



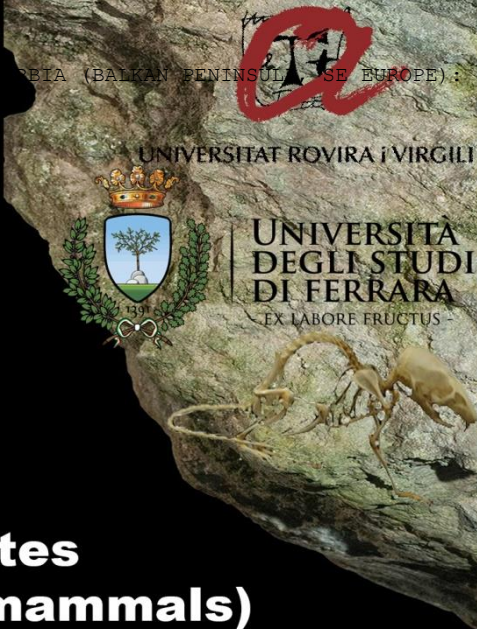
PLEISTOCENE SMALL-VERTEBRATES (AMPHIBIANS, REPTILES, AND SMALL MAMMALS) STUDIES IN SERBIA (BALKAN PENINSULA, SE EUROPE): HISTORY OF RESEARCH, METHODOLOGICAL STATE OF THE ART, AND PALEOCLIMATIC AND PALEOENVIRONMENTAL RECONSTRUCTIONS

Mihailo Jovanovic

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**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 DISSERTATION

Mihailo Jovanović

Tarragona, 2021

**Dissertation Advisors: Hugues-Alexandre Blain
Jordi Agustí**



**UNIVERSITAT
ROVIRA i VIRGILI**



**UNIVERSITÀ DEGLI
STUDI DI FERRARA**

Mihailo Jovanović

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UNIVERSITAT ROVIRA I VIRGILI



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HAGO CONSTAR que el presente trabajo, titulado “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”, que presenta Mihailo Jovanović para la obtención del título de Doctor, ha sido realizada bajo mi dirección en el Departamento de Historia e Historia del Arte de esta Universidad.

I DECLARE that the present work, entitled “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”, presented by Mihailo Jovanović to obtain the title of Doctor, has been carried out under my supervision in the Department of History and History of Art of this University.

March 2021,



Hugues-Alexandre Blain



Jordi Agusti

Director de la Tesis Doctoral/ Director of the Doctoral dissertation

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Abstract

Serbia is a country located at the boundary between Balkan Peninsula and Central European plains. Geologically, the terrain is favorable for the formation of limestone caves where small vertebrate remains are usually recovered, as well as Neanderthals remains occasionally. According to the available data, the small vertebrate remains from Baranica, Hadži Prodanova, Pešturina, and Smolučka caves are the most appropriate for the paleoclimatic reconstructions. I have made an attempt to present AMS dated layers from these sites within the chronological context of the Mousterian-Aurignacian-Gravettian cultural succession. Therefore, changes in the faunal composition have been recognised in relation to the successive cultural context. Taxonomical habitat indexes and bioclimatic analysis have been applied on small mammals. In addition, hierarchical clustering and correspondence analysis have been applied to herpetofaunal assemblages as a comparative proxy for reconstructing the paleoclimate and paleoenvironment. MIS 5 (Smolučka) is found in reconstruction to have been much warmer than present, and the data from the small vertebrates remains in Serbia did not seem to have registered any dramatic climatic oscillations during MIS 3 and early MIS 2. When compared with present local situation, the paleoecological and paleoclimatological reconstructions for these four caves suggest that climate was somewhat colder (presence in the sites of mountain species like *Chionomys nivalis*) and dryer (mainly due to the detection of *Coronella austriaca* and *Lacerta agilis*). The application of taxonomical habitat indexes to the different assemblages suggests that the associated environment was probably more open with the presence of forest species (*Clethrionomys glareolus* and *Apodemus ex gr. sylvaticus-flavicollis*), but never representing more than 10% of the total assemblage. Even during the MIS 2, results suggest that the Balkans had milder and humid climate compared to Central Europe, with average temperature ranging from 2.2

to 4.5 °C lower than presently. Overall, there were no important ecological changes during the transition between Mousterian and Aurignacian, i.e. between Neanderthals and Anatomically Modern Humans. This conclusion is generally in line with common opinion that climate change was not a crucial factor in Neanderthal extinction in the Balkan Peninsula. Instead, it had the effect similar to Iberian and Apennine Peninsulas, where milder climate allowed Neanderthals to find refuge and survive longer than in the rest of the Europe.

