



Early Pleistocene Caniformia from Palan-Tyukan (Azerbaijan)

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ABSTRACT

The Early Pleistocene site of Palan-Tyukan (MNQ18, ca 1.85 Mya) is located in Transcaucasia, northwestern Azerbaijan. In total, more than 300 mammalian bones were collected there by M.V. Sablin in 1986 and 1990. The remains were laid close to each other in a 25 m² lens-like accumulation, in a stratum of normally magnetized (the upper part of the Olduvai subchron) yellowish-grey Lower Apsheron loams. No any excavations have been carried here out since. The present study is based on the analysis of the Caniformia remains. The occurrence of raccoon dog in Palan-Tyukan provides knowledge about the Eurasian stratigraphic range of this taxon: it represents one of the latest records of the species *Nyctereutes megamastoides* (Pomel, 1842) in all of Europe. The bear tooth (was found earlier by N.A. Lebedeva nearby) is ascribed here to the species *Ursus etruscus* Cuvier, 1823. The taxonomic scenario of the Plio-Pleistocene tribe Galictini of Eurasia is intricate and has been debated since the beginning of the last century. The dispute arose mainly due to the scantiness and the sparse nature of their fossil record. The main conclusion about the *Pannonictis nestii* (Martelli, 1906) remains from Palan-Tyukan was reached after a detailed morphological and metrical analysis. Palearctic badger remains were assigned to the species *Meles thorali* Viret, 1950 – the ancestor of the European and Asian badgers. The occurrence of *M. thorali* in Palan-Tyukan represents one of the latest records of the species. The otter material from Palan-Tyukan is here referred to *Lutraeximia* cf. *umbra* Cherin et al., 2016. A Caniformia community of the Palan-Tyukan presents evidence of the wider variety of environments ranging from wooded areas with bodies of water to scrub and even savanna landscape in a relatively humid subtropical climate. The fauna of Palan-Tyukan is an important biostratigraphic reference fauna for mammal zonation in Europe. New discoveries can also help to clarify the taxonomic status of many of these extinct forms.

Keywords: Caniformia, Early Pleistocene, northwestern Azerbaijan, osteological material, Palan-Tyukan, Transcaucasia

Раннеплейстоценовые Caniformia из Палан-Тюкана (Азербайджан)

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РЕЗЮМЕ

Раннеплейстоценовое местонахождение Палан-Тюкан (MNQ18, около 1.85 млн. л.) находится в Закавказье, на северо-западе Азербайджана. Всего здесь в 1986 и 1990 годах М.В. Саблиным было

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собрано более 300 костей млекопитающих. Они залежали вплотную друг к другу внутри линзовидного скопления площадью 25 м² в толще нормально намагниченных (верхняя часть палеомагнитного эпизода Олдувей) желтовато-серых нижеапшеронских суглинков. Настоящее исследование посвящено анализу остатков Caniformia. Присутствие енотовидной собаки в Палан-Тюкане дает представление о стратиграфическом диапазоне данного таксона в Евразии: это – одна из самых поздних находок вида *Nyctereutes megamastoides* (Pomel, 1842) в Европе. Зуб медведя (ранее найденный неподалеку Н.А. Лебедевой) отнесен к виду *Ursus etruscus* Cuvier, 1823. Вопрос о таксономии плио-плейстоценовой трибы Galictini на территории Евразии сложен и обсуждается с начала прошлого века. Дискуссия обусловлена главным образом скудностью и разрозненностью ископаемого материала. После морфологического и метрического анализа сделан основной вывод об остатках *Pannonictis nestii* (Martelli, 1906) из Палан-Тюкана. Остатки палеарктического раннеплейстоценового барсука были отнесены к виду *Meles thoralis* Viret, 1950 – предку европейских и азиатских барсуков. Наличие *M. thoralis* в Палан-Тюкане – одно из самых поздних палеонтологических свидетельств о данном виде. Остатки выдры из Палан-Тюкана отнесены нами к *Lutraeximia cf. umbra* Cherin et al., 2016. Caniformia из Палан-Тюкана обитали в лесной зоне рядом с крупным водоемом, в относительно влажном субтропическом климате. Фауна Палан-Тюкана является важной эталонной фауной для уточнения биостратиграфических зон млекопитающих в Европе. Уточнить таксономический статус многих из этих вымерших форм Caniformia могут лишь новые находки.

Ключевые слова: Caniformia, ранний плейстоцен, северо-западный Азербайджан, остеологический материал, Палан-Тюкан, Закавказье.

