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Pleistocene Canidae (Mammalia, Carnivora) from the Paleolithic Kudaro caves in the Caucasus

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ABSTRACT. The analysis of bone assemblages from the Kudaro Paleolithic sites in Southern Ossetia provides a basis for identification of seven species of canids. The Middle Pleistocene fauna contains *Canis arnensis kudarensis* **subsp. nov**., *C. mosbachensis*, *C. lunellensis*, *Vulpes praeglacialis*, and *V. vulpes*, while the Late Pleistocene fauna contains *Canis lupus*, *Cuon alpinus caucasicus*, and *Vulpes vulpes*. Fossil remains of *Canis arnensis*, *C. mosbachensis*, and *C. lunellensis* represent the latest finds for Eurasia.

KEY WORDS: Canidae, Pleistocene, Paleolithic cave sites, Caucasus, taxonomy.

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Плейстоценовые псовые (Mammalia, Carnivora, Canidae) из Кударских пещерных палеолитических стоянок на Кавказе

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РЕЗЮМЕ. Анализ костного скопления в Кударских палеолитических стоянках в Южной Осетии позволил выявить семь видов псовых. Среднеплейстоценовая фауна включает *Canis arnensis kudarensis* **subsp. nov**., *C. mosbachensis*, *C. lunellensis*, *Vulpes praeglacialis* and *V. vulpes*, в то время как фауна позднего плейстоцена содержит *Canis lupus*, *Cuon alpinus caucasicus* and *Vulpes vulpes*. Находки *Canis arnensis*, *C. mosbachensis*, and *C. lunellensis* являются одними из позднейших в Евразии.

КЛЮЧЕВЫЕ СЛОВА: Canidae, плейстоцен, палеолитические пещерные стоянки, Кавказ, систематика.

Introduction

The canid fauna of Northern Eurasia comprises six recent species: *Canis aureus* L., 1758, *C. lupus* L., 1758, *Cuon alpinus* (Pallas, 1811), *Vulpes lagopus* (L., 1758), *V. corsac* (L., 1768) and *V. vulpes* (L., 1758). Four species (*Canis aureus*, *C. lupus*, *Vulpes corsak* and *V. vulpes*) are known to occur in the Caucasus, where they are widely distributed, with the exception of *V. corsac*, which is confined to the arid regions of Northern Caucasus. One more species, *Nyctereutes procyonoides* (Gray, 1834), has been recently introduced to Caucasus from the Eastern Asia.

In the Late Pleistocene of Western Europe, the canid fauna comprised five species (*Canis lupus*, *Cuon alpinus*, *Vulpes lagopus*, *V. corsak* and *V. vulpes*) (Sommer & Benecke, 2005). *Canis aureus* appeared there only in Holocene (Greek Neolithic). The data on the Pleistocene fauna of north-latitude Eastern Europe and Northern Asia contain *Canis lupus* and *Vulpes lagopus*. It was supplemented by *V. vulpes* in more southern regions, by *V. corsac* in steppe, and by *Cuon alpinus* in mountains of Siberia.

Thus, no considerable difference is revealed between canid taxonomic diversity of the Late Pleistocene and that of the recent epoch. Variation is mainly determined by changes in the range of distribution of several species, which is especially marked for *Cuon alpinus* and *Vulpes lagopus*.

Meanwhile the canid fauna is found to be noticeably more peculiar in the late Early and Middle Pleistocene of Europe. The genus *Canis* includes *C. etruscus* Forsyth Major, 1877, *C. arnensis* Del Campana, 1913, *C. mosbachensis* Soergel, 1925, *C. senezensis* Martin, 1973, and *C. accitanus* Garrido et Arribas, 2008 (Thenius, 1954; Torre, 1967; Kurtén, 1968; Bonifay, 1971; Bishop, 1982; Koufos, 1987; Argant, 1991; Rock & Torre, 1996; Sotnikova, 2001; Garrido & Arribas, 2008; Baryshnikov & Tsoukala, 2010). Recently, it was proposed to classify them into two size-groups (species): small *C. arnensis* (including *accitanus*) and medium *C. etruscus* (including *mosbachensis*) (Brugal & Boudadi-Maligne, 2011). In addition, there were described from China *C. chihliensis* Zdansky, 1924 and *C. variabilis* Pei, 1934; their relationships with the European species are not clear (see Tedford *et al*., 2009). Presumably, these Chinese species may be synonymized with the European ones. For example, *C. mosbachensis* and *C. variabilis* represent chronological contemporaries and are similar in morphology. There are also canid repre-

sentatives belonging to other genera, such as *Lycaon lycaonoides* (Kretzoi, 1938), *Cuon priscus* Thenius, 1954, *Vulpes alopecoides* Forsyth Major, 1877, *V. praeglacialis* Kormos, 1932, *V. praecorsak* Kormos, 1932, 1934 and *V. vulpes* (Kurtén, 1968; Bonifay, 1971; Martínez-Navarro & Rook, 2003).

The Pleistocene history of Caucasian canids is poorly investigated and may be elucidated in a course of examination of the fossil material from the Kudaro cave sites in Caucasus. The Lower Paleolithic sites in the caves of Kudaro 1 and Kudaro 3 in the southern Caucasus were discovered in 1955 by Prof. V. Lioubine (St. Petersburg), who was the leader of long-term multidisciplinary studies there. Extensive fossil material has been collected owing to careful inspection and selective screen-washing of the cave sediments during archeological excavations.

Vereshchagin (1957) identified from Kudaro 1 Cave *Canis* cf. *lupus* and *Vulpes* cf. *vulpes*, which were then supplemented by *Cuon* sp. (Vereshchagin, 1959). Later the large wolf (*Canis lupus*) was identified in the Mousterian layers and small wolf (*C*. cf. *lupus*) was found in the Acheulean layers (Vereshchagin & Baryshnikov, 1980). Baryshnikov (1978, 1986, 1995, 1996) described the new fossil subspecies *Cuon alpinus caucasicus* and provided a detailed characteristics of *Canis* remains, identifying three species within both Kudaro caves: *C.* ex gr. *latrans*, *C*. cf. *etruscus* and *C. lupus*.

This communication deals with the new analysis of the Kudaro canid collection, including the first detailed review of the fossil foxes. This study continues a series of publications dealing with the Pleistocene fauna of Carnivora from Kudaro Paleolithic cave sites (Baryshnikov, 1998, 2010a, b, 2011a, b).

Localities and material

The Kudaro caves are situated in the central part of southern slope of the Greater Caucasus (42°31”N, 43°38”E). The caves are placed virtually one above the other on the left bank of Djedjori River (Rioni River bassin) near Kvaisa City (Southern Ossetia).

Kudaro 1 Cave is located at 1600 m above sea. The thickness of sediments varies in the different parts of the cave from 1.5 to 4.5 m. The deposits contain many limestone detritus markedly corroded in lower stratigraphical levels. Layers 5a–5c, which is composed of yellowish fuscous loam, yielded a Late Acheulean industry. The sediment of layers 3–4, representing grayish loam, yielded Mousterian artifacts.

The cave deposits in their basal portion have been dated by radiothermoluminescence method to 360,000± 90,000 years before present (RTL-379) for layer 5c (Lioubine 1998). Fossil remains from this layer belong to thermophilic mammals (*Macaca* sp., *Ursus thibetanus* G. Cuvier, *Hystrix indica* Kerr, and *H. brachyura vinogradovi* Argiropulo; Baryshnikov, 1998), which corresponds to a warm period in the Middle Pleistocene. It may be compared with the Holstein Interglacial in Western Europe (=Likhvin Interglacial in Eastern Europe), coinciding with the Marine Isotope Stage 11 (405–340 ka BP). Mousterian layer 3a is dated by radiocarbon to 44,150±2,400/1,850 (Gr-6079).

Kudaro 3 Cave, which is situated somewhat lower than Kudaro 1 Cave, contains cave sediments mostly consisting of loam with limestone fragments. The loam color changes from yellow-brown at the bottom to dark gray in the upper part. A small number of the Acheulean artifacts were recovered from layers 5–8, and Mousterian artifacts were recovered from layers 3–4 (Lioubine, 1998).

The geomorphologic data suggest that Kudaro 3 Cave was first opened for occupation by erosion which occurred approximately 50,000–100,000 years after the opening of Kudaro 1 Cave (Nesmeyanov, 1999). The contact zone of the Acheulean and Mousterian layers is dated by two RTL-dates to 252,000±51,000 years and 245,000±49,000 years (Lioubine, 1998), which suggest a considerable time gap between their deposition in the cave.

The examined material includes more than 850 remains of canids. Bone fragments and isolated teeth are predominant. This material is stored in the Zoological Institute, Russian Academy of Sciences (ZIN) in St. Petersburg. For comparison, the fossil and recent collection of ZIN and Pleistocene Canidae material at other museums (see Institutional abbreviations below) has been used.

The bones and teeth were measured by calipers with accuracy of 0.5 mm. Limb bones were measured according to von den Driesch (1976). Tooth dimensions were processed with use of Factor Analysis from STATISTICA 6.0.

Institutional abbreviations: AUT — Aristotle University, Thessaloniki, Greece; CBUL — Claude Bernard University Lyon 1, Villerbann, France; GMY — Geological Museum of the Diamond and Precious Metals Geology Institute, Siberian Branch of Russian Academy of Sciences, Yakutsk, Russia; NMM — Naturhistorisches Museum, Mainz, Germany; IGPR — Institute of Geology and Paleontology, “La Sapienza” University, Roma, Italy; ISAK — Institute of Systematics and Evolution of Animals, Krakow, Poland; IZKM — Institute of Zoology, Academy of Sciences of Moldova, Kishinev, Moldova Republic; MG — Museo Geominero, Instituto Geológico y Minero de España, Madrid, Spain; MHP — Musée de l’Homme, Paris, France; MMBA — Moravsky Museum (Anthropos), Brno, Czech Republic; MNHN — Muséum national d’Histoire naturelle, Paris, France; NHM — Natural History Museum, London, Great Britain; USNM — United States National Museum, Washington DC, USA; ZIN — Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

Measurements. Dental measurements**:** *L* — greatest length, *W* — greatest width, *Lpa* — length of paracone, *Lpad* — length of paraconid, *Ltald* — talonid length. Bone measurements (von den Driesch, 1976): cervical vertebrate: *BFcd* — breadth of the caudal

articular surface, *BFcr* — breadth of the cranial articular surface, *Bpacd* — breadth across the Processus articularis caudalis, *H* — height, *LAPa* — length of the arch including the processus articularis caudalis, *LCDe* — length in the region of the corpus including the dens, *SBV* — smallest breadth of the vertebra; limb bones: *Bcf* — breadth of cuboid facet, *Bd* — breath of the distal end, *BG* — breadth of the glenoid cavity, *Bp* — breadth of the proximal end, *BPC* — breadth across the coronoid process, *DC* — depth of the Caput femoris, *Dd* — depth of the proximal end, *Dp* — depth of the proximal end, *DPA* — depth across the Processus anconaeus, *GB* — greatest breadth, *GL* — greatest length, *GLP* — greatest length of the glenoid process, *LA* — length of the acetabulum including the lip, *LAR* — length of the acetabulum on the rim, *SB* — smallest breadth of the shaft of ilium, *SD* — smallest breadth of the diaphysis in the middle part, *SDO* — smallest depth of olecranon, *SH* — smallest height of the shaft of ilium, *SLC* — smallest length of the neck of the scapula.

Systematics

Family Canidae Fisher de Waldheim, 1817
Genus *Canis* Linnaeus, 1758
†*Canis arnensis* Del Campana, 1913

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: right maxilla with P2–M2 (ZIN 31889-1, layer 5, horizon 3, 1959); three right upper canine (ZIN 31889-2, layer 5, horizon 3, 1959; 36609, layer 5, horizon 6, 1959; 36612, layer 5c, horizon 2, 1980); right P3 (ZIN 36607-2, layer 5, horizon 4, 1959); left M2 (ZIN 36607-3, layer 5, horizon 4, 1959); fragment of left mandible with p2–p4 (ZIN 36611, layer X, horizon 2, 1978); right lower canine (ZIN 36610, layer 5c, horizon 2, 1978); two right p3 (ZIN 36605, layer 5, horizon 3, 1959; 36608, layer 5, horizon 5, 1959); right p4 (ZIN 36607-1, layer 5, horizon 4, 1959); fragment of p4 (ZIN 36604, layer 5, horizon 4, 1958); two right m2 (ZIN 36607-4, layer 5, horizon 4, 1959; 36614, layer 5c, horizon 4, 1984); proximal fragment of radius (ZIN 36613, layer 5c, horizon 1, 1984); proximal fragment of right Mc2 (ZIN 36606-2, layer 5, horizon 4, 1959); left talus (ZIN 36603-1, layer 5, horizon 2, 1957); right calcaneus (ZIN 36606-1, layer 5, horizon 4, 1959); os tarsi centrale (ZIN 36606-3, layer 5, horizon 4, 1959); first phalanx and tooth fragments. Kudaro 3: distal fragment of left humerus (ZIN 36615, layer 8, 1981). Total 23 fossil remains.

Description. Maxilla with P2–M2 (ZIN 31889-1; Fig. 1A) of the fossil small canid was found in the basal layer 5 of the Kudaro 1 Cave, containing the late Acheulean stone industries. Because in the tooth dimensions ZIN 31889-1 resembles a coyote maxilla, it was first determined as *Canis* ex gr. *latrans* Say, 1823 (Baryshnikov, 1986).

Judging from the length of upper tooth row, the muzzle of the small fossil canid was elongated. The infraorbital foramen is located over the border between P3 and P4 (in the recent coyote *C. latrans*, it is usually located over P3). The angle between long axis of the carnassial tooth P4 and that of molar row M1–M2 is more obtuse than in the recent *C. latrans*. The long axis of P4 is directed labial to P3, instead of crossing this tooth as in the recent *C. latrans*. Such position of the upper carnassial tooth is observed in several skulls of the recent jackals *C. adustus* Sundevall, 1847 (ZIN 14689) and *C. aureus* (ZIN 18727).

The cheek teeth are moderately worn. The anterior premolars are narrow, being spaced more widely in comparison with the recent coyote. The diastema between P2 and P3 is 1.5 mm and that between P3 and P4 is 4.0 mm. The carnassial tooth and upper molars are crowded.

There is the alveolus of P1. P2 is trenchant, with very small posterior cusp and lingual cingulum. P3 is larger as compared to P2, the former bearing well-developed posterior cusp, which is more robust than in the recent *C. latrans*. The lingual border of P3 has a cingulum forming a small prominence at the crown posterior end.

The upper carnassial tooth P4 is shorter than the length of upper molar row M1–M2. Paracone is pronounced, its anterior margin bearing a sharp ridge. Metacone and metastyle are comparatively longer than those in the recent *C. latrans*. Carnassial notch is deep. The lingual prominence of the tooth crown is robust; its root is oblique, exceeding the bounds of the crown outside. The protocone is blunt, being not beyond the anterior end of the paracone. The posterior part of lingual border of the crown has an inconspicuous cingulum.

The paracone and metacone of M1 are almost equal in length, the paracone being a little longer and higher. The labial cingulum is developed, which is especially pronounced across the paracone. Protocone, metaconule, and hypocone are well marked. The protoconule is very weak. The trigonid basin is somewhat wider as compared to that in the recent coyote. The anterior margin of the tooth reveals a well-developed cingulum merging with the hypocone. The latter cusp is only slightly lower than the protocone and resembles the entire ridge with two small facets of wear (signs of poor-marked apices).

The anterior margin of the M2 crown is salient; the posterior margin has a pronounced median depression, which is shallower in comparison with the recent jackal *C. aureus*. Paracone and metacone are low, situating almost on the same line, which may be drawn through the apices of protocone and metacone of M1. The labial cingulum is well-developed. The metacone is only slightly smaller than paracone. Trigon is wide, with a shallow basin. Postprotocrista is present, metaconule is absent. Hypocone is well marked. There is a cingulum along the anterior side of the tooth crown, which extends onto the base of hypocone.

The length of tooth row P2–M2 allows comparison of the fossil maxilla ZIN 31889-1 with North American small-size canid-species: the recent coyote *C. latrans* and fossil coyote-like dog *C. lepophagus* Johnston,

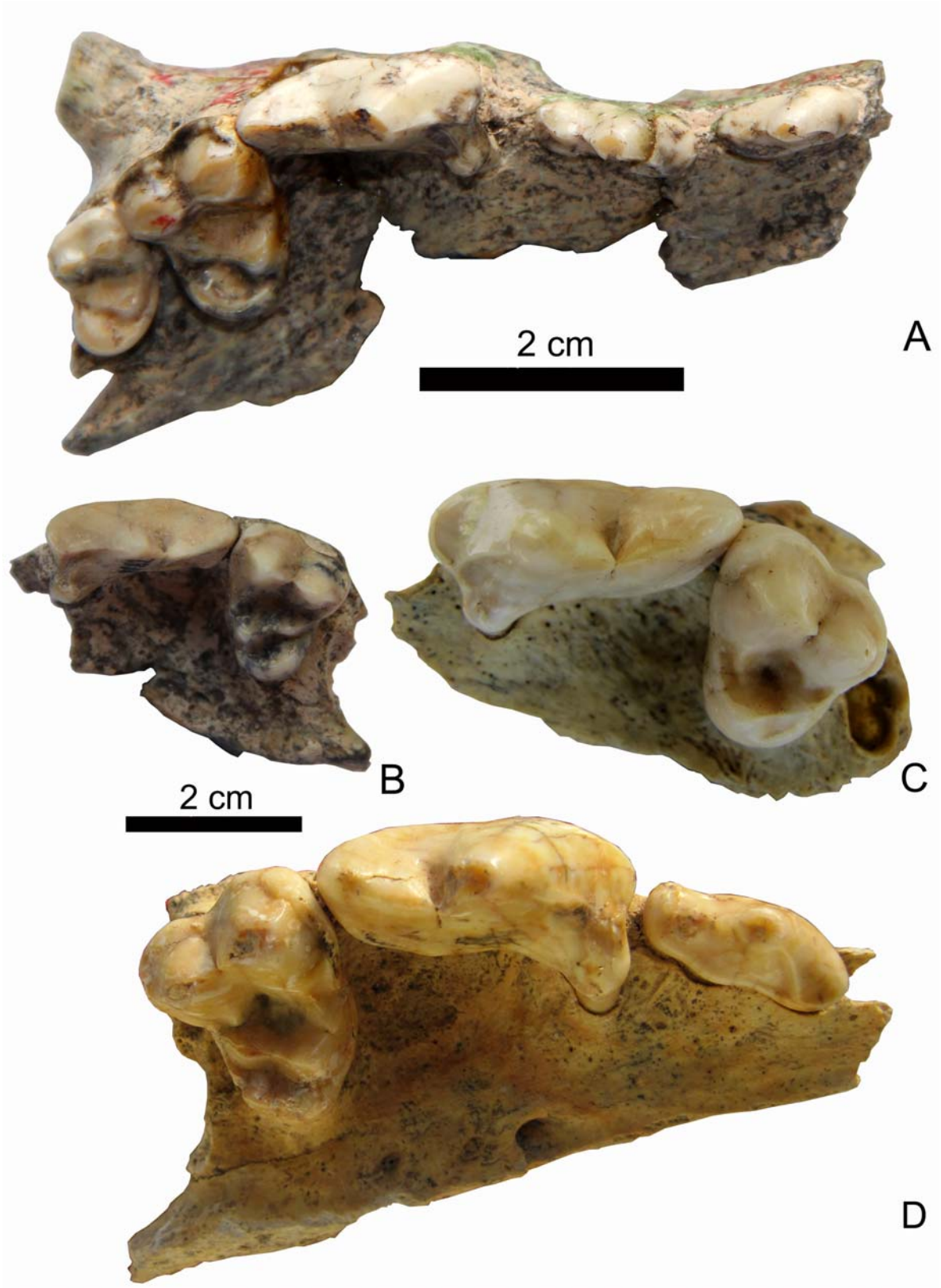

Figure 1. Maxilla fragments *Canis latrans kudarensis* ssp. nov. (A) and C. *mosbachensis* (B) from Kudaro 1 Cave and *Cuon alpinus caucasicus* (C) and *Canis lupus* (D) from Kudaro 3; occlusal view.
A — ZIN 31889-1, holotype; B — ZIN 36621; C — ZIN 34343; C — ZIN 31880.

Table 1. Measurements (in mm) of maxilla in small-sized *Canis*.

Measurements	*C. arnensis kudarensis* subsp. nov.	*C. accitanus*	*C. senezensis*	*C. lepophagus*	*C. latrans*			
	Kudaro 1 Cave, Middle Pleistocene	Fonelas P1, Spain, Early Pleistocene	Senèz, France, Early Pleistocene	Harrell Ranch, Cita Canyon, USA, Late Pliocene	North America, Recent (males and females)			
	ZIN 31889, holotype	MG FP1-2001-0434, holotype (Garrido, Arribas, 2008)	CBUL 210987 (=FSL 3736), holotype	USNM 181495, cast	*n*	lim	M	SD
Length P1–M1			70.0					
Length P2–M2	61.0			59.7	8	56.0–68.0	62.77	4.38
Length P1–P4		51.3	59.1					
Length P2–P4	45.95			43.1				
Length M1–M2	19.4	19.9		20.0	34	18.1–23.0	20.72	1.16
Teeth								
P2 L	10.8	10.9	10.7	9.4	31	9.0–13.0	10.83	0.88
W	4.5	4.2	3.8	4.3	32	3.1–4.9	4.06	0.39
P3 L	12.2	11.6	12.0	12.2	31	10.4–13.7	12.21	0.99
W	4.6	4.5	4.5	4.4	31	3.3–8.2	4.56	0.86
P4 L	18.3	18.5	19.0	17.8	35	16.4–22.5	19.53	1.24
Lpa	11.6		12.0	10.25	35	10.4–14.1	12.50	0.85
W	9.7	8.6	9.9	9.1	35	7.8–11.1	9.78	0.79
M1 L	11.6	12.5	12.0	11.4	35	10.8–14.3	12.96	0.83
Lpa	6.0		6.7	6.25	34	5.6–7.5	6.70	0.44
W	15.1	14.4	14.7	14.9	35	13.4–17.7	15.75	1.02
M2 Length	7.45	7.2		7.35	36	6.4–8.6	7.52	0.55
W	10.2	9.5		10.1	36	9.2–12.1	10.93	0.79

1938 (Tab. 1). At the same time, the length of P2–M2 and the length of P2–P4, of the specimen from Kudaro Cave 1 exceed the recent *C. aureus* from the Caucasus. Length M1–M2 and length P4 is smaller than these measurements in *C. arnensis* from Gerakarou in Grecce (Koufos, 1987).

Notably, the isolated upper canine (ZIN 31889-2) was recovered near the maxilla ZIN 31889-2, both presumably belonging to the same individual. Dimensions of this canine (length 8.5 mm, width 5.4 mm) are typical of the female of recent coyote. There are two other upper canines (ZIN 36609, 36612) of similar size, which were found in the middle and upper parts of the cave layer 5. These specimens resemble in measurements the canine of the fossil canid *C. lepophagus* (USNM 181495) from Harrell Ranch in USA (Tab. 2). Measurements of Kudaro specimens are also fall into the limits of size variation of upper canines in the recent *C. latrans* (length 7.8–10.5 mm, width 4.5–6.2 mm, n=30).

Two isolated upper cheek teeth from middle part of layer 5, P3 (ZIN 36607-2) and M2 (ZIN 36607-3), were assigned to a coyote-like canid, since their length and width correspond to dimensions of intact P3 and M2 from the maxilla ZIN 31889-1 (Tab. 3). P3 has rather small posterior cusp. Postprotocrista of M2 is weak, metaconule is absent on this tooth and its hypocone is large.

Among West European small fossil canids, similar tooth measurements were recorded in coyote-like species: *C. senezensis* from locality Senéz in France (Martin, 1973) and *C. accitanus* from locality Fonelas P1 in Spain (Garrido, Arribas, 2008) (see Tab. 1). Both localities are noticeably older than Kudaro 1 Cave, their age being ascertained near 1.8 Ma (Brugal, Boudadi-Maligne, 2011) or near 2.0 Ma for Senéz (biochron MNQ18; Palombo & Valli, 2004; Delson *et al*., 2006). The teeth of *C. arnensis* known from the Early Pleistocene sites in European Mediterranean are only slightly larger.

