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New Data on Large Mammals of the Pleistocene Trlica Fauna, Montenegro, the Central Balkans

I. A. Vislobokova and A. K. Agadjanian
Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: ivisl@paleo.ru, aagadj@paleo.ru

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Abstract—A brief review of 38 members of four orders, Carnivora, Proboscidea, Perissodactyla, and Artiodactyla, from the Pleistocene Trlica locality (Montenegro), based on the material of excavation in 2010–2014 is provided. Two faunal levels (TRL11–10 and TRL6–5) which are referred to two different stages of faunal evolution in the Central Balkans are recognized. These are (1) late Early Pleistocene (Late Villafranchian) and (2) very late Early Pleistocene–early Middle Pleistocene (Epivillafranchian–Early Galerian).

Keywords: large mammals, Early–Middle Pleistocene, Central Balkans

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INTRODUCTION

The study of the mammal fauna from the Trlica locality (Central Balkans, northern Montenegro), situated 2.5 km from Pljevlja, provides new information improving the knowledge of historical development of the terrestrial biota of Europe in the Pleistocene and biochronology. In addition, this study is of interest in connection with the fact that Trlica belongs to archeological sites of an early stage of penetration of Hominini (genus *Homo*) into Europe.

The locality was discovered in the 1960s in Pleistocene deposits infilling karstic cavern in Triassic limestones. It was studied by a research team headed by Dimitrijević from University of Belgrade (1990; Dimitrijević et al., 2006). Based on the material of excavation in 1988, 1990, and 2001, the following large mammals were determined in this fauna: *Canis etruscus, C. falconeri, Vulpes* sp., Mustelidae gen. et sp. indet., *Ursus etruscus, Pachycrocuta brevirostris, Homotherium* cf. *crenatidens, Panthera* cf. *gombaszoegensis*, *Elaphantidae* indet., *Palaeoloxodon antiquus, Stephanorhinus hundsheimensis, Equus stenonis, E.* cf. *major, Alces* cf. *carnutorum*, *Cervus elaphus, Eucladoceros giullii*, cf. Rupicaprini, *Bison (Eobison)* sp., and two new species of the musk oxen, *Megalovis balcanicus* and *Soergelia intermedia* (Forsten and Dimitrijević, 2002–2003; Crégut-Bonnoure and Dimitrijević, 2006; Argant and Dimitrijević, 2007). Horses, a rhinoceros, bovids, and small mammals have been described (Codrea and Dimitrijević, 1997; Forsten and Dimitrijević, 2002–2003; Dimitrijević et al., 2006; Crégut-Bonnoure and Dimitrijević, 2006; Argant and Dimitrijević, 2007; Bogićević and Nenadić, 2008). The fauna was assigned in different works to the end of the Early Pleistocene–beginning of the Middle Pleistocene (Dimitrijević, 1990; Forsten and Dimitrijević, 2002–2003; Dimitrijević et al., 2006); the MNQ20–MNQ22 zones (Codrea and Dimitrijević, 1997); terminal Early Pleistocene (Crégut-Bonnoure and Dimitrijević, 2006; Argant and Dimitrijević, 2007), *Mimomys savini-pusillus* Zone (Bogićević and Nenadić, 2008); or Epivillafranchian (Kahlke et al., 2011).

Since 2010, Trlica has been studying within the framework of the Program of Cooperation of the Russian Academy of Sciences and Montenegro Academy of Sciences and Arts. The head of the Russian part is Academician A.P. Derevjanko. Employees of the Institute of Archeology and Ethnography of the Siberian Branch of the Russian Academy of Science, Moscow State University, and Borissiak Paleontological Institute, of the Russian Academy of Sciences (PIN) participated in excavation. I.A. Vislobokova and A.K. Agadjanian (PIN) identified large and small mammals, respectively. The results of excavation were published in a series of papers (Derevjanko et al., 2011, 2012a, 2012b, 2013). Excavation is headed by M.V. Shunkov. The section is divided into 12 layers, layers 5–11 of which contain mammal fossils (Derevjanko et al., 2012). Due to the level-by-level collection of fossil material, the taxonomic list of the Trlica Fauna is considerably improved and expanded, changes in the mammal composition throughout the section are traced, and the age of the locality is specified. Our studies have shown that the lower bone-bearing layers of the section contain a mammal fauna of the latter half of the Early Pleistocene and the upper bone-bearing layers are not younger than the beginning of the early Middle Pleistocene. Here, we regard them as two faunal levels, TRL11–10 and TRL6–5,

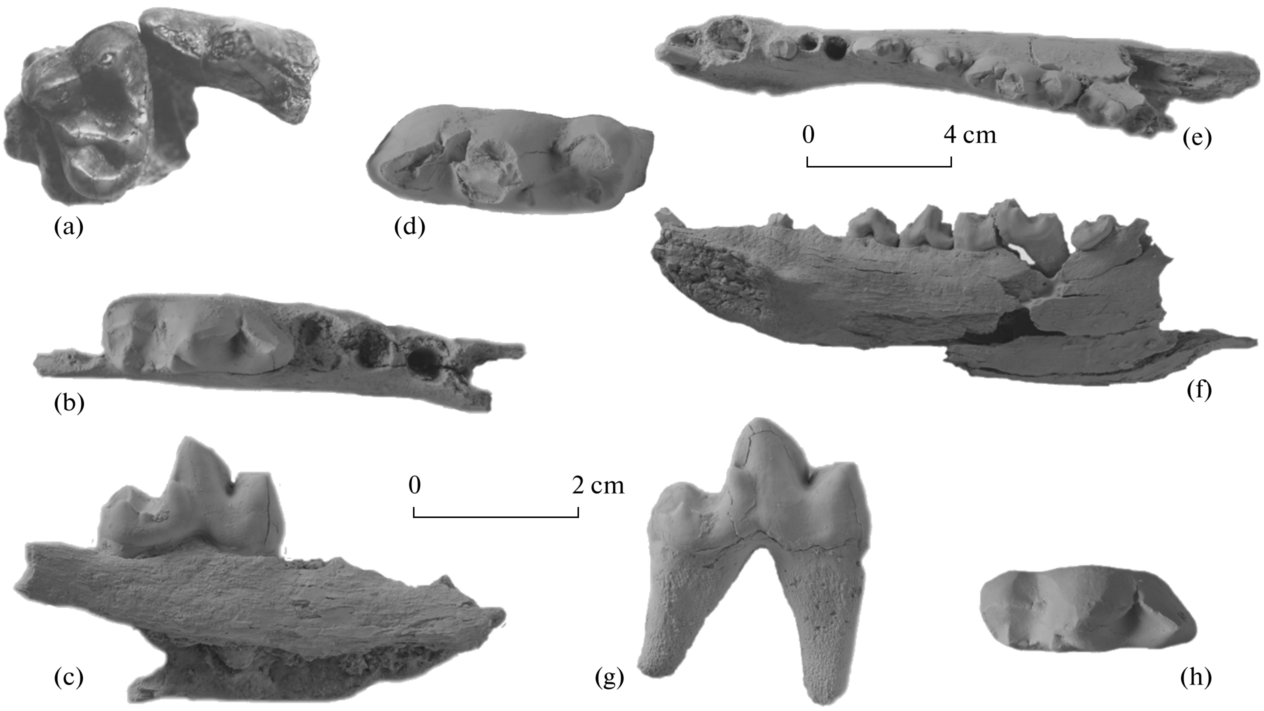

Fig. 1. Canidae from the Trlica locality (Montenegro), Pleistocene: (a–c) *Canis etruscus* Forsyth Major, 1877: (a) specimen TRL 2012/10/1, maxillary fragment with P^4 and M^1, ventral view; (b, c) specimen TRL 12/10/2, mandible fragment with M_1: (b) dorsal and (c) internal views; (d–f) *Lycaon lycanoides* (Kretzoi, 1938), specimen TRL 2011/10/3: (d) M_1, dorsal view; (e, f) mandible: (e) dorsal and (f) internal views; (g, h) *Canis* sp., specimen TRL 11/10/4, M_1: (g) internal and (h) dorsal views.

distinguished by the taxonomic composition of large mammals.

The present paper provides a brief review of large mammals from Trlica based on the material collected in 2010–2014 and the faunal composition of levels TRL11–10 and TRL6–5. Comparisons involve the material housed in the PIN; Geological Institute of the Russian Academy of Sciences; Vernadsky Geological Museum, Moscow; Paleontological Museum of Rome University "La Sapienza"; Staatliches Museum für Naturkunde, Stuttgart; Aristotle University of Thessaloniki; and published data. A detailed analysis of biostratigraphic and zoogeographical aspects of the Trlica Fauna will be provided in future publications.

In the present paper, we adhere to the modern International Stratigraphical Chart, according to which the lower boundary of the Pleistocene is dated 2.6 Ma and the boundary between the Early and Middle Pleistocene is dated 0.78 Ma. The ideas of different authors concerning the age of particular faunas are formalized, given in brackets, with the references to respective publications. In the present study, the following abbreviations for tooth measurements are accepted: (L) length (mesiodistal), (W) width (buccolingual), (H) height. The measurements are given in mm.

BRIEF TAXONOMIC REVIEW

In the material collected in 2010–2014, more than 1000 large mammal specimens from layers 5–11 of Trlica are determined and 38 species of four orders (Carnivora, Proboscidea, Perissodactyla, and Artiodactyla) are recorded. The distribution of species over the beds are shown in Table 1.

Order Carnivora

The **family Canidae** is represented in Trlica by five forms.