INTRODUCTION

The Early Pleistocene site of Palan-Tyukan (MNQ18, ca 1.85 Mya) is renowned for its record of several mammalian taxa. It is located in the vicinity of the Palan-Tyukan range, Samukh District, Ganja-Qazakh region, northwestern Azerbaijan, Transcaucasia (geographical coordinates – 41°05'53" N 46°16'39" E). In total, more than 300 mammalian bones were collected there by M.V. Sablin in 1986 and 1990. The remains were laid close to each other in a 25 m² lens-like accumulation, in a stratum of normally magnetized (the upper part of the Olduvai subchron) yellowish-grey Lower Apsheron loams. The available data indicate that the remains accumulated during a single sedimentary cycle and have been buried in situ. The deposits can be described in a simplified manner as lacustrine. After the body of water dried out, the bones were sealed in the loam. The thickness of the loams containing the bones varies between 50 and 20 cm. Apart from numerous bones of large mammals, a few fragments of ostrich eggs, some fragments of shells of pond turtle *Emys orbicularis* (Linnaeus, 1758), and also shells of freshwater mollusk *Corbicula fluminalis* (O.F. Müller, 1774) were recovered (Sotnikova and Sablin 1993). It seems that the freshwater waterbody was not di-

rectly connected with the Akchagyl-Apsheironsky Basin of the ancient Caspian Sea (Lazarev et al. 2019). The fossil fauna of Palan-Tyukan is already described in previous studies (Sablin 1990; Kuzmina and Sablin 1991; Sotnikova and Sablin 1993; Iltsevich and Sablin 2022). The presence of fossil bones in the sediments is also mentioned by Lebedeva (1972, 1978), who studied the geology of the basin. The detailed information on the latest geological, paleontological studies in the Southern Part of the Caspian Region and palaeoenvironmental reconstructions are presented by van Baak et al. (2013), Bukhsianidze and Koiava (2018), Lazarev et al. (2019).

MATERIAL AND METHODS

The fossils described here are housed at the Zoological Institute of the Russian Academy of Sciences (ZIN, Saint Petersburg, Russia) and Geological Institute of the Russian Academy of Sciences (GIN, Moscow, Russia). All osteological material is fossilized to the same degree, which indicates similar burial conditions. The bulk of the determined remains are teeth and limb bones. Craniodental and postcranial measurements were taken to the nearest 0.1 mm with a digital caliper following von den Driessch (1976).

SYSTEMATIC PALEONTOLOGY

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Canidae Fischer, 1817

Genus *Nyctereutes* Temminck, 1838

Nyctereutes megamastoides (Pomel, 1842)

Type locality: Perrier-Les Etouaires, France.

Age of the type locality: Late Pliocene, MN 16.

Description. The remains belong to two adult individuals.

Upper teeth. The paracone and the metacone of the right M1 (ZIN 34171-1, L=10.0 mm; W=12.7 mm) are partly destroyed, but equal in size; the protocone is large; the protoconule is evident (Fig. 1A). The hypocone has a large base and is separated from the lingual cingulum by a small furrow. The cingulum is strong on the buccal and on the mesial sides. The small fragment of the second right M1 (ZIN 34171-4) is too small for any precise description. The left M2 (ZIN 34171-2, W=8.4 mm) possesses a larger paracone compared to the metacone, a large protocone and smaller protoconule and metaconule (Fig. 1B). The tooth is slightly damaged (part of enamel on the distal wall of the metacone is missing; the reconstructed M2 length is approximately 7.0 mm). Lingually, there is a cingulum-like hypocone. The left C1 (ZIN 34171-5, L=6.0 mm; W=4.5 mm) is broken, and considerably compressed buccolingually (Fig. 1C).

Right hemimandible. The specimen ZIN 34171-3 (Fig. 1D, E and F) is not complete. The m3 (L=4.1 mm; W=3.7 mm), the m2 (L=8.0 mm; W=5.6 mm) and part of the m1 (W_{tal} =6.1 mm) are the only teeth present. The mandibular thickness (on m1) is 6.8 mm. In occlusal view, the lower tooth row appears straight. The masseteric fossa is relatively deep. The m1 talonid has a simplified structure; the hypoconid and entoconid are large (with hardly any difference in height between them). The apices of the hypoconid and entoconid are located on the same transverse axis. Between the metaconid and entoconid, there is one accessory cuspid. The m2 is bean-shaped in occlusal view, with a conspicuous mesiobuccal cingulid (Fig. 1F). The protoconid and metaconid are large and almost equal in size. On the talonid, there is a large hypoconid and a medium-sized metaconid. In occlusal view, the m3 appears oval.

Right ulna. The specimen ZIN 34171-6 is not complete. The lateral coronoid process is greatly reduced in comparison to the medial one (Fig. 1G). The medi-

al coronoid process is rather thin and compressed mediolaterally instead of expanding medially. The greatest breadth across the coronoid process is 16.6 mm.

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Ursidae Fischer de Waldheim, 1817

Genus *Ursus* Linnaeus, 1758

Species *Ursus etruscus* Cuvier, 1823

Type locality: Upper Valdarno, Italy.

Age of the type locality: Early Pleistocene, MNQ18.

Description. The remains belong to one adult individual.

Lower tooth. The right m3 shape is egg-like (GIN 886/30, L=17.7 mm; W=16.5 mm) (Sotnikova and Sablin 1993). The specimen is slightly damaged (the distal wall of the talonid and part of enamel on the occlusal surface is missing) and heavily worn (Fig. 2A). The reconstructed m3 complete length may be of approximately 18.2 mm.

