New paleoecological perspectives on Late Pleistocene Neanderthals in northern Balkans: the rodent assemblages from Smolućka cave (Serbia)

Mihailo Jovanović, Katarina Bogićević, Draženko Nenadić, Jordi Agustí,·Christian Sánchez Bandera, Juan Manuel López García, Hugues Alexandre Blain

ORIGINAL PAPER

New paleoecological perspectives on Late Pleistocene Neanderthals in northern Balkans: the rodent assemblages from Smolućka cave (Serbia)

Mihailo Jovanović[1,2,3] · Katarina Bogićević[4] · Draženko Nenadić[5] · Jordi Agustí[1,2,6] · Christian Sánchez-Bandera[1,2] · Juan Manuel López-García[1,2] · Hugues-Alexandre Blain[1,2]

Abstract

During the Late Pleistocene, the Balkans came to be an important region with many isolated areas, enabling fauna, alongside Neanderthals, to thrive in the area. This work is focused on paleoenvironmental and paleoclimatic changes that occurred in the northern Balkan Peninsula with a special focus on fossil record from Smolućka cave aging from MIS 5 to MIS 3. Based on available data, an attempt has been made to establish a synthetic chronological context for the faunal assemblages recovered from Smolućka cave. Tentative attribution of layer 5 to MIS 5 relies on the interstadial pattern of our reconstructions, with favorable climate conditions for a large diversity of species and with mean annual temperature (MAT) reaching up to 3 °C higher than present values and abundant rainfall in the area. Cold conditions for MIS 4 are not present in Smolućka, although layer 4 (late MIS 5 or early MIS 4) shows somewhat dryer and cooler climate when compared with other layers. Layers 3z and 3 (MIS 3) are characterized by temperate and humid conditions together with a complex system of mosaic habitats with high environmental heterogeny but generally favorable conditions for a large diversity of life. Although still not fully chronologically constrained, Smolućka cave presents an interesting opportunity for future research, in the time period when only Neanderthals occupied the Balkans and thrived in local conditions. The transition between the Neanderthals and anatomically modern humans has not yet been established but can be expected in future research.

Keywords MIS 5 to MIS 3 · Small mammals · Climate · Landscape · Middle Paleolithic · Balkan Peninsula

This article is part of the Topical Collection on *Microvertebrate Studies in Archaeological Contexts: Middle Paleolithic to early Holocene past environments*.

✉ Mihailo Jovanović
mica.rex@gmail.com

1. Institut Català de Paleoecologia Humana I Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain

2. Departament d'Història i Història de l'Art, Universitat Rovira I Virgili, Avinguda de Catalunya 35, 43002 Tarragona, Spain

3. University Business Academy in Novi Sad-Faculty of Social Sciences, , Boulevard of Art, no. 2a, 11070 Belgrade, Serbia

4. Department of Palaeontology, University of Belgrade-Faculty of Mining and Geology, Kamenička 6, 11000 Belgrade, Serbia

5. Department of Regional Geology, University of Belgrade-Faculty of Mining and Geology, Kamenička 6, 11000 Belgrade, Serbia

6. Institució Catalana de Recerca I Estudis Avançats (ICREA), Barcelona, Spain

Introduction

The climate system is dynamic and variable, comprised of a maze of connected components and subsystems (Tierney et al. [101]). Since it is such a complex system, its modeling is very difficult. Examining the results of various climate models requires a large amount of data on past climates (Kohfeld and Harrison [58]). In the last decades of the twentieth century, two of the most important paleoclimatic discoveries are (1) the identification of Marine Isotope Stage (MIS) 5 as a period of minimum ice volume which extended from ca. 130 to 75 ka and has been divided into five substages, three warm episodes (MIS 5e, MIS 5c, and MIS 5a; as warm or warmer than present interglacial) alternating with two cold episodes (MIS 5d and MIS 5b) (i.e., Sánchez-Goñi [91]), and (2) the identification of abrupt climate changes during the last glacial cycle in the North Atlantic region during the MIS 3 and 2. These are now known as Dansgaard-Oeschger and Heinrich events (Bond et al. [20]; Dansgaard et al. [34]; Bond and Lotti

19). Greenland Stadials (GS) and Greenland Interstadials (GI) periods are the Greenland expressions of the characteristic Dansgaard–Oeschger events that represent cold and warm phases of the North Atlantic region (Rasmussen et al. 85). In the meantime, the specific patterns of Greenland Interstadials (GI) became a stratigraphic standard for the last glacial period (Björck et al. 10; Blockley et al. 12).

Serbia is occupying the territory of the central and northern parts of the Balkan Peninsula. Geographically North Serbia is a large fertile plain (Pannonian Basin), while in the south the landscape is dominated by two main mountain ranges (the Carpatho-Balkan belt in the east and the Dinaric Alps in the west). As a consequence of the variance in the landscape, there is also an observable variance in the preservation of the Late Pleistocene sediments and fauna. Late Pleistocene paleoclimatic reconstructions in Serbia are generally performed by analyzing small vertebrates (Đjurić 2019; Đjurić et al. 2016, 2017; 2008; Bogićević et al. 16, 15, 17; Jovanović 48, 49; Jovanović et al. 50), large mammal fauna (e.g., Dimitrijević 36–38), and occasionally by pollen analysis (Argant and Dimitrijević 5). These remains are mainly found in the cave sediments since both mountain ranges are very favorable for the creation of limestone caves. Another approach in reconstructing the Late Pleistocene climate is analyzing malacofauna from loess sequences of North Serbia (e.g., Marković 64, 63; Marković et al. 65, 67, 66, 68).

The mammalian faunas from the Balkans have been synthesized by Musil (75) and Stewart et al. (98) which improved the understanding of climatic, vegetational, and faunal changes during the period of MIS 3 in Europe. Since small mammal distribution changes in accordance with climate events, they constitute a good proxy for reconstructing past climate changes, and those estimates contribute to understanding the effect of a global climate change at a local scale (e.g., Cuenca-Bescós et al. 31; López-García et al. 62). This study aims to apply the bioclimatic analysis method (Hernández-Fernández 43, 44; Hernández-Fernández and Peláez-Campomanes, 45, Hernández-Fernández et al. 46), the Taxonomic Habitat Index (Evans et al. 41), and Shannon diversity index (Barnes et al. 7) on the Late Pleistocene rodent assemblages from Smolućka cave (Serbia) in order to complete previous studies and understand the climatic and paleoenvironmental changes that occurred during this period in central-north Balkan Peninsula.
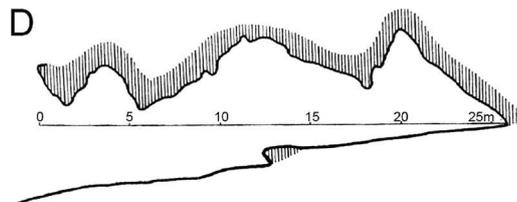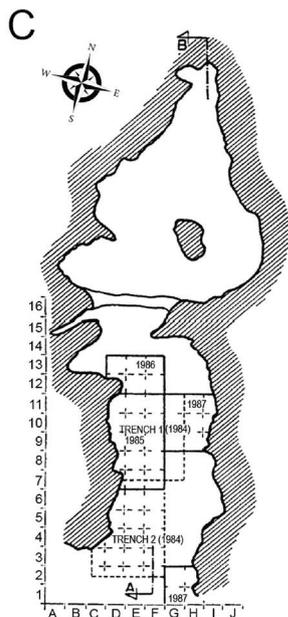
Smolućka cave

Smolućka cave is located about 15 km northeast of the city of Tutin, in the area of the village of Crkvine (Fig. 1B). The entrance to the cave is at an altitude of 945 m above sea level and is located at the end of a small canyon cut through Triassic limestones by the Smolućka River. Small platform is located in front of the cave, a so-called talus, from which the path descends to the bottom of a canyon created by the Smolućka River (Kaluđerović 51–54). Sediments deposited inside the cave formed a total of six layers. It is presumed that the first two layers belong to the Holocene (based on the findings of domestic animals and ceramics), and designated layer 3 is the first one considered to be of Pleistocene age. Among layers 2, 3, and 4, there are three sublayers, established as 2z, 3z, and 4z, which are assumed to be the same or similar age as the main layers. The bottom of the cave has not been reached yet (Fig. 1 C, D, and E).

Numerous bones and Middle Paleolithic (Mousterian) chipped stone artifacts have been collected during the excavations. Description of the chipped stone artifacts is presented by Kaluđerović (53, 54) and Šarić (92). Paleontological examination and identification is performed on around 1200 mammal bone and teeth remains, of which 554 were identified as small mammals, and 644 belonged to large mammals (Dimitrijević 35). These findings are published in numerous papers (Dimitrijević 115, 110, 35, 111, 36, 37; Marković 114; Bogićević 14). Fish, amphibian, and reptile remains are also found, and 120 fossilized remains were identified (Paunović and Dimitrijević 79), but stratigraphical distribution was not consistently recorded. Bird remains have also been found (Malez and Dimitrijević 69). Palynological samples have been negative (Dimitrijević 35). Fossiliferous layers containing small vertebrates are organized chronologically using numerical dating. The first dating done on material from the Smolućka cave is described in Hedges et al. (42). The results came from AMS dating bone on charcoal from layer 5 and showed age older than 38,000 years. Alex (1) has attempted to date remains that have been stored in Belgrade University drawers since the last excavation in 1987. In that research, six samples were dated, two samples from layer 4 (RTD7228B 54,900 ± 3800 (> 49700calBP), RTD7229B 60,200 ± 6000 (> 54700calBP)) and four samples from layer 5 (RTD7224 > 39,170, RTD7225 > 39,170, RTD7226B 53,900 ± 2300 (> 50000calBP), RTD7227 > 39,170).

The position of the cave is very interesting. During the summer months, a permanent and inexhaustible spring appears at the bottom of the canyon just below the cave. The cave is dry with small temperature changes, a large and bright first room, the proximity of drinkable water, a sheltered position in the forest, a platform/talus in front of the entrance suitable for everyday activities, and offering a good view of the surroundings. All these features that must have surrounded the cave also during the Middle Paleolithic could have been appealing to humans and were certainly a

Fig. 1 A–B Geographical location of the Smolućka site and other north Balkans cave sites, cited in this study. 1, Smolućka (Serbia); 2, Pešturina (Serbia); 3,Velika Balanica (Serbia); 4, Mala Balanica (Serbia); 5, Baranica (Serbia); 6, Mujina (Croatia); 7, Krapina (Croatia); 8, Vindija (Croatia). C Map of the excavation sectors and trenches inside the cave. D–E Stratigraphical profile from trench 1 (1985 excavation), adapted after Dimitrijević (35) and Kaluđerović (51)

genuine blessing and of enormous importance in the process of choosing a habitation location (Šarić [92]).