Canis etruscus Forsyth Major, 1877, Etruscan wolf, a medium-sized wolflike dog ancestral to the *Canis mosbachensis*–*C. lupus* lineage. It is represented by jaw fragments with P^4 , M^1, and M_1 from layer 10 (Figs. 1a–1c). The upper carnassial (P^4) has a metastyle triangular in outline and a crest extending from the paracone to metacone. In M^1 the paracone is higher than the metacone; the labial valley is as deep as the lingual valley, but larger than the latter; the cingulum is extended. In the lower carnassial (M_1), the protoconid and paraconid are smaller than in *C. lupus*; the hypoconid and entoconid are connected by a crest (sinous crista). The species was described from the Early Pleistocene (Late Villafranchian) Upper Valdarno, Italy. *C. etruscus* differs from *C. mosbachensis* in

Table 1. Large mammals from Trlica and their position in the section, based on the material collected in 2010–2014

Taxon	Layers						
	5	6	7	8	9	10	11
CARNIVORA							
Canis etruscus						+	
Canis sp.						+	
Lycaon lycanoides						+	
Canidae (?*Vulpus* or *Nyctereutes*)						+	
Mustelidae indet.						+	+
Ursus etruscus						+	+
Ursus deningeri	+						
Pachycrocuta brevirostris				+		+	+
Crocuta sp.			+				
?*Crocuta* sp.		+					
Megantereon cultridens						+	
Homotherium crenatidens						+	+
Panthera onca cf. *gombaszoegensis*						+	+
?*Acinonyx pardinensis*						+	
PROBOSCIDEA							
Elephantidae indet. (?*Archidiskodon meridionalis*)						+	
?*Palaeoloxodon* sp.						+	
PERISSODACTYLA							
Stephanorhinus etruscus						+	+
Stephanorhinus hundsheimensis	+	+					
Equus stenonis						+	+
Equus cf. *major*						+	+
Equus cf. *suessenbornensis*	+	+					
Equus sp. (small)	+						
ARTIODACTYLA							
Cervus ex gr. *C. elaphus* (?*C. acoronatus*)						+	+
Cervus cf. *acoronatus*	+						
Eucladoceros sp.							
Cervini gen.		+	+			+	
Praemegaceros sp.	+	+	+	+		+	+
Praemegaceros cf. *verticornis*	+	+					
Capreolus sp.			+	+		+	+
Libralces cf. *gallicus*						+	+
Bison (*Eobison*) sp.						+	+
Bison cf. *shoetensacki*	+						
Leptobos cf. *etruscus*						+	+
Gazellospira sp.						+	
Caprinae indet.						+	
Caprinae (?Capra)						+	+
Megalovis balcanicus						+	+
Soergelia intermedia						+	+
Ovibovini indet.	+		+	+	+		+
Layers	5	6	7	8	9	10	11

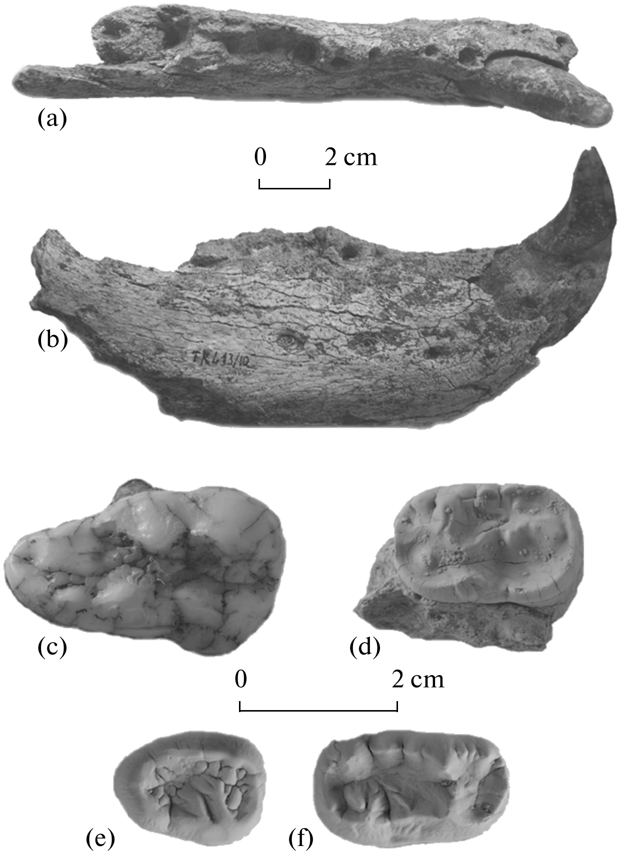

Fig. 2. Ursidae from the Trlica locality (Montenegro), Pleistocene: (a–c, e, f) *Ursus etruscus* Cuvier, 1812: (a, b) specimen TRL 13/10/5, lower jaw with C_1 and alveoli for P_1–M_2: (a) dorsal and (b) external views; (c) specimen TRL2010/10/6, M^2, ventral view; (e) specimen TRL 11/10/7, M_3, dorsal view; (f) specimen TRL 11/10/8, M_2, dorsal view; (d) *U. deningeri* Von Reichnau, 1906, specimen TRL 11/5/9, M_2, dorsal view.

the smaller size, the metastyle outline in P^4, the weaker contact with M^1, the deeper and larger labial valley in M^1; from *C. apolloniensis* in the smaller size, the weaker labial cingulum, and the shorter talonid of M_1; from *C. arnensis* in the larger size and structural details of teeth (in particular, different ratio of the metacone and paracone of M^1) (see Tedford et al., 2009; Cherin et al., 2014). Measurements: specimen TRL 2012/10/1: LP^4, 20.9; WP^4, 10.2; LM^1, 13.9; specimen TRL 12/10/2, WM^1, 17.3; LM_1, 22.7; WM_1 in the middle, 9.2; talonid L, 7.5; talonid W, 8.9. The species *C. etruscus* was widespread in the Early Pleistocene of Eurasia from Spain to China. In Europe, it is typical for the Olivola–Tasso Faunal Units (Rook and Martinez-Navarro, 2010; Cherin et al., 2014). In southeastern Europe, *C. etruscus* has been recorded in Kozarnika Cave, B2-2 Biozone, Bulgaria (ca. 1.6–1.4 Ma: Guadelli et al., 2005; 1.2–0.9 Ma: Kahlke et al., 2011), Gerakorou (MN18/MN19), and Apollonia (MNQ20), Greece (Koufos, 1992a, 2001; Koufos and Kostopoulos, 1997; Kostopoulos et al., 2002; Appolonia: Farneta F.U.: Koufos, 1992b; ca. 1.4–1.1 Ma: Spassov, 2003; ca. 1.1 Ma: Kahlke et al., 2011).

Lycaon lycanoides (Kretzoi, 1938), the ancestor of extant African hunting dog. A right dentary from layer 10 with incomplete I_2, P_1, and P_3–M_2 has a concave dorsal surface between C–P_1 and symphysis characteristic of the genus *Lycaon* and its carnassial M_1 is typical in structure for *L. lycanoides* (Figs. 1d–1f). In M_1, the metaconid is poorly developed; on the talonid, the hypoconid occupies a more central position than in *Canis*, is large and isolated from a relatively small entoconid. M_2 has three peaks, protoconid, and hypoconid located on the same axis, and metaconid. *L. lycanoides* differs from *L. falconeri* (F. Major, 1877) (=*C. falconeri*) from the Late Pliocene of Eurasia in the larger size. Measurements: specimen TRL 11/10/3, LP_2–M_2, 98; LP_1, 7.5; WP_1, 5.0; LP_3, 16; WP_3, 7.5; LP_4, 18.7; WP_4, 8.9; LM_1, 29.5; WM_1 in the middle, 11; talonid L, 9.9; talonid W, 10.7; isolated teeth: LP^4, 25.2; WP^4, 10.8; LM_1, 27.1; WM_1 in the middle, 10.7; talonid L, 9.1; talonid W, 10.1. The species was widespread in the Early–Middle Pleistocene of Eurasia and Africa (Martinez-Navarro and Rook, 2003; Sotnikova and Rook, 2010). Regarding the evolutionary level, *L. lycanoides* from Trlica corresponds to archaic members of the species known, in particular, from Upper Valdarno, Italy. Advanced forms of *L. lycanoides* inhabited Europe and Central Asia at the end of the Early Pleistocene to the beginning of the Middle Pleistocene in association with *Canis mosbachensis* (Sotnikova and Rook, 2010). In the late Early Pleistocene, the Canidae showed a very wide diversity in southern Europe (Koufos, 1992a; Rook and Torre, 1996; Sotnikova and Titov, 2009; etc.).

M_1 of a small dog from layer 10 is referred to *Canis* sp. (Figs. 1g, 1h).

Small Canidae (?*Vulpes* aut *Nyctereutes*) are represented by narrow canines from layer 10. Even smaller canines from layers 10 and 11 are determined as Mustelidae indet.

The **family Ursidae** is represented in Trlica by two species.

