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PLEISTOCENE MAMMAL FAUNA OF THE TRLICA LOCALITY, MONTENEGRO

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Abstract: The paper presents new evidence on the small and large mammal fauna from the Trlica locality, Montenegro, based on our records from the 2010 – 2014 excavations. It is shown that the lower layers of the locality correspond to the Early Pleistocene, and the upper layers are dated as the beginning of the Middle Pleistocene. The results obtained allow us to characterize the environment in which the oldest hominid migrants dwelt in this region of South-Eastern Europe. Within the interval 1.8–1.5 Ma, there was a relatively cool climate in the region. At the beginning of the Middle Pleistocene, the climate became milder; the areas occupied by forests, including broad-leaved forests, increased. The presence of Lagurini throughout the section is evidence of the existence of local areas of steppe in northern Montenegro during the Early Pleistocene and first half of the Middle Pleistocene.

Key words: Montenegro, small and large mammals, Pleistocene, paleogeography, stratigraphy

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Introduction

As the scientist A. P. Derevyanko justly noted, “It seems plausible that, in evolutionary studies, the questions of the origin and evolution of man attract the greatest attention and emotional response” (Derevyanko 2005). They are comparable in importance to questions posed regarding the origin of life. During the past decade, research has strongly supported these statements. To date, several models for the origin and migration pathways of ancient humans have been proposed. According to the data on archeology, anthropology, and molecular genetics, the country where the first anthropoids established themselves and from where the first radiation occurred was Africa. About 2.0–1.8 Ma, ancient humans migrated out of Africa for the first time (Derevyanko 2011). The second great migration wave occurred approximately at 600–400 ka and was connected with the Acheulean culture (Derevyanko 2012). The first “stop” on the migration pathway of ancient man outside Africa was in the northern Arabian Peninsula. Subsequent migrations followed several routes. One passed eastwards around the Iranian Plateau and Turan in the north and then continued to southern Siberia and the Altai. This occurred at about 900–600 ka (Shunkov 2005). Another pathway was along the coasts of southeastern Asia. Westward migration passed through Eastern Europe and the Balkans (Derevyanko 2012a). In each case, the direction and speed of migration were determined by environmental conditions along these pathways. The study of natural conditions, vegetation, and fauna in these regions provides an understanding of the causes and factors which influenced the directions and pathways of these major resettlements.

The The Balkan Peninsula, including Montenegro, are one of the most probable migration pathways of ancient man leading to Central and Western Europe (Kahlke et al. 2011, Spassov 2016, Vislobokova and Agadjanian 2016a, b). This indicates the relative importance and need for study of Pleistocene environments in Montenegro, including vertebrate faunas. One of large localities for Pleistocene fauna in this area is Trlica in northern Montenegro (Text-fig. 1). The study of mammal bone remains from the Trlica locality indicates that the locality contains a representative fauna of two assemblages of different ages. The taphocoenosis of the lower part of the section corresponds to the Early Pleistocene. The taphocoenosis of the upper part is dated to the beginning of the Middle Pleistocene.

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Text-fig. 1. Geographic position of the Trlica locality (a) and its appearance (b).

The Trlica formation taphocoenoses corresponds to the time when early *Homo* penetrated into the eastern Mediterranean. The study of the fauna from this locality characterizes the environments encountered by the most ancient hominid migrators in Europe.

The Balkan Peninsula is a region characterized by positive tectonic shifts during recent geological history. This is distinctly expressed in the modern relief. In Montenegro, deep canyon-like valleys with very steep slopes dominate. Accumulative river terraces are rare and well-developed only in the coastal part of the country. They are mostly composed of shingle strata. In this connection, the Balkans almost lack Late Cenozoic vertebrate localities, which are usually associated with accumulation of lacustrine or alluvial deposits, whereas karstic localities are the most frequent there. They are relatively frequent in Serbia and Greece, and in neighboring Hungary and Romania. They are also known from Montenegro. However, in the study of such localities, the mechanisms of the formation of thanatocoenoses and sedimentary conditions are not always sufficiently analyzed. Simultaneous collecting of bone remains from both small and large vertebrates, primarily mammals, is relatively rare. All the above considerably restricts the possibility for paleogeographical and paleoecological interpretation of any results.

Within the former Yugoslavia, including Montenegro, Late Pleistocene communities of large mammals as well as mammals from the Bronze Epoch and antiquity are well known and have been thoroughly investigated (Basler 1979). Early and Middle Pleistocene assemblages are relatively rare in the fossil record. One such assemblage is from the Trlica locality, with the fauna first came to light at the beginning of the 1980s during road works when a karstic cavity containing abundant mammal bones was uncovered. In 1988, 1990, and 2001 it underwent excavation and the fauna was studied by a team headed by V. Dimitrijević from the Belgrad University (Dimitrijević 1990, Dimitrijević et al. 2003). The researchers proposed that this fauna had accumulated during a relatively short time interval. It was initially assigned to the terminal Early Pleistocene or basal Middle Pleistocene (Dimitrijević 1990, Forsten and Dimitrijević 2002-2003) and, later, to the terminal Early Pleistocene (Codrea and Dimitrijević 1997, Crégut-Bonnoure and Dimitrijević 2006, Argant and Dimitrijević 2007), *Mimomys savini-pusillus* Zone (Bogićević and Nenadić 2008). This fauna was tentatively correlated with the Epivillafranchian (Kahlke et al. 2011). Paleoenvironments were reconstructed based on the faunal composition and pollen-spore analysis from hyena coprolites (Argant and Dimitrijevic 2007). Material from the study of deer in this collection has recently been published (Van der Made and Dimitrijevic 2015).

In 2009, during examination of the loose filler of Trlica cave, a stone flake of Paleolithic appearance, along with bone fragments of Pleistocene animals, were found in a silty sandstone talus (Derevyanko et al. 2010, 2012c). Since 2010, regular examination of this site has been carried out, supported by the Program of Cooperation between the Russian Academy of Sciences and Montenegrin Academy of Sciences and Arts. The leader of studies from the Russian section was the scientist A. P. Derevyanko, research manager of the Institute of Archeology and Ethnography of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk (IAE). Employees of IAE, Lomonosov Moscow State University, and Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN) participated in excavations under the supervision of Prof. Dr. M. V. Shunkov, head of the IAE. The Program included study of the texture and structure of deposits filling the cave, their mineralogical and petrographic composition, plant spores and pollen, the collection and study of fossil remains of large and small mammals (Derevyanko et al. 2011, 2013). The geology of surrounding deposits in adjacent areas was also assessed (Derevyanko et al. 2012c). The Trlica mammals collected during this excavation were described (Vislobokova and Agadjanian 2015, Rossina et al. 2016), and the main material is stored in the PIN.

This paper presents the main results from the study of the mammal fauna from the Trlica locality, based on fossil material collected during excavations between 2010 – 2014. Details of the faunal characteristics of the Trlica section and analysis of taphocoenoses are presented. The main aspects of stratigraphic and paleogeographic distribution of large and small mammals and paleoclimatic conditions are discussed.

Methods

During fieldwork, all sediments taken out of the cave were washed in sieves with 1 × 1 mm mesh. In the laboratory, bones were prepared and cleared with the use of ethanol and acetic acid. Preservation and restoration of particular bone fragments and teeth was carried out using BF-2 glue. The study of small mammals was conducted under a MBS-10 microscope.

Geological setting

The field site is situated in northern Montenegro, on the slope of an intermountain depression of tectonic origin which extends from the northwest to southeast. In the central part, in the vicinity of the town of Pljevlja, it is filled with in excess of 100 m thick deposits of an ancient pond dated to the Miocene. Upward in the section, with angular unconformity and traces of water erosion of Miocene lacustrine deposits, there are 1.5–2 m thick fulvous – brown shingles of alluvial origin. The final beds are overlain by red nonlaminate clays of subaerial origin. They distinctly show at least two horizons of paleosoil. These ancient subaerial beds reach a thickness of 4 m. Upward in the section, they are followed by gray loam, filled in places with poorly sorted detritus, Pleistocene talus. The sides of the valley are composed of Triassic limestones. On the depression axis, is the channel of the Cheotina River, which in the southeastern part of the depression passes along a deep narrow canyon.

The Trlica locality (N 43º 20’ 38.0’’, E 19º 23’ 002’’) is situated 2.5 km southeast of the town of Pljevlja and 1.6 km northeast of the mouth of the Ćehotina River canyon. It is a karstic cavity in Triassic limestone situated at an altitude of 925 m and 151 m above the mouth of the Ćehotina River at the exit of the depression. A dry slope facing southwest has a gradient of 15°–20°. At present, it is covered with a thin pine forest and xerophytic bush. The soil cover on the slope is strongly reduced, and absent in places, exposing blocks of fractured Triassic limestones with abundant caverns, traces of karstic erosion.

The cave was discovered and partly destroyed when the nearby road was under construction. The cave is a closed karstic cavity filled with loose deposits, which were densely compressed by sedimentation and in places strongly cemented. As a result of four-years of excavation, it is possible to conclude that the beds in the cave are rather uniform along the strike, although in places they vary in thickness. A total of 12 main lithostratigraphic units (beds) have been recognized (Text-fig. 2). The section described below was investigated by a team headed by V. A. Ulyanov in 2010 – 2012. The following beds can be recognized going downwards in the section:

Bed 1. Dark brown, with reddish tint, loosely packed, porous intermediate loam moderately enriched by scree – gruss material. The bed is about 40 cm thick.

Bed 2. Scree – gruss horizon, with a moderately loamy basal type filler. Debris includes rock fragments, speleothems structures in the shape of well preserved crusts of transparent crystal calcite. The bed is 35–40 cm thick.

Bed 3. Dark brown, with reddish tint, and reddish brown intermediate to heavy loam. It is rather poor in detrital matter; only rare scree inclusions were observed; small-sized detritus and gruss are almost absent. The lower boundary descends slightly northerly (5–10 degrees), deep into the cave. The bed ranges from 30 to 40 cm thick.

Bed 4. Dark brown heavy loam, moderately enriched by detrital matter. The bed roof is covered by well-pronounced scree – gruss paving, with porous type filler which is evidence of a sedimentation break. The bed is 10–15 cm thick.

Bed 5. Ocherous – yellow heavy loam and yellow intermediate loam, with a brown tint, very similar to “cave terra rossa” (red beds); in the top part, with lenses of yellowish brown intermediate loam. There are several nonconsistent horizons along the strike and dip of weak carbonate cementation. The bed roof is covered by a horizon of fine-clumpy-scree paving, including fragments of spherulitic wandering structures from 3 to 10 cm in diameter. Some spherulites were probably formed directly on the bed surface, evidence that the roof of Bed 5 underwent a long stage of exposure. The middle part of the bed displays traces of activity by large digging animals. The lower part of the bed contains strongly weathered pebbles of sandstone, siltstone, and volcanic rocks. Teeth and bones of large mammals are regularly scattered throughout the strata. As the sediments were washed, bones and teeth of small mammals were also obtained, although they are rather scarce. The bed is 1.0–1.3 m in total thickness.

