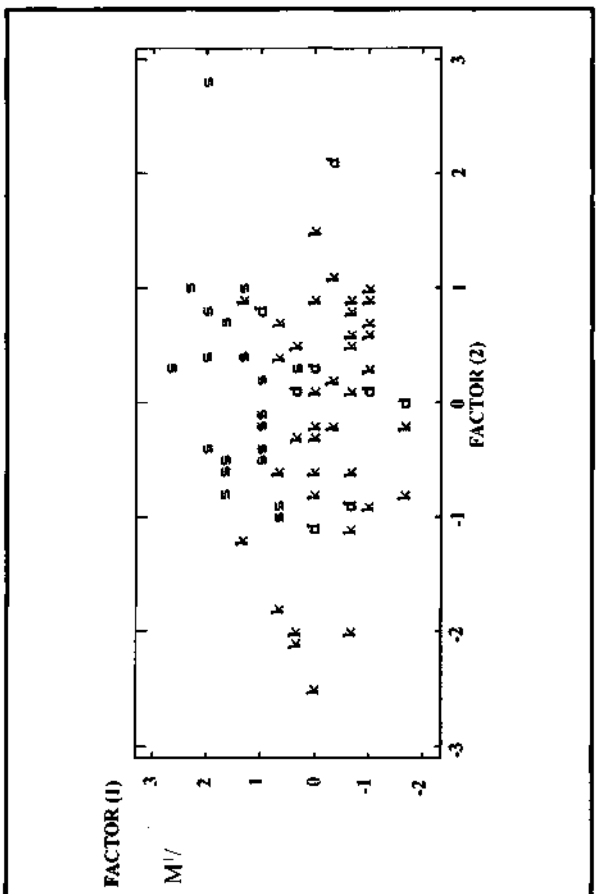

Figure 13. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of upper molar M^1. The symbols are as in Fig. 9.

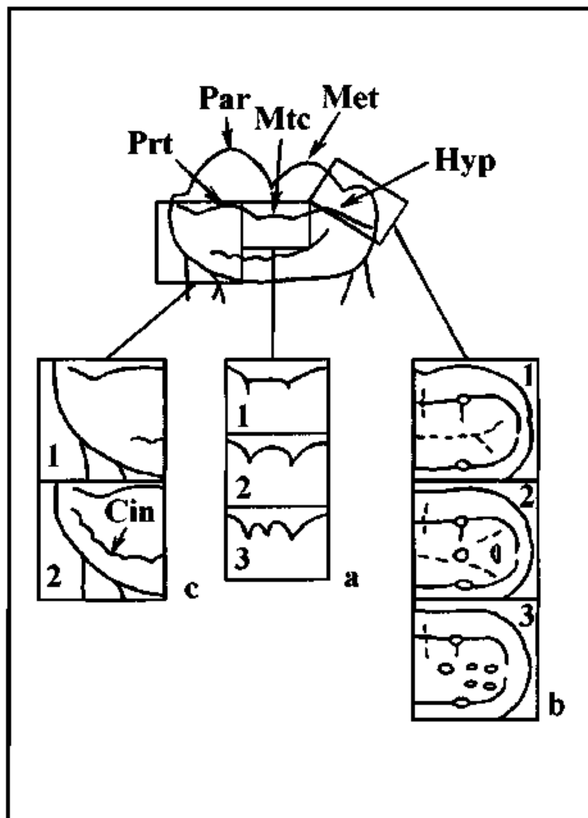

Figure 14. Schematic of first upper molar, M^1, structure, lingual view. The levels of derivation in metaconule (a), posterior portion of longitudinal valley (b) and lingual cingulum (c) are demonstrated. cin–cingulum, Hyp–hypocone, Met–metacone, Mtc–metaconule, Par–paracone, Prt–protocone.

The earliest level of Kudaro 1 is characterized by the least complicated morphotype, B1, which was not observed for samples from Mousterian layers (Fig. 15). Labial and lingual rows of cusps in this morphotype are nearly parallel to each other; the metaconule has a flattened apex; and the lingual cingulum is only weakly developed, although it sometimes spreads to the anterior edge of the base of the protocone. In layers 3 - 5 of Kudaro 3 morphotype B4 is predominant; the archaic morphotypes B1 - 3 decrease in frequency, and in the Mousterian layers they are lacking. In *S. spelaeus* M^1 is wider and more massive and has a more complicated structure. Morphotypes B9 - 10 that have not been noted for the Kudaro caves (Fig. 15a, b, c) are predominant in *S. spelaeus* (Fig. 15d). The presence of a large parastyle and metastyle, and a lingual cingulum are typical of the genus *Spelearctos*. These elements may be lacking in other Ursinae. *Spelearctos* is also characterized by a medial valley that dilates posteriorly and by a sloping inner wall of the crown.

The M^1 is less variable in comparison with other upper cheek teeth. Its transformations in cave bears are related mainly to an increase of the area of the masticatory surface. Labial cusps become larger and lingual cusps are separated. The medial valley becomes wide, and small accessory cusps develop within it.

M^2 (Fig. 16). Five measurements of the crown were taken (Fig. 1). In the Kudaro bear the M^2 is notably shorter and narrower than in *S. spelaeus* with a relatively long metacone (Table 9). A principal components analysis yielded three factors. The percentage of total variance explained is 54. 1 for Factor 1, 22.6 for Factor 2, and 12.1 for Factor 3. Factor score coefficients for standardized variables indicate which variables are important in separating groups of M^2 (Table 10). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 2 (Fig. 17). Differences are apparent for Factor 1. They primarily include the maximum length and breadth of the anterior portion of the tooth. The dispersal of characters in factor space, however, does not suggest a distinct separation of M^2 for the Caucasian and European forms, which was observed in other upper molars. Teeth of European *S. deningeri* from Kozi-Grzbiet fall within the range of variation of the Kudaro bear. Metric differences between cave bears of the Caucasus and Europe in maximum length and maximum width of the crown of M^2 are statistically significant, but within the compared samples from different layers of Kudaro 1 and Kudaro 3 they are slight.

M^2 morphotype (group "C") have been separated based on the presence of a parastyle (Fig. 18a), the shape of the metacone (Fig. 18b), and the degree of development of the lingual cingulum (Fig. 18c). The parastyle is absent (a1) or present (a2). The metacone is simple, with one apex (b1), or complex, with two or three apices (b2). The lingual cingulum is short and weak (c1); in other cases it is distinct, but reaches only the anterior edge of the hypocone (c2), or it is distinct along the entire base of the hypocone (c3).

Nine morphotypes of group "C" were distinguished (C1 - C9): C1 (a1, b1, c1), C2 (a1, b1, c2), C3 (a1, b1, c3), C4 (a1, b2, c2), C5 (a1, b2, c3), C6 (a2, b1, c2), C7 (a2, b1, c3), C8 (a2, b2, c2), C9 (a2, b2, c3).

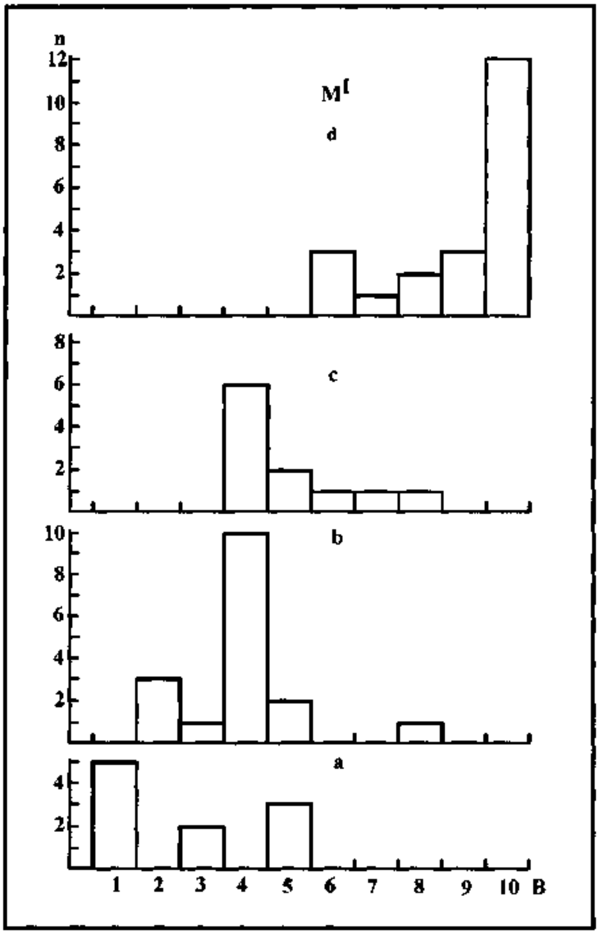

Figure 15. Encountered frequency of morphotypes of group "B". The designations are as in Fig. 11.

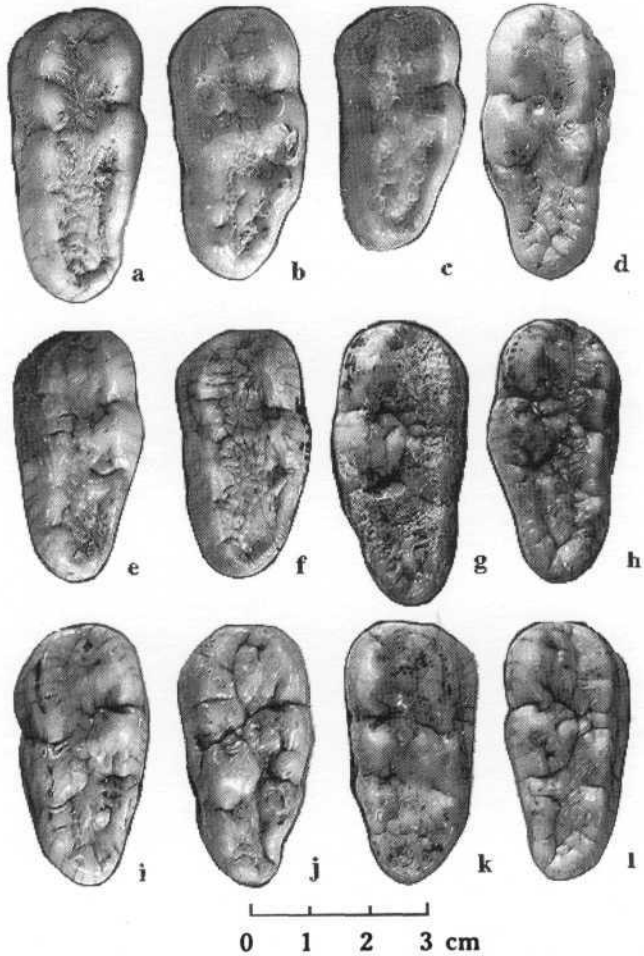

Figure 16. The second upper molar, M^2, occlusal view. The site and level attributions are as in Fig. 8.

Unlike the other upper molars previously considered, M^2 does not exhibit successive temporal changes in predominant morphotype in the Kudaro cave samples. In all layers morphotypes C1 - C3 are most numerous although in deposits of the Mousterian epoch we observe the complicated variants C8 - C9 (Fig. 19b, c), which are absent in Acheulean layers (Fig. 19a). In *S. spelaeus* these complicated variants are most typical (Fig. 19d).

M^2s in the primitive, Pliocene ancestors of cave bears are characterized by moderate length and width and by sharp apices of the paracone and metacone. In *Spelearctos* this tooth becomes wide and long and the paracone and metacone acquire the appearance of massive crushing cusps. The masticatory surface area of the posterior part of the crown, i.e., the talon, increases notably. Other changes in the structure of the M^2 are related to the presence of the parastyle, the separation of the metacone into several parts, the appearance of small cusps in the inner part, and separation of the marginal ridge bordering the talon, which makes it resemble a notched crest. The increase of the area of the talon and appearance of accessory cusps on M^2 is also typical of the recent bamboo bear, *Ailuropoda melanoleuca* David, 1869, which feeds on bamboo leaves and shoots. This trend may be considered as convergent with that observed for *Spelearctos,* although the tooth is shorter in the bamboo bear.

Table 9. Measurements (in mm) of upper molar M^2 in the genus *Spelearctos*.