The upper cheek teeth have been processed using the discriminant analysis of 12 measurements shown in Tab. 1. The analysis incorporated 5 samples: *Canis aureus*, Caucasus, Recent (n=12); *C. latrans*, Recent (n=37); *C. lupus*, Caucasus, Late Pleistocene and Recent (n=44); *C. mosbachensis* from Kudaro caves, Middle Pleistocene (n=3) and from Stránská skála, Czech Republic, Middle Pleistocene (n=12); as well as individual specimens of *C. lepophagus*, Harrell Ranch, USA, Late Pliocene, *C. senezensis*, Senéz, France, Early Pleistrocene, and the maxilla ZIN 31889-1 from Kudaro 1 Cave. On the resulted scatter plot, the samples of *C. latrans*, *C. mosbachensis* and *C. lupus* are distinctly diverged by the Root 1, which involves the length of paracone M1, length of paracone of P4, length of P4, and length of M1 (83.6% of dispersion) (Fig. 2).

Table 2. Measurements (in mm) of upper and lower canines *Canis*.

Localities	Museum number	C1		c1	
		L	W	L	W
C. lepophagus					
Harrell Ranch, Cita Canyon, USA	USNM 181495, cast	9.7	5.4		
C. arnensis kudarensis ssp. nov.					
Kudaro1, layer 5	ZIN 31889	8.5	5.4		
	ZIN 36609	8.6	5.7		
	ZIN 36612	9.6	5.9		
	ZIN 36610			7.9	5.9
C. mosbachensis					
Caucasus					
Kudaro1, layer 5	ZIN 36624	9.7	6.4		
	ZIN 36625			9.6	7.4
	ZIN 36630-1			11.0	6.6
	ZIN 36619			12.5	7.2
	ZIN 36620-1			10.2	6.6
Kudaro 3, layer 8a	ZIN 32023-2			11.8	7.9
Europe					
Perrier, France	MNHN n/n			11.0	6.5
No locality, Czech Republic	ZIN n/n			10.7	7.5
No locality, Czech Republic	ZIN n/n			10.6	6.5
C. lupus					
Caucasus					
Kudaro 1, layer 4	ZIN 36649-1	11.2	7.6		
Kudaro 3, layer 4	ZIN 36651			11.8	8.2
	ZIN 36652			11.3	7.4
	ZIN 36657-1			12.1	7.4
Kudaro 3, layer 3	ZIN 36654	12.0	7.2		
Binagady	ZIN 22384-53	12.0	7.8		
	ZIN 22384-46			14.5	10.6
	ZIN 22384-47			14.0	9.5
	ZIN 22384-51			12.7	9.0
	ZIN 24408-1			12.7	8.3
M. Voronzovskaya, layer 3	ZIN 31978			14.1	9.4
Europe					
Kent Caverns, England	NHM 736	14.1	8.8		
	NHM 850	14.7	9.5		
	NHM 16755	14.1	8.3		
	NHM 15636			13.2	8.1
	NHM 831			13.2	9.1
Gibraltar	NHM 12333			13.6	–
	NHM 12333			11.9	7.8
	NHM 12333			13.1	8.3
Kostenki, European Russia	ZIN 36233	13.4	9.4		
Alasea River, Yakutia, Russia	GMY 5171			14.6	9.1

Therefore, the species differ by metric characteristics of the upper carnassial tooth and first upper molar. *C. aureus*, revealing similar dimensions of upper cheek teeth, is segregated from *C. latrans* by Root 2, which predominantly embraces the length of M1 and length of P3 (9.3% of dispersion). Fossil coyote-like dogs, *C. lepophagus* and *C. senezensis*, do not exceed the range of the sample of *C. latrans*, both fossil taxa locating closer to one another and to *C. aureus* than to the small canid from Kudaro 1 Cave.

The contents of an erosional lens between layers 4 and 5 (lens "X") in Kudaro 1 Cave, containing mixed Acheulean and Mousterian stone industries (Lioubine, 1998), revealed a fragment of right mandible with p2, p3 and a fragment of p4 (ZIN 36611; Fig. 3I, J). The alveolus of p1 is absent. The mandible is robust, belonging to an adult. By the length and thickness at the level of p4 (8.5 mm), it corresponds to the large recent coyote *C. latrans* (ZIN 971); however, the premolar row in the fossil specimen is shorter. The distance from the posterior margin of the canine alveolus to the anterior margin of alveolus of m1 constitutes 41.4 mm compared with 50.9 mm in ZIN 971. The mental foramina are distanced from each other, the first foramen

Table 3. Measurements (in mm) of upper cheek teeth *Canis*.

Localities	Museum number	P1		P2		P3		M1		M2	
		L	W	L	W	L	W	L	W	L	W
C. arnensis kudarensis ssp. nov.											
Kudaro 1	ZIN 36607-2					11.9	4.3				
	ZIN 36607-3									7.4	10.2
C. mosbachensis											
Caucasus											
Kudaro 1, layer 5	ZIN 36631	6.4	4.1								
	ZIN 36640	7.1	4.8								
	ZIN 36626					12.7	5.6				
Europe											
Westbury Quarry Cave, England	NHM 33529					14.3	5.9				
	NHM 1/350					13.8	6.0	14.1	16.7		
	NHM 405							12.7	15.7		
	NHM 78/9							12.8	16.8		
Stránska skála, Czech Republic	MMBA 1378					16.0	6.8				
	MMBA Sch181					13.3	5.5				
	MMBA 1345							14.1	16.8		
	MMBA 1378					16.0	6.8				
	MMBA 1568							14.2	18.1		
	MMBA 1569									8.7	11.9
	MMBA 1587							13.6	16.4		
	MMBA Kn40							13.0	16.0		
	MMBA n/n							14.1	16.8		
C. lunellensis											
Kudaro 3, layer 6	ZIN 36646	6.9	5.0								
	ZIN 31884-5			11.5	5.2						
	ZIN 36647					13.0	6.3				
C. lupus											
Kudaro 3, layer 4	ZIN 31882-1							16.1	ca18.9		
	ZIN 31882-2							15.8	18.8		
	ZIN 31883-3									8.5	11.9

situating below the anterior margin of p2 and second below the posterior margin of p3. The premolars p2–p4 are very narrow, blade-like, not differing by their length from those in the recent *C. latrans* (Tab. 4). The posterior margin of p3 bears supplementary cuspid, which is absent on p2. The premolar p3 is located lower than premolars p2 and p4. By its shortness, ZIN 36611 from Kudaro 1 Cave resembles the mandible of jackal (*C. aureus*); though, the mental foramina of jackal are approximate and its premolars are markedly wider.

Principal components analysis was performed for 5 samples on the basis of 8 mandible measurements given in Tab. 4. The analysis included samples of recent coyote *Canis latrans*, North America (n=5), recent jackals: *C. aureus*, Caucasus (n=16), *C. mesomelas* Schreber, 1775, East Africa (n=4), and *C. adustus*, East Africa (n=2), as well as ZIN 36611. In the factor space samples of jackals were divided by Factor 1, which includes all measurements except the mandible height beyond p2 (76.5% of dispersion). Jackals were separated from the coyote by Factor 2, including three measurements: length of p2–p4, width of p3, and width of p4 (9.6% of dispersion). On the scatter plot, the mandible fragment from Kudaro 1 Cave placed near the sample of *C. latrans* and is clearly separated from all jackal species (Fig. 4).

Within the Kudaro collection, isolated lower teeth are represented by the canine (ZIN 36610) whose parameters are characteristic of *C. latrans*. Also found were lower premolars p3 and p4 (Fig. 3M, N) which correspond in their length and width to the same teeth of the recent coyote (Tab. 5) and reveal well-developed posterior cups. Meanwhile, the fragment of premolar p4 (ZIN 36604) is widened in the posterior portion, as in jackal (*C. aureus*), resembling this species in the width of the tooth crown.

Two lower molars m2, both right ones, are determined as belonging to the Kudaro small canid (Tab. 6).

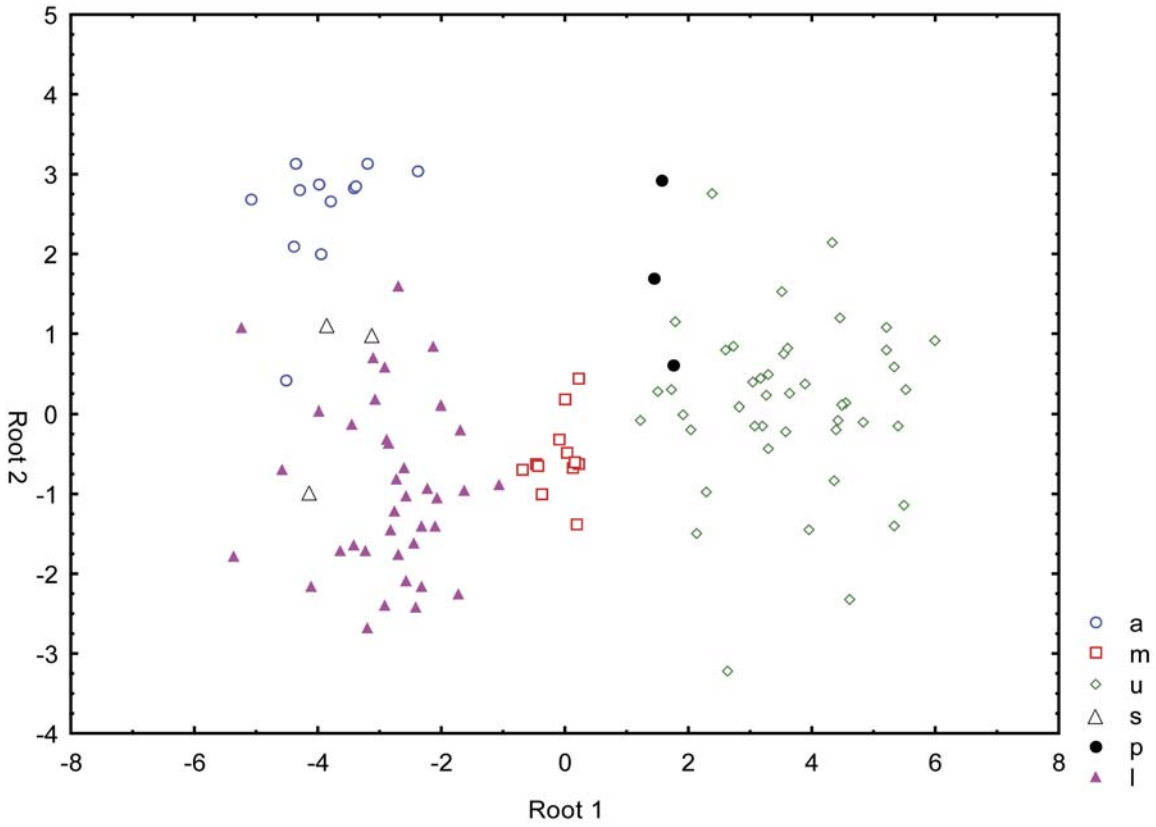

Figure 2. Scatter plot of canonical scores of Root 1 and Root 2 from discriminant analysis for upper tooth row P2-M2 in *Canis*. a — *C. aureus*, Recent; l — *C. latrans*, Recent; m — *C. mosbachensis*, Stránská skála; p — *C. mosbachensis*, Kudaro 1 Cave; s — *C. lepophagus* and *C. senezensis* (above), and *C. arnensis kudarensis* ssp. nov. (below); u — *C. lupus*, Caucasus, Late Pleistocene and Recent.

The fossil specimens are wider in comparison with teeth of the recent *C. latrans* owing to the more pronounced development of the labial cingulid. This character aligns them with the teeth of *C. aureus*. The metaconid and protoconid are approximately equal in size and exhibit equal height. Both Kudaro specimens are smaller compared to the m2 of *C. mosbachensis*, whose sample from Stránská skála in Czech Republic shows length variation 9.4 mm to 10.9 mm and of the width variation 6.7 mm to 7.8 mm (Tab. 6).

Several limb bones of a small fossil dog, which were found in Kudaro 1 Cave, show no difference with those of the recent gold jackal *C. aureus* (Tab. 7). The proximal end of radius (ZIN 36613) is only slightly

Tables 4. Measurements (in mm) of mandibles in small *Canis*.

Measurements	*C. arnensis kudarensis* ssp. nov.	*C. latrans*		*C. aureus*		*C. adustus*	*C. mesomelas*
	Kudaro 1 Cave, Middle Pleistocene	USA, recent		Caucasus, recent		Africa, recent	Africa, recent
	ZIN 36611	ZIN 971	ZIN 5943	ZIN 16899	ZIN 18721	ZIN 14689	ZIN 9330
Length p2–p4	ca32.1	39.7	34.3	31.3	30.7	25.1	30.1
Height before p3	15.1	15.3	14.3	15.2	13.6	12.9	14.0
Teeth							
p2 L	8.6	10.1	8.9	9.2	8.8	6.6	7.7
W	3.2	4.8	3.6	4.1	3.9	2.7	3.4
p3 L	10.5	11.6	9.7	10.4	9.6	7.1	8.7
W	3.7	4.7	3.8	4.4	4.0	3.2	3.7
p4 L	ca11.0	12.3	11.0	11.4	11.1	8.6	9.8
W	ca4.5	5.9	4.6	5.5	4.8	3.9	4.4

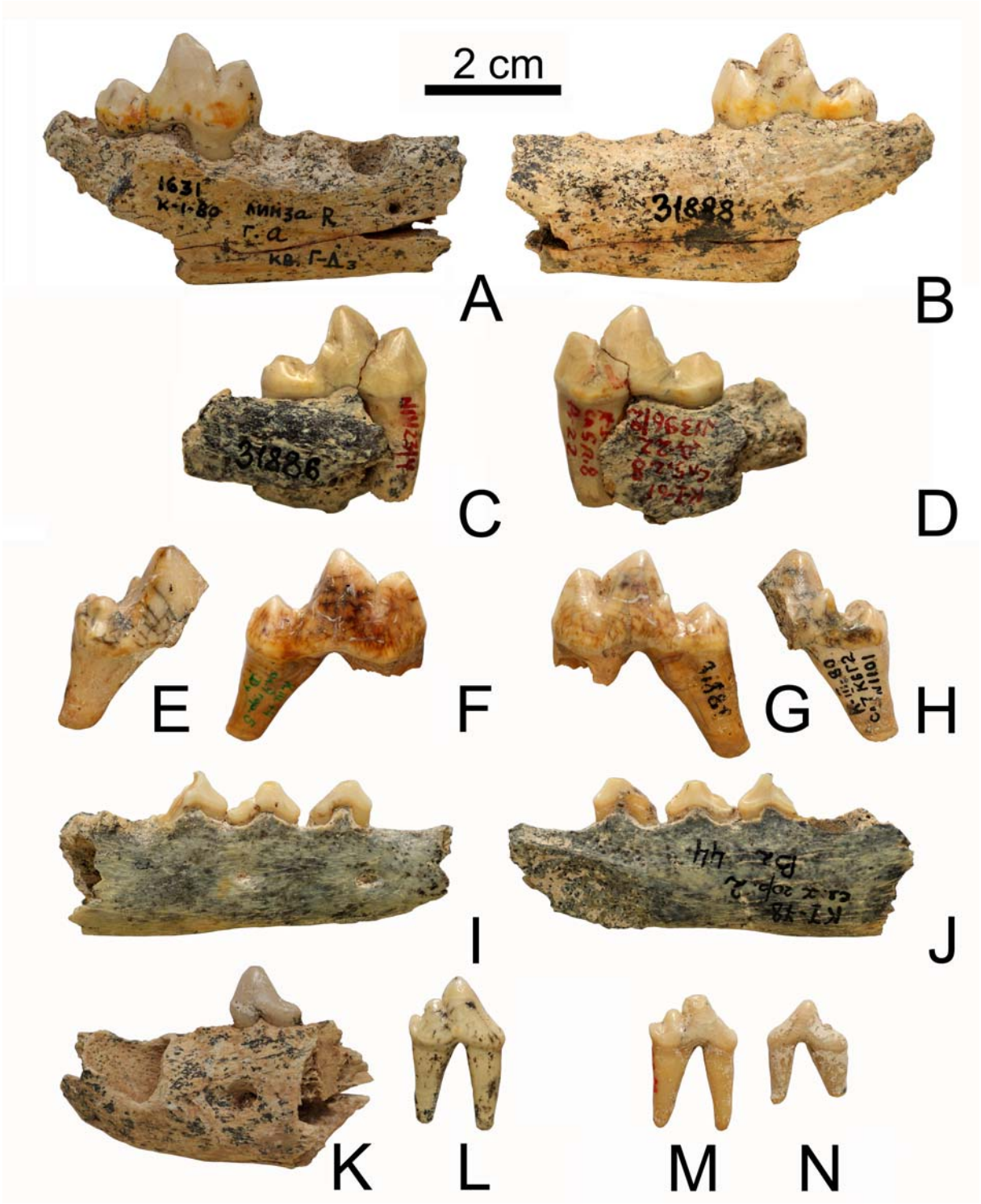

Figure 3. Mandible fragments and lower cheek teeth of *Canis arnensis kudarensis* ssp. nov. (I, J, M, N), *C. mosbachensis* (A–D, K–L), *C. lunellensis* (E, H) and *C. lupus* (F, G) from Kudaro caves; labial (A, D, E, F, I, K–N) and lingual (B, C, G, H, J) views.

A, B — ZIN 31888-1; C, D — ZIN 31886; E, H — ZIN 36645; F, G — ZIN 31881; I, J — ZIN 36611; K — ZIN 32023-1; L — 36629; M — ZIN 36607-1; N — ZIN 36607-2.

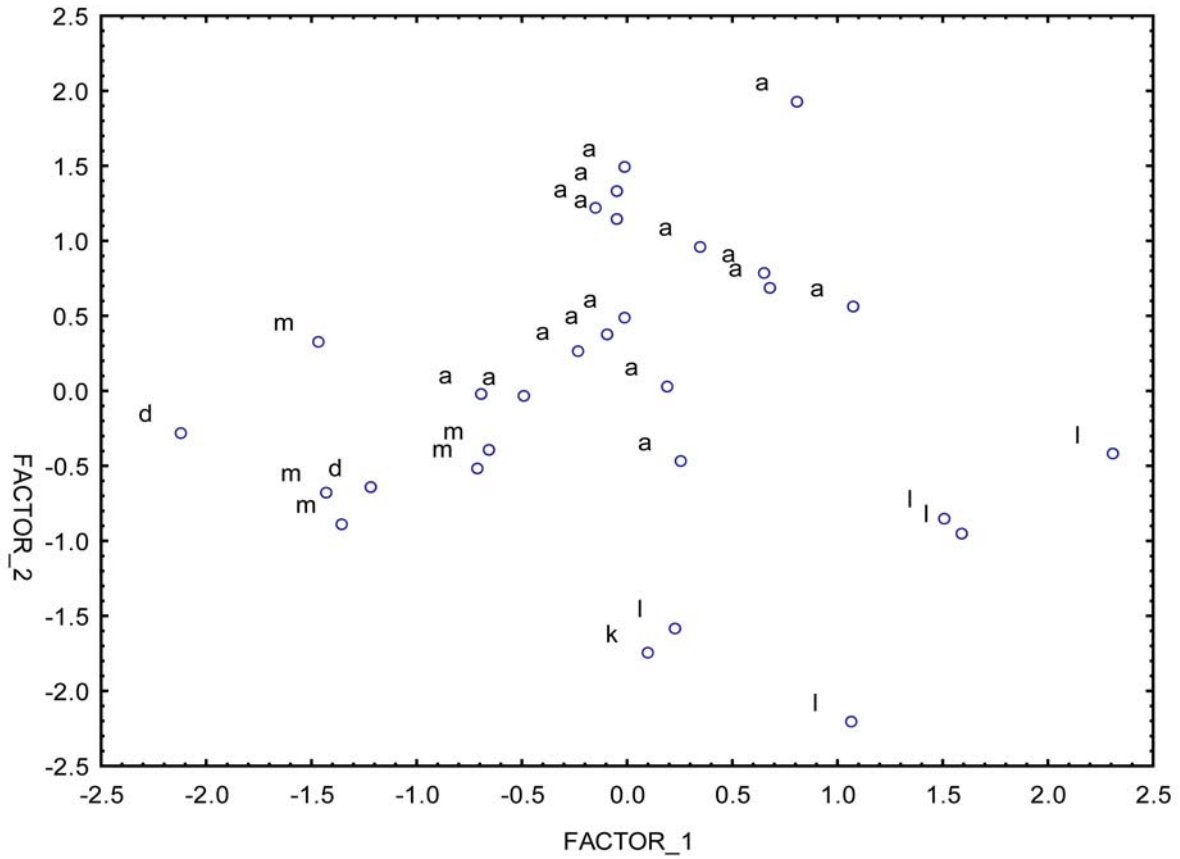

Figure 4. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of mandible in *Canis*.
a — *C. aureus*, Caucasus, Recent; d — *C. adustus*, Recent; k — *C. arnensis kudarensis* ssp. nov., Kudaro 1 Cave; l — *C. latrans*, Recent; m — *C. mesomelas*, Recent.

narrower than that of *C. lepophagus* from Red Light Bolson in USA (Kurtén, 1974). Left talus (ZIN ZIN 36603-1) and right calcaneus (ZIN 36606-1) resemble in the length and width these bones of the recent *C. aureus*, the caput tali being, however, shorter and collum tali narrower in the fossil talus.

The only bone of this small canid has been found in Kudaro 3 Cave, in layer 8. This is a distal fragment of the humerus (ZIN 36615), whose width is similar to that in the recent jackal *C. aureus*.

The study reveals that the small canid from Kudaro caves resembles the recent coyote (*C. latrans*) by the dimensions of upper and lower cheek teeth, differing significantly from jackal (*C. aureus*), which provides a possibility to assign it to a group of coyote-like dogs.

The coyote-like canid from Kudaro caves diverges with the recent *C. latrans* in the wider upper premolar P2 (vestibulo-lingual diameter relative greatest length) and comparatively shorter P4, i.e. the Kudaro small canid is characterized by less carnivorous dentition (Baryshnikov, 1986). In addition, this canid has a comparatively long M2, enlarged metacone of M1, and another position of the upper carnassial tooth P4 (see above).

Teeth of the Kudaro small canid morphologically differ from those of fossil coyote-like dogs from North America. The Pliocene species *C. leptophagus* and *C. thooides* Tedford et al., 2009 are characterized in more archaic dentition. In addition, the Kudaro canid reveals differences with *C. lepophagus* by such apomorphic characters for Canini as the position of protocone of P4 not beyond the anterior end of paracone and markedly enlarged paracone of M1 (Tedford *et al*., 2009). *C. edwardii* Gazin, 1942 from the Early and Middle Pleistocene was noticeably larger (its minimum length parameters of P4 and M1 exceed corresponding measurements of ZIN 31889-1) (see Tedford *et al*., 2009).

A comparison of the small canid from Kudaro 1 Cave with miniature fossil dogs from Europe shows that the former, by dimensions of the carnassial P4, were smaller than *C. arnensis* from sites in Italy (Poggio Rosso, Tasso, Upper Valdarno, Bucine) and Greece (Gerakarou) (see Brugal & Boudadi-Maligne, 2011). At the same time, there is considerable morphometric similarity with the fossil species *C. accitanus* and *C. senezensis* from Southern Europe (Martin, 1973; Garrido & Arribas, 2008).

Brugal & Boudadi-Maligne (2011) stated that European fossil coyote-like species may represent a single species, *C. arnensis*, and the observed biometric differences between them are explained by sexual and geographic variability. Since ZIN 31889-1 belongs to a

Table 5. Measurements (in mm) of lower premolars in small and medium sizes *Canis*.

