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PLEISTOCENE FELIDAE (MAMMALIA, CARNIVORA) FROM THE KUDARO PALEOLITHIC CAVE SITES IN THE CAUCASUS

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ABSTRACT

The Kudaro Paleolithic site complex in Southern Ossetia includes five species of felids: *Panthera onca gombaszoegensis, P. spelaea, P. pardus, Felis silvestris* and possibly *Lynx lynx*. The fossil jaguar *P. onca gombaszoegensis* was identified from the lowest stratigraphic level of the Middle Pleistocene (Likhvian = Holsteinian Interglacial). Remains of *P. pardus* and *Felis silvestris* were recovered from all layers. *Panthera spelaea* and *Lynx lynx* represent northern migrants appeared there at the end of the Middle Pleistocene and Late Pleistocene respectively.

Key-words: Caucasus, Felidae, Paleolithic cave sites, Pleistocene, systematics

ПЛЕЙСТОЦЕНОВЫЕ КОШАЧЬИ (MAMMALIA, CARNIVORA, FELIDAE) ИЗ КУДАРСКИХ ПЕЩЕРНЫХ ПАЛЕОЛИТИЧЕСКИХ СТОЯНОК НА КАВКАЗЕ

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РЕЗЮМЕ

Из комплекса Кударских палеолитических стоянок в Южной Осетии определены пять видов кошачьих: *Panthera onca gombaszoegensis, P. spelaea, P. pardus, Felis silvestris* и, возможно, *Lynx lynx*. Ископаемый ягуар *P. onca gombaszoegensis* присутствует в самом нижнем уровне среднего плейстоцена (лихвинское межледниковье, голштейн). Останки *P. pardus* и *Felis silvestris* обнаружены во всех слоях. *Panthera spelaea* и *Lynx lynx* появляются здесь соответственно в конце среднего плейстоцена и в позднем плейстоцене как северные мигранты.

Ключевые слова: Кавказ, Felidae, палеолитические пещерные стоянки, плейстоцен, систематика

INTRODUCTION

The Felidae Fischer de Waldheim, 1817, comprising 40 recent species (Wozencraft 2005), is represented by 11 species on the territory of the former USSR; most felids are confined to the tropic zone. At present, five species are known to occur in the Caucasus: *Panthera pardus* (L., 1758), *Lynx lynx* (L., 1758), *Felis silvestris* Schreber, 1777, *F. chaus Schreber*, 1777, and *Otocolobus manul* (Pallas, 1776). The first three species are widely distributed, while *F. chaus* occurs in the eastern parts of the Caucasus and *O. manul* is restricted to the semi-desert areas of Armenia and Azerbaijan. Two or three other species became extinct during historic times (Vereshchagin 1959): *Panthera leo* (L., 1758), *P. tigris* (L., 1758) and probably *Acinonyx jubatus* (Schreber, 1775).

In the Late Pleistocene of Western Europe, the Felidae comprised five species (Reumer et al. 2003; Sommer and Benecke 2006): *Panthera leo spelaea*

(Goldfuss, 1810), *P. pardus*, *Lynx lynx*, *L. pardinus* (Temmink, 1827), *Felis silvestris*, and *Homotherium latidens* (Owen, 1846). Information about the Pleistocene cats of Eastern Europe and Northern Asia is scarce. Most of this vast territory was inhabited solely by the cave lion (*P. spelaea*), with the addition in several places of lynx (*L. lynx*). The felids of the Middle and Late Pleistocene of the Caucasus seem to be more diverse, and they have been reassessed as a result of the analysis of the material from the Kudaro caves.

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 (Saint Petersburg), who directed a long-term multidisciplinary project there. The collection of vertebrate fossils from the Kudaro caves encompasses nearly 100 species. The material was collected through careful inspection and sieving of excavated sediments during the archeological excavations.

The first study of the Pleistocene mammals from Kudaro 1 Cave was undertaken by Vereshchagin (1957, 1959), who identified two felid species: *Panthera spelaea* and *P. pardus*. Later, these finds were supplemented by *Felis* cf. *silvestris* (Vereshchagin and Baryshnikov 1980a). Kudaro 3 was found to contain fossils of four species: *P. spelaea, P. pardus, Felis lynx* and *F. silvestris* (Vereshchagin and Baryshnikov 1980b). However, the mentioned identifications were regarded as preliminary, and the collected material has not been thoroughly studied. This communication represents the first detailed review of the felid collections from the Kudaro caves.

This study continues a series of publications dealing with the Pleistocene fauna of Carnivora from the Kudaro Paleolithic cave sites (Baryshnikov 2010a, 2010b, 2011).

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 located virtually one above the other on the left bank of Djedjori River (Rioni River Basin) near Kvaisa City (Southern Ossetia).

Kudaro 1 Cave is located 1600 m above sea level and 260 m above the river level. The cave is Y-shaped with two entrances. The thickness of sediments varies in different parts of the cave from 1.5 to 4.5 m. The deposits contain substantial quantities of limestone rubble, which is more heavily weathered in the lower stratigraphic levels. Layers 5a–5c are composed of yellowish fuscous loam and contained a Late Acheulian industry. The sediment of layers 3–4, representing grayish loam, yielded Mousterian artifacts.

The lowermost cave deposits have been dated by thermo-luminescence to 360,000 ± 90,000 years before present (RTL-379) for layer 5c, and 350,000 ± 70,000 years (RTL-373) for layer 5b (Lioubine 1998). Fossil taxa from layer 5c belong to thermophilous mammals such as *Macaca* sp., *Ursus thibetanus* G. Cuvier, 1823, and two species of porcupine, *Hystrix indica* Kerr, 1792, *H. brachyura vinogradovi* Argiropulo, 1941, and correspond to a very warm period during the Middle Pleistocene (Holsteinian Interglacial in Western Europe [= Likhvian Interglacial in Eastern Europe]) coinciding with the Marine Isotope Stage 11, 405–340 ka BP (Loutre and Berger 2003; Nitychoruk et al. 2006). The Mousterian layer 3a is dated by radiocarbon to 44,150 ± 2,400/1,850 (Gr-6079) (Lioubine 1998).

Kudaro 3, which is situated somewhat lower than Kudaro 1 Cave, represents a long corridor with an underground lake in its deepest portion. The cave sediments mostly consist of loam with limestone fragments. The color of the loam color ranges from yellow-brown at the base to dark-gray at the uppermost part. A small number of Acheulian artifacts were recovered from layers 5–8 and Mousterian artifacts were recovered from layers 3–4 (Lioubine 1998).

The geomorphologic data indicate that Kudaro 3 was initially exposed by erosion that occurred approximately 50,000–100,000 years after the opening of Kudaro 1(Nesmeyanov 1999). The contact zone of the Acheulian and Mousterian layers is dated by RTL-dates of 252,000 ± 51,000 years and 245,000 ± 49,000 years (Lioubine 1998), suggesting a considerable time gap between their deposition in the cave. The bones of Kudaro cave bear (*Ursus kudarensis* Baryshnikov, 1985) from layer 3 were dated by AMS radiocarbon dates of: >41,600 (OxA-19611), 47,900 ± 2,500 (OxA-19612) and 47,700 ± 1,800 (OxA-19613) (A. Stuart, pers. comm.).

The material examined includes more than 200 remains of felids. These are predominantly postcranial bones; mandible fragments and isolated teeth are scarce. This composition of the skeletal elements may be explained by taphonomic characteristics of the Kudaro caves, which provided shelters during the Pleistocene for cave bears and large felids; therefore, the remains of carnivores that perished inside the cave predominate in the layers.

The studied collections are stored at the Zoological Institute of the Russian Academy of Sciences in Saint Petersburg (ZIN). For comparative analysis, the fossil and recent collections at ZIN, as well as Pleistocene felid material at other institutions (see Institutional abbreviations below), have been used.

The bones and teeth were measured by calipers with accuracy 0.5 mm. Limb bones were measured according to von den Driesch (1976). Tooth dimensions were analyzed with use of factor analysis from STATISTIKA 6.0.

Institutional abbreviations. BSPGM, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany; CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; FSM, Florida State Museum, University of Florida, Gainesvillle, USA; GHMT, Georgian National Museum, Tbilisi, Georgia; GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; HLMD, Hessisches Landesmuseum Darmstadt, Germany; IGF, Institute of Geology, University of Florence, Florence, Italy; IGN, Institute of Geology of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia; IGPR, Institute of Geology and Paleontology, "La Sapienza" University, Roma, Italy; ISAK, Institute of Systematics and Evolution of Animals, Krakow, Poland; IQW, Institute of Quarter Paleontology, Weimar, Germany; LGQM, Laboratoire de Geologie du Quaternaire, Marsel-Lumine, France; MMBA, Moravsky Museum (Anthropos), Brno, Czech Republik; MMY, Mammoth Museum, Yakutsk, Russia; MNHN, Muséum national d'Histoire naturelle, Paris, France; NHM, Natural History Museum, London, Great Britain; NHMM, Nature History Museum, Mainz, Germany; NHMSG, Natural History Museum, St. Gallen, Switzerland; NHMV, Natural History Museum, Vienna, Austria; NNHMK, National Natural History Museum, Kiev, Ukraine; PIN, Borissyak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; UCBL, Claude Bernard University Lyon 1, Villerbann, France; USNM, United States National Museum, Washington DC, USA; ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Measurements. Dental measurements: *L* – greatest length, *W* – greatest width, *Lpa* – length of paracone, *Lpad* – length of paraconid. Bone measurements: *Bcf* – breadth of cuboid facet, *Bd* – breath of the distal end, *BG* – breadth of the glenoid cavity, *Bp* – breadth of the proximal end, *DC* – depth of the caput femoris, *Dd* – depth of the proximal end, *Dp* – depth of the proximal end, *GB* – greatest breadth, *GL* – greatest length, *GLP* – greatest length of the glenoid process, *LAR* – length of the acetabulum on the rim, *SD* – smallest breadth of the diaphysis in the middle part, *SH* – smallest height of the shaft of ilium.

SYSTEMATICS

Family Felidae Fischer de Waldheim, 1817

Genus *Panthera* Oken, 1816

Type species. *Felis pardus* Linnaeus, 1758.

Included species. Five modern species: *Panthera tigris* (L., 1758), *P. uncia* (Schreber, 1775), *P. onca* (L., 1758), *P. leo* (L., 1758) and *P. pardus* (L., 1758); and several extinct species.

Distribution. Early Pliocene – Recent, Africa, Eurasia; Early Pleistocene – Recent, North and South America.

Panthera onca (Linnaeus, 1758)

Panthera onca gombaszoegensis (Kretzoi, 1938)

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: right P4 (ZIN 35026, layer 5, horizon 3, 1959); left p3 (ZIN 36429, layer 5, horizon 9, 1961); fragment of scapula (ZIN 36434, layer 5, horizon 8, 1958); right os triquetrum (ZIN 36433, layer 5c, horizon 3, 1980); left calcaneus (ZIN 35028-1, layer 5c, horizon 3, 1978); right calcaneus (ZIN 36437, layer 5, horizon 8, 1958); left os naviculare (ZIN 36430-2, layer 5c, horizon 4, 1988); phalanx 1, anterior (ZIN 36436, layer 5, horizon 5, 1958); phalanx 1, posterior (ZIN 36435, layer 5, horizon 9, 1958); phalanx 1, posterior (ZIN 36431, layer 5, horizon 5, 1961); phalanx 2, anterior (ZIN 36430-1, layer 5c, horizon 4, 1980). Kudaro 3 Cave: fragment of left metatarsal 5 (ZIN 36432, layer 6, 1978). Altogether, 14 fossil remains.

