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Pleistocene Mustelidae (Carnivora) from Paleolithic site in Kudaro Caves in the Caucasus

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ABSTRACT. Kudaro Paleolithic sites in the Southern Ossetia are found to contain five species of mustelids: *Meles meles*, *Martes foina*, *Martes martes*, *Vormela peregusna*, and *Mustela nivalis*. All these species occur in the Caucasus at present time; no difference was revealed in the species composition between faunas of Middle and Late Pleistocene. The fossil and recent populations demonstrate a considerable morphological similarity, except weasel represented by a distinct fossil subspecies *M. nivalis kudarensis* subsp.n.

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

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Плейстоценовые горностаевые (Carnivora: Mustelidae) из Кударских пещерных палеолитических стоянок на Кавказе

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РЕЗЮМЕ. Из Кударских палеолитических стоянок в Южной Осетии определено 5 видов горностаевых: *Meles meles*, *Martes foina*, *Martes martes*, *Vormela peregusna* и *Mustela nivalis*. Все они сохранились на Кавказе до современности; нет видовых различий между фаунами среднего и позднего плейстоцена. Плейстоценовые и современные выборки показывают большое морфологическое сходство, за исключением ласки, плейстоценовая раса которой выделена в новый ископаемый подвид *M. nivalis kudarensis* subsp.n.

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

Introduction

The family Mustelidae is characterized by the greatest taxonomical diversity in the extra-tropical zone of Eurasia in comparison with other carnivorous families. Therefore it is interesting to elucidate the history of this family, especially at its latest, Pleistocene, stage.

At present, seven mustelid species occur in the Caucasus: *Meles meles* (L., 1758), *Lutra lutra* (L., 1758), *Martes martes* (L., 1758), *M. foina* (Erxleben, 1777), *Vormela peregusna* (Güldenstädt, 1770), *Mustela nivalis* L. and stranger *Neovison vison* (Schreber, 1777). Four more species is known for the Northern Caucasus: *Mustela erminea* L., 1758, *M. lutreola* L., 1758 (occurs along the Black Sea coast as far as Sukhum), *M. putorius* L., 1758, *M. eversmanii* Lesson, 1827. The regional Pleistocene fauna of Mustelidae is incompletely known.

The archaeological excavations of the Paleolithic sites in the caves of Kudaro 1 and Kudaro 3 in Southern Caucasus provided a possibility to collect a unique material on the Pleistocene mustelids. These sites were found in 1955 by Prof. V. Lioubine (St. Petersburg) who guided their complex multidisciplinary studies. Since 1974, the author was a member of Lioubine's scientific team.

Both Kudaro caves are situated in the central part of southern slope of the Greater Caucasus. These caves are placed virtually one above other on the left bank of Djedjori River (Rioni River basin) near Kvaisa City (Southern Ossetia).

Kudaro 1 Cave is located at 1600 m up s. l. and 260 m above river level. It is Y-shaped with two entrances. The thickness of sediments varies in the different parts of the cave from 1.5 to 4.5 m. The deposits are found to contain many limestone detritus pronouncedly corroded at lower stratigraphical levels. Layers 5a-5c are formed by yellowish fuscous loam with Acheulian industries. Layers 3–4 represent grayish loam inclosing Mousterian stone artifacts.

The basal part of cave deposits is provided with two dates by radiothermoluminescent method: 360,000± 90,000 years (RTL-379) for layer 5c and 350,000± 70,000 years (RTL-373) for layer 5b (Lioubine, 1998). These dates refer the time of sediment formation to OIS 9 stage. The Mousterian layer 3a is ascertained by the

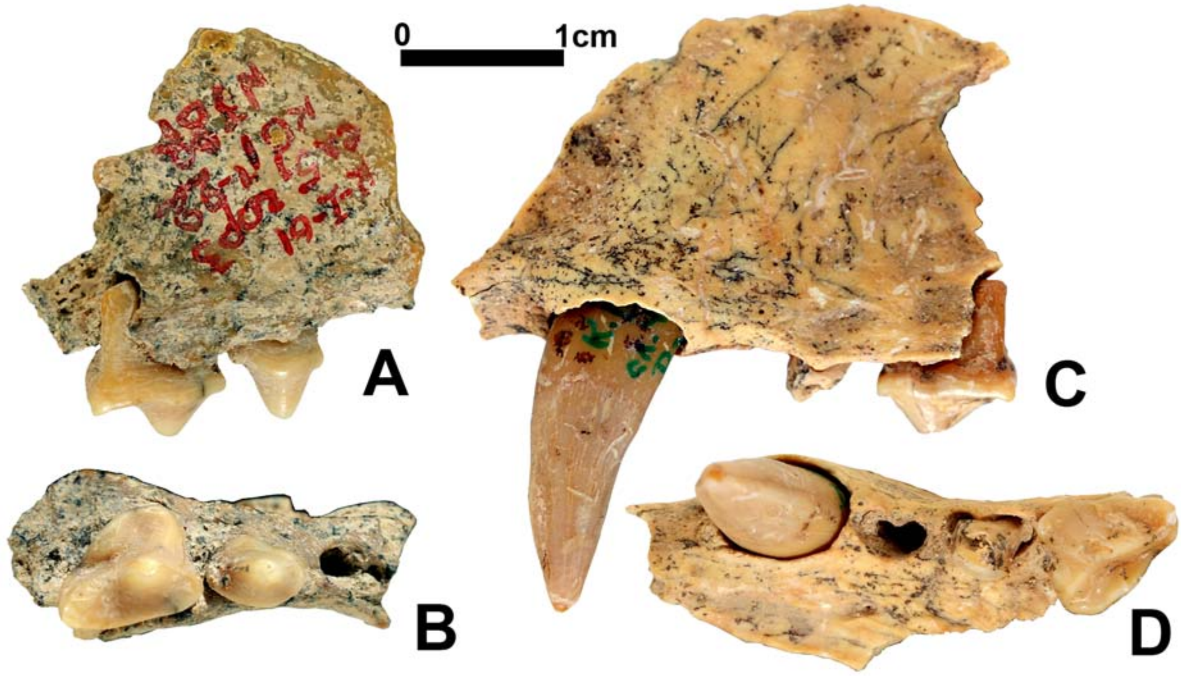

Figure 1. Maxilla fragments of *Meles meles*; right side (A), left side (C) and basal (B, D) views.
A, B — ZIN 36276, Kudaro 1, layer 5, horizon 3, 1961; C, D — ZIN 36278, Kudaro 3, layer 4, horizon 2, 1974.

radiocarbon date 44,150±2,400/1,850 (Gr-6079) (Lioubine, 1998).

Kudaro 3 Cave, which is situated somewhat lower than Kudaro 1 Cave, represents a long corridor with the underground lake in its distant portion. Cave sediments are formed by the loam with admixture of limestone fragments; the loam color is changed bottom-up from yellow-brown to dark gray. Artifacts were in the layers 8–5 (Acheulian) and layers 3–4 (Mousterian), being, however, markedly innumerous than in the Kudaro 1 Cave (Lioubine, 1998).

The geomorphological data suggest the opening of Kudaro 3 Cave by erosion to occur approximately 50–100 thousand years later in comparison with that of Kudaro 1 Cave (Nesmeyanov, 1999). The place of contact of Acheulian and Mousterian layers is dated by two RTL-dates: 252,000±51,000 years and 245,000±49,000 years (Lioubine, 1998).

Fossil collection of vertebrates from Kudaro caves incorporates nearly 100 species, including the Pleistocene *Macaca* sp. which is the only record from the territory of the former USSR (Mashchenko & Baryshnikov, 2002). Both caves considerably differ from each other by the diversity and fragmentation of the paleontological material. The Kudaro 1 Cave, being dry and safe, was more attractive shelter for large carnivores as well as for the Pleistocene hominids, which led not only to bone accumulation, but to more pronounced fragmentation of osteological material in the Kudaro 1 Cave in comparison to that in the Kudaro 3 Cave (Baryshnikov, 1999).

The first study of the Pleistocene mammals from Kudaro 1 Cave was carried out by Vereshchagin (1957, 1959) who identified there four species of mustelids: *Martes* cf. *foina*, *Mustela* cf. *nivalis*, *Meles* cf. *meles*, *Gulo* cf. *gulo*. Later this composition has been supplemented, including as a result *Martes* sp., *Mustela nivalis*, *Mustela erminea*, *Vormela peregusna*, *Gulo* cf. *gulo*, *Meles meles* (small badger) and *Meles* sp. (large badger) (Vereshchagin & Baryshnikov, 1980a). The collection from Kudaro 3 Cave was found to include *Mustela nivalis*, *Mustela* sp., *Martes martes* and *M. foina*, *Gulo gulo*, *Meles meles* and *Meles* sp. (Vereshchagin & Baryshnikov, 1980b). These tentative determinations are specified in a course of the current study, which is not confirmed the presence of *Gulo gulo*, *Mustela erminea* and two forms of badger within the Kudaro mammal fauna

This communication represents the first detailed study of the mustelid collections from Kudaro caves. The examined material is kept in the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Material and methods

The examined collection contains more than 110 fossil remains of mustelids. In both caves, mustelid material has been found in the Middle Pleistocene and Upper Pleistocene deposits.

For the comparison, the collection of ZIN and the material on the Pleistocene badger belonging to Institut