Measurements	Museum number	p1		p2		p3		p4	
		L	W	L	W	L	W	L	W
C. arnensis kudarensis ssp. nov.									
Kudaro 1	ZIN 36605					9.7	4.6		
	ZIN 36608					10.6	4.6		
	ZIN 36607-1							13.2	5.8
	ZIN 36604							–	5.5
C. etruscus									
East Runton, Forest Bed, England	NHM 6170			11.9	5.2				
C. mosbachensis									
Caucasus									
Kudaro 1, layer 5	ZIN 36634	5.4	3.8						
	ZIN 36631	6.4	4.0						
	ZIN 36642					11.8	5.1		
	ZIN 36629							14.1	6.7
	ZIN 36636							–	6.4
Kudaro 1, mixed layers	ZIN 36638-1							13.0	6.7
Kudaro 3, layer 8	ZIN 32023-1			10.2	5.0				
	ZIN 32022-1					12.4	5.7		
Europe									
Westbury Quarry Cave, England	NHM 33640			10.3	3.9	11.5	4.9		
	NHM 33937							13.0	6.4
	NHM 33938							15.2	6.9
	NHM 47519			12.2	5.0				
	NHM 47520							13.5	5.9
Stránska skála, Czech Republic	MMBA 5382-2			12.0	5.2	12.6	5.1	13.7	6.2
	MMBA 5382-5			11.3	5.0				
	MMBA 5382-8					12.1	4.9	13.2	6.2
	MMBA 5382-10							13.5	6.6
	MMBA 5382-13			10.7	4.6	11.5	4.7	12.7	5.8
	MMBA 5382-14			11.2	4.4	12.2	4.7		
	MMBA 1476			11.1	4.5			12.9	5.5
	MMBA 1571							14.7	7.0
	MMBA 1821							14.8	6.6
	MMBA 2097					12.7	5.5		
	MMBA 2394					12.7	6.1		
Kozi-Grzbiet, Poland	ISAK MF/1343							14.0	5.8
C. lunellensis									
Kudaro 3, layer 6	ZIN 31884-4			11.7	5.8	12.6	5.5		

female, it may be suggested that small size of type specimens of *C. accitanus* and *C. senezensis* also implies they are females; this idea maintains the view by Brugal & Boudadi-Maligne (2011).

The small coyote-like dog from Kudaro 1 Cave diverges from *C. arnensis* in several derived characters of dental morphology: the M1 paracone markedly enlarged, p3 lies below p2 and p4. It may result from a large time gap dividing these canids (*C. arnensis* from Western Europe is more than 1 million years older than the Kudaro finding).

I consider the small canid from Kudaro caves to be a later representative of *C. arnensis* (sensu Brugal & Boudadi-Maligne, 2011), surviving in Southern Caucasus until the Middle Pleistocene. Its geographical location, geological age, and characters of dentition provide the basis for a new subspecies, *C. arnensis kudarensis* Baryshnikov **subsp. nov**.

Discussion. The examined fossil material indicates for the first time the presence of fossil coyote-like canid in the Middle Pleistocene mammal fauna of the South Caucasus. This material is distributed throughout layer 5 in Kudaro 1 Cave, including the contact with upper layer 4 ("lens X"). Only a single bone has been found in Kudaro 3 Cave within the lowermost sediment (layer 8).

In the Caucasus region, the postcranial remains from layer 5 in Azykh Cave in Azerbaijan, earlier attributed to *C. aureus* (Gadzhiev & Aliev, 1966), probably belong to *C. arnensis kudarensis*. Vereshchagin (1951), examining the species-rich material on carnivores from the asphalt pit of Binagady near Baku, drew attention to the absence of *C. aureus* there and assumed this species

Table 6. Measurements (in mm) of lower molars in small and medium sizes *Canis*.

Measurements	Museum number	m1			m2	
		L	Ltald	W	L	W
C. arnensis kudarensis ssp. nov.						
Kudaro 1, layer 5	ZIN 36607-4				9.0	6.8
	ZIN 36614				9.2	6.9
C. mosbachensis						
Caucasus						
Kudaro 1, layer 5	ZIN 31888	23.9	7.5	9.2		
	ZIN 31886	23.9	7.4	9.3		
	ZIN 36623-1				9.8	6.9
	ZIN 36618				9.7	7.4
	ZIN 31887				9.9	7.6
	ZIN 36641				10.9	7.8
Europe						
Westbury Quarry Cave, England	NHM 33640	21.8	6.1	7.8		
	NHM 33642	22.9	6.0	8.9		
	NHM 33937	22.4	6.7	9.4		
	NHM 33938	25.4	8.3	10.2		
	NHM 47518	23.3	6.7	8.9		
	NHM 375/75	24.0	6.9	9.7		
Stránska skála, Czech Republic	MMBA 5382-3				10.1	7.1
	MMBA 5382-4	23.7	6.6	9.3		
	MMBA 5382-12				10.4	7.7
	MMBA 5382-21	22.5	6.3	8.6		
	MMBA 1332	21.1	5.4	7.8		
	MMBA 1342	23.1	6.4	8.8		
	MMBA 1371				10.4	7.0
	MMBA 1438	23.5	6.7	9.1		
	MMBA 1496	24.6	7.2	9.4	10.7	7.8
	MMBA 1819	22.0	6.6	8.3		
	MMBA 2098				10.9	7.5
	MMBA 2101	21.8	6.8	8.3		
	MMBA 5381	23.0	6.2	8.6		
	MMBA Sch132	21.5	6.8	8.4		
	MMBA Fe19	22.7	6.9	9.1		
	MMBA Fe20	22.4	6.7	8.5		
C. lunellensis						
Kudaro 3, layer 7	ZIN 36645	–	6.4	–		
Kudaro 3, layer 6	ZIN 31884-3	24.5	6.3	9.7		

to disperse into Caucasus only in Holocene. Yet, no reliable remains of the Pleistocene age were found there. Fossil coyote-like dogs were never recorded in Northern Caucasus.

Fossil coyote-size canids occurred in Europe in the Early Pleistocene (*arnensis*, *senezenensis*, *accitanus*) and their discovery in the Kudaro fauna assigned to the new subspecies (*C. arnensis kudarensis* subsp. nov.) testify that these small-size canids survive in Eurasia until the middle period of the Middle Pleistocene.

Brugal & Boudadi-Maligne (2011) pointed out the importance of biometrical data for understanding the Pleistocene history of *Canis* in Western Europe. Although body size cannot be used to evaluate phylogenetic relationships, it indicates the breadth of the ecological niche of ancient canids, and may be used in taxonomy as well as for paleoecological reconstructions. The size parameters of *C. arnensis kudarensis* sp. nov. resemble those of the recent species *C. latrans* and *C. aureus*, which indicates that they may have shared the same life style with the Caucasian fossil coyote. *C. arnensis kudarensis* sp. nov. was presumably, a gatherer and lived in small groups. Its food is determined to include small mammals and other vertebrates as well as insects, fruits, and carrion.

The early evolution of the genus *Canis* is not well known. Many species from the Miocene and Pliocene of the North America and Eurasia, previously included into this genus, are now assigned to the genus *Eocyon* (Tedford *et al*., 2009; Sotnikova & Rook, 2011).

First representatives of the genus *Canis* (*C. ferox* Miller et Carranza-Castañeda, 1998) appear in the geological record of the North America in the Late Miocene (late Hemphillian, ca 6.0 Ma) (Tedford *et al*.,

Table 7. Measurements (in mm) of limb bones of Caucasian fossil *Canis*.

Bones	Localities and museum number	Measurements						
		GL	GB	Bp	Dp	SD	Bd	Dd
Fore limb								
C. arnensis kudarensis								
Humerus	Kudaro 3 (ZIN 36615)						28.6	
Radius	Kudaro 1 (ZIN 36613)			16.4	10.2			
Mc2	Kudaro 1 (ZIN 36606-2)			8.0	11.0			
C. mosbachensis								
Pisiform	Kudaro 1 (ZIN 31888-2)	20.9	11.5					
Mc4	Kudaro 3(ZIN 32022-3)					8.3	10.5	11.4
C. lunellensis								
Mc3	Kudaro 3 (ZIN 31884-6)						12.3	
Mc4	Kudaro 3 (ZIN 36644-1)			8.8	14.0	8.2		
C. lupus								
Humerus	Kudaro 1 (ZIN 36667)					17.8		
	Kudaro 3 (ZIN 36655)						42.6	
	Binagady (ZIN 22384-2)						44.7	
	Binagady (ZIN 22384-4)						39.4	
	Binagady (ZIN 22384-5)						42.1	
Radius	Kudaro 3 (ZIN 36658-6)					16.1		
Mc3	Kudaro 1 (ZIN 36650-1)			10.9	15.5			
Mc5	Kudaro 1 (ZIN 36648)			14.1	14.2			
	Kudaro 3 (ZIN 36653)			14.4	13.8	9.1		
Hind limb								
C. arnensis kudarensis								
Talus	Kudaro 1 (ZIN 36603-1)	25.5	17.7					
Calcaneus	Kudaro 1 (ZIN 36606-1)	40.6	15.5					
Navicular	Kudaro 1 (ZIN 36606-3)	9.0	14.5					
C. mosbachensis								
Patella	Kudaro 1 (ZIN 36628-1)	25.1	15.5					
Tibia	Kudaro 1 (ZIN 36632-1)						23.0	16.4
Mt3	Kudaro 1 (ZIN 36635)			11.9	17.4	9.0		
Calcaneus	Kudaro 3 (ZIN 32022-2)	-	21.4					
Mt5	Kudaro 1 (ZIN 36620-2)			10.5				
C. lupus								
Talus	Kudaro 3 (ZIN 36658-1)	33.1	24.5					
Calcaneus	Kudaro 3 (ZIN 36658-2)	55.4	24.1					

2009). To the end of Pliocene (Early and Late Blancan), this species has been replaced by the coyote-like canid *C. lepophagus*, which regards as the ancestor of the recent coyote *C. latrans* (Novak, 1979) or as the ancestor of all fossil species from the genus *Canis* in the North America (Tedford *et al*., 2009). At the end of Pliocene and during the Pleistocene, a group of small dogs with jackal-like dentition (*C. thooides*, *C. feneus* Tedford et al., 2009, and *C. cedazoensis* Mooser et Dalquest, 1975) evolved there. Beginning in the Late Pliocene (late Blancan) and until the Late Pleistocene (Irvingtonian), North America is inhabited by *C. edwardii* Gazin, 1942 sharing synapomorphies with the coyote (*C. latrans*) and with the golden jackal (*C. aureus*) (Tedford *et al*., 2009).

In Africa, the earliest find of *Canis* sp. is dated ca 3.5 Ma (South Turkwel) (Werdelin & Lewis, 2000). It represents the oldest record of the genus *Canis* outside North America, testifying to dispersal of this genus from North America across Eurasia as early as the Early Pliocene.

In Eurasia, a *Canis*-like dog of uncertain taxonomic assessment has been found at Vialette in France, which is dated ca 3.14 Ma (Lacombat *et al*., 2008). However, reliable finds of *Canis*, judging from isolated remains of these canids in St. Vallier (Argant, 2004) and Costa di S. Giacomo (Sardella & Palombo, 2007) are attributed by the end of Pliocene (near 2.2 Ma). In the Early Pleistocene, *lepophagus*-like canids might have migrated to Eurasia through Beringia and given rise to *C. arnensis*.

The molecular data reveal close relationships between *C. latrans*, *C. aureus* and *C. lupus* (Zravý & Řičánková, 2004; Bardeleben *et al*., 2005a), indicating a possible common ancestor of probable Holarctic origin. Phylogenetic analysis, based on the skeletal and dental characters, unites *C. latrans*, *C. aureus* and *C. mosbachensis* into a single clade (Wang *et al*., 2004;

Tedford *et al*., 2009). The Africal jackals (*C. mesomelas*, *C. adustus*) are regarded, on the basis of molecular genetic studies, to be a sister taxon to other species of *Canis* (Bardeleben *et al*., 2005b) or to other *Canis* + *Cuon*/*Lycaon* (Zravý & Řičánková, 2004).

†*Canis arnensis kudarensis* Baryshnikov **subsp. nov**.

Etymology. The name is derived from the Kudaro caves.

Holotype. Maxilla ZIN 31889-1, Kudaro 1 Cave, layer 5; collector V.P. Lioubine, 1959 (Fig. 1A). Holotype measurements are given in Tab. 1.

Diagnosis. Small coyote-like canid, resembling in the size of cheek teeth *C. arnensis* from the Early Pleistocene of Mediterranean Europe, but differing from it by derivative characters of the tooth morphology: the M1 paracone is markedly enlarged, p3 lying below p2 and p4.

Distribution. Middle Pleistocene of Southern Caucasus (Kudaro caves).

†*Canis mosbachensis* Soergel, 1928

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: left maxilla with P4–M2 (ZIN 36621, layer 5, horizon 5, 1957); left upper canine (ZIN 36624, layer 5, horizon 8, 1958); left P1 (ZIN 36640, layer 5c, horizon 2, 1984); right P3 (ZIN 36626, layer 5, horizon 8, 1958); left mandible with p2, p4 and m1 (ZIN 36643, layer 5f, horizon 1, 1987); right mandible fragment with m1 (ZIN 31888-1, layer 5, lens R, 1980); right mandible fragment with m2 (ZIN 36623-1, layer 5, horizon 5, 1958); left lower canine (ZIN 36625, layer 5, horizon 8, 1958); tree right lower canines (ZIN 36619, layer 5, horizon 4, 1957; 36620-1, layer 5, horizon 4, 1957; 36630-1, layer 5, horizon 3, 1959); left p1 (ZIN 36631, layer 5, horizon 3, 1959); right p1 (ZIN 36634, layer 5, horizon 3, 1961); left p3 (ZIN 36642, layer 5f, horizon 1-2, 1987); two right p4 (ZIN 36629, layer 5, horizon 2, 1959; 36638-1, mixed layers, 1980); fragment of right p4 (ZIN 36636, layer 5, horizon 9, 1961); left m1 (ZIN 31886, layer 5, horizon 8); fragment of left m1 (ZIN 36628-3, layer 5, horizon 1, 1959); two left m2 (ZIN 36641, layer 5c, horizon 4, 1986; 31887, layer 5c, horizon 4, 1980); right m2 (ZIN 36618, layer 5, horizon 2, 1957); right pisiform bone (ZIN 31888-2, layer 5, lens R, 1980); right patella (ZIN 36628-1, layer 5, horizon 1, 1959); left tibia (ZIN 36632-1, layer 5, horizon 5, 1959); proximal fragment of right Mt3 (ZIN 36635, layer 5, horizon 6, 1961); right cuneiform (ZIN 36639, layer 5c, horizon 2, 1984). Kudaro 3 Cave: left mandible fragment with p2 (ZIN 32023-1, layer 8a, 1981); right mandible fragment with p3 (ZIN 32022-1, layer 8, 1981); left lower canine (ZIN 32023-2, layer 8a, 1981); fragment of right Mc4 (ZIN 32022-3, layer 8, 1981); left calcaneus (ZIN 32022-2, layer 8, 1981); fragment of left Mt5 (ZIN 36620-2, layer 5, horizon 4, 1957). There are also vertebrae, phalanges and bone fragments; total 110 bones.

Description. Fossil remains of a small wolf from layer 5 in Kudaro 1 Cave have been previously assigned to *Canis* cf. *etruscus* (Baryshnikov, 1986), following the wide interpretation of the species *C. etruscus* Forsyth Major, 1877, owing to the fact that it comprises all European medium-size forms of *Canis* from Late Pliocene to Middle Pleistocene (Bonifay, 1971). It was subsequently pointed out that, regarding the smaller wolf from the Early and Middle Pleistocene as a separate species *C. mosbachensis*, the Kudaro material should be considered to belong to this species (Baryshnikov, 1986: 38).

The left maxilla ZIN 36621 (Fig. 1B) exhibits the length of the upper carnassial tooth P4 (22.2 mm) exceeding the length of this tooth in *C. mosbachensis* from the sample from Stránska skála in the Czech Republic (19.8–21.0 mm, n=5) (Tab. 8), but, nevertheless, falling into the value limits for this parameter in

Table 8. Measurements (in mm) of maxilla in *Canis mosbachensis* and *C. etruscus*.

Measurements	*C. mosbachensis*			*C. etruscus*
	Kudaro 1 Cave, layer 5	Stránska skála, Czech Republic	Westbury Quarry Cave, England	Olivola, Italy
	ZIN 36621	MMBA 1532	NHM 47669	MNHN 1891-11
Length P1–M1			68.6	
Length P1–P4			56.5	
Length P4–M1	34.2			
Teeth				
P2 L			11.9	
W			5.0	
P4 L	22.2	19.9	22.4	19.8
Lpa	14.6	13.0		12.4
W	10.8	10.0	10.3	10.0
M1 L	13.6	13.2	14.4	14.4
Lpa	7.5		8.2	7.7
W	16.3	16.4	16.8	16.4
M2 L				7.5
W				10.4

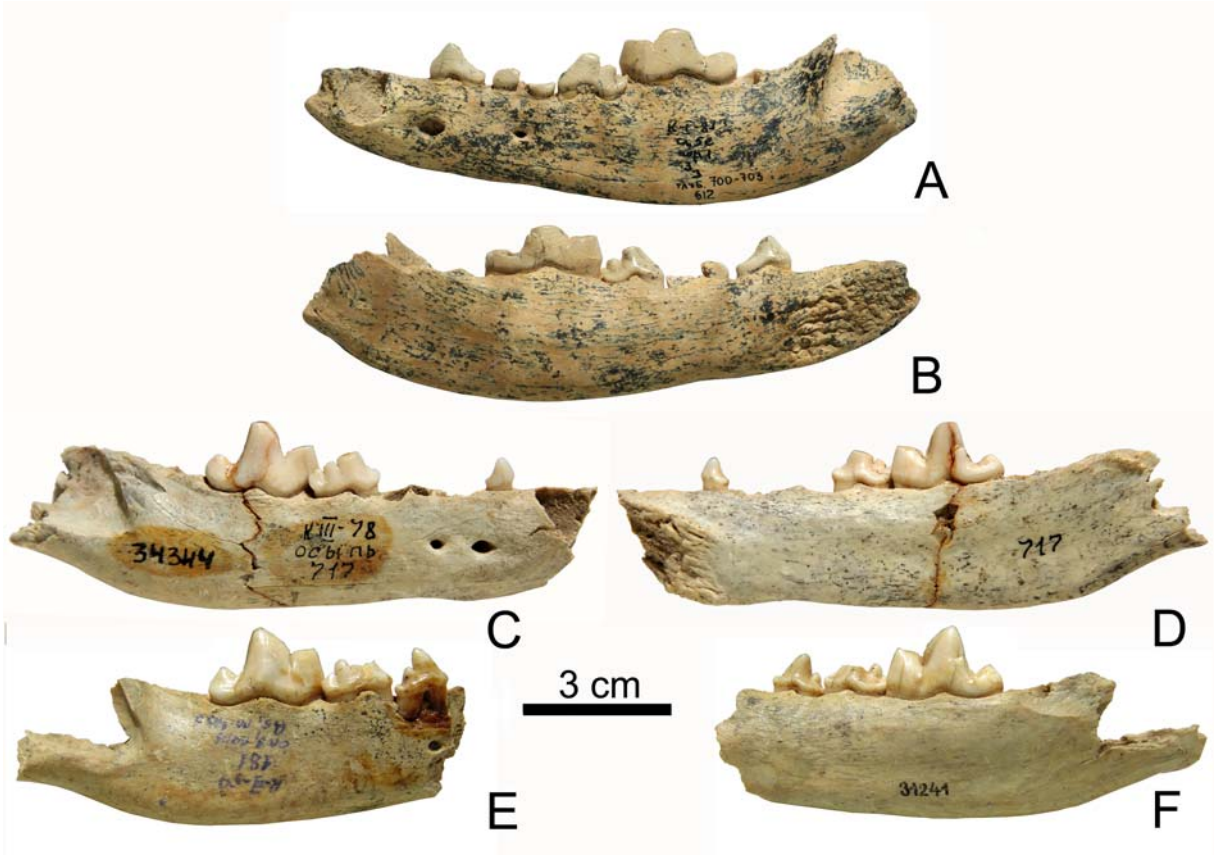

Figure 5. Mandibles of *Canis mosbachensis* from Kudaro 1 (A, B) and *Cuon alpinus caucasicus* from Kudaro 3 (C–F); labial (A, C, E) and lingual (B, D, F) views.
A, B — ZIN 36643; C, D — ZIN 34344; E, F — ZIN 31241, holotype.

the sample from Untermaßfeld in Germany (20.4–23.0 mm, n=9; Sotnikova, 2001). The length and width of the molar M1 lie in the range of minimum values for these measurements in *C. mosbachensis*, in the sample from l'Escale in France (Bonifay, 1971).

The upper canine from Kudaro 1 Cave (ZIN 36624) resembles in its shape that of *C. lupus*, being, however, slightly smaller in the size (Tab. 2). Its length and width are placed within the limits of these measurements in the samples from Untermaßfeld.

P1 is single-cusped. The tooth P3 has the posterior cusp markedly developed. The upper carnasial tooth P4 with small protocone, which is situated approximately at the level of the anterior wall of paracone; there is a distinct concavity between anterior margins of both cusps. There is a weak labial cingulum, showing, however, better development in comparison with that in *C. lupus*. Paracone of M1 is markedly enlarged relatively to metacone. Protocunule is present. Protocone is noticeably higher than metaconule. Hypocone is high and non-divided. The upper margin of the tooth crown bears cingulum, which runs as far as the hypocone and merges with it. The labial cingulum is well-developed and complete.

The length of c1–m3 in the mandible ZIN 36643 (Fig. 5A, B; Tab. 9) from layer 5 in Kudaro 1 Cave does not exceed limits of variation of this length in *C. mosbachensis* from Untermaßfeld in Germany (Sotnikova, 2001). The mandible fragment ZIN 31888-1 (Fig. 3A, B) from layer 5 (lens R) in Kudaro 1 Cave has a similar alveolar length of p3–m1 (48.5 mm) and ramus height in front of m1 (21.3 mm) to specimens of *C. mosbachensis* from Voigstedt in Germany (Thenius, 1965).

The shape and dimensions of lower premolars p1–p4 from the Kudaro collection are the same as those in *C. mosbachensis* (Tab. 5). The premolar p2 is missing a posterior cusp (Fig. 3K); this cusp is small in p3 and well-developed in p4 (Fig. 3L).

Earlier two specimens of the lower carnassial tooth m1 from Kudaro 1 Cave (ZIN 31886 and 31888-1; Fig. 3A–D) have been provisionally assigned to *C. arnensis*, since these specimens occupy an intermediate position by their size between the samples of *C. arnensis* and *C. mosbachensis* (Baryshnikov & Tsoukala, 2010). However, the present study reveals that the lower carnassial tooth m1 from layer 5 in Kudaro 1 Cave corresponds in its dimensions to those of *C. mosbachensis* from Mosbach in Germany, Stránska skála in Czech

Table 9. Measurements (in mm) of mandibles in *Canis mosbachensis*.

Measurements	Kudaro 1 Cave, layer 5e	Westbury Quarry Cave, England	Perrier, France	Stránska skála, Czech Republic	Mosbach, Germany	
	ZIN 36643	NHM 33940	MNHN n/n	MMBA 1477	NMM 1910/411	NMM 1910/113
Length c1–m3	ca.98.7		90.0			
Length p1–m3					87.1	
Length p2–m2	ca.72.9	76.5				
Length p3–m2	ca.60.3					
Length p2–p4	39.9					41.2
Length m1–m3	ca.40.9	40.9	38.7		39.7	38.1
Height before m2	23.8	27.9	21.0		24.6	24.8
Height before p3	19.5	20.9				
Teeth						
p1 L					5.4	
W					4.1	
p2 L	11.3	12.1	11.0	10.9	11.7	11.7
W	4.8	5.6	4.9	4.7	5.2	5.7
p3 L	13.0	13.3	12.3	12.3	13.9	12.7
W	–	5.8	5.1	5.1	6.4	6.0
p4 L	14.0	14.8	13.9	14.1		14.7
W	6.2	7.1	6.1	6.5		6.9
m1 L	23.9	25.3	23.4	23.3	24.9	23.8
Lpad	8.6	–	7.4	–	–	–
Ltald	6.8	8.5	7.2	6.4	6.9	6.8
W	9.5	10.9	8.5	8.2	9.8	9.2
m2 L		10.5	10.0	9.4	10.5	9.8
W		8.3	7.3	6.7	7.7	6.8
m3 L						4.5
W						4.5

Republic and from Westbury Quarry in England (Tab. 6). The paraconid blade is turned inwards by a smaller angle than in the recent *C. lupus* from Caucasus and in *C. lupus* from the Late Pleistocene locality of Binagady in Azerbaijan. The anterior part of the tooth crown is distinctly sloped; as a result, its labial wall forms an angle. Both aforementioned characters were regarded by Thenius (1954) as characteristic of *C. mosbachensis*; however, those were found to be variable. The protoconid steeply descends to the talonid, anterior and posterior ridges of the former apically meet one another at a sharper angle compared to that in recent *C. lupus*. The protostylid is developed. The metaconid is robust; in the superior view, it oversteps the bounds of the crown contours. Within the sample taken from the Upper Pleistocene (Mousterian) layers in the Kudaro caves and in Binagady, the metaconid is less robust and does not exceed the limits of tooth-crown contours. The talonid is comparatively longer than that in the tooth of the recent Caucasian *C. lupus*. The talonid basin is deep and more closed from the lingual side in contrast to *C. lupus*. The hypoconid is higher than the entoconid and slightly shifted forwards, its outer wall is steep. There is a tiny entoconulid. The small hypoconulid shelf bears a short well-developed transverse ridge (postcristid) connecting hypoconid and entoconid. There is a weakly developed cingulid at the hypoconid base, which extends beyond the posterior margin of the talonid.