Description. There are two isolated teeth assigned to the fossil jaguar *P. onca gombaszoegensis*. The upper carnassial tooth P4 (ZIN 35026, Fig. 1A, B) with a damaged parastyle. Its length and width correspond to those of *P. o. gombaszoegensis* from other localities (Table 1). The labial margin of the crown is straight in occlusal view. The protocone is

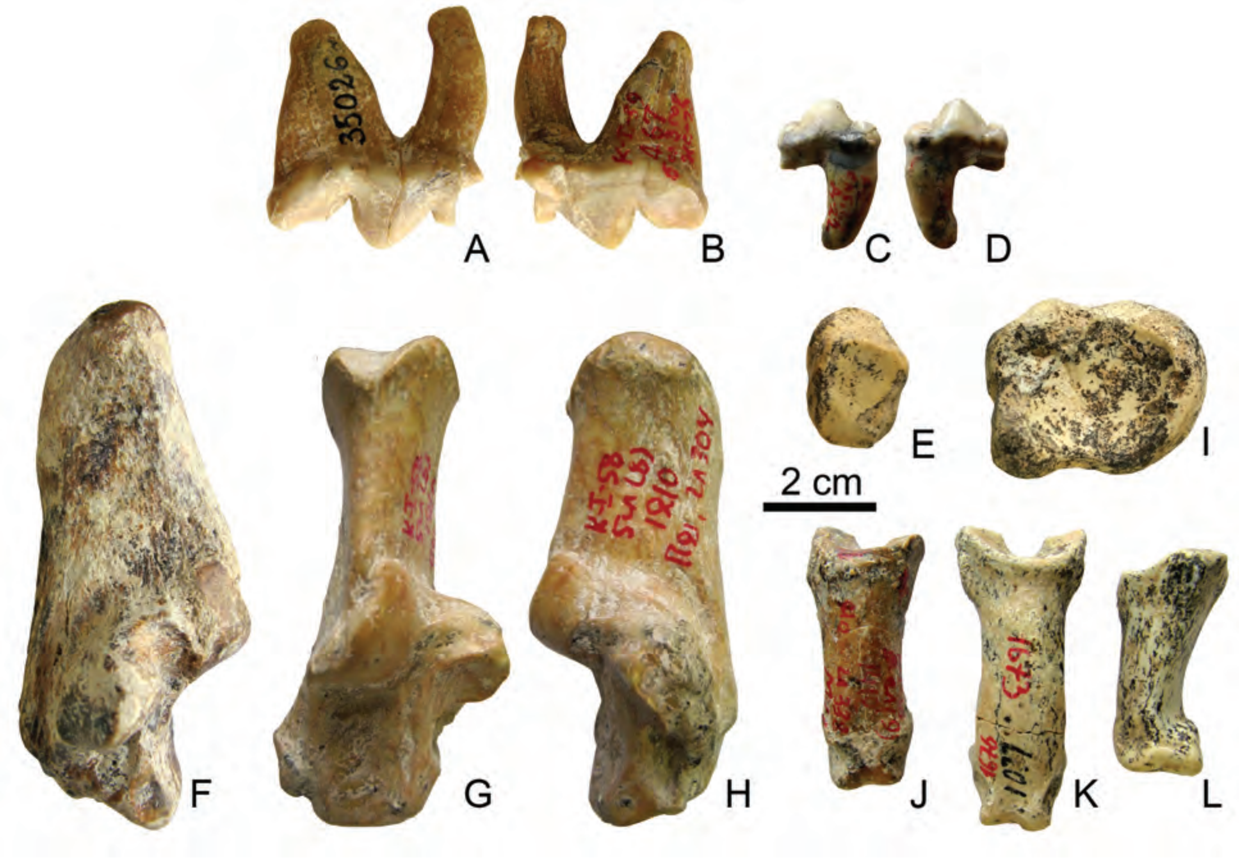

Fig. 1. Fossil remains of *Panthera onca gombaszoegensis* from Kudaro 1 Cave: A–D: cheek teeth: A, B – right upper premolar P4 (ZIN 35026); C, D – left lower premolar p3 (ZIN 36429); labial (A, C) and lingual (B, D) views; E–L – postcranial bones: E – right os triquetrum (ZIN 36433); F – left calcaneus (ZIN 35028-1); G, H – right calcaneus (ZIN 36437); I – left os naviculare (ZIN 36430-2); J – phalanx 1, posterior (ZIN 36435); K – phalanx 1, anterior (ZIN 36436); L – phalanx 2, anterior (ZIN 36430-1); proximal (E, I), dorsal (G, J–L) and medial (F, H) views.

relatively small, located at the level of the anterior margin of the paracone. The length of ZIN 35026 significantly exceeds that of the upper carnassial tooth of *P. pardus* from the Pleistocene of Europe (Kotsakis and Palombo 1979).

The lower premolar p3 (ZIN 36429, Fig. 1C, D) does not differ in size from the same premolar in *P. o. gombaszoegensis* (Table 1). The tooth exhibits a high protoconid and two small cusps anterior and posterior to the protoconid, respectively. The anterior blade of the protoconid is oriented along the axis of the crown.

The fragment of a scapula (ZIN 36434), which is markedly more robust in comparison with the scapula of fossil leopard (*P. pardus*) from the Kudaro cave (see Table 8), has been tentatively assigned to *P. o. gombaszoegensis*.

The left calcaneus (ZIN 35028-1, Fig. 1F) is noticeably smaller than this bone in the tiger (*P. tigris*) and lion (*P. leo*), but considerably larger than that of the recent jaguar. Measurements of this fossil specimen are similar to those of *P. o. augusta* from the Pleistocene of Florida (Table 2). ZIN 35028-1 is partially damaged, which complicates morphological comparisons.

The right calcaneus (ZIN 36437, Fig. 1G, H) corresponds in its dimensions to the calcaneus of recent *P. onca*. The difference from the calcaneus of *P. pardus* is reflected in the more robust and wider distal end of this bone. In addition, the surface of the cuboid facet is less oblique with respect to the longitudinal axis than in *P. pardus*.

There are several autopodial bones intermediate with respect to size between those of the tiger and lion, on the one hand, and those of the leopard, on

Table 1. Measurements (mm) of upper premolar P4 and lower premolar p3 of Pleistocene *Panthera onca*. Designations: (–) – measurement is not available; n/n – no number.

Locality	Museum number and/or reference	P4			p3	
		L	Lpa	W	L	W
P. onca gombaszoegensis						
Caucasus						
Kudaro 1, layer 5	ZIN 35026	32.3	11.4	16.5		
Kudaro 1, layer 5	ZIN 36429				16.9	8.0
Akhalkalaki, Georgia	GHMT n/n (Hemmer et al. 2001)				16.6	7.8
Europe						
L'Escale, France	LGQM CD66/795	30.8	12.0	17.0		
	LGQM CD66/1142	31.4	11.4	19.6		
	LGQM CD66/764	32.4	12.5	–		
	LGQM CD66/763a				16.8	8.1
	LGQM CD66/763b				17.1	8.7
	LGQM CD66/771				17.7	8.5
Château, France	(Argant, 1991)				15.4	7.7
					15.6	8.4
Untermassfeld, Germany	IQW 1984/20268 (Hemmer 2001)	32.0	12.1	18.4		
	IQW 1983/19169 (Hemmer 2001)				14.8	7.4
	IQW 1992/24137 (Hemmer 2001)				15.9	7.2
	IQW 1995/25343 (Hemmer 2001)				15.6	8.0
	IQW 1986/21782 (Hemmer 2001)				18.3	9.1
Mosbach, Germany	HLMD WT231 (Hemmer et al. 2003)				14.4	7.6
Westbury-Sub-Mendip, England	NHM M.33978 (Bishop 1982)				17.3	8.2
	NHM M.33979 (Bishop 1982)				16.8	7.5
	NHM (Bishop 1982)	33.0	–	18.5		
Asia						
Lahuti, Tajikistan	GIN 3848/362-67 (Sotnikova and Vislobokova 1990)				15.8	7.1
P. onca toscana						
Santa Maria near Tasso, Italy	IGF 851, holotype (Hemmer et al. 2010)				16.5	9.5
P. onca georgica						
Dmanisi, Georgia	GHMT 2027, holotype (Hemmer et al. 2010)				16.5	8.1
P. onca augusta						
Niobara River, North America	USNM 125, type (Kurtén1965b)	33.2	12.9	16.7		

the other hand. These bones, assigned to *P. o. gombaszoegensis*, include the os triquetrum (ZIN 36433, Fig. 1E; greatest anatomical length 25.3 mm), os naviculare (ZIN 36430-2, Fig. 1I), and the proximal portion of the metatarsal 5 (ZIN 36432; Bp = 20.9 mm). In their proportions, these bones correspond to those of recent *P. onca*; although, the fossil specimens are substantially larger. The measurements of os naviculare are comparable to those of *P. o. gombaszoegensis* from the Pleistocene of France (Table 2). The measurements of phalanx 1 (ZIN 36436, GL = 49.5 mm, Bp = 21.3 mm; ZIN 36435, GL = 43.1 mm, Bp = 19.0 mm; ZIN 36431, phalanx 1 of fifth finger, GL = 42.6 mm, Bp = 17.4) and phalanx 2 (ZIN 36430-1, GL = 37.4 mm, Bp = 17.5 mm) (see Fig. 1J-L) also fall within the range of these values in *P. o. gombaszoegensis* (Argant 1991).

At other Caucasus localities, fossil jaguar is represented by two mandibles. The material from the early Middle Pleistocene of Akhalkalaki was assigned to *P. o. gombaszoegensis* (Hemmer et al. 2001), and a mandible from the Early Pleistocene locality of Dmanisi was described as a new subspecies *P. o. georgica* (Hemmer et al. 2010). On the basis of the ratio between the width and length of p3, the specimen from Kudaro 1 (47.3%) corresponds to that from Akhalkalaki (47.0%) and falls within the range of variation of this index in *P. o. gombaszoegensis* from various European localities (see Hemmer et al. 2010). *Panthera onca toscana* (Schaub, 1949) from the Early Pleistocene of Europe and *P. o. augusta* (Leidy, 1872) from the Pleistocene of North America possess a significantly wider premolar, corresponding to that in the recent jaguar (mean value 54.4%, n = 10). ZIN 36429 differs from *P. o. georgica* with respect to the lower crown of p3 (protoconid height along outer side measuring 8.7 mm). According to the ratio between the height and length of p3, the jaguar from Kudaro 1 (51.5%) is markedly smaller than *P. o. georgica* (59.4%) and *P. o. gombaszoegensis* from Mosbach in Germany (58.3%) (Hemmer et al. 2003, 2010).

Discussion. The morphological and metric characters of the fossil jaguar from the Kudaro caves provide the basis for its assignment to the subspecies *P. onca gombaszoegensis*. The remains are confined to the basal layer 5c at Kudaro 1. Kudaro 3 yielded a single bone from layer 6; however, the coloration and degree of mineralization suggest that this bone was redeposited from the lower layers.

This material represents the youngest record of the fossil jaguar in the Southern Caucasus. In the Northern Caucasus it is unknown.

The presence of *P. o. gombaszoegensis* in Europe is documented in localities of widely varying age from the Early Pleistocene (Late Villafranchian) to the Middle Pleistocene (Bishop 1982; Argant 1991; Kahlke et al. 2011). In Central Asia, this subspecies was identified at the locality of Lakhuti, dated to the later Early Pleistocene (lowermost part of the Cromerian s. l.; Sotnikova and Vislobokova 1990).

Table 2. Measurements (mm) of limb bones of Pleistocene *Panthera onca*. Designation: (–) – measurement is not available.

Bone	Locality	Museum number and/or reference	GL	GB	Bcf	GD	GLP	BG
		P. o. gombaszoegensis						
Scapula	Kudaro 1, layer 5	ZIN 36434					47.2	30.6
Calcaneus	Kudaro 1, layer 5	ZIN 35028-1	93.6	40.0	ca27.8			
	Kudaro 1, layer 5	ZIN 36437	73.5	37.1				
	Château, France	Coll. Château G.7-35 (Argant 1991)	91.5	–	–			
Naviculare	Kudaro 1, layer 5	ZIN 36430-2		30.6		38.3		
	Château, France	Coll. Château F.7-3 (Argant 1991)		31.4		36.4		
		P. onca augusta						
Calcaneus	Kendrick, USA	FSM 8891 (Kurtén 1965b)	89.5	34.6	24.2			

Fossil jaguar occupied various habitats in Europe and the Caucasus from gallery forests, shrubs to woodland savanna, open grasslands and mountain ranges (Hemmer et al. 2010). Palynological data, obtained for layer 5c in Kudaro 1, provided a basis for reconstructing warm forest-steppe landscapes with savanna elements for this time period (Lioubine 1998).