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Mustelidae Fischer, 1817

Subfamily Mustelinae Fischer, 1817

Genus *Pannonictis* Kormos, 1931

Species *Pannonictis nestii* (Martelli, 1906)

Type locality: Upper Valdarno, Italy.

Age of the type locality: Early Pleistocene, MNQ18.

Description. The remains belong to one adult individual.

Left hemimandible. The specimen ZIN 34173 (Fig. 2B, C and D) is only partly preserved. The m1 (L=13.0 mm; L_{tri} =8.4 mm; W=5.5 mm), the m2 (L=3.3 mm; W=3.6 mm) and part of the p4 are the only teeth present. The horizontal branch has been fractured, damaging the robust p4. The hemimandible appears stout and low. The inferior mandibular margin rises gently just beneath the m1 talonid. The height of mandibular rami (on m1) is 14.9 mm; the mandibular thickness (on m1) is 7.3 mm; the massive index (height mandible corpus below m1 / breadth mandible corpus at m1) is 2.0. The masseteric fossa almost reaches the m2. The m1 is moderately worn. The protoconid is stout and well developed. The paraconid is well developed too (Fig. 2D). The metaconid is not in line with the protoconid but located slight-

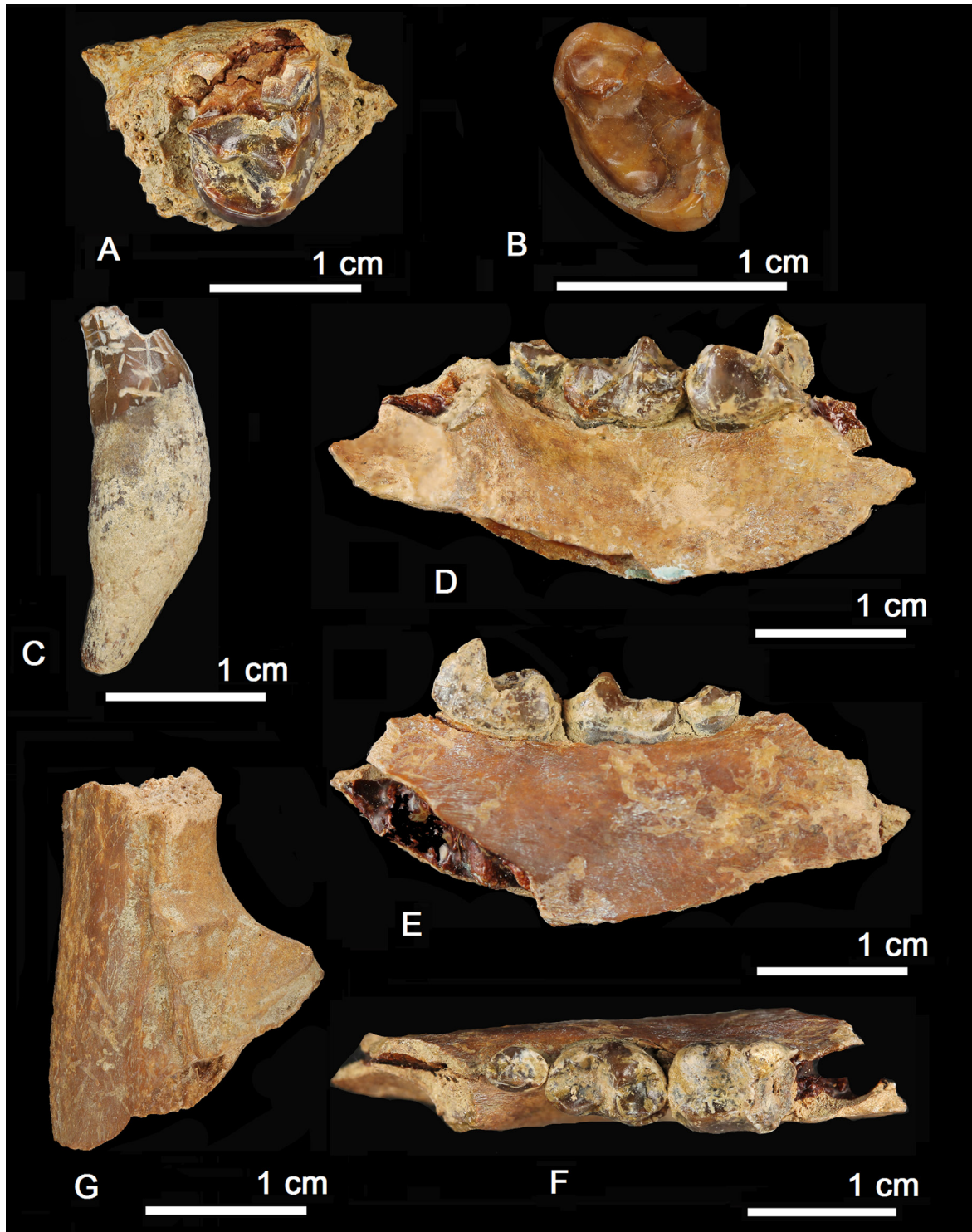


Fig. 1. *Nyctereutes megamastoides* from Palan-Tyukan, MNQ18 (Azerbaijan). A – ZIN 34171–1, right maxillary fragment with M1, occlusal view; B – ZIN 34171–2, left M2, occlusal view; C – ZIN 34171–5, left C1, buccal view; D – ZIN 34171–3, right hemimandible with m2-m3 and talonid of m1, lingual view; E – ZIN 34171–3, right hemimandible with m2-m3 and talonid of m1, occlusal view; F – ZIN 34171–3, right hemimandible with m2-m3 and talonid of m1, lingual view; G – ZIN 34171–6, fragment of right ulna, right lateral view.

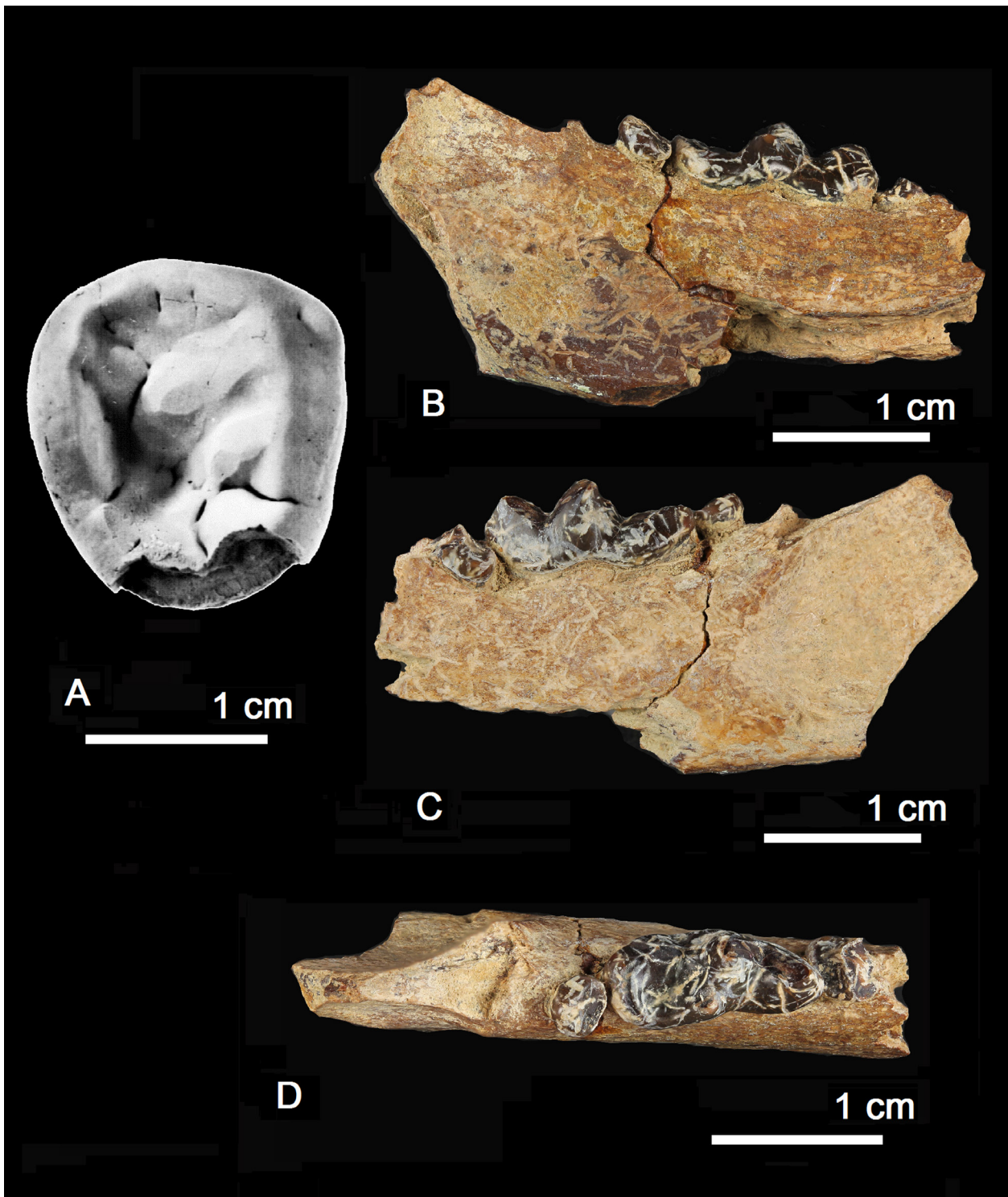


Fig. 2. *Ursus etruscus* from Palan-Tyukan, MNQ18 (Azerbaijan). A – GIN 886/30, right m3, occlusal view (according to Sotnikova and Sablin (1993)). *Pannonictis nestii* from Palan-Tyukan, MNQ18 (Azerbaijan). B – ZIN 34173, left hemimandible with m1-m2 and fragment of p4, buccal view; C – ZIN 34173, left hemimandible with m1-m2 and fragment of p4, lingual view; D – ZIN 34173, left hemimandible with m1-m2 and fragment of p4, occlusal view.

ly posterior to the latter. The talonid is complete and we can see the well developed hypoconid. The m2 is round-shaped in occlusal view.