The lower molar m2 is slightly shorter than that of *C. mosbachensis* from European localities (Tab. 6). The protoconid is larger and taller than the metaconid, with the only exception for the specimen (ZIN 36641) with the metaconid exceeding the protoconid in height. The talonid exhibits a basin and a distinct hypoconid. The labial cingulid is well developed, especially in the anterolabial part of the crown, where it is more pronounced than in the recent *C. lupus* from Caucasus.

Bones of the postcranial skeleton are few and fragmentary. Their dimensions are smaller compared to those of the same bones in *C. lupus* from the Late Pleistocene layers in Kudaro caves and resemble postcranial bone parameters of *C. mosbachensis* from Untermaßfeld (Sotnikova, 2001). In the fragment of the second cervical vertebra (axis) (ZIN 36734), the breadth at the cranial articulatory surface constitutes 34.6 mm.

By its size and dental morphology, the small wolf from the Middle Pleistocene fauna of Kudaro caves may be assigned to *C. mosbachensis*. Tooth measurements fall into the limits of their variation for the samples of this species from these European localities:

Westbury Quarry in England, l'Escal in France, Untermaßfeld, Süßenborn and Voigstedt in Germany, Hundsheim in Austria, and Stránská Skála in Czech Republic (Soergel, 1928; Thenius, 1954, 1965; Schaefer, 1969; Bonifay, 1971; Musil, 1972; Bishop, 1982; Sotnikova, 2001). At the same time, the length of the lower carnassial tooth m1 from Kudaro caves is smaller than that in C. *etruscus* from the localities of Olivola and Upper Valdarno in Italy (Tab. 10) and Ozernoe in Ukraine (De1 Campana, 1913; Torre, 1967; Baryshnikov, 1986).

Discussion. Bone remains of *C. mosbachensis* are recorded only in the lowermost levels of both Kudaro caves: in layer 5 of Kudaro 1 Cave and in layers 8–8a of Kudaro 3 Cave. These findings testify the presence of this species in Southern Caucasus in the middle part of Middle Pleistocene, i.e. its survival there longer than in Western Europe.

The Mosbach small wolf was, presumably, a less specialized predator in comparison with *C. lupus*. It was capable of hunting smaller ungulates and hares, rodents, and birds and consuming carrion, fruits, and other vegetable food.

In the Southern Caucasus, *C. mosbachensis* appears to include the small wolf from the Early Pleistocene locality Akalkalaki in Georgia, whose remains were described as the new species *C. tengesii* (Vekua, 1962). The length of m1 teeth (22.2 and 23.0 mm) of this species corresponds to that of *C. mosbachensis*. In the Northern Caucasus, *C. mosbachensis* has been identified in the Middle Pleistocene locality of Treugolnaya Cave, on the basis of two specimens of m1 measuring 21.9 and 23.0 mm (Baryshnikov, 1994).

Several researchers assign medium-size wolves from the Early and Middle Pleistocene of Europe to a single species *C. etruscus* (Bonifay, 1971; Pons Moya, 1987; Brugal & Boudadi-Maligne, 2011). Other authors regard the Middle Pleistocene wolf as a separate species *C. mosbachensis* (Musil, 1972; Sotnikova, 2001; Tedford *et al*., 2009) or subspecies *C. lupus mosbachensis* (Thenius, 1954; Kurtén, 1969; Kurtén & Poulianos, 1977). Brugal & Boudadi-Maligne (2011) point out that *C. etruscus mosbachensis* differs from *C. lupus* in the ratio of the length of the trenchant portion of the lower tooth row (premolars p1–p4 + m1 trigonid) to the length of its crushing portion (m1 talonid + molars m2-m1). Sotnikova (2001) notes *C. mosbachensis* has a more derived lower carnassial tooth m1 compared to the carnassial tooth of *C. etruscus* and, in contrast to *C. lupus*, shows a trend to the complication of cusps on the talonid of m1. The latter peculiarity is clearly traced in the material from Kudaro 1 Cave.

Tedford *et al*. (2009), in their phylogenetic analysis, link *C. mosbachensis* to the species *C. variabilis* Pei, 1934 from China (Zhoukoudian locality 1) and to *C. palmidens* Teilhard de Chardin et Piveteaua, 1930 from China (Sangkanhe near Nihowan), considering these species as a sister group to the clade *C. aureus*/*latrans*, which is derived by these authors from *C. edwardii*.

†*Canis lunellensis* Bonifay, 1971

Referred specimens. Middle Pleistocene, Kudaro 3 Cave: left maxilla with isolated P3, P4 and M1–2 (ZIN 31885-2, 3, 4, layer 7, 1981); left maxilla with P2–M2 (ZIN 31884-1, layer 6, 1980); right maxilla with P4–M2 (ZIN 31885-1, layer 7, 1981); left P1 (ZIN 36646, layer 5, horizon 2, 1974); left P3 (ZIN 36647, layer 5, 1978); right P3 (ZIN 31884-5, layer 6, 1980); left mandible with p2–m2 (ZIN 31884-2, layer 6, 1980); right mandible with p2 and p3 (ZIN 31884-2, layer 6, 1980); fragment of right m1 (ZIN 36645, layer 7, 1980); right m1 (ZIN 31884-3, layer 6, 1980); distal fragment of right Mc3 (ZIN 31884-6, layer 6, 1980); proximal fragment of left Mc4 (ZIN 36644-1, layer 6, 1980); in total, 15 fossil fragments were examined.

Description. Earlier the fossil remains of the small wolf from layers 6–7 of the Kudaro 3 Cave were assigned to *C. lupus* ssp. of the same evolutionary stage as *C. lupus lunellensis* from Lunel-Viel (Baryshnikov, 1986). This taxon is sometimes considered to have a species rank *C. lunellensis* (Palombo & Valli, 2004), which is used in the present study.

The maxillary fragments (ZIN 31884, 31885-2) from layers 6 and 7 in Kudaro 3 Cave have P4 and M1 longer compared to those in ZIN 36621 (*C. mosbachensis*) (Tab. 11), which corresponds to measurements of these teeth in *C. lunellensis* from Lunel-Viel (Bonifay, 1971). The upper carnassial teeth P4 within the Kudaro maxillas are nearly equal in length with the molar row M1-M2 (97.4–100.9%, n=3); at the same time, the specimens of P4 from Lunel-Viel virtually are always longer than the molar row. In the recent *C. lupus* from Caucasus, P4 is approximately equal in length with M1–M2 (92.2–109.4%, n=39) (Baryshnikov, 1986)

Major axes of P3 and P4 coincide. P2 is worn, and it is hard to ascertain the level of development of its posterior cusp. The tooth P3 exhibits this cusp markedly developed. The upper carnassial tooth P4 resembles in its shape the corresponding tooth of *C. lupus*. Its protocone is situated at the level of the anterior margin of the tooth crown. This cusp may be large (ZIN 31885-1; Fig. 6B) or non-developed (ZIN 31884-1; Fig. 6A). The depression between anterior margins of the paraconid and protoconid is shallow. M1 has a large inner portion and well developed complete anterolingual cingulum (in *C. lupus* it is less marked and interrupted). There is a distinctive parastyle. The paraconule is present. The hypocone is high and may be occasionally divided. The labial cingulum is well developed and complete.

The mandible ZIN 31884-2 from layer 6 of Kudaro 3 Cave falls, by the length of the lower carnassial tooth m1 (Tab. 10), into the area of minimum length values for this tooth in *C. lunellensis* from Lunel-Viel and corresponds in alveolar length of m1–m3 to specimens of *C. mosbachensis* from Untermaßfeld (Sotnikova, 2001).

The lower premolar p2 is characterized by a posterior cusp and p3 has two posterior cusplets. The lower

Table 10. Measurements (in mm) of mandibles in *Canis etruscus* and *C. lunellensis*.

Measurements	*C. etruscus*		*C. lunellensis*
	Ponte Molle, Italy	Olivola, Italy	Kudaro 3 Cave, layer 6
	IGPR n/n	MNHN 1891-11	ZIN 31884-2
Length c1–m3			
Length p2–m2			
Length p3–m2			61.4
Length p2–p4			
Length m1–m3	41.0	ca39.0	39.3
Height before m2	27.4	24.5	
Height before p3	22.0		
Teeth			
p2 L	11.2		
W	5.5		
p3 L			12.8
W			6.0
p4 L			14.9
W			7.6
m1 L	25.6	23.6	24.1
Lpad	8.7	7.3	8.0
Ltald	7.4	7.3	5.7
W	10.0	9.7	9.4
m2 L	10.9	10.2	10.9
W	7.5	7.6	7.4

Table 11. Measurements (in mm) of maxilla in *Canis lunellensis* and *C. chihliensis*.

Measurements	*C. lunellensis*			*C. chihliensis*
	Kudaro 3 Cave, layer 7	Kudaro 3 Cave, layer 7	Kudaro 3 Cave, layer 6	Locality 64, Fengwo near Huanglu, China
	ZIN 31885-1	ZIN 31885-2,3	ZIN 31884-1	MEU 3496, holotype
Length P1–M2			81.7	
Length P4–M2	43.0		42.7	46.0
Length P4–M1	36.3		35.3	
Length M1–M2	24.0	24.1	23.3	
Teeth				
P2 L			12.0	
W			5.3	
P3 L		14.4	13.8	14.0
W		6.1	5.7	6.3
P4 L	23.0	22.9	23.0	23.9
Lpa	15.9	15.4	14.9	15.3
W	13.2	12.45	11.5	13.3
M1 L	15.0	14.6	14.3	16.6
Lpa	7.9	7.9	7.7	8.8
W	20.2	19.5	18.2	19.2
M2 L	8.2	8.9	8.7	9.3
W	12.9	13.35	12.2	13.0

carnassial tooth m1 is morphologically similar to that of the recent *C. lupus*. The talonid of ZIN 31884-2, 31884-3 and 36645 (Fig. 3E, H) is more shortened with regard to the tooth greatest length than in *C. mosbachensis*. Both specimens show worn talonid; however, it may be hypothesized that it had no entoconulid and possessed shallow talonid basin. No clear postcristid on the hipoconulid shelf is observed. In *C. lunellensis* from Lunel-Viel, the entoconulid is also absent (Bonifay, 1971).

Tooth measurements of *C. lunellensis* from Kudaro 3 Cave conform to their minimum values in recent *C. lupus* from Caucasus. The length of P4 in the latter species varies from 22.8 to 29.0 mm (n=39), the length of m1 is measured 24.2–31.0 mm (n=40). In *C. lunellensis* from Lunel-Viel, these dimensions constitute 21.7–24.8 mm (n=14) for P4 and 23.8–27.4 mm (n=12) for m1 (Bonifay, 1971). Thus, *C. lunellensis* and *C. lupus* are similar in length of the carnassial teeth, differing, however, in their proportions.

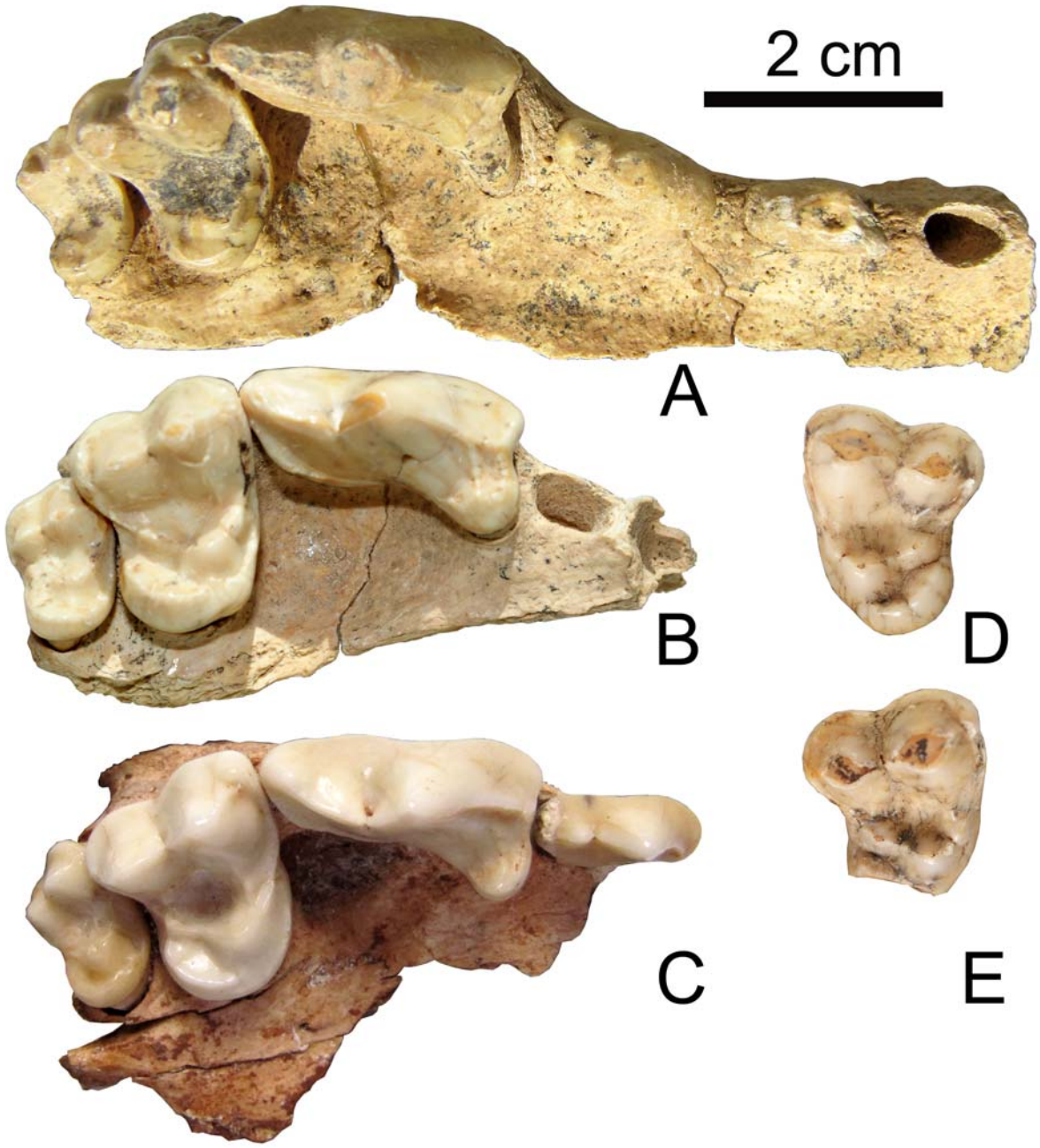

Figure 6. Maxilla fragments (A–C) and upper molar M1 (D, E) of *Canis lunellensis* (A, B) and *C. lupus* (D, E) from Kudaro 3 Cave, and *C. chihliensis* (C); occlusal view.
A — ZIN 31884-1; B — ZIN 31885-1; C — MEU 3496, holotype; D — ZIN 31882-2; E — ZIN 31882-1.

Discriminant Analisys was performed on the basis of three measurements of m1 (L, Ltald, W) for 6 samples of *C. mosbachensis*, *C. lunellensis*, and *C. lupus*. In the resulting scatterplot of canonical scores, the teeth of *C. mosbachensis* from Kudaro caves are grouped together with the teeth of this species from European localities (Fig. 7). These are well separated from teeth of *C. lupus* by Root 1 (measurements L, W; 95.4% of dispersion), i.e. by the total size. The sample of *C. lunellensis* from layers 6–7 of Kudaro 3 Cave locates near *C. mosbachensis* and does not exceed the bounds of variation of recent Caucasian *C. lupus*.

C. lunellensis from Kudaro 3 Cave resembles in size and morphology the upper cheek teeth of *C. chihliensis* Zdansky, 1924 from the Early Pleistocene of China (Tab. 11; Fig. 6C). Both species are characterized, in particular, by a pronounced development of the anterolingual cingulum in M1.

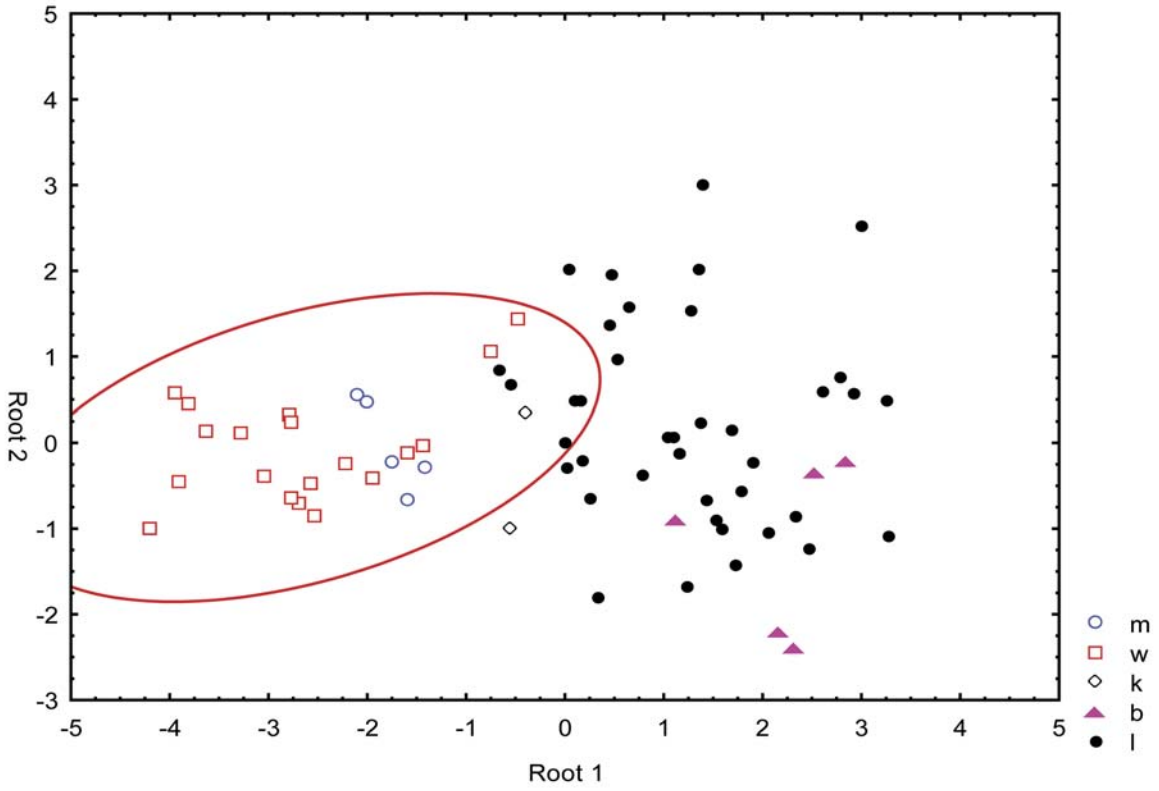

Figure 7. Scatterplot of canonical scores of Root 1 and Root 2 from discriminant analysis of lower carnassial tooth m1 in *Canis*. *C. mosbachensis*: m — Kudaro 1, layer 5, w — Westbury Quarry and Stránska skála; *C. lunellensis*: k — Kudaro 3, layer 6–7; *C. lupus*: b — Binagady, l — Caucasus, recent.

Discussion. Bones of a small wolf from the Middle Pleistocene layers 5–7 in Kudaro 3 Cave are assigned to *C. lunellensis.* This species, therefore, occurred in Caucasus until nearly the end of the Middle Pleistocene (Saalian, OIS 7, near 0.20–0.25 Ma; Baryshnikov, 2002).

Presumably, a considerable portion of large carnivore tooth-marks found on the bones from the lower layers of Kudaro 3 Cave was created by *C. lunellensis*. One bone (calcaneus ZIN 31885-5 from the layer 7 of the Kudaro 3 Cave) of *C. lunellensis* has the pathological enlargement of proximal end.

The small wolf *C. lunellensis* has been described from the Lunel-Viel collection as a subspecies *C. lupus lunellensis* (Bonifay, 1971). Later, new material was found resembling this subspecies in measurements and geological age (Rameaux, Coudoulous I, Balaruc VII and La Fage localities) (Argant, 2009; Brugal & Boudadi-Maligne, 2011). Some researchers believe this small wolf should be treated as a separate species *C. lunellensis*, confined to the biochon MNQ23a–MNQ23b, i.e. to the middle and late Galerian, approximately 0.6–0.4 Ma (Palombo & Valli, 2004). The discoveries from the Kudaro caves are consequently the youngest for this taxon.

Most researchers include *C. lunellensis*, as a subspecies, in *C. lupus* (Tedford *et al*., 2009; Brugal & Boudadi-Maligne, 2011). *C. chihliensis*, which is described from Locality 64 in China (Zdansky, 1924), has been also compared with to *C. lupus* (Tedford *et al*., 2009). Hence, both taxa may be regarded as ancestral to *C. lupus*.

Canis lupus Linnaeus, 1758

Referred specimens. Late Pleistocene, Kudaro 1 Cave: right C1 (ZIN 36649-1, layer 4, 1958); left p3 (ZIN 36649-2, layer 4, 1958); right Mc3 (ZIN 36650-1, layer X-4, horizon 1, 1978); left Mc5 (ZIN 36648, layer 3b-c, 1957). Kudaro 3 Cave: skull fragment with incisor alveolar sockets (ZIN 36684-5, layers 3–4, 1975); right maxilla with P3–M1 (ZIN 31880, layer 3, horizon 2, 1959); two left C1 (ZIN 36657-1, layer 4f, 1978; 36654, layer 3b, horizon 2, 1977); left M1 (ZIN 31882-2, layer 4, horizon 5, 1975), right M2 (ZIN 31882-1, layer 4, horizon 5, 1975), right M2 (ZIN 31883-3, layer 4f, 1980); left mandible fragment with p3–m1 (ZIN 31883-1, 2, layer 4f, 1980); two left c1 (ZIN 36651, layer 4, horizon 3, 1959; 36652, layer 4, horizon 6, 1975); right m1 (ZIN 31881, layer 4, horizon 5, 1974); right humerus fragment (ZIN 36655, layer 3e, horizon 2, 1977); radius fragment (ZIN 36658-6, mixed layers, 1978); right Mc5, sad. (ZIN 36653, layer 3, horizon 2, 1977); left talus (ZIN 36658-1, mixed layers, 1978); right calcaneus (ZIN 36658-2, mixed layers, 1978); several vertebrates, phalanges and small bone fragments. Total 130 fossil remains.

Description. Remains of *C. lupus* are not numerous in the Kudaro caves, being represented by several teeth and postcranial bone fragments. Tooth dimensions and morphology provide a basis for division of these findings into two groups.

Specimens of the first group are confined to the lowermost horizons of layer 4 of Kudaro 3 Cave. Two isolated upper molars M1 (ZIN 31882; Fig. 6D, E) exceed in their length those of *C. lunellensis* from Kudaro 3 Cave. Their metastyles are less developed and antero-lingual cinguli are interrupted.