Locality		Maximum length (1)	Length of paracone (2)	Length of metacone (3)	Breadth of frontal part (4)	Breadth of caudal part (5)
S. deningeri						
Kudaro 1,	n	10	10	12	11	12
layer 5c	min	38.0	10.30	7.0	19.8	16.5
	max	47.8	14.30	13.0	24.6	22.6
	M	43.19	12.51	10.87	21.95	20.06
	SD	3.01	1.24	1.49	1.27	1.64
Kudaro 3,	n	14	14	14	12	12
layer 5	min	40.1	11.3	7.7	20.7	19.8
	max	46.5	13.6	12.6	22.9	22.7
	M	43.15	12.45	10.1	21.86	21.11
	SD	1.92	0.70	1.54	0.76	1.02
Kudaro 3,	n	23	25	24	24	22
layers 3-4	min	39.0	9.6	7.4	19.2	17.9
	max	47.8	14.9	12.2	24.7	23.5
	M	42.89	12.62	10.46	21.97	20.00
	SD	2.21	1.59	1.18	1.38	1.50
S. spelaeus						
Odessa	n	20	20	20	20	20
	min	41.6	12.1	8.8	19.9	16.0
	max	51.7	14.9	13.8	26.2	23.0
	M	46.70	13.54	10.64	23.83	21.03
	SD	3.10	0.82	1.48	1.81	1.55

Table 10. Factor score coefficients for standardized variables in principal components analysis of specimens of upper molar M^2.

Measurements	Factor 1	Factor 2	Factor 3
1	0.326	0.108	0.137
2	0.245	-0.360	- 0.985
3	0.102	-0.755	0.709
4	0.351	0.062	0.058
5	0.264	0.410	0.397

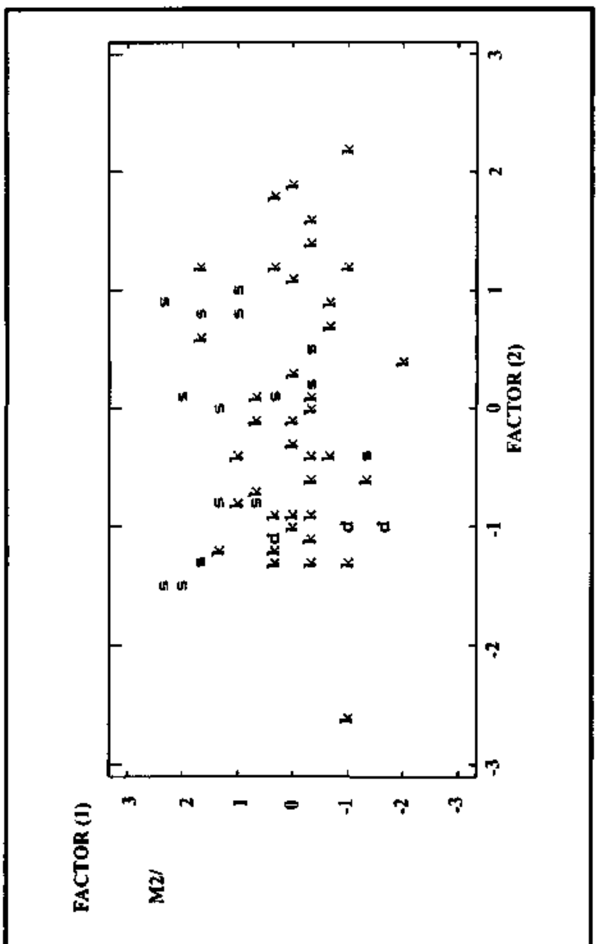

Figure 17. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of upper molar M^2. The symbols are as in Fig. 9.

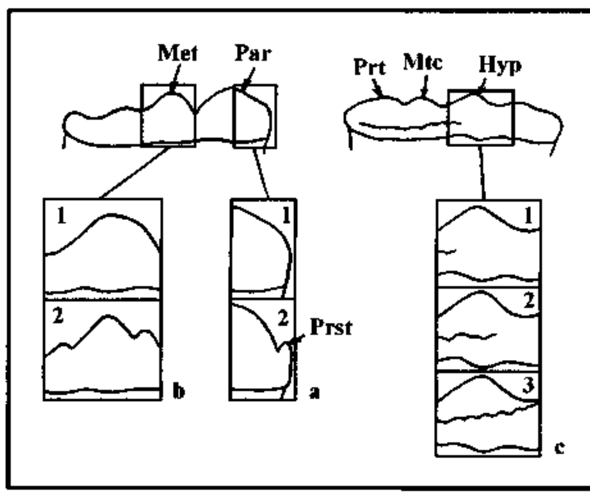

Figure 18. Schematic of second upper molar, M^2, structure, labial (on the left) and lingual (on the right) views. The levels of derivation in parastyle (a), metacone (b) and lingual cingulum (c) are demonstrated. Hyp – hypocone, Met – metacone, Mtc – metaconule, Par – paracone, Prst – parastyle.

Increase in sizes and complication of crown structure for M^2 in cave bears are related to increased reliance on plant foods (i.e., shredding and grinding of coarse herbaceous food). The last molar played the major role in this masticatory process. Its adaptive transformations, therefore, could have taken place in an earlier stage of the evolution of *Spelearctos* than analogous changes in other molars of the upper tooth row.

Lower Molars. Only isolated fragments of mandibles were studied, which did not permit analysis of asymmetry in their wear for both left and right tooth rows. With progressive grinding, erosion zones appear first on the labial side of crowns of M_1 and M_2, then on the lingual tubercles of these molars, then they spread to the masticatory surface of M_3. Grinding appears on P_4 lastly.

I distinguish five stages of wear for lower molars (Fig. 20): I – erosional facets are small and arranged only on apices of the main cusps of M_1 and M_2; II – worn areas are larger and cover the paraconid, protoconid, and hypoconid of M_1 and on M_2 they cover the labial area of the masticatory surface, sometimes forming a narrow continuous stripe; single traces of wear are found on M_3; III – all cusps of the trigonid and talonid of M_1 are covered by erosion; on M_2 a continuous zone of wear stretches in the form of a band along the labial edge of the crown, separate facets only occur lingually; M_3 begins to wear only in the region of the protoconid and hypoconid; IV – zones of wear join only along the labial walls on all molars, and on the M_1 and M_2 they are also connected by transverse ridges composed on eroded lingual cusps; P_4 begins to wear away; V – crowns of all molars are strongly worn over the entire masticatory surface.

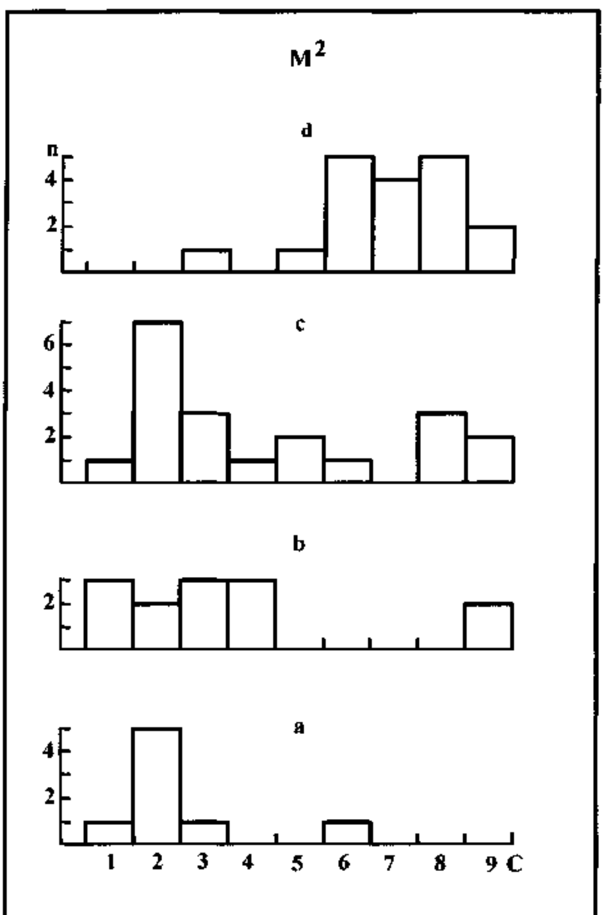

Figure 19. Encountered frequency of morphotypes of group "C". The designations are as in Fig. 11.

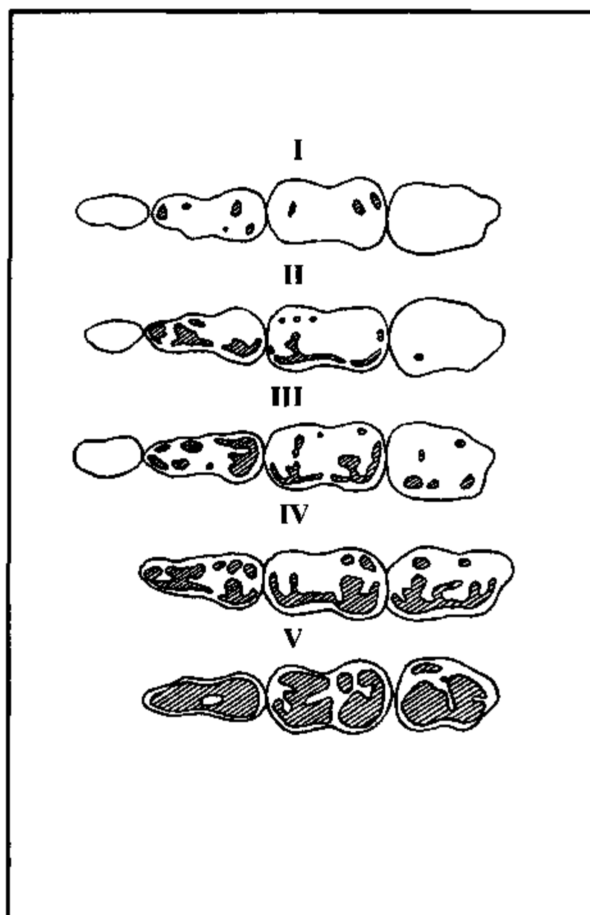

Figure 20. Stage of wear I - IV in lower cheek teeth. Marks of wear (dentin facets) are shaded.

The frequencies of jaws with various degrees of tooth wear are as follows: Kudaro Cave 1, Acheulean: stage I – 3 specimens; Kudaro Cave 3, Mousterian: stage II – 2 specimens, stage III – 3 specimens, stage IV – 2 specimens, stage V – 2 specimens. These data support previous interpretations that all age groups of bears are represented in the Kudaro caves.

P_4 (Fig. 21). Three measurements of the tooth crown were taken (Fig. 1). Their comparison shows that bear teeth from the Kudaro caves are much smaller and are relatively narrower than noted for *S. spelaeus* (Table 11) and differences of the maximum length and maximum width of the crown are statistically significant. A principal components analysis yields two factors. The percentage of total variance explained is 60.6 for Factor 1 and 31.7 for Factor 2. Factor score coefficients for standardized variables indicate which variables are important in separating groups of P_4 (Table 12). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 2 (Fig. 22). Differences are apparent for Factor I which includes maximum length and maximum breadth. Premolars from Kozi-Grzbiet are within the range of variation for P_4 from the Caucasus. For the Kudaro material an increase in the mean values of crown width from the lower layers to the more recent ones is observed. The differences between samples from layer 5c in Kudaro 1 and layer 4 in Kudaro 3 are statistically significant.

