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MIDDLE PLEISTOCENE *URSUS THIBETANUS* (MAMMALIA, CARNIVORA) FROM KUDARO CAVES IN THE CAUCASUS

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ABSTRACT

A comparison of fossil teeth of Asian black bear (*Ursus thibetanus*) from the Middle Pleistocene layers of Kudaro 1 Cave and Kudaro 3 Cave with those from other Caucasian and West European localities showed a marked morphological similarity, allowing the studied material to be referred to the subspecies *U. t. mediterraneus*. This fossil subspecies is distinguished from the recent subspecies *U. thibetanus* by its larger tooth size. The morphology of the metapodial bones from the Kudaro Caves suggests that during the Middle Pleistocene in the Caucasus the Asian black bear led an arboreal mode of life.

Key words: Caucasus, Kudaro caves, Middle Pleistocene, Paleolithic sites, *Ursus*

СРЕДНЕПЛЕЙСТОЦЕНОВЫЙ *URSUS THIBETANUS* (MAMMALIA, CARNIVORA) ИЗ ПЕЩЕР КУДАРО НА КАВКАЗЕ

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РЕЗЮМЕ

Сравнение ископаемых зубов *Ursus thibetanus* из среднеплейстоценовых слоев пещер Кударо 1 и Кударо 3 с зубами гималайского медведя из других местонахождений Кавказа и Западной Европы показало их значительное морфологическое сходство, что позволяет отнести изученный материал к подвиду *U. t. mediterraneus*. Этот ископаемый подвид отличается от современных подвидов *U. thibetanus* более крупными размерами зубов. Строение метаподиальных костей из Кударских пещер позволяет предполагать, что плейстоценовый гималайский медведь вел более древесный образ жизни, чем современный.

Ключевые слова: Кавказ, пещеры Кударо, средний плейстоцен, палеолитические стоянки, *Ursus*

INTRODUCTION

The Asian black bear (*Ursus thibetanus* G. Cuvier, 1823) is now confined to the forest regions of Southern and Southeastern Asia, reaching north-eastwards to the Amur River basin in Russia and the Japanese Islands (excluding Hokkaido).

In the Pleistocene, the geographical distribution of *U. thibetanus* was considerably more extensive than today. Fossil remains of the Asian black bear are found in southern Siberia (near Baikal Lake) and in southern Europe, from where it spread northward into Germany and the Middle Urals (Erdbrink 1953; Kurtén 1968; Fistani and

Crégut-Bonnoure 1993; Crégut-Bonnoure 1996, 1997; Baryshnikov 2002).

The West European Pleistocene records of Asian black bear, which were described as various taxa: *Ursus mediterraneus* Forsyth Major, 1873, *Plionarctos* (?) *stehlini* Kretzoi, 1941, *Ursus schertzi* Dehm, 1943, *U. (Plionarctos) telonensis* Bonifay, 1971, *U. thibetanus kurteni* Crégut-Bonnoure, 1997, *U. t. vireti* Crégut-Bonnoure, 1997 (Forsyth Major 1873; Kretzoi 1941; Dehm 1943; Bonifay 1971; Crégut-Bonnoure 1997), are now referred to *U. thibetanus* (Crégut-Bonnoure 1996, 1997; Baryshnikov 2007). These records are from two stratigraphic levels and correspondingly can be assigned to two subspecies: *U. thibetanus stehlini* Kretzoi, 1941 (= *U. telonensis*)

from the early Middle Pleistocene (Cromerian, Elsterian) and *U. t. mediterraneus* Forsyth Major, 1873 (= *U. schertzi*, *U. thibetanus kurteni*, *U. t. vireti*) from the late Middle and Late Pleistocene (Holsteinian, Saalian, Eemian). The Pleistocene fauna of Eastern Europe is known to include the subspecies *U. t. permjak* which was established to describe a small black bear from the Last Interglacial of the Urals, Russia (Baryshnikov 2002).

The Asian black bear was identified for the first time from the Pleistocene of the Caucasus on the basis of a left mandible from Azykh Cave (layer 5), Azerbaijan (Gadzhiev and Aliev 1966) (Fig. 1). Subsequently this specimen was described as a new species *U. karabach* (Vereshchagin and Tikhonov 1994).



Fig. 1. Location map showing finds of *Ursus thibetanus* from the Pleistocene of the Caucasus.

Then remains of Asian black bear were found in Kudaro 1 Cave and Kudaro 3 Cave in the Southern Caucasus and Treugolnaya Cave (layer 5b) in the Northern Caucasus. Both were attributed to *U. mediterraneus* (Baryshnikov 1992, 1994). The material from the Acheulean layers of Treugolnaya Cave is dated to the early Middle Pleistocene (Hoffecker et al. 2003).

The present paper deals with the morphological analysis of *U. thibetanus* material from the Kudaro Caves, in the collections of the Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, in the light of these new discoveries.

LOCALITIES AND MATERIAL

Kudaro 1 Cave and Kudaro 3 Cave are situated in the central part of the southern slope of the Greater Caucasus. These caves are placed almost one above another on the left bank of the Djedjori River (Rioni River basin) near Kvaisa City in Southern Ossetia. Both caves were excavated in 1955 – 1990 for their Palaeolithic archaeology by Prof. V. Lioubine (Saint Petersburg).

Kudaro 1 Cave is located at 1600 m a. s. l. in the forest zone. The thickness of sediments varies in different parts of the cave from 1.5 to 4.5 m. Layers 5a–5c are formed by yellowish grey-brown loam with limestone detritus and Late Acheulean stone industries. Layers 3–4 comprise grayish loam with Mousterian stone artifacts (Lioubine 2002).