Two lower carnassial teeth m1 (ZIN 31881, 31883-2; Fig. 3F, G) from the same stratigraphical level correspond by the greatest length (25.6 mm, 26.1 mm) to the largest specimens of *C. lunellensis* from Lunel-Viel in France (Bonifay, 1971) and correspond to mean value of this measurement of *C. lupus* from Middle Pleistocene locality La Fage in France (Martin, 1975). They are smaller in this measurement than the teeth of the wolf in the sample from Binagady in Azerbaijan (27.0–29.7 mm, *n*=5) and are placed near the lower limit for the values of this measurement in the recent *C. lupus* from Caucasus (25.2–31.0 mm, *n*=38). In the length and width, these teeth are similar to the teeth of *C. lunellensis* from Lunel-Viel. Both Kudaro specimens noticeably diverge in shape. ZIN 31881 has a deep talonid basin, well-developed entocolulid, and protocristid. These characters associate it with *C. mosbachensis*. The second specimen ZIN 31883-2 resembles this tooth in *C. lupus*: its talonid basin is shallow and more opened on the lingual side in comparison with *C. mosbachensis*; entocolulid and protocristid are absent. In the scatterplot of canonical scores, obtained as a result of Discriminant Analysis, both Kudaro specimens are placed between the samples of *C. mosbachensis* and *C. lupus* and fall into the limits of variation of the measurements of *C. lupus* (Fig. 7).

Gray wolves from the second group of fossil remains from upper stratigraphical levels show size and tooth morphology similar to those of the recent Caucasian subspecies *C. lupus cubanensis* Ognev, 1922. For example, one of these parameters is the alveolar width of the of upper-incisor row (32 mm) in the skull fragment ZIN 36684-5.

The maxilla ZIN 31880 (Fig. 1D) found in layer 3 of Kudaro 3 Cave is characterized by the greatest length of the upper carnassial tooth P4 (24.6 mm) inconspicuously exceeding that of corresponding teeth within the sample from the Binagady locality (23.8 mm, 23.8 mm, *n*=2) and falling into the range of variation of this dimension in the recent *C. lupus* from Caucasus (22.8–29.0 mm, *n*=39). Similar size of P4 is known for the Late Pleistocene wolves from the West-European localities (Bigaj, 1963); their contemporaries were larger in European Russia (Tab. 12). The anterolingual cingulum of M1 is interrupted. Its labial cingulum is well developed at the basis of metacone and extremely weak at the basis of protocone, as in the recent *C. lupus*.

Discriminant Analysis performed on the basis of three measurements of m1 (L, Ltal, W) reveals that nearly all fossil teeth of *C. lupus* from Binagady in Azerbaijan are located on the graph within the area of the sample of recent *C. lupus* from Caucasus (Fig. 7), with only two fossil specimens differing in the longer talonid.

Vereshchagin (1951) described the wolf from Binagady as the fossil subspecies *C. lupus apscheronicus*,

Table 12. Measurements (in mm) of maxilla in Late Pleistocene *Canis lupus*.

Measurements	Kudaro 3 Cave, layer 3	Bunagady, Azerbaijan		Kostenki, Voronezh Region, European Russia		Bern-burg, Germany	Zoolithen, Germany		Khapta-shinsky Yar, Yakutia, Russia
	ZIN 31880	ZIN 21919-1	ZIN 22384-53	ZIN 34327, "*brevis*" holotype	ZIN 36233	NHM 38144	NHM 403	NHM 404b	GMY 3728
Length P3–M1	53.6	51.6	53.2	59.9					
Length P4–M1	38.3	36.0	37.5	42.0					
Length M1–M2		23.5	25.0	25.6		25.7	24.0	27.3	
Teeth									
P2 L		13.0		15.7	14.8	14.5			
W		5.7		6.8	6.7	6.3			
P3 L	16.2	14.4		17.5		15.7			17.5
W	7.0	6.5		8.0		7.2			7.3
P4 L	24.6	23.8	23.8	27.7	27.2	25.5	23.8	26.8	26.7
Lpa	16.8	15.7	15.1	19.3	18.4	8.1	7.8	9.4	8.5
W	13.5	13.1	10.6	17.6	14.6	12.8	15.0	16.3	13.4
M1 L	15.3	14.9	16.4	16.8	17.6	16.7	15.9	17.8	16.2
Lpa	8.1	8.0	8.8	9.4	8.8	8.8	9.0	10.2	8.4
W	19.8	19.4	20.4	22.1	20.6	20.2	18.0	21.0	20.5
M2 L		8.1	8.5	9.4		9.7	7.9	9.7	9.5
W		13.5	12.8	13.3		13.4	10.7	12.6	12.9

Table 13. Measurements (in mm) of lower cheek teeth in Late Pleistocene *Canis lupus*.

Measurements	Museum number	p3		p4		m1			
		L	W	L	W	L	Lpad	Ltald	W
Caucasus									
Kudaro 1, layer 4	ZIN 36649-2	13.7	5.8						
Kudaro 3, layer 4	ZIN 31883-1,2	12.9	5.9	14.0	7.3	26.1	8.0	8.0	9.8
	ZIN 31881					25.6	7.8	6.7	9.6
M. Vorontsovskaya	ZIN 31977			15.7	8.3				
	ZIN 31978	13.8	7.2			29.3	10.5	8.5	11.7
Binagady	ZIN 22384-43					29.7	10.5	8.5	11.5
	ZIN 22384-46	13.8	6.6	16.7	8.6	29.0	11.1	8.1	11.6
	ZIN 22384-47	13.7	7.4	15.4	8.5	28.0	9.7	6.2	11.4
	ZIN 22384-51	13.2	6.8	15.6	8.0	28.4	10.2	6.2	11.2
	ZIN 24408-1	12.5	6.3	15.3	7.6	27.0	9.6	7.1	11.1
Il'skaya 1, Northern Caucasus	ZIN 16569	14.9	7.2	16.1	8.5				
Europe									
Tornewton, England	NHM 40345	13.7	6.6	16.4	7.5	28.6	–	5.1	10.9
Kent's Cavern, England	NHM 15636	14.5	7.0	16.3	8.4	29.5	–	7.9	12.2
	NHM 849	13.5	6.7	15.8	7.8				
Zoolithen, Germany	NHM 403a	14.4	7.1	15.8	8.1	28.1	–	7.3	12.1
	NHM 404	14.3	7.1	16.5	8.5	29.0	–	7.2	12.1
	NHM 404c	14.1	7.4	17.1	8.9	30.4	–	8.6	12.6
Bernburn, Germany	NHM 38144	13.6	6.7	16.5	7.9	28.8	–	7.7	11.2
Wierzchowska Górna, Poland	ISAK 5967	12.8	5.7	14.8	6.4	24.5	–	7.5	10.1
	ISAK 5967	12.9	5.0	14.4	6.3	24.0	–	6.4	9.9
Vykhvatintsy, Moldova	IZKM n/n	13.2	6.6	15.9	8.4				
	IZKM n/n			16.1	8.1	27.0	9.7	7.9	11.5

regarding the presence of alveolus of M3 in two specimens from 33 examined as a primitive trait. He noted that the wolf from Binagady is distinguished from the recent subspecies *C. l. cubanensis* by skull proportions: comparatively longer braincase, longer upper tooth row, wider palate, and shorter temporal constriction.

The upper molar M1 demonstrates the interrupted anterolingial cingulum in both examined skulls from Binagady (ZIN 21919-1 and 22384-53). The talonid of m1 is markedly worn in most mandibles. Two unworn specimens are characterized by the talonid basin shallower as compared to *C. mosbachensis*; the entoconulid is developed in ZIN 22381-40 and absent in ZIN 22384-46. Measurements of m1 are given in Tab. 13.

Discussion. The paucity of bone remains of *C. lupus* in the Kudaro caves may be explained by their coming into the cave only on occasion. Wolf might have been sporadic prey of large cats (cave lion and leopard) using these karst cavities as shelters (see Baryshnikov, 2011).

Fossil remains of wolf occur throughout all Late Pleistocene cave layers, beginning with the earliest ones (lowermost horizons of layer 4 in Kudaro 3 Cave). The time of formation of these early levels is assigned to the Last Interglacial (Baryshnikov, 2002), but their age may be even older.

Wolf is represented in faunal lists for many Paleolithic sites of the Southern Caucasus (Bronzovaya, Bizonovaya, Medvezhiya and Verkhnyaya caves, Ortvala, Gvardzhikas-Klde in Georgia, Dashsalakhly in Azerbaijan, Erevanskaya in Armenia) and Northern Caucasus (Il'skaya, Barakaevskaya). The earliest record of the species in the Caucasus is associated with layer 5 of Azhych Cave in Azerbaijan, being ascribed to the second half of the Middle Pleistocene (Mindel-Riss and Riss) (Lioubine, 1989), and with the locality of Binagady near Baku dated by the Latest Interglacial (Eem) (Baryshnikov, 2002).

The appearance of *C. lupus* in Western Europe has been considered an important biostratigraphical marker of the late Middle Pleistocene (*lupus*-event; Azzaroli, 1983). However, this opinion was later replaced with the view that the most important events of the canid radiation took place earlier, during the latest Pliocene (Sardella & Palombo, 2007).

The subspecies *C. lupus lunellensis* is frequently regarded as the earliest European wolf (Bonifay, 1971; Tedford *et al*., 2009). Other researchers give this wolf the status of a separate species *C. lunellensis*, associating the earliest record of *C. lupus* with the local fauna of the upper complexes of grotte Caune de L'Arago in France, which correlates with OIS 9, near 0.30–0.35 Ma (Palombo & Valli, 2004), or in Pietra F.U. (about MIS 10-8) in Italy (Petronio *et al*., 2011). The earliest North American records of *C. lupus* are the arctic fossils from Yukon Territory (Old Crow) in Canada and from Alaska (Cripple Creek Sump), which date to the middle Pleistocene (Tedford *et al*., 2009).

The subsequent evolution of *C. lupus* was accompanied by an increase in size and comparative lengthening of its muzzle. The large fossil wolf has been described on the basis of the material from the Upper Paleolithic site Kostenki 1 (layer 1) in European Russia as the extinct subspecies *C. lupus brevis*, which is characteristic by shortened limbs (Kuzmina & Sablin, 1994). In the late Pleistocene, wolves inhabiting the northern part of Europe and the Arctic area of Siberia were not strictly predators, but also scavenged carcasses of mammoths, rhinos, and other megafauna. Presumably, they were more strongly pronounced osteophages than the recent animals (Baryshnikov *et al*., 2010).

The study of mitochondrial DNA of the recent *C. lupus* in Europe revealed two geographically overlapped haplogroups (Pilot *et al*., 2010). One of them also includes all fossil wolf samples from Western Europe. In North-America, this haplogroup was associated with a distinct wolf ecomorph becoming extinct to the end of the Pleistocene (Leonard *et al*., 2007).

Genus *Cuon* Hodgson, 1838

Cuon alpinus (Pallas, 1811)

†*Cuon alpinus caucasicus* Baryshnikov, 1978

Referred specimens. Late Pleistocene, Kudaro 1 Cave: skull fragment (ZIN 34350, layers 3–4, 1957); right I3 (ZIN 36665, layer 3a, 1961); right C1 (ZIN 36660, layer 3a, 1957; ZIN 36662, layer 3b, 1958), left C1 (ZIN 36736-1, layer 3b, 1961); left P1 (ZIN 36661-2, layer 3a, 1958), left P1 (ZIN 36659, layer 3c–4, 1957); left mandible with p4–m1 (ZIN 34339, layer 3a, 1959); right c1 (ZIN 36736-2, layer 3b, 1961); right p1 (ZIN 36661-1, layer 3a, 1958); atlas (ZIN 36738, layer X, horizon 4, 1978); left humerus (ZIN 36669, layer 3c, 1961); humerus fragment (ZIN 36667, mixed layers, 1977); left ulna ((ZIN 36733-1, layer 4, 1958); right ulna (ZIN 36739, layer X-2, horizon 1, 1980); left scaphoid (ZIN 36664-2, layer 3, 1959); right pelvis (ZIN 36668, layer X, horizon 4, 1978); left tibia (ZIN 36737-2, layer 3c, 1961); left calcaneus (ZIN ; 36730-1, layer 3c, 1958); right Mt2 (ZIN 36731-1, layer 3c–4, 1958); left Mt3 (ZIN 36663, layer 4, 1958); left Mt4 (ZIN 3666, lens "Z", 1961).

Kudaro 3 Cave: left maxilla with P4–M1 (ZIN34343, layers 3–4, 1975); left C1 (ZIN 36705-6, mixed layers, 1978; 36708-6, mixed layers, 1957); right C1 (ZIN 36684-4, layers 3–4, 1975); left mandible with p3-m1 (ZIN 31241, layer 3, horizon 3, 1959, holotype); left mandibles with p4–m1 (ZIN 34340, layer 4, horizon 2, 1974; 34342, layers 3–4, 1975); left mandible with p2, m1 (ZIN 34341, layers 3–4, 1975); left mandible with p1, p2, p4 (ZIN 34338, layer 4, horizon 3, 1959); left mandible fragment with p2 (ZIN 36675-1, layer 3, 1959); right mandible with p1, p4–m1 (ZIN 34344, mixed layers, 1978); left c1 (ZIN 36683, layer 4, horizon 3, 1974); right c1 (ZIN 36678, layer 3, horizon 2, 1974; 36696-1, layer 3e, horizon 1, 1977); right p1 (ZIN 36699, layer 3a, 1978); right p2 (ZIN 36703-2, layer 4d, 1978); axis (ZIN 36703-1, layer 4d, 1978; 36677-1, layer 3, horizon 1, 1974; 36679-2, layer 3, horizon 2, 1974; 36682-1, layer 4, horizon 2, 1974; 36697-1, layer 3e, 1977); right scapula fragments (ZIN 36705-3, mixed layers, 1977); left scapula fragments (ZIN 36692-1, layer 3d, 1977; 36696-3, layer 3e, horizon 1, 1977; 36708-4, mixed layers, 1957;); left humerus (ZIN 31241-2, layer 3, horizon 3, 1959; 36674, layer 3, horizon 5, 1959; 36684-1, layers 3–4, 1975; 36708-1, mixed layers, 1957); right humerus (ZIN 36679-1, layer 3, horizon 2, 1974; 36708-3, mixed layers, 1977); left ulna (ZIN 36698-1, layer 4a, 1977; 36677-2, layer 3, horizon 1, 1974; 31241-3, layer 3, horizon 3, 1959; 36705-7, mixed layers, 1978); right ulna (ZIN 36670-1, layer 2, 1959; 36697-2, layer 3e, 1977); left radius (ZIN 31241-4, layer 3, horizon 3, 1959; 36705-4, mixed layers, 1978); right radius (ZIN 36698-2, layer 4a, 1977; 36670-2, layer 2, 1959); left pisiform (ZIN 36704, layer 4d, 1979); left Mc2 (ZIN 36681-1, layer 3, horizon 4, 1974; 36702-4, layer 4ab, 1978); right Mc3 (ZIN 36673-3, layer 3, horizon 4, 1959); left Mc4 (ZIN 36698-4, layer 4a, 1977); left Mc5 (ZIN 36684-2, layers 3–4, 1975); right Mc5 (ZIN 36692-3, layer 3d, 1977); right pelvis (ZIN 36688-1, layer 3c, horizon 1, 1977); pelvis fragments (ZIN 31241-5, layer 3, horizon 3, 1959; 36681-3, layer 3, horizon 4, 1974); right femur (ZIN 36692-2, layer 3d, 1977; 36700-2, layer 3e, horizon 1, 1978); patella (ZIN 36688-5, layer 3c, horizon 1, 1977); left tibia (ZIN 36705-1, mixed layers, 1978; 36708-2, mixed layers, 1957); left tibia (ZIN 36702-3, layer 4ab, 1978); fibula fragments (ZIN 36691-4, layer 3c, horizon 3, 1977; 36685-2, layers 3–4, 1975); left talus (ZIN 36694-1, layer 3e, horizon 1, 1977; 36691-2, layer 3c, horizon 3, 1977); right talus (ZIN 36680-5, layer 3, horizon 3, 1974; 36695-1, layer 3e, horizon 1, 1977; 36693, layer 3d, 1977); left calcaneus (ZIN 36701, layer 3e, horizon 2, 1978; 36706, layer 4d, 1980; 36671-1, layer 3, horizon 1, 1959; 36672-2, layer 3, horizon 2, 1959); right calcaneus (ZIN 36676-1, layers 2–3, 1974); left navicular (ZIN 36676-3, layers 2–3, 1974; 36692-4, layer 3d, 1977); right navicular (ZIN 36691-3, layer 3c, horizon 3, 1977); left Mt2 (ZIN 36681-2, layer 3, horizon 4, 1974; 36700-1, layer 3e, horizon 1, 1978; 36671-2, layer 3, horizon 1, 1959); right Mt2 (ZIN 36698-3, layer 4a, 1977); left Mt3 (ZIN 36676-2, layers 2-3, 1974; 36691-1, layer 3c, horizon 3, 1977); right Mt3 (ZIN 36672-1, layer 3, horizon 2, 1959; 36685-1, layers 3–4, 1975); left Mt4 (ZIN 36708-5, mixed layers, 1957; 36684-3, layers 3–4, 1975; 36705-8, mixed layers, 1977; 36687, layer 4, horizon 5, 1975); right Mt4 (ZIN 36671-3, layer 3, horizon 1, 1959; 36702-1, layer 4ab, 1978); left Mt5 (ZIN 36682-4, layer 4, horizon 2, 1974; 36705-5, mixed layers, 1978; 36686, layer 4, horizon 3, 1975); right Mt5 (ZIN 36689-1, layer 3, horizon 3, 1974; 36690-1, layer 3c, horizon 2, 1977; 36705-2, mixed layers, 1978; 36707, mixed layers, 1981). Total is 205 fossil remains.

Description. The fossil skull fragment ZIN 34350 resembles skulls of the recent subspecies *C. a. alpinus*

Table 14. Measurements (in mm) of maxilla *Cuon alpinus*.

Measurements	*C. a. caucasicus*, Late Pleistocene	*C. a. alpinus*, Recent				*C. a. hespericus*, Recent			
	Kudaro 3, layers 3–4	Russian Far East				Tian-Shan and Altai			
	ZIN 34343	*n*	lim	M	SD	*n*	lim	M	SD
Length P4–M1	31.7	9	30.6–33.2	31.80	1.00	9	30.1–33.0	31.47	1.01
Teeth									
P4 L	21.2	9	19.9–21.6	20.73	0.62	9	19.8–21.6	20.61	0.66
Lpa	12.9	9	12.2–13.7	12.93	0.42	9	12.2–14.5	12.86	0.70
W	10.5	9	9.3–10.9	10.10	0.57	9	9.0–10.5	9.80	0.46
M1 L	13.0	9	12.3–14.2	13.08	0.76	9	12.2–13.9	13.08	0.50
Lpa	7.1	9	6.7–7.9	7.19	0.40	9	6.8–7.9	7.42	0.35
W	14.2	9	13.0–14.2	13.63	0.40	9	13.3–14.6	13.79	0.44

Table 15. Measurements (in mm) of upper and lower canines and premolars Late Pleistocene *Cuon alpinus*.

Localities	Museum number	Measurements, mm									
		C1		P1		c1		p1		p2	
		L	W	L	W	L	W	L	W	L	W
Caucasus											
Kudaro 1	ZIN 36660	10.4	6.5								
	ZIN 36662	10.6	6.7								
	ZIN 36735	11.1	6.8								
	ZIN 36736-1	10.8	6.9								
Kudaro 3	ZIN 36684-4	11.0	6.8								
	ZIN 36708-6	11.2	6.8								
	ZIN 36705-6	10.7	7.0								
Kudaro 1	ZIN 36661-2			6.8	4.9						
	ZIN 36659			6.4	4.7						
Kudaro 1	ZIN 36736-2					10.8	6.7				
Kudaro 3	ZIN 36683					10.9	7.3				
	ZIN 36678					11.3	7.1				
	ZIN 36696-1					10.9	6.7				
Kudaro 1	ZIN 36661-1							5.2	3.8		
Kudaro 3	ZIN 36699							5.9	3.8		
	ZIN 36703-2									9.4	5.2
	ZIN 36675-1									8.8	5.1
Europe											
Caune de l'Arago, France	MHP 1558					10.7	6.6				
	MHP 6214					10.3	6.9				

by its greatest width at the occipital condyles (41.1 mm) and by the height of the occiput (64.6 mm). The maxilla ZIN 34343 (Fig. 1C) is indistinguishable in size and shape of the upper molars from continental subspecies of the recent *C. alpinus* (Tab. 14), being, however, markedly smaller in comparison with the fossil subspecies *C. a. antiquus* Mattew et Granger, 1923 from the late Middle Pleistocene of China (Colbert & Hoojer, 1953). The comparison between the Kudaro find and European fossil dholes in the length and width of M1, as well as in the proportion of these dimensions, revealed it to be more similar to *C. a. europaeus* Bourguignat, 1868 from the Late Pleistocene than to *C. priscus* Thenius, 1954 and *C. a. fossilis* Nehring, 1890 from the Middle Pleistocene (Nehring, 1890; Thenius, 1954; Argant, 1991; Pérez Ripoll *et al*., 2010).

The width of the upper canine (6.5–7.0 mm, *n*=5; Tab. 15) does not exceed the bounds of its variation in recent *C. alpinus* (4.9–6.9 mm, *n*=17); however, the mean value of this measurement in the fossil sample is considerably higher, which may be explained by predominance of males within this sample. Measurements of the Kudaro specimens are similar to those of the upper canine in the Late Pleisocene *C. alpinus* from the localities of Parpalló and Santa Maira in Spain (Pérez Ripoll *et al*., 2010).

A series comprising seven fossil mandibles (ZIN 31241, 34338–34342, 34344; Fig. 5C–F, 8) displayed no morphometric difference from the recent *C. alpinus*. The length of the tooth row p1–m1 is analogous to that of the nominative subspecies *C. a. alpinus* (60.7–67.2, *n*=7); meanwhile, the p1–m1 row was found to be

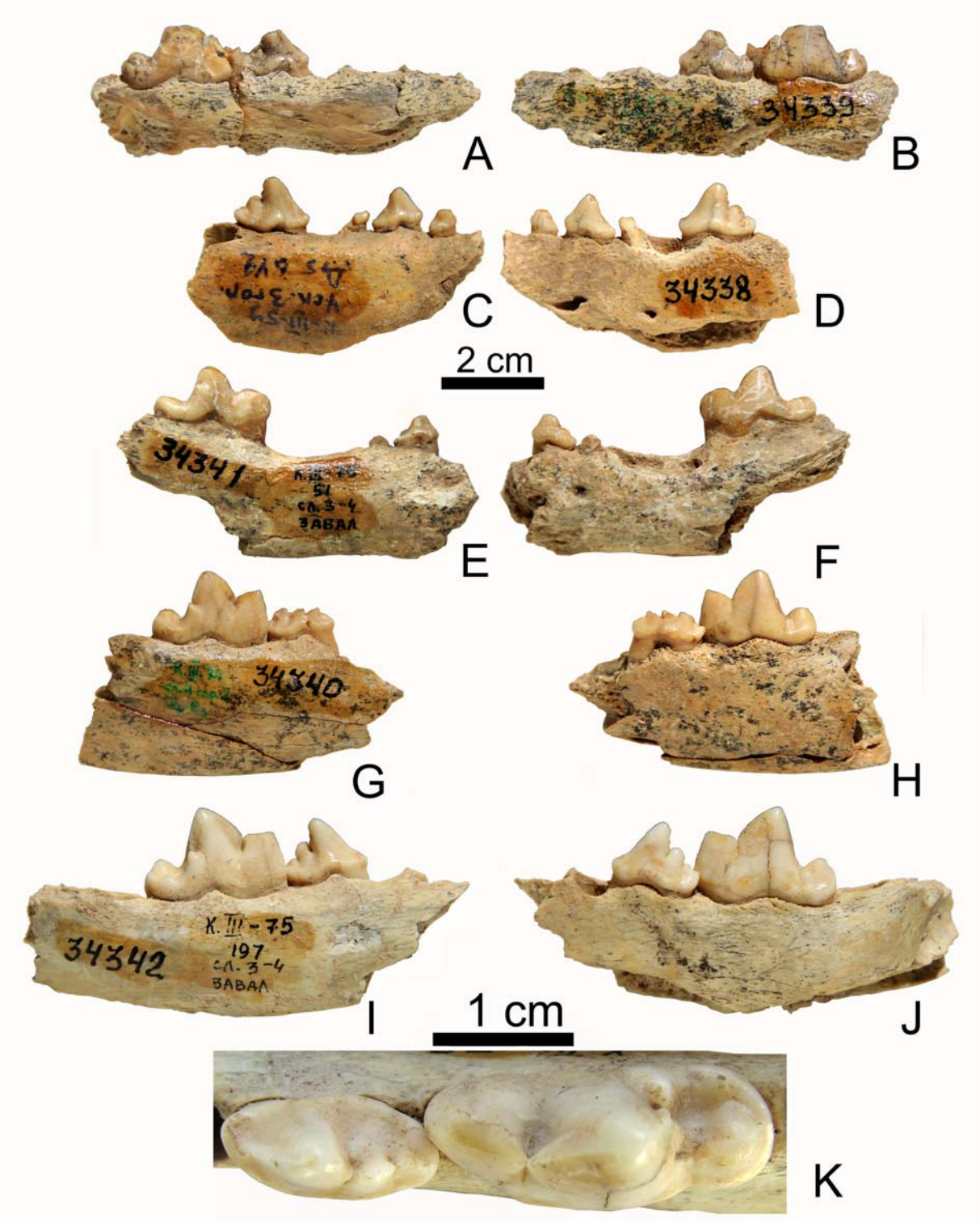

Fig. 8. Mandibular fragments of *Cuon alpinus caucasicus* from Kudaro 3; labial (B, D, F, H, J), lingual (A, C, E, G, I) and occlusal (K) views.
A, B — ZIN 34339; C, D — ZIN 34338; E, F — ZIN 34341; G, H — ZIN 34340; I–K — ZIN 34342.