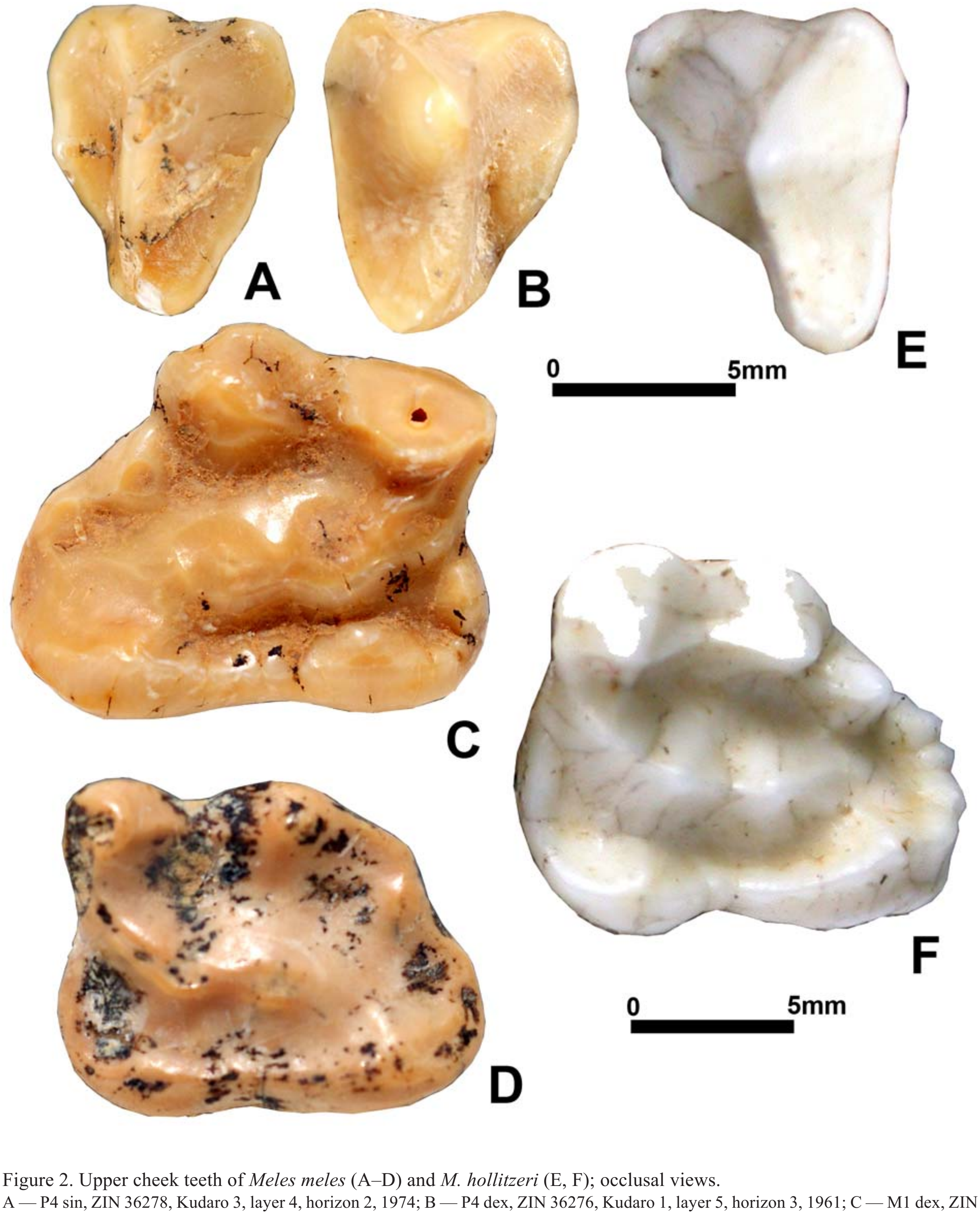

Figure 2. Upper cheek teeth of *Meles meles* (A–D) and *M. hollitzeri* (E, F); occlusal views.
A — P4 sin, ZIN 36278, Kudaro 3, layer 4, horizon 2, 1974; B — P4 dex, ZIN 36276, Kudaro 1, layer 5, horizon 3, 1961; C — M1 dex, ZIN 36277, Kudaro 3, layer 6, 1980; D — M1 sin, ZIN 36275, Kudaro 1, layer 5g, horizon 1, 1987; E, F — P4 and M1 sin, IPUW 2275/14/113, Deutsch-Altenburg 2C1, holotype.

zu Paläeontologie, Universität Wiena, Austria (IPUW) has been used.

The bones and teeth were measured by calipers with accuracy 0.1 mm. Tooth dimensions were processed with use of Discriminant Analysis from STATISTIKA 6.0.

The following designations of measurements are used. Teeth: *L* — length, *Ltl* — length of talonide, *W* — width. Bones: *Bd* — breadth of the distal end, *BFcd* — breadth of the Facies articularis caudalis, *BFcr* — breadth of the Facies articularis cranialis, *Bp* — breadth

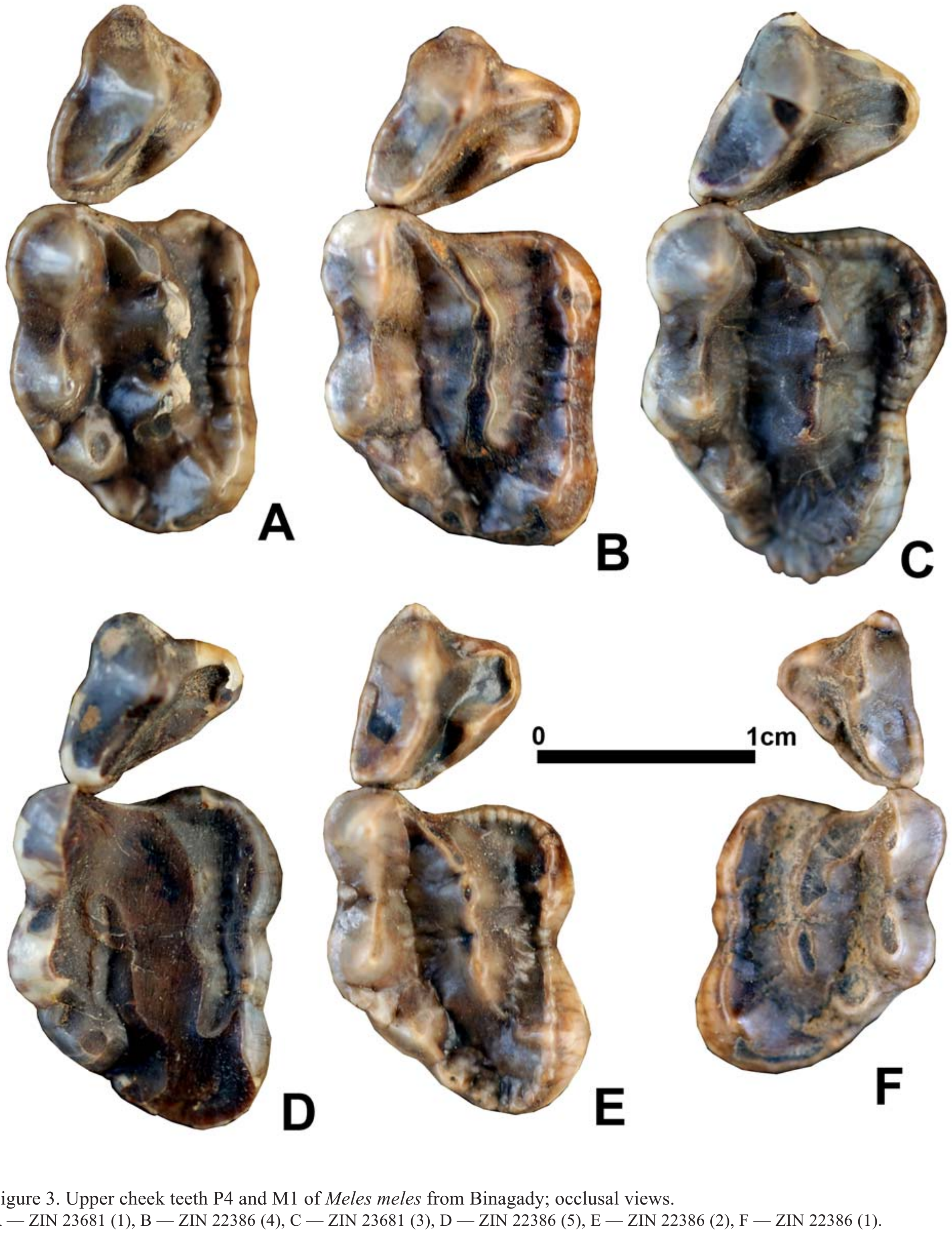

Figure 3. Upper cheek teeth P4 and M1 of *Meles meles* from Binagady; occlusal views.
A — ZIN 23681 (1), B — ZIN 22386 (4), C — ZIN 23681 (3), D — ZIN 22386 (5), E — ZIN 22386 (2), F — ZIN 22386 (1).

of the proximal end, *BPC* — breadth across the coronoid process, *DC* — depth of the Caput femoris, *Dd* — depth of the proximal end, *GL* — greatest length, *H* — height, *LAd* — length of the Arcus dorsalis, *SD* — smallest breadth of middle part of diaphysis, *SDO* — smallest depth of the olecranon, *SH* — smallest height of the shaft of ilium.

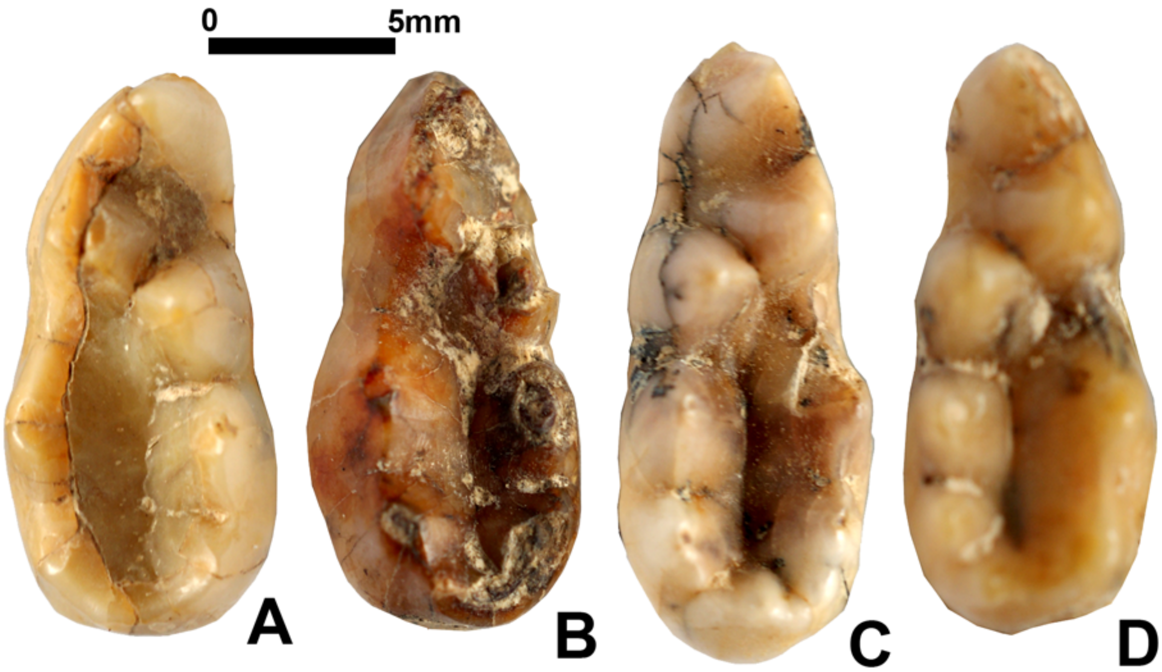

Figure 4. Left (A, B) and right (C, D) lower carnassial tooth m1 of *Meles meles*; occlusal views.
A — ZIN 36280, Kudaro 1, layer 5c, horizon 1, 1984; B — ZIN 36283, Kudaro 1, layer 5a, 1984; C — ZIN 36282, Kudaro 1, layer 5ab, horizon 2, 1987; D — ZIN 36281, Kudaro 1, layer 5, horizon 6, 1958.

Description

Mustelidae Fischer von Waldheim, 1817
Melinae Bonaparte, 1838
Meles Brisson, 1762
Meles meles (Linnaeus, 1758)

Material. Middle Pleistocene, Kudaro 1 Cave: 1 maxilla (ZIN 36276), 2 M2 (ZIN 36375, 36281), 2 mandibles (ZIN 36279, 36284), 4 m1 (ZIN 36280–36283); Kudaro 3 Cave: 1 M1 (ZIN 36277), 1 mandible (ZIN 36285). Late Pleistocene, Kudaro 3 Cave: 1 maxilla (ZIN 26278), 7 mandibles (ZIN 36286–36292). In both caves, sediments contain also numerous limb bones.

Description. Fossil remains of badger are rather numerous in the Kudaro caves, being distributed throughout Pleistocene sediments. It is not unusual because badgers often dig holes near cave entrances. For example, the Holocene layer 1 of the Kudaro 3 Cave contained remains of three individuals, including incomplete skeleton belonging to animal perished in its underground shelter.

The Pleistocene fossils of *M. meles* are represented by skull fragments, isolated teeth, and postcranial bones (Figs 1–8).

There are three maxillary fragments. Two of them possess no alveolus for the first premolar P1; notably, this tooth is absent in 50% of specimens from the sample of recent Caucasian badger (Baryshnikov & Potapova, 1990).

