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The dhole, *Cuon alpinus* (Carnivora, Canidae), from the Upper Pleistocene of the Caucasus

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Abstract. Late Pleistocene remains of *Cuon alpinus* have been recovered from Mousterian sites in the Caucasus, mainly situated between approximately 800 m and 1600 m above sea level. Large *C. a. caucasicus* was distributed in Transcaucasia (Kudaro 1, Kudaro 3 and Tsona caves), while a smaller dhole, *C. alpinus* subsp.?, inhabited the northern Caucasus (Matuzka Cave). The morphology and relative length of the molars of *C. a. caucasicus* are similar to those of dholes from the Middle Pleistocene (*Cuon priscus*, *C. rosi, C. alpinus fossilis* and *C. a. antiquus*). The primitive structure of the teeth of *C. a. caucasicus* supports the hypothesis that western Transcaucasia was a refugium during the Late Pleistocene.

Key words: Carnivora, *Cuon*, Late Pleistocene, Middle Paleolithic, systematics, Caucasus.

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I. INTRODUCTION

The dhole, *Cuon alpinus* (PALLAS, 1811), currently inhabiting eastern Asia from Siberia to Java, was more widely distributed in the Pleistocene, with its range including Europe and North America (KURTÉN 1968; KURTÉN & ANDERSON 1980; YOUNGMAN 1993).

In the Caucasus, fossil remains of *Cuon* sp. were first identified in Kudaro 1 Cave (VERESHCHAGIN 1959). Later, a new Pleistocene subspecies, *C. alpinus caucasicus*, was described from a Mousterian layer in Kudaro 3 Cave (BARYSHNIKOV 1978). At the same time, *C. alpinus* was recovered from Mousterian levels at four other Caucasian sites: Kepshinskaya Cave (BARYSHNIKOV 1978), Tsona Cave (VEKUA et al. 1987), Matuzka Cave (BARYSHNIKOV & GOLOVANOVA 1989) and later at the open site of Ilskaya 1 (HOFFECKER et al. 1991).

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II. LOCALITIES AND MATERIAL

Paleolithic sites with remains of *C. alpinus* are situated on both the southern and northern slopes of the western Great Caucasus (Fig. 1). Numerous specimens are known from the Kudaro caves, at an altitude of approximately 1600 m above sea level (a. s. l.). A lower canine and two fragments of M/1 are present in layer 3 of Matuzka Cave (800 m a. s. l.). Sediments in Kepshinskaya Cave and Ilskaya 1 (both below 500 m a. s. l.) produced only one canine each. The chronostratigraphic position of these Caucasian sites is shown in Fig. 2.

The cave sites of Kudaro 3 and Kudaro 1 were excavated by Prof. V. LIUBIN (St. Petersburg) in 1957-1961 and 1974-1981. He recovered the following number of dhole bones and teeth: Kudaro 3: Layer 6 – 2 specimens, Layer 5 – 1, Layer 4f – 3, Layers 4a-4e – 24, Layers 3-4 – 29, Layer 3 – 67, Layers 2-3 – 5, Layer 2 – 2, Total = 133; Kudaro 1: Layers 4-5a – 1, Layer 4 – 1, Layers 3-4 – 3, Layer 3 – 8, Total = 13.

All fossil material studied is stored in the Zoological Institute, Russian Academy of Sciences (ZIRAS), St. Petersburg.

III. METHODS

Maximum length (L) and width (W) were measured for all cheek teeth. In addition, the length of the M/1 talonid (Lt) on the labial side and the maximum width of the talonid (Wt) were also taken.

In order to further analyse the morphological variability of M/1, the following features were used (Fig. 3): metaconid reduction (1a-1b), presence or absence of a small tubercle on the lingual