Bed 6. Ocherous – brown and reddish brown intermediate loam is saturated with poorly sorted and strongly weathered small pebbles. The bed descends relatively abruptly (at about 10 degrees) deep into the cave. It contains some bones and teeth of large mammals. When washed, bones and teeth of small mammals were also recorded. The bed is 10–15 cm thick.

Bed 7. A gruss – sandy horizon, with a thick travertine cementation. Cementation is most strongly pronounced in the lateral parts (near walls) of the section, where deposits contain strongly weathered gruss and abundant new formations, such as regular black manganous spherical concretions 1–2 mm in size. Bones of large mammals are present, while bones and teeth of small mammals are less frequent. The bed is 15–20 cm thick.

Bed 8. A gruss horizon with light brown sandy filler with reddish tint. The bed contains lenticular inclusions of poorly sorted loamy sand saturated with clayey particles. Bones of large and small mammals are present, but are relatively rare. The bed is 25–30 cm thick.

Bed 9. A pebble – gravel – ligneous horizon with sandy filler. Pebbles are mostly strongly weathered, broken, poorly sorted, which is typical for proluvial beds. Bones of large mammals are recorded. The bed is 35–40 cm thick.

Bed 10. Complex strata of interbedding yellowish brown loams and loamy sands, travertine horizons, with interbeds rich in coprolite inclusions, teeth, and bones of large mammals and well traced scree paving. Bones of small mammals are relatively common. Bed 10 overlies Bed 11 with evident angular unconformity. The bed is up to 60 cm thick.

Bed 11. Dark brown (chocolate) intermediate loam, with lenses and interbeds of greenish gray (olive) and bright ocherous loam, replaced through facies transition by yellowish brown and brown well-sorted loamy sands and sands, including lenses of gravel – gruss matter and rare strongly weathered small pebbles. Loamy – sandy interbeds weakly descend (at about 3 degrees) deep into the cave. The bed displays rather strong post-sedimentation deformations of the subsidence type. Bones of large mammals are somewhat less abundant than in Bed 10. Bones and teeth of small vertebrates are rare. The bed is 60 cm thick.

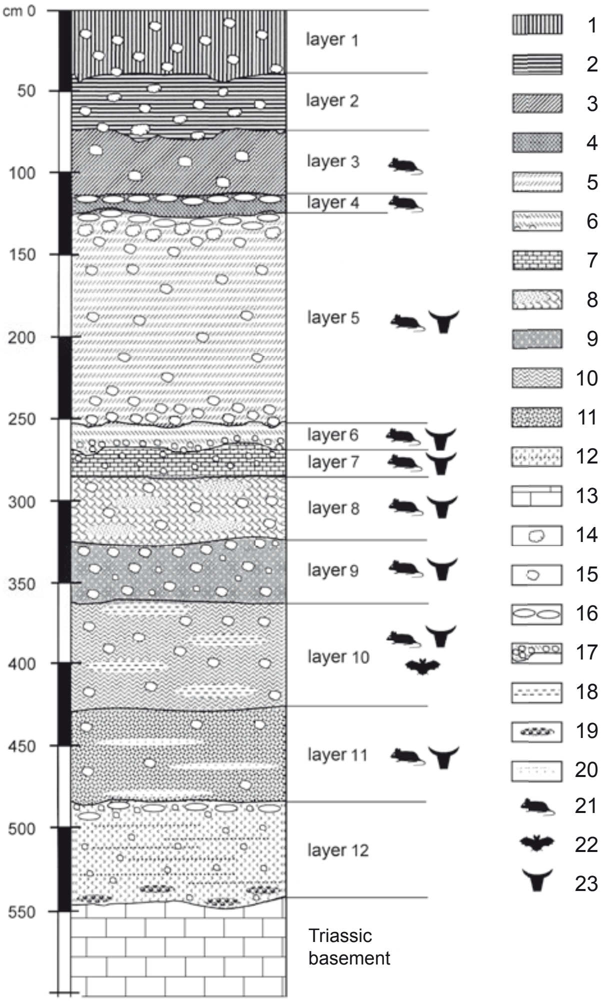
Bed 12. Ocherous well-washed loamy sands and sands filling a narrow fissure between rocky projections of the bedrock walls of the cave. In the upper part of the strata (Bed 12.1), light loamy sands and brown and light yellow fine-grained clayey sands, with thin lenses of gruss – gravel paving cemented by manganese compounds prevail. The texture is crossbedded and lenticular layered. The lower boundary of Bed 12.1 is even, descends southeasterly at an angle of more than 10 degrees. It is tentatively drawn along a manganese horizon of scree – gravel paving, coarsened granulometric composition of sands, the deposit colour undergoes a transition into gray, dark gray, and black – gray. The bed is up to 60 cm thick.

In the lowermost part of the strata (Bed 12.2), gray coarse-grained polymictic sands prevail; at the base of the section, they are brown and dark brown, with abundant gruss and gravel inclusions. In the upper part, at the boundary with Bed 12.1, sand is stained with manganese compounds, becoming black and black-gray. The manganese zone is 10–15 cm thick. Bed 12.2 is crossbedded. In contrast to overlying Bed 11, there is no record of any complete or large fragmentary bones. The exposed part of the bed is 30 cm thick.

As follows from the description, the deposits vary in origin, are characterized by the presence of several, probably long, sedimentation breaks and addition of material from different sources. Most of the filler was brought from outside the cave, while the proportion of deposits of intracave origin is relatively small.

The upper member (Beds 1–4) was mainly formed under subaerial and slightly humid conditions. In origin, it is a red crust of weathering (probably redeposited material from lateritic soil), which passed into the cave through cracks or long narrow vertical karstic canals. This sedimentation model is confirmed by the absence of lamination, sandy lenses, and bones of large vertebrates in the upper member.

Beds 5–6 were formed by diluvial-proluvial processes. Downwards in the section, the proportion of proluvial sedimentation conditions increases considerably. The presence of paving mostly of bones and coprolites of large mammals and also traces of activity by large sized digging animals, are evidence that the cave was periodically inhabited and occupied at least by hyenas and porcupines.



Text-fig. 2. Geological and paleontological characteristics of the Trlica section. Designations: 1. Dark brown, with reddish tint intermediate loam. 2. Dark brown intermediate loam. 3. Dark brown and reddish brown intermediate up to heavy loam. 4. Saturated dark brown heavy loam, moderately enriched with detrital matter. 5. Ocherous – yellow heavy loam. 6. Ocherous – brown and reddish brown intermediate loam. 7. Gruss – sandy horizon. 8. Gruss horizon, with light brown with reddish tint sandy filler, lenticular inclusions of poorly sorted loamy sand, with clayey particles. 9. Gravel – gruss shingle horizon with sandy filler. 10. Yellowish brown interbedding loam and loamy sand. 11. Dark brown (chocolate) intermediate loam, with lenses and interbeds of greenish gray and brightly ocherous loam. 12. Ocherous well-washed loamy sands and sands. 13. Bedrocks (limestones). 14. Pebbles of weathered sandstones. 15. Pebbles. 16. Scree – gruss paving. 17. Small weathered pebble. 18. Lenses of loamy sand. 19. Gruss and gravel cemented by manganese compounds. 20. Sabulous – sandy interbeds. 21. Fossil remains of small mammals. 22. Fossil remains of bats. 23. Fossil remains of large mammals.

Well-pronounced cementation of the material in Bed 7 suggests a significant disturbance of sedimentation conditions and a break in sedimentation between Beds 5–6 and 8–10.

Beds 8–10 were formed mostly as proluvium. Bed 10 is characterized by the presence of paving rich in bone fragments of large herbivores and coprolites of hyenas. In addition, these beds contain bat bones. Perhaps, during the accumulation of Beds 8–10, the cave was inhabited, periodically visited at least by hyenas and porcupines, and bats dwelt under the vault.

Beds 11 and 12 were formed mostly under subaquatic conditions and display deposits of a stream with a variable hydrological mode. Accumulation of deposits corresponds to a stage when the channel of the Ćehotina River was approximately 150 m higher than its present position, probably at a level close to that of the cave. The presence of skeletal remains of large mammals and coprolites of the hyena in Bed 11 is evidence that, during accumulation of these strata, subaquatic conditions in the cave occurred only occasionally. It was periodically inhabited and provided a shelter for hyenas.

Results

Thus, in this section of the Trlica locality, several sets of strata reflecting different sedimentation stages can be recognized; they were connected with different taphonomic processes inside the karstic cavity and paleogeographical stages of the environmental development outside the cave.

Large mammals

The total number of identified specimens is 1,156 bones of large mammals, most of which are teeth, tooth fragments, and less frequently fragments of jaws and postcranial bones. Some bones display the traces of large carnivore teeth. Some small bone fragments passed through the digestive system of carnivores, as indicated by signs of gastric juice activity. This suggests that the major factor resulting in the accumulation of bone specimens in Trlica cave were large carnivores. Thus, it is no surprise that their remains are rather abundant in the taphocoenosis. The proportions of bears, hyenas, large cats, and canids (*Canis* + *Lycaon*) compose 4.41, 2.6, 1.73, and 1.21%, respectively. The occasional presence in the cave of large carnivores is corroborated by the abundance of coprolites in Beds 5–11 inclusive.

Table 1 shows the list of taxa and distribution of large mammal fossil remains, collected between 2010–2014, from beds in the Trlica locality.

The Trlica locality has yielded to date about 30 large mammal taxa from four orders: carnivores (Carnivora), proboscideans (Proboscidea), odd-toed ungulates (Perissodactyla), and even-toed ungulates (Artiodactyla). As Table 1 shows, the general pattern of the oryctocoenosis is determined by various ungulates (first order consumers) from the orders Perissodactyla and Artiodactyla. Second order consumers, predators, are less abundant, but only slightly inferior in diversity to ungulates. The level-by-level description of the faunal composition of large mammals from Trlica is provided below.

In Bed 5, remains of small rhinos of the *Stephanorhinus etruscus*-*S. hundsheimensis* lineage (13 specimens); deer from the red deer group, *Cervus* cf. *acoronatus* (17 specimens), and the bison *Bison* cf. *shoetensacki* (13 specimens) prevail. The bed has also yielded a horse *Equus* cf. *suessenbornensis*, giant deer *Praemegaceros* cf. *verticornis*, and probably a roe deer. Among the carnivores, the bear *Ursus deningeri* has been identified.

Bed 6 contains a similar set of ungulate taxa and also teeth of a hyena similar to the genus *Crocuta*.

Bed 7 contains remains of the rhinoceros *Stephanorhinus* sp. (7 specimens). Among the deer, *Praemegaceros* (6 specimens) and *Cervus* (6 specimens) are common; the roe deer *Capreolus* is also recorded; among Bovidae, the genus *Bison* prevails (12 specimens).

Bed 8 contains remains of a horse and rhinoceros, *Equus* sp., and *Stephanorhinus* sp. (9 specimens). Other remains belong to *Bison* sp., the ovibovine genus *Megalovis* (3 specimens) from the tribe Ovibovini, and Caprinae. Carnivores are represented by the huge hyena *Pachycrocuta brevirostris* (2 specimens).

Bed 9 contains tooth fragments of a rhinoceros and the horse *E.* cf. *stenonis* (1 specimen), and deer. The Bovidae are represented by *Bison* sp. (16 specimens), ?*Leptobos* sp. (5 specimens), and *Megalovis* sp. (2 specimens).