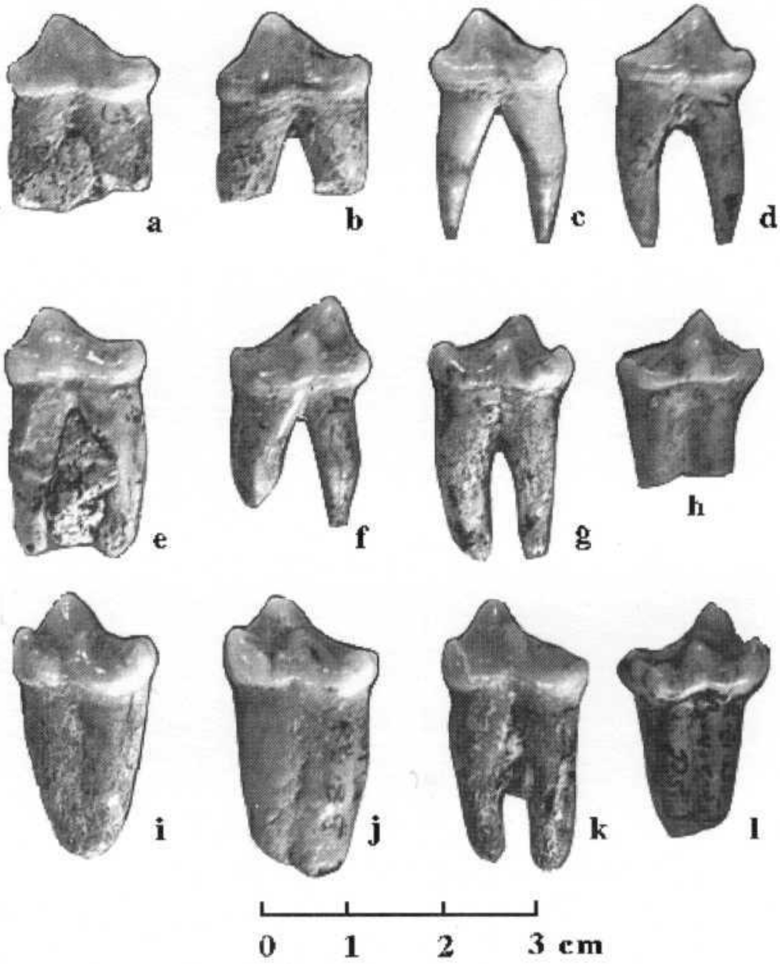

Figure 21. The fourth lower premolar, P_4, lingual view. The site and level attributions are as in Fig. 8.

Table 11. Measurements (in mm) of lower premolar P_4 in the genus *Spelearctos*.

Locality		Maximum length (1)	Maximum breadth (2)	Distance between peak of paraconid and peak of metaconid (3)
S. deningeri				
Kudaro 1,	n	11	10	4
layer 5c	min	11.1	7.9	6.2
	max	15.9	10.0	7.6
	M	14.65	8.77	6.57
	SD	1.32	0.74	0.68
Kudaro 3,	n	10	10	10
layer 5	min	13.8	8.4	2.6
	max	16.2	10.3	8.0
	M	14.87	9.20	5.22
	SD	0.72	0.59	1.71
Kudaro 3,	n	10	11	10
layers 3-4	min	12.6	8.9	3.9
	max	16.2	10.5	6.8
	M	14.62	9.59	5.63
	SD	1.11	0.52	0.95
S. spelaeus				
Odessa	n	30	30	27
	min	13.6	9.6	2.5
	max	18.2	13.0	6.3
	M	16.26	11.44	4.01
	SD	1.33	0.81	0.98

Table 12. Factor score coefficients for standardized variables in principal components analysis of specimens of lower premolar P_4.

Measurements	Factor 1	Factor 2
1	0.479	0.395
2	0.515	0.066
3	-0.236	0.946

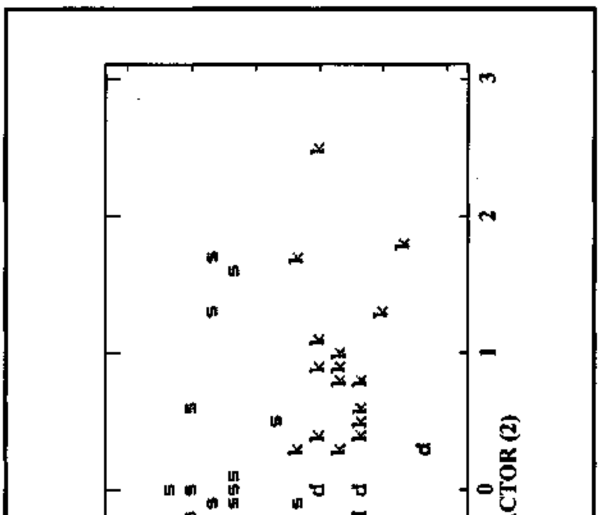

Figure 22. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of lower premolar P_4. The symbols are as in Fig. 9.

Teeth were grouped (morphotypes of group "D") based on the arrangement and size of the metaconid (Fig. 23a) and also on the presence of the "hypoconid" and "entoconid" (Fig. 23b). The paraconid is always present. The metaconid may be absent (a1), look like a weak elevation of enamel on the protoconid (a2), be present in the form of a cusp located far from (a3) or close to (a4) the paraconid; sometimes a small accessory cusp is located between them (a5). The posterior part of the tooth crown (i.e., the "talonid") sometimes lacks tubercles (b1) or only has a "hypoconid" (b2), or only an "entoconid" (b3), or both of these cusps (b4).

The characters noted above form 10 morphotypes of the group "D" (D1 - D10): D1 (a , b1- 2), D2 (a2, b1), D3 (a2, b2 - 4), D4 (a3, bl), D5 (a3, b2), D6 (a3, b3 - 4), D7 (a4, b1), D8 (a4, b2), D9 (a4, b3 - 4), D10 (a5, b1 - 2).

Teeth of simple structure lacking a metaconid are most common in the Acheulean layer of Kudaro 1. The apex of the protoconid is sharp and in this resembles premolars of *Ursus etruscus* and *U. arctos* L., 1758. The most common morphotypes are D1 - D2 (Fig. 24). In the upper Acheulean layer 5 of Kudaro 3, the structure of the P_4 crown is more complicated, and more complicated morphotypes, D3 - D4, predominate. Moreover, three teeth of the most advanced type, D10, have been found. In Mousterian layers 3 - 4 in Kudaro 3, the composition and frequency of occurrence of P_4 morphotypes vary slightly; morphotypes D4 and D6 occur more frequently. In *S. spelaeus* premolars of the D7 morphotype predominate. They were not noted in the Kudaro material. Morphtypes D8 - D10 are also present. In addition, P_4 in *S. spelaeus* from Europe often possesses transverse ridges – metalophid and hypolophid (Rabeder and Tsoukala 1990) – that do not occur on cave bear teeth from the Caucasus.

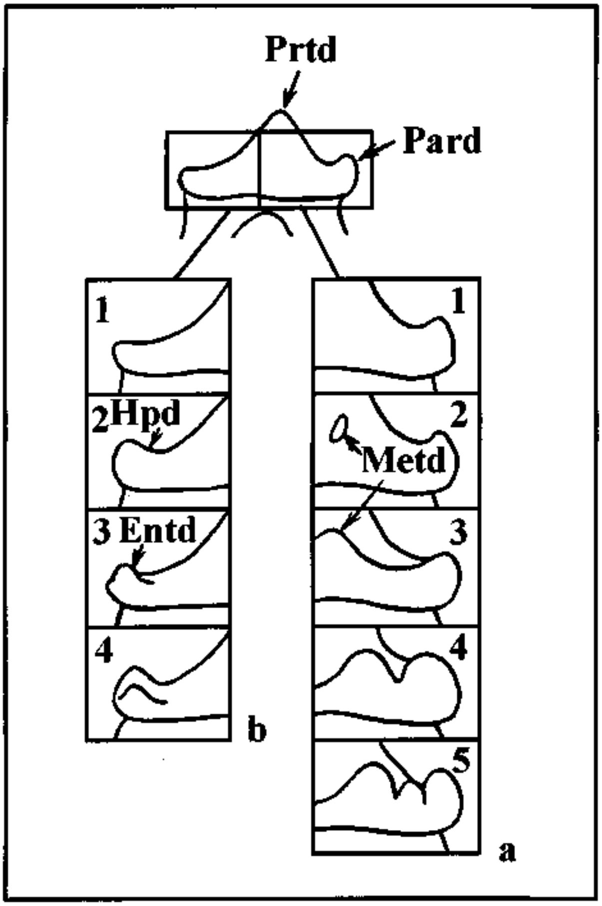

Figure 23. Schematic of fourth lower premolar, P_4, structure, lingual view. The levels of derivation in metaconid (a), hypoconid and entoconid (b) are demonstrated. Entd – entoconid, Hpd – hypoconid, Metd – metaconid, Pard – paraconid, Prtd – protoconid.

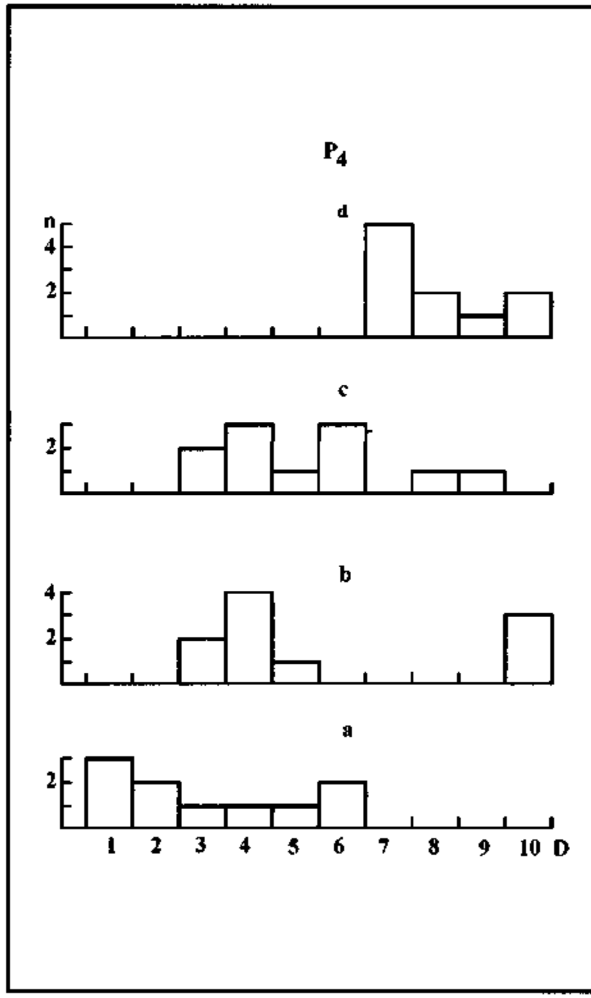

Figure 24: Encountered frequency of morphotypes of group "D". The designations are as in Fig. 11.

Temporal changes in the P_4 of cave bears are related to increases in crown size and number of cusps. Whereas in *U. arctos* this premolar looks like a tall single-cone tooth with a cutting appearance, in *S. spelaeus* it is expanded notably and the apex of the protoconid is more rounded. Paraconid and metaconid with blunt apices develop; accessory cusps on the "talonid" often occur. The structure of the crown becomes somewhat similar to that of the M_1. P_4 plays a more important role in *Spelearctos* in its occlusion with P^4, than in the case of *U. arctos*. Large wear facets on cave bear teeth are situated primarily on the posterior half of the crown. Changes in the size and structure of P_4 are related to the processing of plant food in the genus *Spelearctos*.

M_1 (Fig. 25). Seven measurements of the M_1 crown were taken (Fig. 1). Specimens from the Kudaro caves appeared to be much smaller than teeth of *S. Spelaeus* (Table 14). The area of the crown at the junction of the trigonid and talonid is approximately equal to the width of the trigonid, whereas in *S. spelaeus* this junction is relatively narrower. A principal components analysis yields three factors. The percentage of total variance explained is 72. 1 for Factor 1, 11.6 for Factor 2, and 8.8 for Factor 3. Factor score coefficients for standardized variables indicate which variables are important in separating groups of M_1 (Table 15). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 2 (Fig. 26).