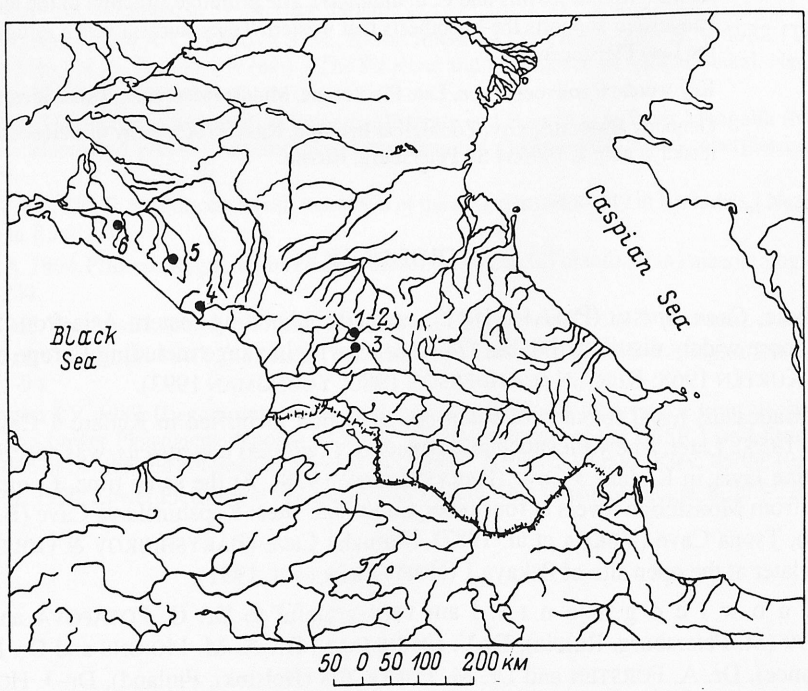

Fig. 1. Finds of *Cuon alpinus* in Paleolithic sites of the Caucasus. 1 – Kudaro 3, 2 – Kudaro 1, 3 – Tsona, 4 – Kepshinskaya Cave, 5 – Matuzka, 6 – Ilskaya 1.

Years Before Present	Oxygen-Isotope Stage	Kudaro 3	Kudaro 1	Kepshinskaya Cave	Matuzka	Ilskaya 1
10.000	1					
	2	Layer 2				
25.000						
45.000	3	↑	↑*		↑	↑
		Layer 3	Layer 3	↑ Layer 3 ↓	Layer 3	
60.000		↓	↓		↓	
	4					Mousterian Layer
73.000		?	?			
		↑	↑			
90.000	5a-5d	Layers 4a-4e	Layer 4			
116.000		↓				
	5e	Layer 4f				
128.000		↓				
	6	?				
195.000	7					
251.000	8	↑** Layer 5				
297.000	9	Layer 6				

Fig. 2. Stratigraphic position of layers with remains of *Cuon alpinus* in Paleolithic sites of the Caucasus. Absolute dates (LIUBIN 1993): (*) Radiocarbon date 44 140 ± 2 400 B.P. (Gr-6079) and (**) Thermoluminescence dates 252 000 ± 51 000 B.P.(RTL-511), 245 000 ± 49 000 B.P. (RTL-534).

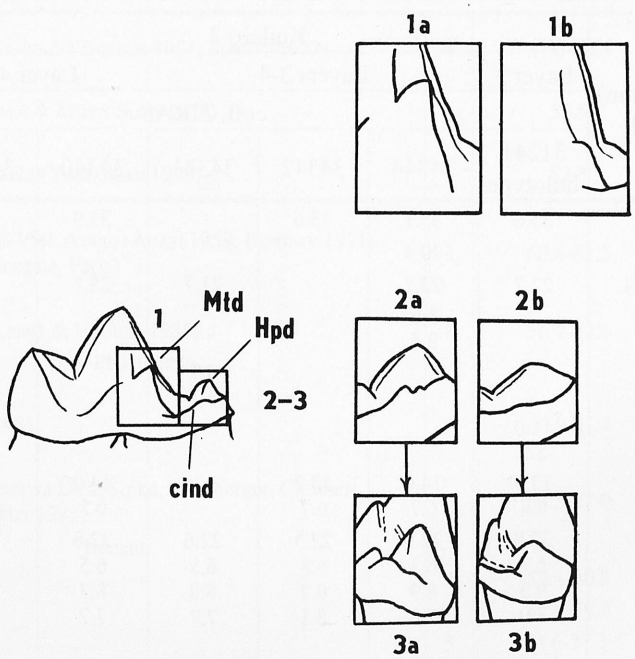

Fig. 3. Morphological variability in the talonid of M/1 in *Cuon alpinus*. Lingual (1, 2) and posterior (3) views. Cind: cingulid, Hpd: hypoconid, Mtd: metaconid.

cingulid of the talonid (2a-2b), and the degree of cingulid development on the posterior side of the hypoconid base (3a-3b).

IV. RESULTS

C r a n i u m. In layers 3 and 4 of Kudaro 1, there is a fragment of an occipital (ZIRAS 34350). The greatest breadth across the occipital condyles of 41.1 mm and the skull height of 64.6 mm are the same as in the Recent subspecies *C. a. alpinus*.

