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A LATE PLEISTOCENE RODENT FAUNA (MAMMALIA: RODENTIA) FROM HADŽI PRODANOVA CAVE NEAR IVANJICA (WESTERN SERBIA)

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Abstract. Hadži Prodanova Cave in western Serbia is a multilayered site which, in addition to Palaeolithic tools, has yielded a relatively rich fauna of small and large vertebrates. In this paper the rodent fauna from this site is described. In total, 13 species of rodents have been found: *Spermophilus* cf. *citelloides, Sicista subtilis, Mesocricetus newtoni, Arvicola* cf. *terrestris, Chionomys nivalis, Microtus arvalis/agrestis, Microtus subterraneus, Clethrionomys glareolus, Apodemus sylvaticus, Apodemus* cf. *uralensis, Spalax* sp.*, Muscardinus avellanarius*. This fauna has a mixed character and includes species of both open and forest habitats, the former being more numerous. According to its overall composition, it is tentatively ascribed to a relatively mild and wet period of the Last Glacial, probably MIS 3.

INTRODUCTION

Hadži Prodanova Cave has been known in the speleological, biospeleological and geomorphological literature for more than a century (Cvijić 1914; Žanel & Stanković 1924; Ršumović 1960), but has attracted more attention only recently, when during preparatory excavations some Palaeolithic artefacts and remains of Pleistocene fauna were found. The goal of these preparatory archaeological excavations was to identify the original position of the Church of St. Archangel Michael, originating from the beginning of the 20th century, so that a new church could be raised on its foundations (Bulić 2006). This work was conducted in cooperation between the Faculty of Philosophy (University of Belgrade), the National Museum of Serbia (Belgrade) and the Institute for Protection of Cultural Heritage from Kraljevo. The excavations were carried out in 2003 and 2004 (Mihailović & Mihailović 2006).

Prehistoric pottery and Pleistocene fauna from this cave were first collected by Mr. Zoran Vučićević from Ivanjica (Mihailović & Mihailović 2006). During the preliminary work some remains of Pleistocene animals (especially cave bear - *Ursus spelaeus*) and artefacts from the Iron Age were reported from the cave entrance and from the main hall.

In 2003 an excavation trench with an area of 16 m^2 and a maximum depth of 2.5 m was dug in the internal part of the cave plateau, the cave entrance and part of the cave hall (Fig. 1b) (Mihailović & Mihailović 2006).

The cave is located in the valley of the Rašćanska river, in the village Šume (Raščići), seven kilometres from Ivanjica (western Serbia) (Fig. 1a). The entrance to the cave lies at an altitude of 630 metres a.s.l., about 40 metres above the floor of the valley (Lješević 2002). It is oriented to the south and is quite narrow and high. Behind it lies the corridor, which is more than 40 m in length. The total length of the cave channels is 345 m (Fig. 1b) (Lješević 2002). The cave was formed in thick-bedded to massive Senonian (Late Cretaceous) limestones. Its morphological characteristics, genesis and hydrological evolution are described in detail in a separate paper (Lješević 2002).

The stratigraphic sequence in this cave is at least 2.5 m thick and has been subdivided into five layers from top to bottom, as follows (Fig. 2):

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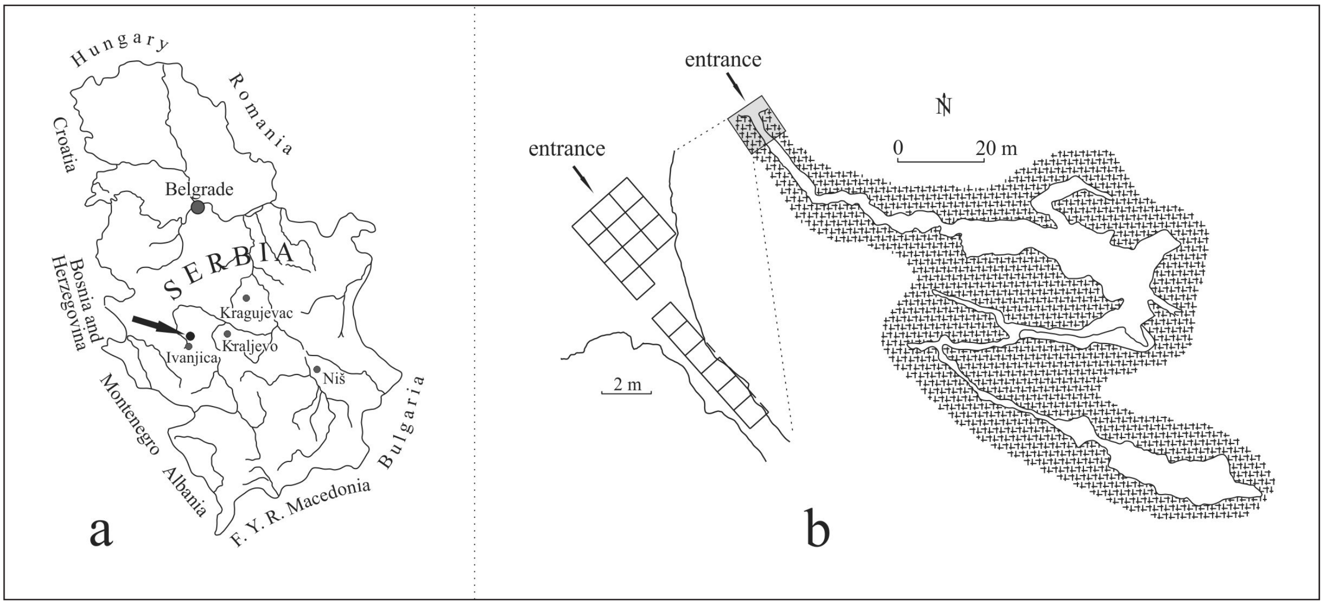


Fig. 1 - (a) Geographic position of the cave. (b) Plan of the cave with the position of the trench.

1- surface deposit of grey clay with rock fragments which contains some modern and Iron Age finds, and rarely bones of Pleistocene animals; it has been formed in Holocene;

2 - brown-yellowish clay with fine debris; contains Late Upper Palaeolithic (Epigravettian) artefacts;

3 - brown clay with coarse detritus and large stone blocks; it contains no archaeological material;

4 - light brown clay with fine detritus and variable amount of fine gravels; it contains Middle Palaeolithic artefacts;

5 - dark brown clay with coarse detritus and large rock fragments which contains Middle Palaeolithic artefacts. In this layer four horizons can be distinguished - a, b, c and d. The plateau is relatively leveled and made up of the same sediments found in the cave entrance (Mihailović & Mihailović 2006). Its surface exceeds 80 m^2 and the deposits are excavated to the depth of 4.4 m but the bedrock has not been reached (Mihailović 2014).

During the excavations of Hadži Prodanova Cave, only a small number (15) of Palaeolithic artefacts was found. The majority of them were collected, not from the interior of the cave, but from the plateau in front of it.

Chipped flint artefacts of Epigravettian type have been found in Layer 2 and Middle Palaeolithic artefacts in Layers 4 and 5 (Mihailović & Mihailović 2006).

Layer 5 yielded two scrapers and artefacts made of quartzite, which definitely identified this collection as Middle Palaeolithic. The presence of implements with abruptly retouched edge in Layer 2 indicates that the collection belongs to the Gravettian or Epigravettian.