Table 1. Taxonomic composition and abundance of large mammal fossil remains from the Pleistocene beds in the Trlica cave, collected between 2010–2014.

Taxon	Bed and number of remains							Total
	5	6	7	8	9	10	11	
CARNIVORA								
Carnivora indet.	1					3		**4**
Ursus sp.	1		1		1	3		**6**
Ursus cf. *etruscus* Cuvier, 1823						32	7	**39**
Ursus deningeri von Reichenau, 1904	1							**1**
Ursidae indet.						5		**5**
Crocuta sp.			1					**1**
?*Crocuta* sp.		2						**2**
Pachycrocuta brevirostris (Gervais, 1850)				2		19	3	**24**
Hyenidae indet.			1			2		**3**
Panthera onca cf. *gombaszogensis* (Kretzoi, 1938)						4	1	**5**
Homotherium crenatidens Fabrini, 1890						10	1	**11**
Megantereon cultridens (Cuvier, 1824)						1		**1**
Felidae indet.		1				2		**3**

Table 1. continued.

Taxon	Bed and number of remains							Total
	5	**6**	**7**	**8**	**9**	**10**	**11**	
Canis etruscus Major, 1877						8		**8**
Canis sp.					1	1		**2**
Lycaon lycaonoides (Kretzoi, 1938)						2		**2**
Canidae indet.	1						1	**2**
Canidae (?*Vulpes* or *Nyctereutes*)	1					3		**4**
Mustelidae indet.						3	1	**4**
PROBOSCIDEA								
Elephantidae indet.	3					7		**10**
?*Archidiskodon meridionalis* (Nesti, 1825)						8		**8**
?*Palaeoloxodon* sp.						2		**2**
Elephantidae indet. (?*Palaeoloxodon*)						1		**1**
PERISSODACTYLA								
Stephanorhinus sp.		3	7	9				**19**
Stephanorhinus hundsheimensis (Toula, 1902)	13	2						**15**
Stephanorhinus etruscus (Falconer, 1868)						104	11	**115**
Rhinocerotidae indet.	1	8			5	1	1	**16**
Equus sp.	2	2		1	1	4	4	**14**
Equus cf. *suessenbornensis* Wüst, 1900	2	3						**5**
Equus stenonis Cocchi, 1867						28	19	**47**
Equus cf. *stenonis* Cocchi, 1867			6		1			**7**
Equus cf. *major* Depéret, 1893						15	22	**37**
Equus sp. (small)	2							**2**
Equidae indet.	3						4	**7**
ARTIODACTYLA								
Praemegaceros sp.	4	13	6	1	2	87	19	**132**
Praemegaceros cf. *verticornis* (Dawkins, 1872)	2	1						**3**
Cervus sp.	3	3	6			13	2	**27**
Cervus acoronatus Beninde, 1937						60	5	**65**
Cervus cf. *acoronatus* Beninde, 1937	17							**17**
Capreolus sp.			1	1		11	1	**14**
?*Capreolus* sp.	1							**1**
Libralces sp.						2		**2**
Libralces cf. *gallicus* Azzaroli, 1952						1	2	**3**
Alcini indet.						3		**3**
Cervidae indet.				1	2			**3**
Bison sp.	6	17	12	1	16			**52**
Bison cf. *shoetensacki* Freudenberg, 1910	13							**13**
Bison (*Eobison*) sp.						98	39	**143**
Leptobos cf. *etruscus* (Falconer, 1868)						29	13	**42**
?*Leptobos* sp.					5			**5**
Bovinae indet.							6	**6**
Bovidae indet.							6	**6**
Gazellospira sp.						1		**1**
Caprinae indet.			1	1		12		**14**
?Caprinae indet.				2				**2**
Caprinae (?*Capra*)						5	1	**6**
Megalovis sp.				3	2			**5**
Megalovis balcanicus Crégut et Dimitrijević, 2006						65	32	**97**
Ovibovini (?*Megalovis*)		3				4	4	**11**
Soergelia intermedia Crégut et Dimitrijević, 2006						13	4	**17**
Soergelia sp.	6							
?*Soergelia* sp.						5		**5**
Ovibovini indet.	7		1	2	5		3	**18**
Bovidae indet.	1	4	1		1	2	5	**11**
Ruminantia indet.					1			**1**
Total	**91**	**62**	**44**	**24**	**43**	**684**	**211**	**1159**

Bed 10 contains the greatest number of fossils and the most representative oryctocoenosis. Among the Carnivora, the bear *Ursus* cf. *etruscus* (32 specimens) and hyena *Pachycrocuta brevirostris* (19 specimens) are most abundant. In addition, there are three species of large cats (Felidae), the jaguar-like *Panthera onca* cf. *gombaszogensis* (4 specimens) and two saber-toothed taxa *Homotherium crenatidens* (10 specimens) and *Megantereon cultridens* (= *M. megantereon*; Palmqvist et al. 2007) (1 specimen), and also two species of large Canidae, the Etruscan wolf *Canis etruscus* (8 specimens) and the hunting dog *Lycaon lycaonoides* (2 specimens). The bed also contains a few small Canidae (probably a fox or raccoon dog) and Mustelidae.

Only Bed 10 yielded tooth fragments of proboscideans (order Proboscidea), which apparently belong to two species of the family Elephantidae, ?*Archidiskodon meridionalis* (= *Mammuthus meridionalis*; Lister et al. 2005) and ?*Palaeoloxodon* sp.

Among the perissodactyls from Bed 10, the majority fossils belong to the horse *Equus stenonis* (28 specimens) and the rhinoceros *Stephanorhinus etruscus* (104 specimens); a large archaic horse, *Equus* cf. *major* (15 specimens) is also present. Among artiodactyls, the following deer are frequent: *Praemegaceros* sp. (87 specimens), *Cervus* sp. (13 specimens), *Cervus acoronatus* (60 specimens), *Capreolus* sp. (11 specimens), and the alcine genus *Libralces* (3 specimens). A large proportion of remains belong to the Bovidae among which the following taxa have been identified: *Bison* (*Eobison*) sp. (98 specimens), *Leptobos* sp. (29 specimens), members of the tribe Ovibovini–Balkan *Megalovis*, or huge *Megalovis balcanicus* (65 specimens), and *Soergelia intermedia* (13 specimens) and two forms of Caprinae or Rupicaprinae, one small and one medium-sized.

Bed 11 also yielded abundant bone material which is similar in composition and proportions of taxa to the oryctocoenosis of Bed 10. Ungulates prevail, including an abundant number of horses (*Equus stenonis*, 19 specimens and *Equus* cf. *major*, 22 specimens) and less abundant rhinoceroses (*Stephanorhinus etruscus*, 11 specimens), both representatives of the order Perissodactyla. Artiodactyls are represented by the bovids *Bison* (*Eobison*) sp. (39 specimens), *Megalovis balcanicus* (32 specimens) and the megacerine deer *Praemegaceros* sp. (19 specimens). In addition, teeth of large *Leptobos* sp., *Soergelia*, and the moose *Libralces* cf. *gallicus* were also found. Carnivores are represented by the bear *Ursus* cf. *etruscus* (7 specimens), the hyena *Pachycrocuta brevirostris* (3 specimens), large felids *Panthera onca* cf. *gombaszogensis* (1 specimen) and *Homotherium crenatidens* (1 specimen), and small Mustelidae.

Small mammals

Small mammals are represented in the Trlica locality by isolated cheek teeth, incisors, jaw fragments, and postcranial bones. A total of 362 identifiable specimens were examined. This allowed establishment of the taxonomic composition of Trlica oryctocoenoses in each bed (Tab. 2).

Table 2 shows that more than 15 small mammal taxa have been identified from the Trlica locality. They include bats, hares and various rodents. Among the rodents, a significant proportion were voles; cheek teeth of the dormice genus *Glis*, and fragmentary incisors and also porcupine cheek teeth are relatively common. The percentages of various small mammal taxa from the Pleistocene beds of Trlica cave are shown in Table 3.

The small mammal taphocoenosis from each bed of the Trlica section is described below.

Table 2 shows that Beds 3 and 4 include individual incisor fragments of small rodents and several cheek teeth which belong to the rootless vole genera *Microtus* and *Lagurus*.

Bed 5 is characterized by the presence of the ancient *Glis sackdillingensis* (17 specimens), a large hamster of the group *Cricetus cricetus* (6 specimens) and a small hamster of the genus *Cricetulus* (2 specimens). The majority of finds in Bed 5 are voles; the rooted vole *Mimomys* ex gr. *intermedius* (6 specimens), the archaic rootless underground vole *Terricola hintoni* (6 specimens), and more advanced *Terricola arvaloides* (2 specimens) are common. In addition, we identified a tooth from *Microtus nivalinus* (1 specimen), a rootless vole having external cement, similar to *Terricola*; a cementless vole from the tribe Lagurini, steppe lemming *Lagurus* ex gr. *transiens* (1 specimen), and a tooth fragment of a porcupine (1 specimen). Incisors from small rodents are abundant (98 specimens). A total of 175 identifiable small mammal specimens were examined. Rooted and rootless voles compose 9.7% and 19.4%, respectively.

Bed 6 is relatively thin, with correspondingly rare bone remains. It has yielded a tooth from the dormouse *Glis sackdillingensis* (1 specimen) and one upper tooth M^3 of a large rooted vole with external cement and a small superficial enamel mark. These are the distinctive characters of M^3 from *Mimomys pliocaenicus.*

Bed 7 corresponds with a long break in sedimentation and bone remains of small mammals are almost absent. The bed yielded only fragmentary teeth of a porcupine.

Bed 8 yielded two molar fragments from the rooted vole genus *Mimomys*.

The lower beds (9–11) differ essentially in the composition of small mammals. In Bed 9, an ancient rooted vole, *Mimomys pliocaenicus* (2 specimens) was identified. Nine specimens are determined as uncertain rooted voles and two teeth are referred to as the vole tribe Microtini.

Bed 10 of the Trlica locality contains the most abundant assemblage. It yielded remains of bats, although rather infrequent (2 teeth, 1 lower jaw fragment, and 5 postcranial bone fragments), which compose 5.9% of bones in the taphocoenosis of Bed 10. V. V. Rossina (personal communication) identified these bone remains as the horseshoe bat *Rhinolophus* cf. *macrorhinus anomalidens* Topál, 1979 and *Myotis blythii longocaninus* Popov, 2004.

The proportion of rooted voles in Bed 10 is 33.2% (44 specimens). The assemblage is dominated by the *Mimomys pliocaenicus* group (24 specimens). The proportion of rootless voles is 8.2% and members of the tribe Microtini compose 7.5% (10 specimens). Rootless voles are represented by the tribe *Lagurini*, which compose less than 1% of the taphocoenosis. The porcupine *Hystrix refossa* is relatively common (14 specimens). Remains of hares play a significant role in the taphocoenosis of Bed 10 (3 specimens), that is 3.7%. They are determined to the genus, *Pliolagus* (= ?*Hypolagus*), allowing a more precise dating of this horizon.

Table 2. Taxonomic composition and number of fossil remains of small mammals from the Pleistocene beds of Trlica cave, collected between 2010–2014.