The cave is located in the hilly Raška region and is typically subjected to humid continental climate. The region is generally among the coolest regions in Serbia but with hydrophilic vegetation. The landscape of the area is characterized by plateaus, hills, numerous mountain areas, gorges, valleys, sinkholes, caves, and rivers with a number of smaller tributaries. Plainland is rare. The south Raška region features a continental mountainous climate. The landscape is habitually mountainous, infused by gorges of the Ibar and Jablanička rivers and some of their tributaries. Winters are usually very cold due to altitude (900–1200 m above sea level). The mean annual temperature (MAT) is 8.9 °C, and the mean annual precipitation (MAP) is 965 mm (https://en.climate-data.org/europe/serbia/crkvine/crkvine-274272/). The average difference between the warmest and coldest months is 20.1 °C.

The exclusive attention to the rodent community that is offered in this study is due to the fact that the current level of knowledge of mammalian communities is more advanced than that of other taxonomic groups in Serbia. Rodents constitute a practically independent community, within the terrestrial vertebrate communities (Valverde [102]). Various authors have confirmed their value as climatic indicators. It is generally assumed that macroclimatic factors of the past can be recognized by studying fossil mammal associations (Weerd and Daams [106]; Andrews et al. [4]; Artemiou [6]; Bonis et al. [18]; Andrews [3]). This assumption is based on the fact that climate imposes a series of habitats which, in turn, impose structure on the community (Walter [105]; Blondel [13]; Currie [32]; Kerr and Packer [56]; Shepherd [95]). Furthermore, many studies have focused on the indirect effects of climate on mammalian communities, such as vegetation types, to explain the organization and differentiation of mammalian communities (Valverde [102]; Fleming [47]; Weerd and Daams [106]; Legendre [112]; Kay and Madden [113]). Therefore, the associations of fossil mammals, especially those of rodents, have been considered as a suitable climatic indicator for qualitative climatic reconstructions (Weerd and Daams [106]; Daams and Meulen [33]; Sesé [93]; Meulen and Daams [72]) and quantitative (Montuire [73]; Montuire et al. [74]).

Material and methods

Faunal list

Descriptions of the rodents from the late Pleistocene of Smolućka cave are presented in a preliminary publication (Dimitrijević [35]) and then completed in an unpublished Ph.D. dissertation (Bogićević [14]). Most of the complementary data concerning other Serbian caves have been collected from previous publications (Jovanović et al. [50]; Jovanović [49]), checked, and updated for this research. Faunal lists used in this research are shown in Table [1].

Bioclimatic analysis

The bioclimatic analysis is used to reconstruct Pleistocene paleoclimate. This method is first introduced by Hernández-Fernández 2 decades ago and later developed to be applicable on Pleistocene sites (Hernández-Fernández et al. [46]) and recently implemented by Royer et al. ([90]). However, we have decided here not to use the new update by Royer et al. ([90]) as there are still some issues to be fixed as raised by Berto et al. ([8]) and Domínguez García et al. (in press). Bioclimatic model is based in the hypothesis that a significant correlation between the climate and the mammals communities exists. According to Hernández-Fernández ([43], [44]), Hernández-Fernández and Peláez-Campomanes ([45]), and Hernández-Fernández et al. ([46]), any mammal assemblages can be included in ten climatic types that can be distributed using the Climatic Restriction Index (CRIi = 1/n, where n is the number of climatic zones where the species are represented and i is the climatic zone where the species appears): I *Equatorial*; II *Tropical with summer rains*; II/III *Transition tropical semiarid*; III *Subtropical arid*; IV *Subtropical with winter rains and summer droughts*; V *Warm-temperate*; VI *Typical temperate*; VII *Arid-temperate*; VIII *Cold-temperate (boreal)*; and IX *Arctic*. After obtaining the distribution of a small mammal fossil assemblage according to each climatic groups (Table [2]), the climatic groups II/III and III are not represented and will not be taken into further consideration. The bioclimatic component (BC; representation level by level of each of the available climates) can be calculated using the following formula:

$$BCi = (\Sigma CRIi) \times 100/S,$$

where S is the number of species by the unit. From the BC, mathematic modeling has been elaborated using a multiple linear regression (Hernández-Fernández and Peláez-Campomanes [45]) which allows, by means of a series of functions, to estimate various climatic parameters.

Four climatic variables have been calculated for each of the Smolućka layer and comparison localities: mean annual temperature (MAT); mean temperature of the warmest month (MTW); mean temperature of the coldest month (MTC); and mean annual precipitation (MAP). Distribution indexes used for calculating these climatic variables are presented in Table [2].

In this research, only one rodent species is extinct (*Spermophilus* cf. *citelloides*); some species no longer live in Serbian territory (*Mesocricetus newtoni*, *Cricetulus migratorius*, and *Hystrix* sp.), but they are still present in other parts of the world. Consequently, modern ecology of the extant species can be used to infer paleoenvironmental and paleoclimatic inferences.

Since this research requires an adaptation from an older terminology, it was necessary to consider taxonomical position of larger taxonomic categories like *Arvicola mosbachensis/amphibius* and *Hystrix* sp., in order to establish their CRIi. Koenigswald and Kolfschoten (57) consider *Arvicola cantianus* (from Pleistocene sediments) as a subspecies of the current *A. amphibius*, in contrast to other authors (Chaline and Sevilla 23; Cuenca-Bescós et al. 30; Rekovets and Nadachowski 86). This position does reflect, however, the great similarity between these species, which is why the occupation of the same climates is assigned to the fossil species as for the current one (IV, VI, VII, and VIII) (Hernández-Fernández et al. 46). However, there might be the possibility that this taxon can be related also in more dry environments (as *A. amphibius* is a quite ubiquitous species, especially when it is in competition with strictly aquatic species). Within the genus *Hystrix*, the occlusal pattern is not useful for establishing similarities between species, given its high intraspecific variability and the small sample size that exists, generally, in the deposits (Weers 103). For this reason, the assignment of current analogues will be made based on belonging to any of the current subgenus (Weers 103). *H. primigenia* and *H. refossa*: they belong to the subgenus *Hystrix* to which three of the current species belong (*H.*

africaeaustralis, *H. cristata*, and *H. indica*) that, together, occupy climatic zones I, II, II/III, III, IV, V, and VII. *H. vinogradovi* belongs to the subgenus *Acanthion* to which the other two present-day species belong (*H. brachyura* and *H. javanica*) that occupy climatic zones I, II, and V. According to Dimitrijević (35), no skeletal remains of the crested porcupine were currently found in Smolućka cave; instead its presence is determined based on the characteristic teeth marks on the long bone of a large mammal and cannot be confused with the marks of the teeth of any other rodent. This is the typical behavior for *H. cristata* as it commonly chews on bones for calcium and to sharpen its incisors (Nowak and Walker 78). However, this is not a solid argument for the presence of *H. cristata*, especially after a recent discovery of *H. vinogradovi* in Pešturina cave layer 4 (Dimitrijević 39). This further implies that without osteological findings, teeth marks on the long bone of a large mammal from layer 5 Smolućka cave (Dimitrijević 35) cannot be assigned to a certain species.

Habitat types

Each small mammal species has different environmental requirements. The species can therefore be divided into ecological groups of similar recent ecological preferences. This method uses the current distribution of small mammals. Paleoenvironmental reconstruction should be based on the composition of entire assemblages, not just on the presence of one or two characteristic species (Popov 81). For this purpose, and in accordance with the primary objective of this research, the rodents have been divided

Table 1 Faunal rodent lists from Smolućka cave (Serbia) with distribution within layers expressed in minimum number of individuals (MNI), percentage within the total assemblage (%), and Shannon diversity index

Species/distribution	Layer 6		Layer 5		Layer 4		Layer 3		Layer 3z	
	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
Spermophilus cf. *citelloides*	1	20	1	12.5	-	-	-	-	1	1.1
Cricetulus migratorius	-	-	-	-	-	-	1	8.8	4	4.6
Clethrionomys glareolus	-	-	-	-	?	?	-	-	2	2.3
Arvicola mosbachensis/amphibius	1	20	-	-	1	2.6	-	-	5	5.7
Microtus arvalis/agrestis	2	40	2	25	22	57.9	6	50	37	42.5
Microtus subterraneus	-	-	2	25	6	15.8	2	16.7	12	13.8
Chionomys nivalis	-	-	1	12.5	4	10.5	2	16.7	7	8
Spalax leucodon	-	-	1	12.5	-	-	1	8.3	1	1.1
Apodemus sylvaticus	-	-	-	-	1	2.6	-	-	2	2.3
Glis glis	1	20	-	-	-	-	-	-	-	-
Muscardinus avellanarius	-	-	-	-	-	-	-	-	1	1.1
Dryomys nitedula	-	-	-	-	-	-	-	-	1	1.1
Sicista subtilis	-	-	-	-	1	2.6	-	-	5	5.7
Spalax leucodon	-	-	1	12.5	-	-	1	8.3	1	1.1
Hystrix sp.	-	-	1	12.5	-	-	-	-	-	-
Shannon diversity index	1.33		1.73		1.33		1.36		1.92	

Table 2 Distribution indexes used for calculating paleoclimatic reconstruction based on the bioclimatic analysis. The values are used from Hernández-Fernández (43, 44) and adapted in accordance with this research from Hernández-Fernández et al. (46)

	I	II	II/III	III	IV	V	VI	VII	VIII	IX
Apodemus sylvaticus	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000	0.000	0.000
Arvicola mosbachensis/amphibius	0.000	0.000	0.000	0.000	0.250	0.000	0.250	0.250	0.250	0.000
Chionomys nivalis	0.000	0.000	0.000	0.000	0.250	0.000	0.250	0.000	0.250	0.250
Clethrionomys glareolus	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
Cricetulus migratorius	0.000	0.000	0.000	0.000	0.333	0.000	0.333	0.333	0.000	0.000
Dryomys nitedula	0.000	0.000	0.000	0.000	0.333	0.000	0.333	0.333	0.000	0.000
Glis glis	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
Hystrix sp.	0.333	0.333	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.000
Mesocricetus newtoni	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
Microtus arvalis/agrestis	x	x	x	x	x	x	x	x	x	x
Microtus subterraneus	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
Muscardinus avellanarius	0.000	0.000	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000
Sicista subtilis	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.000	0.500	0.000
Spalax leucodon	0.000	0.000	0.000	0.000	0.000	0.000	0.500	0.500	0.000	0.000
Spermophilus citelloides	0.000	0.000	0.000	0.000	0.333	0.000	0.333	0.333	0.000	0.000

into five groups, according to their main habitat preferences (Bogićević 14):