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Mustelidae Fischer, 1817

Subfamily Mustelinae Fischer, 1817

Genus *Meles* Brisson, 1762

Species *Meles thoralis* Viret, 1950

Type locality: Saint-Vallier, France.

Age of the type locality: Early Pleistocene, MN 17.

Description. The remains belong to one adult individual.

Upper teeth. The left P4 (ZIN 34168–1, L=9.9 mm; W=8.3 mm) displays a high and buccolingually compressed paracone and a well-developed protocone (Fig. 3A). This specimen has the cuspule on the precingulum at the base of the paracone, and displays a lingual ridge running from the apex of the paracone to the lingual margin of the tooth (A1 category of Baryshnikov et al. 2002). The left M1 (ZIN 34168–2, L=14.4 mm; L_{ext}=9.7 mm; W=11.9 mm) displays a trapezoid occlusal profile (Fig. 3B). The paracone is slightly larger than the metacone, and the metaconule is situated somewhat distolingually to the metacone, thus creating a notch on the labial margin of the crown (B1 or B2 categories of Baryshnikov et al. 2002). The position of the root and the postprotocrista extension are both difficult to trace due to tooth wear. The talon is strongly projected distally.

Left ulna. The specimen ZIN 34168–3 is not complete. The coronoid process is triangular-shaped and more marked in the lateral view (Fig. 3C). The greatest breadth across the coronoid process is 19.4 mm.

Order Carnivora Bowdich, 1821

Suborder Caniformia Kretzoi, 1943

Family Mustelidae Fischer, 1817

Subfamily: Lutrinae Bonaparte, 1838

Genus *Lutraeximia* Cherin et al., 2016

***Lutraeximia* cf. *umbra* Cherin et al., 2016**

Type locality: Pantalla, Italy.

Age of the type locality: Early Pleistocene, MNQ18.

Description. The remains belong to one adult individual.

Upper teeth. The left P4 (ZIN 34247–1, W=9.8 mm) has a triangular contour, is broad, and shows two morphologically distinct portions, the trigon labially and the talon lingually (Fig. 3D). In the trigon, the high paracone is oriented almost vertically. The metacone is not preserved (the reconstructed P4 length is approximately 13.6 mm). The parastyle is very well defined and pointed mesially to the paracone. The talon is broad (L_{tal}=9.8 mm) covering more than two-thirds of the length of the trigonid. The occlusal outline of the left M1 (ZIN 34247–2, L=8.0 mm; W=11.3 mm) is bean-shaped (Fig. 3E). The paracone and the metacone are partially destroyed. The protocone is well developed. The talon is strongly projected distally. The central basin of the talon is concave. The hypocone is on the distolingual corner of the talon. The wear of both teeth is very advanced.

DISCUSSION

The size (Table 1) and the morphological features of the remains of raccoon dog *Nyctereutes* remains from Palan-Tyukan here described (such as the morphology of the M1 and M2 and the simplified structure of the m1 talonid), point to a substantial affinity with the Late Pliocene-Early Pleistocene *N. megamastoides* (Pomel, 1842) of Europe (Kurtén and Crusafont 1977; Monguillon et al. 2004; Titov 2008; Lucenti 2017; Rook et al. 2017; Lucenti et al. 2018). This is also consistent with the stratigraphic history of the species (Lucenti 2018a). The occurrence of *Nyctereutes* in Palan-Tyukan provides knowledge about the Eurasian stratigraphic range of these taxa: it represents one of the latest records of the species *N. megamastoides* in all of Europe (Lucenti 2018a). The favorite habitats of the extant raccoon dog are wet meadows with swampy lowlands, overgrown river floodplains and riverine forests with dense undergrowth.

The bear tooth from Palan-Tyukan is ascribed here to the species *Ursus etruscus*. That specimen was initially determined by Sotnikova and Sablin (1993). The morphological characters and the size of the m3 from Palan-Tyukan suggest similarities with the bear teeth from Upper Valdarno and Dmanisi localities (Table 2). *Ursus etruscus* is the typical ursid species recorded in the faunal assemblages of Eurasia during