The upper carnassial tooth P4 resembles that of the recent *M. meles* from Caucasus by its size and structure (Fig. 2 A, B). Both available specimens belong to the A2 morphotype, which is more characteristic of *M. anakuma* (62% of sample), also appearing in *M. meles* (25% of sample), especially, in Caucasian badgers (Baryshnikov & Potapova, 1990; Baryshnikov *et al*., 2002).

For the comparison the collection from Binagady locality near Baku in Azerbaijan (ZIN 22386, 23681) dated by the last Interglacial (Baryshnikov, 2002) was examined (Fig. 3). Within this collection, the A3 morphotype (n=6) predominates (which is not found in *M. anakuma*); there is also the A2 morphotype (n=1).

Two upper molars M1 have no difference in the lingual length and greatest width from those of the recent Caucasian badger and fossil badger from Binagady (Table 1). Other two specimens from Kudaro caves possess heavily worn or eroded crowns not suitable for measuring. The Kudaro collection of M1 is found to contain teeth of B2 morphotype (n=1) and B4 morphotype (n=1) (Fig. 2 C, D). Within the Binagady sample, the morphotypes of B3 (n=5) and B4 (n=2) were revealed. The recent Caucasian badger is characterized of the B3 and B4 morphotypes. The B2 morphotype occurs extremely rare in *M. meles* and is absent in *M. anakuma* (Baryshnikov & Potapova, 1990).

Two mandibles from Kudaro caves possess alveolus for the first premolar p1, whereas two other specimens have no this alveolus. In *M. meles*, this tooth is as a rule present. All p2 (n=5) from the Kudaro collection are two-rooted and their length not exceeding 4.4 mm; both characters are typical of *M. meles*.

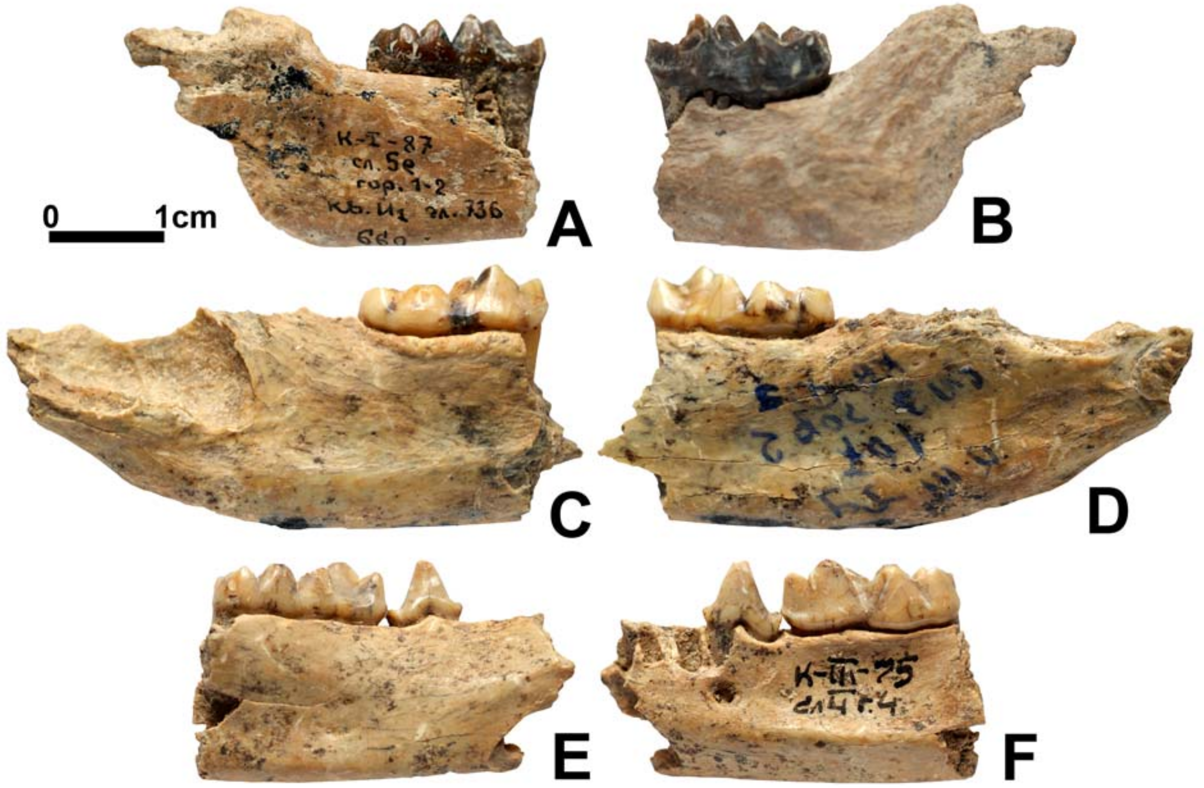

Figure 5. Mandible fragments of *Meles meles*; labial (B, C, F) and lingual (A, D, E) views.
A, B — ZIN 36279, Kudaro 1, layer 5e, horizon 1–2, 1987; C, D — ZIN 36292, Kudaro 3, layer 3, horizon 2, 1959; E, F — ZIN 36289, Kudaro 3, layer 4,horizon 4, 1975.

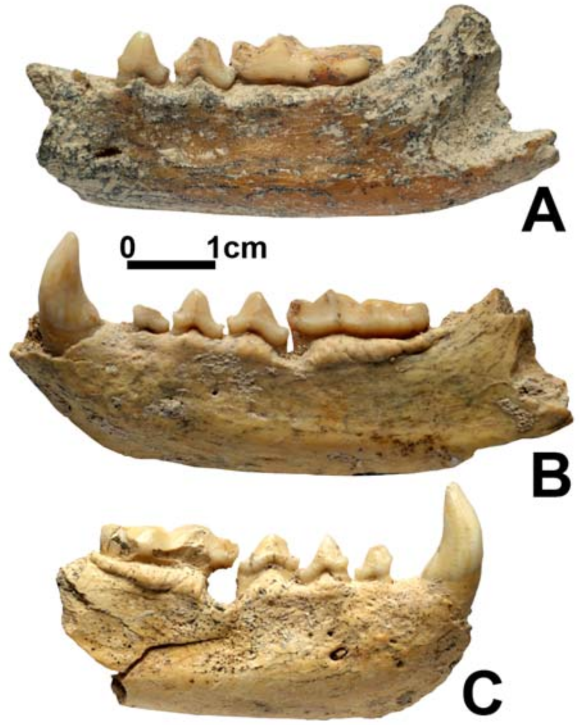

Figure 6. Mandible fragments of *Meles meles*; labial views.
A — ZIN 36283, Kudaro 1, layer 5, 1961; B — ZIN 36286, Kudaro 3, layer 4d, horizon 1, 1978; C — ZIN 36287, Kudaro 3, layer 4d, horizon 1, 1978.

In the sample from Binagady, p1 is present in five out of six findings. Five specimens posses p2 with two roots, two other specimens have conjoined roots. United roots of p2 occasionally occur in the recent badger from Southern Caucasus (Baryshnikov & Potapova, 1990).

The sample of lower carnassial tooth m1 from Kudaro caves is divided into two size groups distinguished by means of the greatest length: 16.83 mm (16.0–17.9 mm, n=7) and 15.23 mm (14.4–16.4, n=7). The larger teeth predominantly occurred in the Upper Pleistocene layers, whereas smaller representatives of the second group were found mostly in the Middle Pleistocene layers (Tabs 2, 3). The difference between two groups is statistically significant ($P<0.00002$). At the same time, one large specimen has been found in the layer 5 of Kudaro 1 Cave and mandibles with large as well as small m1 were revealed in the lower part of the layer 4 in Kudaro 3 Cave.

The study of cranial characters in recent *M. meles* demonstrated that the maximum degree of sexual dimorphism was discovered in the Southern Caucasus subspecies *M. m. canescens* (Abramov & Pusachenko, 2005). Therefore I regard the size groupings of lower carnassial tooth from Kudaro caves to belong to males and females.

In the sample from Kudaro caves, m1 do not differ in the length and width from those teeth in Binagady. No noticeable difference has been also revealed in

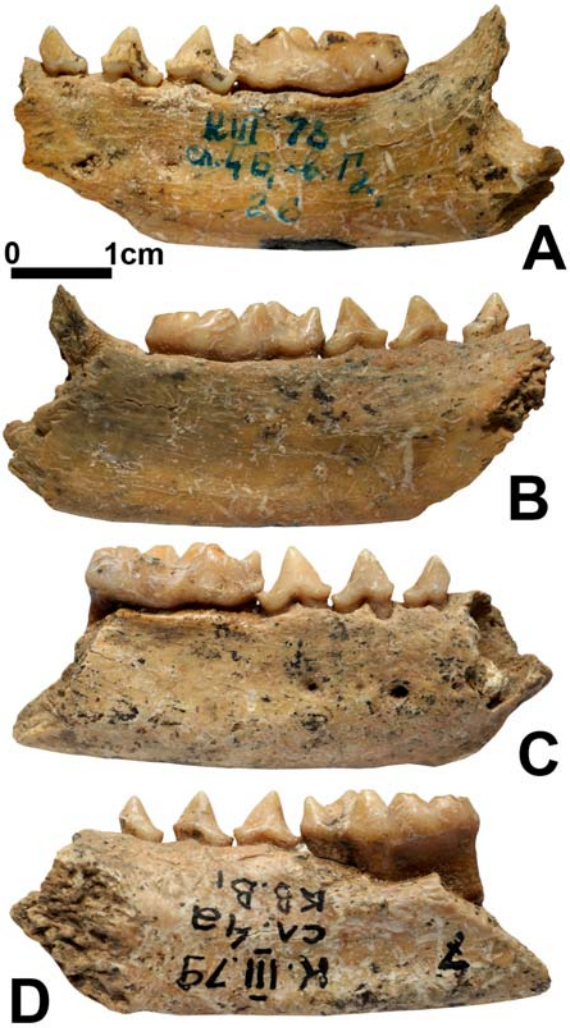

Figure 7. Mandible fragments of *Meles meles*; labial (B, C) and lingual (A, D) views.
A, B — ZIN 36290, Kudaro 3, layer 4b, 1978; C, D — ZIN 36291, Kudaro 3, layer 4a, 1979.

Figure 8. Mandible fragments of *Meles meles*; labial (A, C) and lingual (B, D) views.
A, B — ZIN 36285, Kudaro 3, layer 5, horizon 1, 1959; C, D — ZIN 36288, Kudaro 3, layer 4, horizon 4, 1975.

Table 1. Measurements of upper teeth in genus *Meles*.

Measurements, mm	*M. meles*							*M. hollitzeri*
	Kudaro 1	Kudaro 3		Binagady				Deutsch-Altenburg 2C
	ZIN 36276	ZIN 36277	ZIN 36278	ZIN 22386-2	ZIN 22386-4	ZIN 22386-5	ZIN 23681-1	IPUW 2275/14/113, holotype
C1 L			6.9		7.5	7.7	7.3	
C1 W			5.2		5.6	5.6	5.3	
P3 L	5.4				5.9	5.3	6.1	5.7
P3 W	4.4				3.6	3.4	4.1	4.0
P4 L	8.6		8.5	8.1	8.1	7.1	8.7	8.8
P4 W	7.2		7.4	6.4	7.5	6.7	7.1	7.5
M1 L		14.6	ca14.7	13.7	13.4	14.0	13.6	13.5
M1 W		12.1	-	10.8	11.6	11.5	11.1	11.6

Table 2. Measurements of mandibles and lower teeth of *Meles meles* (males).