A Woodland species (*Clethrionomys glareolus*, *Apodemus* ex gr. *sylvaticus-flavicollis*, *Dryomys nitedula*, *Muscardinus avellanarius*, *Hystrix* sp.)
B Species inhabiting moist meadows (*Arvicola amphibius*, *Microtus (Terricola) subterraneus*)
C Mountain inhabitants and petrophilous species (*Chionomys nivalis*)
D Xero-mesophilous (*Spermophilus* cf. *citelloides*, *Mesocricetus newtoni*, *Microtus gr. arvalis-agrestis*, *Spalax leucodon*)
E Steppe and semi-arid species (*Sicista subtilis*, *Cricetulus migratorius*, *Cricetus cricetus*)

Taxonomic Habitat Index

This method has been first introduced by Evans et al. (41), and it acknowledges that not all species live in only one type of environment, and one species lives in different biotypes and has a preferred habitat. This method is used to assess habitat preferences is the so-called TH (Taxonomic Habitat) Index (Evans et al. 41), which takes into the account that a vast majority of mammal species inhabits several biotopes. The affinity for a particular kind of habitat is expressed in numerals from 0 to 1 (0 if never lives in the mentioned habitat; 1 if lives exclusively in that habitat). Using this method provides more precise data since the distribution of small mammals in nature is complex and it is hard to assign only one kind of habitat for every species. For example, although many species of small mammals tend to live in a coniferous

(boreal) forest, none of them is considered as an indicator of such habitat, so coniferous forests remain "hidden" in the environmental analysis (Andrews and Cook 2).

Data on small mammal distribution preferences are used from Andrews and Cook (2) and adopted in accordance with this research. Indexes used for calculating are presented in Table 3.

Species diversity

The species diversity is measured in terms of richness (i.e., the total number of species in the community) and represents the number of a species and their relative abundance in a given habitat, site, or landscape unit (Whittaker 109). According to Rapoport's rule (Stevens 99, 100), the number of species decreases with increasing latitude and altitude. However, this can only be taken globally and regarding the overall fauna. The species diversity also very much depends on sample size so that small samples cannot give a true picture of the paleoecosystem. One way to measure ecosystem development is to study the relationship between the number of species and the commonness of species in the community, the so-called Shannon diversity index (Barnes et al. 7).

It is most often calculated as follows:

$$H = -\sum_{i=1}^{s} Pi * \ln Pi$$

where *H* is the Shannon diversity index, *S* is the total number of species in the sample, and Pi is the percentage share of the species *i* in the total fauna.

Table 3 Distribution indexes used for calculating the presence of paleohabitats in the layers in Smolućka cave (Serbia). Indexes for *Apodemus* ex gr. *sylvaticus-flavicollis*, *Arvicola mosbachensis/amphibius*, *Microtus arvalis* and *M. agrestis*, *Microtus (Terricola) subterraneus*, *Muscardinus avellanarius*, and *Cricetulus migratorius* are adapted from Andrews (1990). Indexes for *Chionomys nivalis*, *Lagurus*, *Sicista subtilis*, *Spalax leucodon*, *Spermophilus citelloides*, and *Glis glis* are from Jovanović et al. (50). Indexes for the species *Mesocricetus newtoni* and *Dryomys nitedula* are adapted according to their habitat preferences. Symbol "+" indicates the presence and "-" indicates the absence of a species in the layer. *Tu* tundra, *B* boreal forest, *D* deciduous forest, *M* Mediterranean regions, *S* steppe, *Fs* forest-steppe, *A* arid regions, *T* tropical regions, *Mo* mountains

Species/distribution	Tu	B	D	M	S	FS	A	Tr	Mo
Apodemus sylvaticus	0	0	0.2	0.2	0.2	0.2	0.2	0	0
Arvicola mosbachensis/amphibius	0.2	0.3	0.2	0.05	0.1	0.1	0	0	0.05
Chionomys nivalis	0	0	0	0	0.15	0.05	0	0	0.8
Clethrionomys glareolus	0	0.4	0.4	0	0	0.1	0	0	0.1
Lagurus lagurus	0	0	0	0	0.6	0.15	0.1	0	0.15
Microtus arvalis-agrestis	x	x	x	x	x	x	x	x	x
Microtus (Terricola) subterraneus	0	0	0.15	0.23	0.2	0	0.05	0	0.37
Muscardinus avellanarius	0	0	0.7	0.3	0	0	0	0	0
Sicista subtilis	0	0	0	0	0.7	0.2	0.05	0	0.05
Spalax leucodon	0	0.05	0.1	0	0.7	0.1	0	0	0.05
Spermophilus citelloides	0	0	0	0	0.9	0.1	0	0	0
Glis glis	0.05	0.05	0.6	0.1	0.05	0.1	0	0	0.05
Mesocricetus newtoni	0	0	0	0	0.8	0.15	0	0	0.05
Cricetulus migratorius	0	0	0	0.1	0.3	0.1	0.5	0	0
Dryomys nitedula	0	0.2	0.4	0	0	0.2	0	0	0.2

As the studied assemblages present different sample sizes (Table 1), the samples have been standardized by the elaboration of rarefaction (interpolation) and prediction (extrapolation) curves with Hill numbers method (Coldwell et al. 2021; Chao et al. 25) in order to test whether expected species richness are significantly different or not. The curves were drawn on the basis of the integrated sample size and sample-coverage analytic approaches (Chao and Jost 24). Hill numbers include three most widely used species diversity measures, species richness ($q=0$), Shannon diversity ($q=1$), and Simpson diversity ($q=2$), and are increasingly dominated by the frequencies of the more common species. Finally, the bootstrap method is used to construct 95% confidence intervals for the expected interpolated and extrapolated curves (Chao et al. 25). Statistical analyses were processed using the iNEXT (iNterpolation/EXTrapolation) online freeware application R-based version (Chao et al. 26).

Results

Rodent assemblages from Smolućka cave

A total of 15 rodent taxa (if *Microtus arvalis/agrestis* is considered as one species) are represented as fossils. *Microtus arvalis/agrestis* is the most common taxon in the assemblage; it is present in all layers. It is considered that most of the remains belong to *Microtus arvalis*, but presence of *Microtus agrestis* cannot be excluded; therefore, the presence of this taxon is not accounted in Tables 2 and 3. Most representatives in the rodent assemblage from Smolućka cave (seven species: *Cricetulus migratorius*, *Mesocricetus newtoni*, *Arvicola mosbachensis/amphibius*, *Chionomys nivalis*, *Microtus arvalis/agrestis*, *Microtus* (*Terricola*) *subterraneus*, *Clethrionomys glareolus*) are cricetids (Cricetidae). *Apodemus sylvaticus* belongs to Muridae, and *Spalax leucodon* belongs to Spalacidae; together these 9 species compose a large and complex superfamily Muroidea. Other taxa present in the assemblage are *Spermophilus* cf. *citelloides* (family Sciuridae), *Sicista subtilis* (Dipodidae), three members of the Gliridae (*Dryomys nitedula*, *Muscardinus avellanarius*, *Glis glis*), and one member of Hystricidae (*Hystrix* sp.) (Table 1). Among the taxa presented, three species no longer live in Serbian territory. *Mesocricetus newtoni* was much more widespread across Europe during the Late Pleistocene (Kowalski 59); now representatives of this species live only in Romania and Bulgaria (Wilson and Reeder 108). *Cricetulus migratorius* is still present in the Balkans on the Bulgarian territory, but this species is also well distributed in grasslands and arid steppes across Asia (Kryštufek et al. 60). Distribution of *Hystrix* sp. today can be attributed to Italy, North Africa, and sub-Saharan Africa (Cabrera 22; Corbet and Jones 28; Ranck 87; Smit and VanWijngaarden 97; Niethammer 77). In the Mediterranean, it is known from

mainland Italy and the island of Sicily, Morocco, Algeria, and Tunisia; they are also recorded in Ghana, Libya, and along the Egyptian coast.

In this research only one rodent species is extinct, *Spermophilus* cf. *citelloides*. Comparisons between *S. citelloides* and *S. citellus* deserve special attention for two reasons. First, *S. citelloides* appears to be broadly occurring within the same or overlapping geographical areas with *S. citellus* and inhabited essentially the same area as its living counterpart occupies today. Second, the two taxa are superficially similar. In his initial description of *S. citelloides*, Kormos (1916) emphasized the similarities of mandible shape and the structure of the condyloid process of the species to those of *S. citellus* (Sinitsa et al. [96]). These similarities led him to conclude that *S. citelloides* was the closest to the ancestral stock of European ground squirrel. Despite this suggested similarity, a detailed comparison of *S. citelloides* with *S. citellus* reveals numerous differences, particularly in the condyloid process of the mandible. Smolućka cave remains that came out of layer 6, layer 5, and layer 3z are originally classified as *S. citellus* (Dimitrijević [35]) and later reclassified as *S. citelloides* (Bogićević [14]). For the purpose of this research, they are classified as *Spermophilus* cf. *citelloides*, as it seems the most appropriate not to go in to definite attribution of the remains for the research focused on paleoclimatic and paleoenvironmental reconstructions as these two species most likely shared the same habitat preferences.

Paleoclimatic reconstructions

Mean annual temperature (MAT) is estimated to have been 10.5 °C (i.e., + 1.6 °C warmer than today) during the deposition of layer 6, and possibly layer 5 has recorded an even warmer (+ 3.0 °C in comparison with modern values) climate as fauna diversity reaches its peak during that time period (Table 1, Fig. 2). There are also no dramatic oscillations between the mean temperature of the warmest month (MTW) and the mean temperature of the coldest month (MTC) in layer 5, opposite to layer 4 where the general trend of temperature plummeting is recorded. MAT is estimated to have been around 8.0 °C which is a significant drop comparing to the previous layer. Interestingly layer 4 is also a layer with the highest MTW (25.7 °C) and the lowest MTC (− 1.8 °C), suggesting that this layer is strongly influenced by typical continental climate rather than mountainous landscape that defines climate in the vicinity of the Smolućka cave today. Layers 3 and 3z are very different in terms of the nature of the fauna but very similar in calculated climatic parameters, contributing to the postulate that they were deposited simultaneously. MAP values are continuously high, slightly dropping in layer 4 but with no real indications of dry climate (Fig. 2, Table 4).