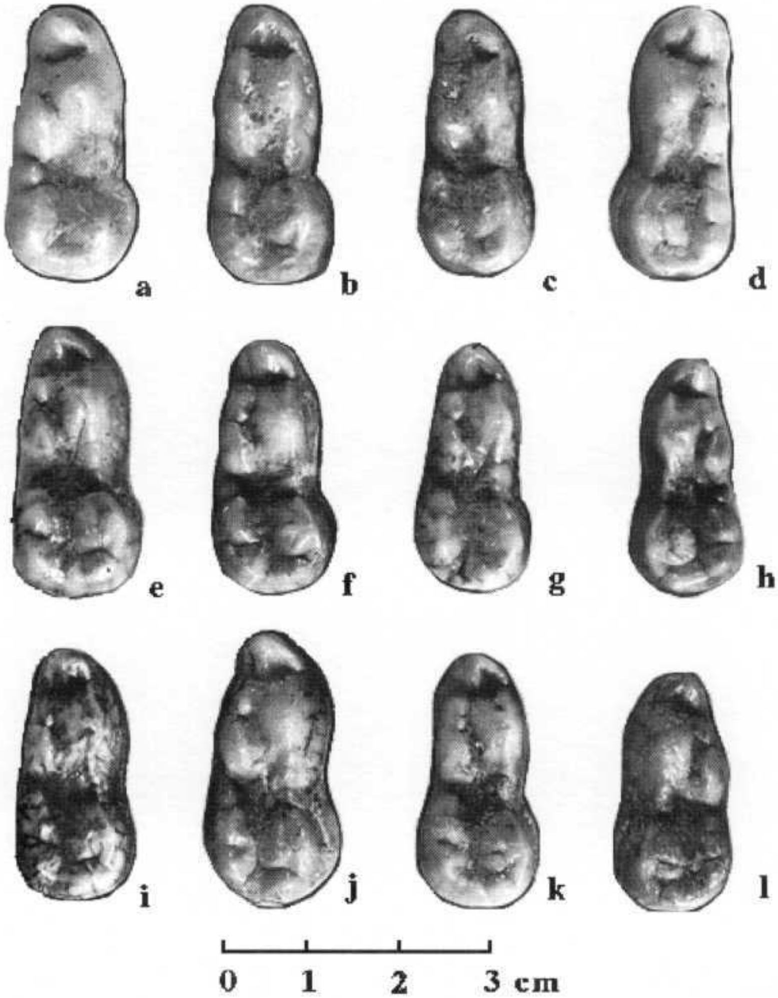

Figure 25. The first lower molar, M_1, occlusal view. The site and level attributions are as in Fig. 8.

Distinctions are apparent for Factor 1. Factor 1 includes the maximum length, the length of the trigonid, the breadth of the trigonid, the breadth of the talonid, and the minimum breadth in the middle part of the crown. The only examined M_1 of *S. deningeri* from Poland is within the range of variation of the Kudaro bear. The maximum tooth length for the Kudaro bear varies slightly within the Acheulean deposits, but decreases considerably in Mousterian layers 3 - 4 of Kudaro 3. The difference between the Acheulean and Mousterian samples is statistically significant (Table 13).

Morphotypes (group "E") were distinguished based on the degree of separation of the metaconid (Fig. 27a) and entoconid (Fig. 27b). The metaconid may be simple, with one apex (a1), but usually it is separated into two and more denticules (a2). The entoconid consists of either two widely spaced cusps if the talonid is narrow (b1), or it may be crest-shaped, having two (b2), three (b3) or four (b4) closely spaced cusps that become successively higher posteriorly, or the entoconid is formed by two separate cusps and sometimes a third anterior and smaller cusp if the talonid is wide with an inner basin (b5).

Combinations of the above characters form seven morphotypes of group "E" (E1 - E7): E1 (a1, b1), E2 (a1, b2 - 3), E3 (a2, b1), E4 (a2, b2), E5 (a2, b3), E6 (a2, b4), E7 (a2, b5).

In *Proarctos ruscinensis* Deperet, 1890 (= *Ursus boecki* Schlosser, 1899) from the early Pliocene of Europe, the M_1 metaconid looks like a single cusp

Table 13. Significance test to differentiate the means of the lower teeth in the genus *Spelearctos*.

+ = P<0.05, ++ = P<0.01

	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Lower premolar P_4			
Maximum length			
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Maximum breadth			
Kudaro 1, layer 5c	-	++	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Lower molar M_1			
Maximum length			
	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Kudaro 1, layer 5c	-	+	++
Kudaro 3, layer 5		++	++
Kudaro 3, layer 4			++
Breadth of talonid			
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Lower molar M_2			
Maximum length			
	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Kudaro 1, layer 5c	-	++	++
Kudaro 3, layer 5		+	++
Kudaro 3, layer 4			++

Table 13. Concluded. Significance test to differentiate the means of the upper teeth in the genus *Spelearctos*.

+ = $P<0.05$, ++ = $P<0.01$

Breadth of talonid			
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		++	+
Kudaro 3, layer 4			++
Lower molar M_3			
Maximum length			
	Kudaro 3, layer 5	Kudaro 3, layer 4	*S. spelaeus*, Odessa
Kudaro 1, layer 5c	-	-	+
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++
Maximum breadth			
Kudaro 1, layer 5c	-	-	++
Kudaro 3, layer 5		-	++
Kudaro 3, layer 4			++

(Ryziewicz 1969), but for *U. etruscus* from the Villafranchian of France (Viret 1954) and in recent *U. arctos*, it usually consists of 2 - 3 cusps, sometimes forming a longitudinal ridge. In layer 5c of Kudaro 1 we find single specimens of M_1 with a single-apex metaconid, but more frequently a large denticle is situated in front of the main cusp of the metaconid. In teeth from the upper layers of the Kudaro caves, the metaconid is usually split and apart from the main cusps there are 2 - 3 additional small cusps joining it.

The entoconid in *U. etruscus* and *U. arctos* has one apex (sometimes two apexes) and is situated far from the trigonid. In samples from the Lower Acheulean layer of Kudaro 1, the entoconid consists of two widely spaced cusps. In Mousterian layers of Kudaro 3, teeth with a crest-shaped entoconid predominate. The entoconid stretches up to the trigonid and has 3 - 4 apices located close to each other. *S. spelaeus* is characterized by a two-apex entoconid, somewhat resembling that of the Kudaro bear of the Acheulean period, but the talonid of the *S. spelaeus* tooth is much wider with an inner basin.

In layer 5c of Kudaro 1 morphotypes E4 - E5 predominate, and primitive variants, E1 - E3, also occur (Fig. 28). In Acheulean layer 5 and Mousterian layers 3 - 4 of Kudaro 3, morphotype E5 predominates; the proportion of archaic teeth is small. Both samples are similar in morphotypes, although morphotype E6, which is absent in the other layers, is represented in layer 5. In European *S. spelaeus* all the specimens studied belong to the more advanced morphotype, E7, which rarely occurs in the Kudaro material.

The samples compared show a successive change of predominant morphotypes that is related to complication of the relief of the masticatory surface of the tooth. However this complication in cave bears as compared to the omnivorous *U. arctos* was not significant and mainly affected the talonid area. The talonid became much wider, the hypoconid increased in size, and the structure of the entoconid became more

Table 14. Measurements (in mm) of lower molar M_1 in the genus *Spelearctos*.

Locality		Maximum length (1)	Length of trigonid (2)	Length of entoconid 1 (3)	Length of entoconid 2 (4)	Breadth of trigonid (5)	Breadth of talonid (6)	Breadth in the middle part (7)
S. deningeri								
Kudaro 1,	n	21	21	20	20	22	27	26
layer 5c	min	25.5	15.7	2.8	3.0	9.2	12.1	9.4
	max	31.0	20.0	6.7	6.6	12.2	15.5	12.5
	M	28.13	17.76	4.28	4.75	11.14	13.72	11.01
	SD	1.77	1.37	1.05	0.87	0.81	1.02	0.87
Kudaro 3,	n	15	15	15	15	15	15	14
layer 5	min	25.7	15.7	2.3	4.0	9.3	12.1	9.1
	max	31.0	19.7	5.2	6.1	12.7	15.4	12.4
	M	28.29	17.62	3.55	4.93	11.13	13.77	11.16
	SD	1.40	1.12	0.74	0.67	0.91	0.93	0.87
Kudaro 3,	n	22	22	16	16	23	23	23
layers 3-4	min	24.7	15.0	2.6	2.5	9.0	12.5	9.9
	max	29.7	18.9	6.9	5.9	11.7	14.8	12.4
	M	27.08	16.99	4.23	4.56	10.94	13.74	11.09
	SD	1.30	0.90	1.26	1.03	0.63	0.62	0.62
S. spelaeus								
Odessa	n	20	20	20	20	20	20	20
	min	29.1	18.5	4.2	4.5	11.0	14.1	10.9
	max	34.1	22.2	6.9	6.8	14.2	17.2	13.2
	M	31.76	19.98	5.35	5.58	12.82	15.54	12.10
	SD	1.40	1.16	0.72	0.56	0.86	0.76	0.64

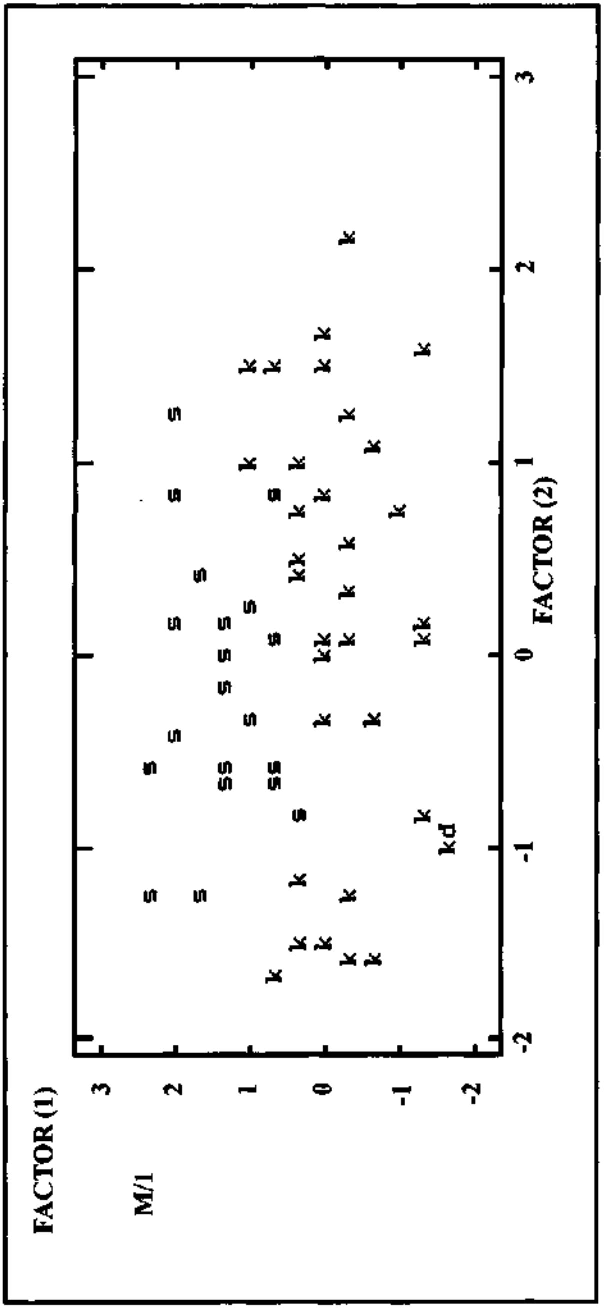

Figure 26. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of lower molar M_1. The symbols are as in Fig. 9.

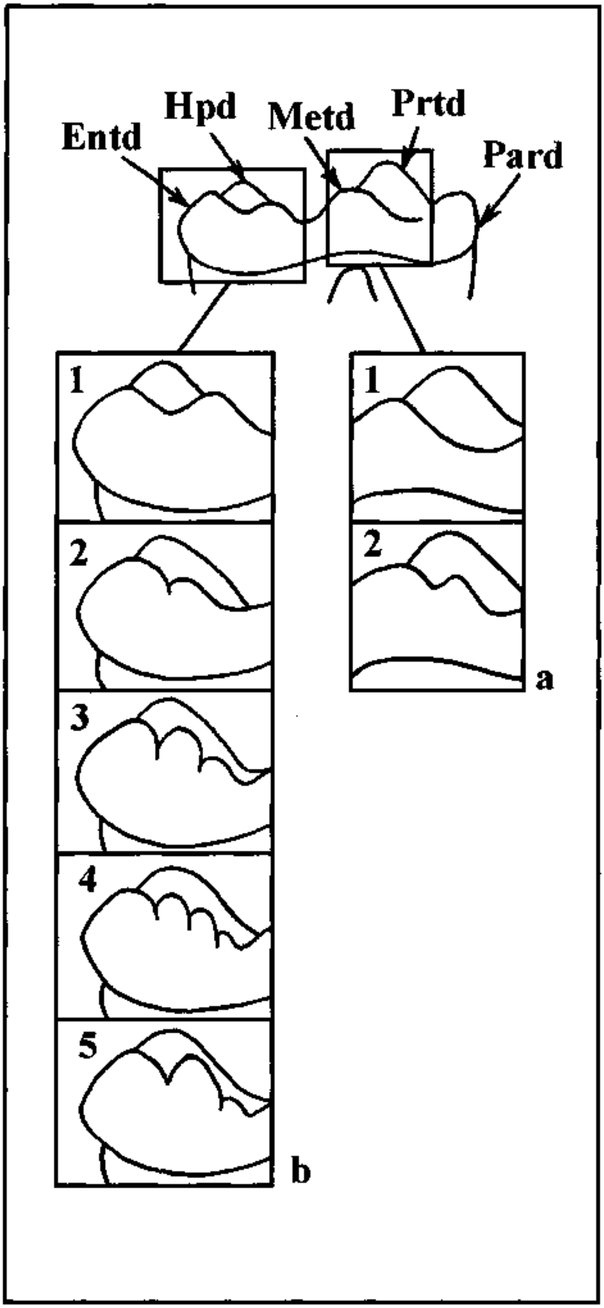

Figure 27. Schematic of first lower molar, M_1, structure, lingual view. The levels of derivation in metaconid (a) and entoconid (b) are demonstrated. The names of cusps are as in Fig. 23.