Concerning the Late Upper Palaeolithic, Hadži Prodanova cave is the only Gravettian/Epigravettian site, besides Šalitrena cave, in the mountainous regions of the Central Balkans (Mihailović & Mihailović 2006).

According to a preliminary taphonomic analysis (Milošević 2010), "human occupation was very brief, maybe only a few hours, which is somewhat more common in the Middle Paleolithic than in the Epigravettian".

The aim of this paper is to describe the association of rodents from this site. Besides rodents, Hadži Prodanova Cave also yielded remains of other small vertebrates (insectivores and reptiles are especially numerous; Bogićević et al. 2016) and large mammals (studied by Prof. V. Dimitrijević and one of the authors of this paper [S. M.]). Preliminary results of the large mammal analysis conducted by V. Dimitrijević showed that the absolutely predominant species in the Pleistocene layers is the cave bear (*Ursus spelaeus*), especially in the upper levels, and somewhat less so in Layers 5b and 5c (Mihailović & Mihailović 2006; Milošević 2010a). This species is the most common in all layers, followed by *Capra*

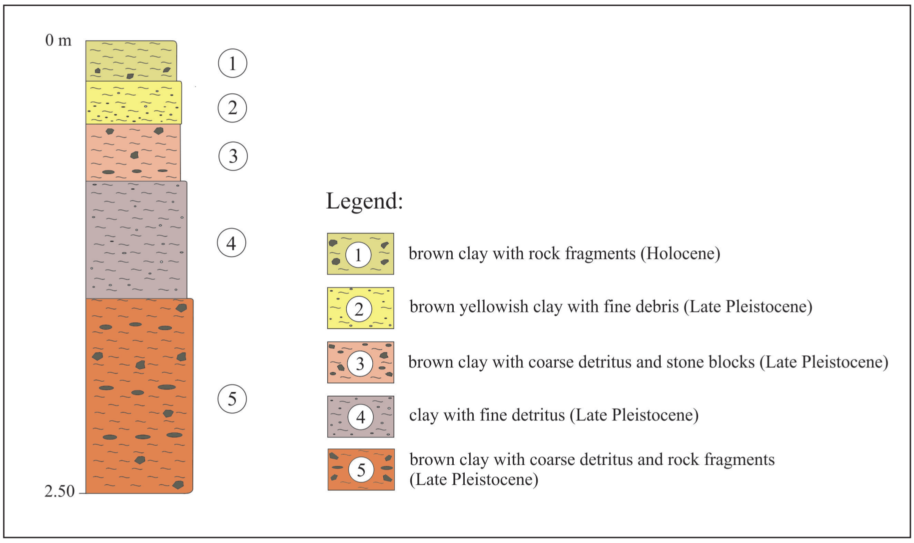


Fig. 2 - Section of the Quaternary deposits in Hadži Prodanova cave.

ibex and *Canis lupus* (Milošević 2010). In Layers 4 and 5 *Rupicapra rupicapra* is rather common. Other species include *Cervus elaphus, Lynx lynx,* and *Crocuta spelaea*. Among birds there are numerous remains of *Pyrrhocorax* sp. (Milošević 2010). Study of this material is still in progress.

The rodent remains in Hadži Prodanova Cave are rather numerous. All the parts of rodent skeleton are found, but some are fragmentary. Most of the teeth are isolated, but there are also some maxillae/mandibles with teeth. Long bones are mostly broken and have sharp edges, but they are rather well preserved, without traces of corrosion and never water-rounded.

Judging by all this, it can be concluded that most of the rodent bones from Hadži Prodanova Cave are prey remains. Nocturnal birds of prey (owls), for example, regurgitate well preserved bones and usually live near cave entrances (Andrews 1990). A more detailed taphonomic analysis is required to reveal which predator is responsible for the accumulation of the rodent and other small vertebrate remains.

Material and Methods

The rodent fauna described in the present paper was collected from the Pleistocene layers (3, 4 and 5) of Hadži Prodanova Cave. During the 2003 excavation season, sediment samples were taken from each layer and horizon (nine samples in total). All samples (approximately 90 kg of sediment) were screen-washed on screens of 2, 1 and 0.5 mm mesh. The residues obtained after washing were sorted under a binocular microscope. All bones were picked out, but for taxonomic identification only teeth and fragments of upper and lower jaws were used. In total, about three hundred teeth are included in this study. Since postcranial elements of most small mammals cannot be identified to the genus or species level, this work was confined to the collected teeth. Remains of other groups of small mammals are still under analysis and will not be described here.

All dimensions (most often length and width) are given in mm. Measurement methods are as described in Nadachowski (1982) for arvicolids, and Maul (2001) for sciurids, cricetids, murids and glirids. The following indices are also used: A/L for the relative length of the anteroconid complex (Meulen 1973), Hsd/L for the relative height of hyposinuid - the buccal posterior tip of enamel-dentine junction line (Rabeder 1981; Maul et al. 1998) and SDQ for the enamel thickness differentiation (Heinrich 1978; Kolfschoten 1990). For arvicolids, the terminology of Meulen (1973) and Nadachowski (1982) is employed; for murids Storch (1987); for sciurids Stehlin & Schaub (1951); and for glirids Bruijn (1967). The names of morphotypes of arvicoline M1 are after Nadachowski (1982, 1984, 1985).

For the purpose of identification, comparative collections of recent and fossil rodent teeth of the Department of Palaeontology, University of Belgrade were used.

The described material is stored at the Department of Palaeontology of the Faculty of Mining and Geology, University of Belgrade under the inventory numbers HPP 3/1-24, 4/1-108, 5/1-14, 5a/1-30, 5b/1-43, 5c/1-51, and HPP 5d/1-11 (the first numbers represent the layer/horizon, the others ordinal numbers of specimens). Data on the geographic distribution of species in the Pleistocene were taken mainly from Kowalski (2001). Relative species abundance was calculated by using MNI (minimum number of individuals, after White 1953).

Systematic palaeontology

Family Sciuridae Gray, 1821
Spermophilus Cuvier, 1825

Spermophilus cf. ***citelloides*** (Kormos, 1916)

Fig. 3a

Material and dimensions:

Layer 5: M$_1$ dext. (2.0x2.5 mm). HPP 5/1

Horizon 5a: M^3 sin. (2.67x2.89 mm) HPP 5a/1; P/M sup. sin. HPP 5a/2.

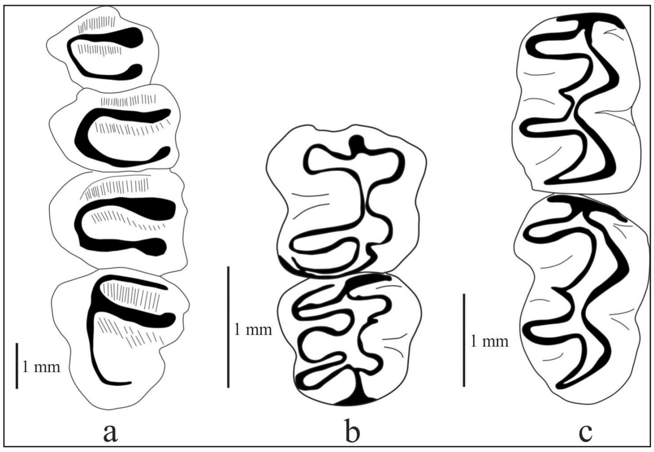


Fig. 3 - (a) *Spermophilus* cf. *citelloides* (Kormos, 1916). max. sin. (P^4-M^3). (b) *Sicista subtilis* (Pallas, 1773). max. dext. (M^1-M^2). (c) *Mesocricetus newtoni* Nehring, 1898. mand. dext. (M_2-M_3).