Resumen

Serbia está situada en el límite entre la Península Balcánica y las llanuras centroeuropeas, y geológicamente, es favorable para la formación de cuevas en las que se suelen recuperar restos de pequeños vertebrados, así como, en ocasiones, restos de Neandertales. Según los datos disponibles, los fósiles de las cuevas de Baranica, Hadži Prodanova, Pešturina y Smolučka son los más adecuados para las reconstrucciones paleoclimáticas. Se ha intentado presentar los niveles fechados por AMS de estos yacimientos dentro del contexto cronológico de la sucesión cultural Musteriense-Auriñaciense-Gravetiense; por tanto, se han reconocido los cambios en la composición faunística en relación con los contextos culturales sucesivos. Se han aplicado índices taxonómicos de hábitat y análisis bioclimáticos sobre los pequeños mamíferos. Además, se ha aplicado la agrupación jerárquica y el análisis de correspondencia a los conjuntos herpetofaunísticos como proxy comparativo para reconstruir el paleoclima y el paleoambiente. El MIS 5 (Smolučka) se ha estimado como mucho más cálido que el actual y que los pequeños vertebrados de Serbia no parecen haber registrado ninguna oscilación climática dramática durante el MIS 3 y principios del MIS 2. Cuando se comparan con la situación actual local, las reconstrucciones paleoecológicas y paleoclimatológicas de estas cuatro cuevas sugieren que el clima era algo más frío (presencia en los yacimientos de especies de montaña como *Chionomys nivalis*) y más seco (principalmente por la presencia

de *Coronella austriaca* y *Lacerta agilis*). La aplicación de índices taxonómicos de hábitat a los diferentes conjuntos sugiere que el entorno asociado era probablemente más abierto, aunque con la presencia de especies forestales (*Clethrionomys glareolus* y *Apodemus ex gr. sylvaticus-flavicollis*), pero nunca representando más del 10% del conjunto total. Incluso durante el MIS 2, los resultados sugieren que los Balcanes tenían un clima más suave y húmedo en comparación con Europa Central, con una temperatura media que oscilaba entre 2,2 y 4,5°C menos que en la actualidad. En general, no hubo cambios ecológicos importantes durante la transición entre el Musteriense y el Auriñaciense, es decir, entre los Neandertales y los Humanos Anatómicamente Modernos. Esta conclusión coincide en general con la opinión común de que el cambio climático no fue un factor crucial en la extinción de los Neandertales en la península de los Balcanes, sino que tuvo un efecto similar al de las penínsulas ibérica e itálica, donde un clima más suave permitió a los Neandertales encontrar refugio y sobrevivir más tiempo que en el resto de Europa.

Résumé

La Serbie est située à la frontière entre la péninsule balkanique et les plaines d'Europe centrale et, d'un point de vue géologique, elle est propice à la formation de grottes où l'on retrouve généralement les restes de petits vertébrés, ainsi que, parfois, des restes de Néandertaliens. D'après les données disponibles, les fossiles des grottes de Baranica, Hadži Prodanova, Pešturina et Smolučka sont les plus favorables aux reconstitutions paléoclimatiques. Un essai d'organisation des couches datées par AMS de ces sites a été faite dans un contexte chronologique de la succession culturelle moustérienne-aurignacienne-gravettienne ; les changements dans la composition faunistique ont donc été reconnus en relation avec les contextes culturels successifs. Des indices taxonomiques d'habitat et des analyses bioclimatiques ont été appliqués aux petits mammifères. De plus, le regroupement