The earliest jaguars (*P. onca*) were found in Eurasia during the Olduvai polarity subchron (1.95 – 1.77 Ma BP) (Spassov 2003; Hemmer et al. 2010). The European jaguars are assigned to the species *P. toscana* from the Early Pleistocene, and *P. gombaszoegensis* from the final Early to early Middle Pleistocene, following one after another (Argant 1991), or alternatively, are considered two chrono-subspecies: *P. gombaszoegensis toscana* and *P. g. gombaszoegensis* (Hemmer 1972), or else *P. onca toscana* and *P. o. gombaszoegensis* (Hemmer et al. 2003). Recently, they have been complemented by the subspecies *P. o. georgica* from the Caucasus (Hemmer et al. 2010).

Approximately one million years ago, jaguars migrated to North America and later reached South America, where they are present today; whereas in the Old World, jaguars became entirely extinct. North American fossil jaguars are assigned to the subspecies *P. o. augusta* (see Kurtén 1965b; Hemmer 2001).

According to results of molecular-genetic studies, *P. onca* is a sister species to the monophyletic group *Panthera leo* + *P. pardus*. A separate position within the genus *Panthera* is occupied by *P. uncia* and *P. tigris* (Pecon-Slattery et al. 2004; Davis et al. 2010). The timing of jaguar divergence from the lion–leopard lineage is estimated at roughly 2.56–3.66 Ma BP, which places the time of jaguar origin earlier than the available paleontological data; the lion and leopard diverged 1.95–3.10 Ma BP (Davis et al. 2010).

Panthera spelaea (Goldfuss, 1810)

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: right talus (ZIN 29515, layer 5, horizon 3, 1959; Vereshchagin [1971, p. 194] erroneously pointed out the number 29074); Kudaro 3 Cave: left p4 (ZIN 36395, layer 5, 1975). Late Pleistocene, Kudaro 3 Cave: fragment of left mandibles with m1 and remain of p4 (ZIN 31904, layer 4, horizon 3, 1975); fragment of left immature mandible with d3 (ZIN 36428, layer 3a, 1978); right scaphoid bone (ZIN 36399-1, layer 4f, 1978); left metacarpal 1 (ZIN 36396, mixed layers, 1957); left metacarpal 2 (ZIN 36398-2, layer 3, horizon 4, 1959); right metacarpal 3 (ZIN 36397-1, layer 3, horizon 2, 1959); left metacarpal 3 (ZIN 36397-2, layer 3, horizon 2, 1959); left metacarpal 4 (ZIN 36397-3, layer 3, horizon 2, 1959); left metacarpal 4 (ZIN 36402, layer 4e, 1978); right metacarpal 4 (ZIN 36398-1, layer 3, horizon 4, 1959); right metacarpal 5 (ZIN 35401, layer 4d, 1980); left metacarpal 5, def. (ZIN 36400, layer 4a-b, 1978); left cuboid bone (ZIN 36397-18, layer 3, horizon 2, 1959); right metatarsal 2 (ZIN 29420-1, mixed layers, 1957); left metatarsal 2 (ZIN 29420-4, mixed layers, 1957); fragment of metatarsal 3 (ZIN 29420-2, mixed layers, 1957); fragment of right metatarsal 4 (ZIN 29420-2, mixed layers, 1957); left metatarsal 4 (ZIN 36403-1, layer 4, horizon 2, 1959); left metatarsal 4 (ZIN 29420-3, mixed layers, 1957); right metatarsal 5 (ZIN 36403-2, layer 4, horizon 2, 1959). In both caves, sediments contain also numerous fragments of vertebrae (mainly caudal vertebrae), ribs and phalanges. Totally 80 fossil remains were collected.

Description. The dentition is similar to that of the recent lion *P. leo*, but tooth size is considerably larger. The isolated p4 (ZIN 36395, Fig. 2B, C) from Kudaro 3 does not differ in its length and width from the examined specimens of this tooth in the cave lion *P. spelaea* (Table 3). The measurements of this tooth are variable; it is generally shorter than m1, being longer, however, in several cases.

The m1 (ZIN 31904, Fig. 2D, E) corresponds in its dimensions to that of the males of *P. spelaea spelaea* (Table 3). The crown of ZIN 31904 is widened at the level of contact of the paraconid and protoconid as a result of the development of a rather small prominence on its lingual side. This prominence is developed in *P. leo* and *P. onca*, but is not characteristic of *P. tigris*. Vereshchagin (1971) noted that recent *P. leo* rather frequently exhibits a well marked cuspid at that place of the crown, which is usually absent in *P. tigris*. In the specimens of *P. spelaea* (n=14) examined by the author, this cuspid is either absent or extremely small.

The fragment of a juvenile mandible with milk tooth d3 (ZIN 36428; Fig. 2A), judging from the mandible height at d3 (25.9 mm), belonged to a lion cub, whose lower carnassial tooth m1 had not yet erupted. In the recent lions, the eruption of permanent teeth begins between the 9th and 12th months (Grzimek 2004). Since the recent lions and tigers (including Siberian tiger, which lives in winter in snow and cold conditions; Yudin and Yudina 2009)

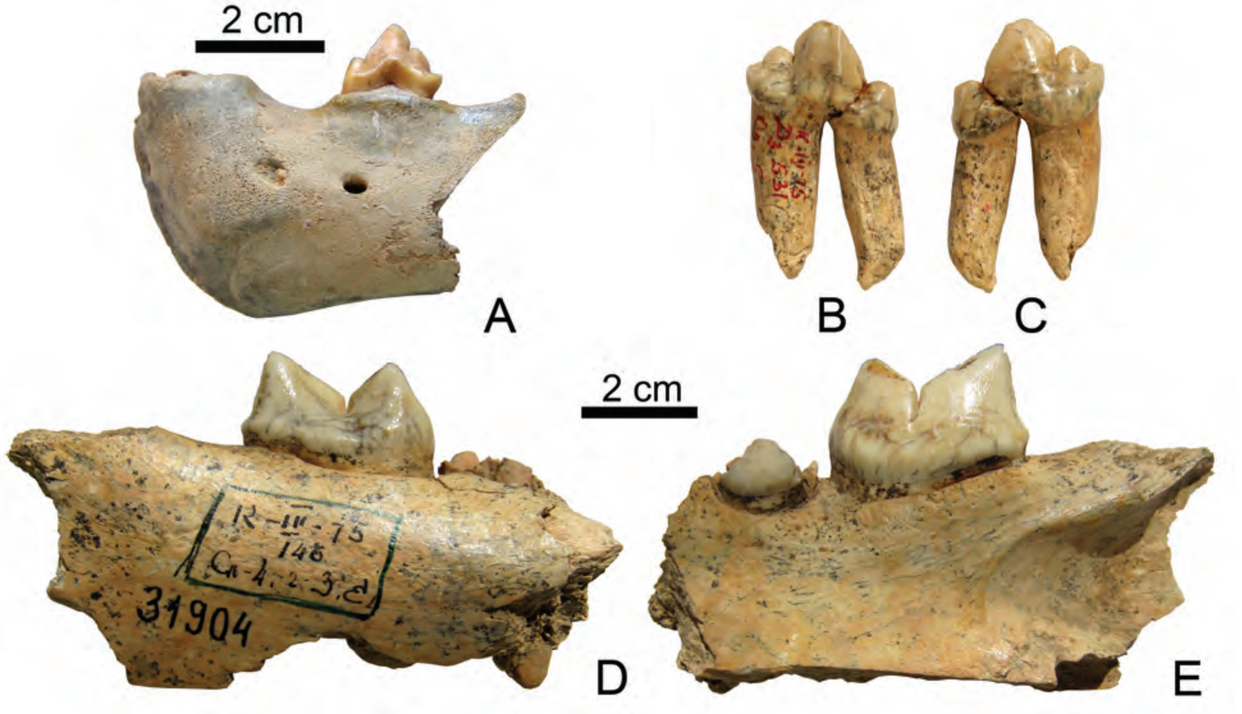

Fig. 2. Lower cheek teeth of *Panthera spelaea* from Kudaro 3 Cave: A – fragment of left mandible with milk teeth d3 (ZIN 36428); B, C – left p4 (ZIN 36395); D, E – fragment of left mandible with m1 (ZIN 31904); labial (A, C, E) and lingual (C, D) views.

mate at any time of the year, it is difficult to define a time of death of this cave lion cub. The measurements of the milk tooth d3 (length 13.0 mm, width 5.8 mm, height 10.0 mm) are comparable to those of recent *P. leo* (ZIN 1455, length 13.4 mm, width 5.4 mm, height 9.2 mm). The same tooth size was found in *P. tigris* (ZIN 36383, length 13.5 mm, width 6.3 mm, height 8.4 mm), its crown, however, being lower.

The postcranial bones of the cave lion from the Kudaro caves are markedly larger than bones of the recent lion (*P. leo*) and tiger (*P. tiger*) (Tables 4 and 5).

The right scaphoid bone (ZIN 36399-1, Fig. 5A, B) is very large (GB=55 mm). The bone is elongated on its proximal-distal axis and exhibits a robust posterior-medial process, such as in recent *P. leo* (in *P. tiger*, the posterior-medial process is more slender and pointed).

The left metacarpal 1 (ZIN 36396, Fig. 3A, B) is similar to that of recent *P. leo*, but more robust.

The left metacarpal 2 (ZIN 36398-2, Fig. 3C, D) possesses a wide dorsal facet on the lateral side of its proximal part for articulation with metacarpal 3, as in recent *P. leo* (in *P. tigris*, this facet is narrower and shorter), but the dorsal margin of the proximal articular surface is convex, as in *P. tigris* (in *P. leo* this margin is saddle-shaped).

Two metacarpals 3, right (ZIN 36397-1, Fig. 3E, F) and left (ZIN 36397-2, Fig. 3G, H), found in the same layer and within the same excavation unit (D-6-7), are assigned to a large individual (male). The dorsal surface of the proximal end lacks a depression, which is present in *P. tigris* (similar to *P. leo*). Facets on the lateral side of the bone at its proximal margin are fused, as in *P. leo* (they are divided in *P. tigris*).

The left metacarpal 4 (ZIN 36397-3, Fig. 3K, L) also is derived from excavation unit D-6-7 and is comparable to ZIN 36397-2. Both specimens are similar with respect to color and weathering, undoubtedly belonging to the same individual (an adult male). In addition, there are two more metacarpals 4: left (ZIN 36402, Fig. 3M, N) and right (ZIN 36398-1, Fig. 3O, P). These bones exhibit similar morphology. The median part of the proximal articular surface, articulating with metacarpal 3, is markedly shifted with regard to the lateral part of the surface, and is
)

Table 3. Measurements (mm) of lower premolar p4 and lower molar m1 of *Panthera spelaea*. Designation: (–) – measurement is not available; n/n – no number.