Measurements, mm	Kudaro 1	Kudaro 3					
	ZIN 36284	ZIN 36288	ZIN 36286	ZIN 36287	ZIN 36292	ZIN 36291	ZIN 36290
Length p2-m2			48.9				
Length p2-m1	33.4		33.2	33.3	36.1		36.3
Height behind p4	15.1	15.1				16.0	16.4
Teeth							
c1 L			7.3	7.0			
c1 W			4.8	5.0			
p2 L			4.4	4.6		4.5	4.9
p2 W			-	2.8		3.2	3.2
p3 L	5.7		5.8	5.6		6.1	6.3
p3 W	3.4		3.4	3.5		3.6	3.5
p4 L	6.6	7.1	7.0	6.9		7.0	7.1
p4 W	4.2	4.3	4.0	4.2		4.2	4.0
m1 L	16.8	16.6	16.2	16.0	16.4	17.9	17.9
m1 Ltl	7.9	7.0	7.9	8.0	7.5	8.9	9.2
m1 W	7.9	7.9	8.2	8.1	7.9	8.7	8.7
m2 L		6.7					
m2 W		6.8					

Table 3. Measurements of mandibles and lower teeth of *Meles meles* (females).

Measurements, mm	Kudaro 1					Kudaro 3	
	ZIN 36282	ZIN 36279	ZIN 36280	ZIN 36283	ZIN 36281	ZIN 36285	ZIN 36289
Height behind p4						11.9	12.9
Teeth							
p4 L							6.7
p4 W							3.9
m1 L	16.4	15.5	14.3	15.0	14.8	15.3	15.2
m1 Ltl	7.8	7.3	6.1	7.5	7.0	7.0	7.2
m1 W	6.8	7.1	7.0	7.2	6.5	7.7	7.1
m2 L						6.3	
m2 W						6.7	

these measurements from the recent subspecies *M. m. canescens*, with except of two mandible fragments found in layer 4a in Kudaro 3 Cave to have the m1 length exceeding maximum value of this measurement in the recent subspecies. Within *M. meles*, such robust teeth possess recent badgers occurring in Europe.

The index of length of the m1 talonid (measured along lingual margin of crown and being divisible by the greatest tooth length) constitutes in average 46.58% (n=14) in the sample from Kudaro caves and 45.68% (n=5) in the sample from Binagady These indices are typical of *M. meles*, whereas *M. anakuma* possesses shorter talonid (Baryshnikov & Potapova, 1970).

Thus, no reliable difference was revealed in the tooth morphology between the Pleistocene and recent Caucasian badgers. This suggests the low rate of the modification of their dental system, which may be explained by stability of food sources.

The fossil postcranial bones from Kudaro caves resemble by their size those of the recent badger (Table 4); however, several markedly larger specimens have been found in Kudaro 1 Cave (layer 4) and in Kudaro 3 Cave (layer 7).

Rabeder (1976) described the species *M. hollitzeri* from the late Early Pleistocene of Austria (Deutsch Altenburg 2C) with the upper check teeth morphologically comparable to *M. meles* (Fig. 2, *e*, *f*). Somewhat archaism of the dentition in this species is expressed only in the larger size of the upper carnassial tooth P4 (with regard to size of M1).

Thus the paleontological data show that badgers morphologically similar to *M. meles* occurred during the whole Pleistocene. Therefore the division of the *M. meles* and *M. anakuma* lineages happened earlier, which conforms to data of molecular-genetic analysis on the early split of these lineages.

Comments. Representatives of the genus *Meles* have been widely distributed in the Palaearctic from the Atlantic coast to Japan. For a long time, this genus was regarded as monotypical. However, studies of the den-

Table 4. Measurements of limb bones of *Meles meles*.

Bones	Measurement, mm	Middle Pleistocene	Late Pleistocene
Fore limb			
Humerus	SD		9.2, 9.8
	Bd	30.0	29.2, 31.6
Ulna	BPC		9.5, 9.5
Radius	Bp	12.2	
	SD	7.6	
Mtc 3	GL	27.1	31.9
	Bd	6.6	8.2
Mtc 4	GL		27.5, 29.3
	Bd		6.7, 7.9
Hind limb			
Tibia	SD		8.9
	Bd		22.3
	Dd		13.7
Talus	GL	21.2	
Mtt 2	GL		27.5, 32.9
	Bd		6.0, 7.5
Mtt 3	GL	29.6, 32.0	
	Bd	5.8, 6.6	
Mtt 4	GL	31.6	29.5
	Bd	7.9	6.0

tal morphology revealed this genus to comprise two species: the European badger *M. meles* (L.) and Asian badger *M. anakuma* Temminck, 1844 (Baryshnikov & Potapova, 1990; Baryshnikov *et al*., 2002). In addition, these species differ from each other by the head pattern and baculum shape (Baryshnikov & Abramov, 1997; Aristov & Baryshnikov, 2002). It was also found that these species are hosts for different flea species (Abramov & Medvedev, 2003).

Molecular genetic analysis revealed two early diverged phylogenetic lineages within the genus *Meles* (Kurose *et al*., 2001; Marmi *et al*., 2006). Their split could be occurred nearly 2.0 or 2.87 million years before present (Sato *et al*., 2003; Marmi *et al*., 2006). These results support division of *Meles* into two species. The ancestor of both recent taxa is considered to be *Meles thorali* Viret, 1954 from the Late Pliocene locality of Saint-Vallier in France (Baryshnikov *et al*., 2002). The age of this locality is ascertained as 2.2 million years (Argant, 2004), which well corresponds to the time of the lineage divergence based on the molecular data.

Other researchers distinguish three species within the genus *Meles*, recognizing two species for the Asian badger: *M. anakuma* from Japanese Islands and *M. leucurus* (Hodgson, 1847) from mainland Asia (Abramov, 2003; Abramov & Pusachenko, 2005, 2006). However morphological and genetic difference between *M. anakuma* and *M. leucurus*, not exceeding, in my opinion, subspecies level may be the result of insular isolation of Asian badgers migrated to the Japanese Islands in the Middle Pleistocene. The young phylogenetic age of the Japanese population is indirectly ascertained by its lower genetic diversity (Kurose *et al*., 2001; Marmi *et al*., 2006).

In the recent Caucasian fauna, there are two subspecies of the European badger: larger *M. meles meles* (L.) in Northern Caucasus and smaller *M. m. canescens* Blanford, 1875 in Southern Caucasus (Heptner *et al*., 1967). Both subspecies differ by cranial characters (Abramov & Pusachenko, 2005, 2006).

Molecular data indicate that badgers of Europe and badgers of Southwest Asia (including Southern Caucasus) divided between 2.37 and 0.45 million years before present (Marmi *et al*., 2006). These data are ascertained by morphological peculiarity of badgers in Southern Caucasus since the Middle Pleistocene, which has been revealed by present study. Therefore, the Great Caucasus Ridge was an important zoogeographic barrier for dispersion of larger mammals, which has been earlier noted for cave bears (Knapp *et al*., 2009).

Martinae Wagner, 1841
Martes Pinel, 1792

The fossil material on martens is represented in Kudaro caves by mandible fragments, isolated canines, and bones of postcranial skeleton, which not always allows identification on the species level. Mandibular dentition is characteristic of the genus *Martes*: the presence of p1, p4 with posterior accessory cusp, and m1 with large metaconid.

There are two marten species in Caucasus: *Martes foina* and *M. martes*. These species reliably differs from each other by a distance between mental foramens (Anderson, 1970; Opatrný, 1972; Gerasimov, 1985). Mandible fragments with unclear position of the mental foramens have been referred to *Martes foina*/*martes* (Fig. 9)

This group was found to include upper (C1) and lower (c1) isolated canines, which correspond by their sizes to those of stone and pine martens (C1: L=4.1–5.1 mm, W=3.2–3.4 mm, n=5; c1: L=4.6–5.4 mm, W=3.1–3.6 mm, n=7). To *M. foina*/*martes* were also ascribed the bones of postcranial skeleton (Tab. 5).

Martes foina (Erxleben, 1777)

Material. Middle Pleistocene, Kudaro 1 Cave: 2 mandibles (ZIN 36262, 36263); Kudaro 3 Cave: 3 mandibles (ZIN 36264-36266). Late Pleistocene, Kudaro 1 Cave: femur fragment (ZIN 36269, layer 4, horizon 8, 1957); Kudaro 3 Cave: 1 mandible (ZIN 36267). Kudaro 3 Cave, mixed layers (ZIN 36268).

Description. The mandibles with approximated mental foramens are determined as a stone-marten (*M. foina*) (Figs 10–12). The minimum distance between these foramens does not exceed 4.0 mm (mean 3.35 mm, 2.8–3.8 mm, n=6).

The Pleistocene sample contains several specimens possessing rather small mandibular height measured

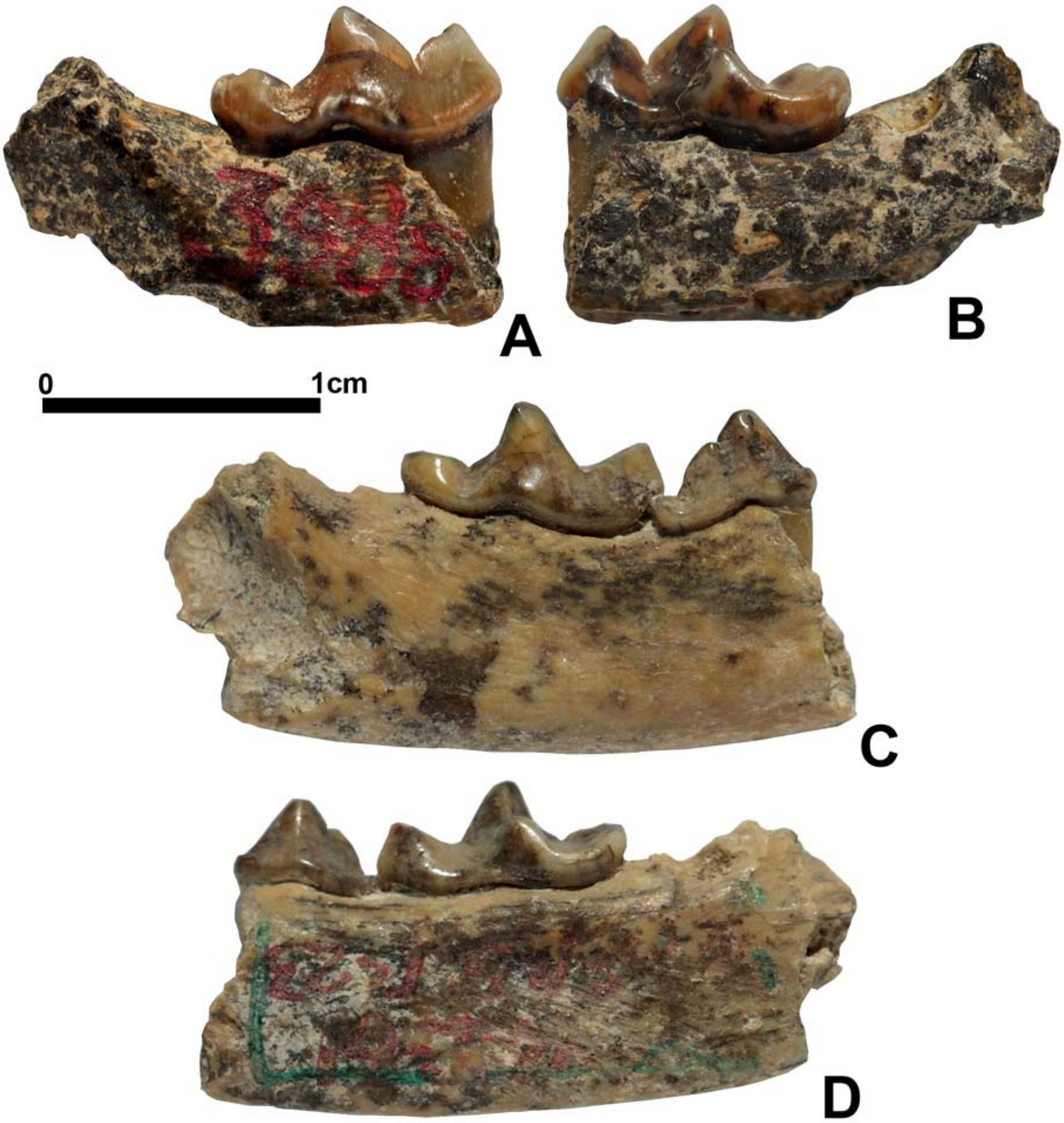

Figure 9. Mandibles of *Martes foina/martes*; labial (A, C) and lingual (B, D) views.
A, B — ZIN 36273, Kudaro 1, layer 5, horizon 1, 1958; C, D — ZIN 36274, Kudaro 1, layer X, 1961.

behind p4; these specimens were assigned to females (Tab. 6).