Taxon	Bed and number of remains								
	3	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
CHIROPTERA									
Rhinolophus cf. *macrorhinus anomalidens* Topál, 1979								2	
Myotis blythii longocaninus Popov, 2004								1	
Chiroptera indet.								5	
RODENTIA									
Glis sackdillingensis Heller, 1930			17	1					
Cricetus sp.			6						
Cricetulus sp.			2						
Mimomys pliocaenicus F. Major, 1902								5	1
Mimomys sp. (ex gr. *pliocaenicus*)				1			2	19	4
Mimomys ex gr. *intermedius* (Newton, 1881)			7						
Mimomys cf. *pusillus* (Méhely, 1914)			4						
Mimomys reidi Hinton, 1910								2	
Mimomys sp. (ex gr. *reidi*)								11	
Mimomys sp.			6			2	9	7	2
Allophaiomys pliocaenicus Kormos, 1933								1	
Terricola hintoni (Kretzoi, 1941)			6						
Terricola arvaloides (Hinton, 1923)			2						
Terricola sp.			1						
Microtus arvalinus Hinton, 1923		1							
Microtini sp.	1	2	14				2	9	
Microtinae gen.									1
Lagurodon aff. *arankae* (Kretzoi, 1954)			1						
Lagurus ex gr. *transiens* Jánossy, 1962			1						
Lagurus sp.		1	9					1	
Hystrix sp.			1		3			5	
Hystrix refossa Gervais, 1852				1				9	3
Rodentia indet.	2	4	98	5				51	3
LAGOMORPHA									
Pliolagus sp.								1	
Leporini gen.								4	
Total	**3**	**8**	**175**	**8**	**3**	**2**	**13**	**133**	**14**

Discussion

Stratigraphy and taxonomy

The results of our study distinctly show that sedimentological and faunal characteristics of deposits in Trlica cave can be divided into three age groups: the first, most ancient strata, corresponds to Beds 11, 10, and 9; the second to Beds 6 and 5; and the third to Beds 4 and 3.

In the lower part of the section, the fauna is most abundant in Bed 10. Elements of this fauna are present in Beds 11, 9, and 8.

The data on stratigraphic distribution of large mammals in Bed 10 suggest that this fauna existed in the second half of the Early Pleistocene. The large mammal fauna from Bed 10 undoubtedly belongs to the Late Villafranchian (1.8–1.2 Ma) of the Mediterranean Zoogeographical Subarea, the beginning of which is connected with the renewal of faunas during the time around the Olduvai Subchrone (1.95–1.77 Ma) of the Matuyama Paleomagnetic Epoch (Text-fig. 3). In Eastern Europe, this interval corresponds to the Psekups Faunal Assemblage of large mammals established by Gromov (1948) and, in Western Europe, to Mammal Zone MNQ 18 (Guérin 2007). The Trlica assemblage TRL 11–10 differs considerably from the Epivillafranchian faunas of Central and South Europe (see Musil 2001a, b, Kahlke et al. 2011, and others).

According to Vislobokova and Agadjanian (2015, 2016b), the fauna from Bed 10 includes:

(1) species and genera that appeared before the Olduvai Subchrone or related forms widespread in the Late Villafranchian (*Canis etruscus*, *Ursus etruscus*, *Homotherium crenatidens*, *Megantereon cultridens*, ?*Archidiskodon meridionalis*, *Stephanorhinus etruscus*, *Equus stenonis*, *E.* cf. *major*, *Praemegaceros*, *Libralces* cf. *gallicus*, *Capreolus*, *Cervus*, *Megalovis*, *Leptobos*, *Gazellospira*);

(2) species that are not known after 1.5–1.3 Ma (*Equus* cf. *major*, *Libralces gallicus*, *Gazellospira*, *Leptobos etruscus*); the upper boundary of their distribution fall within Zone MNQ 18;

Table 3. Proportions of small mammal fossil remains from the Pleistocene beds of Trlica cave, expressed as %.

Taxon	Bed and proportions								
	3	4	5	6	7	8	9	10	11
	%	%	%	%	%	%	%	%	%
CHIROPTERA									
Rhinolophus cf. *macrorhinus anomalidens*								1.5	
Myotis blythii longocaninus								0.7	
Chiroptera indet.								3.8	
RODENTIA									
Glis sackdillingensis			9.7	12.5					
Cricetus sp.			3.4						
Cricetulus sp.			1.1						
Mimomys pliocaenicus								3.8	7.1
Mimomys sp. (aff. *pliocaenicus*)				12.5			15.4	14.3	28.6
Mimomys ex gr. *intermedius*			4						
Mimomys cf. *pusillus*			2.3						
Mimomys reidi								1.5	
Mimomys sp. (ex gr. *reidi*)								8.3	
Mimomys sp.			3.4			100	69.2	5.3	14.3
Allophaiomys pliocaenicus								0.7	
Terricola hintoni			3.4						
Terricola arvaloides			1.1						
Terricola sp.			0.6						
Microtus arvalinus		12.5							
Microtini sp.	33.3	25.0	8.0				15.4	6.8	
Microtinae gen.									7.1
Lagurodon aff. *arankae*			0.6						
Lagurus ex gr. *transiens*			0.6						
Lagurus sp.		12.5	5.1					0.7	
Hystrix sp.			0.6		100			3.8	
Hystrix refossa				12.5				6.8	21.4
Rodentia indet.	66.7	50.0	56.0	62.5				38.3	21.4
LAGOMORPHA									
Pliolagus sp.								0.7	
Leporini gen.								3	
Total	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**	**100**

(3) species that are not known after 1.2–1.0 Ma (*Canis etruscus*, *Megantereon cultridens*, *Homotherium crenatidens*, *Ursus etruscus*, *Stephanorhinus etruscus*, *Equus stenonis*);

(4) species that appeared in the Late Villafranchian and survived up to the Middle Pleistocene (*Lycaon lycaonoides*, *Panthera onca gombaszogensis*, *Pachycrocuta brevirostris*, *Cervus* cf. *acoronatus*, *Bison* subgenus *Eobison*, *Soergelia*);

(5) species that became extinct 1.0–0.8 Ma (*Archidiskodon meridionalis*, *Bison* subgenus *Eobison*);

(6) species described from Trlica (*Megalovis balcanicus* and *Soergelia intermedia*) (Crégut-Bonnoure and Dimitrijević 2006). According to the authors who established them, *M. balcanicus* is somewhat similar to *Megalovis* from Pirro Nord (~1.3 Ma) in Italy and *S. intermedia* is similar to *S. brigittae* from the Apollonia (1–~1.2 Ma) in Greece and the form from Cave Vallonnet (~1 Ma) in France.

Forms that first appeared at the Villafranchian-Galerian boundary or in the Galerian are absent.

The lower age boundary of the fauna is determined by species that appeared at the beginning of the Late Villafranchian; the upper boundary is marked by species that are not known after the first half of the Late Villafranchian. The presence in this fauna of *Equus* cf. *major*, *Libralces* cf. *gallicus*, *Gazellospira*, and *Leptobos* cf. *etruscus* is evidence that it existed before the Epivillafranchian time and probably before 1.5–1.3 Ma (Vislobokova and Agadjanian 2015, 2016a, b). The presence of the following associations *Lycaon lycaonoides-Canis etruscus* and *Equus stenonis-E. major* and the data on the evolution of the *Homotherium crenatidens-H. latidens*, *Megantereon cultridens-M. whitei*, and *Stephanorhinus etruscus-S. hundsheimensis* lineages also confirm this statement (see Lacombat 2006, Palmqvist et al. 2007).

Within the 1.8–1.2 Ma interval in Northern Eurasia, the first occurrence was recorded of certain large mammals that became widespread at the end of the Early Pleistocene and beginning of the Middle Pleistocene (Vislobokova and Tesakov 2013). The Pliocene-Pleistocene boundary and the middle of the Late Villafranchian are marked by essential transformations of various large mammal groups. In Europe, during the Olduvai Paleomagnetic Subchrone, the following taxa appeared: *Canis falconeri*, *Panthera onca*, *Pachycrocuta brevirostris*, *Leptobos etruscus*, *Pseudodama nestii*, and, slightly later, *Lycaon lycaonoides*, *Praemegaceros*, *Soergelia*, and *Bison* (*Eobison*). In Italy, a late form of *Archidiskodon meridionalis* (*A. m. vestinus*) replaced the typical form (*A. m. meridionalis*) soon after the Olduvai paleomagnetic episode (Gliozzi et al. 1997). Certain significant events occurred in carnivores. *Lycaon lycaonoides* coexisted with the wolf *C. etruscus* in the Apennines up to the middle of the Late Villafranchian and, later, from the Pirro Faunal Unit (Pirro F.U.), i.e., approximately 1.3 Ma, coexisted with *C. mosbachensis* (see Gliozzi et al. 1997, Sotnikova and Rook 2010), which replaced *C. etruscus*. In the middle of the Late Villafranchian, *Homotherium crenatidens* was replaced by *H. latidens.*

The presence in the lower faunal horizon of the deer genera and species widespread in Early Galerian ("Epivillafranchian") faunas of Europe and at the beginning of the Middle Pleistocene (*Capreolus*, *Cervus* cf. *acoronatus*, and *Praemegaceros*) correspond with this dating. The deer listed and also the moose *Libralces gallicus* migrated from the east where they had appeared earlier. *L. gallicus* is known from the Late Pliocene (Middle Villafranchian) of the Liventsovka locality in the Azov Region and the Kuruksay locality in Tajikistan (Vislobokova 2008a). *C. cusanoides* from the Untermaßfeld locality in Germany dated to approximately 1 Ma is regarded as the earliest member of the roe deer genus, *Capreolus*, in Western Europe. The earliest member of this genus, the species *C. constantini*, is known from the Udunga locality (MN 16) in Transbaikalia. The most ancient member of the giant deer lineage *Orchonoceros-Praemegaceros – O. gromovi* – is found in Transbaikalia (Udunga) and Mongolia (Shamar) (see Vislobokova 2012). These deer lineages appeared in Central Asia much earlier than in Europe, in the Early Villafranchian against a background of gradual cooling, increase in aridity, and differentiation of landscape-climatic conditions (Vislobokova 2008a, b). The most ancient *Praemegaceros* and *C.* cf. *acoronatus* are known from the Middle Villafranchian of Transbaikalia. The deer *C. abessalomi*, closely related to *C. acoronatus*, inhabited the Caucasus at the beginning of the Late Villafranchian (Dmanisi locality, ~1.77 Ma, Georgia) (Gabunia et al. 2000).