Locality	Museum number	p4		m1		
		L	W	L	Lpad	W
P. s. spelaea						
Kudaro 3, layer 5	ZIN 36395	27.5	14.2			
Kudaro 3, layer 4	ZIN 31904			30.1	16.8	15.2
Binagady, Azerbaijan	ZIN 24409-22, left	25.7	13.5	29.1	17.2	14.9
	ZIN 24409-22, right	25.9	13.3	29.0	16.4	15.0
Bocharov Stream, Sochi, Russia	CCMGE 1/5292			26.8	15.2	14.0
P. s. spelaea (males)						
Kent’s Cavern, England	NHM 16691			30.0	–	14.7
	NHM 1055			29.8	–	15.7
	NHM 17921			30.8	–	15.3
Jaurens, France	UCBL 301035	29.4	13.3	29.9	15.7	15.1
l’Herm, France	MNHN 1903-20	28.6	14.8	31.3	14.9	15.3
Widkirchli, Switzerland	NHMSG n/n	31.3	15.5	31.2	–	16.5
Wierzchowska Górna, Poland	ISAK 6803	30.3	17.0	31.1	18.3	17.0
	ISAK 6804	28.1	14.4	30.9	16.2	16.2
Schusteriucke, Austria	NHMV 002553	29.2	13.4	30.3	–	16.0
Lautscher, Austria	NHMV n/n	31.2	16.1	29.7	–	16.9
Předmosti, Czech Republic	MMBA n/n	27.2	13.2	30.2	15.3	14.1
Kodak, Ukraine	NNHMK 3541, left	25.8	14.1	29.9	16.4	15.5
Saltymakovo, Russia	ZIN 32747	27.8	14.1			
Krasnyi Yar, Russia	ZIN 32746-2	30.2	15.7	32.0	16.8	16.7
Sukhoi Log, Russia	IGN n/n	29.8	14	28.9	–	14.1
Kurtak, Russia	ZIN 36409	27.8	14.7	30.1	16.0	14.9
P. s. spelaea (females)						
Kent’s Cavern, England	NHM 178			26.7	–	12.5
	NHM 16691a			28.0	–	14.8

Table 3. Continued.

Locality	Museum number	p4		m1		
		L	W	L	Lpad	W
Jaurens, France	UCBL 30832			27.9	15.7	14.2
	UCBL 300916			28.0	15.0	14.1
	UCBL 300914	25.7	12.2			
Circeo, Italy	IGPR 1952			25.9	13.7	13.8
Zoolithen Cave, Germany	NHM M272	27.7	14.5	28.1	–	14.4
Wierzchowska Górna, Poland	ISAK 6802	25.1	12.7	27.8	13.6	13.5
	ISAK 6809	24.5	13.0	27.1	14.9	12.8
Předmosti, Czech Republic	MMBA n/n	25.1	12.2	26.7	15.0	12.8
	MMBA n/n	25.9	12.2	27.9	15.3	12.6
Švédův Stůl, Czech Republic	MMBA n/n	25.1	12.4	25.8	13.9	13.4
Starye Duruitory, Moldova	ZIN n/n [SD 9N/1]	25.0	11.9	25.9	13.9	12.4
Krishtaleva, Crimea, Ukraine	NNHMK n/n	25.4	11.6	25.9	14.4	12.4
Shubnoe, Russia	ZIN 29417	26.0	13.4	27.5	13.8	13.5
Medvezhiya Cave, Russia	ZIN 29397-2, cast	27.2	13.1	26.2	13.9	13.6
Krasnyi Yar, Russia	ZIN 32746-3	26.5	12.8	27.0	–	13.3
P. s. vereshchagini						
Berezovka River, Russia	ZIN 31823	27.1	13.6	26.8	15.0	14.5
	ZIN 29405	25.2	12.7	28.5	14.5	14.6
Krestovsky Cape, Russia	private coll.	29.7	16.3	30.2	15.3	15.7
P. fossilis						
Westbury Quarry Cave, England	NHM n/n [F66]			30.5	–	17.0
Mosbach, Germany	NHMM 1951/513	29.9	13.7	ca29.5	–	16.2
	NHMM 1962/634	28.4	14.2			

separated from the latter by a low ridge, as in *P. leo* (in *P. tigris*, both parts are situated almost on the same level and are not subdivided by a ridge).

The right metacarpal 5 (ZIN 36401, Fig. 3Q, R) and a fragment of the left metacarpal 5 (ZIN 36400) were recovered from layer 4. The proximal articular surface is wide, exhibiting a small depression at the plantar end, as in *P. leo* (in *P. tigris*, this surface is narrower and the depression is absent).

The presence of metacarpals (mc3 and mc4) from the same individual in Kudaro 3 provides a basis for morphometric comparison of these bones of the cave

Fig. 3. Metacarpals of *Panthera spelaea* from Kudaro 3 Cave: A, B – left Mc1 (ZIN 36396); C, D – left Mc2 (ZIN 36398-2); E, F – right Mc3 (ZIN 36397-1); G, H – left Mc 3 (ZIN 36397-2); K, L – left Mc4 (ZIN 36397-3); M, N – left Mc4 (ZIN 36402); O, P – right Mc4 (ZIN 36398-1); Q, R – right Mc5 (ZIN 36401); dorsal (B), plantar (A) and lateral (C–R) views.

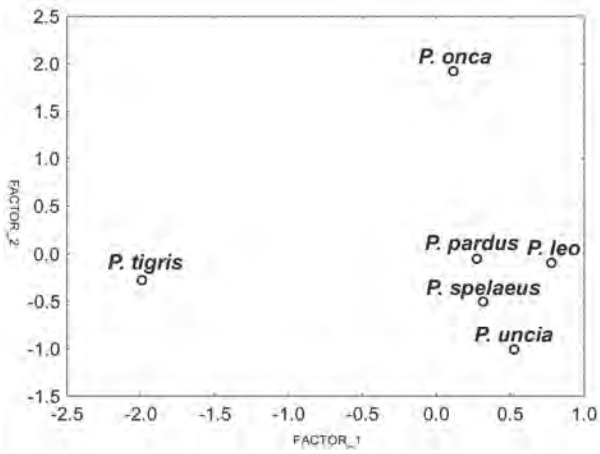

Fig. 4. Plot of factor scores of Factor 1 and Factor 2 from principal components analysis of metacarpal 3 and metacarpal 4 in *Panthera.*

lion with those of other panther-like felids. For this purpose, Principal Component Analysis has been performed, based on 12 measurements of metacarpal 3 and metacarpal 4, for 6 species: the cave lion (*P. spelaea*), the lion (*P. leo*), the tiger (*P. tigris*), the jaguar (*P. onca*), the leopard (*P. pardus*), and the snow leopard (*P. uncia*). This analysis demonstrated that within the first and second factor space, species were distributed in three groups: 1) *P. tigris*, 2) *P. onca*, and 3) the remaining species (Fig. 4). The first group is separated from the others by Factor 1 (49.9% of dispersion), encompassing measurements of mc3 (GL, Dp, Dd) and three measurements of mc4 (GL, Bp, Dd). The second group is segregated by Factor 2 (30.9% of dispersion), which comprises two measurements of mc3 (SD, Bd) and two measurements of mc4 (Dp, SD). The first and second groups contain felids that inhabit forests and thickets (tiger, jaguar). The third group combines felids adapted to open landscapes and mountains (cave lion, lion, snow leopard) or to forests, savanna woodland, and rocky terrain (leopard). The divergence in the structure of the forelimb in species from different groups may be related to locomotion, as well as peculiarities in the use of the forelimbs for taking prey.

The right talus (ZIN 29515, Fig. 5E, F) yields a greatest length of 57.7 mm and greatest breadth of 47.7 mm, which is typical of the size of this bone in *P. spelaea* (Vereshchagin 1971). The posterior end of the depression on the trochlea tali lacks a granular tubercle, as in *P. leo* (this tubercle is developed in *P. tigris*, closing the depression).

The left cuboid bone (ZIN 36397-18, Fig. 5C, D) is large (GL = 34.3 mm) with large facet for articulation with metatarsus 4. As in the recent *P. leo*, the middle facet for articulation with the os cuneiforme 3 is broad, without a "waist" (it is narrow and possesses a waist in *P. tigris*).

Two metatarsals 2, right (ZIN 29420-1, Fig. 5G, H) and left (ZIN 29420-4, Fig. 5I, J), belong to a single individual. The proximal articular surface is not bordered by a bulge at the plantar margin, thus resembling *P. tigris* (*P. leo* exhibits a well-developed bulge).

Metatarsal 3 (ZIN 29420-2) is represented only by a distal fragment.

There are two left metatarsals 4 (ZIN 36403-1, Fig. 5K, L and ZIN 29420-3, Fig. 5M, N), which differ slightly in size. The plantar margin of the proximal end exhibits a distinctive lateral prominence like that in *P. leo* (this prominence is absent in *P. tigris*).

The right metatarsal 5 (ZIN 36403-2, Fig. 5O, P) exhibits a slight division on the proximal end at the plantar margin, also present in *P. leo* (the plantar margin in *P. tigris* is clearly divided into two lobes).

Thus, the morphology of autopodial bones from the Kudaro caves reveals a similarity between the cave lion and the recent lion, with only a few characters resembling those of the recent tiger.

Discussion. The bones of a large lion-like cat occur throughout the Pleistocene layers in the Kudaro caves; however, *P. spelaea* has been identified beginning in the upper part of the Middle Pleistocene levels (layer 5, horizon 3 at Kudaro 1 and layer 5 at Kudaro 3). These remains are common in both caves in the Late Pleistocene levels (layers 3–4). Remains of the cave lion replace those of jaguar in the upper layers, suggesting that the invasion of *P. spelaea* into the Caucasus resulted in the local extinction of jaguar *P. onca gombaszoegensis.*

Panthera spelaea remains were identified in the Southern Caucasus from asphalt deposits at Binagady in Azerbaijan (Vereshchagin 1971). The dimensions of the lower carnassial tooth m1 are comparable for Kudaro and Binagady, falling within the range of metric variability of this tooth in the cave lion (Table 3). However, metacarpals and metatarsals from Binagady are markedly smaller, their measurements being near the minimum values of the same measurements in other samples of *P. spelaea* (Tables 4 and 5). Vereshchagin (1951, 1971) reported similar dimensions for specimens from Binagady. This may be explained by a predominance of females in the sample, but another

Fig. 5. Limb bones of *Panthera spelaea* from Kudaro 3 Cave: A, B – right scaphoid bone (ZIN 36399-1); B, C – left cuboid bone (ZIN 36397-18); E, F – right talus (ZIN 29515); metatarsals: G, H – right Mt2 (ZIN 29420-1); I, J – left Mt2 (ZIN 29420-4); K, L – left Mt4 (ZIN 36403-1); M, N – left Mt4 (ZIN 29420-3); O, P – right Mt5 (ZIN 36403-2); proximal (A), distal (B), dorsal (C, F), plantar (D, E) and lateral (G–P) views.

possibility is size reduction of the local population on the plains of Azerbaijan as a result of isolation from northern populations of this species.

In the Late Pleistocene, *P. spelaea* was distributed throughout Northern Eurasia, as well as in Beringia, inhabiting various biotopes, predominantly tundra-steppe, forest-steppe, and steppe. Vereshchagin (1971) suggested that favorable habitats for these large cats were river valleys with gallery forests bordering open landscapes on the watersheds, because such places are usually characterized by an abundance of various ungulates.