hiérarchique et l'analyse des correspondances ont été appliqués aux assemblages herpétofauniques comme un indicateur comparatif pour la reconstruction du paléoclimat et du paléoenvironnement. Le SIM 5 (Smolučka) est reconstruit comme ayant été beaucoup plus chaud qu'aujourd'hui et les petits vertébrés de Serbie ne semblent pas avoir enregistré d'oscillations climatiques spectaculaires pendant le SIM 3 et le début du SIM 2. Par rapport à la situation régionale actuelle, les reconstructions paléoécologiques et paléoclimatologiques pour ces quatre grottes suggèrent que le climat était un peu plus froid (présence dans les sites d'espèces de montagne comme *Chionomys nivalis*) et plus sec (principalement en raison de la présence de *Coronella austriaca* et *Lacerta agilis*). L'application des indices taxonomiques d'habitat aux différents assemblages suggère que l'environnement associé était probablement plus ouvert, avec toutefois la présence d'espèces forestières (*Clethrionomys glareolus* et *Apodemus ex gr. sylvaticus-flavicollis*), mais ne représentant jamais plus de 10% de l'assemblage total. Même pendant le SIM 2, les résultats suggèrent que les Balkans avaient un climat plus doux et humide par rapport à l'Europe centrale, avec une température moyenne de 2,2 à 4,5 °C inférieure à celles d'aujourd'hui. Dans l'ensemble, aucun changement écologique important n'est intervenu au cours de la transition entre le Moustérien et l'Aurignacien, c'est-à-dire entre l'homme de Néandertal et l'homme anatomiquement moderne. Cette conclusion est généralement conforme à l'opinion commune selon laquelle le changement climatique n'a pas été un facteur crucial dans l'extinction de l'homme de Néandertal dans la péninsule balkanique, mais a eu un effet similaire à celui des péninsules ibérique et apennine, où un climat plus doux a permis aux hommes de Néandertal de trouver refuge et de survivre plus longtemps que dans le reste de l'Europe.

Sažetak

Srbija se nalazi na granici između Balkanskog poluostrva i srednjoevropskih ravnica. Teren je geološki povoljan za formiranje krečnjačkih pećina u kojima se obično pronalaze sitni ostaci kičmenjaka, i ponekad, ostaci neandertalaca. Na osnovu dostupnih podataka, ostaci iz pećina Baranice, Hadži Prodanove, Pešturine i Smolučke, najpogodniji su za paleoklimatske rekonstrukcije. Predstavljen je prikaz datovanja (pomoću AMS metode) slojeva sa ovih lokaliteta u hronološkom kontekstu musterijansko-orinjasijensko-gravetijenske kulturne sukcesije i prepoznate su promene u faunističkom sastavu u odnosu na kulturni kontekst. Na ostacima sitnih sisara primenjene su metode: taksonomski indeksi staništa i bioklimatska analiza. Pored toga, hijerarhijsko grupisanje i analiza korespondencije primenjeni su na herpetofaunalnim skupinama kao uporedni proksi za rekonstrukciju paleoklime i paleookruženja. Rekonstrukcije su pokazale da je MIS 5 (Smolučka) bio znatno topliji nego danas, a čini se da sitni kičmenjaci u Srbiji nisu registrovali nikakve dramatične klimatske oscilacije tokom MIS 3 i ranog MIS 2. U poređenju sa sadašnjom lokalnom situacijom, paleoekološke i paleoklimatološke rekonstrukcije za ove četiri pećine sugerišu da je klima bila nešto hladnija (prisustvo na nalazištima planinskih vrsta poput *Chionomys nivalis*) i suvlja (uglavnom zbog prisustva *Coronella austriaca* i *Lacerta agilis*). Primena taksonomskih indeksa staništa na različite životinjske zajednice sugerišu da je njihovo okruženje verovatno bilo otvorenije, uz prisustvo šumskih vrsta (*Clethrionomys glareolus* i *Apodemus ex gr. sylvaticus-flavicollis*), koje nikada ne predstavljaju više od 10% životinjske zajednice. Čak i tokom MIS 2, rezultati sugerišu da je Balkan imao blažu i vlažniju klimu u poređenju sa Centralnom Evropom, sa prosečnom temperaturom u rasponu od 2,2 do 4,5 °C nižom od trenutne. Sveukupno, nije bilo bitnih ekoloških promena tokom tranzicije između musterijena i orinjasijena, tj. između neandertalaca i anatomski modernih ljudi. Ovaj zaključak je generalno u skladu sa uobičajenim mišljenjem da klimatske promene nisu bile

presudni faktor u izumiranju neandertalaca na Balkanskom poluostrvu. Umesto toga, imale su sličan efekat kao na Iberijskom i Apeninskom poluostrvu, gde je blaža klima omogućavala neandertalcima da pronađu utočište i prežive duže nego u ostatku Evrope.