M a n d i b l e s. Mandibles from the Kudaro caves have a depth in front of the M/1 (Table I) that is less than in any specimens of Late Pleistocene *C. a. europaeus* BOURGUIGNAT, 1868 (BONIFAY 1971). The alveolus for M/2 (L=7.1, 7.5, 7.8 mm) is preserved in these fragments, but the alveolus for M/3 is absent. The length of P/1-M/1 is equal to that in *C. a. alpinus*, and significantly exceeds other Recent subspecies.

D e n t i t i o n. A left maxillary with P4/-M/1 (ZIRAS 34343) is known from Kudaro 3 (layers 3 and 4). In size and morphology, the upper teeth of this specimen do not differ from those of recent *C. alpinus*, but they are notably smaller than *C. a. antiquus* MATTHEW & GRANGER, 1923 from the late Middle Pleistocene of China (COLBERT & HOOIJER 1953). Measurements in mm: P4/-M/1 L=31.8, P4/ L=21.2, W=10.5, M1/ L=13.0, W=14.3.

With one exception (Table I) the mean sizes of the lower molars from the Kudaro caves are greater than those in the Recent subspecies of *C. alpinus* except the nominate one. The nominate subspecies has the same premolar length (P/2 is longer), but the width of the fossil teeth is somewhat

Table I

Measurements of mandibles and lower teeth of *Cuon alpinus caucasicus*

Measurements (mm) and index (%)		Kudaro 3						Kudaro 1
		Layer 3	Layers 3-4			Layer 4		Layer 3
		coll. ZIRAS						
		31241 holotype	34344	34342	34341	34340	34338	34339
P/4-M/1 length		35.6	35.1	35.6		35.9		36.4
P/1-P/4 length			40.4				43.2	
Height anterior to P/4		22.7	23.7		21.7	25.7		
P/1	L		5.6					
	W		3.6					
P/2	L				8.7		9.8	
	W				4.7		5.1	
P/3	L	11.0						
	W	5.5						
P/4	L	13.9	14.0	13.7		14.0	14.6	14.4
	W	6.8	6.7	6.7		6.5	7.2	7.6
M/1	L	22.8	22.9	22.5	22.6	22.8		23.6
	Lt	6.7	6.3	6.8	6.5	6.5		6.7
	W	9.3	8.9	9.2	8.8	8.7		9.1
	Wt	8.0	7.8	8.1	7.7	7.7		8.0
Index								
Length P/2: Length M/1					38.5			
Length P/4: Length M/1		61.0	61.1	60.9		61.4		61.0

less. Comparative analysis of *C. a. caucasicus* and other fossil dholes showed that P/4 and M/1 are longer in *C. priscus* THENIUS, 1954 (Hundsheim, Mosbach, Petralona), *C. rosi* PONS-MOYÁ & MOYÁ-SOLÁ, 1978 (Cueva Victoria), and *C. a. fossilis* NEHRING, 1890 (Heppenloch, Lunel-Viel) from the Middle Pleistocene of Europe (THENIUS 1954; ADAM 1959; BONIFAY 1971; KURTÉN & POULIANOS 1977; PONS-MOYÁ & MOYÁ-SOLÁ 1978). *C. alpinus* cf. *priscus* from Arago cave (P/1-M/2 L=69.9, 70.6; P/2 L=9.5, 9.4; P/4 L=13.8, M/1 L=23.0, 22.2, 23.6 mm; coll. Musée de l'Homme, Paris) is similar in size to specimens of *C. a. caucasicus*. Late Pleistocene *C. a. europaeus* from Europe (Čertova Dira, Sipka, Chokier) has premolars with mean lengths close to *C. a. caucasicus*, but the M/1 is slightly shorter (NEHRING 1891; CORDY 1983). Length ratios of both P/2 and P/4 to M/1 are similar in *C. a.caucasicus* to those in late Middle Pleistocene *C. a. fossilis* and *C. a. antiquus* (Yenchingkuo) and differ noticeably from the same ratios in *C. a. europaeus* (SCHÜTT 1973). A relatively longer P/4 distinguishes *C. a. europaeus* from other fossil and Recent subspecies of *C. alpinus* in the Palaearctic region (Table II).