In the size and proportions, examined mandibles and teeth revealed no difference from those of the recent *M. foina* from Caucasus.

In the analysis of morphotypes elaborated for the evaluation of dental variation in dentition in *M. foina* and *M. martes* from Poland (Wolsan *et al*., 1985), two groups, B1 (n=2) and B2 (n=4) have been identified for p2, which are equally characteristic of *M. foina* and *M. martes*. The morphotypes of p4 were found to be presented by B4 (n=1) and B5 (n=6) groups; these groups are typical of *M. foina* rather than of *M. martes.*

A proximal fragment of femur with short femoral neck from the layer 4 of Kudaro 1 Cave (Bp=13 mm, DC=6.6 mm) was referred to the stone marten. The distance between the femoral head and greater trochanter along the caudal side of the neck constitutes less than 40% of anterior-posterior diameter of the head, which is more characteristic of *M. foina* in comparison with *M. martes* (Gromova, 1950).

Table 5. Measurements of postcranial bones of *M. foina/martes*.

Bones	Measurement, mm	Middle Pleistocene	Late Pleistocene
Atlas	BFcr	19.0	
	BFcd	13.0	
	LAd	6.3	
	H	11.6	
Fore limb			
Humerus	Bp	10.7, 11.3	
	DP	11.2, 11.6	
Ulna	SDO	7.7	7.1, 8.7
	BPC	6.1	6.7, 6.7
Radius	Bp	7.1	6.8
	Bd	7.2	
Hind limb			
Pelvis	SH		6.6, 6.8
Femur	Bp		13.1, 13.8
	DC		6.4, 6.4
	Bd		14.2
Tibia	Bd		8.5

Most findings of *M. foina* are associated with the Middle Pleistocene deposits.

Martes martes (Linnaeus, 1758)

Material. Middle Pleistocene, Kudaro 1 Cave: 2 mandibles (ZIN 36270, 36271); Late Pleistocene, Kudaro 3 Cave: mandible (ZIN 36272).

Description. Mandible fragments with widely spaced mental foramens (5.4 mm, 5.4 mm, n=2) are referred to the pine-marten (Fig. 13). These remains were recovered from the deposits of the Middle and Upper Pleistocene.

There is a single fossil lower carnassial tooth m1, which revealed no difference in the length with those of the recent *M. martes* from Caucasus, being, however, relatively narrower (Tab. 7).

The narrow m1 and widely spaced mental foramens are characteristic of *M. vetus* Kretzoi, 1947 from the early Middle Pleistocene of Western Europe; which occasionally considered as ancestor for *M. martes* as well as for *M. foina* (Anderson, 1970). Molecular genetic analysis unites *M. martes* and *M. zibellina* (L., 1758) into a monophyletic group, which is closely related to *M. americana* (Turton, 1806), whereas *M. foina* occupies an isolated position in the subgenus *Martes* (Stone & Cook, 2002; Saito *et al*., 2003)

Mustelinae Fischer von Waldheim, 1817

Vormela Blasius, 1884

Vormela peregusna (Güldenstädt, 1779)

Material. Middle Pleistocene, Kudaro 1 Cave: 3 C1 (ZIN 36293, layer 5, horizon 1, 1958; ZIN 36294, layer 5, horizon 5, 1961; ZIN 36295, layer 5, horizon 6, 1958), c1 (ZIN 36257, layer 5de, horizon 3, 1987), tibia fragment (ZIN 36258, layer 5, horizon 8, 1958); Kudaro 3 Cave: 2 C1 (ZIN 36261, layer 5, horizon 1, 1959; ZIN 36296, layer 5, 1979). Late Pleistocene, Kudaro 1 Cave: C1 (ZIN 36259, layer 4, 1959); Kudaro 3 Cave: c1 (ZIN 36260, layer 3, horizon 4, 1974).

Description. Middle and Upper Pleistocene layers of Kudaro caves are found to contain isolated canines of middle-sized mustelids. Six specimens, ZIN 36259 (L=3.5 mm, W=2.8 mm), ZIN 36261 (L=3.7 mm, W=2.9 mm), ZIN 36293 (L=3.7 mm, W=2.8 mm), ZIN 36294 (L=3.8 mm, W=3.1 mm), ZIN 36295 (L=4.0 mm, W=2.6 mm), and ZIN 36296 (L=3.7 mm, W=2.9 mm), represent upper canines (C1) and two other specimens, ZIN 36260 (length 3.1 mm, width 2.4 mm) and ZIN 36257 (length 3.1 mm, width 2.5 mm), represent lower canines (c1).

Judging from the length and width measured near the lower margin of enamel crown, the fossil canines may be referred to marbled polecat (*V. peregusna*) or

Table 6. Measurements of mandible and lower teeth of *Martes foina*.

Measurements, mm	Males			Females			
	Kudaro 1		Kudaro 3	Kudaro 3			
	ZIN 36262	ZIN 36263	ZIN 36268	ZIN 36264	ZIN 36266	ZIN 36265	ZIN 36267
Length p2-m1				23.6			
Height behind p4	10.3	9.2	9.4	7.0	7.4	7.5	8.8
Teeth:							
c1 L						4.5	
c1 W						4.0	
p2 L	4.4	4.0	–	4.0		4.3	
p2 W	2.4	2.3	2.3	2.2		2.3	
p3 L	5.3	4.9		4.7	–	4.9	4.9
p3 W	2.7	2.5		2.3	2.4	2.5	2.5
p4 L	6.0	6.1	–	5.7	5.9	5.9	5.4
p4 W	2.9	2.9	2.8	2.8	2.7	2.8	2.8
m1 L	10.1		10.3	9.4			9.7
m1 Ltl	7.7		7.7	7.0			6.9
m1 W	4.2		4.1	3.7			4.0

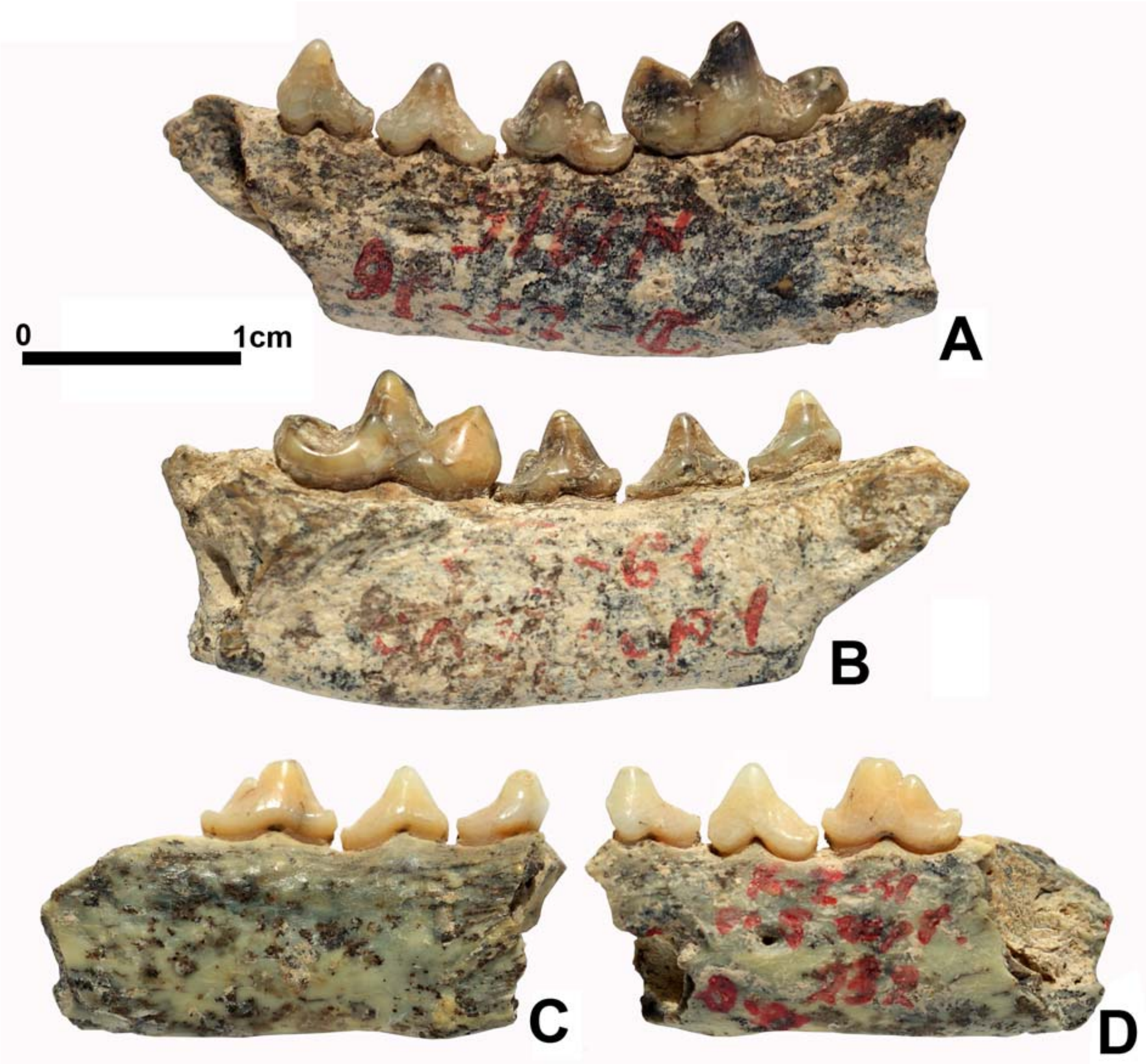

Figure 10. Mandible fragments of *Martes foina*; labial (A, D) and lingual (B, C) views.
A, B — ZIN 36262, Kudaro 1, layer 5, horizon 1, 1961; C, D — ZIN 36263, Kudaro 1, layer 5, horizon 1, 1961.

European polecat (*Mustela putorius* L., 1758), or steppe polecat (*M. eversmanii* Lesson, 1827). The canines from Kudaro caves remarkably smaller than those in *M. eversmanni* from la Fage in Middle Pleistocene of France (Hugueney, 1975).