Two thermoluminescence dates are available for the basal part of the cave deposits: 360,000 ± 90,000 years (RTL-379) for layer 5c and 350,000 ± 70,000 years (RTL-373) for layer 5b (Lioubine 2002) which indicate that the sediment was deposited during marine isotope stage MIS 9. The Mousterian layer 3a has a radiocarbon date 44,150 ± 2,400/1,850 (Gr-6079) (Lioubine 2002).

Kudaro 3 Cave is situated somewhat lower than Kudaro 1. The cave sediments consist of a loam with an admixture of limestone fragments. Artifacts were found in layers 8–5 (Acheulean) and layers 3–4 (Mousterian). The geomorphologic data suggest that Kudaro 3 Cave was exposed by erosion approximately 50–100 thousand years later than Kudaro 1 (Nesmeyanov 1999). The contact between the Acheulean and Mousterian layers is dated by thermoluminescence: 252,000 ± 51,000 and 245,000 ± 49,000 years BP (Lioubine 2002), which suggests a

considerable interval between their depositions in the cave.

The remains of *U. thibetanus* in Kudaro 1 Cave come from the lower part of layer 5 (predominantly from layer 5c). In Kudaro 3 Cave, black-bear remains were recovered from layer 5 and the lowermost part of layer 4 (horizon 6). Therefore, almost all fossil remains of the Asian black bear from the Kudaro caves are associated with Acheulean industries and belong to the late Middle Pleistocene.

The Kudaro caves have yielded two isolated canines, four isolated cheek teeth, two carpal bones, four metacarpals, four metatarsals and several phalanges. This material (apart from the phalanges) is described below.

For comparison I used the collections on the Pleistocene *U. thibetanus* from Europe and Caucasus in the following collections: Aussenstelle Senckenbergmuseum, Weimar, Germany (SMW); Laboratoire de Géologie du Quaternaire, Marsel – Lumine, France (LGQM); Muséum National d'Histoire Naturelle, Institut de Paléontologie, Paris, France (MNHN); Muséum Requier d'Histoire Naturelle, Avignon, France (RMA); Museo di Storia Naturale, Sezione Geologia e Paleontologia, Università di Firenze, Italy (IGF); National Museum, Prague, Czech Republic (NMP); Naturhistorisches Museum, Mainz, Germany (NMM); Naturhistorisches Museum, Wien (NHMW); Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS); Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia (ZIN; Azykh Cave).

In course of the study, the type specimens for the following taxa have been examined: *U. mediterraneus* Forsyth Major, 1873 (P4, IGF 4806V, paratype); *Plionarctos (?) stehlini* Kretzoi, 1941 (left mandible with p4-m3, SMMS 10166, holotype); *U. thibetanus kurteni* Crégut-Bonnoure, 1997 (right upper tooth row P4-M2, RMA n/n, holotype); *U. t. vireti* Crégut-Bonnoure, 1997 (right maxilla with P4-M2, NHMN n/n, holotype); *U. karabach* Vereshchagin et Tikhonov, 1994 (left mandible, ZIN 32549, holotype); *U. thibetanus permjak* Baryshnikov, 2002 (skull, ZIN 35110, holotype). I also studied recent *U. thibetanus* material.

Measurements of teeth were taken as described by Baryshnikov (2006). Limb bones measurements followed the scheme of von den Driesch (1976). The data were processed with the use of Factor Analysis from STATISTIKA 6.0.

DESCRIPTION AND COMPARISONS

Upper teeth. The length (18.6 mm) and width (15.0 mm) of the crown (measured at its base: Fig. 2A) of a right upper canine **C1** (ZIN 36300; Kudaro 1 Cave, layer 5, horizon 6, 1958) is similar to canines of large males of recent *U. thibetanus*. It differs from canines of brown bear (*U. arctos* L., 1758) by the more acute vertical ridge running along the posterior margin of the crown. In addition, the height of the crown (30.8 mm) is lower in ZIN 36300 compared to that in *U. arctos* of similar size.

There are two right upper carnassial teeth **P4**. One specimen comes from Kudaro 1 Cave (ZIN 36301, layer 5c?, 1956), another specimen was found in Kudaro 3 Cave (ZIN 33184, layer 5, horizon 1, 1980). The dimensions of these teeth correspond to those of Pleistocene *U. thibetanus* (Table 1). The crown is triangular in outline (Fig. 2C, D). The main cusps and posterior margin are worn. The paracone is larger than the metacone and possesses three keels: a long anterior keel, a short posterior one, and a weakly developed internal keel. The metacone is narrow and trenchant, being slightly turned with re-