1. INTRODUCTION

This doctoral thesis is focused on paleoclimatic and paleoenvironmental reconstructions based on the data from small vertebrates remains from Marine Isotope Stage (MIS) 5 to MIS 2. In archeological terms, this represents a chronological context of the Mousterian-Aurignacian-Gravettian cultural succession. In climatic terms, this covers a series of climate changes from an interstadial (MIS 5) with favorable climate conditions for a large diversity of species, following temperate conditions in MIS 4 and MIS 3, to the global cooling and the last glacial maximum in MIS 2.

Serbia is a country located in South-East Europe of the southern Pannonian Plain, in the center of the Balkan Peninsula, bordering Hungary (north), Romania (northeast), Bulgaria (southeast), North Macedonia (south), Croatia, and Bosnia and Herzegovina (west), Albania and Montenegro (southwest) (Figure 1.1).

Four mountain systems cover the largest parts of Serbia: Dinaric Alps from northwest to southeast; the Carpathian Mountains and Balkan Mountains in a north-south direction in eastern Serbia, west of the Morava valley. The Morava River flows through the more mountainous southern regions. Ancient mountains along the South Morava belong to the Rilo-Rhodope Mountain system.

Northern Serbia (Vojvodina region) is the southern part of the Pannonian Basin formed after the retreat of the Pannonian Sea (Paratethys) during the Miocene period, with rich, fertile plains and dominated by the Danube River. In Central parts of Serbian hills, low and medium-high mountains are interspersed with numerous rivers and creeks. In East Serbia, the terrain forms limestone ranges of Stara Planina and Serbian Carpathians and in the West

mountains (Zlatibor and Kopaonik) height slowly rises towards the southwest, but they do not form real ridges.

The climate of Serbia is moderate continental with cold, relatively dry winters and warm, humid summers, with diversity on the local level caused by geographic location, relief, and terrain exposition, presence of river and lake systems, vegetation, and urbanization (http://www.hidmet.gov.rs/eng/meteorologija/klimatologija_srbije.php).

Location of river ravines and plains in the northern area of the country enable occasional deep southward protrusion of polar air masses on winters, while hot Saharan air often intrudes over the Mediterranean Sea on summers (<https://www.britannica.com/place/Serbia>).

Significant climatic differences within Serbia can be attributed to geographic characteristics: the proximity to the Mediterranean Sea and Alpes, Pannonian Plain and the valley of the Morava, the Carpathian and Rodope mountains, as well as hilly-mountainous part with ravines and highland plains. Precipitation in Serbia ranges from 560 to 1,900 mm per year, depending on elevation and exposure. Mean annual temperature (1961-1990) for the area with an altitude of up to 300 m amounts to 11°C. The areas with altitudes of 300 to 500 m have a mean annual temperature of around 10.5°C, and over 1,000 m altitude around 6°C. Mean annual precipitation generally rises with altitude. In lower regions, it ranges in the interval from 540 to 820 mm; areas on altitude over 1,000 m receive on average 700 to 1,000 mm, and some mountainous summits in southwestern Serbia up to 1,500 mm. A major part of Serbia has a continental precipitation regimen, with a peak in the earlier summer period, except for the southwest, which receives highest precipitation in autumn. May–June is the rainiest month, with an average of 12 to 13% of the total annual amount. February and October have the least precipitation. Snow cover can occur from late November to early

March, and a majority of days with snow cover is in January (http://www.hidmet.gov.rs/eng/meteorologija/klimatologija_srbije.php).

With 29.1% of territory covered by forest, Serbia is considered today to be a middle-forested country. (<http://www.srbijasume.rs/sumskifonde.html>). According to The National forest inventory of the Republic of Serbia, the most common trees are oak, beech, pines, and firs (<http://upravazasume.gov.rs/wp-content/uploads/2015/12/The-national-forest-inventory-of-the-Republic-of-Serbia.pdf>). Serbia is a country of the rich ecosystem and species diversity covering only 1.9% of the whole European territory. Serbia is home to 39% of European vascular flora, 51% of European fish fauna, 40% of European reptile and amphibian fauna, 74% of European bird fauna, 67% European mammal fauna (<https://www.iucn.org/content/serbian-biodiversityIts>). Opulence of mountains and rivers make it an ideal environment for a variety of animals, many of which are protected including wolves, lynx, bears, foxes, and stags. There are 17 snake species living all over the country (Tomović et al. 2014).