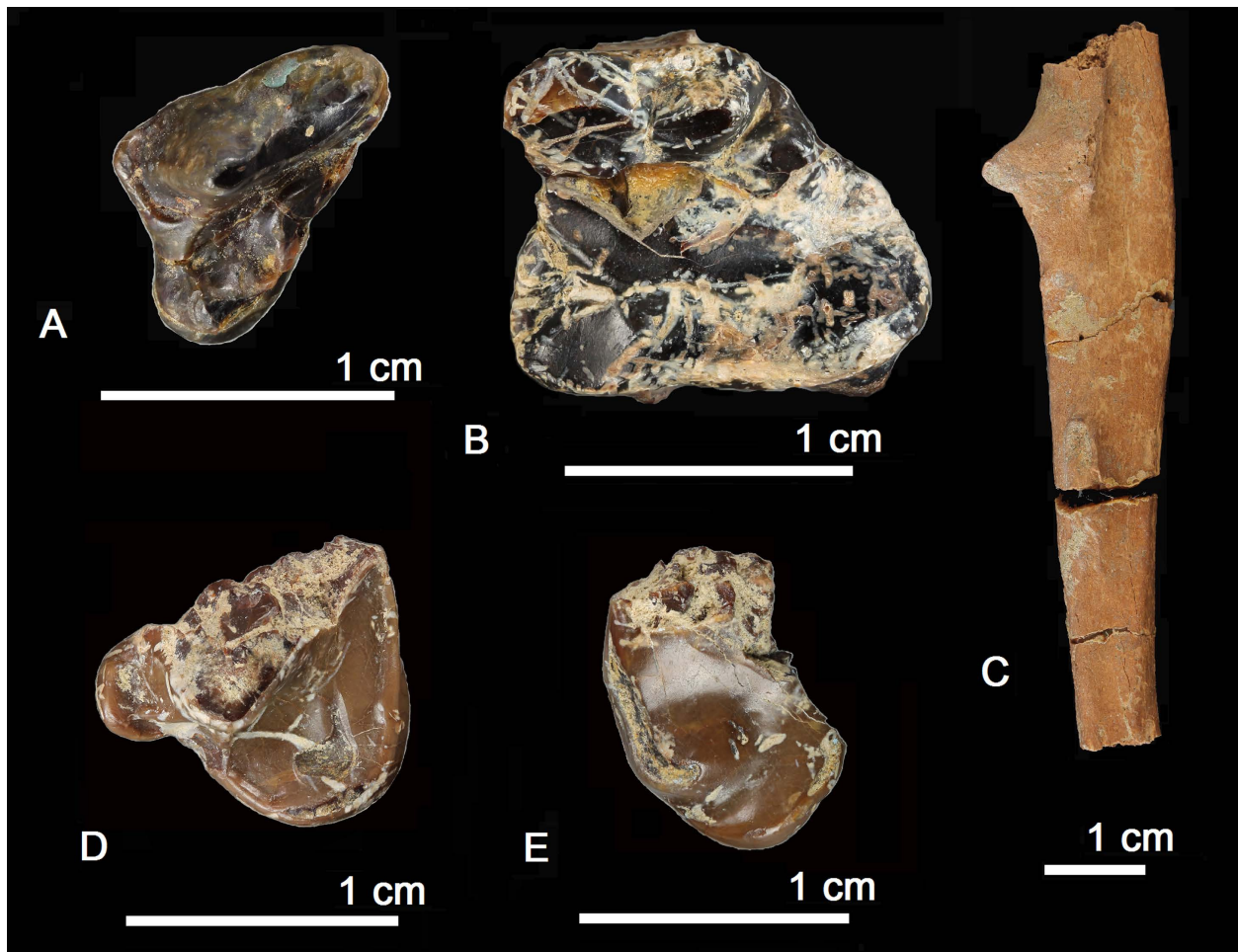


Fig. 3. *Meles thoralis* from Palan-Tyukan, MNQ18 (Azerbaijan). A – ZIN 34168–1, left P4, occlusal view; B – ZIN 34168–2, left M1, occlusal view; C – ZIN 34168–3, fragment of left ulna, right lateral view. *Lutraeximia* cf. *umbra* from Palan-Tyukan, MNQ18 (Azerbaijan). D – ZIN 34247–1, left P4, occlusal view; E – ZIN 34247–2, left M1, occlusal view.

Table 1. Measurements of the teeth (in mm) of *Nyctereutes megamastoides* from various European Late Pliocene-Early Pleistocene localities.

<i>Nyctereutes megamastoides</i>	M1		M2		m2		m3	
	L	W	L	W	L	W	L	W
Palan-Tyukan ZIN 34171–1	10.0	12.7	–	–	–	–	–	–
Palan-Tyukan ZIN 34171–2	–	–	~7.0	8.4	–	–	–	–
Kvabebi K234 L ¹	–	12.1	7.0	8.0	–	–	–	–
Kvabebi K217 L ¹	11.1	12.9	7.7	9.8	–	–	–	–
Kvabebi K217 R ¹	11.4	12.6	7.5	9.0	–	–	–	–
Kvabebi K220 R ¹	11.0	12.6	7.0	8.6	–	–	–	–
Palan-Tyukan ZIN 34171–3	–	–	–	–	8.0	5.6	4.1	3.7
Kvabebi K221 ¹	–	–	–	–	7.9	5.8	4.4	3.8
Kvabebi MG 29–2013/820 ¹	–	–	–	–	8.7	7.5	4.1	4.4
Liventsovka GIN 302/1 ²	–	–	–	–	9,2	7.2	–	–

Data are from: ¹ Rook et al. (2017); ² Sotnikova et al. (2002).