Table 16. Measurements (in mm) of mandibles *Cuon alpinus*.

Measurements	Kudaro 3, layer 3	Kudaro 3, mixed layers	Kudaro 3, layers 3–4		Kudaro 3, layer 4		Kudaro 1, layer 3a	La Caune de l'Arago, France	
	ZIN 31341, holotype	ZIN 34344	ZIN 34342	ZIN 34341	ZIN 34338	ZIN 34340	ZIN 34339	MHP 1558	MHP 6214
Length p1–m2		68.3						70.6	69.9
Length p1–m1		61.4			65.1		65.1		
Length p2–m1				55.6				56.6	56.2
Length p3–m1	46.3			46.3				46.1	46.1
Length p4–m1	35.6	35.1	35.5			35.9	36.4	35.3	35.5
Length p1–p4		40.4			43.2		43.7	41.9	
Height before m1	22.7	23.7		ca.21.7		25.7			23.8
Teeth									
p1 L		5.6			5.6			5.5	5.7
W		3.6			3.6			3.5	3.9
p2 L				8.7	9.8			9.4	9.5
W				4.7	5.1			4.6	4.9
p3 L	11.0							10.5	10.4
W	5.5							5.0	5.7
p4 L	13.9	14.0	13.7		14.6	14.0	14.4	13.8	–
W	6.8	6.7	6.7		7.2	6.5	7.6	6.6	6.7
m1 L	22.8	22.9	22.5	22.6		22.8	23.6	22.2	23.0
Lpad	8.0	8.0	8.5	8.1		8.2	8.7	8.0	7.2
Ltald	6.7	6.3	6.8	6.5		6.5	6.7	6.0	5.9
W	9.3	8.9	9.2	8.8		8.7	9.1	8.8	8.8

noticeably shorter in other recent subspecies. A marked metric likeness of Kudaro mandibles to fossil specimens from grotte La Caune de l'Arago in France is observed (Tab. 16). The height of mandible at m1 in the Kudaro samples is somewhat lower than that in the fossil subspecies *C. a. europaeus* (Bonifay, 1971).

Lower cheek teeth from the Kudaro caves are more robust than in recent subspecies of *C. alpinus*, excepting their largest representative, *C. a. alpinus*. The latter subspecies, however, is characterized by smaller (on average) premolar width. A comparison with fossil specimens from European localities revealed p4 and m1 to be markedly longer in *C. priscus* (Hundsheim, Mosbach, Petralona) and in *C. alpinus fossilis* (Heppenloch, Lunel-Viel) than in *C. a. caucasicus* (Thenius, 1954; Adam, 1959; Bonifay, 1971; Kurtén & Poulianos, 1977). Similarly long p4 and m1 were found in *Cuon* sp. from Cripple Creek Sump in Alaska (Youngmann, 1993).

The resemblance with *C. a. caucasicus* in dimensions of the cheek teeth was established for *C. alpinus* cf. *priscus* from La Caune de l'Arago (Tab. 16) and for two mandibles from the Middle Pleistocene locality Trinchera-Galería in Sierra de Atapuerca, Spain, which were assigned to *C. a. europaeus* (Cervera, 1992).

In the Late Pleistocene European subspecies *C. a. europaeus*, the length of lower carnassial tooth m1 is similar to that of *C. a. caucasicus*; however, the lower premolar p4 of the former subspecies is somewhat longer (Schütt, 1973; Cordy, 1983) (Fig. 9). The ratio of p4 length to m1 length is markedly larger in *C. a. europaeus* (63.5–67.0%, *n*=5) than this index in *C. a. caucasicus* (60.9–61.4%, *n*=5) and in the specimen from Trinchera-Galería (60.8%, *n*=1). In *C. alpinus* from the Late Pleistocene localities of Iberian Peninsula, values of this index vary noticeably (58.9–65.3%, *n*=5; according measurements in Pérez Ripoll *et al*., 2010); however, its maximum values are comparable to those of *C. a. europaeus* from other European sites. Among recent subspecies, *C. a. caucasicus* may by compared with this index to *C. a. alpinus* (58.1–61.2%, *n*=6); at the same time, other subspecies exhibit this proportion less markedly (50.9–59.5%, *n*=28) (Baryshnikov, 1995).

The Kudaro specimens possess one cusp on the lower premolars p1; p2 is characterized by a high main cusp (protoconid) with a small cuspid on the labiodistal side; p4 has a robust protoconid, a diminutive anterior cusp, and two posterior cuspids. Fossil specimens from other localities show size variation of the anterior cusp of p4 (Tedford *et al*., 2009; Pérez Ripoll *et al*., 2010); in the recent *C. alpinus*, this cusp is small.

Lower carnassial teeth m1 from the Kudaro cave collection exhibit a well-developed metaconid, which may be occasionally reduced in the recent *C. alpinus* (in 7 of 41 specimens). The cingulid, running along the lingual wall of talonid, frequently expands beyond the posterior margin of the latter and may reach the hypo-

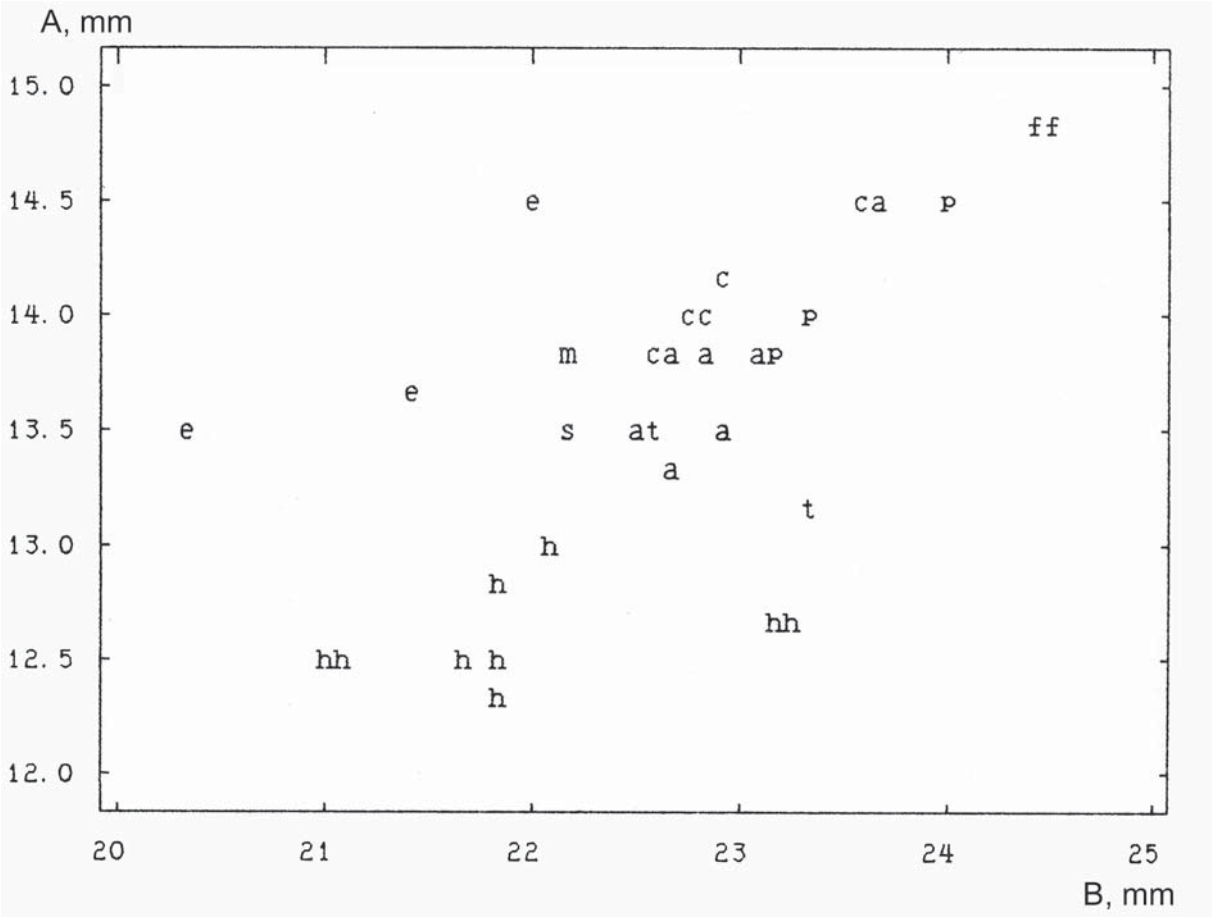

Figure 9. Correlation between greatest length of p4 (A) and greatest length of m1 (B) in *Cuon alpinus*.
Pleistocene: c — *C. a. caucasicus*, Kudaro 1 and Kudaro 3, e — *C. a. europeus*, Čertova Dira, Sipka, Chokier, f — *C. a. fossilis*, Heppenloch, Lunel-Viel, m — *C. alpinus* cf. *priscus*, Arago, p — *C. priscus*, Hundsheim, Mosbach, s — *C. a. europeus*, Atapuerca, t — *C. a. antiquus*, Yenchingkou. Recent: a — *C. a. alpinus*, h — *C. a. hespericus*.

conid base (in recent *C. alpinus*, it generally does not spread beyond the posterior margin of talonid). The hypoconid is large (Fig. 8K). The entoconid is not developed; a small tubercle (in 4 of 5 cases), which may be a rudimentary entoconid, is visible at its place. It is characteristic of *C. priscus* and is recorded in *C. a. fossilis* from Lunel-Viel in France (Thenius, 1954; Bonifay, 1971). The recent *C. alpinus* lacks this small tubercle and it is also absent on fossil teeth from Trinchera-Galería, Obarreta and Cova Negra in Spain (Cervera, 1992; García, 2003; Pérez Ripoll *et al*., 2010).

Summarizing, although the m1 of *C. a. caucasus* from Kudaro caves resembles *C. a. europaeus* from the Late Pleistocene in length and width, the shape of the talonid of this tooth suggests a possible link between the Caucasian subspecies and the archaic species *C. fossilis* (including *C. priscus*) from the Middle Pleistocene.

The best-preserved Kudaro mandible retains the alveolus of m2; no traces of m3 are observed. Judging from the alveolus, m2 had fused roots with a marked groove at their juncture on the labial side. In *C. priscus*, the roots are separate (Thenius, 1954). Adult individuals of the recent *C. alpinus* generally show fused roots of m2; however, these roots are found to be separated in several young animals.

The material from Kudaro caves includes elements of all parts of the vertebral column, with the exception of the tail. Most of the fossil vertebrae are larger in size than those of recent *C. alpinus*, more similar, at the same time, in their robusticity to *C. alpinus* instead of *C. lupus* (Baryshnikov, 1995). The first cervical vertebra (atlas) with small transversarium and several specimens of second cervical vertebra (axis) with widened anterior portion of the processus spinosus (which is characteristic of *C. alpinus*) were examined (Tab. 17; Fig. 10A).

Limb bones from the Kudaro collection (Figs 10–13) exceed corresponding bones of examined skeletons of recent dholes in size, being similar to those of the Late Pleistocene *C. alpinus* from the Iberian localities (Pérez Ripoll *et al*., 2010). Diagnostic characters reflecting osteological differences between *C. alpinus* and *C. lupus* were discussed by Gromova (1950) and Pérez Ripoll *et al*. (2010). Two complete humeri (ZIN 36708-1, 36708-3; Fig. 11A, B) are comparable in their

Table 17. Measurements (in mm) of cervical vertebrates of *Cuon alpinus caucasicus*.

Localities	Museum number	Measurements								
		GL	BFcr	BFcd	LAd	H	LCDe	LAPa	SBV	BPacd
Atlas										
Kudaro 1, layer X	ZIN 36738	40.1	42.3	34.9	20.4	31.0				
Axis										
Kudaro 3, layer 4	ZIN 36682-1		34.0	19.0		ca.42		57.5	26.2	33.7
	ZIN 36703-1		35.9	23.1		45.9	56.1	60.6	28.9	40.7
Kudaro 3, layer 3	ZIN 36697		33.5	19.8		43.1	59.1		26.2	32.0
	ZIN 36677-1		32.0	ca.20		ca.43		58.9	21.5	34.6
	ZIN 36679-2		32.9	22.2					21.0	

Figure 10. Second cervical vertebra (axis) (A) and metacarpal bones (B–F) of *Cuon alpinus caucasicus* from Kudaro 3 Cave; lateral (A–D, F) and medial (E) views.
A — ZIN 36703-1; B — left Mc2, ZIN 36702-4; C — left Mc2, ZIN 36681-1; D — left Mc4, ZIN 36698-4; E — right Mc5, ZIN 36692-3; F — left Mc5, ZIN 36684-2.

Figure 11. Right (A) and left (B) humerus, left ulna (C) and left tibia (D) of *Cuon alpinus caucasicus* from Kudaro 3 Cave; caudomedial (A–B), lateral (C) and medial (D) views.
A — ZIN 36708-3; B — ZIN 36708-1; C — ZIN 36698-1; D — ZIN 36708-2.

greatest length to bones of *C. lupus* from Binagady in Azerbaijan, the width of fossa olecrani in former bones being at the same time approximately equal to its length, and their foramen supratrochleare occupying more than half the space of the fossa olecrani, as in *C. alpinus*. The radius (Fig. 11C) shows tuber olecranoni slightly widened backwards (in *C. lupus* it is markedly widened in the same direction); two ridges extend along the radial shaft from the median prominence restricting incisura radii (a single ridge is observed in *C. lupus*). The longitudinal ridge in the middle portion of the posterior surface of the tibial shaft (Fig. 11D) runs along the centerline or medial to it; this ridge is absent in *C. lupus*. Bones of the limb distal parts are more robust and shorter in *C. a. caucasus* as compared to those of *C. lupus* (Tab. 18, 19).

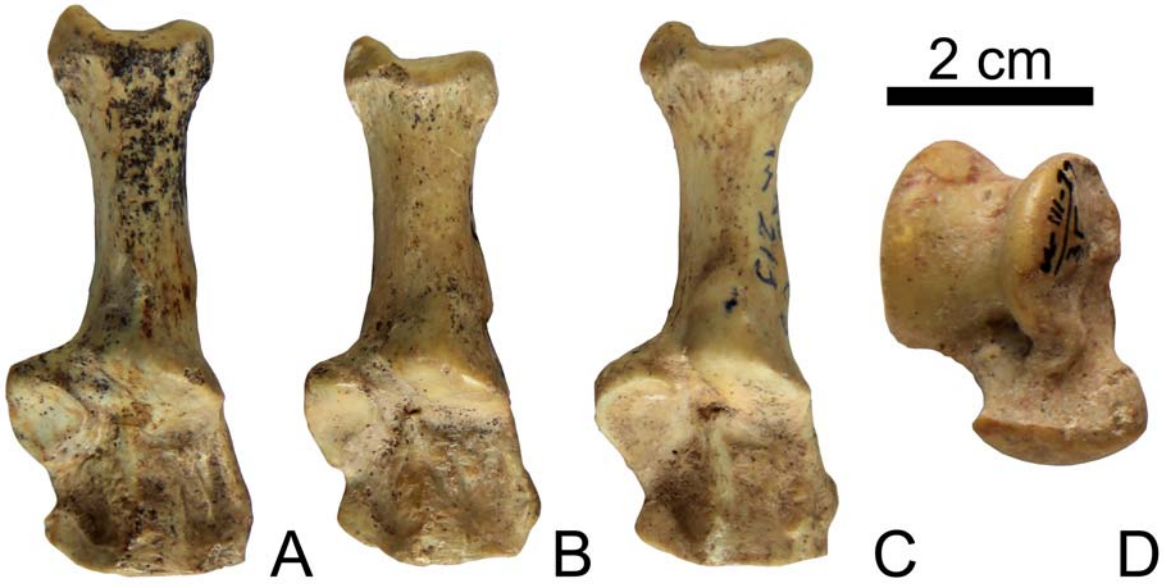

Figure 12. Left calcanei (A–C) and right talus (D) of *Cuon alpinus caucasicus* from Kudaro 3 Cave; dorsal views.
A — ZIN 36672-2; B — ZIN 36701; C — ZIN 36671-1; D — ZIN 36693.

Figure 13. Left (A, B, F, K) and right (C, E, G–J) metatarsal bones of *Cuon alpinus caucasicus* from Kudaro 3 Cave; lateral (L) and medial (A–J) views.
A — left Mt2, ZIN 36671-2; B — left Mt2, ZIN 36681-2; C — right Mt3, ZIN 36672-1; D — right Mt4, ZIN 36671-3; E — right Mt4, ZIN 36702-1; F — left Mt4, ZIN 36687; G–J — right Mt5 (G — ZIN 36707, H — ZIN — 36689-1, I — ZIN — 36690-1, J — ZIN 36705-2); K — left Mt5, ZIN 36705-5.

Table 18. Measurements (in mm) of fore limb bones *Cuon alpinus caucasicus*.

Bones	Localities and museum number (ZIN)	GL	GB	Bp	Dp	SD	Bd	Dd	SLC	GLP	BG	DPA	SDO	BPC
Scapula	Kudaro 3 (36692-1)								29.1	34.7	22.2			
	Kudaro 3 (36696-3)									30.5	21.0			
	Kudaro 3 (36708-4)								27.7	34.4	20.8			
	Kudaro 3 (36705-3)									31.5	18.4			
Humerus	Kudaro 1 (36669)			ca. 34	49.5									
	Kudaro 1 (36667)					17.8								
	Kudaro 3 (36708-3)	196.0		34.6	50.7	15.1	37.3	30.0						
	Kudaro 3 (36708-1)	198.0		34.7	50.8	15.4	37.4	29.9						
	Kudaro 3 (36684-1)					16.3	35.9	28.6						
	Kudaro 3 (36674)						33.9	26.5						
	Kudaro 3 (31241-2)			31.9	46.6									
	Kudaro 3 (36679-1)					14.6	34.9	28.1						
Ulna	Kudaro 1 (36733-1)													18.3
	Kudaro 1 (36739)											32.2	–	17.2
	Kudaro 3 (36698-1)											28.7	24.5	18.9
	Kudaro 3 (36697-2)											34.0	29.5	21.5
	Kudaro 3 (36677-2)											33.6	28.6	21.7
	Kudaro 3 (31241-3)											30.3	26.5	17.0
	Kudaro 3 (36670)											28.8		18.5
	Kudaro 3 (36705-7)													15.0
Radius	Kudaro 3 (36698-2)					15.3	28.5	15.8						
	Kudaro 3 (31241-4)			20.3	13.5		28.0	15.2						
	Kudaro 3 (36670-2)			20.5	13.6									
	Kudaro 3 (36705-4)			20.3	13.2									
Scaphoid	Kudaro 1 (36664-2)		24.9											
Pisiform	Kudaro 3 (36704)	22.0												
Mc2	Kudaro 3 (36702-4)	69.3		10.2	13.8	8.6	11.7	9.8						
	Kudaro 3 (36681-1)	74.2		10.9	15.2	9.4	13.4	12.6						

Table 18 (continued).

Bones	Localities and museum number (ZIN)	GL	GB	Bp	Dp	SD	Bd	Dd	SLC	GLP	BG	DPA	SDO	BPC
Mc3	Kudaro 3 (36673-3)			10.3	13.1	7.9								
Mc4	Kudaro 3 (36698-4)	77.0		8.7	12.5	7.7	10.6	10.9						
Mc5	Kudaro 3 (36684-2)	61.5		13.6	12.7	8.5	12.2	10.5						
	Kudaro 3 (36692-3)	60.6		11.9	12.6	8.6	11.9	10.5						

Table 19. Measurements (in mm) of hind limb bones *Cuon alpinus caucasicus*.

Bones	Localities and museum number	GL	GB	Bp	Dp	SD	Bd	Dd	DC	LA	SH	SB
Pelvis	Kudaro 1 (ZIN 36668)									23.2	20.8	
	Kudaro 3 (ZIN 31241-5)									23.8	23.3	9.7
	Kudaro 3 (ZIN 36688-1)									24.5		
	Kudaro 3 (ZIN 36681-3)										24.2	10.6
Femur	Kudaro 3 (ZIN 36692-2)			48.7					22.7			
	Kudaro 3 (ZIN 36700-2)					15.2			21.7			
Patella	Kudaro 3 (ZIN 36688-5)	19.2	13.1									
Tibia	Kudaro 1 (ZIN 36737-2)						24.8	17.6				
	Kudaro 3 (ZIN 36708-2)	217.6			47.1	15.9	27.8	19.4				
	Kudaro 3 (ZIN 36702-3)						26.3	19.3				
	Kudaro 3 (ZIN 36705-1)						28.2	19.6				
Fibula	Kudaro 3 (ZIN 36691-4)						16.0					
	Kudaro 3 (ZIN 36685-2)						13.9					
Calca-neus	Kudaro 1 (ZIN 36730-1)	51.1	20.8									
	Kudaro 3 (ZIN 36706-1)	47.6	20.6									
	Kudaro 3 (ZIN 36672-2)	53.7	22.5									
	Kudaro 3 (ZIN 36701)	50.9	21.7									
	Kudaro 3 (ZIN 36671-1)	52.4	22.8									
	Kudaro 3 (ZIN 36676-1)		23.2									
Talus	Kudaro 3 (ZIN 36691-2)	29.0	26.9									
	Kudaro 3 (ZIN 36694-1)	31.9	29.4									
	Kudaro 3 (ZIN 36693)	30.2	28.2									
	Kudaro 3 (ZIN 36680-5)	31.5	29.4									
	Kudaro 3 (ZIN 36695-2)	31.9	23.0									
Navi-cular	Kudaro 3 (ZIN 36692-4)	10.4	20.0									
	Kudaro 3 (ZIN 36691-3)	10.8	20.9									
	Kudaro 3 (ZIN 36676-3)	11.0	20.9									
Mt2	Kudaro 1 (36731-1)			9.9	-	7.4						
	Kudaro 3 (ZIN 36698-3)			8.8	15.8	9.0						
	Kudaro 3 (ZIN 36671-2)	79.4		9.7	14.6	8.7	13.2	10.7				
	Kudaro 3 (ZIN 36681-2)	86.0		11.4	17.5	9.5	13.3	12.7				
	Kudaro 3 (ZIN 36700-2)	77.3		9.4	15.5	8.1	11.9	10.4				
Mt3	Kudaro 1 (ZIN 36663)			11.9								
	Kudaro 3 (ZIN 36685-1)			12.2	17.4	9.3						
	Kudaro 3 (ZIN 36672-1)	89.4		11.9	17.4	9.0	11.8	12.0				
	Kudaro 3 (ZIN 36691-1)			11.2		8.8						
	Kudaro 3 (ZIN 36676-2)			12.2	17.5	9.2						

Table 19 (continued).