The first lower molar of *C. a. caucasicus* has a well developed metaconid, which is sometimes reduced in Recent *C. alpinus* (Fig. 3). The lingual cingulid of M/1 usually extends along the hypocone base on the posterior side (not developed in Recent *C. alpinus*) and this cingulid bears a small tubercle (vestigial entoconid?). The latter is characteristic of *C. priscus* and present in *C. rosi* and in a specimen of *C. a. fossilis* from Lunel-Viel (THENIUS 1954; BONIFAY 1971; PONS-MOYÁ & MOYÁ-SOLÁ 1978), but in Recent *C. alpinus* it is for the most part absent.

Table II

Index (%) of P/4 length relative to M/1 length

Subspecies and locality	N	O. R.	M
Middle Pleistocene			
Cuon priscus			
Hundsheim and Mosbach (THENIUS 1954; SCHÜTT 1973)	4	57.6-60.4	59.3
Cuon rosi			
Victoria (PONS-MOYÁ & MOYÁ-SOLÁ 1978)	1	52.5	–
Cuon sp.			
Cripple Creek, Alaska (YOUNGMAN 1993)	1	57.5	–
C. alpinus fossilis			
Heppenloch, Lunel-Viel, Arago (ADAM 1959; BONIFAY 1971; coll. Musee de l'Homme, Paris)	3	60.4-63.5	62.0
C. alpinus antiquus			
Yenchingkuo (COLBERT & HOOIJER 1953)	3	56.7-62.6	59.8
Upper Pleistocene			
C. alpinus caucasicus			
Kudaro (coll. ZIRAS)	5	60.9-61.4	61.1
C. alpinus europaeus			
Mars de Vence, Čertova Dira, Sipka, Ofenberger, Chokier (SCHÜTT 1973; CORDY 1983)	5	63.5-67.0	65.5
Recent			
C. alpinus alpinus	7	58.1-60.3	59.6
C. alpinus hespericus	11	51.8-59.2	56.4
C. alpinus primaeus	5	54.6-57.3	55.7
C. alpinus dukhunensis	3	50.9-58.8	55.9
C. alpinus adustus	6	55.2-59.5	57.0

The following is the distribution of primitive (a) and derived (b) conditions:

Features	1a	1b	2a	2b	3a	3b
C. a. caucasicus, Kudaro caves	5	0	4	1	4	1
C. alpinus, Recent	23	4	1	12	2	10

The lower jaw from Tsona Cave has a reduced metaconid on M/1, but the size of this tooth (L=22.1, W=9.0 mm) is typical of *C. a. caucasicus* (VEKUA et al. 1987).

Two fragments from Matuzka Cave represent significantly smaller (Lt=6.0, 6.5, Wt=6.5, 7.1 mm) M/1 of *C. a. caucasicus*. Both of these specimens have derived morphotypes (1a, 2b, 3b).

V. DISCUSSION AND CONCLUSIONS

The oldest remains of *C. alpinus* from the Caucasus are found in Acheulean layers 5-6 of Kudaro 3. The subspecies identification of this material is impossible due to the lack of teeth.

The subspecific position of the small *C. alpinus* from Matuzka Cave is problematic because of the lack of archaic features in the morphology of the talonid of M/1. It is not clear if this is a case of variability within *C. a. caucasicus* molars, or if it indicates the existence of another form of dhole in the northern Caucasus. A small dhole could have reached the northern Caucasus from eastern Europe, together with other species of the boreal fauna (*Ochotona pusilla*, *Mammuthus primigenius*, *Rangifer tarandus*). This suggestion seems plausible, even in the absence of any reliable finds of Pleistocene *C. alpinus* in either the Russian Plain or the Crimea [the reference for the Kodak open site in Ukraine (PIDOPLICHKO 1951; CORDY 1983) was based on an incorrect identification].

Remains of dholes from Mousterian sites in Transcaucasia belong to the large *C. a. caucasicus*. They are especially numerous in layer 3 of Kudaro 3 and layer 3 of Kudaro 1. The caves were at that time located at the upper border of the forest zone (LUBINE et al. 1985). *C. a. caucasicus* most likely inhabited the upper forest and alpine zones.

The primitive condition of the teeth of *C. a. caucasicus*, which are distinct from the contemporary *C. a. europaeus*, indicate a low rate of morphological change in the dentition of Caucasian dholes. The evolution of *C. alpinus* appears to conform to the previous deduction (BARYSHNIKOV 1989), that western Transcaucasia was a refugium for *C. a. caucasicus* during the Late Pleistocene. This taxon long outlived forms of extinct mammals preserved there: *Hystrix vinogradovi*, *Prometheomys schaposchnikovi kudarensis*, *Spelearctos deningeri.*

REFERENCES

ADAM K. D. 1959. Mittelpleistozäne Caniden aus dem Heppenloch bei Gutenberg (Württemberg). Stuttgarter Beiträge zur Naturkunde, **27**: 1-46.