Ursus etruscus Cuvier, 1812 is represented in Trlica by the greatest number of specimens among carnivores. An incomplete lower jaw with alveoli of P_1 – M_2 and preserved canine, isolated teeth (incisors, canines, premolars, and molars), and limb bones of small and medium-sized bears from layer 10 correspond in morphology and size to this species (Figs. 2a–2c, 2e, 2f). P^4 is large, wide, with a basal cingulum on the labial surface and the protocone displaced slightly posteriorly (a primitive character). The crown of M^2 is oval, slightly elongated, with a weak narrowing at the level of the talon, which has a slightly wrinkled surface. The lower edge of the lower jaw is almost straight. Alveoli of single-rooted P_1, P_2, and P_3 are located at a distance from each other and the alveolus of P_3 is near the anterior alveolus of P_4. M_3 is relatively small, round, with a concave occlusal surface. Measurements: LP^4, 18, 19; WP^4, 13, 14.8; LM^1, 23; WM^1, 16.5; LM^2, 24.6; WM^2, 15; LM_1, 24; WM_1, 13; LM_2, 25; WM_2, 15.5. *U. etruscus* was widespread in the Early Pleistocene. It is recorded in many Late Villafranchian faunas (Mazza and Rustonii, 1992).

A long and narrow M_1 from layer 5.2 and M_2 from layer 5 (Fig. 2d) are referred to the species *Ursus deningeri* Von Reichnau, 1906. In M_2, the entoconid region of the tooth is crescent, consists of three cusps increasing in height posteriorly. Measurements: LM_1, 23.7; WM_1, 11.7; LM_2, 25.35; WM_2, 16. *U. deningeri* occurred in Europe from the end of the Early Pleistocene (Galerian) to the early Middle Pleistocene. The earliest representatives of this species and arctoid bears are known from localities dated approximately 1 Ma. Early arctoid bears are found, in particular, in Untermassfeld (ca. 1 Ma) in Germany, where they are determined as *Ursus rodei* (Musil, 2001). At the beginning of the Middle Pleistocene of southeastern Europe, *U. deningeri* inhabited Kozarnika Cave, levels B2-1-1, in Bulgaria and Petralona Cave in Greece (Baryshnikov and Tsoukala, 2010; Kahlke et al., 2011).

The co-occurrence of *U. etruscus* and *U. deningeri* is recorded in Kozarnika Cave (Guadelli et al., 2005), Bulgaria, and Šandalja 1, Croatia (Malez, 1975). This is probably a transitional stage in the evolution of the *Ursus etruscus*–*U. deningeri* lineage (Spassov, 2003). *U. etruscus* is also recorded in the Apollonia Fauna (Spassov, 2003; Kahlke et al., 2011). A transitional Early Pleistocene form from the Gran Dolina locality (=Trinchera Dolina) Atapuerca, Spain was established as a new species, *U. dolinensis* (Garcia and Arsuaga, 2001).

The **family Hyaenidae** is represented by two hyena genera, *Pachycrocuta* Kretzoi, 1938 and *Crocuta* Kaup, 1828.

The giant hyena *Pachycrocuta brevirostris* (Aymard, 1846) was larger than living spotted hyena *Crocuta crocuta* (Erxleben, 1777). In the number of specimens from Trlica, *P. brevirostris* is only slightly less abundant than the bear *Ursus etruscus*. The teeth of this hyena were found in layers 10 and 11. Its premolars are massive, with inflated crowns and roughly wrinkled (rugose) enamel. The left carnassial (P^4 from layer 10 is large, long, with a massive protocone and protocone root (Figs. 3a, 3b). Left M_1 from layer 11 has a well-developed metaconid and talonid worn strongly externally. Measurements: LP^4, 40; WP^4 with protocone, 28.8; LM_1, 28.2; WM_1, 15.4. The species *P. brevirostris* penetrated into Eurasia from Africa about 1.8 Ma and became widespread in Eurasia in the late Early Pleistocene–Middle Pleistocene.

Left P^3 from layer 7 (Figs. 3c, 3d) is referred to *Crocuta* sp. It is less inflated and higher, with more strongly developed crests than in *P. brevirostris*. It is 26.4 mm long and 18.4 mm wide. Left P_3 and P_4 from layer 6, with narrower crowns than in *Pachycrocuta* and high additional anterior and posterior cusps are determined as ?*Crocuta* sp. P_4 has a small sharp posterointernal cusp is located on the cingulum continuation. Measurements: incomplete length of P_3, 22.5; WP_3, 15.3; LP_4, 27.4; WP_4, 15. The measurements are smaller than in *P. brevirostris* and close to those of the cave hyena *Crocuta crocuta spelaea* (Goldfuss, 1823), the largest hyena of the genus *Crocuta*. *Crocuta* occurred from the Early Pleistocene to Recent. Early *Crocuta* is known from Ubeidiya (ca. 1.5–1.2 Ma) in Israel (Martinez-Navarro et al., 2009). In Europe, the first *Crocuta* appeared at the boundary of the Early and Middle Pleistocene (Palombo et al., 2008); it has been recorded in Gran Dolina, Atapuerca (TD 4-5; ca. 0.8 Ma), Spain, along with the last *P. brevirostris* (Garcia, 2003), and in Ponte Galeria, Italy (Sardella, 2004). *C. crocuta spelaea* is present in the Late Pleistocene fauna of Baranica Cave in southeastern Serbia (Dimitrijević, 2011).

The **family Felidae** is represented by four species. Trlica has yielded two species of saber-toothed cats (Machairodontinae), *Megantereon cultridens* (Cuvier, 1824) [=*M. megantereon* (Croizet et Jobert, 1828)] and *Homotherium crenatidens* (Fabriani, 1890) and also the Pleistocene jaguar *Panthera onca* cf. *gombaszoegensis* (Kretzoi, 1938) and, probably, the Pleistocene cheetah ?*Acinonyx pardinensis* (Croizet et Jobert, 1828).

An upper canine from layer 10 corresponds In morphology and size to *Megantereon cultridens* (Fig. 3e). It is long, thin, laterally flattened, with sharp, but not serrated edges. Its incomplete height (to the break) with the root is 119.7 mm, without the root, 66.4; length, 21.9; width, 11. These measurements are close to the mean values of the species (Palmqvist et al., 2007). *M. cultridens* occurred in the Villafranchian of Eurasia. In the Balkans, it is present in the Middle Villafranchian of the Volax locality of Greece (Spassov, 2003). The latest *Megantereon* is known from the localities of Apollonia (ca. 1 Ma) in Greece (*M. cultridens*: Koufos, 2001; Spassov, 2003; *M. whitei*: Martinez-Navarro et al., 2009) and Untermassfeld in Germany (*M. cultridens adroveri*: Hemmer, 2001). In addition to the European lineage of *M. cultridens*, there was also the African–European *M. ekidoit*–*M. whitei* lineage (Werdelin and Lewis, 2000; Martinez-Navarro et al., 2009; Palmqvist et al., 2009). *M. cultridens* was less specialized than *M. whitei* and differed from it in the proportionally shorter upper canines and the longer premolar row (Palmqvist et al., 2007, 2008). *M. whitei* apparently migrated in Eurasia about 1.8 Ma and gradually replaced *M. cultridens* (Martinez-Navarro and Palmqvist, 1995, 1996; Martinez-Navarro et al., 2009). To date, *M. cultridens* has been reidentified as *M. whitei* from many localities of Europe and the Near East, including Dmanisi (ca. 1.8 Ma) in Georgia, Venta Micene in Spain, Pirro