Table 4 Paleoclimatic reconstruction based on the bioclimatic analysis. Abbreviations: *MAT* mean annual temperature in °C, *MTW* mean temperature of the warmest month in °C, *MTC* mean temperature of the coldest month in °C, *MAP* mean annual precipitation, and *Δ* difference between estimated and modern value

	Layer 6	Layer 5	Layer 4	Layer 3z	Layer 3
MAT (in °C)	10.5	11.9	7.9	9.6	9.1
Today	8.9	8.9	8.9	8.9	8.9
ΔMAT	+ 1.6	+ 3.0	+ 1.0	+ 1.7	+ 0.2
MTW (in °C)	21.1	23.5	25.7	22.5	22.6
Today	18.4	18.4	18.4	18.4	18.4
ΔMTW	+ 2.7	+ 5.1	+ 7.3	+ 4.1	+ 4.2
MTC (in °C)	2.8	5.3	− 1.8	1.5	1.7
Today	− 1.7	− 1.7	− 1.7	− 1.7	− 1.7
ΔMTC	+ 4.5	+ 7.0	− 0.1	+ 3.2	+ 2.4
MAP (in mm)	1247	1431	924	1178	1277
Today	965	965	965	965	965
ΔMAP	+ 282	+ 466	− 41	+ 213	+ 312

Paleoenvironmental reconstructions

Environmental reconstructions based on the rodent assemblages suggest that during MIS 5, there was a patchy landscape with a large representation of steppe inhabitants, humid meadows, scrubland, and rocky mountain habitats around the site (Fig. 3, Table 5). Some taxa such as *Hystrix* sp. indicate that landscape was not only covered with low vegetation, instead occasional forested areas were present as *Hystrix* lives preferentially close to closed habitats rather than in open biotopes with loose soils and stones. *Chionomys nivalis*, *Spalax leucodon*, and *Spermophilus* cf. *citelloides* are typical inhabitants of open environments, with poor and short plant cover and with loose or stony soils. Because the site is close to the main river, water-edge environments are fairly well represented, with the presence of typical inhabitants of wetlands such as *Arvicola mosbachensis/amphibius*. Mountain elements are also the highest in layer 5; coincidently this is the layer with the lowest difference between MTW and MTC suggesting mild mountainous climate rather than harsher continental climate recorded in layer 4 that has both forest (*Clethrionomys glareolus* and *Apodemus* ex gr. *sylvaticus*) and steppe indicators (*Sicista subtilis* and *Mesocricetus newtoni*). Layer 3 is characterized by a high share of steppe inhabitants, while in layer 3z, forest elements are increasing.

Biodiversity

The vicinity of Smolućka cave is currently a complex system of mosaic habitats with extraordinary environmental heterogeny. High altitude, fertile plains, abundant water, and exposure to sunlight, therefore, support wide diversity of

life. In terms of climatology, vegetation and orography contribute to a habiting relatively high number of rodent species in a total of 14 autochthonous species (Petrov et al. 80).

Throughout the different archaeological layers, rodents showed various patterns of appearances and disappearances (Table 1). The value of the Shannon diversity index is the highest in layer 5. The values of the indexes of other layers are approximately the same. But if instead of values for layer 3, we set the value for the sublayer 3z; the chart shows a growth in diversity, therefore, an improvement of conditions relative to layer 4. *Microtus arvalis/agrestis* is the most represented (except in layer 5, where it is equally represented with *Microtus (Terricola) subterraneus*); the frequency of this species decreases in favor of *Microtus (Terricola) subterraneus* during warmer and humid periods. *Chionomys nivalis*, a species characteristic of mountainous areas with karst landscapes, is also common in all layers except in layer 6.

Statistical analyses following the rarefaction and extrapolation with Hill numbers method corroborate the species diversity differences and trends inferred. The biodiversity comparison is based on 10 number of individuals (basic sample size $n = 10$) as double the size of the sample for the layer with the smallest number of individuals (layer 6).

When comparing diversity among the layers based on sample size, slight differences in terms of species richness between the analyzed layers are observed (Fig. S1-A). However, these differences are not statistically significant (i.e., 95% confidence intervals overlap). Despite that, significant differences are detected between layer 5 and 4 ($q = 1$ and $q = 2$ curves and their 95% confidence intervals do not overlap when layer's sample size are standardized). It is remarkable to note that partially overlapping intervals, as the observed in $q = 0$ between layer 5 and 4, do not guarantee no significance (Schenker and Gentleman 94).

According to Shannon and Simpson indices ($q = 1$ and $q = 2$, respectively; Fig. S1-A), layer 4 is less diverse in terms of evenness than the others layers, followed by layer 3. In both cases, this is due to the fact that these assemblages are dominated by the rodent *Microtus arvalis/agrestis*. In the other layers, the species are more equally distributed.

The results obtained were compared with coverage-based rarefaction and extrapolation curves (Fig. S1-C), which confirms the order and significance of the biodiversity indices between the five layers detected in the sample size-based curves (Fig. S1-A). Both curves were linked with the construction of a sample completeness curve (Fig. S1-B), which allow us to examine how the sample completeness varies with sample size. It shows that the estimated sample coverage when the sample size are standardized does not differ significantly between the

five layers (layer 6 = 0.76, layer 5 = 0.67, layer 4 = 0.81, layer 3 = 0.80, and layer 3z = 0.70) due to 95% confidence intervals fully overlap. There is therefore a correspondence between the conclusions regarding the values of biodiversity estimators drawn on the basis of both curve types.

Discussion

Comparison with other proxies

The mammalian fauna from Smolućka cave consists of 42 different species. Arvicolines are the most represented group, but Insectivores (Eulipotyphla) are also quite common, especially in the lower layers, while in the higher layers their number decreases (probably because the climate became drier). Cricetines are not present in layers 5 and 6 (certainly due to a higher humidity), whereas in layers 3 and 4, their number increases (dry climate, which coincides with the disappearance of insectivores). A considerably large amount of carnivore species are present, and the most frequent and present in all layers is the cave bear (*Ursus spelaeus*) who regularly used the cave for habitation. The cave bears preferred to avoid open plains; instead they searched for caves close to the forested or forest-edged terrains (Bieder 9). Carnivores could have also used the cave as a shelter or to occasionally bring their pray to devour it. This is probably how remains of herbivores that were living in the surroundings of the cave got inside the cave when humans were not present. The remains of the herbivores recovered mostly belong to *Cervus elaphus*, *Rupicapra rupicapra*, and *Capra ibex*; these species prefer to live on moorland and mountainsides, as well as grasslands near to woodland. They are more common and diverse in lower layers and almost completely absent in upper layers, except for Capra ibex that also appears in layer 3 but is absent in layer 3z. Layer 5 records the presence of a large bovid (*Bos* or *Bison*), certainly associated to steppe environments, and is consistent with mountainous interglacial environment. Nevertheless, the absence of warm-loving *Dama dama* and *Capreolus capreolus*, documented in other MIS 5 assemblages, as in Pesturina cave (Serbia) (Dimitrijević 39) is worth to be considered as an argument against the proposal to ascribe levels 5 and 6 to a fully interglacial periods, but that most of the large mammals are of cynegenetic origin, and so, in some way, their absence in the Smolućka's assemblage is not a proof of their absence in the environments around the cave. If the MIS 5 age is secured in the future, these absences may constitute a good archaeological or zooarchaeological research question (why on similar climate *Dama dama* and *Capreolus capreolus* are absent in Smolućka). This layer
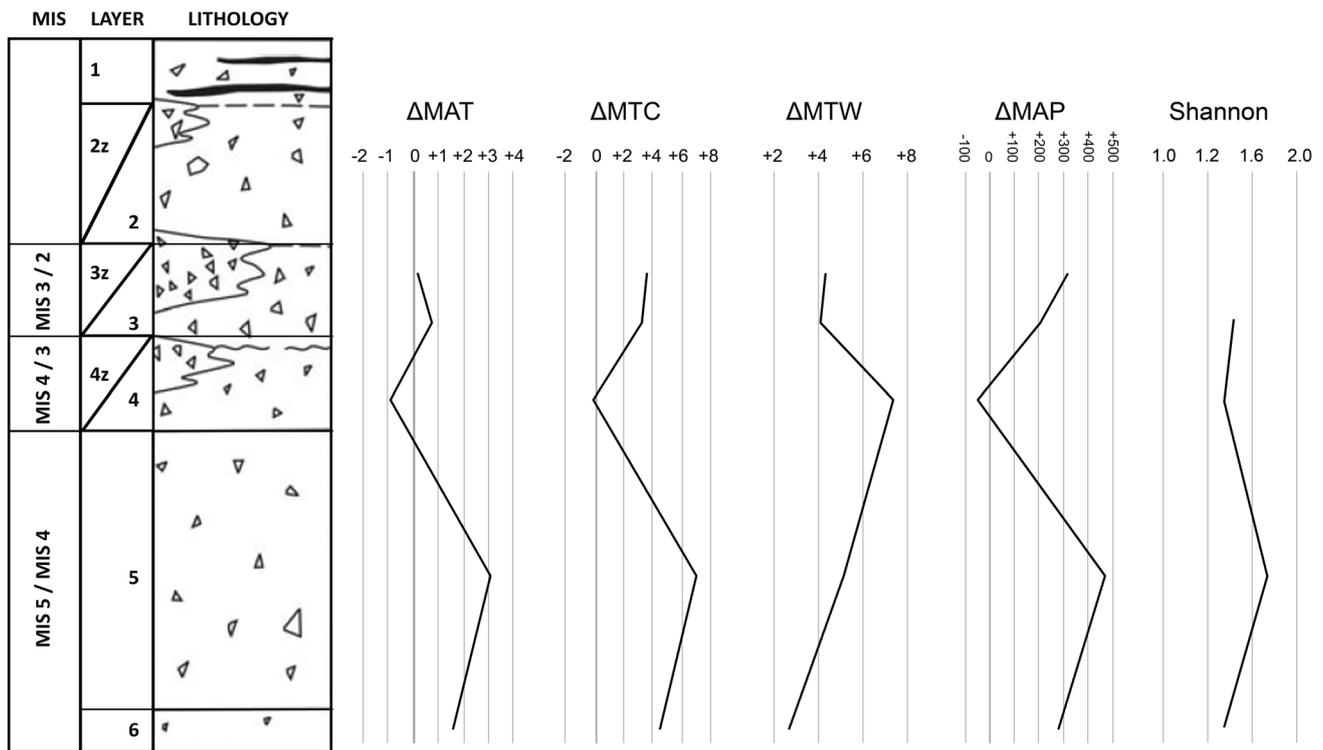
Fig. 2 Paleoclimatic and biodiversity reconstructions for the Late Pleistocene of Smolućka cave (Serbia). Graphical representation showing climatic parameters: ΔMAT, difference between estimated and modern mean annual temperature in °C; ΔMTW, difference between estimated and modern mean temperature of the warmest month in °C; ΔMTC, difference between estimated and modern mean temperature of the coldest month in °C; ΔMAP, difference between estimated and modern mean annual precipitation in mm; and Shannon diversity index

could also be consisted with a relatively mild moment of MIS 5, as there were plenty of climate oscillations.