Horizon 5b: max.sin. (P^4-M^3) L(P^4-M^3): 8.17 mm; P^4 (1.86x2.10); M^1 (1.9x2.45); M^2 (2.0x2.69); M^3 (2.67x2.67). HPP 5b/1; M^1 sin. (2.06x2.56) HPP 5b/2; P_4 dext. (1.78x1.89) HPP 5b/3.

Description. Remains of ground squirrels have been found only in layer 5. Apart from one fragmentary piece of maxilla (Fig. 3a), all other remains are isolated teeth.

Remarks. According to their dimensions, Pleistocene ground squirrels can be placed in two groups: the smaller ones, to which the species *Spermophilus citellus* (Linnaeus, 1766)*, S. citelloides* (Kormos, 1916) and *S. suslicus* (Güldenstaedt, 1770) belong, and the larger ones, such as *S. superciliosus* Kaup, 1839. The dimensions of the molars from Hadži Prodanova cave correspond to the dimensions of the small species *S. citelloides* from various Pleistocene localities in central and southeastern Europe (Heller 1972; Black & Kowalski 1974; Heinrich 1978; Koenigswald 1985; Bogićević et al. 2011). Molars of *S. superciliosus* are decidedly larger (Black & Kowalski 1974; Heinrich 1983).

The representatives of the group of small ground squirels – Pleistocene *S. citelloides* and two recent Eurasian species, *Spermophilus citellus* and *S. suslicus*, have very similar dimensions and morphological features of the cheek teeth. An undivided posterior root in P_4 is sometimes considered as a characteristic of *S. citellus*, while in *S. citelloides* and *S. suslicus* this root is divided into two parts in the majority of cases (50-80%, after Kowalski & Nadachowski 1982). In 80% of P_4 from Burgtonna (ascribed to *S. citelloides*), however, the posterior roots are fused, so this criterion is not entirely reliable for species identification (Koenigswald 1985). A single premolar found in Hadži Prodanova Cave has only two roots. However, there are some slight differences in dimensions between *S. citellus* and *S. citelloides* in that the cheek teeth of the first species (especially $P^4$4 and $M^3$3) are somewhat broader (Jánossy 1976; Heinrich 1978). Since the dimensions of those teeth from Hadži Prodanova Cave are very similar to the *S. citelloides* material from Burgtonna (Heinrich 1978, figs. 17, 19, 20) they are tentatively ascribed to *Spermophilus citelloides.*

During the Late Pleistocene*, S. citelloides* was a rather common element in the rodent faunas of western and central Europe. Remains of this species have been found in several localities in Serbia: Smolućka Cave (cited as *Citellus citellus* and *Citellus* sp.; Dimitrijević 1991, 1997), Baranica (as *Spermophilus* cf. *citelloides*, Bogićević et al. 2011), Vrelska Cave (as *Spermophilus citellus*; Marković & Pavlović 1991; Dimitrijević 1997) and in a fissure filling in the quarry of Kamenjak on Venčac near Arandjelovac (Bogićević 2008).

Family Dipodidae Fischer de Waldheim, 1817
Sicista Gray, 1827

Sicista subtilis (Pallas, 1773)
Fig. 3b

Material and dimensions:

Layer 3: fragment max.dext. (M^1-M^2) (M^1: 1.1x1.0; M^2: 1.07x0.97) HPP 3/1.

Layer 5

Horizon 5a: M^1 dext. (1.1x1.0) HPP 5a/3.
Horizon 5c: mand.dext. (M_1) (1.17x0.83) HPP 5c/1.

Description. Remains of this species are rather scarce in Hadži Prodanova Cave: a fragment of a maxilla (Fig. 3b), a fragment of a mandible with $M_{1,}$ and an isolated molar (M^1).

Remarks. Simple occlusal patterns and the relatively large size of the molars clearly point to *Sicista*. Given the dimensions, the recovered molars can be attributed to *Sicista subtilis* (Pallas, 1773) and not to *Sicista betulina*, for the teeth of the second species are significantly smaller. It is widely accepted that the length of M^1 never exceeds 1.0 mm in *S. betulina*, while it is always greater in *S. subtilis* (Pucek 1982). Both M^1 from the Hadži Prodanova

Cave are longer than 1 mm. The molar dimensions also fit into the size range of the recent *S. subtilis* from Romania (Pucek 1982), or even exceed it. Dimensions of M^1 (length - 1.13; width - 0.83 mm) are very similar to those of the specimen from Caverna Generosa, Italy (Bona & Savoldi 2016).

Molars of *S. subtilis* show some peculiarities in structure (there are no additional "spurs" on the main cusps; cusps are higher and better defined; mesostylid less conspicuous) (Pucek 1982). The M_1 of *S. betulina* has a more rounded occlusal outline, while in *S. subtilis* it has a shallow concavity on the labial side (Kalthoff et al. 2007). A molar from horizon 5c also shows the latter feature.

In Serbia, remains of *S. subtilis* have been found in Upper Pleistocene deposits of Smolućka Cave (Dimitrijević 1991, 1997), Baranica (Bogićević et al. 2011), Vrelska Cave (Marković & Pavlović 1991; Dimitrijević 1997), and Gradašnica Cave (Marković 2008).

Today it lives only in the northeastern part of Serbia, in the area of the Deliblato sands (Ham et al. 1983).

Family Cricetidae Fischer de Waldheim, 1817

Mesocricetus Nehring, 1898

Mesocricetus newtoni Nehring, 1898

Fig. 3c

Material and dimensions:

Layer 3: fragment mand. dext. (M_2-M_3) (M_2: 2.1x1.4; M_3: 2.4x1.47) HPP 3/2.

Layer 4: M^2 sin. (2.1x1.45) HPP 4/1, 2 M^3 sin. (2.07x1.52; 2.03x1.41) HPP 4/2-3.

Layer 5

Horizon 5c: M_2 sin. (2.21x1.38) HPP 5c/2.

Description. Several teeth of medium-sized hamsters have been found in Hadži Prodanova Cave, among them a mandible with two molars (M_2-M_3), and several isolated molars.

Remarks. The cricetid material from Hadži Prodanova Cave can confidently be referred to the genus *Mesocricetus* on the basis of the following characters: intermediate molar size, funnel-like structures between the opposed cusps on the upper molars, M_3 longer than M_2, a well- developed posterior cingulum. The most conspicuous feature of *Mesocricetus* molars is the presence of a ridge on the lower molars, between the metaconid and entoconid–mesolophid. It is usually less distinct in M_1, but more developed in M_2 and M_3 (Fig. 3c).

On the basis of dimensions, two groups of *Mesocricetus* species can be distinguished: a larger "northern" group, to which *M. newtoni* and *M. raddei* (Nehring, 1894) belong and a smaller "southern" group, represented by *M. brandti* (Nehring, 1898), *M. auratus* Waterhouse, 1839 and *M. aramaeus* Bate, 1943 (Popov 2000).

