Pleistocene horses (genus Equus) in the central Balkans

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Abstract. A review of the fossil horses of the genus *Equus* from the central Balkans, a mountainous area comprising Serbia and Montenegro, is presented in this paper. The time period covered by the finds is from the late Early to and including the Late Pleistocene, but the record is not complete: the dated finds are Late Pleistocene in age, while Early and Middle Pleistocene are poorly represented. The horses found resemble those from neighbouring countries from the same time period, probably showing the importance of river valleys as migration routes. The Morava River valley runs in a roughly south-to-north direction, connecting, via the Danube and Tisa River valleys, the Hungarian Pannonian Plain in the north with northern Greece in the south, via the Vardar River valley in Macedonia. In Pleistocene, large mammals, including horses, probably used this route for dispersal.

Keywords: fossil remains, horses, Equus, Pleistocene, Balkans.

Абстракт. У раду су приказани фосилни остаци коња, различитих врста рода *Equus*, који потичу из планинске области централног Балкана, односно територија данашње Србије и Црне Горе. Старост приказаних остатака покрива период од краја старијег плеистоцена до краја плеистоцена. Бројни остаци потичу из горњег плеистоцена, док су налази из средњег и доњег плеистоцена ретки. Налази коња слични су налазима из истог периода суседних области, што вероватно указује на значај долина река као миграционих путева. Долина Мораве пружа се приближно у правцу север–југ, и повезује Панонску низију на северу, преко долина Дунава и Тисе, и јужни део Балканског полуострва, преко долине Вардара у Македонији. Ово је у плеистоцену био један од важних миграционих путева за крупне сисаре, укључујући и коње.

Кључне речи: фосилни остаци коња, *Equus*, плеистоцен, Балканско полуострво.

Introduction: Geographic setting, Pleistocene record, and hiatuses

The Central Balkans is a low to medium high mountainous region on the southern margin of the Pannonian Plain (Fig. 1). It is situated between two mountain belts, the Dinarids and the Carpatho–Balkanids. The dominant feature of the region is the Morava River, flowing from its sources in the south to unite with the Danube in the northeast, its valley connecting rather than separating the East and the West. In Macedonia, it almost meets the Vardar River with its tributaries, flowing south into Greece. The sharp contrast between the continental climate of the Pannonian Plain in the north and the Mediterranean climate in the south becomes here gradually less pronounced. The records of the Pleistocene horses in the Central Balkans is not complete. There are long hiatuses not documented by known deposits or fossils, nor, probably, are all the members of the genus *Equus* once present in the area represented by finds. The Pliocene, the age of the dispersal of *Equus*' in Eurasia (LINDSAY *et al.*, 1980), is represented by a find of *Leptobos* sp. from Čortanovci (DIMITRIJEVIĆ & KNEŽEVIĆ, 1996), by finds of *Anancus arvernensis* (CROIZET & JOUBERT) from Beočin, Sremski Karlovci, and Banovo Brdo (Belgrade) (PA-VLOVIĆ *et al.*, 1976; PETRONIJEVIĆ, 1951, 1952), and of *Zygolophodon borsoni* HAYS from Humka and Kamendol (PETRONIJEVIĆ, 1970), attributed either to Middle or Upper Pliocene. There are no finds of horses.

Two other major stratigraphic stages, Lower and Middle Pleistocene, are poorly represented by fossils.

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Accordingly, the important replacement of stenonid (zebroid) horses by caballoid or true horses, elsewhere locally documented by the sympatry of these two groups, is not known here. There is a single find of typical stenonid horses, dated to the latest Early or earliest Middle Pleistocene, but the rest are all true caballoids.

Trlica

Stenonid horses are represented from a single locality, i. e. Trlica in northern Montenegro (Fig. 1B: 11). The rarity of Lower and Middle Pleistocene deposits in the studied area makes this find unique.

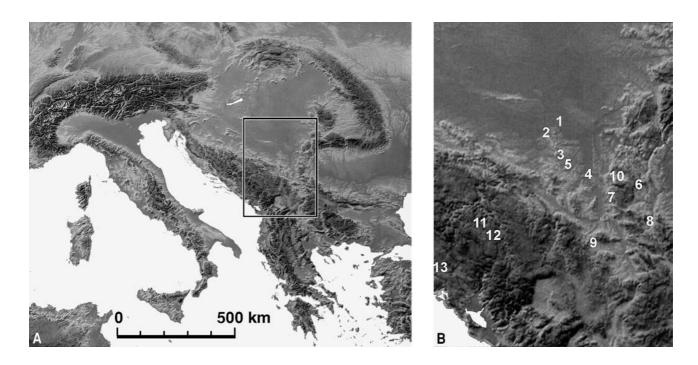


Fig. 1. Geographical position of the area studied (A), and fossil horses sites (B). 1 = Tešića Ciglana, Belgrade; 2 = Ostružnica; 3 = Risovača; 4 = Despotovac; 5 = Gradac, 6 = Baranica; 7 = Ravanička Cave; 8 = Vrelska Cave; 9 = Stubal; 10 = Lazareva Cave; 11 = Trlica; 12 = Medena Stijena; 13 = Crvena Stijena.

The presence of *E. hydruntinus* REGALIA characterizes the Late Pleistocene. The known finds of fossil horses in the Central Balkans are Late Pleistocene in age, either stray finds in loess or alluvia, or material collected during archaeological excavations in caves or rock shelters; more recently palaeontological excavations have been done. The finds have mainly been dated on the basis of archaeological or faunal evidence; we have been able to get some finds radiometrically dated, thanks to the courtesy of HÖGNE JUNGNER of the Dating Laboratory, Helsinki University.

The earliest stage: stenonid horses

Stenonid horses in the Central Balkans are first mentioned in a paper on loess plateaux and sands in Vojvodina (MILOJEVIĆ, 1950). The paper briefly reports on a lower molar, identified by Vladimir Laskarev as *Equus* sp. aff. *stenonis* COCCHI, from the south-west-ern Banat loess plateau. The tooth had not been relocated.

Trlica is a hill composed of Triassic limestone situated north of the city of Pljevlja. A karstic cavern formed in the limestone and filled in with clastic deposits was accidently revealed during construction of the road Pljevlja–Bjelo Polje, in the early 1960's. The deposits, containing mammalian bones and teeth, were excavated during two short field campaigns in 1988 and 1990 (DIMI-TRIJEVIĆ, 1990), and more recently, in 2001.

There are carnivore teeth marks on some of the bones, but not to such an extent that the sample could be regarded as an accumulation in a hyena den. Neither, probably, was it a natural trap, since no complete skeletons or articulated parts of skeletons have been found. The bones are mostly fragmentary, but not markedly worn by water transportation. The bones and teeth were probably scattered in the near vicinity of the locality and were brought into the cavern after a short transport by water and/or gravitation.

The following species have been identified: *Dolomys* dalmatinus KORMOS, Hystrix sp., ?Canis sp., Ursus sp., Pachycrocuta brevirostris (AYMARD), Elephantidae indet., Stephanorhinus cf. hundsheimensis (TOULA), Equus ste-

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nonis, Megacerini indet., ?*Cervus* sp., *Bison* cf. *schoetensacki* FREUDENBERG, *Megalovis* sp., and Caprinae indet. (DIMITRIJEVIĆ, 1990; CODREA & DIMITRIJEVIĆ, 1997); to this list we here add *Equus* cf. *major* BOULE. Large herbivores, particularly ruminants, are the most numerous, while the carnivores and rodents are each represented by a few bones and/or teeth each.

The species found would date the fauna to the late Early or early Middle Pleistocene. The stratigraphic age is more precisely defined by *Stephanorhinus* cf. *hund-sheimensis*, which correlates the fauna with biozones 20–22 (GUERIN, 1980) and MQ3 (late Lower Pleistocene) (AGUSTI *et al.*, 1987). Several layers could be distinguished in the cave profile, showing that conditions were changing during deposition, although probably not during a long time span. The presence of *Hystrix* indicates a temperate climate (MAUL, 1994).

Since the horse sample is small, consisting mainly of isolated cheek teeth, we consider it as a single unit. There are: R PD 3-4 (TRL 88/25/1); L PM2 (TRL 88/20); R and two L PM 3-4 (TRL 90/18/1, 87/5, and 90/11/1); seven R and four L M1-2 (TRL 90/10/2, 96/7, 90/14/2, 90/10/1, 01/11/1); R M3 (TRL 90/7/1); PM/M indet. (TRL 90/12/1, 90/8/1, 88/18/8, 94/2/1, 01/1/1, 01/21/28, and 01/22/43); Lpd3-4 (01/22/2); L pm2 (TRL 90/14/1, 90/9/1, and 01/5/2); three L and four R pm 3-4 (TRL 96/6, 87/7, 88/29/1, 01/22/1, 01/4/3, 01/14/3, and 01/5/1); five L and seven R m1-2 (TRL 87/6, 90/5/1, 88/18/9, 88/26/1, 88/27/1, 90/16/2, 90/6/1, 96/8, 90/13/1, 01/21/29, 01/22/42, and 01/19/4); L m3 (TRL 94/1/1); fragmentary epistropheus (TRL 88/28/1); distal left tibia (TRL 90/17/1), and distal left metapodial (TRL 88/24/1). The material is the property of the Institute for the Protection of Nature, Podgorica, Montenegro.

With the exception of three large specimens, right PM3–4 (TRL 90/18/1), left m1–2 (TRL 90/5/1), and possibly also right m1–2 (TRL 96/8), which we refer to *E*. cf. *major*, (Fig. 2) (Table 1). The rest of the horse sample seems homogeneous. It belonged to a medium-sized horse, which we identify as *E. stenonis* on the basis of dental evidence (Fig. 3) (Table 2), since the bones are few. The distal tibia (TRL 90/17/1) is abraded and therefore appears narrow, but the measurements on the distal metapodial (TRL 88/24/1) are slightly larger than the corresponding means, although within the ranges, of *E. stenonis* from Valdarno, Italy, the hypodigm or type sample.

Table 1. *Equus* cf. *major* BOULE from Trlica. Abbrevations: H = height; Locc. = oclusal length; Bocc. = oclusal breadth; Lprot. = protocon length.

		Н	Locc.	Bocc.	Lprot.
TRL 90/18/1	L PM3/4	57.50	35.75	30.85	12.25
TRL 90/5/1	L m1/2	58.40	31.20	16.30	
TRL 96/8	R m1/2	63.55	31.25	15.60	

Table 2. Trlica *Equue stenonis* COCCHI. The abbreviations are the same as in Table 1.