Table 15. Factor score coefficients for standardized variables in principal components analysis of specimens of lower molar M_1.

Measurements	Factor 1	Factor 2	Factor 3
1	0.188	0.169	-0.014
2	0.182	0.175	0.108
3	0.104	-0.962	0.532
4	0.127	-0.393	-1.127
5	0.188	0.195	0.081
6	0.187	0.057	0.183
7	0.180	0.217	0.118

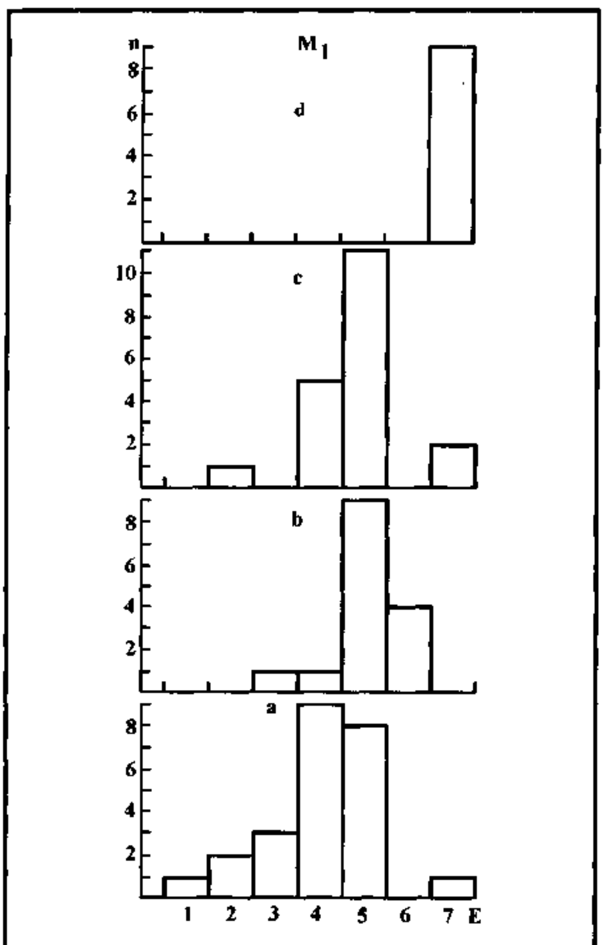

Figure 28. Encountered frequency of morphotypes of group "E". The designations are as in Fig. 11.

complicated. The rate of change in the structure of the crown of M_1 was evidently slow.

M_2 (Fig. 29). Seven measurements of this tooth were made (Fig. 1). Molars from the Kudaro collection are notably smaller in length and width than specimens of *S. spelaeus* (Table 16). Differences between samples from Acheulean and Mousterian levels are also observed. Teeth of Mousterian age are significantly shorter. Samples from Acheulean layer 5 in Kudaro 3 are characterized by a relatively wide talonid. A principal components analysis yields three factors. The percentage of total variance explained is 63.7 for Factor 1, 13.2 for Factor 2, and 10.6 for Factor 3. Factor score coefficients for standardized variables indicate which variables are important in separating groups of M_2 (Table 17). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 2 (Fig. 30). Differences are apparent for Factor 1 that primarily includes maximum length, length of the anterior labial part, and breadth of the anterior part. Strong variation is observed also for two specimens of *S. deningeri* from Kozi-Grzbiet.

For distinguishing morphotypes (group "F"), I used the structure of the entoconid (Fig. 31a) and metaconid (Fig. 31b) complexes of the crown. The entoconid consists of two widely spaced cusps (a1) or there is a third, usually smaller, cusp situated anteriorly (a2), or the small entoconid cuspule is situated in the space between the large, widely spaced cusps (a3), or the entoconid complex is formed by two (a4), or three

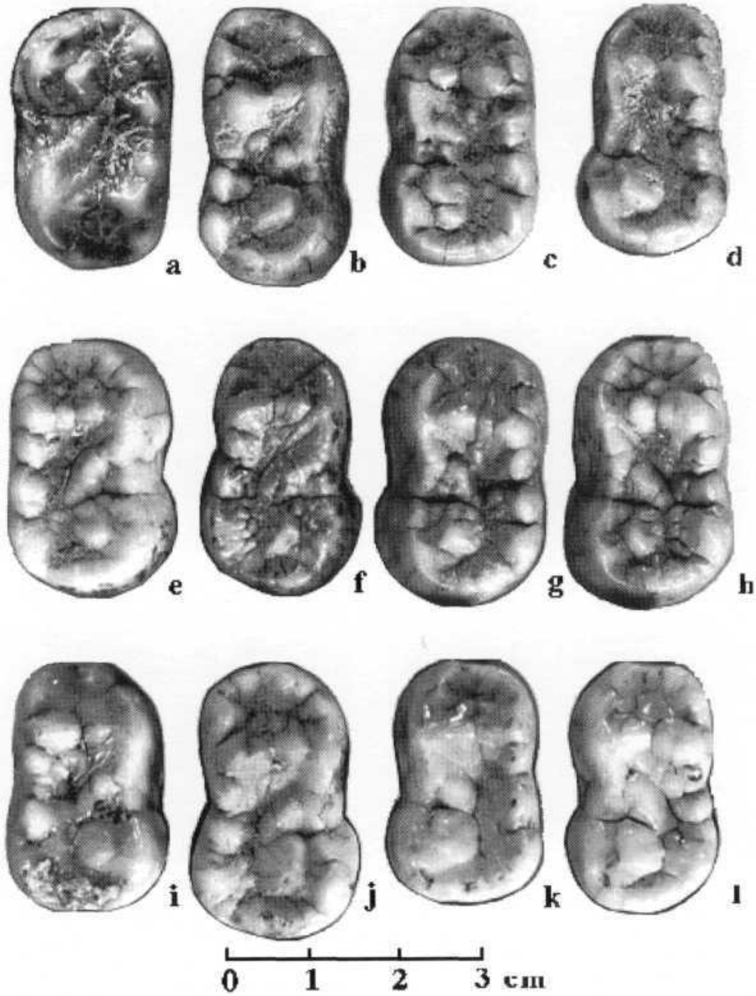

Figure 29. The second lower molar, M_2, occlusal view. The site and level attributions are as in Fig. 8.

(a5) cusps situated close to each other. The metaconid may look like a large denticle weakly divided into two apices (b1), may have the shape of a trident with a tall middle and low anterior apices (b2), or a trident with lateral apices that are of equal height (b3), or lateral denticules are displaced lingually and their bases reach beyond the external wall of the middle denticle (b4), sometimes forming an accessory external cusp (b5).

I distinguish 12 morphotypes of the group "F" (F1 - F12): F1 (a1, b1), F2 (a1, b2), F3 (a1, b3 - 5), F4 (a2, b1), F5 (a2, b2 - 3), F6 (a2, b4 - 5), F7 (a3, b1), F8 (a3, b2 - 3), F9 (a4, b1), F10 (a4, b2 - 3), F11 (a5, b1), F12 (a5, b3 - 4).

Morphotype F3 is regarded as archaic. It occurs more frequently than others in the collections from Acheulean deposits, but is lacking completely in the studied material for *S. spelaeus* (Fig. 32). Samples from layer 5c in Kudaro 1 and from layer 5 in Kudaro 3 are similar in morphotypes. Collections from the Mousterian complex of Kudaro 3 contain a larger proportion of advanced morphotypes, F8 - F11. For *S. spelaeus* nearly all types of teeth are represented, but F10 occurs most commonly among them. Morphotype F12 is also present in *S. spelaeus,* but does not occur in the Kudaro bear.

Table 16. Measurements (mm) of the lower molar M_2 in the genus *Spelearctos*.

Locality		Maximum length (1)	Length of frontal labial part (2)	Length of frontal lingual part (3)	Length of caudal labial part (4)	Length of caudal lingual part (5)	Breadth of trigonid (6)	Breadth of talonid (7)
S. deningeri								
Kudaro 1,	n	18	18	18	18	17	18	17
layer 5c	min	27.4	16.0	13.7	9.9	11.4	15.5	16.1
	max	31.3	19.8	17.4	11.7	14.2	19.3	19.5
	M	29.37	17.82	15.65	10.84	12.98	17.00	17.96
	SD	1.26	0.98	0.96	0.63	0.85	0.96	1.03
Kudaro 3,	n	12	11	11	11	11	12	12
layer 5	min	26.1	15.5	13.5	10.1	10.4	15.3	16.7
	max	30.9	18.4	16.0	12.6	15.0	19.8	20.7
	M	29.08	17.49	14.55	11.04	12.97	17.14	18.87
	SD	1.28	0.84	0.75	0.76	1.25	1.23	0.97
Kudaro 3,	n	30	24	25	24	24	30	30
layers 3-4	min	25.3	15.5	12.1	9.4	10.5	14.7	15.7
	max	30.9	18.8	16.6	12.2	14.5	18.2	19.3
	M	27.97	17.12	14.53	10.87	12.23	16.85	18.02
	SD	1.42	0.91	1.07	0.78	0.89	0.85	0.87
S. spelaeus								
Odessa	n	20	20	20	20	20	20	20
	min	29.4	16.4	14.5	10.9	11.1	16.4	18.0
	max	35.7	21.5	18.4	13.9	16.7	20.8	21.6
	M	32.10	18.86	16.23	12.31	13.34	18.63	19.74
	SD	1.69	1.50	1.12	0.79	1.44	1.16	1.04

Table 17. Factor score coefficients for standardized variables in principal components analysis of specimens of lower molar M_2.

Measurements	Factor 1	Factor 2	Factor 3
1	0.213	0.115	-0.098
2	0.186	0.087	-0.447
3	0.172	0.055	-0.712
4	0.178	-0.445	0.056
5	0.133	-0.769	0.304
6	0.186	0.394	0.345
7	0.175	0.332	0.640

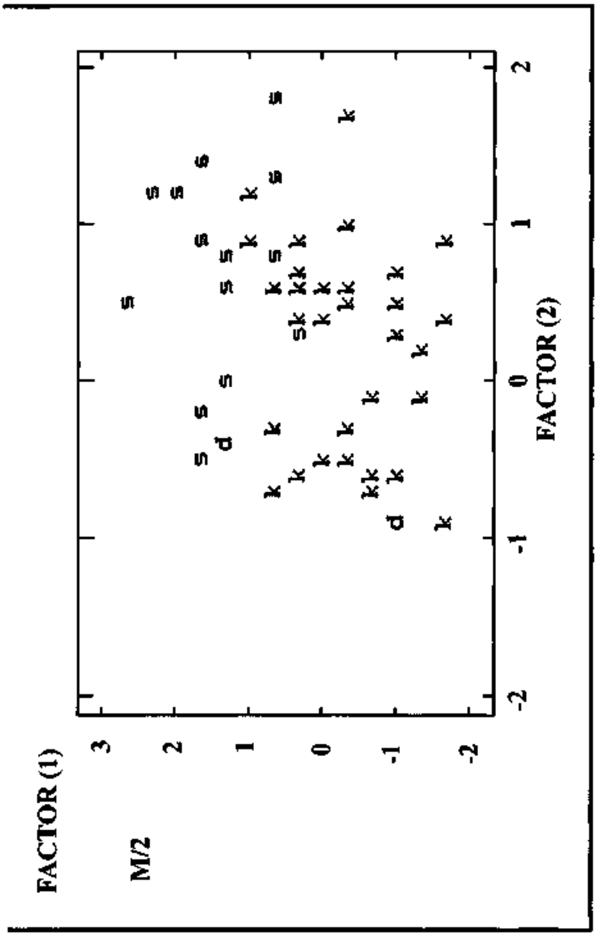

Figure 30. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of lower molar M_2. The symbols are as in Fig. 9.