The molars from Hadži Prodanova Cave are larger than those of "small *Mesocricetus*" species, such as the recent *M. brandti* from the Caucasus (Baryshnikov & Baranova 1983) and the same species from Pleistocene deposits in Turkey (Suata Alpaslan 2011), while "*M. arameus* is amazingly small in comparison with other species of the genus" (Tchernov 1968).

As regards the larger group, the material from Hadži Prodanova Cave is similar to the smaller subspecies of *M. raddei* – *M. raddei nigriculus* (Nehring, 1898) from the Caucasus (Baryšnikov & Baranova 1983) – but it differs from it by a smaller width/length ratio of M_3 (0.64-0.70 in *M. r. nigriculus*; 0.61 in the Hadži Prodanova material), and by the relative length of M_3 (length ratio M_2/M_3 91.3-100 in *M. r. nigriculus*; 87.5 in *Mesocricetus* from Hadži Prodanova Cave).

The dimensions of the molars from Hadži Prodanova Cave are comparable to the dimensions of *M. newtoni* from other Pleistocene localities in Serbia and Bulgaria (Popov 1994, 2000; Dimitrijević 1991; Bogićević et al. 2011 etc.) as well as recent ones from Dobrugia (Romania) (Niethammer 1982).

On this basis, the scarce remains of cricetids from Hadži Prodanova Cave are ascribed to *Mesocricetus newtoni*. The Pleistocene distribution of this species is restricted to the western Balkans – Romania, Bulgaria, Greece, Montenegro and Serbia (Kowalski 2001). It has recently also been found in Italy (Berto & Rubinato 2013).

It is one of the most common and most abundant rodent species in the Upper Pleistocene deposits of Serbia, found at Smolućka (Dimitrijević 1991), Mirilovska (Dimitrijević & Jovanović 2002), Baranica (Bogićević et al. 2011), Vasiljska, Vrelska (Dimitrijević 1997), and Gradašnica Cave (Marković 2008). Mališina Stijena near Pljevlja (eastern Montenegro) is the westernmost Balkan locality at which remains of this species have been found (Bogićević

& Dimitrijević 2004). Today it lives in steppe areas of southern Romania and northern Bulgaria, but not in Serbia (Niethammer 1982).

Family Arvicolidae Gray, 1821
Arvicola Lacépède, 1799

Arvicola cf. ***terrestris*** (Linnaeus, 1758)

Fig. 4a

Material and dimensions:
Layer 4: M^3 sin. (2.45x1.38) HPP 4/5.
Layer 5
Horizon 5a: M^3 dext. HPP 5a/4.

Description. The molars of a large vole from Hadži Prodanova Cave have abundant cement in re-entrant angles.

One of two M^3 (from horizon 5a) is broken (AL is missing and T3 is damaged). The second (Fig. 4a) is slightly damaged. The T4 is in broad connection with PL. The molar has a small buccal syncline - BRA3 and belongs to the more complicated, so-called "exitus" (Nadachowski 1982) morphotype of M^3 with three more or less closed triangles. Enamel differentiation is positive or normal.

The dimensions of a complete M^3 correspond to the dimensions of *A. terrestris* teeth from Temnata Cave (Popov 1994) and Wannenköpfe (Kalthoff et al. 2007), and those of recent and Late Pleistocene representatives of the species from Poland (Nadachowski 1982).

Remarks. Two molars of water vole are tentatively ascribed to *Arvicola* cf. *terrestris*, to which they correspond according to their dimensions and enamel differentiation. The SDQ index (after Heinrich 1978) is usually measured on M_1 (Maul et al. 1998). Since this type of teeth has not been found in Hadži Prodanova Cave, the index has been measured after methods proposed by Kolfschoten (1990). The values for this index (97.67-104.25 in Layer 4 and 83 in Layer 5a) correspond to different populations of *Arvicola terrestris* from Late Pleistocene deposits of Europe (Kolfschoten 1990).

Remains of *Arvicola terrestris* are very numerous throughout Europe, both in warm and cold periods of the Late Pleistocene (Kowalski 2001; Cuenca-Bescós et al. 2008). This species represents the characteristic fossil for the upper part of the Toringian micromammal zone (Fejfar & Heinrich 1983). It has also been found in several caves in Serbia-Baranica (Bogićević et al. 2012), Smolućka and Vrelska Cave (Dimitrijević 1997) and in Montenegro - Crvena Stijena (Malez 1975) and Mališina Stijena (Bogićević & Dimitrijević 2004), but it is never so frequent as, for instance, in some Croatian localities (in Vindija Cave, *A. terrestris* is the most common vole species [Mauch Lenardić 2005]).

Chionomys Miller, 1902

Chionomys nivalis (Martins, 1842)

Fig. 4b

Material and dimensions:
Layer 3: M_1 sin. (L=2.86, a=1.38) HPP 3/11, M_1 dext. (a=1.34) HPP 3/12.
Layer 4: mand.dext. (M_1) HPP 4/11 (L=2.69, a=1.31), mand. dext. (M_1-M_2) (L=2.72, a=1.24), M_1 dext. (L=2.69, a=1.21) HPP 4/11-13.
Layer 5: M_1 sin. (a=1.24) HPP 5/5.
Horizon 5b: M_1 sin. (L=2.62, a=1.24) HPP 5b/10.

Description. The dentine triangles are rather massive. Triangles T1-T4 on M_1 are closed (except on the specimen from layer 5b), while T5 is in some specimens widely connected to the anterior lobe. Most of the M_1 from Hadži Prodanova Cave (5 out of 7 or 71.4%) have anterior parts in the shape of a mushroom or spear (progressive or "nivalid" morphotype; Fig. 4b). The remaining molars show the transient morphotype ("nivalid-ratticeps" after Nadachowski 1984; 28.6%).

Remarks. It is interesting to observe that in all the localities in Serbia in which *Chionomys nivalis* has been recovered (Bogićević et al. 2012; Bogićević 2008; Dimitrijević 1991), the morphotype frequency is very similar to that in Hadži Prodanova Cave. The most frequent morphotype is always "nivalid": Baranica (73.3%), Vrelska cave (71%), Smolućka cave (65%). The second most frequent is the transient "nivalid-ratticeps" morphotype at 35% in Smolućka cave, 23.3% in Baranica and 22% in Vrelska cave, while the morphotype "gud" is extremely rare (3% in Baranica and 7% in Vrelska cave). This morphotype is not present in Hadži Prodanova Cave. This frequency is also rather similar to the distribution of morphotypes in recent populations in Serbia (the mountain Stara planina; Kryštufek 1990).