Such high biodiversity can be explained by geological and orographic reasons. Balkan biodiversity is still poorly understood and is characterized by outstanding levels of endemism, particularly in caves and ancient lakes. At the crossroads of Europe and Asia, they are also renowned as a focus of Pleistocene glacial refugia (Griffiths et al. 2004). Previously, Balkan Peninsula acted as a refugium for the species living in this territory since it was completely isolated from the rest of Europe. The retreat of a large shallow inland sea that stretched from the region north of the Alps over Central Europe to the Aral Sea in Central Asia (Paratethys), opened a large plain which allowed species from Eastern European plains to migrate south and populate Balkans contributing to the richness and diversity of the Balkan fauna. Fossil evidence documenting the mixing of the fauna during the Miocene period is scarce, although it is widely accepted that some of the species currently living in Serbia

migrated to the Balkan Peninsula during this period. It is impossible to identify all of them with certainty as fossil record is not complete. During the Miocene, the Balkans was subjected to the strong tectonic activity which resulted in the formation of two main mountain ranges, Carpatho-Balkan on the East, and Dinarides on the West (Figure 1.1). The composition of the newly formed terrain with high mountain tops and natural barriers, often allowed autochthonous species to find refuges in isolated areas instead of becoming extinct.

The abundance of Mesozoic limestones allowed formation of the caves, (layers usually date from Pleistocene to Holocene) and when interpreted properly represent a valuable source of information about the conditions in the area. Caves in Serbia are usually formed in Mesozoic limestone layers within two mountain ranges, and we can sort them into the caves belonging to Carpatho-Balkan on the East, and Dinarides on the West. Caves in the same zone are usually in short proximity to each other (Figure 1.1).

Small vertebrate remains represent a good proxy for reconstructions of paleohabitats (Lopez-Antoñanzas and Cuenca-Bescós 2002, Cuenca-Bescós et al. 2009, López-García et al. 2015, Rofes et al. 2014, Garcia-Ibaibarriaga et al. 2015, Ivanova et al. 2015, Blain et al. 2008a, Blain et al. 2010). . They are quite common in Late Pleistocene cave sediments in Serbia (Đurić et al. 2016, 2017, Bogićević 2004, Jovanović 2005, Bogićević et al. 2011, 2012, Jovanović 2016, Bogićević et al. 2017, Bogićević 2008, Đurić 2019) They mostly consist of rodent and herpetofaunal remains but also other such as Insectivores (Eulipotyphla), bats, birds, and fish can sometimes be found. My work is including caves: Baranica, Hadži Prodanova, Pešturina, and Smolučka caves. These caves are chosen for their stratigraphical properties and fossil abundance. Osteological remains are not described in this thesis due to them already being described in various works of other researchers closely collaborating with me in my work. Instead, osteological descriptions are planned in further extension of my

work to Velika Balanica and Mala Balanica caves, the material currently being in process of sieving and washing.

1.1 BARANICA (east Serbia)

The site Baranica has been the subject of investigation in my master's thesis (Jovanović 2016). The cave is located in eastern Serbia, in the Balkan mountain range, 4 kilometers south of Knjaževac, on the right bank of the river Trgoviški Timok (Figure 1.1). Altitude is approximately 400 meters above sea level (Mihailović 2004). This area is the base of the western part of Balkan massif which is mainly located in Bulgaria. The mountain range starts from the slopes of Vrška Čuka above Zaječar, and then extends to the southeast, from where it rises abruptly above Knjaževac and turns into a high mountain massif that arches northwest-southeast, reaching the highest height at the top of Midžor. The northeastern slopes are located on the territory of Bulgaria, while the southeastern slopes with hills are located on the territory of Serbia. This is the State protected area, as a natural asset of exceptional importance, due to the exceptional biodiversity. Around 1200 species and subspecies of higher plants live in this area, 115 of which are endemic plant species, over 100 protected and strictly protected species, and more than 50 species that are on the list of endangered European flora. All these species build 52 different forests, shrubby and herbaceous plant communities. As far as animal diversity is concerned, the Balkan massif is a habitat for about 150 species of nesting birds, 30 species of mammals, 7 species of amphibians, 13 species of reptiles, and 26 species of fish. It was declared a nature park in 1997, although the protected area does not cover the area immediately around of the Baranica cave, and cave itself.



Figure 1.1 – Late Pleistocene to Holocene Serbian sites that delivered small-vertebrate assemblages studied in this thesis: 1. Baranica; 2. Hadži Prodanova cave; 3. Pešturina; 4. Smolučka cave; 5. Mala Balanica; 6. Velika Balanica.