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			Locc.	Bocc.	Lprot.
TRL 88/25/1	R D3/4	30.55	43.20	20.60	12.00
TRL 88/20	L PM2	33.00	40.30	26.10	6.70
TRL 87/5	L PM 3/4	68.20	30.85	25.80	10.50
TRL 90/11/1	R PM3/4	38.90	~28.30	~27.20	8.50
TRL 90/8/1	L M1/2	76.60	31.65	24.05	9.65
TRL 88/18/8	L M1/2	~50.50	27.75	-	-
TRL 94/2/1	L M1/2	76.10	29.30	24.25	12.05
TRL 96/7	R M1/2	77.30	29.90	26.80	12.45
TRL 90/14/2	R M1/2	very young	30.80	-	10.10
TRL 90/10/1	R M1/2	65.20	29.05	-	9.70
TRL 90/12/1	R M1/2	>67.50	30.40	25.50	9.40
TRL 90/7/1	R M3	59.50	23.45	>19.20	-
TRL 90/10/2	R M3	>>31.50	-	-	9.25
TRL 90/14/1	L pm2	53.40	34.80	16.60	
TRL 90/9/1	L pm2	18.70	30.75	14.65	
TRL 88/29/1	L pm3/4	40.25	29.15	16.90	
TRL 96/6	R PM3/4	57.60	31.00	15.60	
TRL 87/7	R pm3/4	45.00	31.60	17.05	
TRL 87/6	L m1/2	67.70	~29.00	13.20	
TRL 88/18/9	L m1/2	~62.00	30.80	12.20	
TRL 88/26/1	L m1/2	51.50	-	12.20	
TRL 88/27/1	R m1/2	>41.00	26.80	13.40	
TRL 90/16/2	R m1/2	>68.20	-	-	
TRL 90/6/1	R m1/2	50.80	28.40	14.10	
TRL 90/13/1	R m1/2	>>57.00	31.40	10.75	
TRL 94/1/1	Lm3	60.35	29.30	13.55	

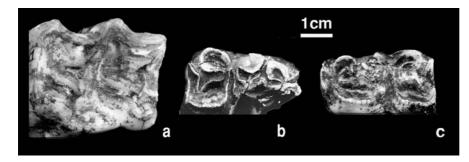


Fig. 2. *Equus* cf. *major* BOULE from Trlica: **a**. L PM3/4 (TRL 90/18/1); **b**. L m1/2 (TRL 90/5/1); **c**. R m1/2 (TRL 96/8).

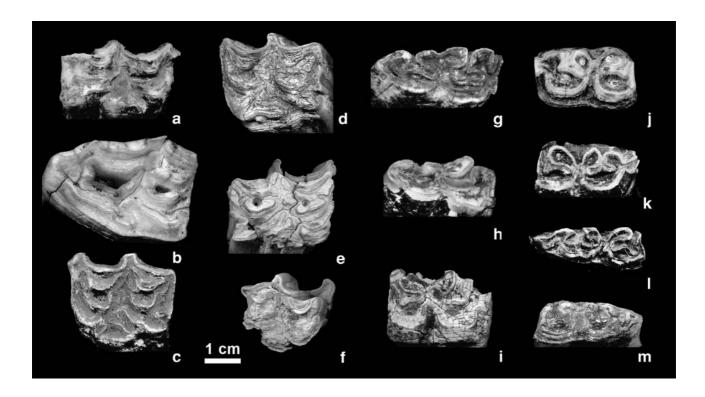


Fig. 3. *Equus stenonis* CoccHI from Trlica: **a**. R D3/4 (TRL 88/25/1); **b**. L PM2 (TRL 88/20); **c**. L PM3/4 (TRL 87/5); **d**. L M1/2 (TRL 94/2/1); **e**. R M1/2 (TRL 90/12/1); **f**. R M1/2 (TRL 90/10/2); **g**. L pm2 (TRL 90/14/1); **h**. L pm2 (TRL 90/9/1); **i**. R pm3/4 (TRL 88/29/1); **j**. L m1/2 (TRL 87/6); **k**. R m1/2 (TRL 90/6/1); **l**. R m1/2 (TRL 90/13/1); **m**. L m3 (TRL 94/1/1).

The unworn upper M1–2 reach approx. 80 mm in crown height. Plotted on their occlusal breadth to length, the cheek teeth fall in the upper range of *E. stenonis* from Valdarno (Figs. 4, 5). The protocones are short (Fig. 3a–f): the mean lengths are 9.41 mm in PM 3–4 and 10.56 mm in M1–2, with a mean plication count of appr. 8 plications, including a pli caballin. In early wear,

the post-protoconal grooves are deep, reaching the prefossettes; the hypocones are lingually indented. The labial styles are not grooved even in PM3-4.

In the lower cheek teeth (Fig. 3g-m), the metaconid-metastylid double knots are typically stenonid, with V-shaped lingual grooves. The double knots tend to droop in pm3-4 and in some of the worn teeth they

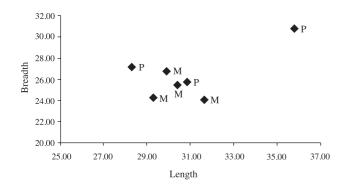


Fig. 4. Occlusal breadth plotted to occlusal length of the upper cheeck teeth of the horses from Trlica. P = premolar, M = molar. Premolar in the upper right belongs to *E. major* BOULE.

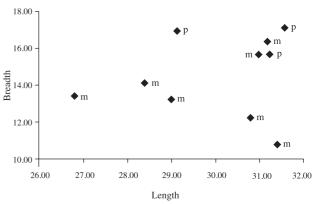


Fig. 5. Occlusal breadth plotted against occlusal length of the lower cheeck teeth of the horses from Trlica. p = pre-molar, m = molar. Molars in the upper right cluster indicate *E. major* BOULE.

take on a caballoid shape. "Protostylids" may be developed in pm2, e.g. TRL 90/14/1, (Fig. 3g) but protostylid plications are not marked in pm3–4 or m1–2. Molar ectoflexids are deep, even ending flat at the double knot, and the plis caballinid disappear with wear.

The large right PM3–4 (TRL 90/18/1) resembles *E. major* in occlusal length, but is narrower (Fig. 2a). The labial styles are massive, but not grooved; the hypocone is lingually indented. The two m1–2 (TRL 90/5/1 and 96/8) (Fig. 2b–c) differ from the other lower molars in that they are of greater length and breadth. We identify these three teeth as *E.* cf. *major*.

Stenonid horses are known from neighbouring regions: Croatia (MALEZ *et al.*, 1992), Northern Greece (TSOU-KALA, 1989; KOUFOS, 1992; KOUFOS & KOSTOPOULOS, 1993; KOUFOS & VLACHOU, 1997; KOUFOS *et al.*, 1997), Bulgaria (SPASSOV, 1997), Rumania (SAMSON, 1975), and Hungary (MOTTL, 1943; KRETZOI, 1954; JANOSSY, 1978). These finds have been dated Middle and Late Villafranchian (Late Pliocene–Early Pleistocene), even late Middle Pleistocene. The latter date may indicate that stenonid horses other than *E. hydruntinus* lived on the Balkans longer than elsewhere in Europe.

Compared with known described occurrences, the Trlica horse shows the closest similarity with finds from bone breccias on the islands of Iz and Vis, Croatia, dated "Villafranchian" (MALEZ et al., 1992), with slender-built stenonids from the Middle Villafranchian of the Mygdonia Basin, Greece (KOUFOS, 1992) and Kislang, Hungary (KRETZOI, 1954), but also with E. stenonis "minor" from Varberg, Hungary (MOTTL, 1943), dated "Altpleistozän", but believed possibly to date from the early Mindel-Riss (Holsteinian) interglacial (JANOSSY, 1969). Other finds, such as the Middle Villafranchian occurrences from Dafnero, Volax, Apollonia, and Sésklo, Greece (KOUFOS & KOSTOPOULOS, 1993; KOUFOS & VLA-CHOU, 1997, KOUFOS et al., 1997, ATHANASSIOU, 2001) appear to be slightly larger than the Trlica horse, those from Petralona, Greece, and Podumci, Croatia (TSOUKALA, 1989; MALEZ et al., 1992), dated Middle Pleistocene, to be slightly smaller. Considerably larger stenonids, identified as E. major, E. robustus POMEL, or E. sp., have been found from the Villafranchian of Rumania, from Osztramos Loc. 7, Hungary, and from Šandalja I and Razine, Croatia (SAMSON, 1975; JANOSSY, 1978; MALEZ et al., 1992). From Kislang, E. cf. stenonis occurs together with a very large stenonid horse, probably E. major.

The later stages: caballoid horses

The loess record

Tešića Ciglana

In an area which in former days was the periphery of the city, but now is part of the centre of modern Belgrade, a brick-works, named Tešića Ciglana, was opened exploiting loess "earth" (Fig. 1B: 1). Pleistocene large mammal remains were found in this earth. LASKA-REV (1926) gave a short description of the find and a list of the species identified. The bones and teeth of animals identified as *Elephas primigenius* BLUMENBACH, *Bos* sp., and *Equus "woldrichi"* ANTONIUS, were scattered on the surface within an area of approximately 75 square meters.

Laskarev was an experienced paleontologist, who contributed significantly to Neogene and Quaternary biostratigraphy of Serbia. His identification of the fossils should be taken seriously, with amendmants for changes in the taxonomy and nomenclature of the species. Thus in addition to the horse, there were remains of *Mammuthus primigenius* and of a large bovid, probably *Bison priscus* (BOJANUS). The generic name "*Bos*" was at that time applied to both aurochs and bison, but *Bison priscus* was much more frequent in the Pleistocene of the region than was *Bos primigenius* BOJANUS.