This species inhabited the mountainous areas of Europe in the Middle and Late Pleistocene

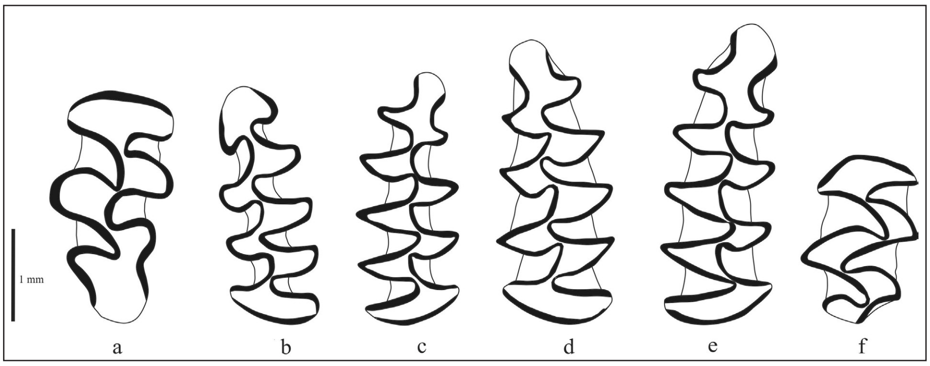


Fig. 4 - (a) *Arvicola* cf. *terrestris* (Linnaeus, 1758). M^3 sin. (b) *Chionomys nivalis* (Martins, 1842). M_1 sin. (c-f) *Microtus* (*M.*) *arvalis* (Pallas, 1778) & M. (M.) *agrestis* (Linnaeus, 1761). (c) M_1 dext. (d) M_1 sin. (e) M_1 dext. (f) M^2 sin.

(Kowalski 2001). It was previously thought (Terzea 1972; Toškan & Kryštufek 2007) that it lived only north of the Danube and Sava rivers during the Late Pleistocene. It appeared in central Europe about 70,000 years ago (Kordos 1995).

Several caves and shelters of Late Pleistocene age in Serbia (Vrelska and Smolućka Cave; Dimitrijević 1991, 1997; Baranica Cave, Bogićević et al. 2012; Gradašnica – Marković 2008) have yielded remains of this species.

Microtus Schrank, 1798
Subgenus *Microtus* Schrank, 1798

Microtus (Microtus) agrestis (Linnaeus, 1761)/ ***Microtus (Microtus) arvalis*** (Pallas, 1778)

Fig. 4c-f

Material and dimensions:

Layer 3: M^2 dext., mand.sin., mand.dext., 2 M_1 sin., 3 M_1 dext. HPP 3/13-20

Layer 4: M^2 sin., 8 mand.sin., 4 mand.dext., 16 M_1 sin., 18 M_1 dext. HPP 4/14-60

Layer 5: mand.sin., mand.dext., 2 M_1 sin., 3 M_1 dext. HPP 5/6-12.

Layer 5

Horizon 5a: mand.dext., 5 M_1 sin., 9 M_1 dext. HPP 5a/7- 21.
Horizon 5b: 2 mand.dext., 2 M_1 sin., 3 M_1 dext. HPP 5b/11-17.
Horizon 5c: 2 mand.sin., 2 mand.dext., 8 M_1 sin., 9 M_1 dext. HPP 5c/7-27
Horizon 5d: M_1 sin., 4 M_1 dext. HPP 5d/2-6.

(Dimensions of M_1 are given in Table 1).

Description. First lower molars (M_1) are characterized by the presence of five closed dentine triangles (T1-T5) on the occlusal surface. Typical "arvalid" morphotypes (Fig. 4c-e) are the most abundant in all layers (100% in layer 3; 83.33% in layer 4; 81.11% in layer 5). The other morphotypes are also present, but in much lower frequencies: "maškii" morphotype: 9.52% in layer 4, 3.78% in layer 5; the morphotype with an additional lingual syncline - LRA6: 4.76% in layer 4; 9.43% in layer 5; "extratriangulatus" morphotype: 3.78% in layer 5; and two transitional morphotypes: "maškii/arvalis" 2.38% in layer 4, and "arvalis/extratriangulatus" 1.89% in layer 5.

The average length of M_1 is 2.74 mm in all three layers.

Apart from M1, two M^2 that have a well-developed "exsul-loop" were also found in Hadži Prodanova Cave (1 in layer 3 and 1 in layer 4; Fig. 4f).

Remarks. The structure of M_1 of these two species (*M. arvalis* and *M. agrestis*) is almost identical, so it is very difficult to distinguish them on the basis of isolated molars. The only unambiguous difference between them is the presence of the so-called "exsul-loop" in M^2, which is well-developed only in *M. agrestis* (Zimmerman 1956).

The M_1 of *M. arvalis* are smaller - the length of M_1 (measured in Recent specimens) ranges from 2.4 to 2.9 mm, while in *M. agrestis* it varies from 2.75 to 3.4 mm (Gromov & Polyakov 1992); in Recent specimens from Slovenia M_1 of *M. arvalis* have mean values of length of 2.68 mm, while the mean is 3.03 in *M. agrestis* (Toškan 2009). In Poland M_1 length in *M. arvalis* is 2.67 mm and in *M. agrestis* 3.05 mm (Nadachowski 1982).

It seems that *M. arvalis* maintained a constant size over the last 100,000 years, while *M. agrestis* gradually increased in size (Mauch Lenardić 2007).

Judging by their minimum, maximum and mean values in length, molars from Hadži Prodanova Cave are much more similar in dimensions to the smaller species. However, the finding of an M^2 with a well-developed "exsul-loop" in layers 3 and 4, as well as M_1 morphotypes with LRA6 and "extratriangulatus" (layers 4 and 5), demonstrates the presence of the species *M. agrestis* in all layers of Hadži Prodanova Cave.

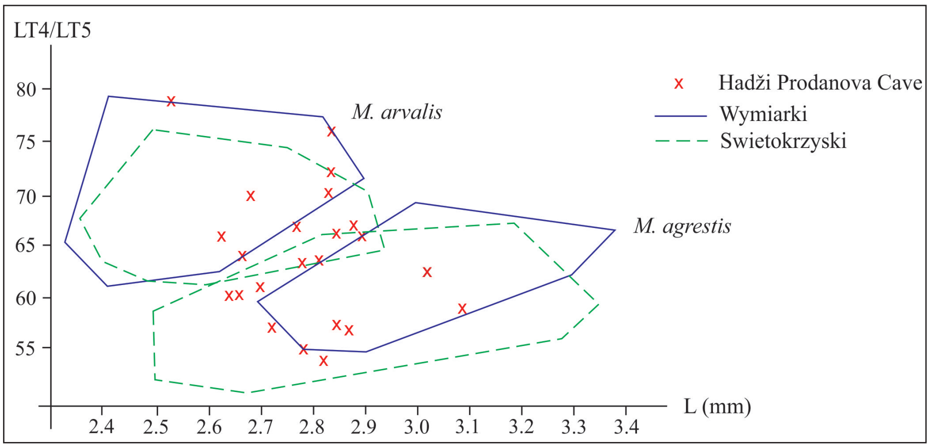


Fig. 5 - Correlation diagram of M_1 length (L) and LT4/LT5 index for two pairs of recent populations of *M. arvalis* and *M. agrestis* (modified after Nadachowski 1984a) and for the fossil specimens from Hadži Prodanova Cave (marked with crosses).

The mean value of the A/L index is 52-54, which can be compared to data from Late Pleistocene localities in Croatia: Vindija Cave, Marlera I, Mujina Cave, where it ranges from 53 to 54 (Mauch Lenardić 2007). According to Nadachowski (1982) the A/L index of both species in Poland remains rather stable at 54, from the early Weichselian till today.

In conclusion, we can say that both species were present in the material from Hadži Prodanova Cave, but *M. arvalis* was significantly more numerous.