Table 4. Measurements (mm) of metacarpal bones of *Panthera spelaea*. Designations: (–) – measurement is not available; n/n – no number.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Mc 1 (*P. s. spelaea*)							
Kudaro 3, mixed layers	ZIN 36396	51.9	24.0	21.5	19.3	20.0	19.5
Secrets Cave, Urals, Russia	Private coll.	42.7	27.3	–	–	20.0	–
		39.6	23.0	–	–	16.7	–
		40.3	22.4	–	–	16.8	–
		47.4	29.0	–	–	22.4	–
		40.8	22.9	–	–	19.4	–
Mc 2 (*P. s. spelaea*)							
Kudaro 3, layer 3	ZIN 36398-2	122.5	27.3	38.4	19.1	27.4	25.5
Binagady, Azerbaijan	ZIN 24409-5	107.2	24.2	29.6	17.8	23.1	20.8
	ZIN 24409-6	107.3	22.9	31.1	14.7	22.9	22.3
Secrets Cave, Urals, Russia	Private coll.	122.7	25.8	36.3	18.0	26.7	22.1
		110.0	24.7	31.6	16.4	23.6	21.4
		115.1	26.7	36.0	16.7	26.3	23.9
Mc 3							
P. s. spelaea							
Kudaro 3, layer 3	ZIN 36397-1	135.1	32.6	32.2	20.6	28.9	26.5
	ZIN 36397-2	134.8	34.2	33.0	20.6	28.9	26.6
Secrets Cave, Urals, Russia	Private coll.	124.8	30.1	30.1	16.6	25.3	23.2
		125.1	28.1	31.8	17.4	26.7	24.8
		126.5	34.0	34.2	16.3	27.6	25.4
		131.5	28.0	32.4	17.1	26.9	25.3
		135.7	26.7	32.1	–	–	–
P. s. vereshchagini							
Yana River, Russia	ZIN 30884	111.2	28.6	26.4	15.7	22.3	21.2
Mc 4 (*P. s. spelaea*)							
Kudaro 3, layer 3	ZIN 36397-3	131.5	26.3	31.3	19.8	26.9	–
	ZIN 36398-1	130.7	27.7	32.5	19.3	27.3	25.9

Table 4. Continued.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Kudaro 3, layer 4e	ZIN 36402	126.1	23.8	29.3	16.7	26.1	26.3
Binagady, Azerbaijan	ZIN 24409-4	117.7	22.9	25.4	16.0	22.5	23.4
	ZIN 24409-10	114.0	21.6	24.2	15.0	21.8	20.7
	ZIN 24409-2	118.2	22.8	25.5	15.6	23.5	23.2
Starye Duruitory, Moldova	ZIN n/n [746]	113.5	23.6	25.4	14.1	22.1	21.6
Kostenki 4, Russia	ZIN 20653-13	–	23.4	28.6	–	–	–
Ulus-Orak, Achinsk, Russia	ZIN 17286	123.0	23.4	28.1	16.0	22.7	24.1
Secrets Cave, Urals, Russia	Private coll.	123.2	25.9	31.0	17.1	26.4	25.1
		123.8	25.5	31.4	17.6	26.5	25.4
		120.2	21.3	25.8	15.1	21.6	–
		114.0	21.3	24.3	14.6	21.5	21.8
Mc 5 (*P. s. spelaea*)							
Kudaro 3, layer 4d	ZIN 36401	105.8	29.4	28.2	16.4	25.7	24.9
Kudaro 3, layer 4a-b	ZIN 36400	–	31.0	29.3	–	–	–
Binagady, Azerbaijan	ZIN 24409-8	87.8	22.9	24.9	12.6	20.6	19.4
	ZIN 24409-9	95.6	24.4	25.5	14.9	21.3	19.7
Wildkirchli, Schwitzerland	MHNSG n/n	109.3	29.2	31.4	18.7	26.3	25.7
Kostenki 4, Russia	ZIN 20653-40	–	28.1	25.1	–	–	–
Secrets Cave, Urals, Russia	Private coll.	105.2	28.7	29.5	16.6	24.3	23.8
		100.7	25.6	23.5	16.6	22.2	–
		103.0	26.0	24.3	15.7	22.1	20.7

As the material from Kudaro indicates, the cave lion inhabited hearts of mountain massifs. The co-occurrence of its remains with those of large ungulates suggests that this felid probably preyed on deer, roe, goat, sheep, and bison in the Caucasus. Occasional hunting for young cave bears is also possible, especially during the winter, as suggested in Europe on the basis of isotopic evidence for the diet of the cave lion (Bocherens et al. 2011). During battles with herbivorous adult cave bears, cave lions might be killed and their carcasses then disarticulated in caves by trampling by cave bear and other visitors (Diedrich 2011).

The cave lion has been documented in the Northern Caucasus (Ilskaya 1, Gubs Shelter No. 1, Mezmaiskaya Cave, Treugolnaya Cave), as well as in the Southern Caucasus (near Sochi City, Akhstyrskaya

Table 5. Measurements (mm) of metatarsal bones of *Panthera spelaea*. Designation: (–) – measurement is not available; n/n – no number.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
Mt 2							
P. s. spelaea							
Kudaro 3, mixed layers	ZIN 29420-1	136.2	27.8	35.9	20.4	28.4	23.7
	ZIN 29420-4	135.6	28.0	31.3	19.6	28.2	24.5
Binagady, Azerbaijan	ZIN 24409-1	122.6	24.3	30.87	16.4	23.1	20.8
Wildkirchli, Schwitzerland	MHNSG n/n	134.5	28.7	33.7	18.3	27.1	23.3
Starye Duruitory, Moldova	ZIN n/n [748]	115.0	22.7	–	15.4	22.2	20.6
Secrets Cave, Urals, Russia	Private coll.	153.0	28.9	40.7	21.6	26.1	23.0
		142.0	27.3	36.6	19.9	24.6	22.7
P. s. vereshchagini							
Malta, Angara River, Russia	ZIN 21846	118.4	22.8	28.8	16.0	22.6	21.5
Bolshoi Liakhovsky Island, Russia	ZIN 4224	117.5	21.8	30.3	15.7	23.1	21.7
Mt 3 (*P. s. spelaea*)							
Kudaro 3, mixed layers	ZIN 29420-2	–	–	–	20.3	27.4	25.4
Binagady, Azerbaijan (Vereshchagin, 1951)	ZIN 24409-1	139	–	–	18	–	–
Volga River, Russia (Vereshchagin, 1951)	ZIN 15691	144	–	–	24	–	–
Ural River, Russia	ZIN 24214-1	137.6	30.4	40.1	19.7	26.1	22.8
Secrets Cave, Urals, Russia	Private coll.	154.0	34.1	44.3	22.6	30.5	28.0
		149.4	31.7	42.9	23.3	30.1	27.2
		144.0	26.6	–	19.8	26.2	–
Mt 4							
P. s. spelaea							
Kudaro 1, mixed layers	ZIN 29420-2	–	–	–	21.4	27.4	25.4
Kudaro 3, mixed layers	ZIN 29420-3	152.3	28.3	37.6	19.7	27.4	25.5
Kudaro 3, layer 4	ZIN 36403-1	147.9	26.7	30.8	18.5	26.9	24.7
Starye Duruitory, Moldova	ZIN n/n [747]	131.8	26.3	33.0	18.9	22.3	22.3
Secrets Cave, Urals, Russia	Private coll.	147.6	25.1	34.5	17.9	23.1	23.5
		161.9	34.4	39.1	20.2	27.7	27.3
		135.5	26.6	28.6	16.3	22.0	22.3

Table 5. Continued.

Locality	Museum number	GL	Bp	Dp	SD	Bd	Dd
P. s. vereshchagini							
Rebrov River, Dm. Laptev Strait, Russia	ZIN 35047	141.6	27.5	33.6	17.4	23.3	21.5
Duvanny Yar, Russia	MMY 270	131.0	25.0	29.5	15.5	21.3	21.6
Mt 5 (*P. s. spelaea*)							
Kudaro 3, layer 4	ZIN 36403-2	138.7	29.4	21.7	14.3	23.5	22.6
Secrets Cave, Urals, Russia	Private coll.	150.6	29.2	21.9	16.1	24.7	25.3
		144.7	27.1	19.7	15.6	21.9	20.5
		142.3	31.1	21.3	15.1	23.4	23.3
		131.2	25.0	19.0	14.8	20.6	17.0

Cave, Sakazhiya Cave, Verchnyaya Cave, Kudaro caves, Tsona Cave, Orozman, Binagady, Taglar Cave) (Vereshchagin 1971; Lioubine 1989; Baryshnikov et al. 1996; Hoffecker et al. 2003).

The results of pollen analysis indicate that climate during the formation of layers 3–4 in the Kudaro caves was unstable. Broad-leaved forests were present during deposition of the lower part of layer 4, while alpine meadows prevailed during formation of the upper part of this layer; layer 3 reflects alternating phases of coniferous forest and subalpine meadows (Lioubine et al. 1985). These data imply that the cave lion inhabited various biotypes in the Caucasus, chiefly meadow, probably with seasonal altitudinal movements.

The large size of fossil bones of the cave lion from Kudaro allows their assignment predominantly to males. The cave lions may have used these caves as shelters for rest and for consumption of prey. The discovery of a juvenile mandible suggests that they also were used as a den for lion cubs.

No cut-marks or other reliable traces of human activity have been observed on the examined cave lion bones. The plantar side of the metatarsal ZIN 29420-2 exhibits numerous short scratches and markings (Fig. 6). Several similar marks also have been found on the dorsal side of this bone, suggesting that they may represent gnaw marks of a large carnivore scavenging in the cave.

The timing of the cave lion extinction in the Caucasus is unclear; presumably, it occurred before the Last Glacial Maximum. In other parts of Eurasia, the cave lion became extinct approximately 14–14.5 thousand years ago, surviving in eastern Beringia somewhat later (Stuart and Lister 2010). It has been suggested that during the Holocene, the southeastern region of the Caucasus was occupied by *P. leo* until historic times (Vereshchagin 1959; Schnitzler 2011).

The Pleistocene cave lion is usually regarded as a subspecies of the recent lion – *P. leo spelaea* (Kurtén 1968; Turner and Antón 1997; Mazák 2010), or being considered by some zoologists to be a distinct species *P. spelaea* on the basis of cranial and dental characters (Vereshchagin 1971; Baryshnikov and Boeskorov 2001; Spassov and Stoytchev 2005; Sotnikova and

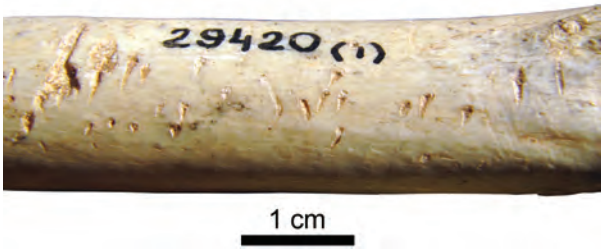

Fig. 6. The metatarsal of the cave lion (*Panthera spelaea*) from Kudaro 1 Cave (ZIN 29420-1) with cut-marks from teeth of a large carnivore; plantar view.

Nikolskiy 2006; Barycka 2008). Lion-like felids are known from the Early Pliocene of Africa (Laetoli), while *P. leo* is firmly dated to the beginning of Pleistocene (Werdelin and Lewis 2005). The ancestor of the Eurasian cave lion is regarded as *P. leo fossilis* (von Reichenau, 1904) or *P. fossilis* from the early Middle Pleistocene of Europe (Schütt and Hemmer 1978; Sotnikova and Nikolskiy 2006), which is sometimes considered as a subspecies of the cave lion: *P. spelaea fossilis* (Baryshnikov and Boeskorov 2001; Barycka 2008).

Molecular genetic analysis has revealed two lion clades: 1) extinct *spelaea* (Northern Eurasia, Alaska and Yukon Territory) and *atrox* (Leidy, 1853) (North America southwards from Alaska), and 2) extant *leo* (Africa and southwest Asia) (Burger et al. 2004; Barnett et al. 2009). The date of the divergence of the lineages of extinct and extant lions is estimated at 600,000 years ago (Burger et al. 2004), whereas the American lion was found to diverge from the cave lion about 340,000 years ago (Barnett et al. 2009). At the same time, cladistic analysis of osteological and dental characters indicates that *P. atrox* and, probably, *P. spelaea* do not belong to the lion lineage, but are successive outgroups to the lion + leopard (Christiansen 2008). In my opinion, these genetic and morphological data suggest the possibility of assigning a species rank to the cave lion – *P. spelaea.*

Panthera pardus (L., 1758)

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: left mandible with p4 and fragment of m1 (ZIN 35029, layer 5ab, 1980); left C1 (ZIN 36445-1, layer 5, horizon 5, 1959); left P3 (ZIN 36457, layer 5c, horizon 3, 1978); left P3 (ZIN 36474, layer 5c, horizon 3, 1980); left c1 (ZIN 36445-2, layer 5, horizon 5, 1959); fragment of right radius (ZIN 36459-1, layer 5b, horizon 2, 1980); fragment of right radius; ZIN 36361, layer 5ab, horizon 3, 1980); right scaphoid (ZIN 36446-3, layer 5, horizon 2, 1959); right scaphoid (36446-4, layer 5, horizon 2, 1959); right metacarpal 1 (ZIN 36447-1, layer 5, horizon 6, 1959); right metacarpal 1 (ZIN 36460, layer 5ab, horizon 2, 1980); left metacarpal 3 (ZIN 36452, layer 5, horizon 4, 1961); left metacarpal 3 (ZIN 36453-4, layer 5, horizon 1, 1961); left metacarpal 4 (ZIN 36454, layer 5, horizon 3, 1961); left metacarpal 4 (ZIN 36449, layer 5, horizon 7, 1958); left patella (ZIN 36450, layer 5, horizon 7, 1958); left talus (ZIN 36453-2, layer 5, horizon 1, 1961); left cuboid (ZIN 36438, layer 5, horizon 5, 1958); right metatarsal 4 (ZIN 36453-3, layer 5, horizon 1, 1961); left metatarsal 4 (ZIN 36451, layer 5, horizon 8, 1958); right metatarsal 5 (ZIN 36448-1, layer 5, horizon 1, 1959); right metatarsal 5 (ZIN 36458, layer 5c, horizon 1, 1980); left metatarsal 5 (ZIN 36444-2, mixed layers, 1957).