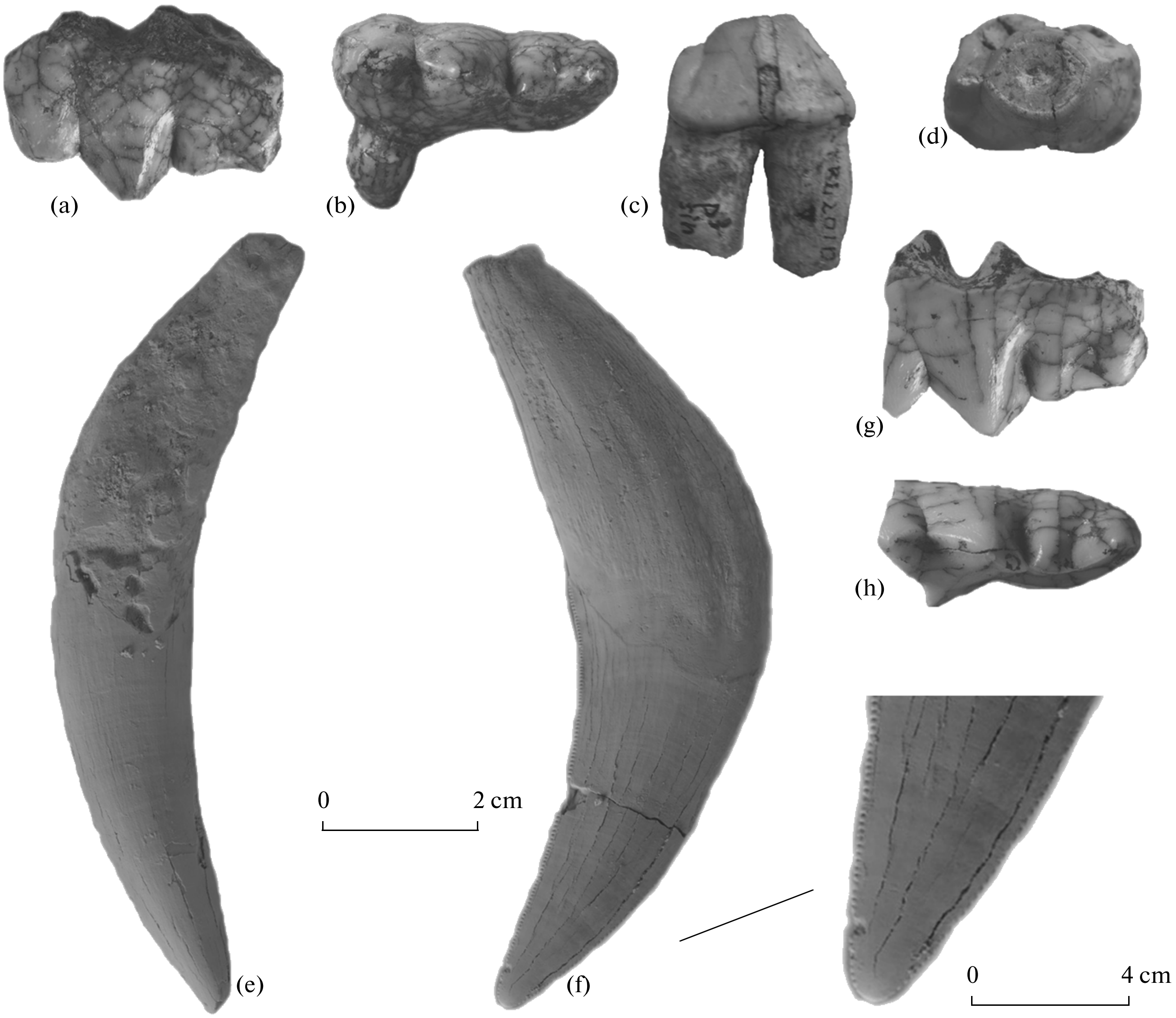

Fig. 3. Hyaenidae and Felidae from the Trlica locality (Montenegro), Pleistocene: (a, b) *Pachycrocuta brevirostris* (Aymard, 1846), specimen TRL 12/10/10, P^4: (a) external and (b) ventral views; (c, d) *Crocuta* sp., specimen TRL 12/7, P^3: (c) external and (d) ventral views; (e) *Megantereon cultridens* (Cuvier, 1824), specimen TRL 13/10/11, C, lateral view; (f–h) *Homotherium crenatidens* (Fabriani, 1890): (f) specimen TRL 12/10/12, C, lateral view; (g, h) specimen TRL 12/10/13, P^4: (g) lateral and (h) ventral views.

Nord in Italy, and Ubeidiya (1.5–1.2 Ma) in Israel (Martinez-Navarro and Palmqvist, 1995, 1996; Sardella, 1998; Palmqvist et al., 2007; Martinez-Navarro et al., 2009).

Homotherium crenatidens is represented by the greatest number of specimens among Felidae from Trlica. Layer 10 has yielded its incisors, canines, and incomplete carnassial P^4. The upper incisors are hooked and the lower incisors are conical and serrated. The upper canine is large, with serrated anterior and posterior edges (Fig. 3f). Its height with the root is 113.8 and without root, 64.3; length, 30.6; width, 13.4. P^4 is large, long, narrow, bladelike (Figs. 3g, 3h). The lower canine is relatively small, with well-pronounced crests, serrated along the posterior edge. The species was common in the Middle and Late Villafranchian of Eurasia. *H. crenatidens* differs from *H. latidens*, which replaced it in the Galerian, in the smaller size and shape of the upper canines. The latest *Homotherium* in Europe are known from the Late Galerian of Italy (the stage of Fontana Ranuccio) (Gliozzi et al., 1997).

Panthera onca cf. *gombaszoegensis* is represented by the upper and lower canines and premolars from layer 10. The upper canine is large, with two weak crests (anterointernal and posterior), almost round, slightly flattened at the crown base; it is 20.5 mm long and 15.7 mm wide. The lower canine has two crests and a groove along the lateral side; it is 9.9 mm long and 13.8 mm wide. The premolar crowns are relatively low. Left P^4 is large, with preparastyle, strongly reduced protocone projection, but with a well-developed protocone root. In P_4, the anterior cusp is high, the protoconid is high and long, with two cusps behind it, the posteriormost cusp is formed by the cingulum. Measurements: LP^4, 28.5; WP^4, 11.2; LP_4, 19.7–20; WP_4, 9.5–9.6; talonid length, 6.6–6.8; LP_3, 15.2. The upper canine is larger than in *P. pardus* (Linnaeus, 1758). According to Palmqvist et al. (2007), in *P. pardus* LC = 10–18 and WC = 8–14. P^4 of the jaguar from Trlica is longer than the mean values of *P. pardus* reported by Palmqvist et al. (2007) and shorter than that of *P. leo* (Linnaeus, 1758). The earliest members of the species are known in Europe from the Upper Valdarno and Olivola localities (ca. 2.0 Ma) in Italy, Dmanisi in Georgia, and Tegelen (2–1.8 Ma) in the Netherlands (Gliozzi et al., 1997; Hemmer et al., 2010). The jaguar from Dmanisi is referred to a separate subspecies, *Panthera onca georgica* (Hemmer et al., 2010). The species became extinct at the beginning of the Middle Pleistocene; the latest European records are known from Gran Dolina, Atapuerca (0.8 Ma) in Spain (Garcia, 2003), Kozarnika Cave, levels B2-1–B1 (0.8–0.4 Ma) in Bulgaria (Gaudelli et al., 2005) and Kudaro Cave in the Caucasus (Baryshnikov, 2011).

An upper canine with a broken off end and a half of right carnassial (P^4) from layer 10 are determined as ?*Acinonyx pardinensis*. The upper canine is relatively small, narrow, slightly flattened; it is 11.2 mm long and 8 mm wide. P^4 almost lacks a preparastyle and has a strongly reduced protocone projection and, apparently, without a protocone root. The length from the anterior crown edge to the middle of the metacone is 12.4 and the paracone is 9 mm long. Complete tooth was probably at most 26–28 mm long. According to the data of Kurten and Crusafont Pairó (1977), P_4 of Villafranchian *A. pardinensis* is 23.3–28.2 mm long; in the *A. pardinensis* (FSL) from Senèze, it is 25.9 mm long. The species occurred from the basal Villafranchian to the early Middle Pleistocene. *A. pardinensis* has been recorded in Dmanisi (Hemmer et al., 2011). In Europe, late *A. pardinensis* (*A. pardinensis pleistocenicus*) is known from Untermassfeld, Germany (Kahlke, 2007).

Order Proboscidea

The **family Elephantidae** is recorded in layer 10, including fragments of small teeth of calves and young elephants. They are determined as Elephantidae indet. (?*Archidiskodon meridionalis*) and ?*Palaeoloxodon* sp. In the shape of plates and enamel thickness (2.0–2.5 mm), most of the fragments correspond to the southern elephant *A. meridionalis* (=*Mammuthus meridionalis* after Lister et al., 2005) (Fig. 4). The species occurred in Europe from the Early Villafranchian to the beginning of the Galerian, MN16b–MNQ19/20.

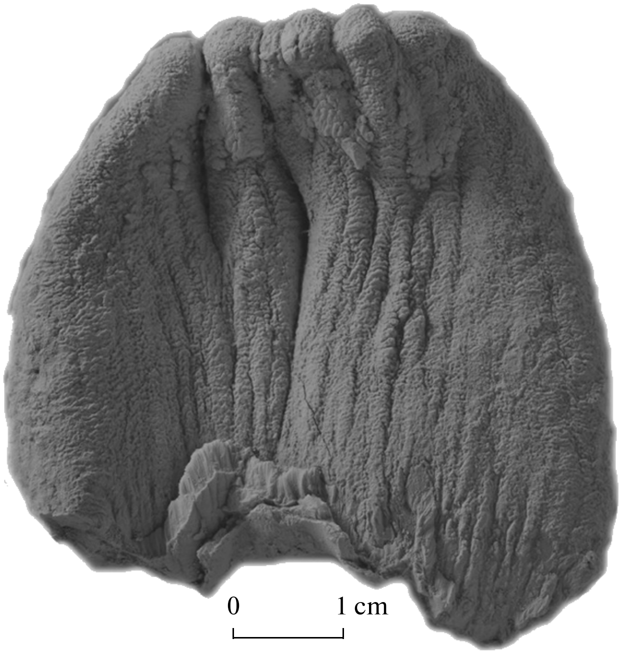

Fig. 4. Elephantidae indet. (*?Archidiskodon meridionalis*) from the Trlica locality (Montenegro), Pleistocene; specimen TRL2011/10/14, tooth plate, probably, the fourth replacement tooth.

The genus *Palaeoloxodon* Matsumoto, 1924, the forest elephant, is probably represented by fragments of the third or fourth tooth (DP^3/M^1) with the "characteristic" plate structure. The crown is narrow. The enamel is about 2 mm thick. Argant and Dimitrijević (2007) included the species *P. antiquus* (=*Elephas antiquus*) in the total list of mammals from Trlica. *Palaeoloxodon* (*P. antiquus*) existed in Europe from the terminal Early Pleistocene to the Late Pleistocene (Van der Made and Mazo, 2001). The earliest records are known, in particular, from Soleilhac (ca. 1.18–0.9 Ma), France. According to the data of Todd (2010), ancestors of *Palaeoloxodon* came from Africa about 2.5 Ma.

Order Perissodactyla

The **family Rhinocerotidae**. The first list of mammals from Trlica includes *Stephanorhinus etruscus* (Falconer, 1859), which was later replaced by *S. hundsheimensis* (Toula, 1903) (=*Dicerorhinus etruscus brachycephalus* Schroeder) (Dimitrijević, 1990; Codrea and Dimitrijević, 1997). In the material collected in Trlica in 2010–2014, both species are present (Table 1; Fig. 5).