Some authors have tried to separate these two species using the size (length) of their M_1 and the asymmetry of the enamel triangles (M_1 of *M. agrestis* are distinctly asymmetric – buccal triangles being smaller than lingual ones; Chaline 1972). For example, Nadachowski (1984a) obtained a complete or almost complete separation of these two species by plotting on a correlation diagram the length of M_1 (L) and the index LT4/LT5 (ratio of the lengths of the fourth and fifth enamel triangles of M_1). We measured the same values in M_1 from Layer 4 and obtained a similar distribution as Nadachowski (Fig. 5), but with some values situated in the overlapping zone. Kočev (1986) had even better results in separation of these species, but it was unclear how he measured the lengths of the opposite enamel triangles. Since our results are not satisfactory, we decided to leave the two species unseparated for now, with remarks that both of them are present in the material.

Microtus arvalis/agrestis are among the most common of all Late Pleistocene rodents in Serbia (they are the second numerous in Hadži Prodanova Cave, after *M. subterraneus*). Their remains have been found in Baranica, Smolućka, Vrelska, Vasiljska and Petnička Caves (Dimitrijević 1997; Bogićević 2008).

Microtus (Terricola) subterraneus

(de Sélys-Longchamps, 1836)

Fig. 6 a-c

Material and dimensions:

Layer 3: 2 M_1 sin., 2 M_1 dext. HPP 3/21-24.

Layer 4: 6 mand.sin., 8 mand.dext., 22 M_1 sin., 12 M_1 dext. HPP 4/61-108.

Layer 5: 2 mand.dext., 4 M_1 sin., 3 M_1 dext. HPP 5/13-14

Horizon 5a: mand.sin., 4 M_1 sin., 4 M_1 dext. HPP 5a/22-30.

Horizon 5b: 4 mand.dext., 10 M_1 sin., 12 M_1 dext. HPP 5b/18-43.

Horizon 5c: mand.sin., 4 mand.dext., 8 M_1 sin., 11 M_1 dext. HPP 5c/28-51

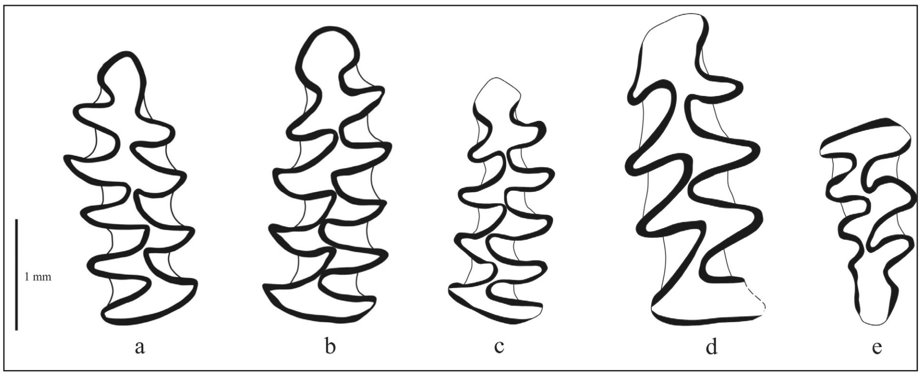
Horizon 5d: mand.sin., 4 M_1 dext. HPP 5d/7-11.

(Dimensions of M_1 are given in Tab. 2).

Description. The first lower molars of a small-sized vole are characterized by the presence of the so-called "*Pitymys*-rhombus" (a broad connection between triangles T4 and T5). In all layers typical "arvalid" morphotypes (combined A, C and D morphotypes after Nadachowski 1982; Fig. 6a, c) prevail and are almost uniformly distributed (80% in layer 3, 80.4% in layer 4 and 79.7% in layer 5). The transitional "arvalid-maškii" morphotype, with slightly narrower anterior cap (Fig. 6b) is the second abundant (13% in layer 4 and 14.5% in layer 5), while all the others are much less numerous.

Remarks. The overall morphology of M_1 resembles that of the recent species *Microtus subterraneus* and *Microtus multiplex* (Fatio, 1905), but based on the length of M_1 it can be concluded that the material from Hadži Prodanova Cave is closer to the smaller species, *Microtus subterraneus*. The overall size ranges and mean values of these molars are very similar to those of Recent and fossil representatives (Niethammer 1982; Ziegler 1995; Nadachowski 1984 etc.). The mean length of M_1 in layers 4 and 5

Fig. 6 - *Microtus* (*Terricola*) *subterraneus* (de Sélys-Longchamps, 1836). (a) M_1 dext. (b) M_1 sin. (b) M_1 sin. (d) *Clethrionomys glareolus* (Schreber, 1780). M_1 sin. (e) M^3 dext.



is 2.51 mm; in layer 3 it is somewhat greater (2.60 mm), probably because of the small sample (only 3 molars), and is comparable to recent specimens from Poland (2.62 mm; A/L – 53; Nadachowski 1982).

Several Late Pleistocene localities in Serbia have yielded remains of this species: Baranica (Bogićević 2008), Smolućka and Vrelska Caves (Dimitrijević 1997), Vasiljska Cave and Pećurski kamen (Brunet-Lecomte et al. 2001).

In central Europe it occurs only in warmer periods of the Late Pleistocene (Kowalski & Nadachowski 1982).

Clethrionomys Tilesius, 1850

Clethrionomys glareolus (Schreber, 1780)

Fig. 6d-e

Material and dimensions:

Layer 3: M^1 dext. HPP 3/10.

Layer 4: M^1 sin., M^1 dext., M^3 sin., M^3 dext., M_1 sin., 2 M_2 sin., M_3 dext. HPP 4/10

Layer 5: 2 M^2 sin. HPP 5/4.

Horizon 5a: M^2 dext. HPP 5a/6.

Horizon 5b: mand.sin. (M_1) (L=2.07, a=0.93), M_1 sin., M_2 sin. HPP 5b/7-9

Horizon 5c: M^1 sin., M^3 sin., M_1 sin. (L=2.31, a=0.9), M_3 dext. HPP 5c/6

Horizon 5d: M_2 sin.,M_2 dext. HPP 5d/1.

Description. Molars of this species differ from all the other voles' molars from this locality by the presence of roots. They are small or completely absent in young individuals and very high in the older ones. Dentine triangles have rounded outlines. The enamel is thinner on convex sides of triangles and thicker on concave ones. Reentrant angles are filled with cementum. The M^1 have 2 roots. In both M_1, T4 and T5 are broadly connected to each other and to ACC (Fig. 6d).

Remarks. It has been claimed that molars of *Clethrionomys glareolus* that lived during warmer periods were smaller and comparable to the dimensions of the Recent ones (Nadachowski 1982). This is also confirmed by the study of remains of Pleistocene *Clethrionomys* from other localities in Serbia. Molars found in the Last Glacial deposits of Baranica and Smolućka Cave are much larger than those from Last Interglacial deposits of Vasiljska Cave (Bogićević 2008). Since molars from layer 5 are rather small, it could indicate that this layer was formed during a warmer period.

No M^1 from Hadži Prodanova Cave has three roots, a characteristic that is observed (Jeannet 1981; Radulescu & Samson 1992) in populations that lived before the Last Glacial period.