Previous researchers proposed that the accumulation of deposits in the Trlica locality occurred over a rather short time interval, thus all the beds can be referred to one stage. However, opinions about their age gradually changed (Crégut-Bonnoure and Dimitrijević 2006). The rhinoceros from Trlica was originally determined as *S. etruscus* (Dimitrijević 1990). Subsequently, it was redetermined as *S.* cf. *hundsheimensis* (Codrea and Dimitrijević 1997). However, it was not indicated which beds yielded 9 isolated teeth in various stages of preservation described by them as from a rhinoceros of the *S. etruscus-S. hundsheimensis* lineage. The species *S. hundsheimensis* is considered to be characteristic of the MNQ 20 – MNQ 22 zones; thus, the locality was dated to the end of the Early Pleistocene (Codrea and Dimitrijević 1997, Forsten and Dimitrijević 2002-2003). The zebra-like horse species *E. stenonis* and *E.* cf. *major* originally determined by Forsten and Dimitrijević (2002-2003) suggest an earlier (Villafranchian) age for the locality. *E.* cf. *stenonis* and probably *E. major* coexisted in the fauna of the Hungarian Kisláng locality (Forsten and Dimitrijević 2002-2003). We assigned the horses from Bed 10 of Trlica to the same species, and the rhinoceros from this bed, to the species *S. etruscus.* The age range of *S. etruscus* is Middle Villafranchian – beginning of the Late Villafranchian. According to detailed biochronology of Italy, *S.* cf. *hundsheimensis* replaced *S. etruscus* soon after the Olduvai paleomagnetic episode. The last representatives of the species *S. etruscus* are recorded in Italy at the Tasso Unite (Tasso F.U., ~1.7–1.6 Ma) (Gliozzi et al. 1997). From the beginning of the Farneta Unite (Farneta F.U., 1.5 Ma), the Apennines were inhabited by small rhinoceroses similar to *S. hundsheimensis* (Gliozzi et al. 1997).

The bison from Trlica was originally determined as *Bison* cf. *schoetensacki* (Forsten and Dimitrijević 2002-2003, Dimitrijević et al. 2003). The presence of this species suggests a significantly later age of the fauna. *B. schoetensacki* appeared at the end of the Early Pleistocene and was widespread in the first half of the Middle Pleistocene. Later, the bison from Trlica was redetermined as *Bison* (*Eobison*) sp. (Argant and Dimitrijević 2007). The subgenus *Eobison* was characteristic of Late Villafranchian faunas (Pirro Nord, Venta Micena, etc.). At the Villafranchian-Galerian boundary, *Bison* (*Eobison*) was replaced by *Bison* (*Bison*). According to our data, the lower faunal horizon contains *Bison* (*Eobison*) and the upper contains *B.* (*Bison*) *schoetensacki* (Vislobokova and Agadjanian 2015).

The large mammal fauna from Bed 11 is similar in taxonomic composition and, hence, in age to the fauna from Bed 10, although it is somewhat less representative. The presence in Bed 11 of *E.* cf. *stenonis* and ?*Leptobos* sp. confirms its Villafranchian age.

Bed 11 yielded only 14 small mammal fragments, out of which five specimens are identified as voles of the group *Mimomys pliocaenicus* one is assigned to Microtini. The presence in the taphocoenosis of a porcupine and the vole genus *Mimomys* makes the assemblage similar to that of Bed 10, suggesting sedimentological and age similarity in Beds 11 and 10.

For estimation of the age of the lower member of the Trlica deposits, the small mammal fauna of Bed 10 is very informative. As shown above, it is characterized by the prevalence of the vole genus *Mimomys* (32.6%), some of which belong to the group *Mimomys pliocaenicus* (17.8%). Rootless voles of the tribe Microtini and Lagurini are also recorded. This allows reliable dating. The vole group *Mimomys pliocaenicus* is characteristic of the first half of the Early Pleistocene, MNQ 18 Zone (Guérin 2007), i.e., the faunal phase of the Villányian of Central Europe (Fejfar and Heinrich 1983). Similar data are known for the Apennines Peninsula (Gliozzi et al. 1997). In later faunas of the Early Biharian, these species are almost absent (Fejfar and Horáček 1983). Consequently, the presumed upper age boundary of the taphocoenosis from Bed 10 is approximately 1.5 Ma (Text-fig. 3).

On the other hand, the presence of Microtini and Lagurini restricts the lower age limit of this community to the Olduvai episode (1.95–1.77 Ma) of the Matuyama Paleomagnetic Epoch, since rootless voles did not occur in Central Europe before this boundary (Agadjanian 2009). Thus, the time span of the small mammal fauna from the lower member of the Trlica locality falls within the interval 1.8–1.5 Ma.

In the lower part of the section, the relatively high abundance of the porcupine *Hystrix refossa* is significant. In Bed 11, the proportion of porcupine is 21% (3 specimens); in Bed 10, it is 6.7% (9 specimens). This large porcupine, with a high crown on the cheek teeth was originally described from the Les Etouaires locality, Perrier, France, which is dated to the Late Pliocene (Villányian, MN 16). To date, *Hystrix refossa* has been recorded in a number of Pliocene and Early Pleistocene localities of Europe (Weers 1994, 2005, Weers and Rook 2003). It is characteristic of warm periods in the Villányian and Biharian (Kowalski 2001). It occurs in Villafranchian localities of former Yugoslavia, including, Montenegro (Malez 1979, Bogićević and Nenadić 2008).

Almost 5% of the taphocoenosis of Bed 10 are bone remains of hares, which belong to the genus *Pliolagus*. It existed in the Pliocene – Early Pleistocene. Hares of this group are characteristic of the Early Pleistocene (Villányian) of Europe (Gureev 1964). In Hungary, for example, they are typical in the Csarnóta 2, Osztramos 7, and Beremend 5 localities. They also occur in Late Villányian faunas: Villány 3, Villány 5, Nagyharsányhegy 2 and 4, etc. (Jánossy 1986). In Poland, these hares are known from the Kielce locality (Kowalski 1958b); in Germany, the latest occurrences are connected with the Untermaßfeld fauna (Maul 2007). They are present in the majority of Pliocene – Early Pleistocene localities of the Don and Volga Basin (Sukhov 1970, 1975, Agadzhanyan 2009).

Only Bed 10 of the lower member of Trlica contains chiropteran remains, which V. V. Rossina identified as two species, *Myotis blythii longocaninus* and *Rhinolophus* cf. *macrorhinus anomalidens*. The first was originally described from the Middle Pliocene of the Muselievo locality in Bulgaria (Popov 2004), which is correlated with MN 15b. The second was from the Early Pleistocene of Osztramos 8 locality in Hungary (Topál 1963, 1979). According D. Jánossy, Osztramos 8 was assigned to the Betfia faunal phase (Jánossy 1986), and hence corresponds to a time interval approximately 1.2–1 Ma.

In a previously published paper on small mammals of Trlica (Bogićević and Nenadić 2008), the following composition of rodents was reported in this locality: *Dinaromys dalmatinus*, *Allophaiomys* cf. *pliocaenicus*, *Mimomys* ex gr. *reidi-pusillus*, *Glis sackdilligensis*, and *Hystrix* cf. *refossa*. Remains of *Dinaromys* occur in both upper (Beds Ia and Ib) and lower parts of the section (Bed IV) (Bogićević and Nenadić, 2008). This approximately corresponds to Beds 5–6 and 10 of the Trlica section. The dormouse *Glis sackdilligensis* was only recorded in Bed Ib, which in general corresponds to our results. Unfortunately, our collections lack reliable remains of *Dinaromys dalmatinus*, although collections from Beds 10 and 9 includes three molars M_3, which possibly belong to *Dinaromys*, judging from their morphology. Thus, this vole could be regarded as an integral component of the Trlica taphocoenosis. At present, the only member of the genus *D. bogdanovi* has a restricted occurrence within the Dinaric Plateau (Gromov and Polyakov 1977, Shenbrot and Krasnov 2005), inhabiting stony detritus and outcrops of rocks on the coasts of the Adriactic Sea up to the upper forest boundary at 1,700–2,200 m above sea level (Görner and Hackethal 1988). Rare fossil remains of *Dinaromys* are known in Early Pleistocene faunas beyond the modern range in the Balkans and Carpathian mountains (Kretzoi 1955, Kowalski 2001). The material from the Trlica locality provides additional data on the early origin of the vole genus *Dinaromys* and its formation in the Dinaric Mountains.

The small mammal fauna from Bed 9 is rather poor, but informative. The proportion of rooted voles is 85% (11 specimens); they include two M^3 molars belonging to the group *Mimomys* ex gr. *pliocaenicus.* Microtini, rootless voles, are only represented by two specimens. Thus, this oryctocoenosis can be dated to the beginning of the Biharian.

Beds 8 and 7 contain a few bone remains of mammals, especially small mammals. The composition of taphocoenoses from these beds resembles that of Beds 9, 10, and 11. They are probably similar in age to the fauna from the underlying beds.

Significant differences however are displayed by Beds 6 and 5. The large mammal fauna from these beds is inferior in abundance and taxonomic diversity to the fauna from Beds 10 and 11. It contains species that were widespread at the end of Early Pleistocene – beginning of the Middle Pleistocene. The Trlica section contains Carnivora indet., *Ursus* sp., *Ursus deningeri*, ?*Crocuta* sp., *Stephanorhinus* cf. *hundsheimensis*, *Equus* cf. *suessenbornensis*, *Praemegaceros* cf. *verticornis*, *Cervus* cf. *acoronatus*, ?*Capreolus* sp., *Bison* cf. *schoetensacki*, and Ovibovini. The genera *Ursus*, *Stephanorhinus*, *Equus*, *Praemegaceros*, and *Bison* are represented here by evolutionarily more advanced species than in the lower faunal horizon. Many of them appeared at the end of the Early Pleistocene and were widespread after the Jaramillo Paleomagnetic Subchrone (see Gliozzi et al. 1997). The first occurrence of some species occurring in the fauna from Bed 5 is recorded in Italy at the beginning of the Galerian, at the level of the Colle Curti locality (~1.1 Ma): *U. deningeri*, *Crocuta*, *Stephanorhinus hundsheimensis*, *Praemegaceros verticornis*, and *Bison* (*Bison*). *S.* cf. *hundsheimensis* from Bed 5 belongs to the group of small rhinoceroses characteristic in Europe during the Early Galerian–beginning of the Middle Galerian.

These beds are also distinguished by the presence of the hyena genus *Crocuta*, which is recorded in the underlying Bed 7.

The data on stratigraphic distribution of large mammals show that the fauna from Beds 6 and 5 (TRL 6–5) are not older than 1 Ma and probably existed after the Jaramillo episode, i.e., later than the 1.07–0.99 Ma boundary (Text-fig. 3). This fauna is similar in composition to faunas of the terminal Early Pleistocene – beginning of the Middle Pleistocene, Epivillafranchian – Middle Galerian of Western Europe. Judging from the presence of *Equus* cf. *suessenbornensis* and the evolutionary level of *S.* cf. *hundsheimensis* and *P.* cf. *verticornis*, it most likely belonged to the beginning of the Middle Pleistocene, 0.78–0.4 Ma interval, and existed after the Brunhes/Matuyama paleomagnetic inversion.

Faunas from the beginning of the Middle Pleistocene were preceded by significant transformations at the 1.2 and

0.8 Ma boundaries. Changes in faunal composition correlate with cooling at the Early-Middle Pleistocene boundary, an increase in amplitude and changes in the frequency of climatic fluctuations soon after the Jaramillo Subchrone (1.07–0.99 Ma) and changes in landscapes. At the beginning of the Middle Pleistocene, *Palaeoloxodon antiquus* became widespread and *A. meridionalis* was replaced by *Mammuthus trogontherii.* The Tiraspol assemblage of Eastern Europe and contemporaneous faunas of Western Europe are characterized by the bear *U. deningeri*, rhinoceros *S.* cf. *hundsheimensis*, coexistence of caballoid horses of the Mosbach type (*Equus* cf. *mosbachensis*) and stenonian horses *E.* aff. *suessenbornensis*, steppe mammoth, various deer *C. acoronatus*, *Praemegaceros verticornis*, broadhead elk *Alces latifrons,* and the short-horned *Bison* (*Bison*) *schoetensacki* (Nikiforova 1971, Kahlke et al. 2011).