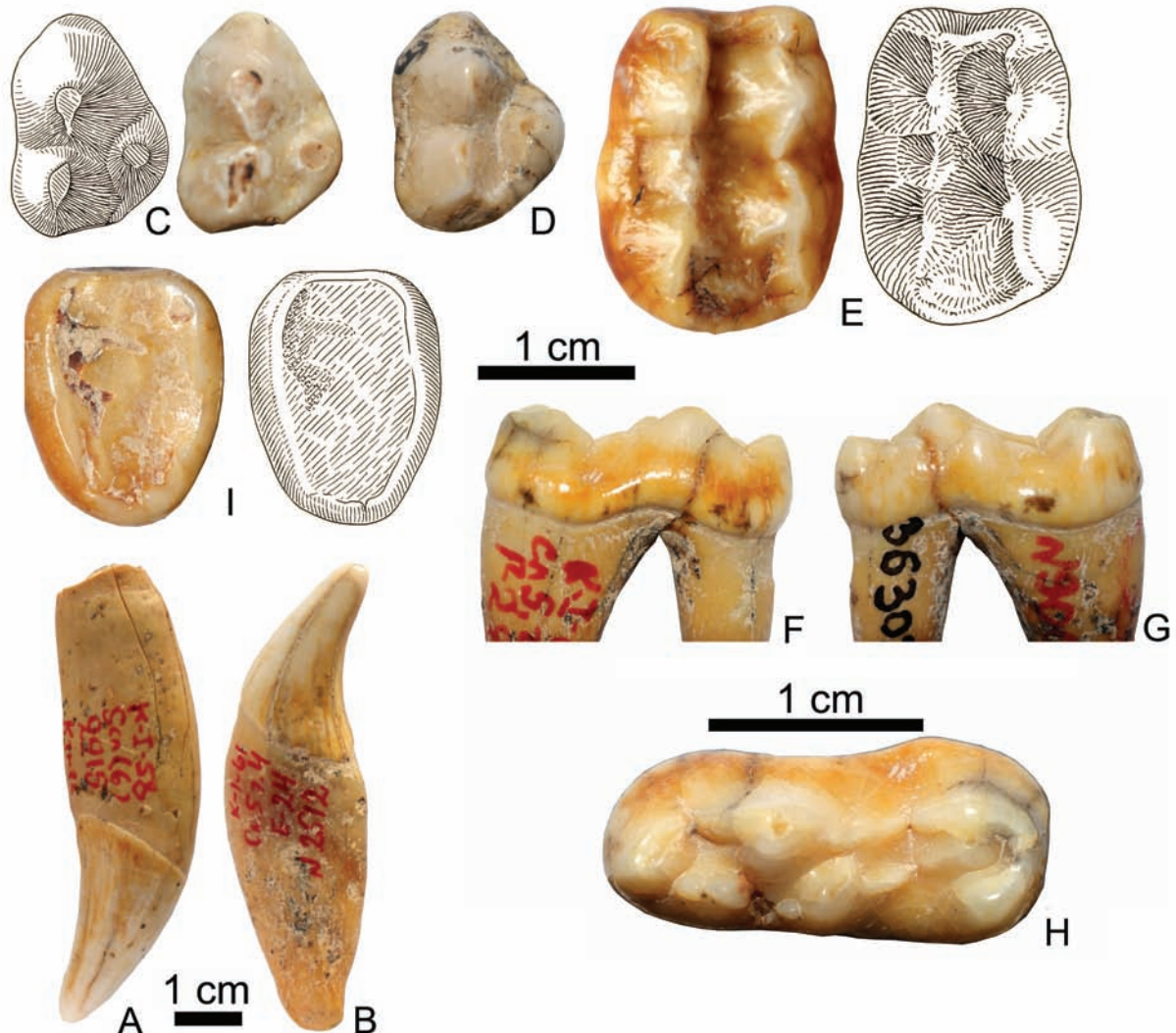


Fig. 2. Teeth of *Ursus thibetanus* from Kudaro caves in labial (A, B, F), lingual (G) and occlusal (C–E, H, I) views: A – right upper canine, Kudaro 1 Cave (ZIN 36300); B – left lower canine, Kudaro 1 Cave (ZIN 33174); C – right P4, Kudaro 3 Cave (ZIN 33184); D – right P4, Kudaro 1 Cave (ZIN 36301); E – left M1, Kudaro 3 Cave (ZIN 33179); F–H – right m1, Kudaro 1 Cave (ZIN 3602); I – left m2, Kudaro 1 Cave (ZIN 33176).

Table 1. Measurements (in mm) of upper premolar P4 of Pleistocene *Ursus thibetanus*.

Localities	Museum number	Greatest crown length	Length of paracone	Greatest crown width	Minimal length between frontal ridge of protocone and caudal side of crown
Kudaro 1 Cave	ZIN 36301	14.5	9.5	10.9	12.0
Kudaro 3 Cave	ZIN 33184	13.7	8.8	9.9	10.9
<i>Ursus thibetanus mediterraneus</i>					
Reale Cave, Italy (type <i>U. t. mediterraneus</i>)	IGF 4806V	15.4	9.4	11.1	10.8
Bruges, France (type <i>U. t. virety</i>)	NHMN n/n	14.2	9.0	9.8	10.9
	NHMN n/n	14.5	9.0	10.0	10.6
Boule Cave, France	RMA n/n	14.1	9.0	10.4	11.7
	RMA C6	14.0	9.1	10.3	11.6
Cèdres Cave, France (type <i>U. t. kurteni</i>)	RMA n/n	14.3	9.2	9.9	11.8
	RMA n/n	15.3	9.9	10.5	11.2
<i>Ursus thibetanus permjak</i>					
Makhnevskaya, Russia (type <i>U. t. permjak</i>)	ZIN 35110	11.4	6.4	7.9	9.7

gard to the long axis of the paracone. The metastyle is absent. Prae- and postprotocrista are pronounced. The protocone is single, rather short, with its apex situated level with the carnassial notch. In ZIN 33184, the protocone is small and shifted towards the labial cusps; in ZIN 36301, the protocone is larger and placed more lingually. A labial cingulum is developed in the posterior part of the crown. Two roots are present.

A principal components analysis carried out on the basis of four measurements of P4 plots both specimens from Kudaro within a sample of *U. t. mediterraneus*, which combines fossil teeth from various European localities (Fig. 3). The scatterplot of Factor 1 and Factor 2 demonstrates a difference between *U. t. mediterraneus* and recent *U. thibetanus* in Factor 1, which includes all tooth measurements (87.3% of dispersion). *U. t. mediterraneus* possesses a larger P4 in comparison with recent *U. thibetanus*; whereas both taxa do not differ in tooth proportions. The isolated position was obtained for *U. t. permjak* from the Urals plotted outside the main scatter which differed from other studied samples in Factor 2 (measurements 2 and 4).

The left upper molar **M1** (ZIN 33179; Kudaro 3 Cave, layer 5, 1975) is represented by the enamel crown. The tooth demonstrates no traces of wear and belongs to a young animal. The crown is low and rectangular in outline (Fig. 2E). The crown anterior margin is slightly concave, whereas the posterior margin is convex. The lingual and labial sides of the crown are nearly equal in length. The posterior part of the tooth is a little wider than the anterior. The crown anterior margin and lingual margin form nearly a right angle.