The most important information about the find is that it came from the lower part of the second loess horizon. The loess deposits in the surroundings of Belgrade constitute the southern margin of the loess cover of the Pannonian Plain. The loess reaches a thickness of over 30 m in places and covers deposits of various ages, mostly Neogene freshwater deposits and Middle Pleistocene fluvio-lacustrine sediments (the so-called "layers with Corbicula fluminalis"). For a long time it was thought that loess deposition began in the Middle Pleistocene Rissian, and was finished at the end of the Pleistocene (LASKAREV, 1922; STEVANOVIĆ, 1977). More recent data indicate an older age. In one of the profiles of the Danube embankment, 15 km downstream from Belgrade, 12 paleosols can be distinguished. Samples of the paleosols were dated by the thermoluminiscence method, which showed that the oldest soil could be equated with the oxygen isotope stage (OIS) 15 (535000 years BP) (BUTRYM et al., 1991). The second Belgrade loess has been correlated with the second loess in the loess profiles from Batajnica, Stari Slankamen, and Neštin, and dated to the second Würm stadial (MARKOVIĆ-MARJANOVIĆ, 1972). The lower part of the second loess in the Mošorin-Surduk Dukatar profile has been dated to 35 900 +/- 500 BP (Lub-1905) and in the Stari Slankamen-Čot profile to 37000 +/- 600 BP (Lub-1892)(BUTRYM et al., 1991). These dates compare closely with the 14C date 36680 +/- 1100 BP (NLJ 306) for the uppermost part of the paleosol beneath the second Belgrade loess (MARKOVIĆ-MARJANOVIĆ, 1976).

There are two sets of maxillary teeth of a horse from the Belgrade loess, one of a mature individual (complete right row, LV 21/2, 21/1, 21/3, 21/10, 21/11, and 21/9 (Fig. 6a), and left PM3–M2, LV 21/25, 21/24, 21/26, and 21/23), and another of a young adult animal (complete right row, LV 21/20, 21/19, 21/21, 21/17, 21/13, and 21/16 (Fig. 6b), and left PM3–M3, LV 21/22, 21/12, 21/18, 21/14, and 21/15). In addition, there are 4 incisors (LV 21/5–21/8), probably belonging to the younger animal, as well as a fragment of an indeterminate incisor

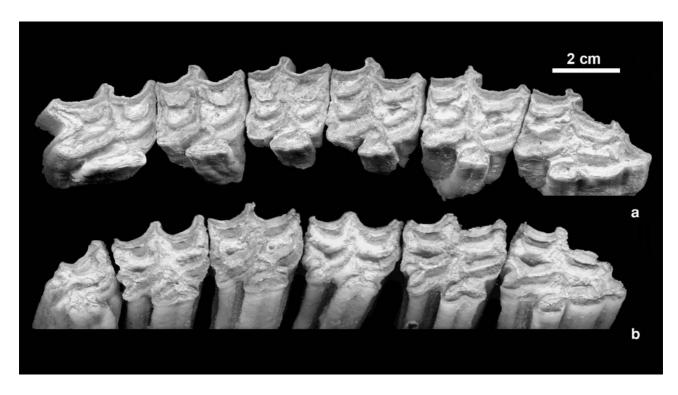


Fig. 6. Upper tooth rows from Tešića Ciglana: **a**. mature individual, right upper tooth row (LV 21/2, 21/1, 213, 21/10, 21/11, 21/9); **b**. young adult individual, right upper tooth row (LV 21/20, 21/19, 21/17, 21/21, 21/13, 21/16).

(LV 21/4). The sample is in the Faculty of Mining and Geology, University of Belgrade.

The teeth, which evidently represent a caballoid horse, although the diagnostic lower cheek teeth are lacking, are medium sized; the total tooth rows measure appr. 165–175 mm at the alveoli. In the mature PM3 (LV 21/1 and 21/25) the protocones are very short, only a little longer than in PM2. In the young adult PM 3 (LV 21/19 and 21/22), the protocones approach those of PM 4 in length. The mean protoconal length of PM3–M2 of the two individuals together is only 11.8 mm (N 8, range 8.97–13.5 mm). The hypocones in PM2–4 are lingually indented and there is a pli hypostyle overhanging the hypoconal groove; the labial styles are angled or grooved, in M1–3 they are simple, but the mesostyles may be slightly grooved lower down. The plication counts are 3–8 plications; in the molars the plis caballin tend to disappear with wear.

The size of the horse teeth from the Belgrade second loess compare best with those of late Late Pleistocene caballoids from Central Europe (FORSTEN, 1991: fig. 4), but are on the small side compared with those of the middle Late Pleistocene, corresponding to the dates of approx. 35 900–37 000 BP and 36 680 BP for the second loess and paleosol, respectively. The species *E. "woldrichi*", to which these specimens were originally referred, is based on a horse skull from Krems, Austria, believed to represent the Late Pleistocene "loess horse" (ANTONIUS, 1912). The species was poorly described, without photographs and measurements, and is probably not valid; in addition its age is unknown. SCHLOSSER (1916), MOTTL (1938, 1941), and VERTES (1950) used the name for fossil horses from Eichstätt, Germany, Bergavölgy and Solymar, Hungary, respectively. The teeth referred to *E. woldrichi* by SCHLOSSER (1916) seem larger than those from the Belgrade loess, while the three specimens referred to MOTTL (1938, table 396) correspond to those of the latter.

A host of different names have been coined for Late Pleistocene medium sized to smallish Eurasian caballoid horses; more recently usually identified as *E. caballus* L. with "subspecies". For fossil forms, GENTRY *et al.* (1996) have proposed *Equus ferus* BODDAERT to replace *E. caballus*, a name originally given to the domestic horse (LINNAEUS, 1758).

Ciglansko Brdo, Smederovo

MARKOVIĆ-MARJANOVIĆ (1970) briefly described a fossil horse from the former brick – yard Jevremović, Ciglansko Brdo, in Smederevo. The site lies 50 m above the Danube riverbed. The Ciglansko Brdo hill shows two lithological members: an upper, 6 m thick series of three loess horizons and two paleosols, and a lower, 18 m thick stratified loess-like clay of aquatic origin, with gastropods and equid remains. The equid remains (parts of limb bones, part of rib, and two jaw fragments (MARKOVIĆ-MARJANOVIĆ, 1970) were found 14 m beneath the topographic surface. By correlating the Ciglansko Brdo lithology with that of the bore-core Kovin (Bolnica), MARKOVIĆ-MARJANOVIĆ (1970) dated the equid from Smederovo to the Mindel 2.

The material cannot be located, but the figures (MARKOVIĆ-MARJANOVIĆ, 1970) show right pm2–pm4 and left pm2–m2 of a caballoid horse, originally identified as the large stenonid E. cf. suessenbornensis WÜST, probably mainly because of the presumed Middle Pleistocene age of the find. Neither the size of the specimens nor the scale of the figures is given. In the left jaw, m1 has a deep ectoflexid reaching to the double knot. Morphologically these teeth do not differ from those of other caballoid forms.

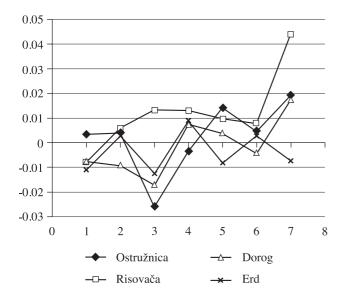


Fig. 7. Simpson's ratio diagram comparing seven measurements on MT III; standard arbitary. Compared are: single Mt III (No. 603) from alluvial of Ostružnica; sample means from Risovača, Erd and Dorog. Measurements (standards in logs in parentheses): 1 = (2.47) total length; 2 = (1.78) proximal breadth; 3 = (1.73) proximal diameter; 4 = (1.75) distal articular breadth; 5 = (1.76) distal protuberance breadth; 6 = (1.64) distal keel diameter; 7 = (1.60) mid–shaft width.

Alluvial deposits

Belgrade surrounding

Material: Left maxillary with PM2–M3 (No. 1591); right mandible with pm2–m2, I2 (No. 1397); and right MT III (No. 603), in the Natural History Museum, Belgrade. Right PM3–4 (ZP 5) and left mandible with pm2–m3 (RGF 87/01), in the Faculty of Mining and Geology, University of Belgrade. The Natural History Museum and the Faculty of Mining and Geology have in their collections remains of Pleistocene large mammals found in alluvial deposits, chiefly in deposits of the greatest rivers in the region, the Danube, Sava, Tisa, and Morava. Most numerous are the massive skeletal parts of the largest animals, e.g. the teeth and bones of mammoth and crania of bison, reflecting the selection of the collectors'; horse remains are scarce. Some specimens have exact data about the circumstance of their finding, while others only have a note on their alluvial origin. Several specimens are considered alluvial finds solely on the basis of the sediment preserved in the bone crevices.

The horse metatarsus (No. 603), in the collections of the Natural History Museum, was found from Ostružnica, a small town west of Belgrade (Fig. 1B: 2). In 1949, when the supporting columns of a railway bridge crossing the Sava River were built here, large mammal fossils were found in deposits known as the «Sava layers» (VESELINOVIĆ-ČIČULIĆ, 1952). Originally dated to the Holocene (LASKAREV, 1938; STEVANOVIĆ, 1977), the «Sava layers» were shown to contain Late Pleistocene mammals identified as *Bison priscus, Mammuthus primigenius,* and *Cervus* sp. (amended) (VESELINOVIĆ-ČIČULIĆ, 1952). According to the museum's inventory book, the metatarsus was found together with *M. primigenius, Megaloceros* sp., and *Bison* sp., indicating a stratigraphic age similar to the find described by VESELINOVIĆ-ČIČULIĆ, (1952).

We compared the bone (No. 603) with metapodials from the Late Pleistocene of the Risovača cave (FORSTEN & DIMITRIJEVIĆ, 1995) and with bones of similar age from Hungary in a Simpson's ratio diagram (Fig. 7). The bone is as large and massive as those compared with it.

Table 3. Maxilary and mandibulary cheek-teeth rows from alluvial deposits of Serbia. The abbreviations are the same as in Table 1.

		Н	Locc.	Bocc.	Lprot.
	PM2	42.00	44.55	26.70	12.05
	PM3	57.10	35.10	30.65	16.85
Left maxilla	PM4	~64.00	32.75	30.45	16.65
1591	M1	56.65	29.80	29.40	16.60
	M2	57.90	28.65	29.10	18.40
	M3	55.20	31.80	24.20	17.85
	PM2	-	32.55	15.20	
Distance dibt.	PM3	-	28.40	16.95	
Right mandible	PM4	-	27.30	16.60	
	M1	-	26.30	15.25	
	M2	-	27.97	14.40	
	PM2	-	32.70	14.05	
	PM3	-	29.50	15.45	
Left mandible 87/01	PM4	_	29.65	14.65	
	M1	_	27.40	13.70	
	M2	_	28.20	13.30	
	M3	~76.30	32.95	11.85	

The upper and lower jaws (Nos. 1591 and 1397) (Figs. 8, 9b) in the Natural History Museum are said to come from alluvial deposits, but lack locality data. There are no data on the mandible (RGF 87/01)(Fig. 9a) held in the Faculty of Mining and Geology, but river pebbles in the canine alveolus and dark sand with muscovite particles in the incisor alveoli and in cracks in the bone, clearly show its alluvial origin.