The age of the small mammal community of Beds 6 and 5 can be determined by the presence of the dormouse *Glis sackdillingensis*, voles *Terricola gregaloides*, *Mimomys* ex gr. *intermedius*, and *Lagurus* ex gr. *transiens*. The four taxa are characteristic for the first half of the Middle Pleistocene, Cromerian on the European Biostratigraphic Scale and Tiraspolian on the scale accepted in Russia.

As mentioned above, in Bed 6, the dormouse *Glis sackdillingensis* and a vole similar to *Mimomys pliocaenicus* co-occur. A similar combination of small mammal taxa apparently corresponds to the early phases of the Middle Pleistocene (early Tiraspol faunas). This suggests that Bed 6 is similar in age to Bed 5 and both belong to the same time stage of the biostratigraphic scale.

The prevalence in the taphocoenosis of Bed 5 of dormouse of the genus *Glis* and pine vole of the genus *Terricola* is evidence of the distribution of broad-leaved forests under relatively warm climatic conditions. At present, the range of the dormouse genus *Glis* covers the entire area of Central Europe, the Balkans, forest regions in the central Russian Plain up to the right bank of the Volga River and the forest belt of the Caucasus (Brink 1968). This species inhabits beech and oak forests, orchards, and vineyards (Görner and Hackethal 1988); this implies that similar biotopes were widespread when Bed 5 had accumulated. The presence of the steppe lemming is evidence of local distribution of open dry biotopes. A hamster resembling *Cricetus cricetus* suggests the existence of meadow biotopes. The presence of porcupine suggests the distribution of fructiferous plants at least within a limited territory and the absence of low temperatures in the winter season.

In general, the small mammal material allows a more accurate estimate of the age of the Trlica locality deposits. In Central Europe, *Mimomys pliocaenicus* was initially described from Upper Val d'Arno in Italy at the end of the 19th century (Major 1902, Heller 1968). The *M. pliocaenicus* Zone corresponds to the Villafranchian from the Triversa (MNQ 17) to Olivola stages (MNQ 18) (see Gliozzi et al. 1997). It was replaced by the *Mimomys pusillus-M. intermedius* Zone. In the Apennine Peninsula, the species *Mimomys pusillus* is characteristic of the Farneta stage (Pietrafitta locality, MNQ 19), which corresponds to the Villányian-Biharian boundary. This change in the community composition occurred after the Olduvai paleomagnetic episode. In Bed 10 of the Trlica locality, *Mimomys pliocaenicus* co-occurs with the rootless vole *Allophaiomys pliocaenicus*. In Italy, the vole *Allophaiomys pliocaenicus* is known from localities of Early Biharian (= Late Villafranchian): Monte la Mesa, Pietrafitta (Farneta F.U.), Cava Pirro, and Soave Cava Sud (Masini and Sala 2007). The faunas listed form an age sequence from earlier Monte la Mesa to younger Soave Cava Sud.

In Spain, the earliest *Allophaiomys* was recorded in the Venta Micena locality, which was dated by the combined method US-ESR, using fossil teeth, as 1.4 Ma (Duval et al. 2011). Later populations of *Allophaiomys* fall into the 1.4–1.2 Ma interval (Duval et al. 2012, Toro-Moyano et al. 2013). Some researchers believe that the upper boundary of the *Allophaiomys pliocaenicus* Zone corresponds to approximately 1.4 Ma and the lower boundary is probably at the level of 1.6 Ma (Gibert et al. 2007, Agustí et al. 2010). In southeastern Spain, *Allophaiomys* is known from a number of localities: Gruta 1, Fuente Nueva 3, and Barranco León 5 (Piñero et al. 2015). These communities also include the mice *Castillomys rivas* and *Apodemus mystacinus* and the dormouse *Eliomys quercinus*. *Allophaiomys* has also been recorded in northern Spain in the well-known small mountain range Sierra de Atapuerca. In karstic cavities in this area, several localities with the co-occurrence of ancient humans, Paleolithic tools, and mammal fauna have been discovered (Rosas et al. 2006, Carbonell et al. 2008). This allowed the establishment of seven faunal horizons which display faunal development during the last 1.5 My (Cuenca-Bescos et al. 2010). The lower horizon (TE9) at the level of "A" is characterized by *Allophaiomys nutensis* similar in evolutionary level to *Allophaiomys pliocaenius*; the later level "A+" contains *Allophaiomys lavocati* (Rosas et al. 2006). The beds of horizon TE9, where tools and a lower jaw fragment from an ancient human have been found, are dated as 1.22 ± 0.16 Ma (Carbonell et al. 2008). Thus, humans appeared in the Iberian Peninsula before the Jaramillo paleomagnetic episode, but later than the Olduvai episode (Gibert et al. 2007) and coincided in time with radiation and migration of the vole *Allophaiomys*. *Allophaiomys* appeared in this area even earlier, within the Early Biharian, but after the Olduvai episode (Gibert et al. 2007). Thus, the data on the appearance and distribution of *Allophaiomys* in Western Europe suggest that Beds 11–10 of the Trlica locality correspond approximately to the 1.5–1.2 Ma time interval.

Late Villányian and Early Biharian localities are also known in Central and Eastern Europe. Betfia (= Püspökfürdö) in the territory of modern Romania was the locality from where the genus *Allophaiomys* was originally described (Kormos 1932). Later, it was found in other localities, including Betfia IX in Romania, Osztramos 2, Osztramos 8, Osztramos 14, and Nagyharsányhegy 2 in Hungary (Jánossy 1986, Terzea 1988). In the listed Hungarian faunas, *Allophaiomys* is accompanied by *Mimomys pusillus*, *Lagurus arankae*, *Hystrix*, etc. Unfortunately, all of these taphocoenoses are of karstic origin, lack dating, and can only indirectly be compared with the chronostratigraphic scale of Europe.

On the Russian Plain, the vole *Mimomys pliocaenicus*, along with *M. reidi*, are present in the Psekups Assemblage (Aleksandrova 1977). In the stratotypic section on the Psekups River, they occur in beds with reverse magnetization, i.e., within the Matuyama Paleomagnetic Epoch (Tesakov

2004). *Mimomys* cf. *pliocaenicus*, along with *M. reidi* and the archaic *Allophaiomys*, were described from the Tizdar locality on the Sea of Azov coast (Tesakov 2004) and Mikhailovka-1 in the Kursk Region (Agadzhanyan 2009) (Text-fig. 3). In the Tizdar locality, two bone horizons have been recognized, the lower (Tizdar 1) and upper (Tizdar 2) horizons, between which there are deposits containing abundant artifacts – the Kermek locality (Shchelinsky et al. 2016). The Paleolithic tools from this locality are intermediate in their characteristics between the Olduvai and Acheulean cultures (Shchelinsky et al. 2016). The underlying Tizdar 1 bone horizon includes remains of Soricidae, Leporidae, *Spermophilus*, *Spalax*, jerboas, *Allophaiomys deucalion*, *Pitymimomys pitymyoides*, *Mimomys* cf. *pliocaenicus*, *M. reidi*, *Borsodia newtoni*, Lagurini, *Ellobius kujalnikensis*, and *Clethrionomys* cf. *kretzoii*. In the Kermek taphocoenosis, *Allophaiomys deucalion*, Lagurini, and *Spermophilus* were recorded. A similar small mammal composition is observed in the upper horizon, Tizdar 2 (Shchelinsky et al. 2016). At the same time, *Allophaiomys deucalion* from Tizdar 2 shows the very primitive characters of rooted voles from Central and Eastern Europe (Tesakov 2004). Available data provide indirect evidence that this fauna corresponds to the 2.1–1.8 Ma time interval (Shchelinsky et al. 2016).

In the type locality of the Taman Faunal Assemblage, the Sinyaya Balka locality, the following taxa have been recorded: the elephant *Archidiskodon meridionalis tamanensis*, large horse *Equus* cf. *major*, giant steppe rhinoceros *Elasmotherium caucasicum*, bison *Bison* sp., deer Cervidae gen., antelope Tragelaphini gen., and voles *Mimomys savini* and *Lagurodon arankae* (Shchelinsky et al. 2008, Titov et al. 2012).

A number of small mammal localities containing *Mimomys pliocaenicus*, *Mimomys pusillus*, *Allophaiomys pliocaenius*, *Prolagurus praepannonicus*, and *P. pannonicus* are known in the central part of the Russian Plain: Mikhailovka-1, Strelitsa-1, Uspenka, Log Denisov, Korotoyak-3a, Korotoyak-3b, Korotoyak-3c, Log Krasnyi, etc. (Agadzhanyan 2003, 2009). Most of them are associated with reverse polarity deposits (Iosifova et al. 2007, Iosifova and Agadjanian 2010) and, hence, correspond to the Matuyama Paleomagnetic Epoch. An exception is provided by Korotoyak-3c which has normal polarity and is comparable with the Jaramillo episode (Iosifova et al. 2009).

Faunas similar in taxonomic composition have also been described in the lower reaches of the Dnieper River, Western Kairy and Ushkalka (both Ukraine), and Margaritovo 1 in the Azov Region. In the Western Kairy and Ushkalka sections, the Matuyama-Brunhes paleomagnetic boundary is recorded above two paleosols and loess, which are underlain by bone alluvium (Markova 2014). The fauna contains *Mimomys savini*, *M. pusillus*, *Eolagurus argyropuloi*, *Borsodia petenyii*, *Lagurodon arankae*, *Prolagurus pannonicus*, *Clethrionomys* sp., and *Allophaiomys pliocaenicus* (Markova 2014).

In lower reaches of the Dniester River, this interval corresponds to the fauna from the village of Roksolany. The locality is confined to alluvium of terrace VII of the Dniester River and contains *Mimomys savini*, *M. pusillus*, *Eolagurus argyropuloi*, *Lagurodon arankae*, *Prolagurus pannonicus*, *Clethrionomys sokolovi*, and *Allophaiomys pliocaenicus* (Markova 2014). The bone horizon underlies the strata of loess, also paleosols, in total number nine, and they include the Matuyama-Brunhes inversion; just above the faunal horizon, there is the Jaramillo episode (Markova 2005). In the bone horizon, an evolutionarily advanced member of the genus *Archidiskodon*, the southern elephant *A. meridionalis tamanensis* is recorded (Markova and Vislobokova 2016).

On the Sea of Azov coast, near the village of Margaritovo, a locality just below the beds containing evidence of the Jaramillo paleomagnetic episode has been described. The taphocoenosis includes *Mimomys savini*, evolutionarily advanced *Allophaiomys* ex gr. *pliocaenicus*, *Lagurodon arankae*, *Clethrionomys hintonianus* (Tesakov et al. 2007), and *Archidiskodon meridionalis tamanensis* (Markova and Vislobokova 2016).