Examined teeth possess the enamel crown lower as compared to that in aforementioned representatives of the genus *Mustela*. Owing to this character, the canines from Kudaro caves have been attributed to *V. peregusna*.

The incomplete tibia (ZIN 36258, Bd=5.3 mm) found in layer 5 of Kudaro 1 was also referred to the marbled polecat basing on the similar dimensions. In addition, the distal part of this bone is more slightly narrowed laterally, than in the representatives of the genus *Mustela*.

Most findings of marbled polecat remains occur in the Middle Pleistocene layers.

At present time, *V. peregusna* occurs in Northern Caucasus and in the eastern part of Southern Caucasus. Fossil skulls of this species have been recovered in the bitumen locality of Binagady in Azerbaijan (Vereshchagin, 1959) and in the Verkhniya Cave in Georgia (Vekua, 1978).

Mustela Linnaeus, 1758
Mustela nivalis Linnaeus, 1766

Material. Middle Pleistocene, Kudaro 1 Cave, layer 5: D4 (ZIN 36255), P4 def. (ZIN 36254), 4 mandibles (ZIN 36247, 36250, 36252, 36253 def.), m1 sin (ZIN 36252); Kudaro 3 Cave, layers 7 and 8a: 2 mandi-

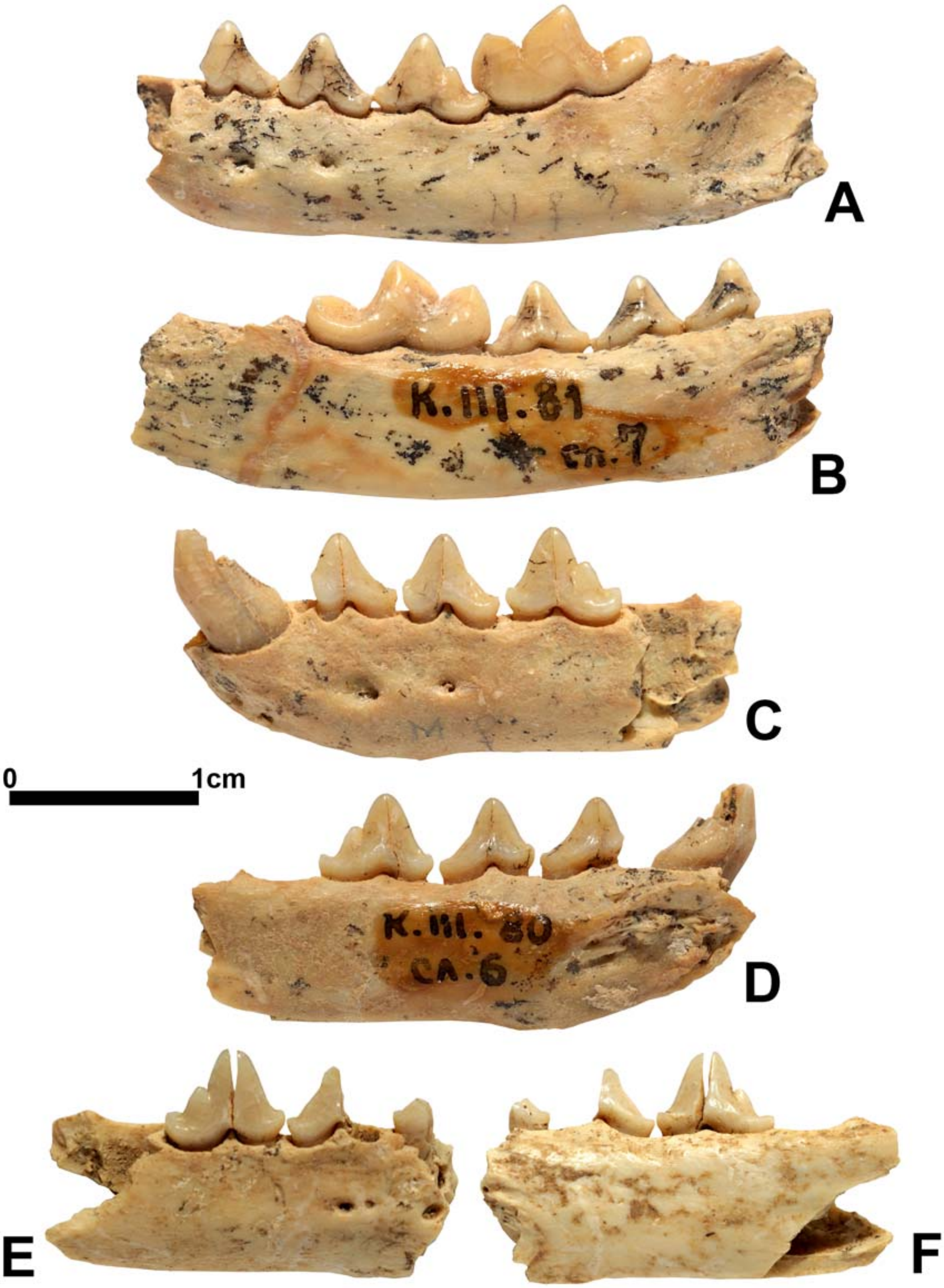

Figure 11. Mandibles of *Martes foina*; labial (A, C, E) and lingual (B, D, F) views.
A, B — ZIN 36264, Kudaro 3, layer 7, 1981; C, D — ZIN 36265, Kudaro 3, layer 6, 1980; E, F — ZIN 36266, Kudaro 3, layer 7, 1981.

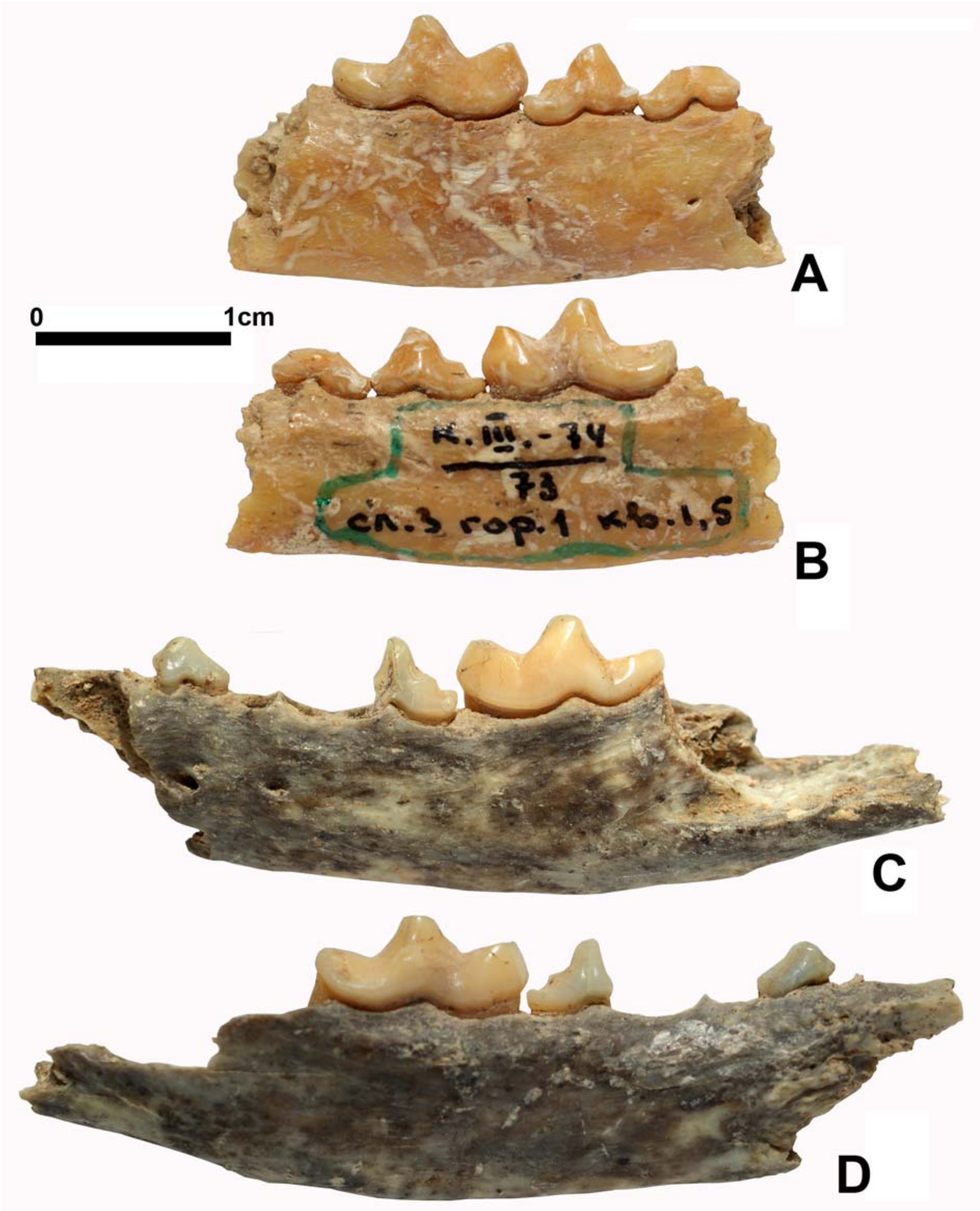

Figure 12. Mandibles of *Martes foina*; labial (A, C) and lingual (B, D) views.
A, B — ZIN 36267, Kudaro 3, layer 3, horizon 1, 1974; C, D — ZIN 36268, Kudaro 3, mixed layers, 1978.

Figure 13. Mandibles of *Martes martes*; labial (A, C, E) and lingual (B, D, F) views.
A, B — ZIN 36270, Kudaro 1, layer 5b, 1984; C, D — ZIN 36272, Kudaro 3, layer 4, horizon 3, 1975; E, F — ZIN 36271, Kudaro 1, layer R, horizon 2, 1984.

Table 7. Measurements of mandible of *Martes martes* and *M. foina/martes*.

Measurements, mm	*M. martes*			*M. foina/martes*	
	Kudaro 1		Kudaro 3	Kudaro 1	
	ZIN 36270	ZIN 36271	ZIN 36272	ZIN 36273	ZIN 36274
Height behind p4			8.4		7.5
Teeth:					
c1 L	4.3				
c1 W	3.6				
p1 L	1.8				
p1 W	1.3				
p2 L			4.2		
p2 W			2.5		
p3 L		4.9			
p3 W		2.2			
p4 L	6.0	5.7		5.9	5.4
p4 W	2.6	2.6		2.9	2.7
m1 L	9.6			10.3	8.9
m1 Ltl	6.7			7.0	6.0
m1 W	3.7			4.2	3.6

bles (ZIN 36248, 36451). Late Pleistocene, Kudaro 1 Cave, layers 4, 3 and X: 11 mandibles (ZIN 26237–26246, 36249), femur (ZIN 36256) (Figs. 14–16).

Description. The species was identified based on the mandibles, which are similar to *M. nivalis* in the size and tooth morphology. The examined mandibles differ from those of *M. erminea* L., 1758 by the smaller size and absence of supplementary root in the middle part of the labial wall of m1, which is characteristic of the ermine (Hugueney, 1975).

By the length of m1, *M. nivalis* from Kudaro caves resembles *M. palerminea* Petenyi, 1864 from Grotte de l'Escale in Middle Pleistocene of France, possessing, however, narrower m1 and smaller p3 and p4 (Bonifay, 1971). The size of m1 in *M. palerminea* from Villàny in Hungary is markedly larger (Hugueney, 1975).