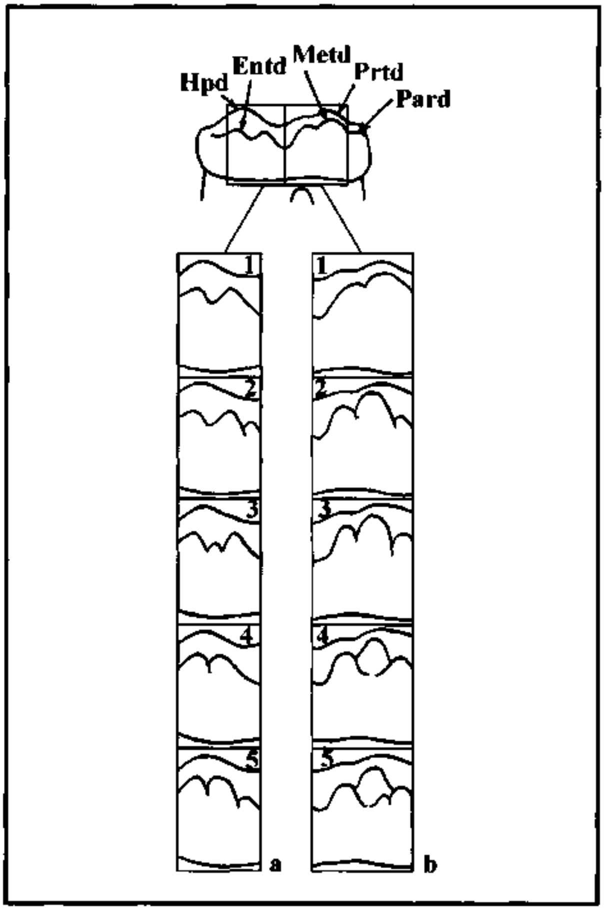

Figure 31. Schematic of second lower molar, M_2, structure, lingual view. The levels of derivation in entoconid (a) and metaconid (b) are demonstrated. The names of cusps are as in Fig. 23.

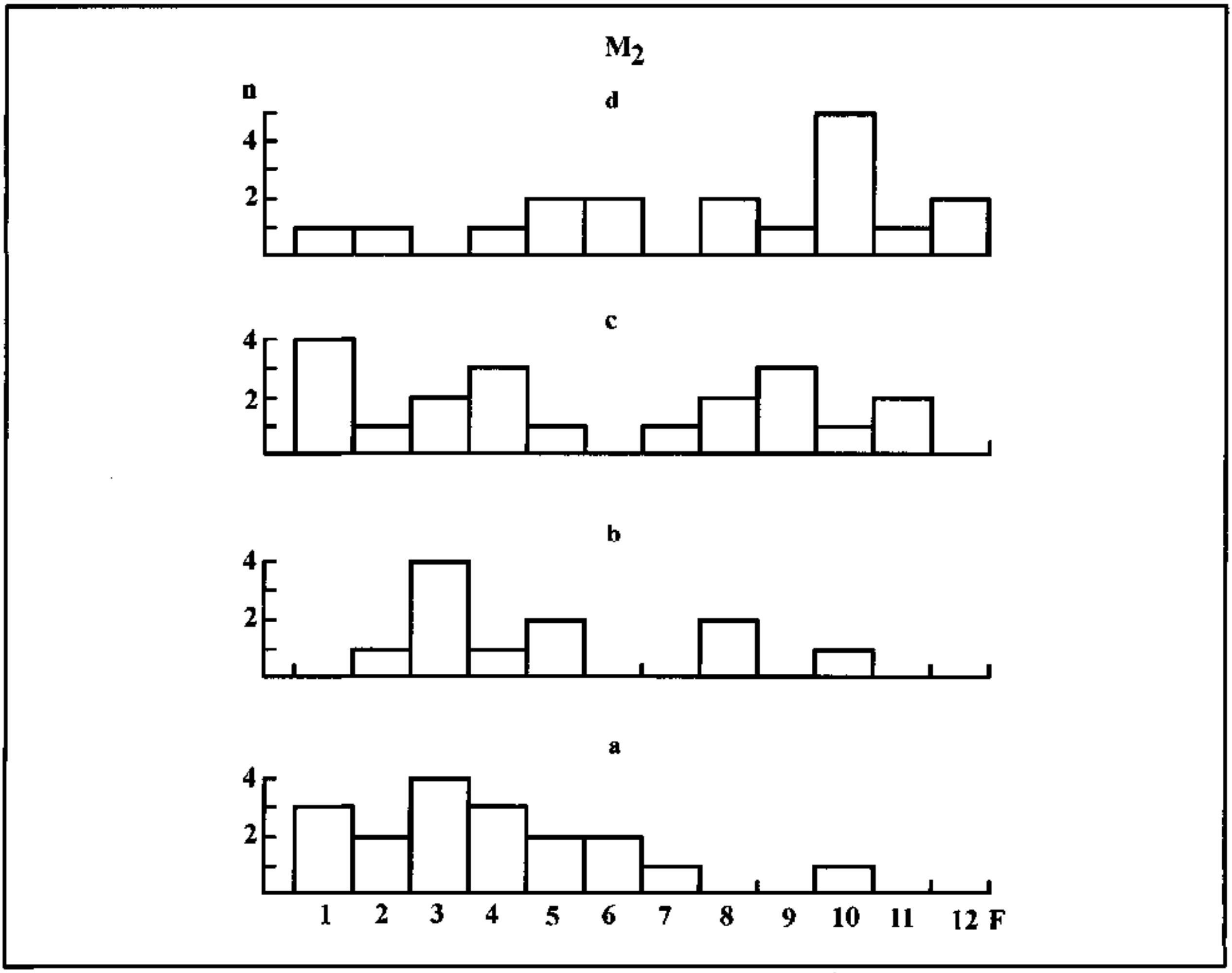

Figure 32. Encountered frequency of morphotypes of group "F". The designations are as in Fig. 11.

In M_2, as well as in other molars, one can trace the direction of changes in the masticatory surface through time. Change manifests itself as an increase in the proportion of complex morphotypes in successively more recent temporal sections. However this tendency is less evident for M_2 than for other molars. In correspondence with the general evolutionary changes of dentition in cave bears, the crown of M_2 increases in width. The metaconid and talonid become relatively wider. The area of the internal fields of the crown increases, and the crown acquires new structural elements. In this morphological transformation M_2 somewhat resembles M^1. This resemblance can be explained by their similar position in the middle of the dental row.

M_3 (Fig. 33). Four measurements were taken (Fig. 1). For maximum length and width, specimens of the Kudaro bear are on the average smaller than those of *S. spelaeus* (Table 18). Significant differences between separate samples from the layers in the Kudaro caves have not been revealed. A principal components analysis yields three factors. The percentage of total variance explained is 84.7 for Factor 1, 8.5 for Factor 2, and 4.6 for Factor 3. Factor score coefficients for standardized variables indicate which variables are important in separating groups of M_3 (Table 19). The separation between specimens from the Kudaro caves and Odessa is shown by a plot of the factor scores for Factor 1 and Factor 3 (Fig. 34). Factor analysis does not yield a distinct separation of metric values for M_3 in the

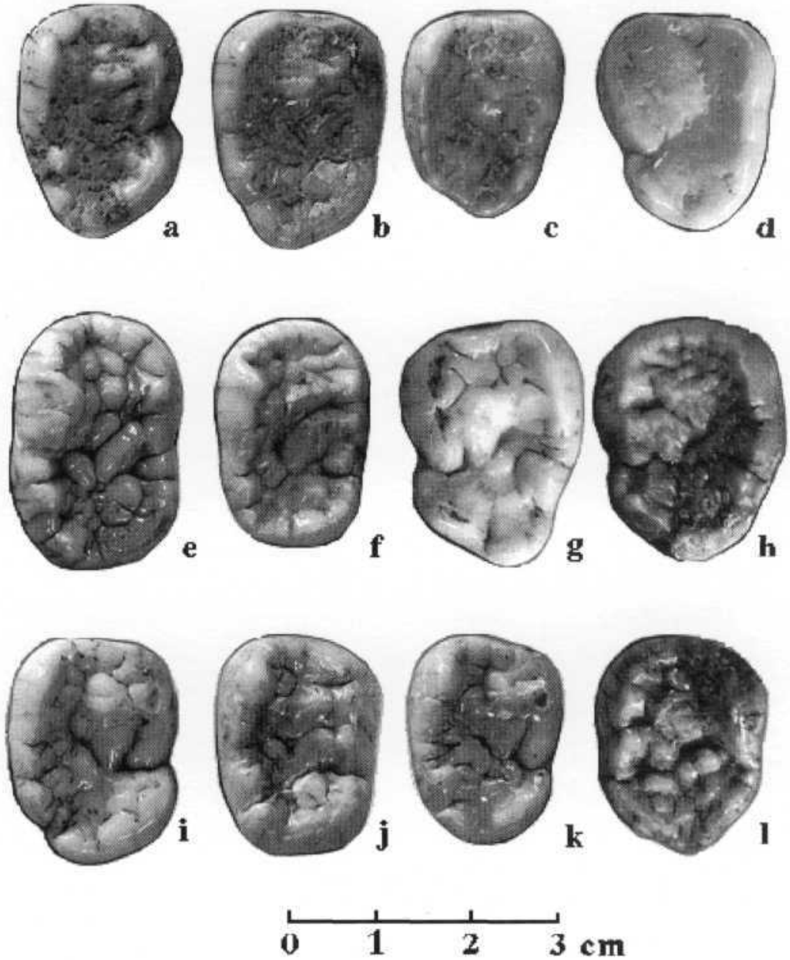

Figure 33. The third lower molar, M_3, occlusal view. The site and level attributions are as in Fig. 8.

Caucasian and European bear. Some distinctions are apparent for Factor 1, which includes all measurements.

The formation of the crown in M_3 is completed later than in other molars. Therefore fossil specimens represented by the crown without roots often occur. Such teeth belong to young individuals, in which M_3 has not erupted. Accordingly, crowns of teeth that were not formed completely were fossilized; as a result we observe notable morphometric variation in the entire M_3 sample.

Morphotypes (group "G") were distinguished based on the structure of the entoconid complex (Fig. 35). It varies from a sloping wavy crest weakly demarcated from the metaconid (a1), to a single cuspule remote from the metaconid (a2), perhaps with a weak frontal (a3), or well-modeled accessory denticle (a4). Each of the considered characters constitutes a morphotype of group "G": G1 (a1), G2 (a2), G3 (a3), G4 (a4).

The masticatory surface of young molars often has a large number of small cusps and folds that are not as well expressed on the teeth of adult bears. These small cusps and folds were not considered in the separation of morphotypes.

Due to the simple structure of the crown and the complexity of distinguishing between morphotypes of M_3, the samples compared do not show distinct differences. Morphotype G2 predominates in all layers of the Kudaro caves (Fig. 36). *S. spelaeus* is characterized by a larger tooth and greater degree of

Table 18. Measurements (in mm) of lower molar M_3 in the genus *Spelearctos*.