Thus, it is evident that, throughout the area from the Russian Plain to the Iberian Peninsula, mammal faunas including *Mimomys pliocaenicus*, *M. pusillus*, *M. reidi*, *Allophaiomys pliocaenicus*, archaic steppe lemmings of the group *Lagurodon arankae*, and *Prolagurus pannonicus*, along with late *Archidiskodon meridionalis* existed from the Olduvai to Jaramillo episodes. It corresponds to the 1.95–0.9 Ma time interval. Judging from the taxonomic composition of small and large mammals, the fauna from the Bed 10 of the Trlica locality corresponds to the first half of this time period.

Beds 6 and 5 of the Trlica locality show a different taphocoenosis composition. As mentioned above, they are characterized by *Glis sackdillingensis*, *Mimomys* ex gr. *intermedius*, *Terricola hintoni*, and *T. arvaloides*, the vole genus *Microtus*, and the steppe lemming *Lagurus* ex gr. *transiens.* The dormouse *Glis sackdillingensis* was originally described from the Sackdillinger Cave locality in Upper Pfalz (Heller 1930, 1933). The taphocoenosis contains the insectivores *Talpa gracilis*, *Beremendia fissidens*, *Neomys* sp., *Sorex runtonensis*, *S. praealpinus*, *Erinaceus*, chiroptera *Myotis bechsteinii*, ?*M. natteri*, rodents *Allocricetus bursae*, *Apodemus sylvaticus*, *Glis sackdillingensis*, *Lemmus*, forest voles of the genus "*Evotomys*" (= *Clethrionomys*), rootless voles "*Pitymys*" (= *Terricola*) *gregaloides*, *Microtus nivaloides*, *M. ratticepoides*, etc. (Heller 1930). The fauna from this locality was compared with the fauna from Forest-Bed in England, i.e., referred to the Cromerian sensu stricto (Heller 1933). Later, the dormouse *Glis sackdillingensis* was found in a number of localities from the Early and first half of the Middle Pleistocene of Europe, for example, in Schernfeld and Hohensülzen in Germany (Dehm 1962, Storch et al. 1973), in Podumci of North Dalmatia (Kowalski 1958a), in karstic faunas of Hungary, where this species was relatively common throughout the second half of the Biharian: Tarkő, Vértesszőlős, and Toringian: Uppony 1 phases (Jánossy 1962, 1963, 1969). In early faunas, this species co-occurs with the rooted voles *Mimomys pliocaenicus*, *M. pusillus*, *Kislangia rex*, etc.; in late faunas, with the rootless vole genera *Terricola*, *Microtus*, and *Lagurus* (Jánossy 1986). In Poland, *Glis sackdillingensis* is present in the Kamyk locality, along with *Allophaiomys* (Kowalski 1963) and in the later Kozi Grzbiet locality (Daoud 1993, Stadnik 2010), along with *Mimomys* cf. *savini*, *Clethrionomys* cf. *glareolus*, *Pliomys* cf. *episcopalis*, *Pitymys gregaloides*, *P. arvaloides*, *Microtus* ex gr. *oeconomus*, *M.* ex gr. *arvalis*, *Lemmus*, and *Dicrosotonyx* (Nadachowski 1985). Judging from the size, *Glis sackdillingensis* from the Kozi Grzbiet fauna is evolutionarily more advanced than the dormouse from the Kamyk Fauna (Daoud 1993). In Italy, this dormouse is also characteristic of faunas of the Biharian, of the *M. pusillus-M. savini* Zone (Gliozzi et al. 1997, Kotsakis 2003, Masini and Sala 2007). An important feature for dating the fauna from Trlica Beds 6 and 5 is the presence of the voles *Mimomys* ex gr. *intermedius*, *Terricola*, and *Microtus.* The vole *Mimomys intermedius* (= *M. savini*) is a rooted vole that is among the latest to appear in the fossil record. It was described for the first time from the stratotype of the Cromerian, i.e., the beds of West Runton Freshwater Bed in Norfolk (Newton 1881, Major 1902), which are the main component of the Cromer Forest-Bed Formation. The fauna from these beds includes the beaver *Trogontherium*, common field mouse *Apodemus sylvaticus*, bank vole *Clethrionomys glareolus*, rooted vole *Mimomys savini* (= *intermedius*), and the rootless voles "*Pitymys*" *arvaloides*, *P. gregaloides*, *Microtus ratticepoides* (= *oeconomus*), *M. arvalinus*, and *M. nivaloides* (Sutcliffe and Kowalski 1976, Stuart 1981). The list of large mammals includes species characteristic for the first half of the Middle Pleistocene, such as the bear *Ursus deningeri*, southern mammoth *Mammuthus* cf. *meridionalis*, *Dicerorhinus etruscus*, giant deer *Megaceros verticornis*, broadhead elk *Alces latifrons*, bison *Bison schoetensacki*, etc. (Stuart 1975, 1992). Subsequently, the mammoth and rhinoceros were redetermined as *Mammuthus trogontherii* and *Stephanorhinus hundheimensis* (Preece and Parfitt 2000). The Forest-Bed Formation shows normal magnetization and is assigned to the lower part of the Brunhes Epoch (Gibbard et al. 2009). The listed mammal composition of the Cromerian stratotype is very similar to that of Beds 5 and 6 in Trlica. It is noteworthy that the beds of the Cromer Forest-Bed Formation include Paleolithic flint tools (Parfitt et al. 2005, Preece and Parfitt 2008), i.e., by that time, humans had already expanded throughout Europe.

Similar communities are also known in the Voigtstedt and Süssenborn localities in Germany and a number of other localities in continental Europe (Kretzoi 1965, Fejfar 1969, Chaline 1972, 1977).

The taxa found in Bed 5, such as *Glis sackdillingensis*, *Terricola hintoni*, *Mimomys* ex gr. *intermedius*, and *Lagurus* ex gr. *transiens*, are characteristic for the first half of the Middle Pleistocene, Cromerian on the biostratigraphic scale of Western Europe (Jánossy 1969, Sutcliffe and Kowalski 1976, Chaline 1977, Stuart 1977, Preece and Parfitt 2000) or Tiraspol on the scale accepted in Russia (Aleksandrova 1971, Agadjanian 1977, 1992, 2009, Markova 2007). At the same time, these communities lack *Allophaiomys* and already show a higher diversity in the *Microtus* members. During the Cromerian (= Tiraspol), *M. pusillus* gradually disappeared from the fossil record and *M. intermedius* increased in number. The co-occurrence in Bed 6 of *Glis sackdillingensis* and the vole *Mimomys pusillus* also corresponds to Early Tiraspol faunas characteristic of the early phases of the Middle Pleistocene. During the history of small mammal fauna establishment, coexistence of *M. pliocaenicus* and *Allophaiomys* corresponds to the Late Villányian phase and the combination *Mimomys-Microtus* is typical for the Early Biharian (Fejfar and Heinrich 1983). Thus, Beds 5–6 of the Trlica locality are dated to the first half of the Middle Pleistocene, Cromerian = Tiraspol (Text-fig. 3).

Beds 1–4 probably belong to the second half of the Middle Pleistocene or beginning of the Late Pleistocene, because they directly overlie Beds 5–6. The presence in Beds 3 and 4 of rare remains of evolutionarily advanced rootless voles (Tab. 2) supports this age estimate.

In general, deposits of karstic filler in Trlica can be clearly divided into three strata differing in age based on the composition of the small mammal fauna. Beds 1–4 belong to the second half of the Middle Pleistocene and, probably, to the beginning of the Late Pleistocene. Beds 5–6 are dated to the first half of the Middle Pleistocene (Cromerian = Tiraspol). They correspond to the Biharian faunal phase or MNQ 20 Zone (Text-fig. 3). Beds 8–11 correspond to the second half of the Early Pleistocene (Late Villafranchian), i.e., the final stage of the Villányian, or MNQ 18 Zone. Thus, the taphocoenoses of Beds 3–4, 5–6, and 9–11 are separated by significant time intervals.

The composition of mammal faunas, like the palynological spectra obtained by N. S. Bolikhovskaya (Derevyanko et al. 2012b), shows that the communities of Beds 10–8 and 6–5 in Trlica existed in warm periods and dwelt in conditions of mosaic landscapes, with widespread forest biotopes. Judging from the palynological data, there were temperature reductions during the accumulation of Bed 12, the upper part of Bed 9 – lower part of Bed 8, and also the upper part of Bed 5; Bed 6 and the basic part of Bed 5 clearly corresponds to the first interglacial of the Middle Pleistocene, MIS 19 (Derevyanko et al. 2012b).

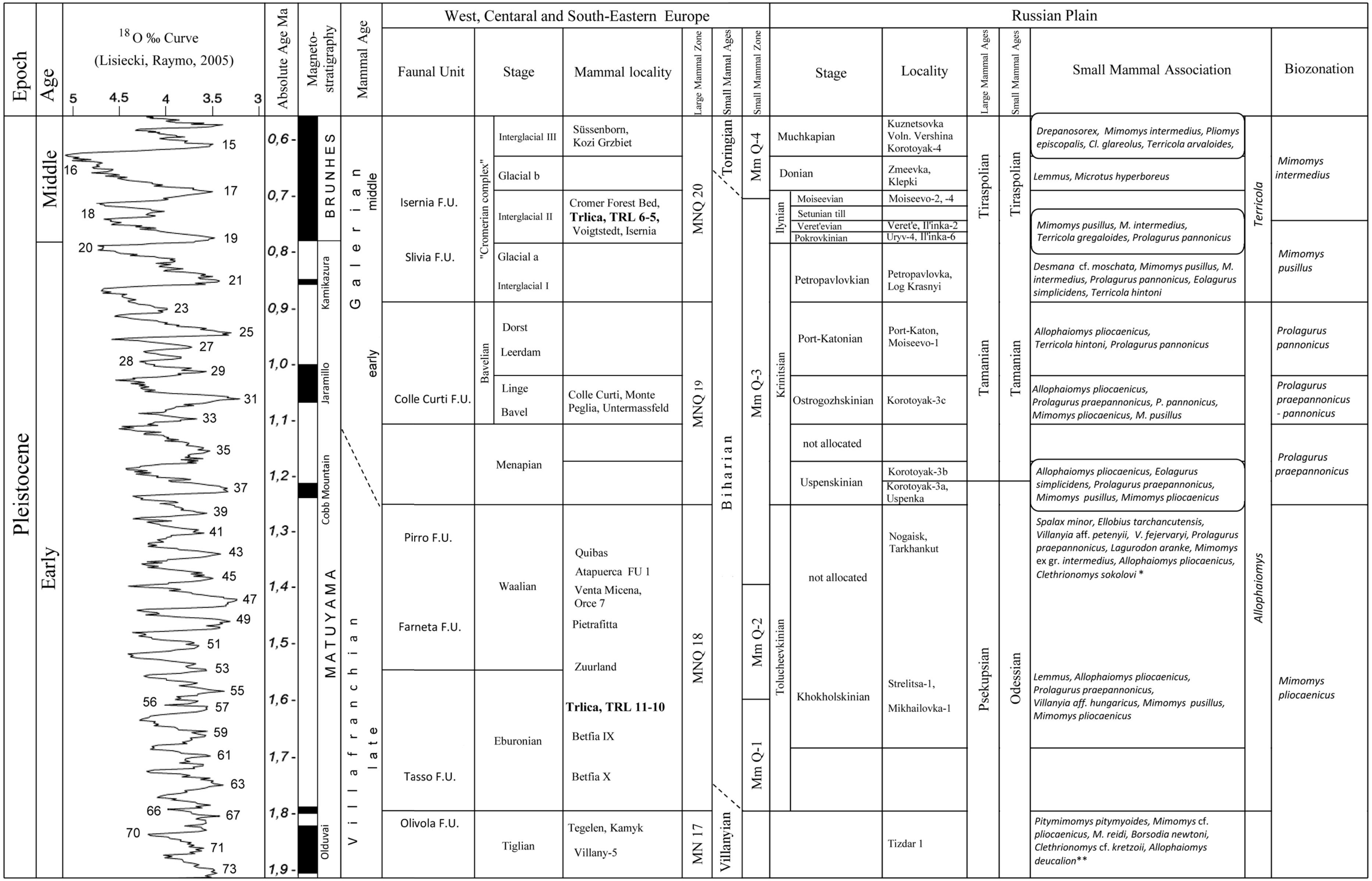
Changes in the large and small mammal composition in the Trlica section correspond to the general trend of gradual cooling during the Pleistocene, although allow for recognition of certain local features during the lifetime of each fauna within these groups.