Hsd/L can be measured only in one M_1 from layer 5b, and its value is 122, similar to the lower values for this species in German localities (Maul et al.1998). M^3 from layer 4 (the only complete specimen) has a length of 1.76 mm. According to Rekovets (1994), length of M^3 in *Clethrionomys glareolus* is, on average, 1.6-1.7 mm, in both fossil and recent specimens. All M^3 from Hadži Prodanova Cave (3 of them) are of a similar structure – with a well developed T5, small BSA4 and BRA4 (Fig. 6e). In two specimens the connection between T3 and T4 is wide, in one (from layer 5c) this connection is somewhat constricted. In recent populations of this species, T3 and T4 are almost always separated (Rekovets & Nadachowski 1995).

Remains of this species have been found in Upper Pleistocene deposits of several caves in Serbia: Smolućka, Vrelska, Vasiljska, Petnička Cave, Baranica and Canetova Cave (Dimitrijević, 1997; Bogićević 2008).

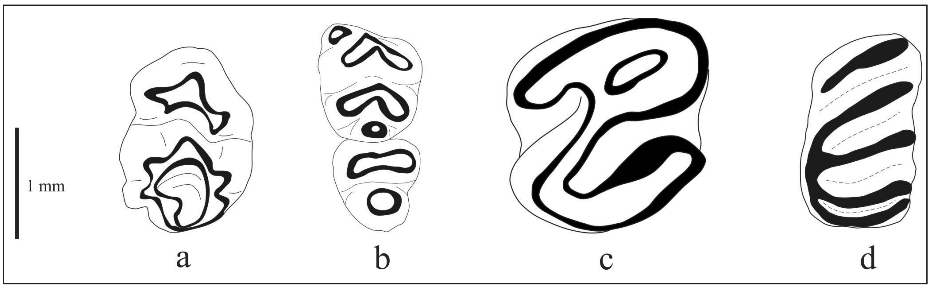


Fig. 7 - (a) *Apodemus sylvaticus* (Linnaeus, 1758). M^1 dext. (b) mand. sin (M_2-M_3). (c) *Spalax* sp. M^2 sin. (d) *Muscardinus avellanarius* (Linnaeus, 1758). M^1 sin.

Family Muridae Illiger, 1811
Apodemus Kaup, 1829
Subgenus *Sylvaemus* Ognev, 1924

Apodemus sylvaticus (Linnaeus, 1758)

Fig. 7a, b

Material and dimensions:

Layer 3: fragment max.dext. (M^1-M^2, fragment M^3; M^1 - 1.71x1.18; M^2 – 1.21x1.14) HPP 3/5, fragment M^1 sin. (L>1.7 mm) HPP 3/6, fragment mandibulae sin. (M_2) (1.07x1.03) HPP 3/7.

Layer 5

Horizon 5c: mand.sin. (M_2-M_3) (M_2 – 1.17x1.07; M_3 – 1.0x0.9) HPP 5c/3, M_2 sin. (1.14x1.07) HPP 5c/4.

Description. Scarce remains of a medium-sized murine were found in Hadži Prodanova Cave. The M^1 and M^2 have four roots. They have no posterior cingula. On M^1 t1 and t3 have small posterior spurs and t1 is connected to t5 (Fig. 7a). On M^2 t1 and t3 are present and t9 is distinct. The M_2 has only one accessory labial cusp, the so-called Sv (Fig. 7b).

Remarks. According to their morphological features and dimensions, these molars from Hadži Prodanova Cave are similar to *Apodemus sylvaticus* and *A. flavicollis* Melchior, 1834.

The L/W ratios of M_2 are closer to those in the species *A. sylvaticus* than to *A. flavicollis* (1.03-1.07 in *sylvaticus*, 1.09-1.12 in *flavicollis* after Pasquier 1974; 1.04-1.09 in Hadži Prodanova molar), and the dimensions of the molars are also more similar to *A. sylvaticus*. The conjunction between the tubercles t4 and t7 on M^1 and the development of the tubercle t9 on M^2 are morphological characteristics (after Pasquier 1974) of *Apodemus sylvaticus*. Thus, the remains from Hadži Prodanova Cave are ascribed to this species.

Remains of *Apodemus sylvaticus* have been found in Upper Pleistocene deposits of several caves in Serbia: Smolućka, Vasiljska, Vrelska, Petnička, Prekonoška, Canetova and Popšička Caves (Dimitrijević 1997; Bogićević 2008).

Apodemus cf. ***uralensis*** (Pallas, 1811)

Material and dimensions:

Layer 4: mand.dext. (M_1-M_2) (M_1 – 1.48x1.0; M_2 – 1.07x1.0) HPP 4/9.

Description. The M_1 has a small anteromedial tubercle (Sm) (similar to *A. sylvaticus* but less developed). Two accessory cusps are present on the labial side, one beside the medial cusp and the other near the posterior loop. The M_2 has only Sv, with no other accessory cusps.

Remarks. The lower molars are very similar in the structure of their occlusal surfaces to *A. sylvaticus*, but since they are somewhat smaller, we tentatively assign them to *Apodemus* cf. *uralensis*. Small representatives of the genus *Apodemus* from Pleistocene deposits of Europe are poorly known. *Apodemus uralensis* has been found in Upper Pleistocene deposits of Bulgaria (Temnata-3) and Slovenia (Črni kal 2 and 3) (Kowalski 2001).

Family Spalacidae Gray, 1821
Spalax Güldenstädt, 1770

Spalax sp.

Fig. 7c

Material and dimensions:

Layer 5

Horizon 5b: M^2 sin. (2.36x2.39) HPP 5b/6.

Horizon 5c: fragment of $M_{1,2}$ dext. HPP 5c/5.

Description. The molars are cylindrical, with a characteristic S-shaped occlusal surface (Fig. 7c) and short roots. The lower molar has two roots.

Remarks. The remains of mole rat are so scarce and fragmented that they cannot be identified to the level of species. They probably belong to *Spalax leucodon*, remains of which have already been found in several caves in Serbia: Baranica, Smolućka, Vrelska and Mirilovska Caves (Dimitrijević 1997; Dimitrijević & Jovanović 2002; Bogićević 2008). This species has also been reported from the Risovača Cave, but its Pleistocene age has not been confirmed (Rakovec 1965).

Family Gliridae Muirhead, 1819
Muscardinus Kaup, 1829

Muscardinus avellanarius (Linnaeus, 1758)
Fig. 7d

Material and dimensions:
Layer 3: M^1 sin. (1.72x1.00) HPP 3/8, M^3 sin. (1.00x1.28) HPP 3/9.

Description. Two glirid molars with flat occlusal surfaces were found in layer 3. The M^1 has an elongated occlusal surface with five transverse enamel crests (Fig. 7d), four main roots and a small one. The anteroloph is separated from the other crests, which are connected lingually. The ridges are separated by deep and wide valleys. The M^3 has four roots and seven narrow ridges that are almost straight and approximately parallel to each other. This tooth is much wider in its anterior part.