Chronological context of Smolućka cave

The oldest layers in these analyses from Smolućka cave are layers 5 and 6. The proposed age of layer 6 according to its superposition corresponds to the "first Würmian stadial" (Dimitrijević [35]). Layer 6 did not provide identifiable material except a small number of osteological finds; therefore, no definite conclusions about the age of this layer are possible. When chronology of the Smolućka cave is compared to other sites in Serbia, presented in Jovanović et al. [50], layer 5 is possibly comparable to Pešturina layer 4, but without new datings from Smolućka specimens, it is not possible to establish any affirmative correlation. However, it is possible to compare fauna lists in order to establish analytical similarities which could pinpoint the time period for the deposition of the layer. In fact, all species from Smolućka layer 5 are also present in Pešturina layer 4, suggesting that these two layers could

have been partially deposited at the same chronological period. Pešturina layer 4 has been thoroughly dated using the ESR method (Blackwell et al. [11]). This layer is known to have two distinct sedimentological depositions (layers 4a and 4b). Pešturina layer 4a based on one horse tooth is placed in MIS 4, while two horse tooth samples that were dated placed layer 4b to penultimate interglacial, stage 5c (Dimitrijević [39]). Sedimentological features and mammalian remains of layer 5 indicate interstadial character of this deposition. According to the Dimitrijević [35], this layer is deposited after the "first Würmian stadial," when warm climate species disappeared from central Europe, and probably the Balkans. After the macroscopic analysis of sediments from layer 5, Šarić [92] concludes that this layer dates to "stadial Würm 2." Taking all this into account and along with the assemblage of fauna in layer 5, it can be concluded that this layer contains MIS 5 elements; therefore, it can be attributed to this stage.

Layer 4 of Smolućka contains osteological material and chipped stone artifacts; the chronology of this layer remained insufficiently defined (Šarić [92]). According

Fig. 3 Paleoenvironmental reconstruction for the Late Pleistocene of Smolućka cave (Serbia) based on the Taxonomic Habitat Indexes
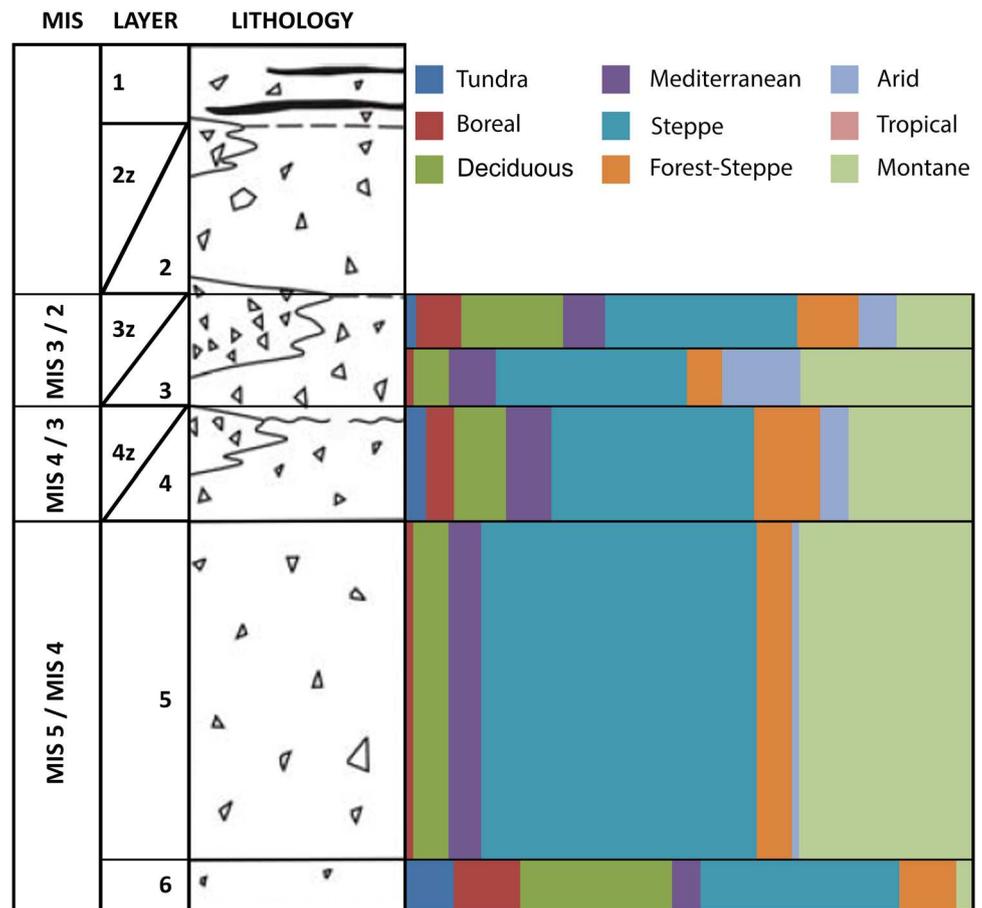

Table 5 Distribution of habitats obtained by calculating indexes from Table 3, presented in percentage (%)

	Tundra	Boreal	Desidous	Mediterranean	Steppe	Forrest-Steppe	Arid	Tropical	Montane
SMP3z	1.6	7.9	17.9	7.3	33.7	10.8	6.6	0	13.9
SMP3	0	1.2	6.2	8.2	33.7	6.2	13.7	0	30.5
SMP4	3.3	5	9.1	8	35.8	11.6	5	0	22
SMP5	0	1.2	6.2	5.7	48.7	6.2	1.2	0	30.5
SMP6	8.3	11.6	26.6	5	35	10	0	0	3.3

to Dimitrijević (35), layer 4 probably belongs to "second Würmian stadial" stage. Macroscopic analysis of sediments confirmed that layer 4 dates from "interstadial Würm 2/3" (Kaluđerović 52; Šarić 92). The most important findings of the chipped stone artifacts in this layer also confirm the Middle Paleolithic age of this layer. When all facts are taken into account, no definitive conclusions about the age of this layer can be made, as there were no clear indicators to attribute whether this layer is deposited during the later intermediate stages of the MIS 5 or during the MIS 4.

In an attempt to determine the relative age of layer 3, the composition of the fauna is examined. Among the large mammalian remains, there are no species of extremely cold fauna, but among the bird remains of two cold species,

Lagopus mutus and *Lagopus lagopus* are found indicating that this layer is not younger than early postglacial. These birds inhabited Balkans in Pliocene and Pleistocene, but after early postglacial they remain only in more northern regions after the retreat of the snow line (Dimitrijević 35). *Lagopus mutus* lives in a high mountain climate zone and is a good indicator of cold climate because it inhabits rocky slopes above the forest line which is today located at about 2000 m above sea level. During Pleistocene, when the Alps were covered with snow and ice, biotype of *Lagopus mutus* was suppressed to lower regions (Malez and Dimitrijević 69). *Lagopus lagopus* is also very important as a climate indicator, it lives in wetlands and wastelands with willows and birches in today's northern Europe. During the Pleistocene, the range of this species was extended far to the south

of Europe (Malez 1963; 1972) Among the rodent remains, layer 3 holds the most "cold elements" compared to other layers (Fig. 3), *Spermophilus* cf. *citelloides*, *Mesocricetus newtoni*, and *Chionomys nivalis* are more common in layers 3 and 3z than in lower layers. This suggests that part of the layer is deposited during MIS 2, but deeper parts of the sediment are more likely to have been deposited during MIS 3. During the excavation of layer 3 a sublayer has been noted (layer 3z in Figs. 1 and 2). The superposition of the sublayer is uneven which makes establishing the age of the sublayer difficult without dating (Dimitrijević 35). The deposition of this sublayer (layer 3z) is considered to be simultaneous with the layer 3.

The two uppermost (layers 1 and 2) of Smolućka cave contain remains of Holocene and Pleistocene fauna indicating mixing in the sedimentation in some point in time; therefore, they are ineligible for this type of analysis.

Implication for paleoclimatic and paleoenvironmental evolution during the Late Pleistocene in Southwestern Serbia

Marine Isotope Stage 5

In layer 6, THI calls attention to a notable rise of Boreal forest inhabitants compared to layer 5 (Fig. 3); this suggests that climate was probably slightly colder than during the deposition of layer 5, and this is supported by bioclimatic analysis results. Habitat surroundings of the Smolućka cave during the deposition of layer 6 were Boreal Forest-Steppe.