Locality		Maximum length (1)	Length of talonid (2)	Maximum breadth (3)	Breadth of talonid (4)
S. deningeri					
Kudaro 1,	n	16	17	18	18
layer 5c	min	20.7	8.2	15.7	14.6
	max	28.2	13.9	20.4	20.4
	M	25.10	10.85	18.48	17.37
	SD	2.23	1.50	1.27	1.55
Kudaro 3,	n	15	15	15	15
layer 5	min	20.0	8.4	16.5	14.4
	max	28.2	12.6	20.6	19.8
	M	24.49	10.35	18.43	16.80
	SD	2.32	1.10	1.37	1.84
Kudaro 3,	n	24	24	24	22
layers 3-4	min	20.7	8.3	16.5	13.2
	max	28.1	13.3	21.1	19.3
	M	24.85	10.74	18.68	17.20
	SD	2.09	1.32	1.14	1.54
S. spelaeus					
Odessa	n	20	20	20	20
	min	21.0	10.2	17.5	16.8
	max	31.4	16.7	22.4	21.3
	M	27.24	12.83	19.95	18.96
	SD	2.80	1.60	1.35	1.44

Table 19. Factor score coefficients for standardized variables in principal components analysis of specimens of lower molar M_3.

Measurements	Factor 1	Factor 2	Factor 3
1	0.277	-0.199	1.699
2	0.260	-1.330	-0.611
3	0.274	0.929	0.313
4	0.276	0.532	-1.441

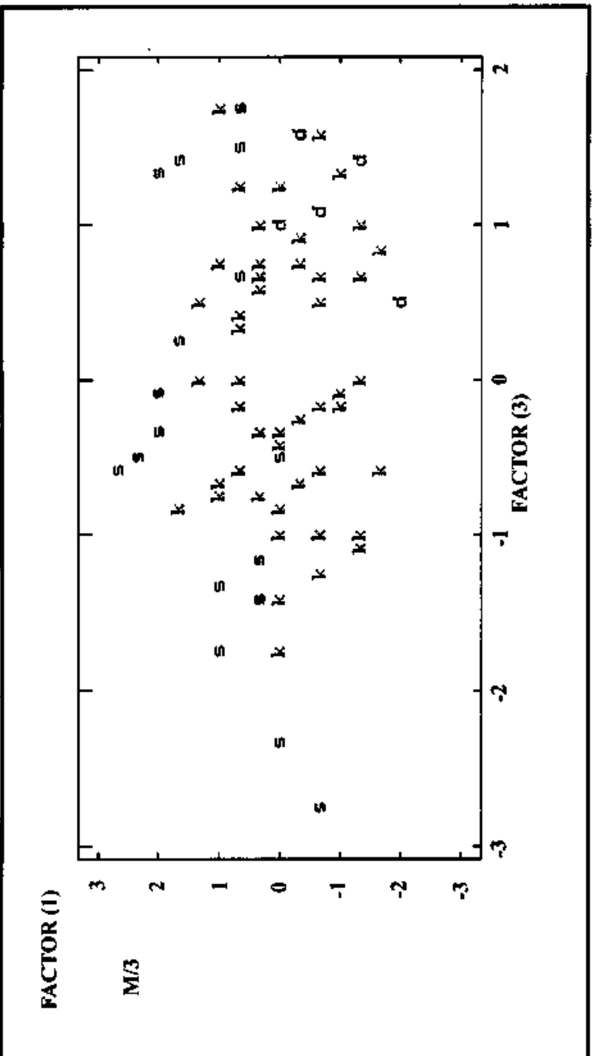

Figure 34. Plot of factor scores of Factor 1 and Factor 3 from principal components analysis of lower molar M_3. The symbols are as in Fig. 9.

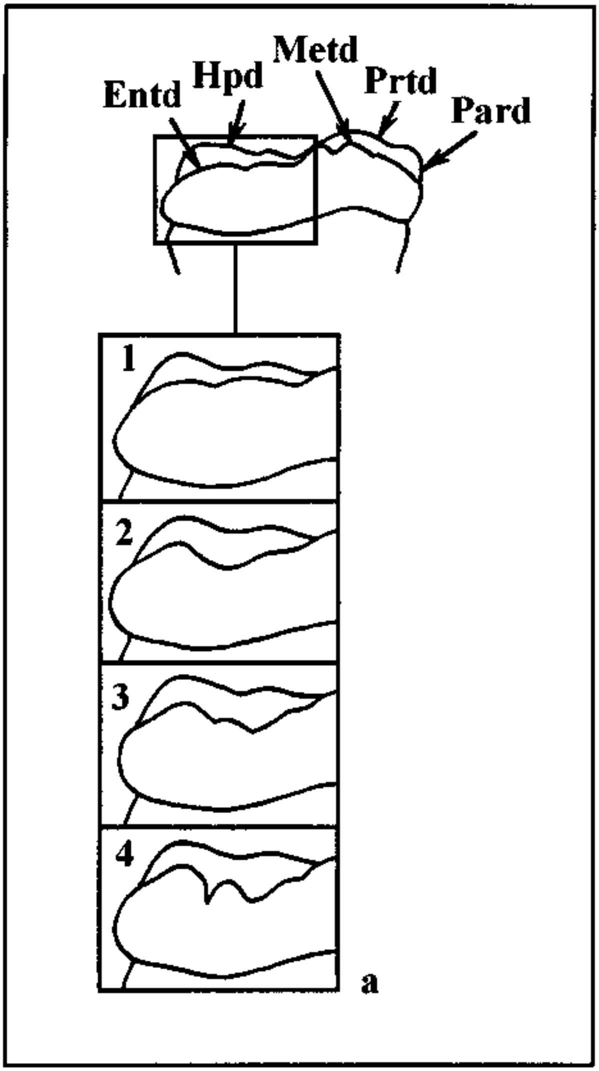

Figure 35. Schematic of third lower molar, M_3, structure, lingual view. The levels of derivation in entoconid (a) are demonstrated. The names of cusps are as in Fig. 23.

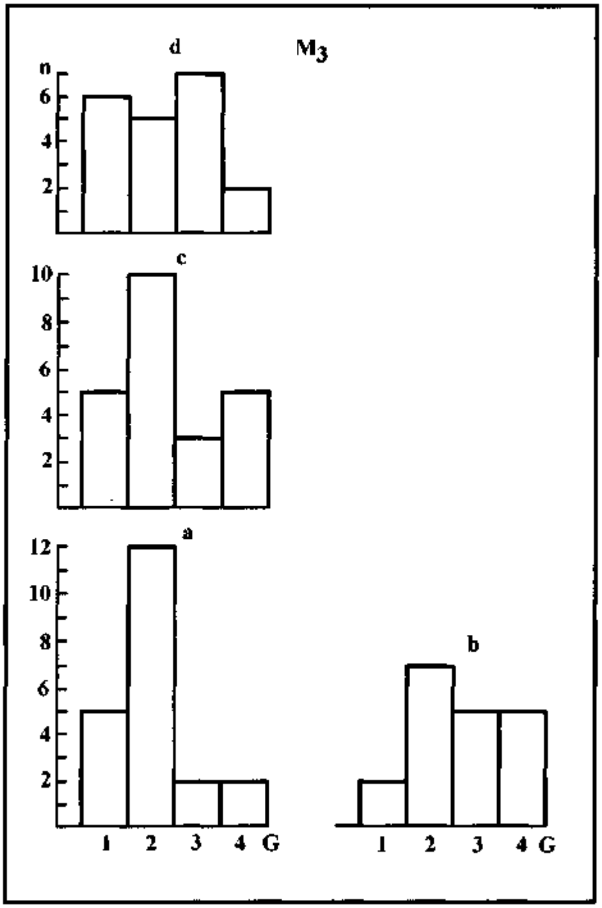

Figure 36. Encountered frequency of morphotypes of group "G". The designations are as in Fig. 11.

differentiation of the trigonid and the talonid. Morphotypes G1 and, particularly, G3 occur somewhat more frequently.

In the evolution of bears of the subfamily Ursinae, I observed an increase in the size of M_3 (Baryshnikov 1992). Small M_3s are characteristic of the Pliocene genus *Proarctos* and of the recent archaic genera and subgenera *Helarctos*, *Melursus*, and *Selenarctos*. This tooth was already large at the evolutionary level of *Ursus etruscus*. A rapid increase in the size of the masticatory surface of M_3 in *Spelearctos* is accompanied by the separation of the talonid. Growth of M_3 corresponded with the elongation of the talon of the M^2, which it contacts during occlusion. The working surface of the tooth is situated horizontally (in early forms it is somewhat bent forward), its relief becomes more complicated, and M_3 in cave bears begins to play a still greater functional role in connection with their specialization in the consumption of plant food.

DISCUSSION

The Evolution of Dentition

The size of molars of bears from the Kudaro caves varies slightly. In only few molars do we observe significant variations of separate parameters from layer to layer, e.g., in M_2. The Kudaro sample as a whole includes much smaller molars than those found in European localities of *S. spelaeus*.

A study of morphotypical variation of different molars of the Kudaro bears shows that nearly all of the molars are characterized by a directed change in the proportion of morphotypes from earliest to more recent levels. This tendency manifests itself in successive change of predominant morphotypes. It is particularly evident for P^4 and M^1 and for P_4.

Simple morphotypes predominate in Acheulean deposits of the Kudaro caves; they are more rare in Mousterian deposits. Similar simple morphotypes of *S. spelaeus* are still more rare or are lacking. On the contrary, complex tooth types seldom occur in ancient levels and acquire still greater "specific weight" as they approach the more recent epoch, that demonstrates the change in the frequency of occurrence of archaic and advanced morphotypes of the Kudaro bears through time. Such a shift in morphotypes has been described many times for Pleistocene rodents, e.g., for the genus *Lagurus* (Maleeva 1976).

Cave bears from the lower Acheulean layer of Kudaro 1 had archaic teeth resembling those of European *S. deningeri*. In later temporal levels molars typical of *S. spelaeus* in the structure and proportions of crowns occur more frequently. The observed trend in the dentition of the Caucasian bear is analogous to the trend observed in cave bears in Europe during the Pleistocene. These changes represent parallel evolution. Changes in molars from the Kudaro layers suggest the phylogenetic unity of populations that existed in different periods. This unity allows us to assume separate evolution of cave bears in the Caucasus in isolation from European populations of *Spelearctos*. Sets of morphotypes from Acheulean and Mousterian layers in both Kudaro 1 and Kudaro 3 are closer to each other than to the set of morphotypes for *S. spelaeus*. Cave bears of the Caucasus never attained the level of morphological specialization of dentition that was characteristic of *S. spelaeus* from the Late Pleistocene of the European continent.

The main evolutionary transformations of the skull and teeth in the genus *Spelearctos* are related to the change from omnivorous feeding to herbivory. Development of dentition proceeded towards complication of the masticatory surfaces of cheek teeth. The large skull and thick sagittal crest and zygomatic arches suggest an increase in the mass of the masticatory musculature, providing for the increased load needed for crushing and grinding plant food. The evolution of the masticatory apparatus of cave bears occurred evidently in a relatively short period. Therefore, it did not affect the microstructure of enamel of cheek teeth, which does not differ in *S. spelaeus* from that of typical predators (Koenigswald 1992).

Morphological changes in the upper molars of cave bears were more significant than changes in the lower molars. Ficarelli (1981) assumes that the process of transition from *Ursus etruscus* to advanced forms of cave bears involved upper molars alone. Transformation of the upper dental row occurred apparently in the direction from the last molar to the first one. Thus in the Kudaro material morphotypical differences in samples of M^2 from different layers are less marked than in other molars. Active transformation of M^2 structure in all probability occurred at an earlier stage of the evolution of bears than the one that is represented by the Kudaro material.

For mandibular teeth the sequence of structural changes of their crowns was analogous to that of the upper cheek teeth, i.e., proceeded from M_3 to P_4, but rates of transformation of teeth were considerably slower on all cheek teeth, except for P_4.

The development of accessory cusps, crests, and other small formations on mammal molars, used for separating morphotypes, marks a developmental threshold (Wolsan 1988). It is related to the circumstance that additional structures appear when the crown of the tooth attains a certain length. We can observe a cumulative effect, i.e., the greater the length of the crown beyond the threshold, the more the accessory formations on it are developed (Baryshnikov and Averianov 1992). In the Kudaro material this pattern is observed only in the upper molars (M^1 and M^2). In M^1, tooth length increases notably as the structure of the crown becomes more complicated: B1 (M = 25.3 mm; n = 4), B4 (M = 26.7 mm; n = 16), B5 (M = 27.9 mm; n = 7), B6 (M = 28.9 mm; n = 4). Statistically significant differences are observed between average values of tooth length for morphotypes B1 and B4 (t = 4 .23), B4 and B6 (t = 2.69). On M^2, the increase in crown length for different morphotypes is smoother: C1 (M = 41.5 mm, n = 5), C2 (M = 42.3 mm, n = 14), C3 (M = 43.0 mm, n = 8), C4 (M = 43.5 mm, n = 4), C6 (M = 45.6 mm, n = 7). There are significant differences only in the length of extreme variants of morphotypes Cl and C6 (t = 2.48).