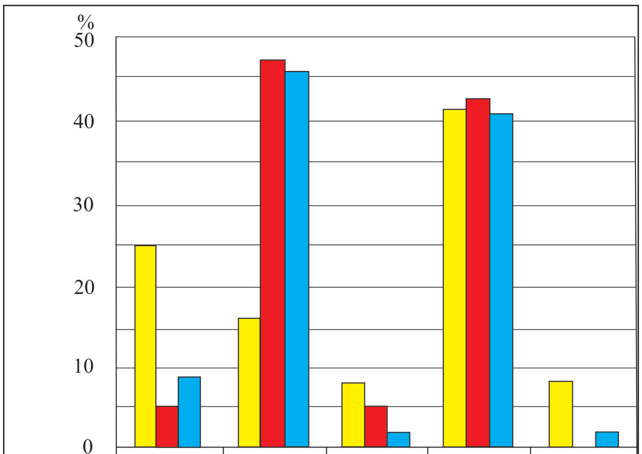
Remarks. On the basis of their morphological features and dimensions these molars can be identified as belonging to *Muscardinus avellanarius.*

Remains of *Muscardinus avellanarius* are rather rare in Upper Pleistocene cave deposits of Serbia. Only a few isolated teeth are known from Baranica (Bogićević et al. 2011), Smolućka, and Vasiljska Caves. A single tooth has been found in the Petnička Cave, Vrelska cave (Bogićević 2008; Dimitrijević 1997) and in Gradašnica (Marković 2008).

PALAEOECOLOGICAL IMPLICATIONS AND AGE OF FAUNA

Hadži Prodanova Cave is characterized by a rodent fauna in which *Microtus subterraneus* has the highest frequency (45-45.9%) in layers 4 and 5, and is the second most abundant in layer 3. *Microtus arvalis/agrestis* is the commonest in layer 3 (33.3%) and the second most common in layers 4 and 5.

The rodent species have been divided into five ecological groups (Fig. 8):



	A	B	C	D	E
🟨 layer 3	24.9	16.7	8.3	41.6	8.3
🟥 layer 4	5	47.6	5.1	42.6	-
🟦 layer 5	9	46	2	41	2

Fig. 8 - Distribution of rodents with different ecological preferences in layers 3, 4 and 5 of Hadži Prodanova Cave. A) forest species; B) species inhabiting wet meadows and river banks; C) mountain dwellers, D) inhabitants of intermediate (xero-mesophilous) environment, E) inhabitants of steppe and semi-arid regions.

A - forest dwellers: *Apodemus sylvaticus, A.* cf. *uralensis, Clethrionomys glareolus, Muscardinus avellanarius*;

B - species inhabiting moist meadows and river banks: *Microtus subterraneus, Arvicola* cf *terrestris*;

C - mountain dwellers and petrophilous species (*Chionomys nivalis*);

D - inhabitants of intermediate (xero-mesophilous) environments: *Microtus arvalis* and *agrestis, Mesocricetus newtoni, Spalax* sp., *Spermophilus* cf. *citelloides*;

E - steppe and semi-arid species: *Sicista subtilis.*

We can summarize the characteristics of the rodent fauna in the following way:

The ecological characteristics of layers 4 and 5 are strikingly similar to each other (all the ecological groups show similar frequencies in both layers), while in layer 3 an increase of steppe species can be observed. Species typical of humid environments (A+B) predominate in layers 4 and 5 and are also rather abundant in layer 3, although less so than those inhabiting drier habitats (group C).

There are no representatives of cold climates (such as lemmings, *Microtus gregalis*, etc.) and inhabitants of steppe, semi-arid and dry regions, like *Spermophilus, Sicista* and cricetids are rare. Especially interesting is the low percentage of cricetids, which are rather common in other Late Pleistocene assemblages in Serbia, where sometimes three species are present (*Cricetus cricetus, Mesocricetus newtoni* and *Cricetulus migratorius*). Only one species of cricetid has been found in Hadži Prodanova Cave, M*esocricetus newtoni*, and it is rather rare.

Of representatives of forest biotopes, *Clethrionomys glareolus* is present in all layers, although at a low frequency, while a glirid species (*Muscardinus avellanarius*) is found only in layer 3.

Almost all rodent species found in Hadži Prodanova Cave are still extant. Only S*permophilus citelloides* is extinct, whereas some species no longer inhabit western Serbia (*Sicista subtilis, Mesocricetus newtoni, Microtus agrestis*). The rather modern composition and appearance of the fauna (only one extinct species present, predominance of progressive morphotypes among vole molars, absence of the third root in M^1 of *Clethrionomys glareolus*) points to a Late Pleistocene rather than Middle Pleistocene age for the fauna.

Comparison of the fauna from Hadži Prodanova Cave with a typical "glacial" fauna from Baranica Cave and an "interglacial" one from Vasiljska Cave, led to the following conclusions: the fauna from Hadži Prodanova cave, although including forms that indicate a humid and temperate climate, is still a fauna with a predominance of voles, typical representatives of a cold climate. Inhabitants of forests and warm-loving forms, so numerous in the interglacial fauna from Vasiljska Cave, appear only sporadically, so it is more probable that we are dealing here with a glacial fauna, although from one of the warmer periods in the interval MIS 5e-MIS 3. Even so, the predominance of *M. subterraneus* and the absence of cricetids, the genus *Lagurus* and other typically steppe forms, differentiates this fauna from Last Glacial faunas in the Balkan Peninsula.

Rodent faunas from Middle Palaeolithic localities in central and eastern Europe are described in an article by Musil (2010). Faunas from the Last Interglacial (MIS 5e) from Croatia and central Europe have lived in the conditions of "continuous forest in its vicinity, climate ... warmer than today," which obviously is not the case with the fauna from Hadži Prodanova Cave.

However, there is an obvious similarity to MIS3 ("interstadial") faunas: "both interstadials (11 and 12) are characterized by a park landscape and alternating open steppe and small forest areas" (Musil 2010). Particularly similar is layer 11a from Bacho Kiro Cave (Bulgaria), which corresponds to interstadial 11 (Hengelo) ("mildly warm climate and forest steppe"). This level, with an absolute age of >43,000 years B.P., is the only stratum in the whole profile of Bacho Kiro where *M. subterraneus* is more numerous than *M. arvalis*, which is considered a sign of a progressive warming and an increase in humidity (Kowalski 1982).

This suggests that layers 4, 5 (and possibly 3) were most probably deposited during MIS 3 and not during MIS 5, as suggested elsewhere (Mihailović & Bogićević in press.) Layer 3 was formed in somewhat drier conditions, so it may be associated with climate changes at the end of MIS 3 or beginning of MIS 2. However, it should be remembered that climate changes in the Balkan Peninsula were not extreme (Miracle et al. 2010) and mammal faunas from colder and warmer periods did not show significant differences, so an earlier age (MIS 4), although less probable, should not be excluded.

Of course, this conclusion should be viewed cautiously and needs to be confirmed by radiometric dating.

CONCLUSIONS

The rodent fauna from Hadži Prodanova Cave is characterized by its mixed character. At first, voles are the most common group, which is characteristic of glacial period rodent faunas in the Balkans. Nevertheless, it differs from typical glacial faunas (such as those in Baranica Cave; Bogićević et al. 2011) by the absence or low frequency of arid and steppe-dwelling species, while its most abundant species, *M.subterraneus*, is considered to be associated with warming periods of the Pleistocene (Kowalski 1982; Nadachowski 1982).

The whole association was formed during a temperate and relatively humid period, but colder and drier than today (less forests, presence of forms that no longer inhabit western Serbia), so it could tentatively be placed in one of warmer periods within the Last Glacial (probably MIS 3).

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