The analysis and comparison of the large mammal composition in Beds 5–6 and Beds 9–11 lead to certain conclusions about the environment at the time when these faunas existed. For this purpose, the ratios of horses (Equidae), deer (Cervidae), and Ovibovini in the two strata were compared. The results of these comparisons are shown in Table 4.

Table 4 shows that during the accumulation of Beds 9–11, the proportions of horses and ovibovines increased, while that of deer decreased. On the contrary, the accumulation of Beds 5–6 coincided with the prevalence of deer and lower proportions of horses and ovibovines. Horses are typical grazers, inhabitants of open biotopes, a typical component of grassy biomes. Deer are mainly browsers, inhabitants of forests and their ecotonal biomes. Extant ovibovines (tribe Ovibovini) occupy the Arctic tundras. During the Late Pleistocene glaciation, their range covered the territory from

Table 4. Proportions of various herbivore groups in taphocoenoses of Beds 5–6 and 9–11 of the Trlica locality.

Beds	Taxa		
	Equidae	Cervidae	Ovibovini
5–6	9.21 %	28.95%	8.55%
9–11	10.31%	22.19%	14.79%



* Topachevskiy 1973 ** Shchelinsky et al. 2016

Text-fig. 3. Chronostratigraphic position of the Trlica mammal assemblages (TRL 11–10 and TRL 6–5) and their correlation with main European fossil mammal sites.

the Atlantic to Chukotka (Kahlke 1994). Villafranchian members of the tribe were a component of thermophilic faunas, resembling the composition of African savanna faunas, but probably belonged to the group of species with the primary adaptation for cold conditions. The range of *Soergelia* expanded out of Europe, where it was recorded for the first time in the territory of Germany, the Czech Republic and Romania, up to the lower reaches of the Kolyma River (Kahlke 1969, Sher 1971). The genus *Megalovis* occurred from the Apennines to China. The range of *M. balcanicus* was confined to mountain regions of the Balkan Peninsula. The somewhat cooler conditions during the accumulation of the lower beds in Trlica in comparison with the preceding Middle Villafranchian faunas and some Late Villafranchian faunas of Western Europe is evidenced by the presence of some other migrators from the eastern regions, which are at the base of the boreal lineages (*Cervus* cf. *acoronatus* and *Capreolus*) (Markova and Vislobokova 2016).

Thus, it is plausible that, during the accumulation of Beds 9–11, the proportion of open landscapes was somewhat greater than during the accumulation of Beds 5–6, when the proportion of forested biotopes was higher. Similar conclusions follow from the composition of the small mammal fauna. The high proportion of the dormouse *Glis sackdillingensis* in Beds 5–6 and complete absence of dormice in Beds 9–11 are evidence of considerably milder and warmer conditions during the accumulation of Beds 5–6 compared to that of underlying beds. This suggests that there was an upward shift along the slopes of the forest belt and the belt of nival biotopes, probably occurring with specific climatic warming. This statement is supported by palynological data (Derevyanko et al. 2012b), which suggest that Beds 6 and 5 correspond to the first interglacial of the Middle Pleistocene, MIS 19 (Text-fig. 3).

However, the effect of climatic fluctuations should not be overstated. Bone remains of bats from Bed 10 include the genus *Rhinolophus*. The modern fauna includes 68 species of this genus. Their range is limited to the Old World and covers the Mediterranean, Africa, India, China, and the entire southeastern Asia. The northern boundary of the range of horseshoe bats passes through the Transcarpathians, Crimea, Caucasus, Turkmenistan, Uzbekistan, and western Tajikistan (Gromov and Baranova 1981, Görner and Hackethal 1988, Benda et al. 2011). Possibly, an ancient horseshoe bat, *Rhinolophus*, dwelt in conditions with a more severe climate, although this assumption looks questionable. Another bat species from Bed 10 is *Myotis blythii longocaninus*. At present, the range of *Myotis blythii* covers Spain, Switzerland, Austria, Italy, the southern European part of the USSR, North Africa, Near East, Central Asia, and the Altai (Bobrinsky et al. 1965, Gromov and Baranova 1981, Görner and Hackethal 1988). It dwells under more continental conditions than *Rhinolophus*. However, in general, these data suggest that climatic conditions in northern Montenegro in the Cheotina River valley in the Early Pleistocene were favorable, without long cold periods in the climatic dynamics.

Taphonomy and Paleogeography

The presence of different sedimentation stages in the Trlica locality is connected with different taphonomic processes inside the karstic cavity and paleogeographical stages in the development of environments outside it.

Beds 12 and 11 are deposits of a channel with a changeable hydrological mode. It appears that the alluvial matter of these beds was accumulated at the level of the cave, when the Cheotina River channel was approximately 150 m higher than its recent position. The absence in Bed 12 of large mammal bones and hyena coprolites suggests that, in the period of accumulation of these strata, subaquatic conditions in the cave prevailed. During accumulation of Beds 10–8, the cave was periodically inhabited. It was visited at least by hyenas and bats under the vault.

Beds 10–5 were formed due to the periodical influx of slope deposits. Beds 4–1 were also formed by washout of slope deposits, mostly paleosoil, but in a more stable and slow regime.

A remarkable feature is the existence of paving horizons in Beds 12 and 10, and in the roof of Beds 5 and 4. Paving is a horizon of flattened rock, fragments of large mammal bones, and coprolites of carnivores. It is formed as a result of a long break in the accumulation of mineral matter from external sources and gives evidence of a significant break in sedimentation. Another important parameter indicative of a break in sedimentation is the strong travertine cementation characteristic of Bed 7, the presence in this bed of strongly weathered grusses and abundant manganous concretions. Travertine beds are also recorded in Bed 10. In addition, deposits of Bed 10 overlie the loam of Bed 11 with angular unconformity. All this is evidence of significant breaks in sedimentation and the fossil record of the locality in question.

Taphocoenoses of particular beds of Trlica include both large and small mammals; the mechanisms and sources of accumulation of bone fragments were different in the specific animal groups. Carnivores used the karstic cavity as a shelter or made it a den to bring up their young, as evidenced by the abundance of teeth of young animals and coprolites mostly of hyenas. Bones of large herbivores, deer and bovids, were apparently brought to the cave by large carnivores, as indicated by the significant fragmentation of bones and bite marks on them (Crégut-Bonnoure and Dimitrijević 2006; original data). In addition, some fragments of large bones show traces of contact with gastric juices.

Bone remains of small mammals come from pellets of birds of prey and, probably, also from excrement of terrestrial carnivores. In particular, bone remains of dormice found in Beds 5 and 6 probably came from pellets of owls. All living dormice are nocturnal and twilight animals inhabiting trees (Airapetiants 1983, Görner and Hackethal 1988) and, hence, nocturnal birds of prey, owls, are the most probable producers of pellets with these remains. At the same time, owls successfully prey on other terrestrial rodents, for example, voles which are also recorded in the taphocoenoses of the Trlica locality. The pellet origin of small mammal bones, except for bats, is corroborated by the fact that some bone fragments show traces of digestion by gastric juices and clearly passed through the digestive system of predators.

The chiroptera material despite the small sample size, allow for certain taphonomic conclusions to be made (Rossina et al. 2016). A pellet origin of chiropteran bones is highly unlikely, since the bones and teeth of bats lack any trace of the effect of gastric juices. In addition, Bed

10 contains fine postcranial bones of Chiroptera, excluding the possibility that they passed through the digestive tract of predators. Apparently, bats were dwellers of the cave. However, the cave was not occupied by large bat colonies, as follows from the rarity of their bone remains. Chiroptera only periodically occupied the cave which apparently had sufficient space between the floor and vault for the flight of horseshoe bats dwelling there. The movement of the majority of Rhinolophidae on a firm surface is restricted because of the morphology of their limbs; they cannot run or walk on firm substrates (Kuzyakin 1950). They usually suspend themselves directly after their flight to the vault of the shelter and then move head over heels along it for at most several meters, using the hind legs (Hall 1989). Under a hanging animal, there should be a significant air space because to start a flight, the bat needs a certain distance for passive falling, which is then followed by rapid expansion of wings providing active flight (Kuzyakin 1950). All this suggests that the karstic cavity of Trlica periodically had enough space between the floor and vault of the cave, providing conditions for the life of both large mammals and hominids.

Conclusions

The study of the mammal fauna from the Trlica locality in northern Montenegro, based on our records from excavations between 2010 – 2014 has shown that it consists of representative faunas of two different assemblages. The earlier assemblage, TRL 11–10, corresponds to the Early Pleistocene and falls within the interval 1.8–1.5 Ma, with most cold snaps in MIS 58 and 52. The younger assemblage, TRL 6–5, is characteristic for the beginning of the Middle Pleistocene, starting from MIS 19. The time of these assemblages are the time of migration of early *Homo* into the Mediterranean. The results of the study provide additional evidence on the environmental condition during the earliest dispersal of ancient hominids in the territory of South-Eastern Europe. In the Early Pleistocene, there was a relatively cool climate. The presence of temperate (close to boreal) eastern immigrants in TRL 11–10, such as *Praemegaceros*, *Cervus* cf. *acoronatus*, *Capreolus*, as well as the first appearance of lemmings of the genus *Lemmus* on the Russian Plain during this time, testifies to the cool conditions (cold snap) which stimulated the East-to-West migration. The faunal exchanges between Europe and Africa also increased during cooling, partly due to some reduction in the Mediterranean Sea level. The presence of some carnivores demonstrates the existence of a steady connection between faunas of Africa and Europe during this time. At the beginning of the Middle Pleistocene the climate in northern Montenegro became milder; the areas occupied by forests, including broad-leaved forests, increased. The presence of Lagurini fossil remains throughout the section is evidence of the existence of local steppe sites in northern Montenegro during the Early Pleistocene and first half of the Middle Pleistocene.

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