In the upper and lower dental rows of cave bears from Kudaro we observe the complication of structure of fourth premolars. The crowns begin to acquire more complex structure typical of molars. "Molarization" of the upper and lower fourth premolars occurred as a result of processing of plant food. Spreading of the masticatory function of the molars to the premolars promoted increased dental efficiency. "Molarization" of premolars is characteristic of nearly all phytophagous mammals, e.g., horses and kangaroos. "Molarization" is observed in other bears that have changed to plant food diets. For instance, in *Ailuropoda melanoleuca*, not only crowns of fourth premolars, but also those of the second and third premolars acquired complex molar-like structure. In bamboo bears the molarization process occurred at the earlier stage of the evolution of the Ursidae, before anterior premolars were lost. The anterior premolars of the ancestors of cave bears were strongly reduced in size and later disappeared completely.

Cave bears occupied different landscapes. In the Caucasus they inhabited forest and mountain meadow biotopes with abundant herbaceous food, nuts, and berries. On the European plains, in the Alps, and in the Urals natural conditions were less favorable; periglacial steppe, forest-steppe, or tundra-steppe landscapes were predominant. Bears inhabiting these regions were feeding on tougher plant foods, mainly cereals. This led to the complication of the masticatory surface of molars in *S. spelaeus*. Also, small *S. rossicus* occurred in more arid steppe biotopes of Eastern Europe. Its molars are characterized by a large number of accessory cusps. The skull of a young animal of this species found on the right bank of the Volga River (Baryshnikov, Shkatova, and Shadrukhin 1992), had marked wear facets on its teeth, whereas in skulls of *U. arctos* of the same individual age molars are not worn. Because S. *rossicus* ate tough steppe grasses, the wear was more rapid.

Geographic Variation

Based on skull sizes, I distinguish some geographic groups of cave bears from the Late Pleistocene in Eastern Europe and the Caucasus.

The smallest cave bear was *S. rossicus* (condylobasal length in the male is less than 390 mm), which inhabited steppe biotopes. In faunas of Western Europe that have more forest character, *S. rossicus* is not yet found. The nominative subspecies occurred in the Last Interglacial in Ukraine, Northern Caucasus, and the Volga River region. In the Middle Urals *S. rossicus uralensis* (Vereshchagin, 1973) lived until the late Würm. It is distinct by possessing archaic features in the structure of the dentition (Baryshnikov et al. 1992). From *S. spelaeus* this steppe species differs not only by its small size, but also by morphology of cheek teeth (as an example, the entoconid of M_1 has a similar structure in *S. deningeri*), different ratio of hind and forelimb lengths, and also by the form of the os penis (Borissiak 1932; Vereshchagin 1973).

Large forms of cave bears constituted three allopatric local groups. Large *S. deningeri kudarensis* (condylobasal length in males 420 - 451 mm) inhabited the Caucasus, where it could find the most favorable conditions in the mountain forests of Kolchida.

S. spelaeus spelaeus, with males reaching the largest cave bear sizes (condylobasal length in males 430 - 475 mm) was distributed in forest-steppe, tundra-steppe, and forest landscapes of Central and Eastern Europe. The other large subspecies *S. spelaeus kanivetz* (Vereshchagin, 1973)(condylobasal length in males 440 - 495 mm, n = 5) occurred in the Northern and Middle Urals. Possibly we should place bears of the mountain area of the Crimea in a separate subspecies, *S. spelaeus crimaeus* (Bachisky, 1962) as suggested by me earlier (Baryshnikov 1987). Condylobasal length of its skull is unknown.

Changes in morphological and morphometric features of cave bears in space during the Middle Pleistocene are difficult to trace because few complete skulls have been found. Cave bears from the Middle Acheulean of Kudaro 1 seem to be somewhat smaller than the nominative subspecies *S. deningeri deningeri* from Germany and have somewhat different proportions of the skull as compared to *S. deningeri romeviensis* from France (Prat and Thibault 1976). Morphotypical differences in the structure of molars between these forms have not been clarified.

Taxonomy of Cave Bears of the Caucasus

This study shows the distinctiveness of the cave bear from the Paleolithic of the Caucasus. In sizes and proportions of the skull and size and structure of the molars, it differs notably from *S. spelaeus* from the European Late Pleistocene. It possesses some features typical of the Middle Pleistocene *S. deningeri* to which it should be referred.

Comparative analysis of molars from different layers of the Kudaro caves shows their genetic continuity and stratigraphic differences, related to the change of dental features of Caucasian populations of the genus *Spelearctos*. The degree of morphometric and morphotypical variability suggests presence of two chronological forms of the Kudaro bear, one succeeding the other, and each having subspecies taxonomic rank. The more ancient subspecies includes materials from the Middle Acheulean layer 5c in Kudaro 1. This form is characterized by predominance of the simple archaic morphotype on the upper and lower molars. Its teeth have a more carnivorous appearance and P^4 and M_1 have structures more suited to cutting. Cave bears of the Acheulean complex from Kudaro 1 may be placed in a new subspecies, *S. deningeri praekudarensis* Baryshnikov subsp. nov.

Bears from the fauna of Mousterian layers 3 - 4 in Kudaro 3 belong to the subspecies *S. deningeri kudarensis* Baryshnikov, 1985. It is characterized by the predominance of more complicated molar morphotypes and an increase in the width of the crowns, on which accessory structures occur much more frequently.

Bears from Acheulean layer 5 of Kudaro 3 are characterized by a set of intermediate characters, but more closely resemble *S. deningeri praekudarensis*. The chronostratigraphic positions for subspecific forms of cave bears in the Kudaro caves are shown in Figure 37.

Taxonomic notations for cave bears from the Paleolithic of the Caucasus are as follows:

Genus *Spelearctos* E. Geoffroy, 1833

1828. *Spelaeus* Brookes, *Cat. Anat. Zool. Mus.*:31. Nom. nudum.

1833. *Spelearctos* E. Geoffroy, *Rev. Ency.*, 59:81 [Species is not mentioned.–GFB]

1835. *Spelearctus* E. Geoffroy, *Etud. Natural.*: 92. *Ursus speleus* Cuvier = *U. spelaeus* Rosenmüller.

1842. *Spelaearctus* Gloger, *Hand. Naturg.*, (1841), 1: xxviii, 54. Pro *Spelearctos* Geoffroy, 1833.

1926. *Spelaearctos* Soergel, *Neues Jahrb. Mineral. Geol. Paläontol.*, 54 (Abt. B):117. Pro *Spelearctos* Geoffroy, 1833.

Type of the genus: *Ursus spelaeus* Rosenmüller, 1794 (cave near Gaylenreuth, Germany).

Years Before Present	Oxygen-Isotope Stage	Kudaro 1	Kudaro 3	Subspecies of cave bear
10,000	1			
	2		Layer 2	
25,000				?
				↑
45,000	3	↑* 44,150+/-2,400	↑	
		Layer 3	Layer 3	*Spelearctos deningeri kudarensis*
60,000		↓	↓	
	4			
73,000		?	?	
		↑	↑	
90,000	5a-5d	Layer 4	Layers 4a-4e	
116,000		↓	↓	
	5e		Layer 4f	
128,000			↓	↓
	6		?	Transitional form between *S. deningeri praekudarensis* and *S. d. kudarensis*
195,000				
	7			
251,000			↑* 245,000+/-49,000 252,000+/-51,000	
	8	↑		
297,000		Layer 5a	Layer 5	
	9	↑	?	↑
347,000		* 350,000+/-70,000	↑	
	10	Layer 5b		
367,000		↑* 360,000+/-90,000		*Spelearctos deningeri praekudarensis*
	11			
440,000		Layer 5c	Layers 6-8	
	12			
472,000		↓	↓	↓
	13	?		?
502,000			?	
	14		↑	
542,000				
	15		* 560,000+/-112,000	
592,000			Layer 8a	

Figure 37. Stratigraphic position of cave bear subspecies from Paleolithic sites in the Kudaro caves.

Number of species and distribution: The genus includes 3 species: *S. deningeri* (von Reichenau,1904) (Middle Pleistocene of Europe, West and Central Asia, Late Pleistocene of the Caucasus), *S. rossicus* (Borissiak, 1930) (Middle and Late Pleistocene of Eastern Europe, Urals, Kazakhstan, and southern portions of Western Siberia), *S. spelaeus* (Rosenmüller, 1794) (Late Pleistocene of Europe including the Urals).

Note: In Brookes' (1828) catalogue the name *Spelaeus antiquorum* occurs. Neither the generic nor specific name was accompanied by a description or illustration (nomen nudum). The name *Spelaeus* is not available from Kretzoi's (1945:77, 1947:286) papers because there is no description of the taxon and no type species is designated (Article 13 of the Code). Rosenmüller (Rosenmüller and Heinroth 1794) cited the new species *Ursus spelaeus* as "mihi" and the name should probably be ascribed to him alone, rather than to "Rosenmüller et Heinroth," as it is customarily cited (see, for example, Erdbrink 1953; Kurtén 1968).

Spelearctos deningeri (von Reichenau, 1904)

1904. *Ursus deningeri* von Reichenau, *Jahrb. nassau. Ver. Naturkunde, Jg.* 57:11.

Terra typica: Mosbach in Germany, early Middle Pleistocene.

***Spelearctos deningeri praekudarensis* subsp. nov.**

Holotype: Male skull without zygomatic arches, with damaged neurocranium, ZIRAS No. 33161 sen. ind., Kudaro Cave 1, layer 5c, horizon 1, Middle Acheulean. Collector G. Baryshnikov, 1986 (Fig. 2).

Paratype: Complete female skull No. 31894 ad. ind., Kudaro Cave 1, layer 5c, horizon 5, collector G. Baryshnikov, 1983 (Fig. 3); fragment of male skull No. 31896 ad. ind., Kudaro Cave 1, layer 5c, horizon 2-3, collector G. Baryshnikov, 1980; mandible ZIRAS No. 33162 subad. ind., Kudaro Cave 1, layer 5c, horizon 2, collector G. Baryshnikov, 1986 (Fig. 6a).

Diagnosis: Neurocranium is wide. Upper cheek teeth have dominant morphotypes Al - A2, B1 - B3. Lower cheek teeth have dominant morphotypes D1 - D2, E4. P_4 is narrow (usually less than 9.5 mm), M_1 and M_2 are relatively long.

Distribution: Apart from terra typica, apparently, Acheulean deposits in Kudaro 3 (layers 7 - 8) in Transcaucasia, and in Treugoinava Cave (layers 4 - 5) in the North Caucasus.

Geologic age: Middle Pleistocene (Mindel and Mindel-Riss).

Material: All remains from layer 5c in Kudaro 1.

***Spelearctos deningeri kudarensis* (Baryshnikov, 1985)**

1985. *Ursus spelaeus kudarensis* Baryshnikov, *Sov. Archeol.* 3:10.

Holotype: Male skull, ZIRAS No. 31260 sen. ind., Kudaro Cave 3, layer 4, horizon 4, Mousterian. Collector V. Liubin, 1959 (Fig. 4).

Diagnosis: Neurocranium is wide. Upper cheek teeth have dominant morphotypes A9 - A10, B4 - B5. Lower cheek teeth have dominant morphotypes D4 - D6, E5. P_4 wide (usually more than 9.5 mm), M_1 and M_2 comparatively short.

Distribution: Mousterian cave sites in Transcaucasia – Kudaro 3 (layers 3 - 4), Kudaro 1 (layers 3 - 4), Machagua, Akhshtyrskaya, Malaya Vorontsovskaya, and in the Northern Caucasus – Matuzka, Mezmaiskaya.

Geologic age: Late Pleistocene (Riss-Würm and Würm).

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