The most worth mentioning layer in Smolućka cave is layer 5. Composition of the fauna suggests favorable climate conditions for a large diversity of species. The most notable in the rodent assemblage is the presence of *Hystrix* sp. Although the presence of the *Hystrix* sp. during the late Pleistocene has been considered uncertain in the past, it has been proven that it lived in the Balkans (Dimitrijević 39), with findings in caves: Praška Grobina in Slovenia (Rakovec 84), Veternica in Croatia in the layer assigned to MIS 5 (Miracle and Brajković 71), and deeper parts of Pešturina layer 4 are also assigned to MIS 5. Today Crested Porcupine mostly inhabits North Africa, while in Europe it is only present in Italy (Niethammer 77). This species is indicative of a warm and dry climate, possibly as bioclimatic analysis showed even on average warmer than today. Supportive of this, THI results show that forest was much less represented in MIS 5 than in MIS 4 but still present (Fig. 3). The composition of the large mammal fauna from layer 5 is not completely consistent with small vertebrate fauna. There is a complete lack of findings of warm-loving large mammals that are expected to be living in the area (e.g. *Capreolus capreolus* and *Dama dama*). Based on available information, we can only speculate about this phenomenon. More than half of all skeletal remains of *Ursus spelaeus* came from this layer, suggesting that they inhabited the cave for the majority of the time. The latest isotopic analysis of fossil collagen from the bones collected in three Romanian caves indicates that the cave bear (*Ursus spelaeus*) was exclusively herbivorous (Naito et al. 76). Hence, the middle/large-sized herbivore remains were perhaps conveyed by true carnivores or Neanderthals themselves. Nevertheless, the composition of the large mammal fauna should not be considered contradictory to an interglacial climate, as there are numerous factors to be considered, such as biogeographic properties of the area and possible inconsistent presence of Middle Paleolithic groups. Generally, migration of the large mammal species during the last interglacial in Northwestern Balkans is a complex issue and rarely conceptualized with small vertebrate findings.

Marine Isotope Stages 5 or 4

The exact age of layer 4 is still undetermined. It is very difficult to find a corresponding layer of a similar age for comparison. All seven species identified in this layer are also found in younger layer 3z, unlike layer 3 with which they share only two species (*Microtus (Terricola) subterraneus* and *Chionomys nivalis*). Using the method "habitat types" as a reference, two species found both in layers 4 and 3z (*Clethrionomys glareolus* and *Apodemus* ex gr *sylvaticus-flavicollis*) have the highest probability of living in a forest habitat, but one species (*Sicista subtilis*) mostly occurs in treeless habitats, shrubland, and grassland (Cserkész et al. 29). Compared to other layers in Smolućka cave, layer 4 has the lowest species diversity value (Bogićević 14). A low species diversity value can indicate the disappearance of species that could not adapt in new living conditions (López Antoñanzas and Cuenca-Bescós 61; Williams et al. 107). The difference in climate between layer 5 and layer 4 can be determined through analysis of the difference in fossil findings. Four species (*Spermophilus* cf. *citelloides*, *Microtus arvalis/agrestis*, *Spalax leucodon*, and *Hystrix* sp.) are present in layer 5 but are no longer recorded in layer 4; instead, four other species appear (*Mesocricetus newtoni*, *Arvicola amphibius*, *Apodemus* ex gr. *sylvaticus-flavicollis*, and *Sicista subtilis*). This change indicates a drop in MAT between 1 and 4 °C, depending on which species of *Hystrix* is present in layer 5, and a drop in MAP as layer 4 is the driest. Change in the habitat ratio is also noted between these two layers as THI shows a significant drop in forest extension during the transition between layer 5 and layer 4 (Fig. 3). Deposition of layer 4 probably represents long-lasting climate shifts, but the exact time period could not be defined.

Marine isotope stages 3 or 2

Bioclimatic analysis for Smolućka layers shows very similar climate components between layer 3 and layer 3z, with MAT comprised between 9.1 and 9.6 °C and MAP around 1200 mm. Compared to the older layers, climate is more temperate, with a lower difference in temperature between the warmest and the coldest months (21 °C in layer 3 compared to 27.5 °C in layer 4). An interesting addition to paleoclimatic reconstruction on these entities is noted when THI is introduced (Fig. 3). Although MAT and MAP are quite similar, THI reveals a significant change in surrounding habitats between layer 3 and layer 3z. Layer 3 is dominated by steppe and arid elements, whereas in layer 3z forest elements are raising, therefore, a more closed environment. Using the method "habitat types" as a reference, 30% of the species (*Clethrionomys glareolus*, *Apodemus sylvaticus*, *Dryomys nitedula*, and *Muscardinus avellanarius*) found in layer 3z have the highest probability of living in forest habitats, while none of the species from layer 3 have such a preference. Instead, the composition of the fauna in layer 3 clearly indicates a mountainous steppe as a more likely habitat surrounding the cave. It is unknown which factor could have triggered the change of habitats. Perhaps forest habitats from layer 3z are represented due to climate change that has occurred during a short-term time interval. Nevertheless, the deposition of the layers 3 and 3z, when all facts are accounted for, should be considered simultaneous. Sites containing MIS 3 depositions are most studied and explained in Jovanović et al. (50). The fact is that we cannot determine the exact age of the deposition of the MIS 3 Smolućka layers and establish an affirmative correlation with either early MIS 3 or late MIS 3 (Mousterian or Aurignacian), but on general, climatic parameters and the list of species appearing in the fossil record are similar. Layers 3 and 3z compared to calculated MIS 3 values (MAT and MAP) from Baranica, Hadži Prodanova, and Pešturina caves are similar but slightly higher. MAT is around 1–1.5 °C higher, while precipitation is around 200 mm higher in Smolućka. These results are somewhat unexpected due to Smolućka being located at a higher altitude than the other sites. All of the species represented in Smolućka also are present in other sites.

Smolućka in a wider Balkan context

It could be speculated that layers from Smolućka cave share chronological context with some of the other archaeological sites in Western Balkans. Mujina cave, in Western Dalmatia (Croatia), is systematically excavated and well-dated Middle Paleolithic site in the eastern Adriatic. Its

stratigraphic sequence covers the period between 45 and 39 uncalibrated ka (Karavanić et al. 55; Boschian et al. 21), corresponding to the younger layers from Smolućka (layers 4, 3, and 3z). Similar to Smolućka cave, no diagnostic hominin remains are found but numerous lithic industries prove hominin presence as this locality was used as a hunting site, only sporadically visited by humans (Boschian et al. 21). Neanderthals frequented Mujina cave more intensively during the deposition of the first part of the sequence, partly corresponding to Heinrich event H5, whereas their presence was episodic in later phases when the cave was shared with carnivores. No cultural horizons younger than the Mousterian were found in the site (Boschian et al. 21). Chronological evidence from Mujina cave suggests that Neanderthals, generally accepted as the makers of Mousterian industries, were still present in the Dalmatian area at least until 43–42 cal ka BP, roughly the same time Neanderthals persisted in the territory of Serbia (Mihailović 70; Alex 1), thus overlapping with Uluzzian and Protoaurignacian industries in Italy (Villa et al. 104). Potential associations between lithic industries and hominin remains of the Croatian Middle Paleolithic sites are important for the Balkan context of the Smolućka cave. The stone tools from Smolućka cave may possibly be correlated with most famous sites like Krapina or Vindija in NW Croatia. Unfortunately, no fossil hominins were unearthed in Smolućka in 1985.

Conclusions

Smolućka cave has long been recognized as an important archaeological site. Systematic archaeological excavations have been organized in the past, but the paleontological importance of this site has been sometimes overlooked in recent years. Smolućka can be considered as one of the most abundant Late Pleistocene sites in Serbia, especially concerning the diversity in small vertebrate remains.

The application of the bioclimatic analysis method and the Taxonomic Habitat Index to the Late Pleistocene rodent assemblages from the successive layers from Smolućka Cave indicates some depiction of environmental change in central Balkans between MIS 5 and MIS 3. Tentative attribution of layer 5 from Smolućka cave to MIS 5 relies on combined methods suggesting interstadial favorable climate conditions for a large diversity of species, with mean annual temperature (MAT) reaching up to 3 °C higher than present values. Cold conditions for MIS 4 have not been evidenced in the cave, even if layer 4 shows somewhat drier and cooler climate when compared with other layers. MIS 3 (layers 3z and 3) is characterized by temperate and humid conditions together with a complex system of mosaic habitats with high

environmental heterogeneity but generally favorable conditions for a large diversity of life.

Although not fully chronologically constrained, Smolućka cave presents an interesting opportunity for future research of the period when only Neanderthals occupied the Balkans and thrived in local conditions. The presence of Neanderthals on the territory of Serbia has been recently confirmed for the Late Pleistocene (MIS 5c) layers of Pešturina Cave near Niš (Radović et al. [82]) and has been suggested for the Middle Pleistocene layers of the nearby Velika Balanica (Radović et al. [83]; Roksandic et al. [88]). New excavations and multidisciplinary studies currently conducted at Smolućka cave, which include systematic dating via ESR (instead of the ^{14}C AMS method), could contribute this work and address numerous problems that have been encountered.

Declarations

References

Alex BA (2016) Establishing contexts of encounters: radiocarbon dating of archaeological assemblages with implications for Neanderthal-modern human interactions. Dissertation, Harvard University

Andrews P, Cook J (1990) Owls, caves and fossils: predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene cave faunas from Westbury-sub-Mendip, Somerset. University of Chicago Press, Chicago

Andrews P (1995) Mammals as palaeoecological indicators. Acta Zool Crac 38:59–72

Andrews P, Lord JM, Evans EMN (1979) Patterns of ecological diversity in fossil and modern mammalian faunas. Biol J Linn Soc Lond 11:177–205

Argant J, Dimitrijević V (2007) Pollen analyses of Pleistocene hyaena coprolites from Montenegro and Serbia. Geoloski Anali Balkanskoga Poluostrva 68:73–80

Artemiou C (1984) Mammalian community Palaeoecology: a review of recent methods with special reference to Miocene mammalian faunas of Europe. Paléobiologie Continentale 14:91–109

Barnes BV, Zak DR, Denton SR, Spurr SH (1998) Nutrient cycling Forest Ecology, 4th edn. John Wiley & Sons Inc, New York

Berto C, Szymanek M, Blain H-A, Pereswiet-Soltan A, Krajcarz M, Kot M (2021) Small vertebrate and mollusc community response to the Holocene climate and environment changes in the Kraków-Częstochowa Upland (Poland). Quaternary International

Bieder R (2005) Bear. Reaktion Books, London, p 192

Björck S, Walker MJ, Cwynar LC, Johnsen S, Knudsen KL, Lowe JJ, Wohlfarth B (1998) An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. J Quat Sci 13:283–292

Blackwell BA, Chu S, Chaity I, Huang YE, Mihailović D, Roksandić M, Dimitrijević V, Blickstein J, Huang A, Skinner AR (2014) ESR dating ungulate tooth enamel from the Mousterian Layers at Pešturina, Serbia. Paleolithic and Mesolithic research in the Central Balkans, 1st edn. Dušan Mihailović, Belgrade, pp 21–38