The main labial cusps are acute, with distinct longitudinal keels. The paracone is markedly higher than the metacone. The anterior keel on the metacone is slightly shorter than the posterior one. The parastyle is robust while the metastyle is inconspicuous.

The lingual and labial rows of cusps are nearly parallel to one another. A narrow valley dividing these rows opens forwards. Its posterior part is occupied by a rugose field. The protocone, mesocone, and metaconule are ridge-shaped. The mesocone is single, with a lingual cingulum situated at its base. There is a minute additional cusp behind the metaconule.

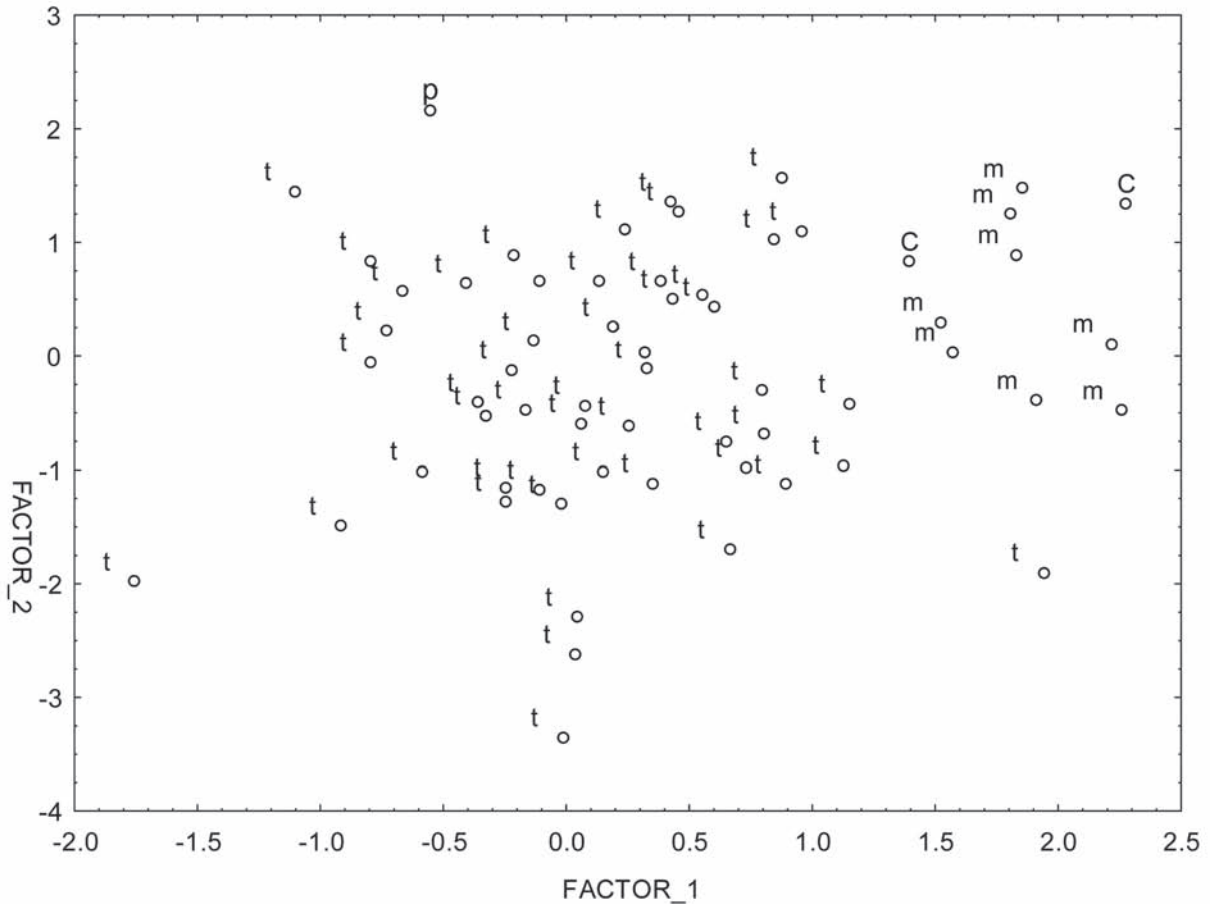


Fig. 3. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of upper premolar P4. Abbreviations: c – Kudaro caves; m – *Ursus thibetanus mediterraneus*; p – *U. t. permjak*; t – *U. thibetanus*, recent.

ZIN 33174 is slightly larger than the examined specimens of *U. t. stehlini* and *U. t. mediterraneus* (Table 2).

In recent *U. thibetanus*, M1 possesses similar structure, differing, however, by smaller size and more developed metastyle. Its lingual cingulum is only occasionally present (in 5 of 24 cases).

Lower teeth. The length (19.3 mm) and width (13.1 mm) of the crown in the left lower canine c1 (ZIN 33174; Kudaro 1 Cave, layer 5, horizon 4, 1961) correspond with canines in large males of recent *U. thibetanus*. In the fossil specimen, the crown is slightly extended backwards, its apex is blunt and base is narrow (Fig. 2B). The tooth root is more than half as long as a whole tooth, which measures 68.5 mm.

The lower canine from Kudaro 1 Cave is similar in size to that from Azykh Cave, and slightly smaller than a canine fragment from Treugolnaya Cave

(Table 3). Specimens from the Pleistocene localities of Europe vary considerably in crown length and width, which may be explained by a pronounced sexual dimorphism in size of the lower canine in *U. thibetanus*. No difference was found in canine dimensions between *U. t. stehlini* and *U. t. mediterraneus*. The Caucasian specimens do not exceed the limits of measurements for these subspecies from the European Pleistocene.