The teeth and tooth fragments of *Stephanorhinus etruscus* come from layers 10 and 11. The parastyle fold of the upper molars is deep; the crochet lacks branching at the end; the crista is weak, almost absent on worn teeth; in incomplete slightly worn P^3, it branches. In M^3, the crista is weak; the anticrochet is hardly discernible; the crochet is long, curves towards the crista; the anterior cingulum is massive; the posterior cingulum is weak. The upper molars have ectostyle. The cingula are well pronounced. The enamel is

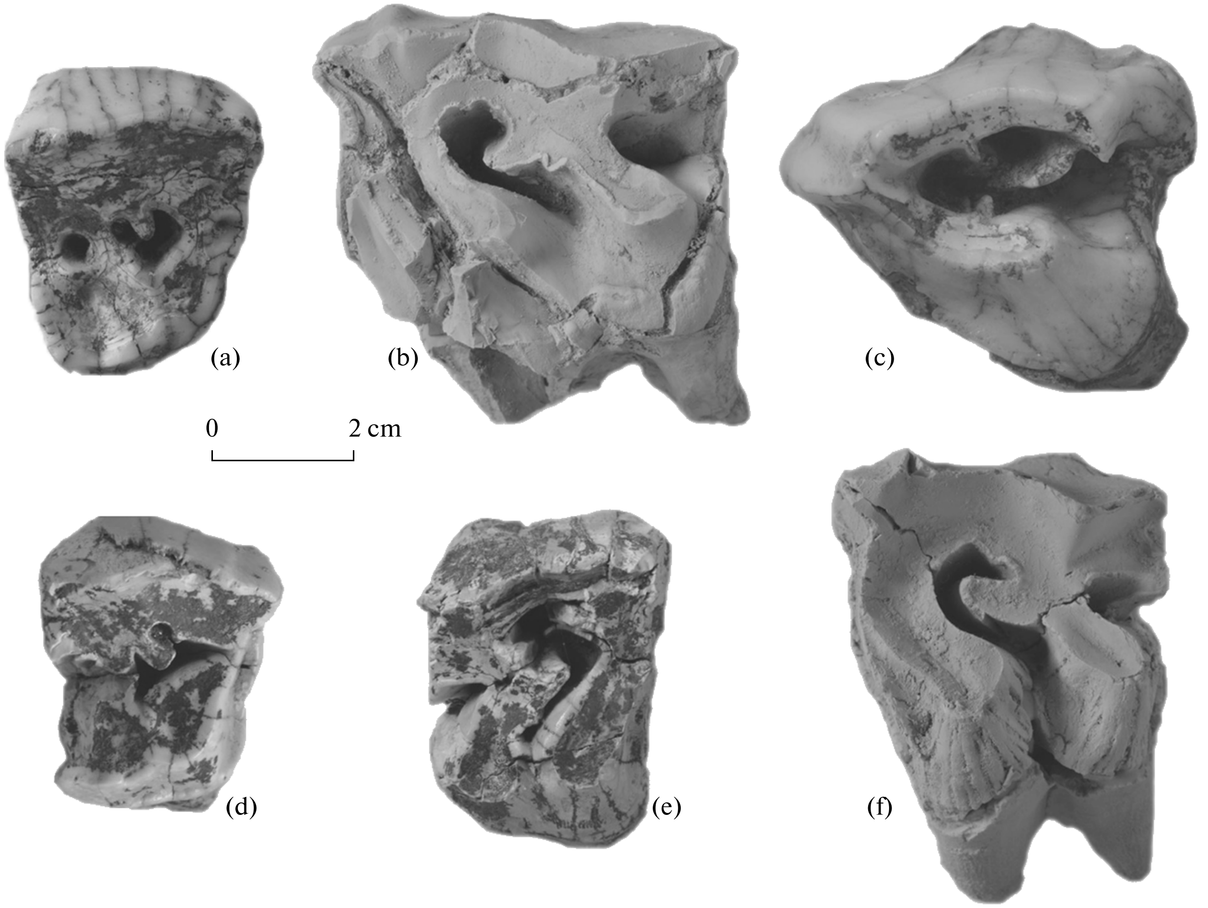

Fig. 5. Rhinocerotidae from the Trlica locality (Montenegro), Pleistocene:(a–c) *Stephanorhinus etruscus* (Falconer, 1859): (a) specimen TRL 12/10/15, P^2; (b) specimen TRL 12/10/16, M^2; (c) specimen TRL 12/10/17, M^3; (d–f) *S. hundsheimensis* (Toula, 1903): (d) specimen TRL 2011/5.2/18, P^3; (e) specimen TRL 2011/5.2/19, P^2; (f) specimen TRL 2011/5.2/20, M^2; ventral view.

wrinkled. Measurements: LP^2, 32.4; WP^2, 41.7; LP^3, 38.7, WP^3, 49.73; LP^4, 40.8; WP^4, 55.3; LM^1, 44.8; WM^1, 54; LM^2, 60.5; WM^2, 54; LM^3, 57.56; WM^3, 53.3; LP$_4$, 49.4; WP$_4$, 30.2. The species was widespread in Europe from the end of the Early Villafranchian to the beginning of the Late Villafranchian. In Italy, *S. etruscus* occurred up to the level of Farneta Faunal Unit, ca. 1.5 Ma, and, then, was replaced by small rhinoceroses, intermediate in size between *S. etruscus* and *S. hundsheimensis* (Pietrafitta, Pirro, and Colle Curti localities), which existed up to 1 Ma and was similar in morphology to Middle Pleistocene *S. hundsheimensis* (Fortelius et al., 1993; Mazza et al., 1993; Gliozzi et al., 1997; Lacombat, 2006). According to the data of Guérin (2004), *S. etruscus etruscus* is characteristic of the Villafranchian, MNQ16–MNQ19 zones, and *S. etruscus brachycephalus*, of the MNQ20–MNQ22 zones, from 1 to 0.5 Ma.

Stephanorhinus hundsheimensis is represented by deciduous and permanent teeth from layers 5 and 6, including left P^4 and M^1 from the same tooth row found in layer 5. Measurements: LP^2, 30.3; WP^2, 27.5; LP^3, 32.7; WP^3, 45.5; LP^4, 37, 37.2; WP^4, 46, 48.5; LM^1, 41.5; WM^1, 51; LM^2, 45.5, WM^2, 54.3. *S. hundsheimensis* differs from *S. etruscus* in the smaller size, slightly higher crowns, more advanced structure of deciduous and permanent teeth, i.e., the stronger developed fold of the paracone and crista, the presence of an anticrochet, the narrower exit of the groove separating the protocone and hypocone, the weaker styles, the absence of an entostyle on the upper molars, and in the finer wrinkled enamel. The crista of P^4 branches; in M^1 it is fused with the crochet. *S. hundsheimensis* from Trlica corresponds in size to the forms of the middle of the Late Villafranchian, in particular, rhinoceroses from Pietrafitta (stage Farneta, 1.5–1.3 Ma) described by Mazza et al. (1993). The upper premolars are smaller than in the forms from Isernia (ca. 0.6 Ma) and M^1 and M^2 fall into the lower limit of size variation of these forms, as obtained by Ballatore and Breda (2013).

The existence of the phyletic lineage *S. etruscus* (=*S. etruscus etruscus*)–*S. hundsheimensis* (=*S. etrus-*

cus brachycephalus), which was proposed by Guérin (2004, 2007), seems questionable to some experts (Fortelius et al., 1993; Lacombat, 2006). In the dental structure, *S. hundsheimensis* is close to *S. etruscus* and *S. hemitoechus*. The three species are characterized by wrinkled enamel, distinct folds and styles, relatively narrow exits of the valley, and frequent presence of a small cingulum below the exit of the posterior valley on the lower molars (Fortelius et al., 1993). *Stephanorhinus hemitoechus* is known since the Galerian, frequently existing in European faunas of the Middle and Late Pleistocene. It was larger than *S. hundsheimensis* and had some convergent similarity to the wooly rhinoceros *Coelodonta antiquitatis* (Fortelius et al., 1993).

The **family Equidae**. In the material collected in 2010–2014, the genus *Equus* is represented by four species of stenonid (zebroid) horses. In addition to the species *Equus stenonis* Cocchi, 1867 and *Equus* cf. *major* Boule, 1893 previously described from Trlica (Forsten and Dimitrijević, 2002–2003), these are two more horse species (Table 1; fig. 6).

Incisors and cheek teeth of *Equus stenonis*, a medium-sized horse, have been found in layers 10 and 11. The tooth size, the double loop shape, and protocone length (length indexes) correspond to this species. In unworn P^3 and P^4, the protocone is 9.4 mm long and the index of its length is 0.56. Teeth of *Equus* cf. *stenonis* are present in layers 7 and 9. The species was widespread in the Villafranchian. Regarding the evolutionary level, the horse from Trlica is close to the stenonid horse from the Late Villafranchian of Gerakarou assigned to the subspecies *E. stenonis mygdoniensis* (Koufos, 1992b) and is more primitive than *E. apollonensis* from Apollonia, which is considered to be intermediate between *E. stenonis* and *E. suessenbornensis* (Koufos et al., 1997).

The species *Equus* cf. *major* is represented by teeth of a large horse from layers 10 and 11. The crowns of unworn teeth are relatively low. In the Middle and Late Villafranchian, large stenonid horses of several species and different ecological groups, including *E. major, E. liventzovensis, E. bressanus*, and *E. stenonis vireti* existed (Azzaroli, 1990; Koufos and Vlachou, 1997; Forsten, 1999; Eisenmann, 2003, 2004). The majority of researchers believe that the species *E. major* and *E. bressanus* are synonyms. The last (instead of *Equus* cf. *major*) is included in the faunal list of Trlica provided by Kahlke et al. (2011) in a review on Early and Middle Pleistocene faunas. We retain for large horses of Trlica the species name reported by Forsten and Dimitrijević (2002–2003).