Blockley SP, Lane CS, Hardiman M, Rasmussen SO, Seierstad IK, Steffensen JP, Svensson A, Lotter AF, Turney CS, Ramsey CB, Members I (2012) Synchronisation of palaeoenvironmental records over the last 60,000 years, and an extended INTIMATE event stratigraphy to 48,000 b2k. Quat Sci Rev 36:2–10

Blondel J (1986) Biogeografía y Ecología, Revised. Academia, León

Bogićević K (2008) Pleistocenski glodari (Rodentia) Srbije. Dissertation, University of Belgrade

Bogićević K, Nenadić D, Mihailović D (2012) Late Pleistocene voles (Arvicolinae, Rodentia) from the Baranica Cave (Serbia). Geol Carpath 63(1):83–94

Bogićević K, Nenadić D, Mihailović D, Lazarevic Z, Milivojević J (2011) Late Pleistocene rodents (Mammalia: Rodentia) from the Baranica Cave near Knjaževac (eastern Serbia): Systematics and palaeoecology. Riv Ital Di Paleontol e Stratigr 117:331–346

Bogićević K, Nenadić D, Milošević S, Mihailović D, Vlastić S, Tošović R (2017) A Late Pleistocene rodent fauna (Mammalia: Rodentia) from Hadži Prodanova Cave near Ivanjica (western Serbia). Riv Ital Di Paleontol e Stratigr 123:23–38

de Bonis L, Bouvrain G, Geraads D, Koufos G (1992) Multivariate study of late Cenozoic mammalian faunal compositions and paleoecology. Paleontologia i Evolució 24–25:93–101

Bond GC, Lotti R (1995) Iceberg discharges into the North Atlantic on millennial time scales during the last glaciation. Science 267:1005–1010. https://doi.org/10.1126/science.267.5200.1005

Bond G, Heinrich H, Broecker W, Labeyrie L, McManus J, Andrews J, Huon S, Jantschik R, Clasen S, Simet C, Tedesco K, Klas M, Bonani G, Ivy S (1992) Evidence for massive discharges of icebergs into the North Atlantic Ocean during the last glacial period. Nature 360:245–249

Boschian G, Gerometta K, Ellwood BB, Karavanić I (2017) Late Neandertals in Dalmatia: site formation processes, chronology, climate change and human activity at Mujina Pećina, Croatia. Quat Int 450:12–35

Cabrera A, Spain, & Museo Nacional de Ciencias Naturales (Spain). (1932). *Los mamíferos de Marruecos*. Madrid

Chaline J, Sevilla P (1990) Phyletic gradualism and developmental heterochronies in a European Plio/Pleistocene *Mimomys* lineage (Arvicolidae, Rodentia). In International symposium evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia), pp. 85–98.

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. Ecology 93:2533–2547

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr 84:45–67

Chao A, Ma KH, Hsieh TC (2016) iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User's Guide published at http://chao.stat.nthu.edu.tw/wordpress/software download/

Corbet GB, Jones LA (1965) The specific characters of the crested porcupines, subgenus *Hystrix*. Proc Zool Soc Lond 144:285–300

Cserkész T, Kitowski I, Czochra K, Rusin M (2009) Distribution of the Southern birch mouse (*Sicista subtilis*) in East-Poland: morphometric variations in discrete European populations of superspecies S. subtilis. Mammalia 73:221–229

Cuenca-Bescós G, Canudo JI, Laplana C (1995) Los arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno inferior, Atapuerca, Burgos, España). Rev Española De Paleontol 10:202–218

Cuenca-Bescós G, Rofes J, García-Pimienta J (2005) Environmental change across the Early-Middle Pleistocene transition: small mammalian evidence from the Trinchera Dolina cave, Atapuerca, Spain. Geol Soc London, Special Publ 247:277–286

Currie DJ (1991) Energy and large-scale patterns of animal- and plant-species richness. Am Nat 137:27–49

Daams R, van der Meulen AJ (1984) Paleoenvironmental y paleclimatic interpretation of micromammal faunal successions in the Upper Oligocene y Miocene of North Central Spain. Paléobiologie Continentale 14:241–257

Dansgaard W, Johnsen SJ, Clausen HB, Dahl-Jensen D, Gundestrup NS, Hammer CU, Hvidberg CS, Steffensen JP, Sveinbjörnsdottir AE, Jouzel J, Bond G (1993) Evidence for general instability of past climate from a 250-kyr ice-core record. Nature 364(6434):218–220

Dimitrijević V (1985) Kvartarna fauna iz Smolućke pećine. Novopazarski zbornik, 9: 19-20.

Dimitrijević V (1988) Prvi nalazak stepske zviždare – Ochotona pusilla (Pallas) (Lagmorpha, Mammalia) u Srbiji. Geološki anali Balkanskog poluostrva, 51: 379–386

Dimitrijević V (1991) Quaternary mammals of the Smolućka cave in southwest Serbia. Palaeontol Jugoslav 41:1–88

Dimitrijević V (1993) Result of Investigating Vertebrate Fauna from the Paleolithic Habitat of Smolućka cave near Novi Pazar. Starinar, 42/1991: 9–17

Dimitrijević V (1995) Gornjopleistocenski sisari iz pećinskih naslaga Srbije. Dissertation, University of Belgrade

Dimitrijević V (1997a) Gornjopleistocenski sisari iz pećinskih naslaga Srbije. Geološki Anali Balkanskog Poluostrva 61:179–370

Dimitrijević V (1997b) Pleistocenska sisarska fauna na području istočne Srbije. In: Lazić M (ed.) Arheologija istočne Srbije, Donji Milanovac, Belgrade, pp 45–55

Dimitrijević V (2021) Ključna dopuna faunističke sekvence srednji-kasni pleistocen Srbije: ostaci sisara iz naslaga pećine Pešturina (Jelašnica, istočna Srbija). Posebna Izdanja Srpske Akademije Nauka i Umetnosti, Odeljenje Za Matematiku, Fiziku i Geo-Nauke, Zbornik Odbora Za Kras i Speleologiju 11:91–102

Domínguez García Á C, Laplana C, Sevilla P, Álvarez-Vena A, Collado Giraldo H (in press) Small mammals of the Holocene sequence of Postes Cave (SW Spain): biogeographic and palaeoenvironmental implications for southwestern Iberia. Historical Biology

Evans EMN, Van Couvering JAH, Andrews P (1981) Palaeoecology of Miocene sites in western Kenya. J Hum Evol 10:99–116

Hedges REM, Housley RA, Bronk CR, van Klinken GJ (1990) Radiocarbon dates from the Oxford AMS system: Archaeometry datelist 11. United Kingdom. doi:https://doi.org/10.1111/j.1475-4754.1990.tb00468.x.

Hernández-Fernández M (2001a) Bioclimatic discriminant capacity of terrestrial mammal faunas. Glob Ecol Biogeogr 10:189–204

Hernández-Fernández M (2001b) Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico. Dissertation, Universidad Complutense de Madrid

Hernández-Fernández M, Peláez-Campomanes P (2005) Quantitative palaeoclimatic inference based on terrestrial mammal faunas. Glob Ecol Biogeogr 14:39–56

Hernández-Fernández M, Álvarez-Sierra MÁ, Peláez-Campomanes P (2007) Bioclimatic analysis of rodent palaeofaunas reveals severe climatic changes in Southwestern Europe during the Plio-Pleistocene. Palaeogeogr Palaeoclimatol Palaeoecol 251:500–526

Fleming TH (1973) Numbers of mammal species in North y Central American forest communities. Ecology 54:555–563

Jovanović M (2016) Paleoenvironmental reconstruction based on small vertebrates remains from Baranica cave. Master degree Dissertation, University of Belgrade

Jovanović, M, 2021. Pleistocene small-vertebrates (amphibians, reptiles, and small mammals) studies in Serbia (Balkan Peninsula, SE Europe): history of research, methodological state of the art, and paleoclimatic and paleoenvironmental reconstructions. Doctoral Thesis, 159 pp. University Rovira i Virgili.

Jovanović M, Bisbal-Chinesta JF, Đurić D, Bogićević K, Nenadić D, Agustí J, Blain H-A (2020) Pleistocene herpetofaunal studies in Serbia (Balkan Peninsula, SE Europe): state of the art and perspectives. Quat Sci Rev 233:106235

Kaluđerović Z (1985) Istraživanja Smolućke pećine 1984–1985. Novopazarski Zbornik 9:5–18

Kaluđerović Z (1986) Izveštaj o arheološkom istraživanju Smolućke pećine 1986. Novopazarski Zbornik 10:225–226

Kaluđerović Z (1987) Izveštaj o istraživanju arheološkog nalazišta Smolućka pećina kod Tutina, 1987. godina. Novopazarski Zbornik 11:221–222

Kaluđerović Z (1993) Paleolithic in Serbia in the Light of the recent Research. Starinar 42:1–8

Karavanić I, Miracle PT, Culiberg M, Kurtanjek D, Zupanič J, Golubić V, Paunović M, Lenardić JM, Malez V, Šošić R, Janković I (2008) The Middle Paleolithic from Mujina Pećina, Dalmatia, Croatia. J Field Archaeol 33:259–277

Kay RF and Madden RH (1997) Mammals and rainfall: paleoecology of the middle Miocene at La Venta (Colombia, South America). Journal of Human Evolution, 32: 166–199

Kerr JT, Packer L (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252–254

Koenigswald WV, Kolfschoten TV (1996) The *Mimomys-Arvicola* boundary and the enamel thickness quotient (SDQ) of *Arvicola* as stratigraphy markers in the Middle Pleistocene. In: Turner (ed.) The Early Middle Pleistocene in Europe. Balkema, Rotterdam, pp 211–226

Kohfeld KA, Harrison SP (2000) How well can we simulate past climates? Evaluating the models using global palaeoenvironmental datasets. Quat Sci Rev 19:321–346

Kowalski K (2001) Pleistocene Rodents of Europe Folia Quarter 72:3–389

Kryštufek B, Bukhnikashvili A, Sozen M, Isfendiyaroglu S (2008) *Cricetulus migratorius*. In: IUCN Red List of Threatened Species, 2015.2 edn. Gland, Switzerland: IUCN