A right lower carnassial tooth **m1** was found in Kudaro 1 Cave (ZIN 36302; layer 5, horizon 7, 1961) (Fig. 2F, G). It is narrow, with a slight contraction between the trigonid and the paraconid. The metaconid is a robust cusp separated from the protoconid, with two to three smaller cusps in front of it. A ridge, crossing the talonid basin, runs from the metaconid to the hypoconid (Fig. 2H). The entoconid is single, being well distanced from the metaconid. Both characters

Table 2. Measurements (in mm) of upper molar M1 of Pleistocene *Ursus thibetanus*.

Localities	Museum number	Greatest crown length	Length of anterior part of crown	Length of paracone	Greatest crown width
Kudaro 3 Cave	ZIN 33179	20.9	9.4	6.7	16.0
<i>Ursus thibetanus stehlini</i>					
Mauer, Germany	SMNS 31183	–	–	9.3	16.8
	NMM 1959/627	19.6	9.7	6.9	14.4
<i>Ursus thibetanus mediterraneus</i>					
Bruges, France (type <i>U. t. virety</i>)	NHMN n/n	19.2	9.2	6.9	14.8
Boule Cave, France	RMA n/n	19.1	9.5	6.9	14.5
Cèdres Cave, France (type <i>U. t. kurteni</i>)	RMA C6	19.8	9.5	6.4	15.8

Table 3. Measurements (in mm) of lower canine c1 of Pleistocene *Ursus thibetanus*.

Localities	Museum number	Length	Width
Kudaro 1 Cave	ZIN 33174	19.3	13.1
Azykh Cave (type <i>U. karabach</i>)	ZIN 32549	19.7	13.9
Treugolnaya Cave	ZIN n/n	21.0	–
<i>Ursus thibetanus stehlini</i>			
Mauer, Germany (type <i>U. t. stehlini</i>)	SMNS 10166	20.0	13.6
	SMNS 31186	21.6	16.2
	NMM 1999/42, cast	23.4	15.2
Cimay, France	LGQM 118	25.9	15.3
Laaerberg, Austria	NHMW 1992/3282	18.5	12.0
Chlum 4, Czech Republic	NMP Ra2121	22.1	14.6
	NMP Ra2132	22.8	13.8
	NMP Ra2133	20.5	14.9
<i>Ursus thibetanus mediterraneus</i>			
Bruges, France (type <i>U. t. virety</i>)	NHMN n/n	24.4	15.0
	NHMN n/n	19.6	14.4
	NHMN n/n	20.4	14.3
	NHMN n/n	19.3	13.9
	NHMN n/n	20.6	13.9
Eringsdorf, Germany	SMW 1966/51134	17.1	10.5
	SMW 1966/8472	18.6	10.6

are typical of the dental morphology of *U. thibetanus*. The labial cingulum is well developed.

ZIN 36302 is markedly shorter in comparison with the carnassial tooth m1 in the type specimen of *U. karabach*. The latter possesses the longest crown of all the specimens examined (Table 4).

A principal components analysis on the basis of four measurements of m1 places the tooth from Kudaro 1 Cave into a group comprising samples of *U. t. stehlini* and recent *U. thibetanus* (Fig. 4). The isolated position of *U. karabach* in the scatterplot is determined by the outstanding length of its m1 and wide trigonid.

Table 4. Measurements (in mm) of lower molar m1 of Pleistocene *Ursus thibetanus*.

Localities	Museum number	Greatest crown length	Length of trigonid	Greatest width of trigonid	Greatest width of talonid
Kudaro 1 Cave	ZIN 36302	19.6	13.3	7.9	9.1
Azykh Cave (type <i>U. karabach</i>)	ZIN 32549	22.3	14.8	9.7	10.8
<i>Ursus thibetanus stehlini</i>					
Mauer, Germany (type <i>U. t. stehlini</i>)	SMNS 10166	20.7	14.2	8.1	9.0
	NMM 1999/42	20.5	13.8	–	10.4
Cimay, France	LGQM 118	21.6	14.1	9.0	10.5
	LGQM 32	21.4	14.4	8.3	10.5
Laaerberg, Austria	NHMW 1992/3282	18.8	12.4	7.2	8.7