Description. Among the available leopard mandibles, ZIN 35029 (Fig. 7A, B) from the Middle Pleistocene level possesses a tooth row p3-m1 somewhat longer (55.4 mm) than that of the mandible ZIN 31905 (52.2 mm), which, on the basis of coloration and degree of mineralization, is derived from the upper layers of the cave and may be assigned to the Late Pleistocene. The recent Caucasian subspecies *P. pardus ciscaucasica* (Satunin, 1914) is characterized by a p3-m1 length from 44.3 to 52.4 mm (n = 9). Hemmer (1971) provides higher values for this parameter: 52 and 56 mm. Both specimens from the Kudaro caves yield or exceed the maximum values for this dimension in the recent Caucasian leopard. The specimen ZIN 35029 is distinguished from the fossil jaguar *P. onca gombaszoegensis* by a shorter diastema and a smaller height of the ramus behind m1 (Table 6). This height does not exceed 32.3 mm (n = 9) in the modern Caucasian subspecies *P. p. ciscaucasica.*

The mandible ZIN 31905 (Fig. 7C, D), owing to the dimension of the canine, may be ascribed to a male. By the size and proportions of cheek teeth, this specimen is similar to the recent *P. p. ciscaucasica.*

The upper canine C1 (ZIN 36445-1, length 14.8 mm, width 12.1 mm, lateral height of crown 29.4 mm; Fig. 8A) and lower canine c1 (ZIN 36445-2, length 12.9 mm, width 11.6 mm; Fig. 8B) were found within the same stratigraphic level and in close proximity to each other, probably belonging to a single individual. Judging from their size, the latter was a male. Similar dimensions were recorded for fossil canines of *P. pardus* from Triagalnata Cave in Bulgaria, also regarded as belonging to males (Spassov and Raychev 1997).

There are two premolars P3, which noticeably differ in size (Table 7). The measurements of ZIN 36457 correspond to maximum values of those in the recent *P. pardus,* whereas measurements of ZIN 36474 are characteristic of the females of *P. p. ciscaucasica.* Although ZIN 36457 is partly broken on the lingual margin of the crown, there are indications that the parastyle is shifted lingually. In ZIN 36474, this cusp is situated on long axis of the tooth. Both Kudaro

Table 6. Measurements (mm) of mandibles of Pleistocene *Panthera pardus* and *P. onca gombaszoegensis*. Designation: (–) – measurement is not available.

Measurements	*P. pardus*			*P. onca gombaszoegensis*					
	Kudaro 1, layer 5ab	Kudaro 3, mixed layers	Triagalnata (Spassov, Raychev 1997)	Rabenstein (Hemmer 1971)	Untermassfeld (Hemmer 2001)			Mosbach (Hemmer et al. 2003)	Akhalkalaki (Hemmer et al. 2001)
	ZIN 35029	ZIN 31905	MCT 3859	BSPGM 1894 I 501	IQW 1983/ 19169	IQW 1992/ 24137	IQW 1995/ 25343	HLMD WT231	GHMT n/n
Total length		145.1	134.0	ca173					
Alveolar length c1-m1		80.1							
Length row p3-m1	55.4	52.2		58	59.5		58.6		
Height of the vertical ramus		66.7							
Height of the mandible behind m1	32.2	32.4	28.0	38	37.5				ca39
Height of the mandible in front of p3		29.9	26.5	38	33.5		33.7		
Diastema length	12.3	12.6	10.1	16	ca22	19.1	ca16		
Teeth									
c1 length		15.4			18.5	18.2	17.3		
c1 width		12.3							
p4 length	19.8	18.9	17.8	21.4	21.8	22.9	22.0	21.8	21.4
p4 width	9.6	10.1	8.5	10.4	10.7	11.3	10.7	10.1	11.0
m1 length	alv20.5	20.5	18.1	21.2	22.3		23.0	23.1	23.4
m1 length of paraconid	–	11.1	9.2	11.5	12.3		12.1	–	–
m1 width	–	9.0	8.1	11.0	11.3		11.2	–	11.6

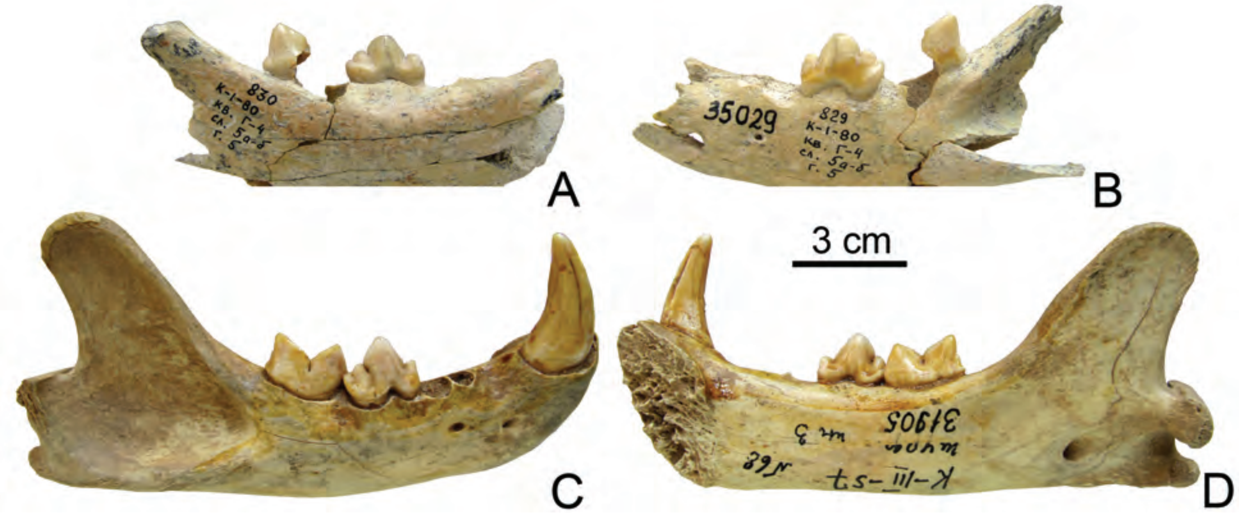

Fig. 7. Mandible fragments of *Panthera pardus* from Kudaro 1 Cave (A, B) and Kudaro 3 Cave (C, D): A, B – left mandible (ZIN 35029); C, D – right mandible (ZIN 31905); labial (B, C) and lingual (A, D) views.

Table 7. Measurements (mm) of teeth of Pleistocene *Panthera pardus*. Designation: (–) – measurement is not available.

Locality	Museum number	P3		p4		m1		
		L	W	L	W	L	Lpa	W
Caucasus								
Kudaro 1, layer 5c	ZIN 36457	18.5	8.9					
	ZIN 36474	15.9	8.0					
Kudaro 1, layer 5ab	ZIN 35029			19.8	9.6			
Kudaro 3	ZIN 31905			18.9	10.1	20.5	11.1	9.0
Europe								
Genista Cave, Gibraltar	NHM 47704	18.7	8.6					
	NHM 47693			18.4	8.6	19.7	–	9.4
Tower Rock Shelter, Gibraltar	NHM 13223			16.2	8.5	19.1	–	8.6
Jaurens, France	UCBL 301060	17.3	7.8					
	UCBL 301094			18.4	8.6	19.7	10.4	18.8
	UCBL 301063					21.0	10.7	8.4

specimens do not exceed the length and width limits of variation for these parameters in the fossil subspecies *P. p. incurve* from South Africa (Ewer 1956). In jaguar (*P. onca*), P3 is generally lacking a parastyle.

The dimensions of premolar p4 from mandibles ZIN 35029 and ZIN 31905 do not exceed the range of variation in the recent subspecies *P. p. ciscaucasica* (length 16.8–19.7 mm, width 8.2–10.0 mm, n = 9). The Pleistocene leopard from European localities is characterized by similar length (16.1–18.7 mm, n = 5) and similar width (7.5–9.1 mm, n = 6) of p4 (Hemmer 1971). The same size of this tooth was recorded

Fig. 8. Remains of *Panthera pardus* from Kudaro 1 Cave (A–G, J, M–O) and Kudaro 3 Cave (H, I, K, L): A – right upper canine (ZIN 36445-1); B – left lower canine (ZIN 36445-2); C – left scaphoid bone (ZIN 36446-3); D – left scaphoid bone (ZIN 36446-4); E – right metacarpal 1 (ZIN 36447-1); F – right metacarpal 1 (ZIN 36460); G – left metacarpal 2 (ZIN 36456); H – right metacarpal 5 (ZIN 36439-2); I – left talus (ZIN 36439-1); J – right talus (ZIN 36453-2); K – left talus (ZIN 36443-1); L – right metatarsal 2 (ZIN 36442-1); M – left metatarsal 4 (ZIN 36451); N – left metatarsal 5 (ZIN 36444-1); O – left metatarsal 5 (ZIN 36444-2); labial (B), lingual (A), lateral (G, M), medial (H, L) and dorsal (E, F, I–M, N, O) views.

in the fossil African leopard *P. p. incurve* (Ewer 1956). In fossil jaguar *P. onca gombaszoegensis*, the length (21.4–24.4 mm, n = 12) and width (10.0–11.9 mm, n = 12) of p4 are significantly larger. A large mandible from Rabenstein in Germany, which was first referred to *P. pardus* (Hemmer 1971), has been revised later by Hemmer et al. (2003, p. 45) and now belongs to *P. onca gombaszoegensis*. Measurements of p4 in the Rabenstein mandible correspond to those of the fossil jaguar (Table 4).

The lingual margin of the crown in m1 in the mandible ZIN 31905 is straight and the apex of the paracone of this tooth is shifted anteriorly compared to its position in *P. onca gombaszoegensis* (see Spassov and Raychev 1997). A small metaconid is developed, being absent in the fragment of m1 in ZIN 35029 and in the recent *P. p. ciscaucasica*. This cusp has been recorded in the specimen of *P. onca gombaszoegensis* from Untermassfeld (Hemmer 2001), and sometimes is present in tiger (*P. tigris*).

The Kudaro caves yielded several leopard limb bones, predominantly broken, which do not differ in terms of metric characteristics from limb bones in the recent *P. pardus* (Table 8).

Two right scaphoid bones (ZIN 36446-3, 36446-4; Fig. 8C, D) from the Middle Pleistocene level are noticeably smaller than in the recent jaguar *P. onca*. In addition, the posterior-medial process in the specimens from Kudaro 1 is more pointed than that in *P. onca*.

The talus (ZIN 36453-2, Fig. 8J) from the Middle Pleistocene layers and two tali (ZIN 36439-1, 36443-

Table 8. Measurements (mm) of limb bones of *Panthera pardus* from the Kudaro caves. Designation: n/n – no number.

Bone	Museum number	GL	GB	Bp	Dp	SD	Bd	GLP	BG	LAR	SH	DC
Middle Pleistocene												
Radius	ZIN 36459-1			23.8	15.9							
	ZIN 36461			28.5	19.6							
Scaphoid	ZIN 36446-3								27.8			
	ZIN 36446-4								27.5			
Patella	ZIN 36450	38.5	25.1									
Cuboid	ZIN 36438	18.9	18.3									
Talus	ZIN 36453-2	41.5	34.8									
Late Pleistocene												
Scapula	ZIN n/n							37.2	22.0			
Humerus	ZIN 36455					22.4	65.6					
Pelvis	ZIN 36440									31.9	35.8	
Femur	ZIN n/n			46.0								22.1
Tibia	ZIN 36441-1			51.0								
Talus	ZIN 36443-1	41.3	35.5									
	ZIN 36439-1	41.4	35.0									
	ZIN n/n	38.5	32.4									
Cuboid	ZIN 36443-3	18.7	18.5									

1; Fig. 8I, K) from the Late Pleistocene layers display no morphological differences from this bone in the recent Caucasian leopard, being, at the same time, smaller than the talus of the recent jaguar (*P. onca*).