Legendre S (1986) Analysis of mammalian communities from the Late Eocene y Oligocene of Southern France. Palaeovertebrata, 16 (4): 191–212

López Antoñanzas R, Cuenca-Bescós G (2002) The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals. Palaeogeogr Palaeoclimatol Palaeoecol 186:311–334

López-García JM, Blain H-A, Cuenca-Bescós G, Ruiz-Zapata MB, Dorado-Valiño M, Gil-García MJ, Valdeolmillos A, Ortega AI, Carretero JM, Arsuaga JL, Bermúdez de Castro JM, Carbonell E (2010) Palaeoenvironmental and palaeoclimatic reconstruction of the Latest Pleistocene of El Portalón Site, Sierra de Atapuerca, northwestern Spain. Palaeogeogr Palaeoclimatol Palaeoecol 292:453–464

Marković Z (1997) Pleistocenske Cricetinae Srbije. pp 43 Magistarska teza, Univerzitet u Beogradu, Beograd

Marković SB (2001) Paleosols of Srem region. In: Miljković N, Marković SB (eds.) Soils of Srem region (Vojvodina, Yugoslavia). Institute of Geography, Novi Sad, pp 133–155 (in Serbian with English summary)

Marković SB (2000) Paleogeografija kvartara na teritoriji Vojvodine. Dissertation, Institut za geografiju PMF, Novi Sad

Marković SB, Heller F, Kukla GJ, Gaudenyi T, Jovanović M, Miljković LJ (2003) Magnetostratigraphy of Stari Slankamen loess section. Zbornik Radova Instituta Za Geografiju 32:20–28

Marković SB, McCoy WD, Oches EA, Savić S, Gaudenyi T, Jovanović M, Stevens T, Walther R, Ivanisević P, Galović Z (2005) Paleoclimate record in the Late Pleistocene loess-paleosol sequence at Petrovaradin Brickyard (Vojvodina, Serbia). Geol Carpath 56:545–552

Marković SB, Oches EA, Gaudenyi T, Jovanović M, Hambach U, Zöller L, Sümegi P (2004) Paleoclimate record in the Late Pleistocene loess-paleosol sequence at Miseluk (Vojvodina, Serbia). Quaternaire 15:361–368

Marković SB, Oches EA, Sümegi P, Jovanović M, Gaudenyi T (2006) An introduction to the Upper and Middle Pleistocene loess-paleosol sequences in Ruma section (Vojvodina, Serbia). Quat Int 149:80–86

Malez V, Dimitrijević V (1990) Gornjopleistocenska avifauna iz Smolućke pećine (JZ Srbija, Jugoslavija). Rad JAZU 449(24):35–76

Mihailović D (ed) (2014) Palaeolithic and Mesolithic Research in the Central Balkans. Serbian Archaeological Society, Belgrade

Miracle P, Brajković D (2010) The palaeoecological significance of the Pleistocene mammalian fauna from Veternica Cave, Croatia. Revision of the Lagomorpha, Canidae. Mustelidae and Felidae Geologia Croatica 63:207–224

van der Meulen AJ, Daams R (1992) Evolution of Early-Middle Miocene rodent faunas in relation to long-term palaeoenvironmental changes. Palaeogeogr Palaeoclimatol Palaeoecol 93:227–253

Montuire S (1996) Rodents y climate II: Quantitative climatic estimates for Plio-Pleistocene faunas from Central Europe. Acta Zool Crac 39:373–379

Montuire S, Michaux J, Legendre S, Aguilar J-P (1997) Rodents y climate. 1. A model for estimating past temperatures using arvicolids (Mammalia: Rodentia). Palaeogeogr Palaeoclimatol Palaeoecol 128:187–206

Musil R (2003) The Middle and Upper Palaeolithic game suite in Central and Southeastern Europe. In: van Andel TH, Davies W (eds) Neanderthals and modern humans in the European landscape during the last glaciation: archaeological results of the stage 3 project. McDonald Institute for Archaeological Research, Cambridge, pp 167–190

Naito YI, Meleg IN, Robu M, Vlaicu M, Drucker DG, Wißing C, … Bocherens H (2020) Heavy reliance on plants for Romanian cave bears evidenced by amino acid nitrogen isotope analysis. Sci Rep 10(1):1–10

Niethammer J (1982) *Hystrix cristata* Linnaeus, 1758 — Stachelschwein. In: Niethammer J., Krapp F. (eds) Handbuch der Säugetiere Europas. Band 2/I. Rodentia I (Cricetidae, Arvicolidae, Zapodidae, Spalacidae, Hystricidae, Capromyidae). Akademische Verlagsgesellschaft, Wiesbaden, pp 588–605

Nowak RM, Walker EP (1999) Walker's Mammals of the World (Vol. 1). JHU Press, Baltimore and London

Paunović M, Dimitrijević V (1990) Gornjopleistocenska fauna nižih vertebrata iz Smolućke pećine u JZ Srbiji. Rad JAZU 449(24):77–88

Petrov BM, Kambasković D, Gradojević Z, Vasić V (1992) Mammals of Yugoslavia: insectivores and rodents. Natural History Museum, Belgrade

Popov VV (1994) Quaternary small mammals from deposits in Temnata-Prohodna Cave system. Temnata Cave. In: Ginter B Kozlowski JK Laville H (ed) Excavations in Karlukovo Karst Area, 1st edn. Krakow, Poland, pp 11–53

Radović P, Lindal J, Mihailović D, Roksandic M (2019) The first Neanderthal specimen from Serbia: maxillary first molar from the Late Pleistocene of Pešturina Cave. J Hum Evol 131:139–151

Radović P, Lindal J, Mihailović D, Roksandic M (2020) Hominin fossil material from the Middle Pleistocene of Velika Balanica Cave (Serbia) and its implications for human evolution in Europe (abstract). Serbian Archaeological Society 43rd Annual Meeting, 14–16 October 2020, Subotica (Serbia), pp 78–79

Rakovec I (1961) Mladopleistocenska favna iz Parske golobine v Pivški kotlini. Slovenska Akad. znanosti in umetnosti, Ljubljana

Rasmussen SO, Bigler M, Blockley SP, Blunier T, Buchardt SL, Clausen HB, Cvijanovic I, Dahl-Jensen D, Johnsen SJ, Fischer H, Gkinis V (2014) A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quaternary Science Reviews 106:14–28

Rekovets L, Nadachowski A (1995) Pleistocene voles (Arvicolidae) of the Ukraine. Paleontologia i Evolució 28:145–246

Ranck GL (1968) The rodents of Libya Taxonomy, ecology and zooge-ographical relationships. Smithsonian Institution Press, Washington D.C.

Roksandic M, Lindal J, Radović P, Mihailović D (2020) New hominin finds from Velika Balanica and Kozja Cave, Serbia. Canadian Association for Physical Anthropology / L'Association Canadienne d'Anthropologie Physique (CAPA/ACAP), 48th Annual Meeting, Paleoanthropological Society of Canada / Société Canadienne d'Anthropologie (PASC/SCPA), 5th Annual Meeting: London (ON, Canada), pp 58

Royer A, Yelo BAG, Laffont R, Fernández MH (2020) New bioclimatic models for the quaternary palaearctic based on insectivore and rodent communities. Palaeogeogr Palaeoclimatol Palaeoecol 560:110040

Sánchez-Goñi MF (2007) 13. Introduction to climate and vegetation in Europe during MIS5. In: Sirocko F Claussen M Sánchez-Goñi MF Litt T (ed) Developments in Quaternary Sciences Vol. 7 The Climate of Past Interglacials, 1st edn. Amsterdam, Netherlands, pp. 197–205

Šarić J (2013) Smolućka cave: unpublished chipped stone artifacts from excavations in 1987. Starinar 63:9–21

Sesé C (1991) Interpretación paleoclimática de las faunas de micromamíferos del Mioceno, Plioceno y Pleistoceno de la Cuenca de Guadix-Baza (Granada, España). Estud Geol 47:73–83

Schenker N, Gentleman JL (2001) On judging the significance of differences by examining overlap between confidence intervals. American Statician 55:182–186

Shepherd UL (1998) A comparison of species diversity and morphological diversity across the North American latitudinal gradient. J Biogeogr 25:19–29

Sinitsa MV, Virág A, Pazonyi P, Knitlová M (2021) Redescription and phylogenetic relationships of *Spermophilus citelloides* (Rodentia: Sciuridae: Xerinae), a ground squirrel from the Middle Pleistocene-Holocene of Central Europe. Hist Biol 33:19–39

Smit CJ, VanWijngaarden A (1981) Threatened mammals in Europe. Akademische Verlagsgesellschaft, Wiesbaden

Stewart JR, Van Kolfschoten M, Markova A, Musil R (2003) The mammalian faunas of Europe during oxygen isotope stage three. In: Van Andel TH, Davies W, Aiello L (eds) Neanderthals and modern humans in the European landscape during the last glaciation. Michigan, USA, pp 103–130

Stevens GC (1989) The latitudinal gradients in geographical range: how so many species co-exist in the tropics. Am Nat 133:240–256

Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. Am Nat 140:893–911

Tierney JE, Poulsen CJ, Montañez IP, Bhattacharya T, Feng R, Ford HL, Hönisch B, Inglis GN, Petersen SV, Sagoo N, Tabor CR (2020) Past climates inform our future. Science 370:6517. https://doi.org/10.1126/science.aay3701

Valverde JA (1967) Estructura de una comunidad de vertebrados terrestres. Monografías De La Estación Biológica De Doñana 1:1–219

Van Weers DJ (1994) The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus *Hystrix*. Scr Geol 106:35–52

Villa P, Pollarolo L, Conforti J, Marra F, Biagioni C, Degano I, Lucejko JJ, Tozzi C, Pennacchioni M, Zanchetta G, Nicosia C (2018) From Neandertals to modern humans: new data on the Uluzzian. PLoS ONE 13:e0196786

Walter H (1970) Vegetationszonen und Klima. Eugen Ulmer, Stuttgart

van de Weerd A, Daams R (1978) Quantitative composition of rodent faunas in the Spanish Neogene y paleoecological implications (I y II). Proc Kon Ned Akad Wetensch, B 81:448–473

Williams SE, Marsh H, Winter J (2002) Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rain forest. Ecology 83:1317–1329

Wilson DE, Reeder DM (eds) (2005) Mammal species of the world: a taxonomic and geographic reference (Vol. 1). JHU Press, Baltimore

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 21:231–251