Bones	Localities and museum number	GL	GB	Bp	Dp	SD	Bd	Dd	DC	LA	SH	SB
Mt4	Kudaro 1 (ZIN 36666)			11.6	15.5							
	Kudaro 3 (ZIN 36702-1)	87.4		11.6	14.8	8.6	11.0	11.0				
	Kudaro 3 (ZIN 36687)	85.1		10.3	13.5	7.9	10.1	10.8				
	Kudaro 3 (ZIN 36684-3)			10.9	14.9	8.6						
	Kudaro 3 (ZIN 36671-3)	87.4		12.1	15.0	9.2	11.7	12.0				
	Kudaro 3 (ZIN 36708-5)			10.7	16.3	8.8						
	Kudaro 3 (ZIN 36705-8)	94.9		11.5	16.1	8.5	12.0	12.3				
Mt5	Kudaro 3 (ZIN 36682-4)	76.7		9.7	10.3	8.1	10.4	9.4				
	Kudaro 3 (ZIN 36686)			11.0	11.9	7.7						
	Kudaro 3 (ZIN 36690-1)	75.5		11.9	13.1	7.8	11.3	10.1				
	Kudaro 3 (ZIN 36707)	81.6		10.4	12.9	8.0	11.3	10.6				
	Kudaro 3 (ZIN 36705-2)	78.5		11.6	14.3	8.4	11.7	10.5				
	Kudaro 3 (ZIN 36705-5)	75.7		10.5	12.6	7.9	11.7	10.3				
	Kudaro 3 (ZIN 36689-1)	75.7		11.7	13.0	7.4	11.0	10.1				

Discussion. Fossil remains of *C. alpinus* are widespread in Upper Pleistocene layers 3–4 of both Kudaro caves; this species may comprise several earlier fragmentary fossils from layer 5 of Kudaro 3 Cave. The lower portion of layer 4 yielded fewer finds of dhole bones in comparison with layer 3, when these caves were situated, judging from the palynological data, at the upper border of forest belt (Lioubine, 1989).

The Pleistocene representatives of *C. alpinus* were larger than the recent animals, being heavier, stronger and hardier predators. Presumably, similar to recent Caucasian dholes, they lived in packs, migrating great distances. The abundance and variety of bone fragments, including several vertebrae arranged in anatomical order, suggest burial of the complete carcasses or their large fragments in the Kudaro caves. Most probably, these burials took place at the time of seasonal migrations of dholes to the upper belt of mountain forest and alpine meadows.

In the Caucasus, lower carnassial teeth of *C. alpinus* have been also found in Tsona Cave in Georgia (Vekua *et al*., 1987) and in Matuzka Cave in the Northern Caucasus (Baryshnikov, Golovanova, 1989). The specimen from Tsona Cave shows a reduced metaconid; nevertheless, the tooth dimensions (L=22.1 mm, W=9.0 mm) are typical of *C. a. caucasus*. Two fragmented teeth m1 from Matuzka Cave are noticeably smaller and exhibit shape characteristic for the recent *C. alpinus*.

C. alpinus is regarded as the descendant of *C. priscus* from the Middle Pleistocene of Europe (Fontana Ranuccio F.U. in Italy, near 0.5 Ma; Brugal & Boudadi-Maligne, 2011; Petronio *et al*., 2011), which inhabited Eurasia and, via Beringia, came to North America, reaching the northeastern part of Mexico (San Josecito Cave) (Tedford *et al*., 2009).

As a result of cladistic analysis, *Cuon* was combined in a single cluster with the recent genus *Lycaon* and with the extinct genus *Xenocyon* (Tedford *et al*., 2009). Molecular analyses also affiliate *Cuon alpinus* with *Lycaon pictus* (Temminck, 1820), placing these species together with wolves, coyotes, and jackals in a group of wolf-like canids (Zravý & Řičánková, 2004; Bardeleben *et al*., 2005). Tropical populations of *C. alpinus* from the Asian mainland comprise two major phylogeographical groupings (Iyengar *et al*., 2005).

Genus *Vulpes* Frisch, 1775

†*Vulpes praeglacialis* (Kormos, 1932)

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: right m2 (ZIN 36600-2, layer 5, horizon 9, 1958), distal fragment of right humerus (ZIN 36598-1, layer 5, horizon 5, 1959), proximal fragment of right ulna (ZIN 36600-1, layer 5, horizon 9, 1958), fragment of right radius (ZIN 36599, layer 5, horizon 6, 1958), fragment of left metacarpal 4 (ZIN 36600-3, layer 5, horizon 9, 1958), left calcaneus (ZIN 36598-2, layer 5, horizon 5, 1959); total 6 remains.

Description. The lower molar m2 (ZIN 36600-2) of a small fox from the lower part of layer 5c is markedly smaller in length and width than the specimens of this tooth of the red fox *V. vulpes* found in Kudaro caves. The length of ZIN 36600-2 is smaller than the mean value of this dimension calculated for the sample of the recent *V. vulpes* (L., 1758) from the Caucasus, whereas the width of the fossil tooth is located within the area of minimum width parameters of m2 for the recent sample. At the same time, ZIN 36600-2 shows no size difference with this tooth of *V. praeglacialis* from the Early and Middle Pleistocene of Europe (Tab. 20).

Layer 5c was found to contain several bone fragments of small-fox limbs. The humerus (ZIN 36598-1) corresponds in width of the distal epiphysis (Bd=18.5 mm) to that of recent arctic fox *V. lagopus* (L., 1758) and *V. praeglacialis* from grotto l'Escale in France (Bonifay, 1971).

The ulna fragment (ZIN 36600-1), in the dimensions of the olecranon (SDO=11.4 mm, DPA=13.3 mm), is similar to the ulna of *V. lagopus* and corsak fox, *V. corsak* (L., 1768). Unlike the fossil *V. vulpes* from Kudaro 1, in *V. lagopus* the upper margin of olecranon is not elevated posteriorly and forms, thus, nearly a

Table 20. Measurements (in mm) of lower molar m2 in Pleistocene *Vulpes*.

Species	Locality and reference	L	W
V. praeglacialis	Kudaro 1, layer 5 (ZIN 36600-2)	6.5	4.8
	Kalkberg (Kormos, 1932)	5.6	4.4
	Brassó (Kormos, 1932)	6.3	4.3
	l'Escale (Bonifay, 1971)	6.4	4.8
		6.8	5.1
		6.8	4.9
		6.0	4.9
		6.4	4.2
		6.1	4.8
		6.5	4.6
		5.0	4.1
		5.1	4.3
	Stránská skála (Musil, 1972)	5.9	4.2
	Hundsheim (Thenius, 1954)	7.1	4.5
	Cal Guardiola (Madurell-Malapeira *et al*., 2009)	6.6	4.9
V. vulpes	Kudaro 1, layer 5	7.2	5.8
		7.2	5.4
	Kudaro 3, layers 3–4	6.8	5.5
		6.7	4.8
		7.6	5.2
		6.9	5.7
	l'Escale (Bonifay, 1971)	7.1	5.4
		6.5	5.0
		7.6	5.6
		7.7	5.4
		8.8	6.4
		8.5	5.5

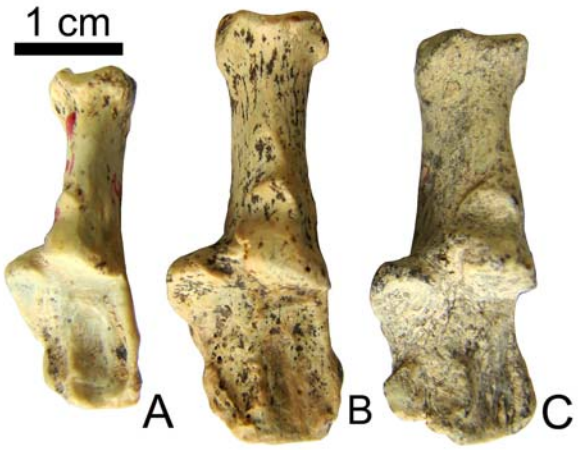

Figure 14. Left calcanei of Pleistocene foxes *Vulpes praeglacialis* (A) and *V. vulpes* (B, C) from Kudaro 1 Caves; dorsal views.
A — ZIN 36598-2; B — ZIN 36542-1; C — ZIN 36529-1.

right angle with the posterior (palmar) margin of this bone.

The proximal fragment of a radius (ZIN 36599), with measurements (Bp=9.4 mm, Bd=5.8 mm), is noticeably smaller than this bone in *V. vulpes* and resembles *V. lagopus*.

The fragment of a metacarpal 4 (ZIN 36600-3) is similar in size (SD=3.2 mm, Bd=4.3 mm, Dd=5.6 mm) to Mc4 of the recent *V. lagopus*.

The calcaneus (ZIN 36598-2; Fig. 14A) from layer 5 is markedly smaller (GL=28.0 mm, GB=10.8 mm) in comparison with this bone in *V. vulpes* from Kudaro caves (Fig. 14B, C), revealing similarity in length and width with that of *V. praeglacialis* from grotto l'Escale (Bonifay, 1971). It is larger and more robust than the same bone in *V. corsak* and raccoon dog *Nyctereutes procyonoides* (Gray, 1834), both latter species having a calcaneus, as a rule, shorter than 27 mm. In addition, the fossil bone differs from the calcaneus of *N. procyonoides* in the development of a longitudinal ridge on the dorsal wall of bone distal part, which is absent in the raccoon dog. By its size, ZIN 36598-2 corresponds to the calcaneus of *V. lagopus*; however, the distal part (below coracoid facet) of the fossil specimens is longer. The length of distal part constitutes 55.7% of the length of proximal part; at the same time, this ratio does not exceed 52% in *V. lagopus*. The correlation between the length of the distal part and maximum width of calcaneus is calculated as 94.5%, being less than 90% in *V. lagopus*. These indices link the fossil bone with that of the recent *V. vulpes* (Gromova, 1960).

Discussion. Isolated remains of a small fox found in the lower part of layer 5 in Kudaro 1 Cave reveal a metric resemblance to *V. praeglacialis* and indicate, for the first time, the presence of this species in Caucasus. These fox remains are also similar in size to the recent *V. lagopus*, differing from the latter by several morphological characters.

The earliest fossil foxes are recorded in Europe in the middle Villafranchian (Les Etouaires, Villaroya, Saint-Vallier, Val d'Arno, Varshets, Dafnero 1) with *V. alopecoides* Forsyth Major (biochron MN16b-18; Bonifay, 1971; Spassov, 2003; Argant, 2004; Palombo & Vialli, 2004). Later, it was replaced by *V. praeglacialis* resembling in size the recent polar fox, but differing from it in the details of structure of the cheek teeth, including a larger m2 (Kormos, 1932). The species has been found in numerous European localities of the Early Pleistocene (Venta Micena, Cal Guardiola, Fuente Nueva-3, Barranco León, Quibas, Kalkberg, Beremend, Püspökfürdö, Brassó, Stránská skála 1) and Middle Pleistocene (l'Escale, Vergranne, Hundsheim, Heppenloch, Achenheim, Petralona) (biochron MNQ20-23b; Kormos, 1932; Thenius, 1954; Bonifay, 1971, 1983; Kurtén & Poulianos, 1977, 1981; Martínez-Navarro *et al.,* 2003; Palombo & Vialli, 2004; Calero *et al*., 2006; Madurell-Malapeira *et al*., 2009).

Vulpes vulpes (Linnaeus, 1758)

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: upper cheek teeth (ZIN 36485, 36486), fragment of left mandible with m1–m2 (ZIN 36497, layer 5, horizon 5, 1958), lower cheek teeth (ZIN 36487, 36496-2, 36503-36506); Kudaro 3 Cave: upper cheek teeth (ZIN 36518-1), lower cheek teeth (ZIN 36518-2, 36593-11).

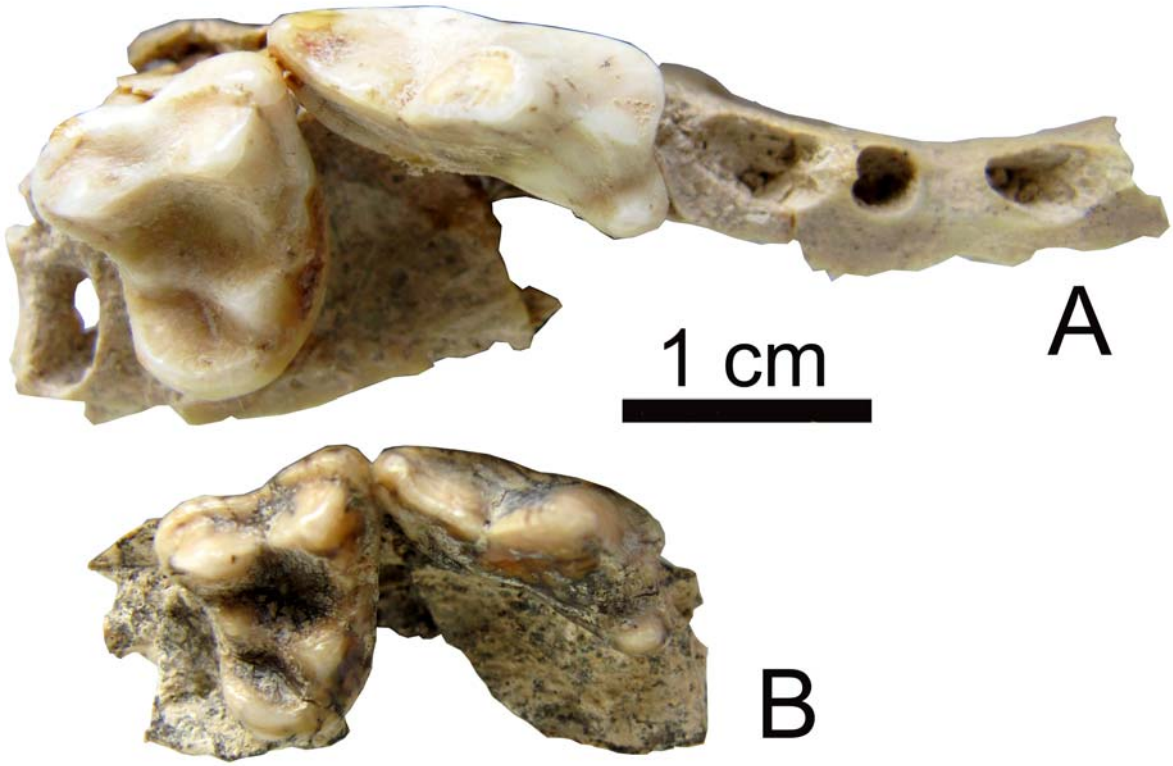

Figure 15. Maxilla fragments with P4-M1 of *Vulpes vulpes* from Kudaro 3 (A) and Kudaro 1 (B); occlusal view.
A — ZIN 36492; B — ZIN 36488.

Late Pleistocene, Kudaro 1 Cave: fragment of right maxilla with P4–M1 (ZIN 36488, layer 4, 1961), upper cheek teeth (ZIN 36484-1, 36489-3), fragment of left mandible with p3–p4 (ZIN 36495, layer 3c, 1958), fragment of left mandible with p3def–p4 (ZIN 36493, layer 3, 1957), fragment of left mandible with p1–m1 (ZIN 36501, layer X-3, 1980), fragment of right mandible (ZIN 36499-1, layer 4, 1961), fragment of right mandible with p2 (ZIN 36500-1, mixed layers, 1961), fragment of left mandible with p4 (ZIN 36502-1, layer X-1, horizon 4, 1980), lower cheek teeth (ZIN 36494-2, 36498-3,4, 26503, 36507); Kudaro 3 Cave: fragment of left maxilla with P4–M1 (ZIN 36490, layer 3c, horizon 1, 1977), fragment of right maxilla with P4–M2 (ZIN 36492, layer 3e, horizon 1, 1978), upper cheek teeth (ZIN 36489-3, 36491-3, 36584-2), fragment of left mandible (ZIN 36491-1, layer 3e, horizon 1, 1977), fragment of left mandible with p2 and m2 (ZIN 36508, layer 3, horizon 3, 1959), fragment of left mandible with p4 and m2 (ZIN 36509, layer 4, 1959), fragment of left mandible with p3–p4 (ZIN 36510-1, layer 3, horizon 4, 1974), fragment of right mandible with p2 and p4 (ZIN 36511, layer 4, horizon 5, 1975), fragment of right mandible with p2–m2 (ZIN 36517, mixed layers, 1979), fragment of right mandible with m2 (ZIN 36512-1, layer 4, horizon 3, 1975), lower cheek teeth (ZIN 36513–36516).

All layers of both caves also are found to contain isolated canines (~ 60), large fragments of limb bones (> 70), and portions of vertebrae, phalanges, and small bone fragments. A total of approximately 365 fossil remains have been collected.

Description. Numerous fossil remains of *V. vulpes* are represented in both Kudaro caves, primarily by fragmented bones and isolated teeth, which complicate the description of Pleistocene Caucasian red fox.

Fossil maxillary fragments (ZIN 36488, 36492; Fig. 15) exhibit no difference in the shape as well as in the length of the tooth row P4–M1 (21.2 mm and 21.6 mm, respectively) with maxillae of recent *V. vulpes*. In the fossil specimens, the protocone of P4 is markedly shifted forward, extending beyond the level of the anterior margin of the paracone; the metastyle blade is short (Fig. 16).

The recent Caucasian fauna includes three subspecies of red fox (*V. v. caucasica* Dinnik, 1914, *V. v. alpherakyi* Satunin, 1906 and *V. v. alticola* Ognev, 1926) (Aristov & Baryshnikov, 2001). The red fox from Kudaro caves resembles, with respect to the mean value of the length of upper teeth P4 and M1, *V. v. alticola*, which is found in the Lesser Caucasus and in the Armenian Highland; however, the latter subspecies is characterized by significantly wider teeth (Tab. 21).

The available mandible fragments from Kudaro caves suggest a rather small size for fossil *V. vulpes*

Table 21. Measurements (in mm) of upper cheek teeth in Pleistocene and recent *Vulpes vulpes* from Caucasus.

Measurements		Middle and Late Pleistocene	Recent subspecies (males and females)		
		Kudaro 1 and Kudaro 3	*V. v. caucasica*	*V. v. alpherakyi*	*V. v. alticola*
P2, L	*n*	2	22	5	14
	lim	7.8, 7.9	7.5–9.4	7.6–8.9	7.7–9.5
	mean	–	8.58	8.12	8.45
	SD	–	0.47	0.65	0.51
P2, W	*n*	2	22	5	14
	lim	2.9, 2.9	2.6–3.4	2.7–3.0	2.6–4.3
	mean	–	3.04	2.90	3.05
	SD	–	0.21	0.12	0.41
P3, L	*n*	5	23	6	14
	lim	8.5–9.5	8.4–9.9	8.3–9.2	8.1–9.7
	mean	9.11	9.22	8.77	8.99
	SD	0.44	0.42	0.39	0.51
P3, W	*n*	5	23	6	14
	lim	3.1–4.0	2.8–4.1	3.2–3.5	2.9–3.7
	mean	3.49	3.31	3.38	3.27
	SD	0.44	0.32	0.14	0.26
P4, total length*	*n*	8	23	6	14
	lim	13.4–14.9	13.1–15.8	12.8–14.4	13.3–15.8
	mean	14.37	14.77	13.69	14.36
	SD	0.53	0.66	0.52	0.70
P4, L	*n*	9			
	lim	13.0–14.3			
	mean	13.40			
	SD	0.41			
P4, Lpa	*n*	9	23	6	14
	lim	7.9–8.8	7.7–9.1	6.7–8.5	7.3–8.7
	mean	8.33	8.31	7.62	8.08
	SD	0.24	0.42	0.65	0.47
P4, W	*n*	8	23	6	14
	lim	5.8–6.7	5.4–7.5	5.2–6.6	6.0–7.6
	mean	6.34	6.55	5.90	6.60
	SD	0.34	0.51	0.48	0.48
M1, L	*n*	4	23	6	14
	lim	9.1–9.8	8.3–10.2	8.5–9.6	8.8–10.0
	mean	9.50	9.26	9.12	9.51
	SD	0.32	0.49	0.49	0.42
M1, Lpa	*n*	4	23	6	14
	lim	4.4–5.0	4.3–5.7	4.4–5.3	4.6–5.5
	mean	4.74	4.97	4.74	5.04
	SD	0.23	0.37	0.33	0.28
M1, W	*n*	4	23	6	14
	lim	10.9–11.8	10.2–12.1	10.4–11.4	10.4–12.9
	mean	11.34	11.23	10.93	11.51
	SD	0.41	0.56	0.42	0.67
M2, L	*n*	1	23	6	14
	lim	5.1	4.4–8.0	4.6–55	4.4–6.0
	mean	–	5.34	5.12	5.22
	SD	–	0.67	0.35	0.53
M2, W	*n*	1	23	6	14
	lim	7.6	6.7–9.0	7.3–8.7	7.5–10.0
	mean	–	7.96	8.05	8.54
	SD	–	0.59	0.55	0.69

* Distances between protocon and posterior end of tooth.

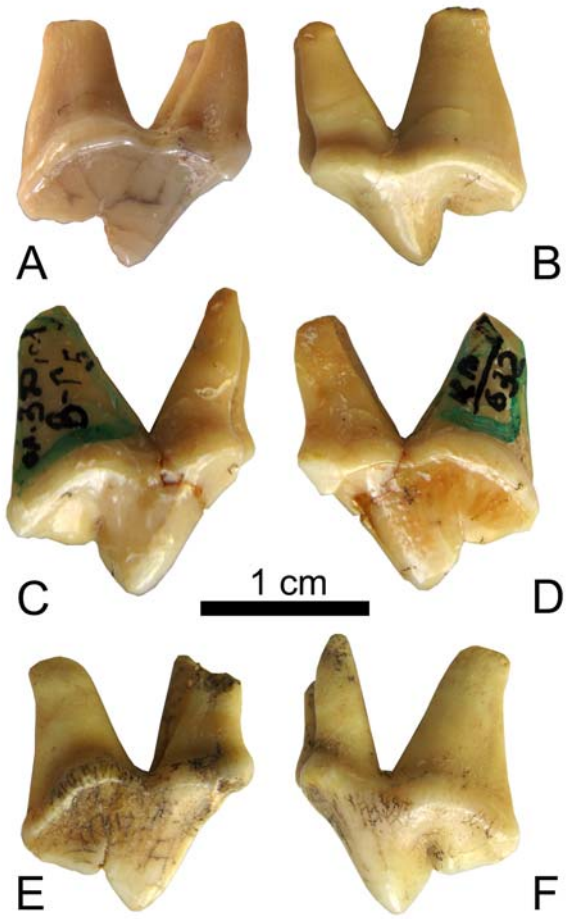

Figure 16. Upper carnassial tooth P4 of *Vulpes vulpes* from Kudaro 1 (A, B) and Kudaro 3 (C–F); labial (B, D, E, H, J, K) and lingual (A, C, F, G, I, L) views.
A, B — ZIN 36486; C, D — ZIN 36491-3; E, F — ZIN 36489-3.

(Tab. 22). The length of p1–m1 (46.9–50.1 mm, *n*=3) falls into the range of variation for this measurement in modern red fox from the Caucasus (42.7–55.0 mm, *n*=40). The shape of the mandibles and development of the posterior additional cusp on p3–p4 also corresponds to the modern species (Fig. 17).

With respect to the length of the premolar p4 and the length of the molar m2, the red fox from Kudaro caves resembles *V. v. alticola*, although the lower carnassial tooth m1 is longer and comparatively narrower in the fossil collection (Tab. 23).

The length of upper cheek teeth P4 and M1 and the length of the lower carnassial tooth m1 of red fox from Kudaro caves are similar to those in the fossil subspecies *V. vulpes jansoni* Bonifay from grotte de l'Escale in France (Bonifay, 1971).

Szuma (2004), examining morphological variability of the occlusal surface of the talonid in m1 of *V. vulpes* in the Holarctic, identified in recent red fox from the Caucasus the presence of morphotypes "P1", "P3" and "P4", the last being present nearly in half of the studied specimens (*n*=27). The Kudaro collection (Fig. 18) revealed morphotypes "P1" (2 specimens), "P2" (1), "P3" (3), and "P4" (5), which show that the frequency of occurrence of the morphotypes in the fossil sample is similar to that in the recent Caucasian *V. vulpes*. Therefore, the dental characters of the red fox are highly conservative and reveal minimal change throughout time. In recent *V. vulpes*, the geographical variation of morphotype char-

Table 22. Measurements (in mm) of mandibles of Pleistocene *Vulpes vulpes*.