The mandibles (No. 1397 and RGF 87/01) come from medium-sized caballoid horses, with the premolar rows measuring alveolarly 86.7 and 90.5 mm, respec-

tal teeth row PM2–M3 measures alveolarly 194.3 mm, but these teeth are less worn than those of the two previous specimens, as shown by the still deep post-protoconal groove in PM3, reaching towards the prefossette (Fig. 8, Table 3). The protocones of PM3–M2 vary between 16.85–18.4 mm in length, the plication counts between 11–13 plications, including well-developed plis caballin. The hypocones are lingually indented and plis hypostyle are indicated; in M3 the pli hypostyle closes the hypoconal groove as a lake. Premolar labial styles are well grooved, also molar styles may be

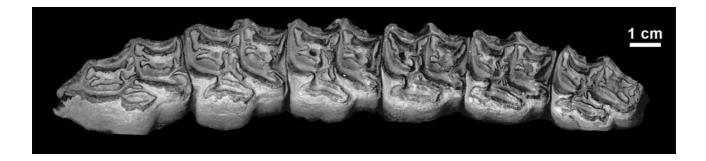


Fig. 8. Left upper cheek-teeth from alluvial deposits (No.1591).



Fig. 9. Lower cheek-teeth from alluvial deposits: a, left mandible (RGF 87/01); b, right mandible (1397).

tively (Table 3). The total pm2–m3 row of RGF 87/01 measures 177.6 mm. The pm2 lack "protostylids" and m2–3 have shallow ectoflexids. These jaws and teeth correspond in size and morphology to those of late Late Pleistocene caballoid horses of Eurasia, identified under several local names but probably synonymous with *E. ferus*. In terms of size, they also correspond to the uppers from the Belgrade second loess. Left mandible (RGF 87/01) has been δ 13C dated to > 40 000 BP (Hela–506 & Hela–507) (JUNGNER, pers. comm.).

No. 1591, δ 13C dated to 36300+/-1700 BP (Hela-505) (JUNGNER, pers. comm.), represents a larger horse, the to-

grooved at some point along the crown. A single PM 3–4 (ZP 5) from the Sava River is also large, but has a short protocone, measuring 11.65 mm. These specimens, with PM3–4 occlusal lengths of 32–35 mm, correspond in size to large horses from the Late Pleistocene caves of Hungary, from caves and rock shelters in Serbia and Montenegro, identified as *E*. sp. and *E. mosbachensis-abeli* REICHENAU-ANTONIUS (RAKOVEC, 1965; MALEZ, 1975; FORSTEN & DIMITRIJEVIĆ, 1995), and to large Middle Pleistocene horses from neighbouring Greece and Rumania, identified as *E. abeli* ANTONIUS and *E. insulidens* SAMSON (MELENTIS, 1966, SAMSON, 1975).

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Despotovac

A L PM3–4 (LV 20), in the Faculty of Mining and Geology, University of Belgrade, was collected by Laskarev, most probably when surveying the Despotovac area (Fig. 1B: 4), where important Neogene mammalian fossils were found (LASKAREV, 1949). The tooth is appr. 90 mm high, large, with a long protocone and grooved labial styles, resembling those of No. 1591.

Stubal

Three large upper horse cheek-teeth, R and L PM3-4 (ZP 6/1 and 6/3) and L M1-2 (ZP 6/2), probably from a single young adult individual, were found by ŽIVADIN PETRONIJEVIĆ, a Serbian Neogene mammal specialist, in Stubal, a village near Blace in Central Serbia (Fig. 1B, 9). Little is known about the circumstances of the finding, except that the teeth come from loose sediment, most probably alluvial sands. The crowns are high, from >84 to 98 mm, and the protocones long, range 15–16.4 mm.

Cave deposits of Serbia

The Late Pleistocene fossil record is best known from caves, both because the cave environment furnished favourable conditions for fossilization and because archaeological excavations have focussed on caves. The cave faunas are mostly rich and diverse, and Palaeolithic artefacts, where found, make dating and age comparisons feasible.

Fossil remains of mammals have been discovered in more than 25 caves in Serbia, with 25 large mammal and 32 small mammal species identified (DIMITRIJEVIĆ, 1997a, 1998). Horses have been found from six cave localities: Risovača, Gradac (Jerinina Cave), Vrelska, Lazareva, Ravanička, and Baranica caves. The remains from Risovača (Fig. 1B: 3) were described earlier (RA-KOVEC, 1965; FORSTEN & DIMITRIJEVIĆ, 1995).

Jerinina Cave

The Jerinina Cave or the Cave under Jerinina hill is situated in the village Gradac near Kragujevac (Fig. 1B: 5), 11 m above the Lepenica River, at an altitude of 128 m. Late Pleistocene mammal remains and Paleolithic flint and bone artifacts were found during archeological excavations in 1952–53 (GAVELA, 1988).

The fossil mammal remains from the Jerinina cave are kept in the National Museum, Belgrade. The following species have been identified: *Castor fiber* (LIN-NAEUS), *Marmota marmota* (LINNAEUS), *Canis lupus* LIN-NAEUS, *Vulpes vulpes* (LINNAEUS), *Ursus spelaeus* (RO-SENMÜLLER & HEINROTH), *Crocuta spelaea* (GOLDFUSS), Panthera spelaea (GOLDFUSS), Mammuthus primigenius, Rhinoceros sp., Equus hydruntinus, E. ferus, Sus scrofa LINNAEUS, Megaloceros giganteus (BLUMENBACH), Cervus elaphus LINNAEUS, and Bos primigenius (MARKOVIĆ-MARJANOVIĆ, 1968; GAVELA, 1988, amended).

The equid material consists of one R PD3–4 (No. 216); L and three R PM2 (Nos. bb, 63,139, and 321); three R and four L PM3–4 (Nos. 140, 213, 244, 154, 188, 214, and 870); three R and six L M1–2 (Nos. 190, 219, 266, 44, 50, 187, 189, 267, and bb); two L M3 (Nos. 191 and 192); three L pd3–4 (Nos. bb, 371, and 432); L and three R pm3–4 (Nos. 64, 186, 212, and 322); four R m1–2 (Nos. bb1, bb2, 155, and 156); R and three L m3 (Nos. bb, 141 211, and 274); epistropheus (No. 220); proximal R radius (No. 284).

Except for the second phalanx, the horse bones show severe damage attributed to *Crocuta* gnawing. The epistropheus is gnawed along the neural spine, and the caudal articular surface and processes show similar damages. The lateral part of the trochlea tali and the plantar surface of the astragalus show grooves made by *Crocuta* teeth. The lateral side of the proximal end of the radius is chewed off and there are two pits on the proximal articular surface, probably made by *Crocuta* canines. The radius also shows scratches, but they are not so clear nor in a characteristic position as to be classified with certainty as butchering marks, and they could have been made by stone ertefacts.

The horse teeth are large, corresponding in size to those from the Risovača, Baranica, and Ravanička caves (Fig. 10) (Table 4). Two R lowers (Nos. bb1 and bb2) (Fig. 10n–o), although worn, are particularly large; they may be m1 and m2 (alternatively, mp4 and m1) of one individual. In this sample, the protocones are medium long (mean 14.8 mm), the plication counts slightly high (mean appr. 9.8 plications). The ectoflexids tend to be shallow in the lower molars.

The astragalus (No. 98) is medium sized, but the medial phalanx (No. 284), with a total length of 58.4 mm, is as large as the bones from Risovača.

Lazareva Cave

The Lazareva Cave, sometimes referred to in the literature as Zlotska Cave, is located at the foot of the Kučaj mountain, 3 km northwest of the village Zlot, on the left side of the Lazareva River, a tributary of the Zlotska River (Fig. 1B: 10). The entrance is at an altitude of 291 m or 6.7 m above the Lazareva riverbed (LAZAREVIĆ, 1978). The total length of the Lazareva Cave is 1540 m (PETROVIĆ & GAVRILOVIĆ, 1965).

This cave has attracted visitors and researchers for a long time (CVIJIĆ, 1893; ŽUJOVIĆ, 1889, 1929). A detailed speleological survey preceded its opening to tourists in 1953 (PETROVIĆ, 1958; PETROVIĆ & GAVRILO-VIĆ, 1965; LAZAREVIĆ, 1978), and archaeological exca-

		Jerinina Baranica				Crvena Stijena				
		N	М	SD	Ν	М	SD	N	М	SD
PM2	Locc.	4	41.075	1.108	6	40.12	1.46	4	40.1	1.07
	Bocc.	4	25.8	0.85	5	25.7	1.97	4	26.7	0.707
PM3/4	Locc.	3	30.88	_	11	30.88	2.93	9	32.2	1.71
	Bocc.	5	28.6	1.949	11	29.6	1.7	10	28.87	1.58
M1/2	Locc.	6	29.2	1.87	12	28.03	2.36	10	28.3	1.329
	Bocc.	5	27.5	1.15	13	27.32	1.19	8	27.26	1.917
M3	Locc.	1	30.05	_	4	31.7	1.29	7	29.6	2.46
	Bocc.	1	~24.95	_	5	25.3	1.19	7	23.9	1.439
PM3-M2	Lprot.	14	14.8	1.258	24	13.95	1.62	20	13.68	1.249
PM2-M3	n.plic	6	9.3	6.12	18	8.7	2.55	20	9.9	3.97
	Locc.	_	-	_	2	35.95	_	3	34.37	2.02
pm2	Bocc.	_	-	_	2	17.35	_	3	16.4	1.04
pm3/4	Locc.	5	30.5	1.15	4	30.075	1.601	18	30.98	1.517
	Bocc.	5	17.97	0.27	4	17.325	1.18	18	17.28	0.845
m1/2	Locc.	3	28.37	1.258	2	30.05	_	21	28.75	0.937
	Bocc.	3	16.37	0.76	2	15.2	_	21	14.99	0.568
m 3	Locc.	2	33.275	_	2	33.15	_	6	32.6	3.2
	Bocc.	2	14.82	_	2	13.7	_	6	12.7	1

Table 4. Cheek-teeth of cabballoid horses from cave and rock-shelter deposits of Serbia and Montenegro. Abbreviations: N = number of specimens; M = mean; SD = standard deviation.

vations were done in 1963, 1964, and 1968, revealing Iron and Bronze Age remains (TASIĆ, 1971).