BARYSHNIKOV G. F. 1978. [The dhole of the Caucasus.] Trudy Zoologicheskogo Instituta AN SSSR, **79**: 79-84. (In Russian).

BARYSHNIKOV G. 1989. Les mammifères du Paleolithique inférieur du Caucase. L'Anthropologie (Paris), **93**: 813-830.

BARYSHNIKOV G. F., GOLOVANOVA L. V. 1989. Mammals of the Mousterian site Matuzka in the Kuban Caucasus. Trudy Zoologicheskogo Instituta AN SSSR, **198**: 3-55. (In Russian with English summary).

BONIFAY M.-F. 1971. Carnivores quaternaires du sud-est de la France. Mémoires du Museum national d'Histoire naturelle, Paris, **21**: 43-377.

COLBERT E. H., HOOIJER D. A. 1953. Pleistocene mammals from the limestone fissures of Szechwan, China. Bulletin of the American Museum of Natural History, **102**: 1-134.

CORDY J.-M. 1983. Decouverte de *Cuon alpinus europaeus* Bourguignat dans le Quaternaire de Belgique. Mémoires de la Société Préhistorique Franaise, **16**: 49-53.

HOFFECKER J., BARYSHNIKOV G., POTAPOVA O. 1991. Vertebrate remains from the Mousterian site of Ilskaya 1 (Northern Caucasus, USSR): New analysis and interpretation. Journal of Archaeological Science, **18**: 113-147.

KURTÉN B. 1968. Pleistocene Mammals of Europe. London: Weidenfeld and Nicolson. 317 pp.

KURTÉN B., ANDERSON E. 1980. Pleistocene Mammals of North America. New York: Columbia University Press. 442 pp.

KURTÉN B., POULIANOS A. 1977. New stratigraphic and faunal material from Petralona Cave with special reference to the Carnivora. Anthropos (Athens), **4**: 47-130.

LIUBIN V. P. 1993. The chronostratigraphy of the Caucasian Paleolithic. Rossiiskaya Arkheologia, 2: 5-14. (In Russian with English summary).

LUBINE V. P., TCHERNIACHOVSKI A. G., BARYSHNIKOV G. F., LEVKOVSKAIA G. M., SELIVANOVA N. B. 1985. La grotte de Koudaro 1 (resultats de recherches pluridisciplinaires). L'Anthropologie (Paris), **89**: 159-180.

NEHRING A. 1891. Diluviale Reste von *Cuon, Ovis, Saiga, Ibex* und *Rupicarpa* aus Mähren. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, **2**: 107-155.

PIDOPLICHKO I. 1951. [Ice age.] Vol. 2. Kiev, Izdatelstvo AN Ukrainskoi SSR. 264 pp. (In Russian).

PONS-MOYÁ J., MOYÁ-SOLÁ S. 1978. La fauna de Carnivoros del Pleistoceno medio (Mindel) de la cueva Victoria (Cartagena, Espana). Acta Geologica Hispanica, **13**: 54-58.

SCHÜTT G. 1973. Fossil mammals of Java. V. Pleistozäne Caniden (Carnivora, Mammalia) aus Java. Proceedings, Koninklijke Nederlandse Akademie van Wetenschappen, **76**: 446-471.

THENIUS E. 1954. Die Caniden (Mammalia) aus dem Altquartär von Hundsheim (Niederösterreich) nebst Bemerkungen zur Stammesgeschichte der Gattung *Cuon*. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **99**: 230-286.

VEKUA A. K., GABELAYA Ts. D., MUSKHELISHVILI A. T., MAMATSASHVILI N. S. 1987. Paleolithic vertebrate fauna of the cave Tsona. Peshchery Grusii, **11**: 92-100. (In Russian with English summary).

VERESHCHAGIN N. K. 1959. [Mammals of the Caucasus: History of the evolution of the fauna.] Moscow-Leningrad, Izdatelstvo AN SSSR. 704pp. (In Russian).

YOUNGMAN P. 1993. The Pleistocene small carnivores of eastern Beringia. Canadian Field Naturalist, **107**: 139-163.