Table 2. Measurements of the teeth (in mm) of *Ursus etruscus* from various European localities (the initial phase of Early Pleistocene).

<i>Ursus etruscus</i>	m3	
	L	W
Palan-Tyukan GIN 886/30 ¹	17.7	16.5
Dmanisi D 5355 ²	20.7	17.0
Dmanisi D1277 ²	22.4	14.7
Dmanisi D1278 ²	20.5	15.6
Dmanisi D1029 ²	18.4	14.0
Dmanisi D36 L ²	19.1	15.3
Dmanisi D36 R ²	19.2	15.0
Dmanisi D355 L ²	18.4	17.2
Dmanisi D355 R ²	18.5	17.3
Dmanisi D1020 ²	18.3	14.6
Dmanisi D2219 ²	17.9	15.3
Upper Valdarno IGF 906 ³	18.8	14.5
Upper Valdarno IGF 4595 ³	22.7	15.0

Data are from: ¹ Sotnikova and Sablin (1993); ² Medin et al. (2019); ³ Baryshnikov (2007).

the Early Pleistocene (Baryshnikov 2007; Wagner 2010; Madurell-Malapeira et al. 2014; Medin et al. 2017; Wagner et al. 2017; Koufos et al. 2018; Medin et al. 2019). The species was a forest and ecotonal animal and had an omnivorous diet, feeding on both plants and mammals depending upon availability. A regular consumption of fish from the lacustrine systems also could have played a significant role in the diet of *U. etruscus* (Palmqvist et al. 2008).

Pannonictis remains have been recovered from 25 Early Pleistocene Eurasian sites (Martelli 1906; Sotnikova 1980; Stuart 1982; Rook 1995; Sotnikova et al. 2002; García et al. 2008; García and Howell

2008; Titov 2008; Colombero et al. 2012; Peters and de Vos 2012; Madurell-Malapeira et al. 2014; Lucen-ti 2018b). The taxonomic scenario of the Plio-Pleistocene tribe Galictini of Eurasia is intricate and has been debated since the beginning of the last century. The dispute arose mainly due to the scantiness and the sparse nature of their fossil record. The main conclusion about the *Pannonictis* remains from Palan-Tyukan was reached after a detailed morphological and metrical analysis. The adult left hemimandible originally assigned to *Enhydriactis ardea* (Bravard, 1828) by Sotnikova and Sablin (1993) is very similar to the hemimandibles from Liventsovka (Sotnikova et al. 2002), Upper Valdarno (Martelli 1906), Pietrafitta (Rook 1995) and Atapuerca (García and Howell 2008), all assigned to *Pannonictis nestii* (Table 3), a smaller and more slender species of the *Pannonictis* genus (Colombero et al. 2012). A strictly aquatic life of the species, comparable to the style of otters, is not likely, but semiaquatic habitats close to lakes are suggested, similar to those of their phylogenetic descendant, the American *Galictis* species (Peters and de Vos 2012).

On the basis of the morphological characters, we attribute the badger remains from Palan-Tyukan to the extinct *Meles thorali* (Sotnikova and Sablin 1993). The Early Pleistocene fossil record of European badgers is scanty and poorly known (Viret 1950; Madurell-Malapeira et al. 2009, 2011). Nevertheless, in a recent taxonomical review (Madurell-Malapeira et al. 2011), all Early Pleistocene (MN17-MNQ18) Palearctic badger remains were assigned to the species *M. thorali* – the ancestor of the European and Asian badgers (Baryshnikov et al. 2002; Abramov and Puzachenko 2013). The split between these two

Table 3. Measurements of the hemimandible and the m1 (in mm) of *Pannonictis nestii* from various European Early Pleistocene localities.

<i>Pannonictis nestii</i>	H _{M1} m1	W _{M1} m1	m1		
			L	L _{tri}	W
Palan-Tyukan ZIN 34173	14.9	7.3	13.0	8.4	5.5
Upper Valdarno IGF 916 ¹ (holotype)	14.8	6.35	11.75	–	5.2
Pietrafitta 1745 ¹	13.25	6.7	12.6	–	5.55
Pietrafitta 1750 ¹	14.5	7.05	12.5	–	5.25
Pietrafitta 1776 ¹	11.95	5.35	11.50	–	4.8
Liventsovka RSU 98 ²	15.1	7.1	13.5	–	–
Atapuerca ATA98-TE-J30-19 ³	13.3	7.3	12.6	9.0	5.1
Atapuerca ATA00-TE9-L30-54 ³	14.5	7.7	14.0	9.7	5.2
Pirro Nord PU 120257 ⁴	13.9	6.6	12.6	8.4	5.6

Data are from: ¹ Rook (1995); ² Sotnikova et al. (2002); ³ García and Howell (2008); ⁴ Colombero et al. (2012).