The Pleistocene layers of the Lazareva Cave have not been systematicaly excaved, but scattered remains of several Pleistocene mammalian species have been reported, such as *Ursus spelaeus*, *Panthera spelaea*, and *Crocuta spelaea* (CVIJIĆ, 1893, 1895; ŽUJOVIĆ, 1929). One cave visitor happened to be ŽIVADIN PETRONIJEVIĆ, who collected an equid tooth and four canines of *Ursus spelaeus*, which are now in the collections of the Faculty of Mining and Geology, University of Belgrade. Two equid teeth from the same locality, found by an unknown collector, are held in the Natural History Museum, Belgrade.

The horse material consists of two R PM3–4 (Nos. bb and ZP 7/1) and L M3 (No. bb). The premolars are large, with short protocones measuring 11.35 and 14.5 mm, grooved mesostyles, hypocones with faint lingual marking and plis hypostyle.

Ravanička Cave

The cave is located in the immediate vicinity of the Ravanica monastery (Fig. 1B: 7). The entrance is at an altitude of 235 m, only 6 m above the riverbed of Rava-

nica, a tributary of the Morava River. The total length of the cave is 1049 m (PETROVIĆ, 1976).

ĆIRIĆ (1952) described cave bear remains from the Ravanička Cave. Two equid teeth from this locality, found by ŽIVADIN PETRONIJEVIĆ, are in the collections of the Faculty of Mining and Geology, University of Belgrade. The teeth are L PM3–4 (ZP 2/2) of a caballoid horse and R M3 (ZP 2/1) of *E. hydruntinus*. In the Natural History Museum, Belgrade, there is a total of five teeth, L and R PM3–4, L M1–2, and L pm3–4 (Nos. 377, 375, 376, and 380) of a horse and R PM3–4 (No. 378) of *hydruntinus*. The uppers of the horse are large, with long protocones and 5–11 plications, including marked plis caballin.

Baranica

The cave is situated in the wider surroundings of the town Knjaževac, on the right bank of the Trgoviški Timok River, at an altitude of 260 m (Fig. 1B: 6). The entrance is in the form of a low rock-shelter, while behind it a network of cave channels is developed.

Archaeological excavations were done in 1994, 1995, and 1997 (SLADIĆ & JOVANOVIĆ, 1996; MIHAILOVIĆ *et al.*, 1997). Four stratigraphic layers were distinguished

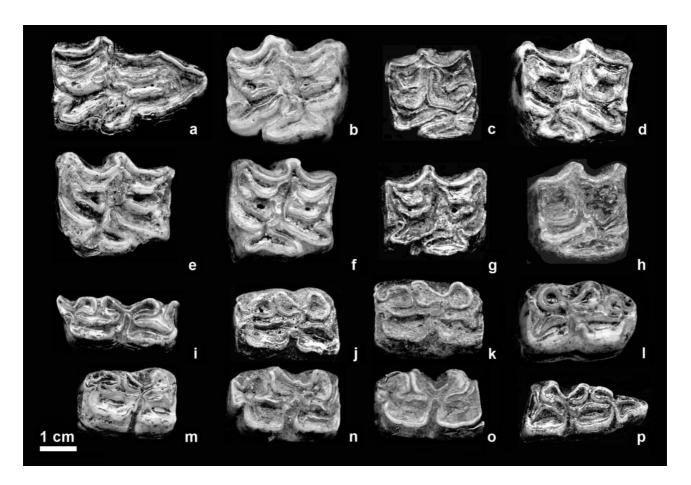


Fig. 10. The caballoid horse from Jerinina Cave: **a**. R P2 (139); **b**. R P3/4 (244); **c**. R P3/4 (213); **d**. L P3/4 (214); **e**. L M1/2 (267); **f**. L M1/2 (44); **g**. R M1/2 (219); **h**. R M1/2 (266); **i**. R d4 (371); **j**. R pm3/4 (322); **k**. R pm3/4 (212); **l**. L pm3/4 (64); **m**. R m1/2 (156); **n**. R m1/2 (bb1); **o**. R m1/2 (bb2); **p**. L m1/2 (211).

to a depth of 2.2 m. Flint artefacts were found, as well as an extremely rich and diverse fauna of both large and small mammals, birds, frogs, fish, and gastropods. Among the flint artefacts from layer 2, characteristic early Upper Palaeolithic types can be distinguished, indicating an age < 41000 BP (MIHAILOVIĆ *et al.*, 1997).

Some of the large mammal bones were water worn, probably from having been transported down from the upper levels of the cave by underground water currents. Tooth marks and gnawing damage could be seen on other bones, mostly caused by cave hyena.

Some ten metres above the cave entrance in the same carbonate rock, a road cuts through a karst cavern, which was excavated in 1997. Animal remains recovered showed strong predator selection and were damaged by gnawing to such an extent that it was concluded that the place was a cave hyena den and raptor haunt. It is supposed that it was connected with the lower cave and it has accordingly been named Baranica II. The palaeontological finds from the lower cave and the cavern are marked "BAR" and "BAR II", respectively.

The faunal content from the two parts of Baranica are largely similar, and include the following species:

Spermophillus citellus (LINNAEUS), Dryomys nitedula (PALLAS), Sicista subtilis (PALLAS), Nannospalax leucodon (NORDMANN), Apodemus sylvaticus (LINNAEUS), Cricetus cricetus (LINNAEUS), Mesocricetus newtoni (NEH-RING), Cricetulus migratorius (PALLAS), Clethrionomys glareolus (SCHREBER), Arvicola terrestris (LINNAEUS), Terricola subterraneus (DE SELYS-LONGSCHAMPS), Microtus arvalis (PALLAS), Microtus nivalis (MARTINS), Castor fiber, Lepus sp., Canis lupus, Vulpes vulpes, Ursus sp., Martes martes (LINNAEUS), Mustela nivalis LIN-NAEUS, Crocuta spelaea, Panthera spelaea, P. pardus (LINNAEUS), Mammuthus primigenius, Dicerorhinus sp., Equus sp. (caballoid), E. hydruntinus, Cervus elaphus, Megaloceros giganteus, Bos primigenius, Bison priscus, Capra ibex LINNAEUS (DIMITRIJEVIĆ, 1997b, 1998).

The fossil material from Baranica cave is kept in the Knjaževac Regional Museum. The horse material consists mainly of isolated teeth (Fig. 11) (Table 4). There are two L PD2 (BAR 97/81/1 and BAR II 97/10/6); two L and three R PD3–4 (BAR 97/30/3, BAR II 97/11/9, 97/24/1, 97/3/4, and 97/11/19); two R and four L PM2 (BAR II 97/11/11, 97/12/1, 97/10/1, 97/26/1, 97/9/14, and 97/2/2); ten L and four R PM3–4 (BAR 97/12/2, 97/13/2,

BAR II 97/26/2, 97/10/4, 97/9/9, 97/8/88, 97/8/2, 97/10/3, 97/16/2, 97/29/1, 97/8/10, 97/7/24, 97/11/1, and 97/11/4); five R and six L M1-2 (BAR II 97/30/2, 97/9/13, 97/27/1, 97/11/10, 97/11/2, 97/1/13, 97/10/2, 97/16/3, 97/16/1, 97/8/11, and 97/30/3); four L and three R M3 (BAR 97/13/1, BAR II 97/4/2, 97/16/4, 97/3/2, 97/11/5, 97/8/12, and 97/11/16). R and three L pm2 (BAR 97/80/3, BAR II 97/30/1, 97/10/5, and 97/8/13); one L and three R pm 3-4 (BAR 97/80/1, BAR II 97/11/15, 97/11/6, and 97/27/2), L and R m1-2 (BAR 97/80/2 and BAR II 97/9/10); L and two R m3 (BAR 97/11/8, BAR II 97/17/1, and 97/29/2), upper and lower incisors (BAR 10/10, BAR II 97/3/1, 97/11/14, 97/11/12, 97/27/3, 97/9/15, 97/11/18, 97/16/7, 97/16/6, 97/11/13, and 97/17/2); R and L distal tibiae (BAR II 97/7/77, 1/11, 97/8/65); R and two L astragali (BAR II 97/11/7, 97/16/8, and 97/8/29); proximal L and distal MT III

(BAR II 97/2/10 and 97/14/1); and a scaphoid (BAR 97/1/5).

The teeth are large and among them are single particularly large specimens, like those from the Jerinina Cave, e.g. two L PM3–4 (BAR II 97/9/9 and 97/26/2), which although worn measure 35×32 mm and 33×31.7 mm occlusally; also R PM3–4 (BAR 97/12/2) is large. We regard these specimens as large variants. The protocones are medium long, but occasionally they may be short, e.g. in R PM3–4 (BAR II 97/7/24) and R M1–2 (BAR II 97/27/1), which measure 10.9 and 10.8 mm, respectively. The plication counts vary between 4–12 plications. In M3, the hypoconal groove closes as a lake, with or without including the postfossette; there is often a hypostylar foramen.

Of the few limb bones, an astragalus (BAR II 97/8/29), distal tibia (1/11), and distal MT III (97/14/1) are large,

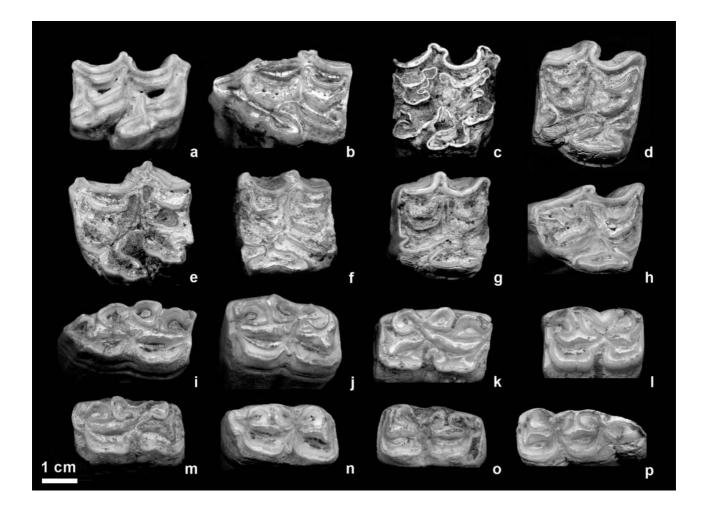


Fig. 11. The caballoid horse from Baranica Cave: **a**. R D3/4 (BAR II 97/3/4); **b**. L PM2 (BAR II 97/10/1); **c**. R PM3/4 (BAR II 97/11/1); **d**. R PM3/4 (BAR II 97/11/4); **e**. R PM3/4 (BAR 97/12/2); **f**. L M1/2 (BAR II 97/10/2); **g**. R M1/2 (BAR II 97/11/10); **h**. R M3 (BAR II 97/8/12); **i**. L pm2 (BAR 97/80/3); **j**. R pm3/4 (BAR 97/80/1); **k**. L pm3/4 (BAR II 97/11/15); **l**. R pm3/4 (BAR II 97/27/2); **m**. R pm3/4 (BAR II 97/11/6); **n**. R m1/2 (BAR 97/80/2); **o**. L m1/2 (BAR 97/9/10); **p**. L m3 (BAR II 97/17/1).

while the proximal MT III (97/2/10), with a breadth of 52 mm, is medium sized.