Measurements	Kudaro 1		Kudaro 3				Petralona, Greece
	Layer 5	Layers 3–4	Layers 3–4				
	ZIN 36497	ZIN 36501	ZIN 36511	ZIN 36508	ZIN 36491-1	ZIN 36517	AUT PEC1600
Length p1–m3		52.3		61.4		59.3	
Length p1–p4		37.1	32.5		34.8	34.1	
Length m1–m3				27.4		26.4	23.7
Length m1–m2	23.3						
Height behind m1	15.8		13.4				
Teeth							
p1 L		3.65			3.9		
W		2.25			2.8		
p2 L		8.65	8.4	8.55	9.3	8.9	
W		3.0	3.3	3.3	3.3	3.4	
p3 L		8.95			10.0	9.4	
W		3.1			3.4	3.4	
p4 L		8.95	9.1		10.0		8.5
W		3.8	4.0		4.0		3.8
m1 L	15.3	15.0				16.05	14.2
W	6.5	6.0				6.15	5.7
m2 L	7.2			7.65		6.95	6.5
W	ca. 5.8			5.2		5.75	5.3

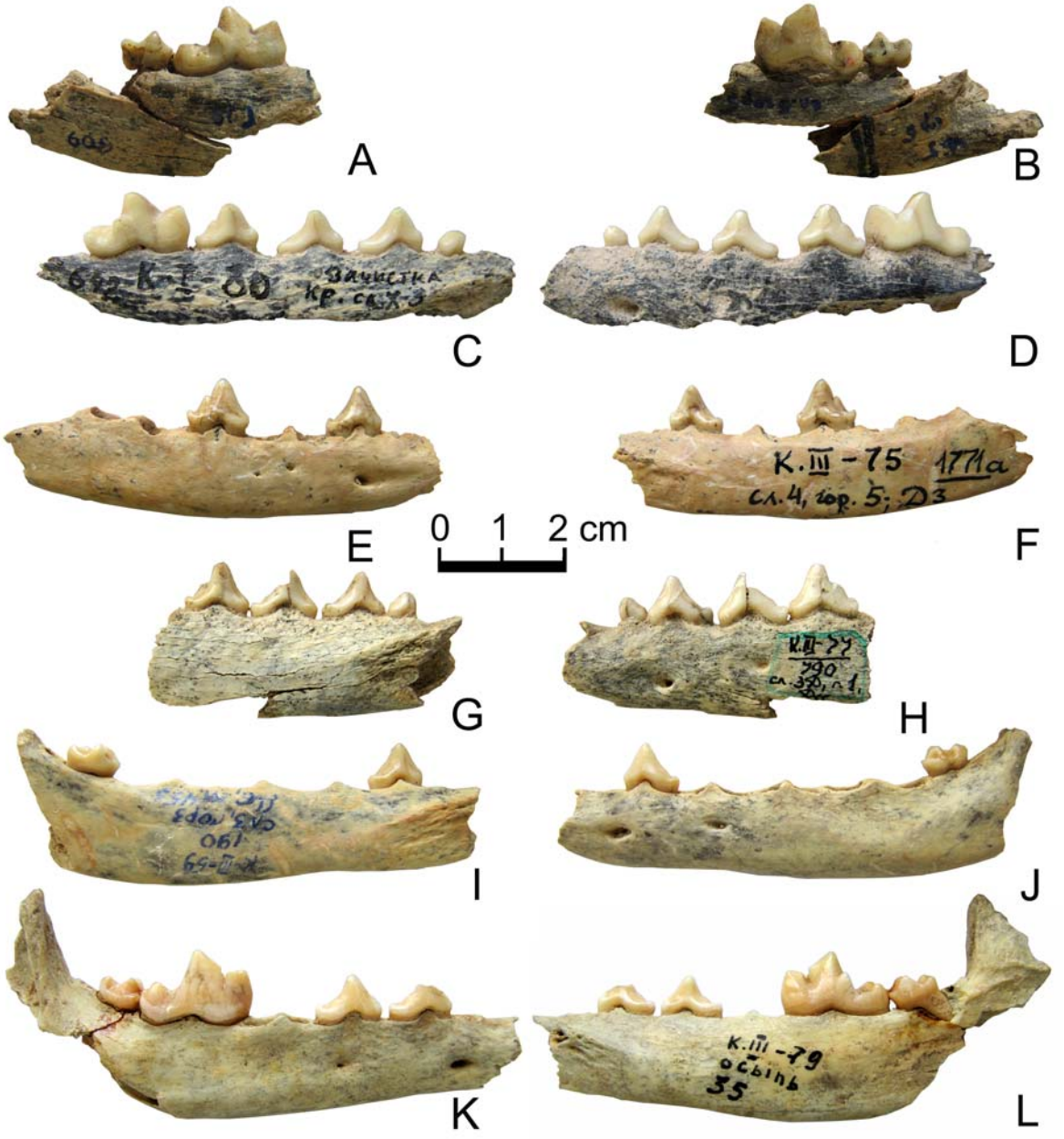

Figure 17. Fragments of mandibles of *Vulpes vulpes* from Kudaro 1 (A–D) and Kudaro 3 (E–L); labial (B, D, E, H, J, K) and lingual (A, C, F, G, I, L) views.
A, B — ZIN 36497; C, D — ZIN 36501; E, F — ZIN 36511; G, H — ZIN 36491-1; I, J — ZIN 36508; K, L — ZIN 36517.

acters is found to correspond to changes in geo-climatic factors (Szuma, 2007, 2008).

The male red fox is somewhat larger than the female, which is indicated by the size of the upper and lower canines (Fig. 19). The frequency distribution of the width of the upper canine in the Kudaro sample reveals that males and females are almost equally represented, whereas frequency distribution of the width of lower canine suggests predominance of females.

The dimensions of the limb bones reveal that the size of the fossil specimens only slightly exceeds that of recent red fox from the Caucasus (Tab. 24).

Therefore, no marked difference was found between fossil *V. vulpes* from Kudaro and the modern Caucasian representatives of this species. In addition, I failed to find reliable metric differences between Middle and Late Pleistocene red fox.

Table 23. Measurements (in mm) of lower cheek teeth in Pleistocene and recent *Vulpes vulpes* from Caucasus.

Measurements		Middle and Late Pleistocene	Recent subspecies (males and females)		
		Kudaro 1 and Kudaro 3	*V. v. caucasica*	*V. v. alpheraki*	*V. v. alticola*
p1, L	*n*	4	20	5	12
	lim	3.6–3.9	3.2–4.2	3.4–4.0	3.2–4.3
	mean	3.78	3.73	3.79	3.66
	SD	–	0.27	0.25	0.33
p1, W	*n*	4	20	5	12
	lim	2.2–2.8	1.7–3.3	2.4–2.8	2.1–2.8
	mean	2.48	2.39	2.55	2.43
	SD	–	0.30	0.16	0.19
p2, L	*n*	12	23	6	13
	lim	7.8–9.3	5.2–9.1	7.3–8.7	7.1–8.9
	mean	8.42	7.96	8.03	8.01
	SD	0.49	0.73	0.53	0.43
p2, W	*n*	12	23	6	13
	lim	3.0–3.4	2.5–3.3	2.7–3.2	2.7–3.9
	mean	3.17	3.03	2.99	3.12
	SD	0.15	0.21	0.20	0.32
p3, L	*n*	11	23	6	13
	lim	8.5–10.3	8.3–9.7	8.0–9.5	7.5–9.4
	mean	9.33	8.80	8.61	8.82
	SD	0.55	0.41	0.60	0.52
p3, W	*n*	11	23	6	13
	lim	3.0–3.5	2.6–3.5	2.9–3.4	2.7–3.7
	mean	3.28	3.18	3.13	3.21
	SD	0.16	0.23	0.19	0.29
p4, L	*n*	16	23	6	13
	lim	8.8–10.1	8.4–10.1	8.6–9.9	8.3–10.1
	mean	9.37	9.26	9.02	9.21
	SD	0.38	0.40	0.49	0.46
p4, W	*n*	16	23	6	13
	lim	3.4–4.2	3.2–4.3	3.7–4.3	3.5–4.3
	mean	3.87	3.87	3.91	3.92
	SD	0.26	0.27	0.21	0.30
m1, L	*n*	11	23	6	13
	lim	15.0–16.7	13.4–16.1	13.1–15.9	13.4–16.4
	mean	15.79	14.86	14.45	15.15
	SD	0.55	0.73	0.98	0.71
m1, Ltald	*n*	11	23	6	13
	lim	4.3–5.4	3.8–5.2	3.8–5.0	4.0–5.1
	mean	5.00	4.38	4.45	4.64
	SD	0.32	0.34	0.43	0.42
m1, W	*n*	11	23	6	13
	lim	5.1–6.5	5.2–6.6	5.5–6.3	5.5–6.4
	mean	5.99	5.93	5.89	6.01
	SD	0.43	0.35	0.31	0.28
m2, L	*n*	9	23	6	13
	lim	6.5–7.6	6.1–7.5	6.6–7.2	5.7–7.9
	mean	7.01	6.84	6.86	7.04
	SD	0.33	0.42	0.18	0.59
m2, W	*n*	9	23	6	13
	lim	4.8–5.8	4.5–5.6	4.9–5.7	4.4–6.4
	mean	5.29	5.03	5.18	5.64
	SD	0.36	0.29	0.32	0.58

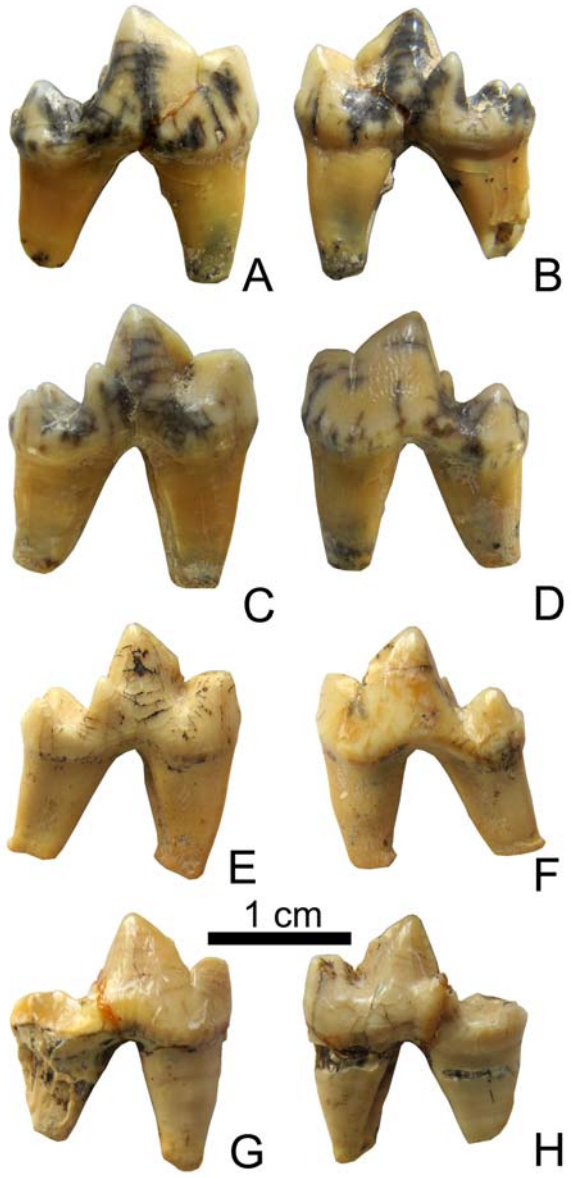

Figure 18. Lower carnassial tooth P4 of *Vulpes vulpes* from Kudaro 1 (A–D) and Kudaro 3 (E–H); labial (A, D, F, G) and lingual (B, C, E, H) views.
A, B — ZIN 36506-1; C, D — ZIN 36503; E, F — ZIN 36518-2; G, H — ZIN 36593-11.

Discussion. Remains of *V. vulpes* occur in all layers of both Kudaro caves. These fossils are the most numerous among examined species of canids.

The bones of red fox may have accumulated in several ways. The animals often dig holes inside caves, near the entrance, and may perish there. Foxes also could have been hunted by ancient hominins; however, no cut-marks or any other signs of butchering were found on the bones. The primary agent of accumulation probably was large carnivores. For examples, in the southern part of Russian Far East, red fox is recorded as the prey of wolf (*Canis lupus*) and, less commonly, of tiger (*Panthera tigris*) and leopard (*P. pardus*) (Yudin, 1992; Pikunov & Korkishko, 1992; Yudin & Yudina, 2009). Foxes also are attacked by eagles and large owls (Yudin, 1986).

Vulpes vulpes is found in many sites of the Southern Caucasus (Bronzovaya, Medvezhiya, Verkhnayay, Dzhchula and Sakazhiya in Georgia, Erevanskaya in Armenia, Binagady and Taglar in Azerbaijan), as well of the Northern Caucasus (Barakaevskaya) (Vereshchagin, 1959; Lioubine, 1989). Vereshchagin (1951) recorded two species of fox in the Binagady fauna: *Vulpes corsak* and *V. vulpes* aff. *alpherakyi*, indicating considerable morphological similarity between fossil red fox and the recent subspecies *V. v. alpherakyi*, comprising animals from semi-desert plains of Azerbaijan. Presumably, the subspecies of *V. vulpes* evolved in the Southern Caucasus as early as the Late Pleistocene.

The genus *Vulpes* is known in North America from the Late Miocene (*V. kernensis* Tedford et al., 2009, *V. stenognathus* Savage, 1941) (Tedford *et al*., 2009). Small foxes are recorded in the Pliocene and early Pleistocene fauna of Eurasia (Bonifay, 1971; Qiu & Tedrord, 1990). The origin of *V. vulpes* is associated with the Old Word, and this species is derived from the Late Pliocene *V. alopecoides* Del Campana, 1913; in the Late Pleistocene, this species dispersed to North America (Kurtén & Anderson, 1980).

The molecular phylogeny of canids reveals the monophyly of the genus *Vulpes*, species of which exhibit limited variability (Zravý & Řičánková, 2004). Another molecular study shows that the basal position to *Vulpes* is occupied by the genus *Fennecus* and *Vulpes vulpes* is clustered with *V. corsak* (Bardeleben *et al*., 2005b).

Conclusions

The Kudaro caves yield more canid species than other sites in the Caucasus and adjacent regions. Seven canid species have been identified here: *Canis arnensis kudarensis* ssp. nov., *C. mosbachensis, C. lunellensis, C. lupus, Cuon alpinus caucasicus, Vulpes praeglacialis,* and *V. vulpes*. Only two species (*Canis lupus* and *Vulpes vulpes*) have survived in the Caucasus until the present.

The Kudaro fauna does not contain *Vulpes corsak*, which is recorded for the Pleistocene of eastern areas of Southern Caucasus (Binagady). As in other Caucasian sites, the arctic fox *Vulpes lagopus*, a typical representative of mammoth biome, did not occur here.

Baryshnikov (2002) established several faunal units (f. u.) for the Pleistocene of the Caucasus. The earliest finds of canids in Kudaro caves (Kudaro 1 Cave, layer 5c and Kudaro 3 Cave, layer 8) are assigned to the Kudaro f. u., which is characteristic of the middle Middle Pleistocene: *Canis arnensis kudarensis* ssp. nov., *C. mosbachensis, Vulpes praeglacialis,* and *V.*

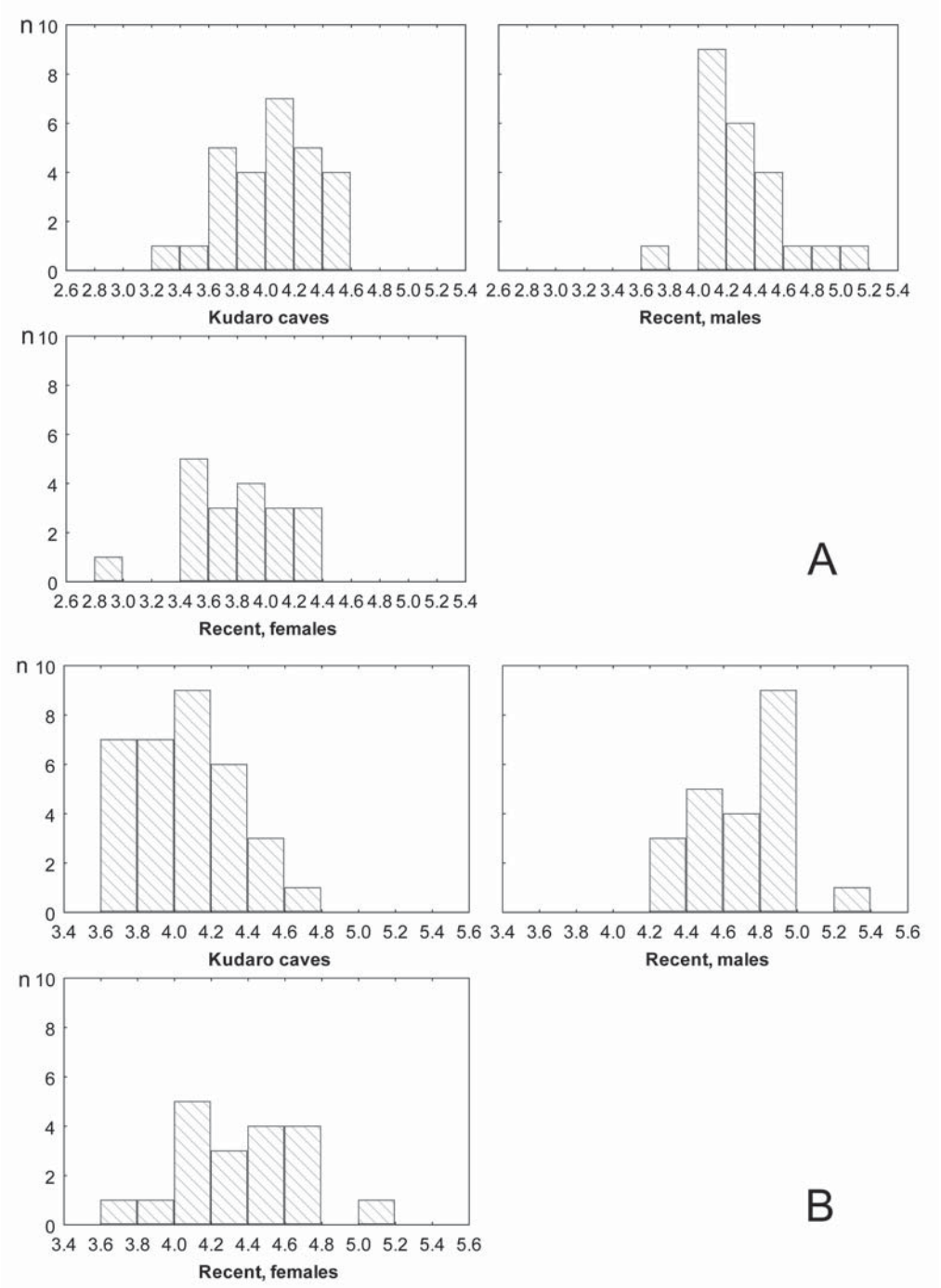

Figure 19. Frequency distribution of upper (A) and lower (B) canines width (in mm) of *Vulpes vulpes* from Caucasus: Pleistocene (Kudaro 1 and Kudaro 3) and Recent.

vulpes. It was replaced by the Kvaisa f. u. (Kudaro 3 Cave, layers 5–7) of the late Middle Pleistocene age, comprising *C. lunellensis* and *V. vulpes*. At the same time, *Canis arnensis*, *C. mosbachensis*, and *C. lunellensis* survived in the Southern Caucasus longer than in Europe, which was a factor of local environmental conditions. The Late Pleistocene Binagady f. u. and Chasaval f. u. (Kudaro caves, layers 3–4) include three species: *Canis lupus, Cuon alpinus caucasicus,* and *Vulpes vulpes*. Therefore, only *Vulpes vulpes* has been found at all levels within the caves.

The majority of the identified species are characteristic of the Caucasus and Mediterranean European regions. At the same time, *Canis lupus* and *Cuon alpinus*

Table 24. Measurements (in mm) of limb bones of Pleistocene and recent *Vulpes vulpes* from Caucasus.

Bones	Measurements	Kudaro 1 and Kudaro 3				Binagady				Recent (males and females)			
		n	lim	M	SD	*n*	lim	M	SD	*n*	lim	M	SD
Fore limb													
Scapula	SLC	2	14.7, 16.7	–	–	6	14.0–15.8	14.92	0.60				
	GLP	2	16.4, 18.5	–	–	6	16.0–17.5	16.67	0.62				
	BG	2	9.0, 11.4	–	–	6	8.9–11.0	10.11	0.73				
Humerus	Bp	2	19.5, 20.0	–	–	2	19.3, 19.4	–	–	4	15.9–17.4	16.32	0.72
	Dp	2	24.2, 24.5	–	–	2	23.7, 23.8	–	–	4	23.1–24.9	23.8	0.77
	Bd	4	18.5–21.2	19.92	1.33	2	18.6, 19.1	–	–	4	18.7–20.4	19.41	0.72
	Dd	4	13.5–15.1	14.17	0.70	2	13.5, 14.9	–	–	4	13.7–15.8	14.31	0.99
Radius	GL	1	115.5	–	–	1	112.2	–	–	4	108.0–114.4	111.0	2.72
	Bp	11	10.2–12.0	11.12	0.60	2	10.5, 10.9	–	–	4	10.6–11.3	11.05	0.31
	Dp	13	6.3–7.5	7.08	0.34	2	7.0, 7.0	–	–	3	6.7–6.9	6.80	–
	SD	4	7.2–10.2	8.45	1.27	3	8.0–8.7	8.37	–				
	Bd	2	11.6, 14.8	–	–	1	14.4	–	–	3	13.6–14.2	14.02	–
	Dd	2	7.9, 7.9	–	–	1	8.3	–	–	3	7.4–8.3	7.90	–
Ulna	DPA	7	14.0–15.7	15.07	0.61	16	14.1–16.0	15.06	0.58	3	14.2–14.7	14.43	–
	SDO	5	12.4–13.5	13.10	0.45	16	12.2–13.6	12.89	0.46	3	11.7–12.9	12.40	–
	BPC	8	7.8–10.2	8.89	0.77	16	8.1–10.3	8.97	0.63	3	8.1–10.3	8.93	–
Mc2	GL	3	37.7–48.1	37.7	–	1	48.5	–	–				
	SD	3	4.3–4.9	4.70	–	1	4.0	–	–				
Mc3	GL	4	44.2–48.1	46.20	1.59					3	42.4–44.6	43.37	–
	SD	3	3.5–4.8	3.93	–					3	3.4–3.6	3.50	–
Mc5	GL	4	36.5–45.6	41.42	4.01					4	35.3–38.9	36.52	1.67
	SD	4	3.9–5.3	4.65	0.60					4	4.0–4.3	4.15	0.13
Hind limb													
Pelvis	LA	3	11.5–15.6	13.33	–	10	11.9–14.4	13.33	0.81	4	11.6–13.4	12.32	0.76
	SH	2	12.1, 13.1	–	–	9	9.6–12.1	10.98	0.71				
Femur	Bd	1	25.5	–	–	1	19.0	–	–				
Tibia	Bp	1	20.4	–	–								
	SD	1	8.3	–	–								
	Bd	6	14.5–18.0	15.52	1.34	14	13.7–15.2	14.37	0.50	4	13.4–15.2	14.28	0.83
	Dd	7	10.1–12.2	10.71	0.79	14	9.2–11.8	10.53	0.81	4	9.6–11.0	10.30	0.62
Talus	GL	2	18.9, 20.0	–	–					4	17.1–18.7	17.65	0.72
	GB	2	11.4, 13.1	–	–					4	10.9–12.8	11.85	0.88
Calcaneus	GL	11	30.6–33.5	32.25	1.18					4	27.7–30.3	28.97	1.12
	GB	14	10.7–13.6	12.22	0.92					4	10.6–12.6	11.60	0.82

may be regarded as the northern invaders of the Caucasus region.

During formation of the Kudaro cave sediments, representatives of the genus *Canis* exhibit changes in the size and morphology of their cheek teeth, which provide a basis for recognizing the replacement of several taxa over time; in contrast, the genus *Vulpes* (*V. vulpes*) exhibits conservatism in its dental characteristics.

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