Equus cf. *suessenbornensis* is represented in Trlica by teeth of a large stenonid horse from layers 5 and 6, which differs from *E. major* and *E. apollonensis* in the more plicate enamel. Measurements: LM_1, 27.2; WM_1, 14.7. *E. suessenbornensis* occurred in the Early and Middle Galerian. In Eastern Europe, the earliest finds of the horse similar to *E. suessenbornensis* are known from the Taman Assemblage, 1.2–0.8 Ma. In the crown height *Equus* cf. *suessenbornensis* from Trlica is more primitive than these horses.

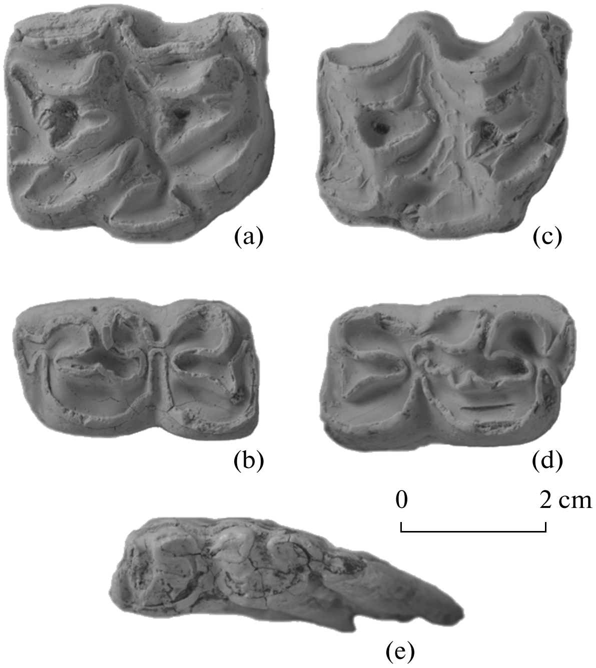

Fig. 6. Equidae from the Trlica locality (Montenegro), Pleistocene: (a) *Equus* cf. *major* Boule, 1893, specimen TRL 2012/11/21, maxillary tooth; (b) *E. stenonis* Cocchi, 1867, specimen TRL 2012/11/22, mandibular tooth; (c, d) *E. suessenbornensis* Wüst, 1901: (c) specimen TRL 2011/5/23, maxillary tooth; (d) specimen TRL 2011/5/24, M_2; (e) *Equus* sp. (?*E. altidens*), specimen TRL 2011/5/25, M_3; (a, c) ventral and (b, d, e) dorsal views.

A small horse *Equus* sp. is represented by two slightly worn last lower molars (M_2 and M_3) from layer 6. These teeth with a double loop of relatively equal lobes and a deep external groove (ectoflexid), adjoining the incisure of the linguoflexid are similar in size and morphology to those of *E. altidens*, in particular, *E.* cf. *altidens* from the Pirro Nord in Italy (De Giuli et al., 1986). The species *E. altidens* occurred in Western Europe in the Early Pleistocene–early Middle Pleistocene (De Giuli et al. 1986; Forsten, 1999). The absence of data on the structure of a complete tooth row of the small horse from Trlica prevents identification to species.

Order Artiodactyla

The **family Cervidae**. Among the Cervidae from Trlica, the subfamily Cervinae was most diverse. Three genera have been recorded: *Cervus* Linnaeus, 1758, *Eucladoceros* Falconer, 1868 (Cervini), and *Praemegaceros* Portis, 1920 (Megacerini).

A large deer of the genus *Cervus* ex gr. *C. elaphus* L. (?*C. acoronatus* Beninde, 1937) is represented by incisors and cheek teeth from layer 10. A few specimens of *C.* cf. *acoronatus* have been found in layers 5 and 6.

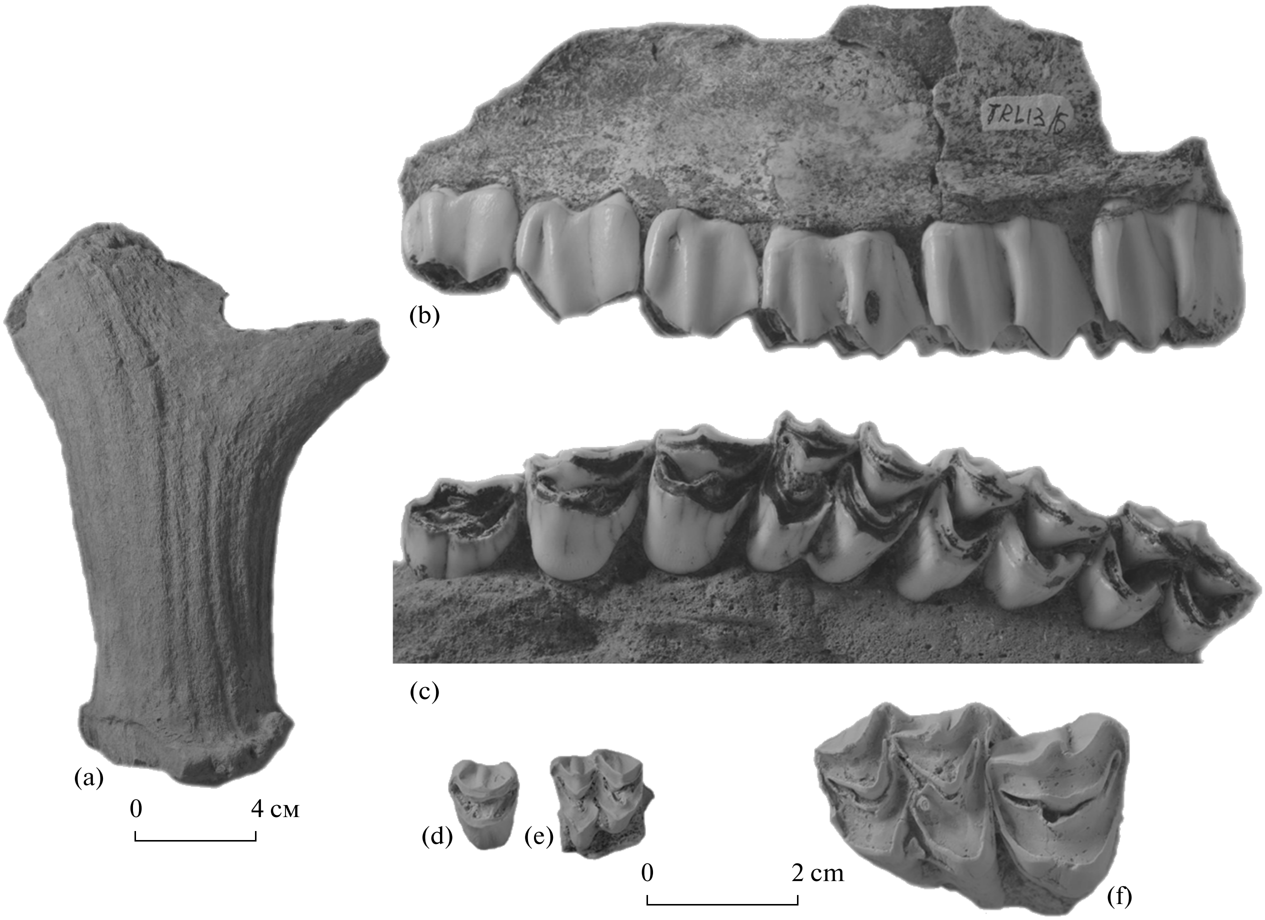

Fig. 7. Cervidae from the Trlica locality (Montenegro), Pleistocene: (a) *Praemegaceros* cf. *verticornis* (Dawkins, 1872), specimen TRL 13/6/26, antler base, laterointernal view; (b, c) *Cervus* cf. *acoronatus* Beninde, 1937, specimen TRL 13/6/27, maxilla with P^2–M^3: (b) external and (c) ventral views; (d, e) *Capreolus* sp.: (d) specimen TRL 11/10/28, P^4; (e) specimen TRL 11/10/29, M^3; (f) *Libralces* cf. *gallicus* Azzaroli, 1952, specimen TRL 2011/10/30, P^4–M^1, ventral view.

In specimen TRL 13/6/27, the upper tooth row is 130.8 long (Figs. 7b, 7c). The species *C. acoronatus* appeared in Eurasia about 2–1.8 Ma and was widespread in the Early Pleistocene–early Middle Pleistocene. In Asia, the earliest *C. acoronatus* are known from the Itantsa Assemblage in Transbaikalia, along with the first *Praemegaceros* (Vislobokova, 2008).

Eucladoceros sp. is represented by teeth corresponding in size to *E. teguliensis* (Dubois, 1904) (=*E. senezensis* Deperet, 1910 and *E. ctenoides* Nesti) from the Middle and Late Villafranchian. The faunal list of Trlica based on early collections includes *E. giulii* Kahlke, 1997 (Crégut-Bonnoure and Dimitrijević, 2006) originally described from Untermassfeld (Kahlke, 1997, 2001).

Several teeth corresponding in size to the fallow deer are identified as Cervini gen. indet. (layers 6, 7, and 10).