Vrelska Cave

The cave is in the town Bela Palanka, at an altitude of 545 m (PETROVIĆ, 1976) (Fig. 1B: 8). Since 1986 it has been repeatedly explored by hydrogeologists, who found the remains of Pleistocene mammals. In 1990 paleontological excavations were done in the cave, revealing a fauna of mammals, birds, reptiles, amphibians, and fish (MARKOVIĆ & PAVLOVIĆ, 1991; DIMITRIJEVIĆ, 1997a). The material collected during the hydrogeological works (mainly *Ursus spelaeus*) is kept in the Bela Palanka Regional Museum, while the spoils of the excavations are kept in the Natural History Museum, Belgrade.

There are only two tooth fragments of horses: an upper PM/M and a lower pm/m. Although broken, the protocone and the metaconid–metastylid double knot, respectively, clearly show caballoid features.

Rock-shelters of Montenegro

Pleistocene vertebrate remains are known from only a few cave localities in Montenegro (DIMITRIJEVIĆ, 1997c), which mainly comprise the remains of the cave bear, but another type of karst localitiy, rock-shelters, have yielded rich and diverse Pleistocene faunas.

Excavations have been done in the Crvena Stijena rock shelter in the Trebišnjica River valley (BENAC, 1975), the Odmut Cave in the Piva valley (SREJOVIĆ, 1977), the rock-shelters Mališina Stijena and Medena Stijena in the Ćehotina Gorge (RADOVANOVIĆ, 1986; MI-HAILOVIĆ, 1996), and the Trebački Krš rock shelter in the Lim valley (DJURIČIĆ, 1996). These sites are situated in mountainous areas, at an altitude of more than 500 m. They are multilayered and contain numerous flint artefacts and faunal remains (MALEZ, 1975; MALEZ et al., 1988; DIMITRIJEVIĆ, 1996, 1999; MIHAILOVIĆ & DIMITRIJEVIĆ, 1999). The composition of the fauna, especially the frequency of the various mammal species, is largely influenced by the hunting and subsistence strategies of Palaeolithic and Mesolithic human societies, which enjoyed the advantages of these natural shelters.

Medena Stijena

The Medena Stijena rock shelter is situated about 20 km south–east of Pljevlja, in the Ćehotina canyon, at an altitude of 780 m (Fig. 1B: 12). Upper Palaeolithic chipped stone assemblages were found in several layers of the lower stratigraphic complex, and Mesolithic and Eneolithic/Bronze Age archaeological material in the upper stratigraphic complex of the rock shelter (MIHAILOVIĆ, 1996). The poor preservation of the bones, due both to predepositional fragmentation and depositional conditions, has meant in that less than 5% of the 1747 pieces of bone and teeth collected could be assigned to species. The following species were found in the lower stratigraphic complex: *Ursus arctos* LINNAEUS, *Equus* sp. (caballoid), *Sus scrofa*, *Cervus elaphus*, *Bison priscus*, *Bos/Bison*, *Capra ibex*, and *Rupicapra rupicapra* (LIN-NAEUS) (DIMITRIJEVIĆ, 1996).

A single equid R pm2 (MS 88/95/1) and a proximal MC III (MS 86/109/1) were found in the lowermost layer, together with artefacts of Early Epigravettian type (mainly dated 25 000–13/12 000 BP) (MIHAILOVIĆ, 1996). The fossils belong to the City Museum of Pljevlja, Montenegro. Although fragmentary, the pm2 appears large to medium in size; the proximal breadth of the metacarpal is 50 mm, indicating medium size.

Crvena Stijena

The Crvena Stijena rock shelter is in the Trebišnjica River valley, near the village of Petrovići, western Montenegro, at an altitude of approximately 700 m (Fig. 1B: 13). Archaeological excavations there were done in 1955–1964 (BENAC, 1975). The locality comprises one of the most complete Middle to Late Pleistocene sequences in Europe, with more than 20 m of deposits and 31 distinguished layers, without as yet having reached bedrock. Most of the layers contain both Palaeolithic artefacts and Pleistocene faunal remains. The following mammal species have been identified in layers V-XXXI: Lepus timidus varronis MILLER, L. europaeus (PALLAS), Marmota marmota, Arvicola scherman exitus MILLER, Microtus arvalis, M. nivalis, Apodemus flavicollis (MEL-CHIOR), Canis lupus, Cuon alpinus europaeus BOURGUI-GNAT, Ursus cf. spelaeus, U. arctos priscus GOLDFUSS, U. cf. mediterraneus FORSYTH MAJOR, Meles meles (LINNAEUS), Crocuta spelaea, Lynx lynx (LINNAEUS), Panthera pardus, Equus caballus germanicus NEHRING, E. mosbachensis-abeli group, Coelodonta antiquitatis (BLUMENBACH), Dicerorhinus kirchbergensis (JAEGER), Sus scrofa, Megaceros giganteus, Dama dama (LIN-NAEUS), Alces cf. alces LINNAEUS, Cervus sp., Capreolus capreolus (LINNAEUS), Bison priscus, Bos primigenius, Rupicapra rupicapra, Capra ibex, Ovis sp. (MA-LEZ, 1975, partly amended).

The equid material is kept in the Institute of Quaternary Geology and Palaeontology, Zagreb, Croatia, and lacks collection numbers. It consists of: three R and L PM2; six R and L PM3–4; six R and five L M1–2; four R and six L M3; L and two R pd 3–4; R and two L pm2; six R and eight L pm3–4; ten R and twelve L m1–2; four R and three L m3. There are no limb bones.

The horse material comes from layers XX–XXV of Crvena Stijena, believed to span the late Riss Glacial – ?Amersfoort Interstadial, i.e. mainly the last Interglacial (BRUNNACKER, 1975) or the marine oxygen isotope stage (OIS) 5e. Maximal frequency of the horse is in layer XXIV, believed to correspond to the Interglacial, with a high frequency also in layers XXI–XXII, believed to correspond to the Würm I (OIS 5). According to BRUN-NACKER (1975), the climate of layer XXII was still relatively warm.

The horse is dentally as large as those from the Risovača, Jerinina, and Baranica caves (Table 4). In a phenogram, constructed on the basis of ten upper check tooth measurements (Fig. 12), these samples cluster together. The protocones are medium long, the plication counts slightly high. Although the coefficients of variation ($100 \times s$ /Mean) for M3 and m3 occlusal lengths are high, probably because specimens in different stages of wear were included in the calculations, there are no morphological indications of two different caballoid species in the sample, nor has *E. hydruntinus* been found here.

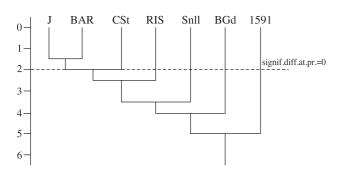


Fig. 12. Phenogram, constructed on the basis of 10 upper cheek tooth measurements. Scale in standard deviation units. Abbreviations: J = Jerinina Cave; BAR = Baranica; CSt = Crvena Stijena; RIS = Risovača; Snll = Šandalja II; BGd = Tešića Ciglana; 1591 = Left maxillary from alluvial deposits near Belgrade.

Equus hydruntinus REGALIA

The presence of the small Middle to Late Pleistocene stenonid, *Equus hydruntinus*, was previously established in the Risovača Cave, near Arandjelovac in Central Serbia (RAKOVEC, 1965; FORSTEN & DIMITRIJEVIĆ, 1995). The coexistence of this species with a much larger, caballoid horse also characterizes the caves Baranica, Jerinina, and Ravanička. A further similarity lies in the low number of *hydruntinus* remains found in relation to those of caballoid horse remains found, as is the case with most European finds of *hydruntinus*. In the Ravanička Cave, there were two *hydruntinus* teeth compared with only five caballoid specimens, but the sample in its entirety is too small to be conclusive regarding their original frequency. Whenever caballoid horse remains are

found in large numbers in a cave, *hydruntinus* is generally also present, Crvena Stijena being an exception.

Material: Baranica Cave (Fig. 13a–I): L PM2 (BAR II 97/1/10); L and R PM3–4 (BAR II 97/3/3 and 97/8/3), two L and four R M 1–2 (BAR 97/25/1, BAR II 97, BAR II 97/12/3, 1/10, 97/7/7, and 97/16/5); R pm 3–4 (BAR II 97/9/12); L distal tibia (BAR II 97/8/65), and R astragalus (BAR II 97/11/7); pm2 (BAR II 97/8/13) may also belong to *hydruntinus*. Ravanička Cave (Fig. 13n–0): R M3 (ZP 2/1) and R PM 3–4 (No. 378), and Gradac (Jerinina Cave) (Fig. 13m) R M1–2 (No. 61).

All over its range in Europe, the Middle East, and the Caucasus, Equus hydruntinus is identifiable by its dental morphology, although a single tooth may resemble small/much worn specimens of the caballoid horse. The protocones, although short, may have an anterior extension, a "heel", particularly in the molars. The protoconal length, i.e. the development of the heel, is variable within samples. A separate "subspecies", E. hydruntinus davidi Alimen was established, believed to differ in having relatively long protocones (ALIMEN, 1946), but significant differences in the protoconal length between local samples have not been demonstrated. The lower cheek teeth are typically stenonid with V-shaped lingual grooves, protostylid plications indicated, and mostly deep molar ectoflexids. Occasionally, the molar ectoflexids may be shallow, resembling those of the Asiatic Wild Ass, E. hemionus PALLAS. Generally small, the limb bones vary locally in size, but the slender metapodials and proximal phalanges are characteristic, an additional resemblance with E. hemionus.