The mean of the length of m1 from Kudaro caves (4.45 mm, 3.5–5.1 mm, n=15) only slightly exceeds this measurement in *M. nivalis* from la Fage (4.15 mm, 3.24–4.96 mm, n=183) in Middle Pleistocene of France (Hugueney, 1975).

The lower carnassial tooth m1 has no metaconid; small talonid bears a single tubercle (hypoconid). The talonid is longer than that in the recent weasel from Caucasus, the ratio between trigonid length and the greatest length of m1 constituting in the Pleistocene weasel, in average, 74.09% (71.7–78.4%, n=16) and 76.38% (73.3–83.3%, n=18) in the recent weasel from Caucasus. The difference between samples in this index is statistically reliable (P<0.001). The talonid reduction may be regarded as a development of carnivorous specialization of dentition in evolution of *M. nivalis*.

Fossil remains of *M. nivalis* were found in both caves in the Middle Pleistocene and Upper Pleistocene layers. No difference in the morphology was observed between weasels from these levels.

The fossil specimens are divided into two dimensional groups (Tabs 8, 9). Analogous division has been earlier proposed for *M. nivalis* from Pleistocene layers in Matyzka Cave in Northern Caucasus (Baryshnikov & Golovanova, 1989). It was regarded that two forms of weasel occur in Caucasus and the taxonomic difference between smaller and larger Caucasian weasels reaches specific level (Vereshchagin, 1959). Therefore fossil dimensional groups were referred to different species: *M. nivalis* and *M. boccamela* Bechstein, 1800 correspondingly.

In the revision of *M. nivalis*, all the Caucasian weasels have been referred to a single subspecies, *M. nivalis caucasica* (Barett-Hamilton, 1900), on the basis

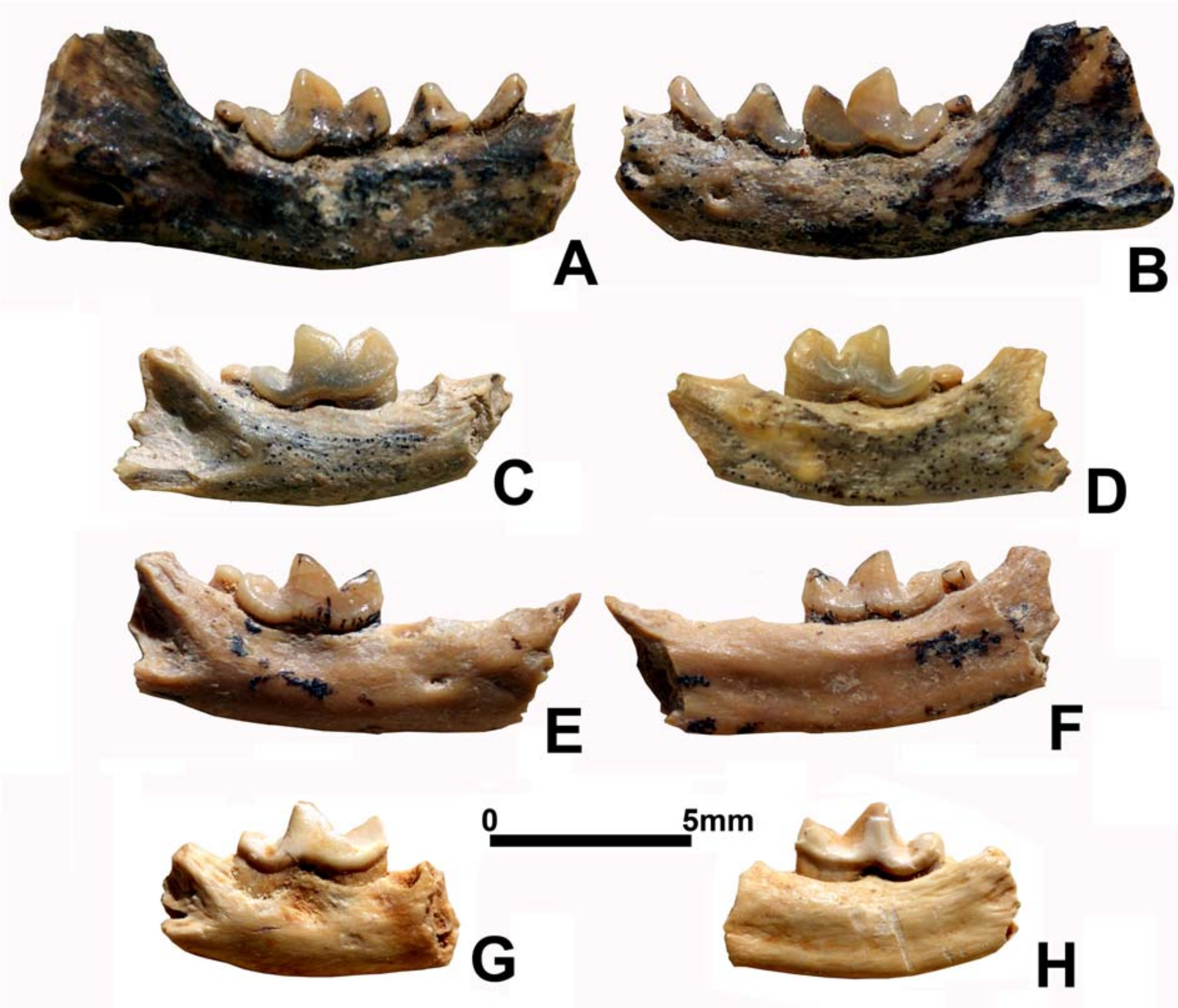

Figure 14. Mandibles of *Mustela nivalis kudarensis*, subsp.n.; labial (B, C, E, G) and lingual (A, D, F, H) views.
A, B — ZIN 36242, Kudaro 1, layer 4, 1959; C, D — ZIN 36249, Kudaro 1, layer X-1, horizon 4, 1980; E, F — ZIN 36247, Kudaro 1, layer 5f, horizon 1, 1987; G, H — ZIN 36251, Kudaro 3, layer 8a, 1981.

of morphological characters (Abramov & Baryshnikov, 2000). The molecular analysis distributed weasels from this region into different clusters (Kurose *et al*., 2005). One comprised specimens from Georgia, Turkey, Turkmenistan, Ukraine, and European Russia, whereas another cluster groups together animals from Georgia, Turkmenistan, and Kazakhstan.

The discriminant analysis based on three measurements of m1 (greatest length, length of trigonid, greatest width) demonstrated association of larger fossil form from Kudaro caves with males of the recent Caucasian weasel, whereas the smaller fossil form is grouped together with females (Fig. 17). The difference in size between genders seems to be considerable. In addition, females possess narrower m1 (with respect to its length).

Dimensions of large Pleistocene weasel exceed those of recent males from Caucasus. The average value of height of mandible behind p4 in fossil sample (3.92 mm, 3.4–4.2 mm, n=10) pronouncedly exceeds that in the recent sample (3.34 mm, 2.5–3.8 mm, n=10). The lower carnassial tooth m1 of large Pleistocene weasel is longer (measuring, in average, 4.79 mm, 4.5–5.1 mm, n=11) as compared to this tooth in the recent Caucasian males (4.44 mm, 4.2–4.7 m, n=16).

The upper carnassial tooth P4 (ZIN 36254) with broken protocone from layer 5de of Kudaro 1 Cave was referred to *M. nivalis.* This tooth resembles that in *Vormela peregusna* by the greatest length (6.5 mm) and posterior width (2.6 mm) but possesses the more pronounced cingulum at the base of metastylar blade, which is characteristic of the species belonging to the genus *Mustela*.

The upper deciduous tooth D4 (ZIN 36255, length 2.7 mm, width 1.1 mm) from the layer 5f of Kudaro 1 Cave has been also ascribed to *M. nivalis* basing on its size and structure.

The robust size is characteristic of the femur belonging to *M. nivalis* from layer 3c of Kudaro 1 Cave

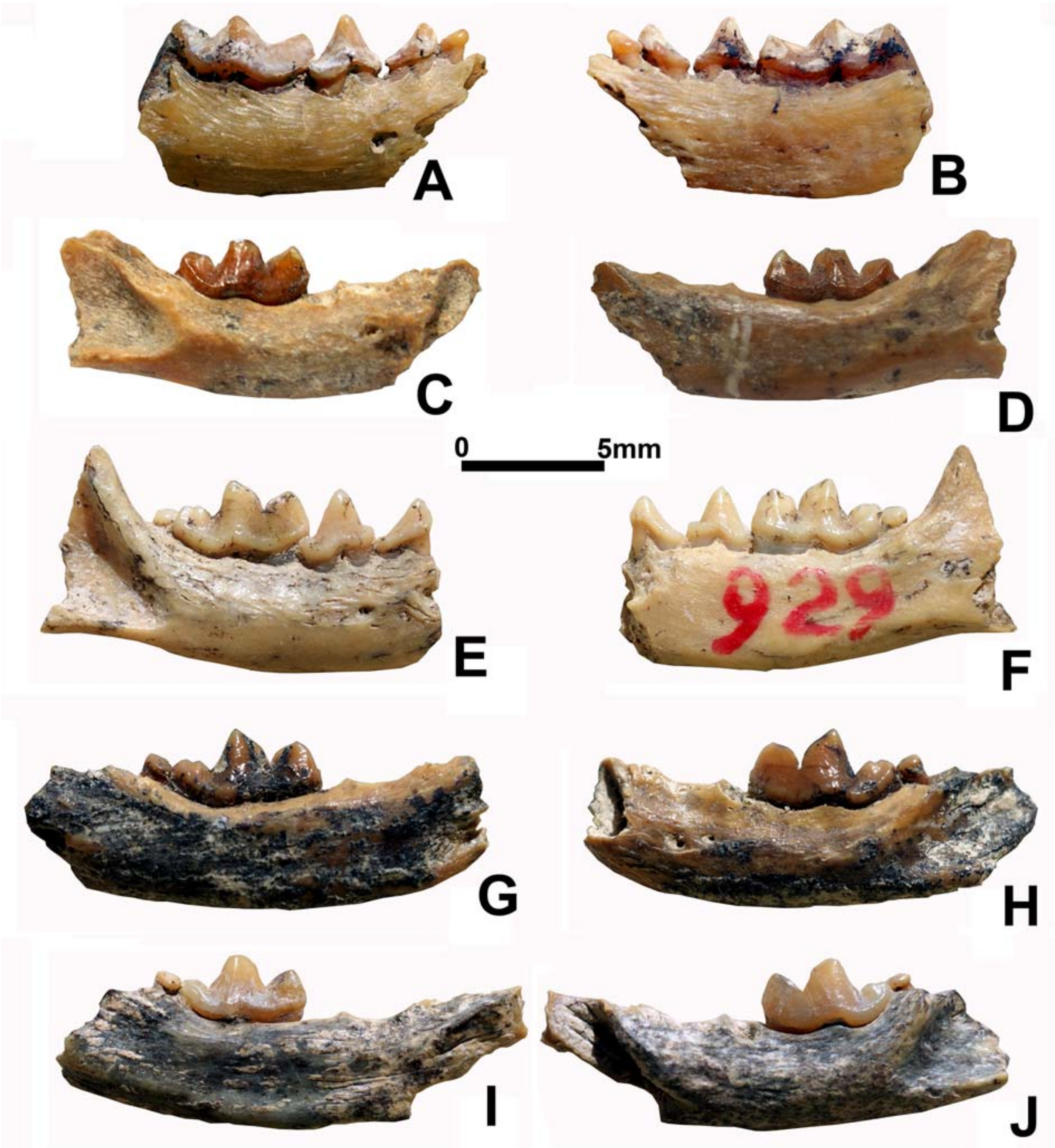

Figure 15. Mandibles of *Mustela nivalis kudarensis*, subsp.n.; labial (A, C, E, H, J) and lingual (B, D, F, G, I) views.
A, B — ZIN 36237, Kudaro 1, layer 3a, 1959, holotype; C, D — ZIN 36238, Kudaro 1, layer 3b, 1959; E, F — ZIN 36239, Kudaro 1, layer 3b–c, 1958; G, H — ZIN 36241, Kudaro 1, layer 3c, 1959; I, J — ZIN 36246, Kudaro 1, layer X, horizon 3, 1978.