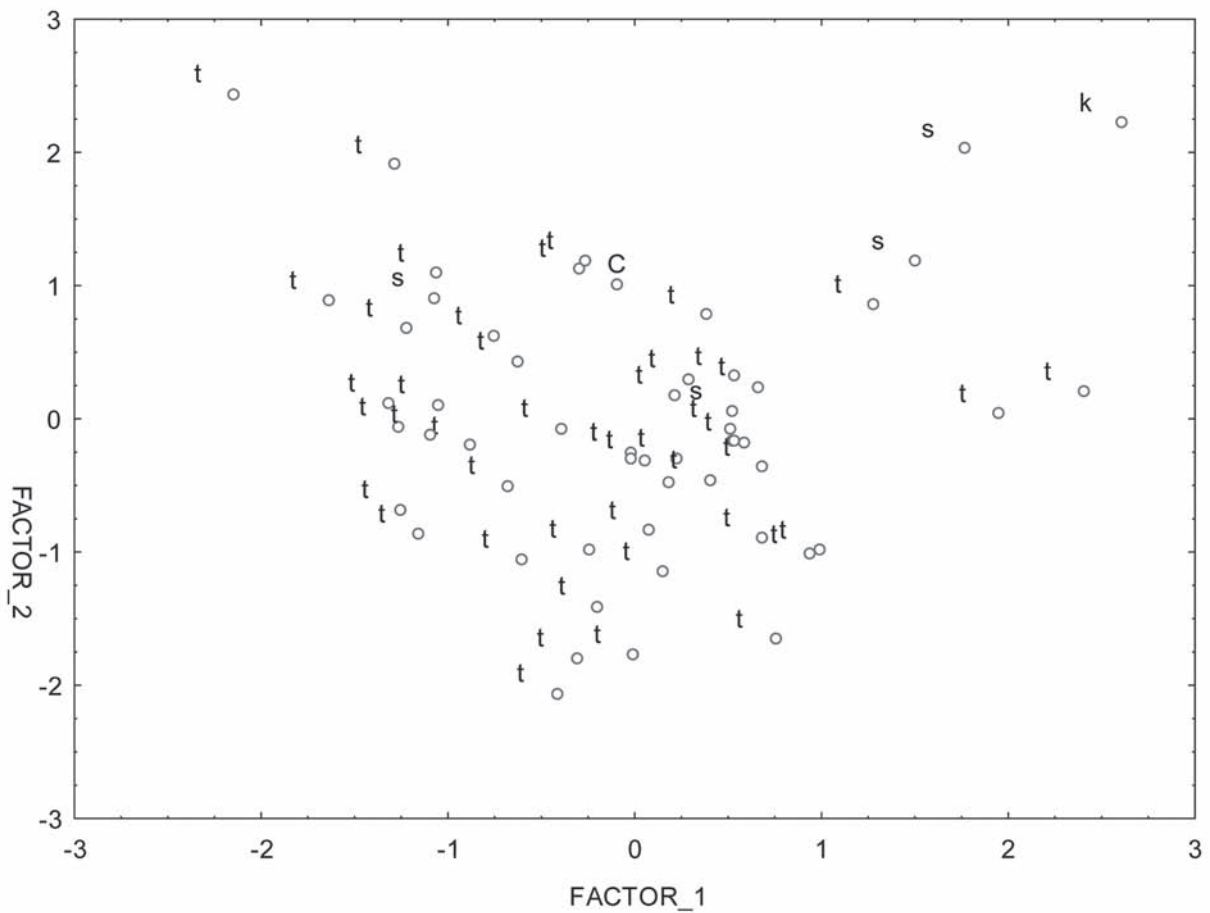
**Fig. 4.** Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of lower molar m1. Abbreviations: c – Kudaro 1 Cave; k – *Ursus karabach*; s – *U. thibetanus stehlini*; t – *U. thibetanus*, recent.

Table 5. Measurements (in mm) of lower molar m3 of Pleistocene *Ursus thibetanus*.

Localities	Museum number	Greatest crown length	Greatest crown width
Kudaro 3 Cave	ZIN 33176	16.1	12.5
Azykh Cave (type <i>U. karabach</i>)	ZIN 32549	19.2	13.6
<i>Ursus thibetanus stehlini</i>			
Mauer, Germany (type <i>U. t. stehlini</i>)	SMNS 10166	16.2	12.7
Cimay, France	LGQM 118	16.6	12.4
	LGQM 185		
<i>Ursus thibetanus mediterraneus</i>			
Cèdres Cave, France (type <i>U. t. kurteni</i>)	RMA n/n	17.5	12.9
Orgnac 3, France	RMA n/n, cast	16.9	12.6

Measurements on the left lower molar **m3** (ZIN 33176; Kudaro 1 Cave, layer 5c, horizon 2, 1978) are characteristic of recent *U. thibetanus*. The masticatory surface is triangular, with wear facets (Fig. 2I). The tooth crown is low, with a straight anterior margin. A border surrounding the crown is uninterrupted and slightly elevated near the metaconid. Two roots are present.

The m3 from Kudaro 1 Cave is the smallest of the Pleistocene samples (Table 5), whereas the type specimen of *U. karabach* is the largest.

Podial bones. There are two capitata bones (os carpale distale 3, = os capitatum), left and right from a single individual, from Kudaro 3 Cave (ZIN 33185-5, 33185-6; layer 5, horizon 1, 1980) (Fig. 5A–D). These specimens correspond with recent *U. thibetanus* in length (18.5, 18.6 mm), breadth (11.8, 12.1 mm) and depth (22.0, 23.2 mm). One specimen (ZIN 33185-6) shows pathological modifications to its anterior (dorsal) margin. The caput of each bone is narrow, with a weakly developed ridge in the articular surface, slightly shifted backwards as in *U. thibetanus*. The anterior (dorsal) margin is wide and flattened. The posterior (volar) margin is more pronounced compared to that of recent *U. thibetanus* (in *U. arctos*, this margin is flat).

The studied metacarpal and metatarsal bones do not exceed the dimensions of recent *U. thibetanus* (Table 6) and are shorter than those of *U. arctos*.

The left first metacarpal (**Mc 1**) (ZIN 33180; Kudaro 3 Cave, layer 5, 1975) morphologically resembles *U. thibetanus*, differing by less roughness of the proximal end, more rounded dorsal surface of the caput

(trochlea metacarpi), and the more pronouncedly oblique medial margin of the distal epiphysis (Fig. 5E, F). The proximal end is comparatively wide (wider than in *U. arctos* of comparable size).

The left second metacarpal (**Mc 2**) (ZIN 33187; Kudaro 3 Cave, layer 4f, 1980) is broken proximally (Fig. 5G, H). The dorsal margin of the diaphysis is less arched than in recent *U. thibetanus*. The metacarpal caput is more pronounced (in recent *U. thibetanus* it is slightly flattened); its medial margin is more pronouncedly oblique as compared to those of recent *U. thibetanus*.

In the left third metacarpal (**Mc 3**) (ZIN 33183; Kudaro 3 Cave, layer 5, 1978) the articular surfaces for the second and fourth metacarpals are identical in shape to recent *U. thibetanus*, whereas the proximal articular surface (facies articularis) is narrower (Fig. 5I, J).

The right fourth metacarpal (**Mc 4**) (ZIN 33188; Kudaro 3 Cave, mixed layers, 1980) is typical of recent *U. thibetanus* (Fig. 5K, L).