Teeth of *Praemegaceros* sp. are present in almost all beds and particularly abundant in layer 10. A fragment of a large left antler with a broken off highly positioned first tine from layer 6 (Fig. 7a) and a lower jaw from layers 8–9 are similar in morphology and size to those of *P. verticornis* (Dawkins, 1872) and determined as *P.* cf. *verticornis*. Measurements: anteroposterior diameter of the antler base, 60; its transverse diameter, 65. The genus *Praemegaceros* occurred from the Late Pliocene to the beginning of the Holocene and *P. verticornis* is recorded at the end of the Early Pleistocene and early Middle Pleistocene (Vislobokova, 2008, 2012, 2013).

The roe deer (Capreolinae) is represented by incisors and cheek teeth from layers 7, 8, 10, and 11, which are determined as *Capreolus* sp. (Figs. 7d, 7e). In Asia, the earliest *Capreolus* (*C. constantini*) is known from the Early Villafranchian of Udunga, MN16, in Transbaikalia (Vislobokova et al., 1995); in Europe, this is *C. cusanoides* described from Untermassfeld (Kahlke, 2001).

Moose (Alcinae) are represented by the genus *Libralces* Azzaroli, 1952. Layer 10 has yielded an upper jaw fragment with P^4 and M^1 resembling in size

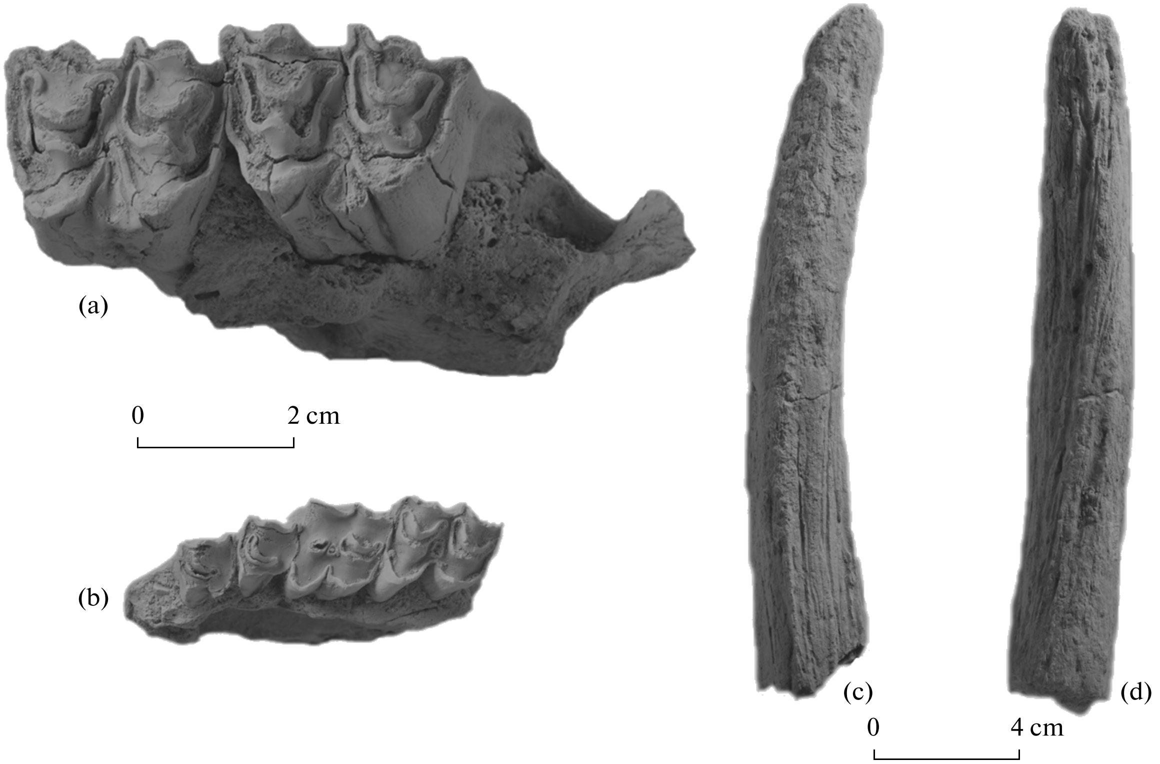

Fig. 8. Bovidae from the Trlica locality (Montenegro), Pleistocene: (a) *Leptobos* cf. *etruscus*, specimen TRL 2013/10/31, maxillary fragment with M^2–M^3; (b) Caprini (?*Capra*), specimen TRL 2011/10/33, maxilla with P^3–M^3; ventral view; (c, d) *Gazellospira* sp., specimen TRL 2013/10/32, horn: (c) anterior and (d) posterior views.

and morphology *L. gallicus* Azzaroli, 1952 (=*Cervalces gallicus* after Breda and Marchetti, 2005) (Fig. 7f). They are smaller and more primitive than in *Cervalces carnutorum* (Laugel, 1862) and *C. latifrons* (Johnson, 1874). Measurements: LP^4, 21.4; WP^4, 24.6; LM^1, 24.5; WM^1, 28.2. *L. gallicus* is described from Senèze, France. This predecessor of *C. carnutorum* and *C. latifrons* occurred in the Middle–Late Villafranchian (MNQ17–MNQ18) (Breda and Marchetti, 2005). The faunal list of Trlica based on early collections includes *C.* cf. *carnutorum* (Crégut-Bonnoure and Dimitrijević, 2006). It remains uncertain which part of the section it comes from; they were probably found above layer 10.

The **family Bovidae**. Based on the material collected in Trlica in 2010–2014, the presence of three bulls (Bovinae) of two genera has been established, *Bison* H. Smith, 1827 and *Leptobos* Rütimeyer, 1878.

The faunal list of Trlica initially included *Bison* cf. *schoetensacki* Freudenberg, 1910 (Forsten and Dimitrijević, 2002–2003; Dimitrijević et al., 2006) and, later, *Bison* (*Eobison*) sp., which was described by previous researchers (Crégut-Bonnoure and Dimitrijević, 2006; Argant and Dimitrijević, 2007). According to our data, Trlica has both species.

Abundant teeth and tooth fragments of a small primitive bison from layers 10 and 11 are determined as *Bison* (*Eobison*) sp.

B. cf. *schoetensacki* is represented by several molars from layer 5. The species *B. schoetensacki* occurred in the Galerian (Gliozzi et al., 1997).

Leptobos cf. *etruscus* (Falconer, 1868) is represented by teeth and tooth fragments from layers 10 and 11 and an incomplete humerus and metacarpal and the first phalanx from layer 11. The teeth are relatively large, with relatively low crowns and very weak cement covering enamel. The upper molars have well-developed ribs, high rounded styles and high and wide entostyles (Fig. 8a). Measurements: LM^2, 30.52; WM^2, 25.6; LM^3, 33.6; WM^3, 24.8; LM_3, ca. 42, WM_3, ca. 15; transverse diameter of the humeral trochlea, 97.6; transverse diameter of upper end of metacarpal, 67.9; its anteroposterior diameter, 42; first phalanx length, 68.5. It corresponds in size to the forms of the beginning of the Late Villafranchian, in particular, *L. etruscus* from Fonelas P-1 (MNQ18, ca. 1.8 Ma) in Spain (Garrido, 2008). *L. etruscus* differs from other species in the large size and structural details of the skull and horn. This species occurred in Europe in the first half of the Late Villafranchian. In the Central Balkans, *Leptobos* sp. has been recorded in the Čortanovci locality (Dimitrijević and Kneževič, 1996). In Greece, the latest *Leptobos* is known in the Late Villafranchian of Livakos (Koufos and Kostopoulos, 1997).

Antelopes (Tragelaphinae) are represented by the genus *Gazellospira* Pilgrim et Schaub, 1939. An incomplete left horn of a spiral-horned antelope with broken off lower and upper ends with characteristic characters of the genus (from layer 10), very weakly heteronomously twisted horn axis and two keels (weaker anteroexternal and more strongly developed posteroexternal) is determined as *Gazellospira* sp. (Figs. 8c, 6d). The anteroposterior diameter at the base is 32.2 mm and the transverse diameter is 31.5 mm. It differs from *Pontoceros* and *Spirocerus* in the weaker torsion of the horn and, in addition, from *Pontoceros* in the twisting type. The genus *Gazellospira* was widespread in the Villafranchian of Eurasia, where it was represented by the species *G. torticornis* (Aymard, 1854), which occurred from the Pyrenean Peninsula to Black Sea Region. In the Balkan Peninsula, *G. torticornis* is found in the Middle Villafranchian of the Volax, Vatera, and Sesklon localities and in the Late Villafranchian of Alikes in Greece (Koufos and Kostopoulos, 1997; Koufos, 2001).

The subfamily Caprinae is represented by two forms of small and medium-sized goats (Caprini) and two musk oxen species (Ovibovini), *Megalovis balcanicus* Crégut-Bonnoure et Dimitrijević, 2006 and *Soergelia intermedia* Crégut-Bonnoure et Dimitrijević, 2006.

Very small hypsodont teeth from layer 10 are determined as Caprini indet. An incomplete maxilla with P^3–M^2 (with labially disrupted P^3 and P^4) (Fig. 8b) and isolated teeth from layers 10 and 11 are referred to as Caprinae (?*Capra*). Caprinae (?*Capra*) is similar in size to small antelopes from Gerakarou and extant *Rupicapra*. The Caprinae were common in Villafranchian faunas of mountain regions. Various small and medium-sized Caprinae occurred in Late Villafranchian and later faunas of southeastern Europe (Kostopoulos, 1997; Fernandes and Crégut-Bonnoure, 2007). Rupicaprini, Ovini, and Caprini have been found in Kozarnika Cave (Fernandes and Crégut-Bonnoure, 2007) and in Slivintsa in Bulgaria (Spassov, 2003).