The few *hydruntinus* teeth listed above do not differ from the teeth described from elsewhere of the species' range, either in their size or morphology (Fig. 13). The mean protoconal lengths are: PM3–4 7.98 mm, M1–2 9.25 mm; there may be a short heel. The plication counts vary between 6–11 plications; the plis caballin were obliterated early by wear.

The astragalus from Baranica (BAR II 97/11/7) compares closely with that from the Rissian of La Adam Cave, Rumania, (SAMSON, 1975: table 14).

The Equus hydruntinus is believed to have preferred dry and temperate climatic conditions, but the species has been found in France under glacial conditions also (PRAT, 1968). In the Bacho Kiro Cave, Bulgaria, hydruntinus occurs from layer 7 to and including layer 13, dated from 29150 +/- 950 BP to >47000 BP (MOOK, 1982; GINTER & KOZLOWSKI, 1982), and under climate conditions varying from cool-dry or cold-humid to warm-dry and warm-humid (KOWALSKI, 1982). The maximum frequency of hydruntinus is in layer 11, dated > 40 000 BP (MOOK, 1982), when the climate was becoming warmer and increasingly humid, preceding the maximum cold of layer 12 (KOWALSKI, 1982; GIN-TER & KOZLOWSKI, 1982). It is not known from which layers of the Risovača, Baranica, Ravanička, and Jerinina caves hydruntinus derives, neither the age nor the climatic conditions are known.

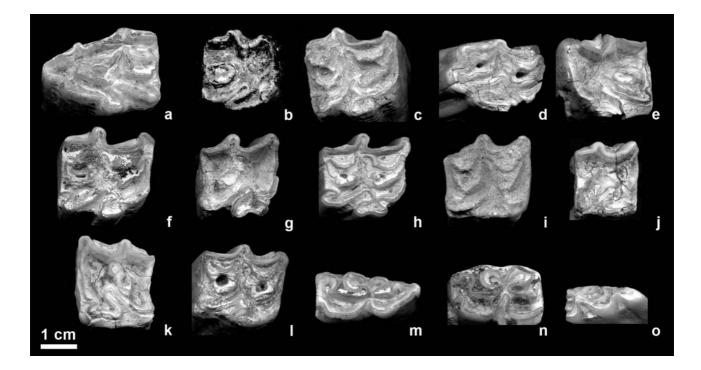


Fig. 13. *E. hydruntinus* REGALIA from cave deposits of Serbia. Baranica Cave: **a**. L PM2 (BAR II 97/1/10); **e**. L PM3/4 (BAR II 97/3/3); **f**. R PM3/4 (BAR II 97/8/3); **g**. R M1/2 (BAR 97/25/1); **h**. R M1/2 (BAR II 97/7/7), **i**. R M1/2 (BAR II 1/10); **j**. L M1/2 (BAR II 97/12/3); **k**. L M1/2 (BAR II 97); **l**. R M1/2 (BAR II 97/16/5); **m**. R pm2 (BAR II 97/8/13); **n**. R pm3/4 (BAR II 97/9/12); **o**. L m1/2 (BAR II 97/3/26); Jerinina Cave: **b**. R M1/2 (61); Ravanička Cave: **c**. R PM3/4 (378); **d**. R M3 (ZP 2/1).

Pleistocene/Holocene discontinuity in the horse record

In the Central Balkans, as well as elsewhere in Europe, the records indicate that the caballoid horses disappeared at the end of the Pleistocene. There are no finds of caballoid horse from the Early Holocene faunas of Serbia, although due to extensive archaeological excavations these faunas are much better known than those from the Late Pleistocene. The *Equus hydruntinus* survived and locally in the Neolithic even formed an important part of the fauna and of man's subsistence (BÖKÖNYI, 1984).

The further history shows, once again, the caballoid/stenonid turnover. The latest representative of the stenonid horses, *E. hydruntinus*, became extinct in the Middle Neolithic (BÖKÖNYI, 1974) or as late as in the Copper Age in Spain (BOESSNECK, 1967), while the caballoid horse reappeared in the Eneolithic, this time as domesticated animals.

Discussion

The taxonomy of the caballoid horses from the European Pleistocene is still in disarray, due to the morphological uniformity of these animals. There are size differences, probably partly clinal, partly temporal. A number of species names have been coined, mainly on the basis of the size of the horse and its stratigraphic age, but specimens (mainly isolated teeth and limb bones) from the type localities or referred to various species cannot be morphologically clearly differentiated from one another and are connected by forms intermediate in size, thus depriving the names of meaning and usefulness. However, at a number of localities, two caballoid forms, differing in size, seem to have occured in sympatry (see discussion in FORSTEN, 1993), indicating distinct species.

The caballoid horses from the Central Balkans fall into two size groups, as judged on the basis of the teeth: large forms mainly from the caves and rock shelters and medium sized forms from alluvia and loess. The large forms resemble Late Pleistocene large horses from Hungary, e.g. from Erd, Tata, Dorog, Istalloskö, Lengyel, Tokod–Nagybereg, and Bodrogkeresztur, dated 30 000–40 000 BP, from Subalyuk, Kecskesgalya, and Kalman–Lambrecht, dated 50 000–95 000 BP, and from Szuhogu, dated to the Holsteinian Interglacial (e.g. JA-NOSSY, 1986). The medium-to-small forms resemble those from Kiskevely, Pilisszanto, Szelim, and Ságvár, dated to the last Glacial and early Late Glacial. From the Rumanian Late Pleistocene, SAMSON (1975) identified the large *E. transilvanicus* Theoder and the medium-sized *E. spelaeus* Owen. Single, very large bones have been found from the late Late Pleistocene (SAM-SON, 1975: Tables 12, 15).

On the basis of limb massivity and protoconal lengths, SPASSOV & ILJEV (1997, 1998) tried to differentiate Pleistocene species of Equus in an Equus germanicus/latipes Nehring-Gromova Group, massively built with long protocones, and an E. gmelini Antonius Group, more gracile in build and with short protocones. They showed (SPASSOV & ILJEV, 1998) that the protoconal length can be roughly correlated with the dental occlusal length (their Fig. 3), as pointed out earlier (FORSTEN, 1982), and that a positive correlation between the MC III diaphysal breadth and length (their Fig. 4), in both cases with only small differences in the proportions between representatives assigned to the two groups. They concluded that the domestic horse is polyphyletic, deriving from both groups. Polyphyly of the domestic horse was suggested earlier (LUNDHOLM, 1949; GROVES, 1974), but considered unlikely on genetic and molecular grounds (FORSTEN, 1988).

In the present material, short protocones occur in both maxillas (LV 21/) from the Belgrade loess, the mean protoconal length in PM3-M2 is 11.8 mm, range 8.97-13.5 mm, in the PM 3-4 (ZP 5) from the Sava River alluvia, the protocone length is 11.65 mm, in the two PM 3-4 (No. bb and ZP 7/1) from the Lazareva Cave, the lengths are 11.35 and 14.5 mm, respectively, and in the PM 3-4 and M1-2 (BAR II 97/7/24 and 97/27/1) from the Baranica Cave, the lengths are 10.9 and 10.8 mm, respectively. Except for the mature maxilla from the Belgrade loess and the No. bb from the Lazareva Cave, with worn teeth measuring 22.3-31.8 mm and 35.1 mm in crown height, respectively, the teeth are only moderately worn, with crown heights of 51.7-75.2 mm, indicating that in these specimens the short protocones are not due to wear. The teeth from the Sava River, Lazareva and Baranica caves are large, the PM3-4 measuring 31.1-34 mm occlusally. Where limb bones are known, e.g. from Risovača, Jerinina, and Baranica II, they are also large and massive (For-STEN & DIMITRIJEVIĆ, 1995).

We do not believe that rhe European Pleistocene horses of the genus *Equus* can be differentiated into the two groups of SPASSOV & ILJEV'S (1997, 1998), simply based on the basis of the protoconal length. In addition, the type specimen of *E. germanicus*, a skull (in the Berlin Humboldt Museum MB 1972.31.86; NEH-RING, 1884: pl. 5) from Unkelstein near Remagen, Germany, has short protocones. Especially within local samples, we believe that more evidence is required for species differentiation. To avoid competition for resources, sympatric species ought to occupy different ecological niches, particularly among caballoid horses, with wide ecological requirements; this should be re-

flected in the morphology. Where seemingly two taxa of caballoid *Equus* occur, they usually differ noticeably in size (e.g. MUSIL, 1962). In some of the cave samples, e. g. Jerinina and Baranica, single teeth do differ in that they are larger than the rest. We consider here these specimens large variants within taxonomically homogeneous samples, but acknowledge their difference in size.

The dated specimens do not support a decrease in size with time, as observed in the caballoid horses in other areas (FORSTEN, 1991, 1993), rather an oscillation in size is indicated. The earliest find described here, the horse from Crvena Stijena, dated to the Last Interglacial or approx. 120 000 BP, is large. It is matched in size by stratigraphically younger horses from the Risovača (> 36400 BP, Malez in litt.) and Baranica caves (< 41000 BP), and by No. 1591 from alluvium (36300 BP). The two medium-sized jaws (No. 1397 and RGF 87/01) from alluvia, dated > 40000 BP, correspond in size to the uppers (LV 21) from the Belgrade second loess, dated appr. 36-37 000 BP. Taking into account the slight uncertainty with radiometric dates, all these rather differently sized finds could be roughly contemporaneous. The majority of the dated finds from the Central Balkans thus fall in the middle Late Pleistocene or OIS 3, approx. 30-50000 BP, comprising the interstadials Denekamp, Hengelo, and Moershoofd with colder stadials in between (ZAGWIJN, 1989).

Conclusions

The earlist stage in the records of the Pleistocene horses in the Central Balkans is represented by the late Early Pleistocene stenonid horses. Remains were found of two species, *Equus major* and *Equus stenonis* and from a single locality Trlica in northern Montenegro.

The next stage is represented by the existence of solely caballoid horses throughout The middle and beginning of the Upper Pleistocene. The remains were found mostly in alluvial and cave deposits. There are two size groups: large forms mainly from caves and rock shelters and medium–sized forms from the alluvial and loess deposits. A size decrease with time is not confirmed in the Central Balkan caballoids.