The left first metatarsal (**Mt 1**) (ZIN 33175; Kudaro 1 Cave, mixed layers, 1978) is broken proximally (Fig. 5M, N). The diaphysis is curved, with a rounded cross-section. The metatarsal caput (trochlea metatarsi) is pronounced and narrow; a median ridge running along its plantar side is more marked than in recent *U. thibetanus*.

There are two second metatarsals (**Mt 2**), left (ZIN 33181; Kudaro 3 Cave, layer 5, 1975) and right (ZIN 33177; Kudaro 3 Cave, layer 4, horizon 6, 1975) (Fig. 5O–R). The lateral and medial articular platforms of the proximal end do not differ from recent

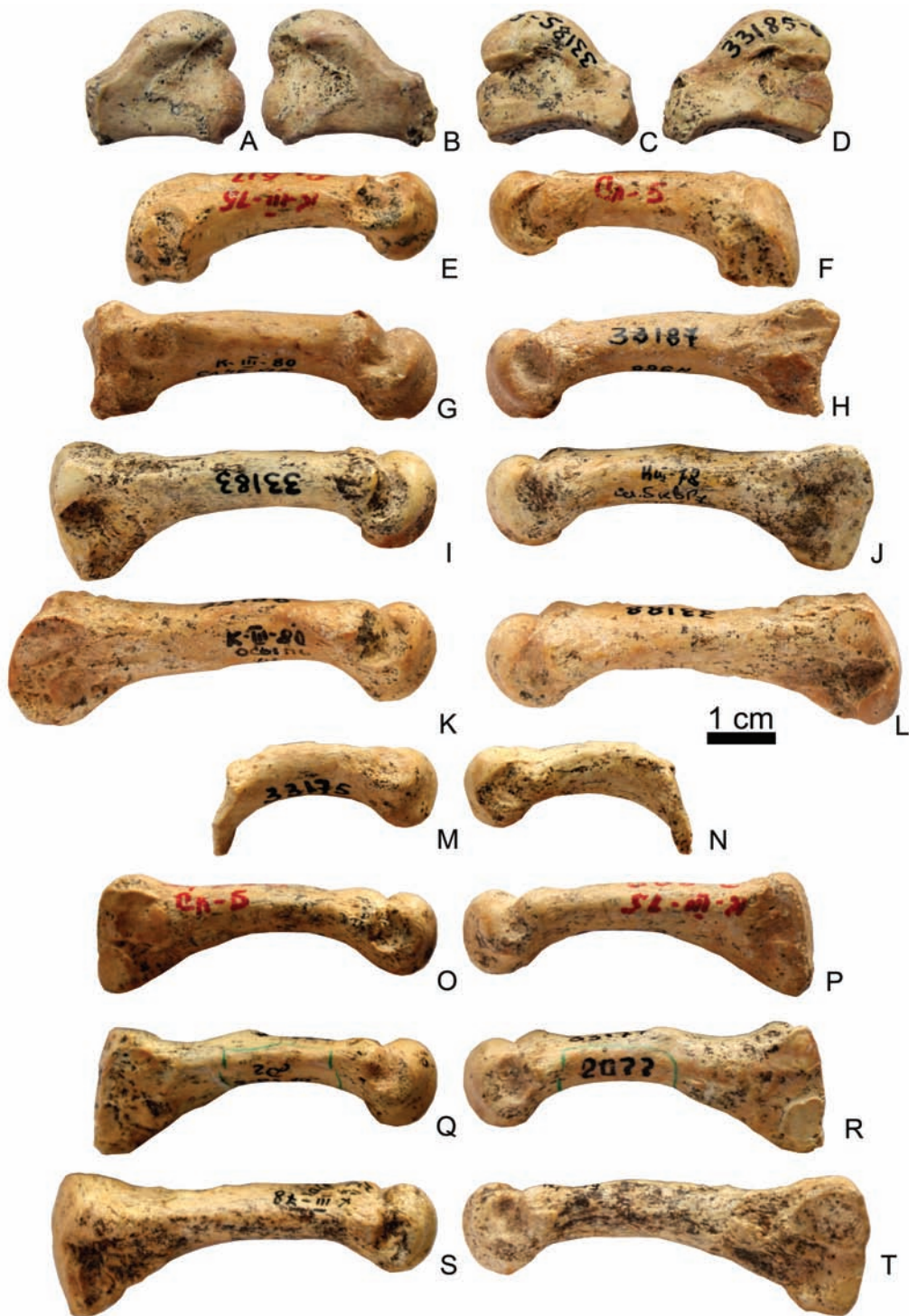


Fig. 5. Limb bones of *Ursus thibetanus* from Kudaro caves; lateral views: A, C – left capitate bone, Kudaro 3 Cave (ZIN 33185-5); B, D – right capitate bone, Kudaro 3 Cave (ZIN 33185-6); E, F – left Mc1, Kudaro 3 Cave (ZIN 33180); G, H – left Mc2, Kudaro 3 Cave (ZIN 33187); I, J – left Mc3, Kudaro 3 Cave (ZIN 33183); K, L – right Mc 4, Kudaro 3 Cave (ZIN 33188); M, N – left Mt 1, Kudaro 1 Cave (ZIN 33175); O, P – right Mt2, Kudaro 3 Cave (ZIN 33181); Q, R – left Mt2, Kudaro 3 Cave (ZIN 33180); S, T – left Mc3, Kudaro 3 Cave (ZIN 33182).

Table 6. Measurements (in mm) of metacarpal (Mc) and metatarsal (Mt) bones of *Ursus thibetanus*.