Megalovis balcanicus was described from Trlica based on fragments of skulls, horns, and many isolated teeth; the holotype of species is a skull fragment with horns (Crégut-Bonnoure and Dimitrijević, 2006). Layers 10 and 11 have yielded many isolated teeth of this species. *M. balcanicus* resembles somewhat *Megalovis* from the Pirro Nord Fauna, Italy. *M.* aff. *balcanicus* is present in Kozarnika Cave, apparently B2-2 Biozone (1.6–1.4 Ma) along with *Soergelia* aff. *intermedia* (Fernandes and Crégut-Bonnoure, 2007).

The holotype of *Soergelia intermedia* is a right lower jaw with P_2–M_3 from Trlica (Crégut-Bonnoure and Dimitrijević, 2006). Layers 10 and 11 have yielded isolated teeth corresponding in morphology and size to this species. In morphology, *S. intermedia* is similar to *S. brigittae* from Apollonia 1, Greece, and *Soergelia* from Vallonnet, France (Crégut-Bonnoure and Dimitrijević, 2006).

Remains of Ovibovini indet. are present in layers 5, 7, 8, and 9.

DISCUSSION

The data on the evolutionary level and stratigraphic range of particular species suggest that faunas from the lower and upper parts of the bone-bearing strata differ in geological age and allow the recognition of two faunal stages: (1) the fauna from the lower part of the section, including layers 11 and 10, TRL11–10, and (2) the fauna from the upper part of the section, layers 7–5, TRL7–5.

The TRL11–10 fauna contains *Canis etruscus, Canis* sp., Canidae (*Vulpes* aut *Nyctereutes*), Mustelidae indet., *Lycaon lycanoides, Ursus etruscus, Pachycrocuta brevirostris, Megantereon cultridens, Homotherium crenatidens, Panthera onca* cf. *gombaszoegensis*, ?*Acinonyx pardinensis*, Elephantidae indet. (?*Archidiskodon meridionalis*), ?*Palaeoloxodon* sp., *Stephanorhinus etruscus, Equus stenonis, Equus* cf. *major, Praemegaceros* sp., *Cervus* sp. (ex gr. *elaphus*), *Eucladoceros* sp., Cervini gen., *Capreolus* sp., *Libralces* cf. *gallicus*, Bison (*Eobison*) sp., *Leptobos* cf. *etruscus, Gazellospira* sp., *Megalovis balcanicus, Soergelia intermedia*, Caprini indet. (small form), and Caprini (?*Capra*).

This fauna belongs to the upper Early Pleistocene, Late Villafranchian, in the interval 1.8–1.4 Ma (Table 2). This conclusion is supported by the presence of *Libralces* cf. *gallicus*, *Leptobos etruscus*, *Gazellospira*, associations of *Lycaon lycanoides*–*Canis etruscus* and *Equus stenonis*–*E. major*, and the data on the evolution of the *Canis etruscus*–*C. mosbachensis, Ursus etruscus*–*U. deningeri, Homotherium crenatidens*–*H. latidens*, and *Stephanorhinus etruscus*–*S. hundsheimensis* lineages. In the species composition, the TRL11–10 fauna is similar to Late Villafranchian faunas of Europe and the Caucasus: Saint Vallier, MNQ18 (France), Tegelen (Netherlands), Olivola–Tasso Faunal Units (Italy), Dmanisi (Georgia), Gerakarou (Gerakarou Formation, red beds = Olivola–Tasso Faunal Units; Platanochori Formation, conglomerates = Farneta Faunal Units), Livakos and Alikes (Greece) (Gliozzi et al., 1997; Koufos and Kostopoulos, 1997; Gabunia et al., 2000; Spassov, 2003; Palombo et al., 2006; Kahlke et al., 2011). In southeastern Europe, an approximately coeval fauna is known from Kozarnika Cave, B2-2 level (1.6–

Table 2. Distriburtion of large mammals in the Early Pleistocene and beginning of the Middle Pleistocene

Ma		1.8	1.5–1.4	1.2–1.1	1.0–0.9 0.78
Genera and species	Pleistocene				
	Early				Middle
	Villafranchian			Epivillafranchian	
				Galerian	
	Middle	Late		Early	Middle
	MNQ 17	MNQ 18	MNQ 19	MNQ20	MNQ21
Canis etruscus	▬	▬	▬		
Lycaon lycanoides		▬	▬	▬	▬
Ursus etruscus	▬	▬	▬		
Ursus deningeri				▬	▬
Megantereon cultridens	▬	▬			
Homotherium crenatidens	▬	▬	▬		
Pantera onca gombaszoegensis		▬	▬	▬	▬
Acinonyx pardinensis	▬	▬	▬	▬	▬
Pachycrocuta brevirostris		▬	▬	▬	▬
Crocuta				▬	▬
Archidiskodon meridianalis	▬	▬	▬	▬	▬
Palaeoloxodon antiquus				▬	▬
Stephanorhinus etruscus	▬	▬			
S. cf. *hundsheimensis*			▬	▬	
S. hundsheimensis					▬
Equus stenonis	▬	▬	▬		
Equus major	▬	▬			
Equus suessenbornensis				▬	▬
Libralces gallicus	▬	▬			
Capreolus	▬	▬	▬	▬	▬
Cervus acoronatus		▬	▬	▬	▬
Praemegaceros	▬	▬	▬	▬	▬
Praemegaceros verticornis				▬	▬
Megalovis	▬	▬	▬	▬	▬
Megalovis balcanicus		▬	- - -	- - ?	
Soergelia		▬	▬	▬	▬
Soergelia intermedia		▬	- - -	- - ?	
Gazellospira torticornis	▬	▬			
Bison (*Eobison*)		▬	▬		
Bison (*Bison*)				▬	▬
Bison (*Bison*) *schoetensacki*				▬	▬
Leptobos etruscus		▬			
Trlica layers		TRL11–10			TRL6–5

1.4 Ma) (Gaudelli et al., 2005; Fernandes and Crégut-Bonnoure, 2007).

The absence in the TRL11–10 fauna of forms that appeared in Europe at the end of the Late Villafranchian (the wolves *Canis mosbachensis–C. variabilis*, arctoid and cave bears, the horse *Equus suessenbornensis*, and the bison *Bison schoetensacki*) is evidence that it is more ancient than Epivillafranchian faunas, such as Apollonia in Greece and Untermassfeld in Germany (Koufos and Kostopoulos, 1997; Kahlke et al., 2011). In addition, Trlica is definitely more ancient than Apollonia in the evolutionary level of horses and bisons. Untermassfeld shares many species with the TRL11–10 fauna, although, judging from available data (Kahlke, 2007; Kahlke et al., 2011), *Ursus, Canis*, and Alcinae are represented by more advanced species: *Ursus rhodei, Canis mosbachensis*, and *Alces carnutorum* (*=Cervalces carnutorum*).

The TRL6–5 fauna includes *Ursus deningeri, Crocuta* sp., *Stephanorhinus hundsheimensis, Equus* cf. *suessenbornensis, Cervus* cf. *acoronatus, Praemegaceros* cf. *verticornis*, ?*Capreolus* sp., *Bison* cf. *schoetensacki*, and Ovibovini indet.

The presence in the TRL7–5 fauna of forms that appeared for the first time at the Villafranchian–Epivillafranchian boundary, at the beginning of the Galerian (*U. deningeri, Crocuta, E.* cf. *suessenbornensis, Bison* cf. *schoetensaki*) (Palombo et al., 2006) is evidence that it should be dated at most 1.2 Ma. The fauna belongs to the Galerian faunal stage (terminal Early Pleistocene–beginning of the Middle Pleistocene).

CONCLUSIONS

In the material collected in the Trlica locality from 2010 to 2014, 38 large mammal belonging to four orders and ten families have been determined, i.e., Carnivora (Ursidae, Hyaenidae, Felidae, Canidae, and Mustelidae), Proboscidea (Elaphantidae), Perissodactyla (Rhinocerothidae and Equidae), and Artiodactyla (Cervidae and Bovidae); 29 of them come from lower, layers 10 and 11.

It is shown that faunas from the upper and lower parts of the bone-bearing strata differ in age. Two faunal levels (TRL11–10 and TRL6–5), which belong to two stages in the faunal evolution of the Central Balkans are established, i.e., (1) Late Villafranchian, 1.8–1.2 Ma, and (2) transitional between the Early and Middle Pleistocene, when the faunal composition changed considerably; many Villafranchian species disappeared and a number of extant genera (in particular, *Crocuta*) appeared.

The faunal levels differ in the taxonomic composition of mammals and the presence of different species of bears, rhinoceroses, and horses: *Ursus etruscus, Stephanorhinus etruscus, Equus* cf. *major*, and *E. stenonis* in the lower faunal level and *U.* cf. *deningeri, S. hunscheimensis, E.* cf. *suessenbornensis*, and, probably, *E.* cf. *altidens* in the upper faunal level.

A significant part of taxa in the Trlica Fauna are recorded for the first time, including *Megantereon cultridens,* ?*Acinonyx pardinensis, Lycaon lycanoides, Libralces* cf. *gallicus*, *Praemegaceros*, *Cervus* cf. *acoronatus, Capreolus*, and *Gazellospira* in the lower faunal level and *Crocuta*, *Ursus deningeri, Praemegaceros* cf. *verticornis, Bison* cf. *schoetensacki*, and *Leptobos* cf. *etruscus* in the upper faunal level.

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