Several fossil metacarpal and metatarsal bones (Fig. 8G, H, L–O) resemble those of the recent jaguar in terms of length (Table 9). However, these bones in *P. pardus* are more slender and less widened at the proximal and distal ends in comparison with *P. onca*.

Discussion. The study of the *P. pardus* collection from Kudaro, comprising two mandibles, several teeth, and isolated bones, revealed no metric differences with the Late Pleistocene and recent Caucasian leopards. Middle Pleistocene leopards probably were more robust.

Panthera pardus remains occur in all layers, exceeding the number of other felid remains. The remains belong predominantly to adults; only isolated bones were assigned to immature animals. The remains that may be sexed belong primarily to males and rarely to females. The age and sex composition of the sample suggests that the Kudaro caves served as shelters for leopards resting there during the day or hiding their prey.

The recent geographic range of *P. pardus* encompasses Africa, as well as Southwest, Southern, and Eastern Asia. Although leopard once inhabited the entire Caucasus, it now survives only in southern portions of this region and is extremely rare.

In the Southern Caucasus leopard bone remains are known from many cave localities: Akhstyrskaya Cave in Russia, Bronzovaya Cave, Medvezhiya Cave and Verkhnyaya Cave in Georgia, Azykh Cave (layer 5) and Dashsalakhty in Azerbaijan (Lioubine 1989). In the cave deposits of the Northern Caucasus, leopard remains are rare, known for example in Mezmaiskaya Cave and in Treugolnaya Cave (Baryshnikov et al. 1996; Hoffecker et al. 2003).

There is the opinion that the earliest leopard-like specimens come from East Africa (Laetoli) and dated to about 3.5 Ma BP (Werdelin and Levis 2005), which is somewhat earlier than the estimated time of divergence for the lineages of *P. pardus* and *P. leo* on the basis of molecular phylogeny (Davis et al. 2010). However, the finds from Laetoli were assigned by Hemmer et al. (2004) to early Old World pumas. In Africa the fossils unambiguously assigned to *P. pardus* are dated to approximately 2.0 Ma BP (Werdelin and Levis 2005). Molecular-phylogenetic evidence suggests that the origin of the modern *P. pardus*

Table 9. Measurements (mm) of metacarpal and metatarsal bones of *Panthera pardus* from the Kudaro caves. Designation: (–) – measurement is not available.

Bone and museum number	GL	Bp	Dp	SD	Bd	Dd
Mc 1 (Middle Pleistocene)						
ZIN 36460	33.1	16.1	12.7	11.3	13.0	11.7
ZIN 36447-1	32.5	15.0	11.7	10.5	12.4	11.6
Mc 2 (Late Pleistocene)						
ZIN 36456	72.6	14.8	20.0	10.3	16.3	14.2
Mc 3 (Middle Pleistocene)						
ZIN 36453-4	–	18.0	19.6	–	–	–
ZIN 36452	–	–	–	11.1	17.0	15.4
Mc 4 (Middle Pleistocene)						
ZIN 36454	–	14.6	17.6	–	–	–
ZIN 36449	–	14.6	18.8	–	–	–
Mc 5 (Late Pleistocene)						
ZIN 36439-2	62.3	15.5	16.9	9.2	14.7	14.4
Mt 2 (Late Pleistocene)						
ZIN 36442	87.6	15.6	20.9	10.8	15.0	15.0
Mt 4 (Middle Pleistocene)						
ZIN 36451	98.3	18.7	22.7	11.6	15.9	15.8
ZIN 36453-3	–	–	–	10.9	13.5	13.9
Mt 5 (Middle Pleistocene)						
ZIN 36462	–	21.6	16.5	12.0	–	–
ZIN 36458 (juv.?)	–	14.5	10.8	–	–	–
ZIN 36444-2	96.6	18.9	16.3	9.6	14.2	14.8
ZIN 36448-1 (subad.)	–	17.7	13.8	8.7	–	–
Mt 5 (Late Pleistocene)						
ZIN 36444-1	89.1	19.3	13.9	9.0	13.7	14.3

lineage in Africa probably dates to 470,000–825,000 years ago, and the subsequent migration into and across Asia to roughly 170,000–300,000 years ago (Uphyrkina et al. 2001). The finds from Kudaro and from the European locality Mauer (ca. 0.6 Ma BP, see Wagner et al. 2010) in Germany (Kurtén 1968; Turner and Antón 1997) indicate a significantly earlier appearance of this species in Eurasia.

The results of craniometrical analysis revealed that the modern Caucasian leopard belongs to the subspecies *P. p. ciscaucasica*, whose distribution embraces Caucasus, northern Iran and Turkmenistan (Khorozyan et al. 2006). A similar view has been articulated on the basis of molecular-genetic studies (Rozhnov et al. 2011).

Genus *Lynx* Kerr, 1792

Type species. *Felis lynx* Linnaeus, 1758.

Included species. Four modern species: *L. pardinus* (Temminck, 1827), *L. lynx* (L., 1758), *L. rufus* (Schreber, 1777) and *L. canadensis* Kerr, 1792; and 3–4 extinct species.

Distribution. Early Pliocene – Recent, Eurasia and North America; Late Pliocene – Middle Pleistocene, Africa (Morocco).

Lynx lynx (L., 1758)

Referred specimens. Late Pleistocene, Kudaro 3 Cave: first phalanx, anterior (ZIN 36472, layer 3–4, 1975).

Description and Discussion. The lynx has been identified on the basis of a single first phalanx of forelimb found in the fallen cave sediments of the layers 3–4. The bone is slightly eroded. Its color and fossilization indicate that the specimen originates from the upper levels of the cave strata. The phalanx ZIN 36472 (GL = 29.6 mm, Bp = 9.6 mm) resembles in the dimensions that of the recent *L. lynx* (ZIN 32198, female; GL = 27.3 mm, Bp = 8.7 mm).

Fossil remains of *L. lynx* are scarce in the Paleolithic sites of the Caucasus: in the Sakazhia and Bronzovaya caves in Georgia and in Azykh Cave (layer 5) in Azerbaijan (Vereshchagin 1959; Lioubine 1989).

The molecular genetic data ascertain the monophyly of the genus *Lynx*, with the bobcat (*L. rufus*) from North America occupying the isolated position within this genus (Pecon-Slattery et al. 2004). *Lynx issiodorensis* (Croizet et Jobert, 1828) from the Late Pliocene of Eurasia and North America is regarded to be the ancestor of the recent species (Kurtén 1978; Werdelin 1981). *Lynx issiodorensis* and *L. pardina* are considered to be most closely related phylogenetically (Ficcarelli and Torre 1977).

The lynx from the Late Pleistocene of the Western Europe is referred to *L. spelaea* (Boule, 1906) or to *L. pardina spelaea* (Bonifay 1971; Werdelin 1981; Kurtén and Granqvist 1987; Argant 1991). The taxonomic position of the lynx from the Late Pleistocene of the Eastern Europe and Siberia was not established. The lower cheek teeth from Altai (Denisova Cave) do not differ in their dimensions from those of the recent *L. lynx* from this region (Derevianko et al. 2003). The same tooth size was revealed in the lynx mandible from Kostenki 21 in European Russia; however, the presence of a small metaconid on m1 makes this find similar to *L. pardina spelaea* and to the recent *L. lynx* from Central Asia (Sablin 1999).

Genus *Felis* Linnaeus, 1758

Type species. *Felis catus* Linnaeus, 1758.

Included species. Five modern wild species: *F. bieti* Milne-Edwards, 1892, *F. chaus* Schreber, 1777, *F. margarita* Loche, 1858, *F. nigripes* Burchell, 1824, *F. silvestris* Schreber, 1777 (including *F. lybica* Forster, 1780), and domestic cat, *F. catus*; classification of extinct representatives of the genus *Felis* is not elaborated, several species were described.

Distribution. Late Miocene – Recent, Eurasia and Africa; domestic cat is worldwide.

Felis silvestris Schreber, 1777

Referred specimens. Middle Pleistocene, Kudaro 1 Cave: left juvenile mandible with d3 (ZIN 36463, layer 5c, horizon 4, 1980). Kudaro 3 Cave: right m1 (ZIN 36467, layer 5, 1975); fragment of right radius (ZIN 36469, layer 7, 1981). Late Pleistocene, Kudaro 3 Cave: right ulna (ZIN 36468-1, layer 4, horizon 4, 1975); right pisiform bone (ZIN 36466, layer 4, horizon 4, 1974); fragment of left tibia (ZIN 36468-2, layer 4, horizon 4, 1975); left calcaneus (ZIN 36468-6, layer 4, horizon 4, 1975); right metatarsal 2 (ZIN 36468-4, layer 4, horizon 4, 1975); left metatarsal 4 (ZIN 36468-3, layer 4, horizon 4, 1975); left metatarsal 5 (ZIN 36468-5, layer 4, horizon 4, 1975); and several phalanges. Totally 20 remains have been collected.

Description. Layer 5c of Kudaro 1 yielded a juvenile mandible fragment of European wild cat (ZIN 36463, Fig. 9A, B) with the milk tooth d3, alveoli for d4, and m1 in the initial stage of eruption. The ramus height behind d3 (10.1 mm) exceeds this measurement (8.9 mm) in a cub of the recent subspecies *F. sylvestris caucasica* Satunin, 1905 from the Caucasus (ZIN 2473). The dimensions of the fossil d3 (length 5.7 mm, width 2.3 mm, height 3.9 mm) also exceed those of ZIN 2473 (4.5 mm, 2.0 mm and 4.1 mm, correspondingly). The tooth m1 in ZIN 36463 contained within the alveolar cavity is longer than 8.2 mm. A jungle cat *F. chaus* specimen of similar individual age (ZIN 19028) exhibits a more robust juvenile mandible (ramus height behind d3 11.7 mm; d3 length 6.1 mm, d3 width 2.4 mm, d3 height 4.3 mm).

The large fossil subspecies *F. sylvestris hamadryas* Kurtén, 1977 was described from Petralona Cave in Greece (layer 11, probably early Cromerian). The lengths of its two known lower carnassial teeth are 10.1 mm and 10.2 mm respectively (Kurtén and Poulianos 1977). Presumably, the European wild cat from Kudaro 1 is similar to this subspecies.

The isolated lower carnassial tooth m1 (ZIN 36467, Fig. 9C, D) from layer 5 in Kudaro 3 Cave has a small talonid, which is usually inconspicuous in recent *F. s. caucasica*. The measurements of the fossil m1 are as follows: length 8.6 mm, width 3.9 mm. These dimensions do not exceed the range of variation in *F. s. caucasica* (males and females): length 8.3–9.8 mm (mean 8.64 mm, n = 18), width 3.3–4.3 mm (mean 3.73 mm, n = 18). Comparable size is found in two isolated m1 teeth collected from the Holocene deposits at Kudaro 1: ZIN 36464 (mixed layers, 1987; Fig. 9E, F), length 9.3 mm, width 4.1 mm; ZIN 36465 (layer 1, 1959), length 8.2 mm, width 3.3 mm.

Two m1 teeth of Late Pleistocene *F. silvestris* from the cave of Jaurens in France are characterized by following measurements: length 10.2 mm, width 4.3 mm (UCBL 301097) and length 8.2 mm, width 3.9 mm (UCBL 301153). Similar lengths for m1 are found in *F. silvestris* from other Late Pleistocene localities in France (Observatoire, Grimaldi), specifically 9.2 mm to 10.0 mm (Bonifay 1971). Localities of the same age in Britain contain specimens of this tooth measuring between 7.0 mm and 9.5 mm (Kurtén 1965a).