Bone	Greatest length (GL)	Proximal breadth (Bp)	Proximal depth (Dp)	Smallest breadth of the diaphysis (SD)	Distal breadth (Bd)	Distal depth (Dd)
Mc 1						
Kudaro 3	45.0	17.8	15.8	9.3	13.9	12.8
Recent (n=6)	39.1–47.0	15.2–20.9	13.7–17.0	7.5–9.7	11.5–13.8	10.1–12.4
Mc 2						
Kudaro 3				10.2	16.1	13.6
Recent (n=6)				9.9–10.9	14.0–16.8	11.8–14.8
Mc 3						
Kudaro 3	57.3	12.1	19.0	9.5	15.0	13.9
Recent (n=6)	54.8–67.8	10.9–13.9	17.6–21.0	8.9–10.4	13.6–17.5	12.3–15.4
Mc 4						
Kudaro 3	61.9	13.9	19.0	9.9	16.3	14.3
Recent (n=6)	51.9–70.6	11.7–14.2	16.7–21.8	9.9–11.1	13.0–17.7	12.2–15.5
Mt 1						
Kudaro 3				7.7	12.6	12.0
Recent (n=6)				7.5–10.7	11.3–15.9	9.3–12.8
Mt 2						
Kudaro 3	48.8, 49.6	10.5, 10.7	17.4, 18.1	8.7, 8.9	14.7, 14.7	11.7, 12.4
Recent (n=6)	47.7–58.8	10.0–12.6	14.9–19.7	7.7–10.7	13.2–16.4	10.6–14.0
Mt 3						
Kudaro 3	55.9	14.2	19.5	9.9	15.0	12.8
Recent (n=6)	52.1–64.8	11.2–15.8	17.2–20.8	7.4–10.8	12.4–16.0	11.1–14.1

U. thibetanus; although the proximal articular surface are narrower and lack the deep incision of the dorsal margin. The diaphysis shows noticeable dorso-plantar flattening. The medial ridge of the caput is more slender and less curved than in *U. thibetanus*.

The left third metatarsal (**Mt 3**) (ZIN 33182; Kudaro 3, layer 5, 1978) is more robust than in recent *U. thibetanus* (Fig. 5S, T). The proximal articular surface is typical of the third metatarsal of the Asian black bear, although its plantar part is wider and the medial incision deeper. The metatarsal caput is pronounced and its median ridge more shifted dorsally than in recent *U. thibetanus*.

In summary, the morphology of podial bones of the fossil *U. thibetanus* from Kudaro caves corresponds with that of recent *U. thibetanus*, differing only in few details. The fossil specimens are more ro-

bust (especially metatarsals), with more pronounced articular caputs. Many metacarpals and metatarsals show a larger proximal diameter and more flattened diaphysis. A spherical articular caput on the metapodial bones suggests more mobile fingers in the fossil Caucasian black bear. A similar shape is characteristic of the arboreal Malayan sun bear *Helarctos malayanus* (Raffles, 1821) and the fossil Caucasian black bear was probably a better tree climber than the recent *U. thibetanus*.

DISCUSSION AND CONCLUSION

The present study shows that the tooth morphology of specimens of *U. thibetanus* from Kudaro caves is identical to material from other Caucasian and West European localities. In addition, the analysis of den-



Fig. 6. Left first metatarsal of *Ursus thibetanus* from Kudaro 1 Cave (ZIN 33175) with gnaw marks made by a large rodent (porcupine?).

tal material, including the type specimens, shows no marked differences between the Pleistocene taxa *U. t. mediterraneus*, *U. t. stehlini*, *U. t. kurteni*, *U. t. vireti*, and *U. karabach*, suggesting them to be a single taxon of subspecies level. A pronounced similarity between *U. t. mediterraneus* and *U. t. stehlini* has been noted previously (Thenius 1958; Baryshnikov 1992, 2007; Wagner 2004). Only the subspecies *U. t. permjak* has different tooth size and proportions.

Thus, two fossil subspecies can be recognized for Europe and the Caucasus: *U. t. mediterraneus* Forsyth Major, 1873 (= *stehlini*, *kurteni*, *vireti*, *karabach*) (Middle and Late Pleistocene, Western Europe and Caucasus) and *U. t. permjak* Baryshnikov, 2002 (Late Pleistocene, Eastern Europe). The taxonomic position of Early Pleistocene Asian black bear from Europe remains unclear.

Ursus thibetanus mediterraneus is noticeably similar in tooth morphology to recent subspecies of *U. thibetanus*, except that the former has larger cheek teeth. Presumably, the dental system of *U. thibetanus* evolved slowly. However, the morphology of the fossil metacarpals and metatarsals from the Kudaro caves suggest that the Pleistocene Asian black bear in the Caucasus had peculiar locomotory adaptations.

In the Kudaro caves, fossil remains of *U. thibetanus* are associated with forest and thermophilous mammal species, such as *Rhinolophus* sp., *Macaca* sp., *Apodemus* sp., *Ursus deningeri praekudarensis* (Baryshnikov), *U. arctos*, *Stephanorhinus hundsheimensis* (Jäger), *Capreolus capreolus* (L.), *Cervus elaphus* L., *Bison* sp. (Lioubine 2002). Two species of porcupine

have also been found: the large porcupine (*Hystrix indica* Kerr) and the small porcupine (*H. brachyura vinogradovi* Argyropulo). A metatarsal fragment of *U. thibetanus* from Kudaro 1 Cave (ZIN 33175) has been gnawed by a large rodent, most probably, a porcupine (Fig. 6). The association of *U. thibetanus* and *H. brachyura vinogradovi* has been demonstrated in many European Pleistocene localities, including Makhnevskaya Cave in the Middle Urals (Baryshnikov 2003). Both species could have come to Europe and the Caucasus from South-East Asia.

During the Pleistocene in the Caucasus the Asian black bear inhabited high forests, where it probably foraged on the ground as well as in the trees and used tree hollows as winter dens. When danger threatened it could have escaped by climbing tall trees.

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