Table 4. Measurements of the upper teeth (in mm) of otters.

Species	P4		M1	
	L	W	L	W
<i>Lutraeximia</i> cf. <i>umbra</i> , Palan-Tyukan ZIN 34247–1	~13.6	9.8	–	–
<i>Lutraeximia</i> cf. <i>umbra</i> , Palan-Tyukan ZIN 34247–2	–	–	8.0	11.3
<i>Lutraeximia umbra</i> , Pantalla SBAU 337654 L ¹	13.9	10.6	9.6	11.2
<i>Lutraeximia umbra</i> , Pantalla SBAU 337654 R ¹	13.8	10.9	9.2	11.3
<i>Lutrogale cretensis</i> GIA 2/1974 ¹	14.6	12.2	10.6	13.8
<i>Lutrogale perspicillata</i> MNB 5822 ¹	14.2	10.0	10.0	14.1
<i>Lutrogale perspicillata</i> MNB 30675 ¹	14.1	10.5	10.4	14.5
<i>Lutrogale perspicillata</i> MNB 14277 ¹	12.9	9.3	8.8	14.0
<i>Aonyx capensis</i> MNB 5328 ¹	13.4	11.4	12.5	18.4
<i>Aonyx capensis</i> MNB 30729 ¹	13.3	11.3	11.9	17.2
<i>Aonyx capensis</i> MNB 30730 ¹	13.7	11.5	12.4	18.0

Data are from: ¹ Cherin et al. (2016).

extant species took place around 1.8 Mya in the top of the Olduvai subchron through a vicariance process prompted by palaeoclimatic changes. This interpretation is supported by molecular data (Del Cerro et al. 2010; Sato et al. 2012). Thus, the occurrence of the species in Palan-Tyukan represents one of the latest records of this species. Modern badgers often settle in forests and avoid open landscapes. These animals often live in the vicinity of a body of water: a lake, a swamp or a river.

The otter material from Palan-Tyukan originally assigned to *Aonyx* sp. by Sotnikova and Sablin (1993) is here referred to *Lutraeximia* cf. *umbra*. Although remains of this genus had never been reported from Transcaucasian Early Pleistocene sites, we can state with reasonable certainty that P4 ZIN 34247–1 and M1 ZIN 34247–2 belong to *Lutraeximia* cf. *umbra* for the following reasons: 1. From the dimensional point of view, the P4 is relatively broad and with a large talon, M1 is rather small and not enlarged. The taxonomic attribution of both the P4 and M1 is unequivocally supported by its strong morphometric affinities (Table 4) with the upper teeth of the extinct medium-sized otter *Lutraeximia umbra* described so far (Cherin et al. 2016); 2. This species, together with the living *Lutrogale perspicillata* (I. Geoffroy Saint Hilaire, 1826), form a wide monophyletic clade, which most probably also includes several other Eurasian extinct taxa only known through fragmentary remains (Willemsen 1992; Cherin et al. 2016; Cherin 2017); 3. The phylogenetic reconstructions of *Lg. perspicillata* show that the above monophyletic clade already existed in the initial phase of the Early Pleis-

tocene (Koepfli et al. 2008; Moretti et al. 2017). The species *Le. umbra* may have had a much larger geographic distribution in Eurasia (including Transcaucasia) during the MNQ18 standard zone. Predicted body mass for this extinct otter is about 13.6 kg and it was animal which fed on fish, but invertebrates (shellfish and crustaceans) formed an important part of the diet too (Cherin et al. 2016).

CONCLUSION

The fauna of Palan-Tyukan is an important biostratigraphic reference fauna for mammal zonation in Europe. It is considered to be the typical MNQ18 standard zone, often called the early Late Villafranchian: the remains of the raccoon dog *N. megamastoides* and the badger *M. thoralis* are not found in deposits younger than 1.8 Mya. New discoveries can also help to clarify the taxonomic status of many of these extinct forms. In general, the fauna of Palan-Tyukan is about the same age to faunas of Valea Granceanului (Romania), Gerakarou 1, Sesklo (Greece), Olivola, Upper Valdarno (Italy) and Fonelas P-1 (Spain) which existed during the interval 1.95–1.8 Mya (Rook and Martiinez-Navarro 2010; Ferring et al. 2011; Koufos 2014; Madurell-Malapeira et al. 2014; Koufos and Kostopoulos 2016; Vislobokova et al. 2020). Seemingly, the accumulation of the mammalian remains at Palan-Tyukan was formed simultaneously by slowly-flowing water during the Lower Apsheron regression epoch (Ali-Zade et al. 1972; Lebedeva 1972, 1978; van Baak et al. 2013; Svitoch 2015; Lazarev et al. 2019). A Caniformia community of the

Palan-Tyukan presents evidence of the wider variety of environments ranging from wooded areas with bodies of water to scrub and even savanna landscape in a relatively humid subtropical climate (Filippova 1997; Bukhsianidze and Koiava 2018; Sablin 2020; Sablin and Iltsevich 2021a, 2021b).

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