Comparable size of m1 (length 8.0–8.6 mm, width 3.8–3.8 mm, n = 3) is reported for *F. silvestris* from Lunel-Viel (Holsteinian) in France (Kurtén 1965a). Bonifay (1971) described a new species of small cat *F. monspessulana* Bonifay, 1971 from the same locality; however, the lengths of p3-m1 (21.3 mm, 21.5 mm) and m1 (7.5 mm, 8.2 mm) the new species are very similar to those of *F. silvestris*.

Smaller parameters were recorded for the fossil cat *F. minuta* Schmerling, 1834 from the Late Pleistocene of France (Argant 1991).

The limb bones excavated from the Pleistocene layers of the Kudaro caves (Fig. 9G–I) show no morphological and metric differences from those of the recent European wild cat from the Caucasus (Table 10).

An exploratory test unit yielded felid remains assigned to domestic cat (*F. catus*) in the uppermost (Holocene) layer at Kudaro 2, which is situated between the caves of Kudaro 1 and Kudaro 3. The right mandible (ZIN 36470-1, Fig. 9J) is large (total length = 60.6 mm, length p3-m1 = 20.9 mm), resembling that of the European wild cat, although it is

Table 10. Measurements (mm) of limb bones of *Felis silvestris* from the Kudaro caves.

Bone	Museum number	GL	GB	Bp	Dp	SD	SDO	DPA	BPC
Ulna	ZIN 36468-1						12.3	14.3	11.1
Radius	ZIN 36469			9.4		6.1			
Os pisiforme	ZIN 36466	11.2		6.3					
Tibia	ZIN 36468-2					9.3			
Calcaneus	ZIN 36468-6	36.6	15.6						
Mt 2	ZIN 36468-4			7.1	8.5				
Mt 4	ZIN 36468-3			7.8	10.2	6.1			
Mt 5	ZIN 36468-5			9.5	8.8				
1 phalanx, post.	ZIN 36468-7	22.6		7.8					

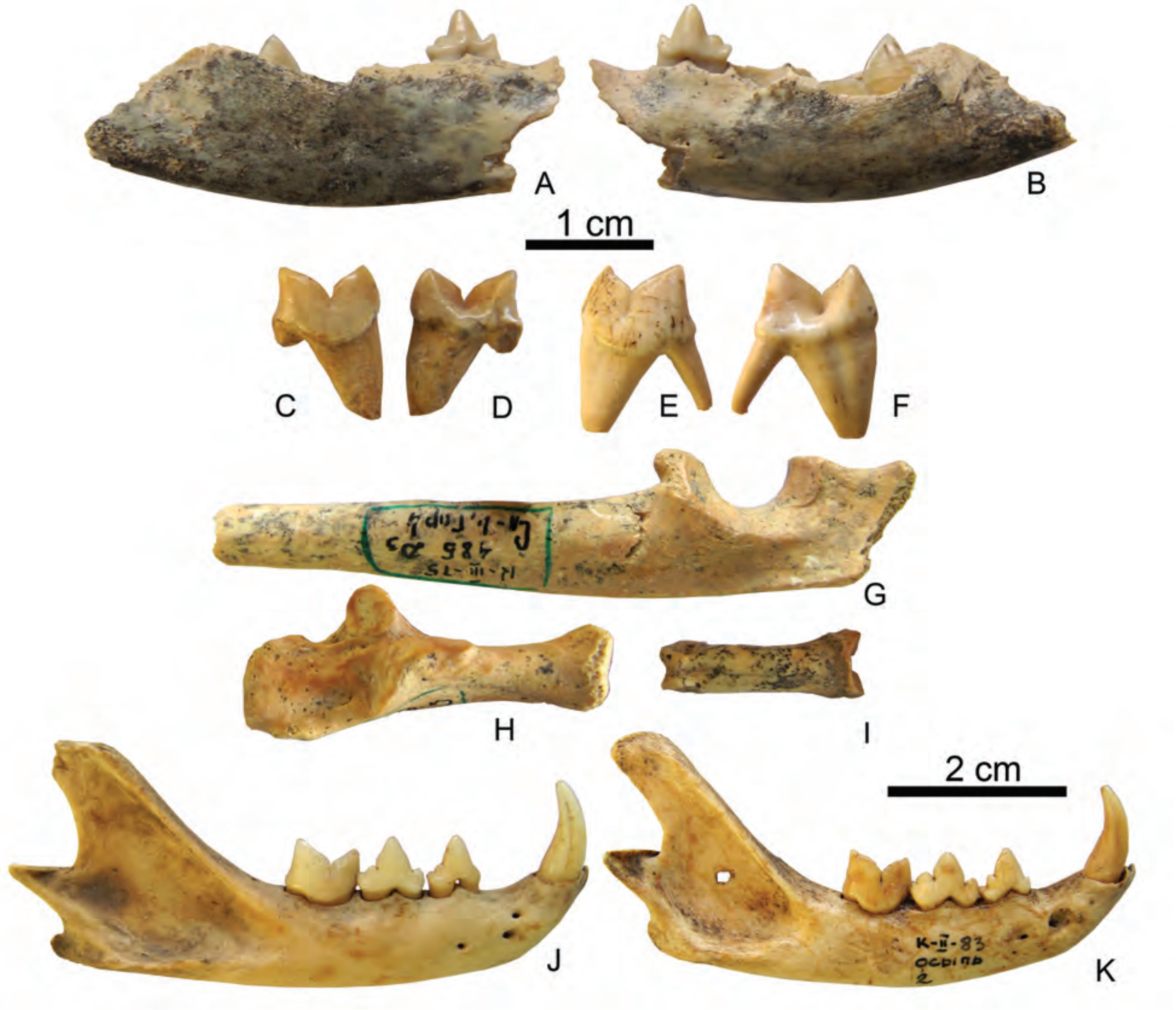

Fig. 9. Remains of *Felis silvestris* (A–I) and *F. catus* (J, K) from Kudaro 1 Cave (A, B, E–F), Kudaro 3 Cave (C, D, G–I) and Kudaro 2 Cave (J–K): A, B – left juvenile mandible (ZIN 36463); C, D – right m1 (ZIN 36467); E, F – left m1 (ZIN 36464); G – right ulna (ZIN 36468-1); H – left calcaneus (ZIN 36468-6); I – 1 phalange (ZIN 36468-7); J – left mandible (ZIN 36470-1); K – left mandible (ZIN 36471); labial (B, C, E, J, K), lingual (A, D, F), medial (G) and dorsal (H, I) views.

characterized by small carnassial tooth m1 (length 7.7 mm, width 3.4 mm). The length of this tooth falls at the minimum range of the length of m1 in *F. silvestris caucasica*. Another right mandible (ZIN 36471, Fig. 9K) is markedly smaller (total length 54.5 mm, length p3-m1 20.1 mm), with a miniature m1 (length 7.3 mm, width 3.4 mm), which is typical of the domestic cat.

Discussion. Remains of *F. silvestris* occur throughout the stratigraphic sequence in the Kudaro caves. In their size and shape, these remains exhibit no differences from those of *F. s. caucasica*, with exception of the material from layer 5c in Kudaro 1, which is comparable in size to the fossil subspecies *F. s. hamadryas*.

Felis silvestris inhabits broad-leaf and mixed forests in Europe, the Caucasus, and Asia Minor, as well as arid regions of Africa and Southwest and Central Asia. Its occasional fossils have been identified in the Caucasus at Akhstyrskaya Cave and the grotto Kholodnyi near the Black Sea coast (Vereshchagin 1959). *Felis* cf. *lybica* has been identified from Middle Pleistocene layer 5a in Treugolnaya Cave in the Northern Caucasus (Hoffecker et al. 2003).

A *Felis*-like small cat (*F. attica* Wagner, 1857, *F. christolii* Gervais, 1848–1852) is known in Europe from the Late Miocene (Rook et al. 1991; Ginsburg 1999). In Africa (Toros-Menalla in Chad), these cats also appeared during the Late Miocene (ca. 7 Ma BP; Peigné et al. 2008). The geological dating of these fossil finds corresponds to the estimated molecular age (4.8–8.55 Ma BP) of the divergence of the domestic cat lineage (Johnson et al. 2006). The time of divergence of the *F. silvestris* lineage, based on molecular phylogeny, is estimated at roughly 0.89–2.16 Ma BP (Johnson et al. 2006).

The analysis of cytochrome *b* sequences revealed close relationships of the domestic cat (*F. catus*) and the Asiatic wildcat (*F. s. ornata* Gray, 1832) as well as of *F. silvestris* and *F. margarita* (Agnarsson et al. 2010).

CONCLUSIONS

Five felid species have been identified from the Kudaro caves: *Panthera onca gombaszoegensis*, *P. spelaea*, *P. pardus*, *Felis silvestris*, and probably *Lynx lynx*. The three latter species have survived in the Caucasus until the present.

The fossil remains of *P. pardus* and *P. spelaea* are numerous compared to the other species which are represented by isolated finds, the bone material being heavily fragmented. *Panthera onca gombaszoegensis* was found only in the lowermost level of the Middle Pleistocene deposits (Likhvian=Holsteinian Interglacial). *Panthera pardus* and *Felis silvestris* were recorded throughout the sequence in both caves, whereas *P. spelaea* and *Lynx lynx* occur only in the upper levels and may be regarded as northern invaders of the Caucasus region.

In order to better document the Pleistocene history of the Caucasian Felidae, we can complement the stratigraphic record for the Kudaro caves with the information from other sites.

The Early Pleistocene locality Dmanisi in Georgia contains *Megantereon cultridens* (Cuvier, 1824), *Homoterium crenatidens* (Fabrini, 1890), *Acinonyx pardinensis* (Croizet et Jobert, 1828), and *Panthera onca georgica* (Vekua 1995; Hemmer et al. 2010, 2011). At the end of the Early Pleistocene, the subspecies *P. onca gombaszoegensis* was present in Akhalkalaki in Georgia (Hemmer et al. 2001). The North-Caucasian Taman mammalian fauna of this geologic age includes *Panthera* sp. (Vereshchagin 1959), which has been attributed to *P. onca gombaszoegensis* by Hemmer et al. (2003).

The fauna of the first half of the Middle Pleistocene is represented by finds from the basal sediment in Kudaro 1 (layer 5c): *Panthera onca gombaszoegensis*, *P. pardus*, *Felis silvestris*. The fauna of the second half of the Middle Pleistocene is found in the upper part of layer 5 in Kudaro 1 and layers 5–7 in Kudaro 3: *Panthera spelaea, P. pardus, Felis silvestris*, and from layer 6 in Azykh Cave in Azerbaijan, containing *Panthera pardus*, *Lynx lynx,* and *Felis chaus* (Lioubine 1989). The Middle-Pleistocene Felidae of the Northern Caucasus are represented by isolated bones from Treugolnaya Cave: *Felis* cf. *lybica* (layer 5a) and *Panthera spelaea* (layer 4b) (Hoffecker et al. 2003).

The Late Pleistocene cats known on the basis of material from layers 3–4 in both Kudaro caves and from other Mousterian and Upper Paleolithic sites in the Southern Caucasus, are including *Panthera spelaea*, *P. pardus*, *Lynx lynx*, *Felis silvestris*. Besides that, *Acinonyx jubatus* should be added to this list. Remains of *A. jubatus* have been identified from Binagady near Baku in Azerbaijan (Vereshchagin 1951). Felids of the Late Pleistocene age are represented in the Northern Caucasus by *Panthera pardus* and *P. spelaea* (Vereshchagin 1959; Baryshnikov et al. 1996). The cave lion became extinct at the end of the Pleistocene, while other species survive in the modern Caucasian fauna.

The Holocene is characterized by the expansion of *Panthera tigris* and *P. leo* to the southeastern portions of the Caucasus (Vereshchagin 1959). The later history of the Caucasian felid fauna is characterized by the whole (lion, cheetah, and tiger) or partial (leopard) disappearance of large cats as a result of hunting or destruction of natural habitat by recent economic activity.

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