In the Upper Pleistocene, the stenonid line is again present, this time with the species *Equus hydruntinus*.

At the end of the Pleistocene, the caballoid horses disappeared, while the *Equus hydruntinus* continued to exist into the Neolithic.

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Резиме

Плеистоценски коњи (род *Equus*) централног Балкана

На подручју централног Балкана, које обухвата планинске области Србије и Црне Горе, налазили су се, током плеистоцена, значајни миграциони путеви којима су се ширили крупни сисари прилагођени на хладну климу. Кроз ову област, смештену између два планинска појаса, Динарида и Карпато–Балканида, протеже се долина Мораве, спајајући, Панонску низију на северу, преко долина Дунава и Тисе, и северну Грчку на југу, преко долине Вардара у Македонији (сл. 1а). Оштри климатски контраст између континенталне климе Панонске низије и медитеранске климе на југу се овде постепено ублажава.

Фосилни налази коња (род *Equus*) до сада откривени на подручју централног Балкана покривају период од касног раног до краја млађег плеистоцена. Налази из раног и средњег плеистоцена су ретки, док из млађег плеистоцена потичу бројни остаци, нарочито из пећинских наслага.

Најранији налази представљени су стенонидним коњима касног старијег плеистоцена. Представник ове развојне линије коња први пут је поменут у раду о лесним платоима и пешчарама Војводине (Мп.ојеvić, 1950), где се наводи да је пронађен доњи молар, на основу кога је Ласкарев одредио врсту *Equus* sp. aff. *stenonis* Соссни.

Бројни остаци, укључујући зубе и неколико костију ванкранијалног скелета, откривени су на локалитету Трлица у северној Црној Гори (сл. 16: 11). Одређене су две врсте: Equus cf. major BOULE (сл. 2) и Equus stenonis (сл. 3). Врста Equus cf. major крупнија форма, одређена је на основу једног горњег премолара и два доња молара, који се по својим димензијама јасно разликују од зуба E. stenonis (сл. 4, 5). Е. stenonis је врста средње крупног раста. Висина круне неистрошених горњих првих и других молара достиже приближно 80 mm. Протокон је кратак (сл. 3а-ф): средња вредност дужине је 9,41 mm код РМ 3-4 и 10,56 mm код М1-2, а средња вредност броја набора 8, укључујући и кабалоидну бору. У раном стадијуму трошења пост-протоконалне бразде су дубоке, и досежу префосете; хипокони су лингвално увучени. Лабијални стили немају жљебове ни на РМЗ-4.

Остаци стенонидних коња познати су из суседних области: Хрватске (Malez *i dr.*, 1992), северне Грчке (Tsoukala, 1989; KouFos, 1992; KouFos & Kostopoulos, 1993; KouFos & Vlachou, 1997; Kou-Fos *i dr.*, 1997), Бугарске (Spassov, 1997), Румуније (Samson, 1975) и Мађарске (Mottl, 1943; Kretzoi, 1954; Janossy, 1978). Датовани су у период од средњег и касног вилафранка (млађи плиоцен – старији плеистоцен) до касног средњег плеистоцена. Ово би могло да значи да су стенонидни коњи, старији од *E. hydruntinus* REGALIA, живели на простору Балкана дуже него у другим деловима Европе.

У следећем стадијуму стенонидне коње замењује кабалоидна развојна линија. Кабалоидни коњи средњег и млађег плеистоцена су у новије време најчешће називани *Equus caballus* LINNAEUS, често уз одредбу подврсте, мада је коришћено и мноштво различитих имена. Ми се придржавамо предлога који су дали GENTRY *i dr.* (1996) да се за фосилне форме користи назив *Equus ferus* BODDAERT, јер је као *E. caballus* примарно описан домаћи коњ (LINNAEUS, 1758).

Остаци кабалоидних коња, *Equus ferus*, на подручју централног Балкана, потичу из лесних, алувијалних и пећинских наслага.

У лесним наслагама на територији Београда, на локалитету Тешића циглана, пронађени су остаци крупних сисара – мамута, бовида и коња. Остатке коња Ласкарев (1926) је приписао врсти Едииз "woldrichi" Антония. Значајан је податак да су остаци пронађени у доњем делу другог лесног хоризонта, с обзиром да је овај лесни хоризонт у новије време датован на профилима Мошорин-Сурдук Дуркатар у 35900 +/- 500 BP (Lub-1905) и Стари Сланкамен-Чот у 37000 +/- 600 BP (Lub-1892) (ВUткум et al., 1991). Остаци су представљени низовима максиларних зуба, од којих је један леви и један десни припадао старијој одраслој (сл. 6а), а други леви и десни млађој одраслој јединки (сл. 6б). Положај појединачних зуба у зубном низу је реконструисан, с обзиром да су пронађени ван вилица. Осим премолара и молара, пронађени су и горњи секутићи, 4 примерка која по истрошености зубних круна одговарају млађој јединки, и један фрагментован. Морфолошке особине зуба указују на средње крупног кабалоидног коња. Средња дужина протокона је 11,8 mm. При томе, протокони РМЗ старије јединке су врло кратки, док се дужина РМЗ протокона млађе јединке приближава дужини протокона РМ4. Лабијални стили на премоларима су угласти и жљебљени, док су на моларима једноставни, изузев мезостила који у доњем делу круне слабо ужљебљен. Број набора је 3-8, а на моларима кабалоидна бора има тенденцију нестајања са трошењем.

Из алувијалних наслага потичу остаци из Остружнице (метатарзус), и појединачни налази зуба из Деспотовца и Стубала. Место наласка максиле и мандибуле из збирке Природњачког музеја, и мандибуле из збирке Рударско-геолошког факултета није познато, али се, на основу шљунка и песка сачуваног у коштаним шупљинама може закључити да потичу из речних наслага. Метатарзус из Остружнице одговара по величини и пропорцијама налазима горње плеистоценске старости из Рисоваче и налазима исте старости из Мађарске (сл. 7). Максила из збирке Природњачког музеја (сл. 8) припадала је крупној форми. Датована је методом d13C y 36300+/-1700 BP (Hela-505) (JUNGNER, YCMEHO саопштење). Коњима нешто мањег раста припадале су доње вилице из збирке Природњачког музеја (Сл. 9б) и Рударско-геолошког факултета (сл. 9a), која је датована методом d13C y > 40000 BP (Hela-506 & Hela-507) (JUNGNER, усмено саопштење).

Најбројнији остаци потичу из пећинских наслага, захваљујући делом повољним условима фосилизације, делом усредсређености археолошких ископавања на пећине. Истовремено то су и налази за које има и највише података о старости, захваљујући богатој и разноврсној фауни, и налазима палеолитских артефаката. Фосилни остаци сисара пронађени су у више од 25 пећина у Србији, а одређено је 25 врста крупних и 32 врсте ситних сисара (DIMITRI-JEVIĆ, 1997а, 1998). Остаци коња пронађени су у Рисовачи, Јерининој (Градац), Лазаревој, Раваничкој пећини, Бараници (сл. 11) и Врелској пећини.

Зуби коња из Рисоваче (RAKOVEC, 1965; FORSTEN & DIMITRIJEVIĆ, 1995), Јеринине пећине (сл. 10), Баранице (сл. 11) и Раваничке пећине припадају крупној форми (табела 4). На примерцима из Јеринине пећине протокон је средње дужине (средња вредност 14,8 mm), средња вредност броја набора релативно висока (9,8), а ектофлексид на доњим моларима претежно плитак. На примерцима из Баранице, протокон је средње дужине, а број набора варира од 4 до 12. Појединачни примерци су врло крупни, као на пример два десна доња молара из Јеринине пећине (bb1 и bb2)(сл. 10н–о), или два горња лева (BAR II 97/9/9 и 97/26/2) и један горњи десни премолар (BAR 97/12/2) из Баранице.

Плеистоценски остаци кичмењака Црне Горе познати су из свега неколико пећинских локалитета (Димитријевић, 1997ц), и представљени су већином само остацима пећинског медведа, али су релативно бројни и разноврсни у наслагама поткапина, као што су Црвена Стијена (Велас, 1975), Одмут у долини Пиве (Srejović, 1977), Малишина и Медена Стијена у кањону Ћехотине (Радовановић, 1986; Мінацоvić, 1996) и Требачки Крш у долини Лима (DJURIČIĆ, 1996).

У Меденој Стијени пронађен је један доњи десни премолар и фрагмент метакарпуса у слоју са артефактима раног епиграветијена (DIMITRIJEVIĆ, 1996). Оба налаза одговарају коњима средње крупног раста. У Црвеној Стијени релативно бројни остаци коња пронађени су у слојевима XX–XXV, за које се наводи старост касни Рис –?Амерсфорт интерстадијал, односно последњи интерглацијал (BRUN-NACKER, 1975). По величини, зуби одговарају примерцима из Рисоваче, Јеринине пећине и Баранице (табела 4). На фенограму, конструисаном на бази мера 10 горњих југалних зуба, ове вредности се групишу заједно (сл. 12).

Као и другде у Европи, и на централном Балкану фосилни налази указују да кабалоидни коњи нестају крајем плеистоцена. Њих нема ни у раним холоценским фаунама Србије, док је представик стенонидне линије, *Equus hydruntinus* REGALIA, преживео локално све до неолита (Вökönyi, 1984).

Присуство ове врсте у горњем плеистоцену од раније је познато из Рисоваче (RAKOVEC, 1965, Forsten & Dimitrijević, 1995). Као и у Рисовачи, коегзистенција ове врсте са много крупнијим, кабалоидним коњем карактерише и Бараницу, Јеринину и Раваничку пећину (сл. 12). Сличност се оглада и у малом броју налаза остатака Equus hydruntinus у односу на налазе кабалоидних коња. Морфологија зуба је карактеристична, мада појединачни налази могу да буду слични малим, односно врло истрошеним зубима кабалоидног коња. Протокон је кратак, али може бити антериорно извучен ("пета"), нарочито на моларима. Доњи премолари и молари имају типичну стенонидну морфологију, са лингвалним жљебом у облику слова "V", наглашеним набором протостилида, и углавном дубоким ектофлексидом.

Даља историја показује још једну промену у заступљености коња кабалоидне и стенонидне развојне линије. Последњи представник стенонидних коња, *E. hydruntinus*, изумире у неолиту (Вöкönyi, 1974), док се већ у енеолиту поново појављују кабалоидни коњи, овога пута као припитомљена врста, *Equus caballus*.