(measurements, mm: GL=29.6, Bp=6.6, DC=3.0, SD=2.2, Bd=5.7).

The revealed morphological difference provides grounds to refer the Pleistocene weasel from Caucasus to a separate subspecies.

†*Mustela nivalis kudarensis* **subsp.n.**

Etymology. The name is derived from the Kudaro caves.

Holotype. Mandible ZIN 36237, Kudaro 1 Cave, layer 3a; collector V.P. Lioubine, 1959 (Fig. 15 A, B). Holotype measurements are given in Tab. 8.

Paratypes. Mandibles ZIN 36238, 36239, 36240, 36241, 36242, 36243, 36244, 36245, 36246, 36247, 36248, 36249, 36250, 36251.

Diagnosis. Differs from the Recent subspecies *M. nivalis caucasica* from Caucasus by more robust size and elongated talonid of m1 (ratio between trigonid

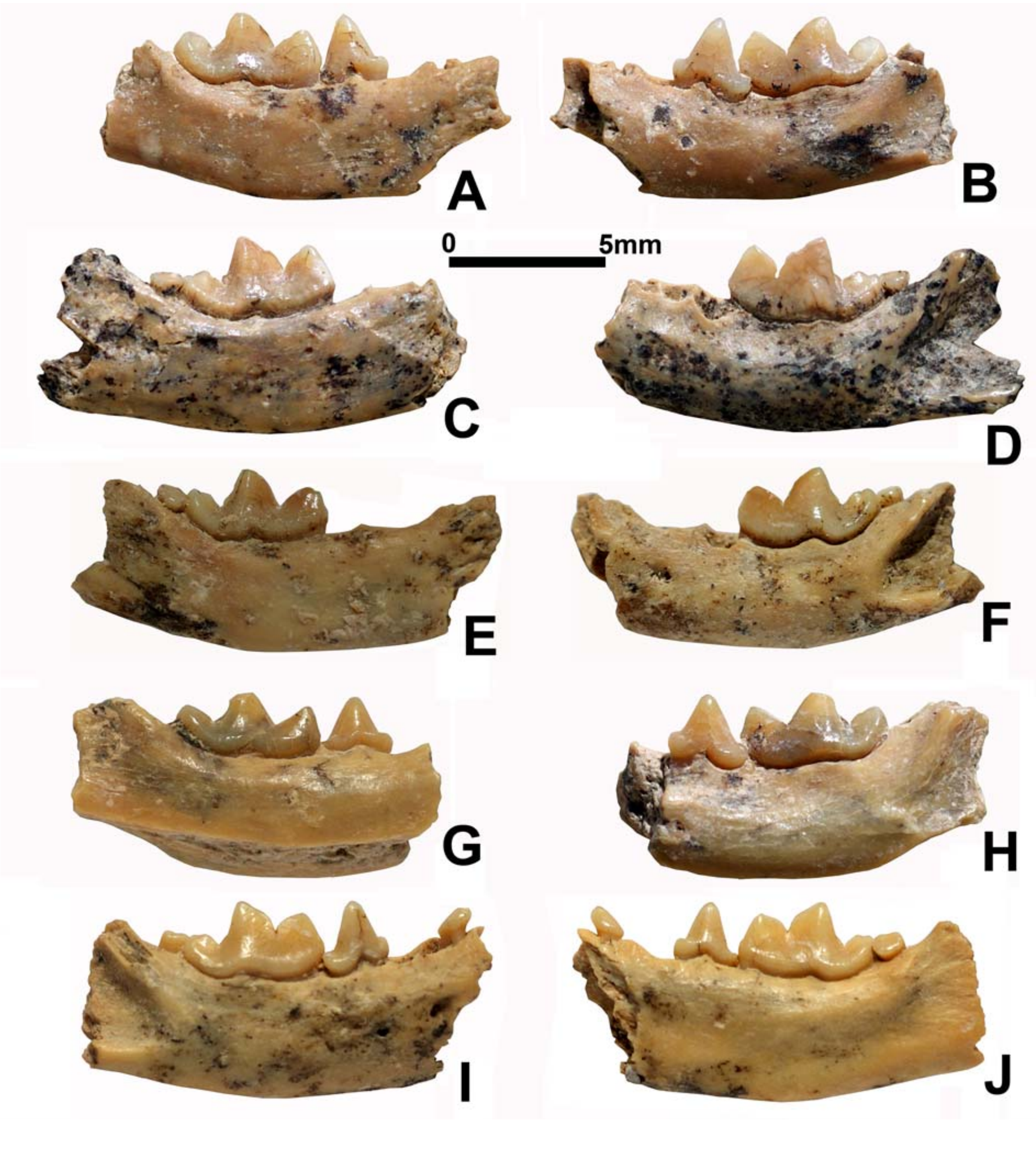

Figure 16. Mandibles of *Mustela nivalis kudarensis*, subsp.n.; labial (B, D, E, G) and lingual (A, C, F, H) views.
A, B — ZIN 36245, Kudaro 1, layer 4b, 1958; C, D — ZIN 36244, Kudaro 1, layer 4b, 1958; E, F — ZIN 36243, Kudaro 1, layer 4b, 1957; G, H — ZIN 36250, Kudaro 1, layer 5, horizon 5, 1959; I, J — ZIN 36248, Kudaro 3, layer 7, 1981.

length and greatest length constituting 74.09%, being 76.38% in the Recent weasel).

Distribution. Middle and Late Pleistocene of Southern Caucasus (Kudaro 1 Cave, Kudaro 3 Cave) and possible Northern Caucasus (Matuzka Cave).

Discussion

The study of the Pleistocene fauna of Kudaro cave sites demonstrates the presence of five mustelid species from 6 aborigines known of the Southern Caucasus. The absence of river otter, *Lutra lutra*, may be explained by taphonomic reasons. At the same time, *Vormela peregusna* does not occur in Southern Ossetia at present time; the marbled polecat now inhabits more eastern, arid areas of the Southern Caucasus.

No confirmation is given to the presence of wolverine, *Gulo gulo* (L., 1758), in Kudaro caves, spreading to the western part of Southern Caucasus in the Late Pleistocene (Smirnov, 1918; Burchak-Abramovich &

Table 8. Measurements of mandible and lower teeth of *Mustela nivalis kudarensis* (males).

Measurements, mm	Kudaro 1										Kudaro 3
	ZIN 36237, holotype	ZIN 36238	ZIN 36239	ZIN 36240	ZIN 36241	ZIN 36243	ZIN 36244	ZIN 36245	ZIN 36246	ZIN 36250	ZIN 36248
Length p2–m2				10.5		10.1			11.8		10.0
Length p2–m1	10.5	9.1		9.7	9.8	9.1		10.0	10.0		9.2
Height behind p4	4.0	3.7	4.0	4.2	4.0	3.7	4.1	3.4	3.9		4.2
Teeth:											
c1 L				2.5				2.1			2.8
c1 W				1.5				1.4			1.3
p2 L	1.3										1.2
p2 W	0.9										0.9
p3 L	1.9		2.0								
p3 W	1.3		1.1								
p4 L	2.6		2.6					2.6		2.6	2.2
p4 W	1.6		1.3					1.4		1.4	1.3
m1 L	5.0	4.6	4.8	4.5	5.1	4.7	5.0	4.9	4.7	4.9	4.5
m1 Ltl	3.7	3.3	3.5	3.4	3.7	3.5	3.7	3.5	3.5	3.6	3.4
m1 W	2.0	1.7	1.7	1.9	1.9	1.8	1.9	1.8	1.8	1.9	1.8
m2 L			1.0	1.0	0.9		1.1		0.9		1.0
m2 W			0.9	0.9	1.0		1.0		0.9		1.0

Table 9. Measurements of mandible and lower teeth of *Mustela nivalis kudarensis* (females).

Measurements, mm	Kudaro 1				Kudaro 3
	ZIN 36242	ZIN 36247	ZIN 36249	ZIN 36252	ZIN 36251
Length p2-m2	8.4	8.6			
Length p2-m1	7.7	8.0			
Height behind p4	2.8	2.7	2.5		2.5
Teeth:					
c1 L					
c1 W					
p2 L					
p2 W					
p3 L	1.3				
p3 W	0.9				
p4 L	2.0				
p4 W	1.0				
m1 L	3.7	3.7	3.8	3.5	3.8
m1 Ltl	2.9	2.7	2.9	2.6	2.8
m1 W	1.3	1.3	1.2	1.2	1.1
m2 L	0.8	0.7	0.8		
m2 W	0.7	0.7	0.6		

Bendukidze, 1971) and representing a marker of the mammoth fauna. Nowadays this species occurs 2000 km northwards.

The examined Pleistocene populations show a considerable morphological similarity with recent populations, with only *M. nivalis* being represented in the Kudaro cave sites by an especial fossil subspecies.

Thus the Pleistocene and recent associations of the mustelid species in Kudaro caves demonstrate no noticeable difference from each other. This resemblance throughout 350 thousand years makes it possible to suggest that the environment of Southern Caucasus underwent no significant changes during interchange of Glacial and Interglacial epochs and this region might be a refuge for many mammal species, such as rhinoceros and cave bears (Guerin *et al*., 1992; Baryshnikov, 1998). Refugial character of the southern areas of Europe and Caucasus in the glacial epochs has been established as a

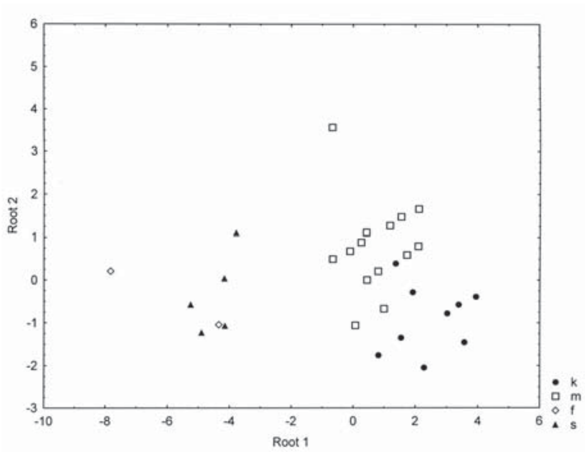

Figure 17. Scatter plot of canonical scores of Root 1 and Root 2 from discriminant analysis for lower carnassial tooth m1 of *Mustela nivalis*.
M. n. kudarensis subsp.n., Kudaro caves: k — large weasels, s — small weasels; *M. n. caucasica*, Recent, f — females, m — males.

result of molecular genetic studies (e.g. for brown and cave bears, Taberlet & Bouvet, 1994; Knapp *et al*., 2009).

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