Presently, the vicinity of the cave is a mosaic of fertile plains and low-medium vegetation, with tall vegetation present mostly on the banks of the river Trgoviški Timok. True forests are not present in close proximity of the cave but are visible in the distance, mostly consisting of deciduous trees.

This area has a humid continental climate. Going from the higher to the lower altitude, the average temperature increases, and the humidity decreases. The warmest month is July with an average temperature of 21.1°C, whereas the coldest month is January with an average temperature of 0.1°C. The mean annual temperature is 11.2°C. The average annual rainfall is 605 mm. There are 306 sunny days and 30 days with snow in a year (<https://en.climate-data.org/europe/serbia/knjazevac/knjazevac-31866/>).

The entrance of the cave is directly exposed to the sun throughout the most of the day. Along with the absence of predators, this creates favorable conditions for large diversity of reptiles. On sunny days the rocky hills with low vegetation are teeming with lizards and snakes. Positioned north of the cave, on a slightly higher altitude there is a rocky hill surrounded by forest vegetation with natural water springs. These natural settings contribute to the complexity of the mosaic of habitats, as they create conditions favorable for water-edge and forest requiring organisms, such as frogs, toads, newts, salamanders, turtles, and tortoises (Figure 1.2). The data linked to the distribution of the herpetofauna are collected from domestic and foreign authors (Ratnikov 1996, Tomović et al. 2014, Vukov et al. 2013). Based on these works, we can conclude that the area where Baranica is located is correlated with the Eastern European platform in terms of the dynamics of the distribution of herpetofaunal species. Ljiljana Tomović, Tanja Vukov, and the other authors (Tomović et al. 2014), presented the data on the distribution of herpetofauna in Serbia. In the region where Baranica cave is located today it is difficult to approximate the number of species present, and the presence of some species may vary.



Figure 1.2 – Natural habitats and associated herpetofauna in the vicinity of Baranica cave.

According to Vukov (Vukov et al. 2013) and Tomović (Tomović et al. 2014), there are 20 herpetofaunal species; two frogs (*Rana dalmatina*, and *Pelophylax ridibundus*), three toads (*Bombina bombina*, *Pseudepidalea viridis* and *Bufo bufo*), one newt (*Lissotriton vulgaris*),

one salamander (*Salamandra salamandra*), one turtle (*Emys orbicularis*), one tortoise (*Testudo hermanni*), one anguid lizard (*Anguis fragilis*), three lacertids (*Podarcis muralis*, *Lacerta viridis*, and *Darevskia praticola*), one skink (*Ablepharus kitaibelii*), and six snakes (*Coronella austriaca*, *Natrix tessellata*, *Natrix natrix*, *Zamenis longissimus*, *Dolichophis caspius*, and *Vipera ammodytes*). According to Petrov (Petrov 1992), three species of Insectivores (Eulipotyphla) (*Sorex minutus*, *Crocidura suaveolens*, and *Crocidura leucodon*), and 6 species of rodents (*Microtus arvalis*, *Spalax leucodon*, *Apodemus flavicollis*, *Apodemus sylvaticus*, *Mus hortulanus*, and *Muscardinus avellanarius*) live in the area of Baranica cave.

Archeological excavations of the site were carried out from 1994-1997 by the Archeological Institute, the Faculty of Philosophy in Belgrade, and the Knjaževac Museum. It is a composite system of three small caves connected to each other – Baranica I, II, and III. The entrance into Baranica II is situated some 20 m above Baranica I (Dimitrijević 2011). An open profile 2.5 m deep in Baranica I was created in which four layers were separated. A large number of vertebrate remains (large and small mammals, birds, reptiles, amphibians, and fish) were collected. The first layer is of Holocene age, while the other three belong to the Upper Pleistocene (Bogićević et al. 2011, 2012; Đurić et al. 2016, Đurić et al. 2017). A detailed chronology of the site is elaborated in Chapter III. A total of four layers were detected (Figure 1.3).

The research of the cave was performed within the project "Prehistory of the Knjaževac region" (whose leader was the late academician D. Srejić), organized by the Faculty of Philosophy in Belgrade and Museum in Knjaževac, and began in 1994 to explore in archeological terms little known area of Stara planina, Tresibaba, Tupižnica, and the Timok basin.

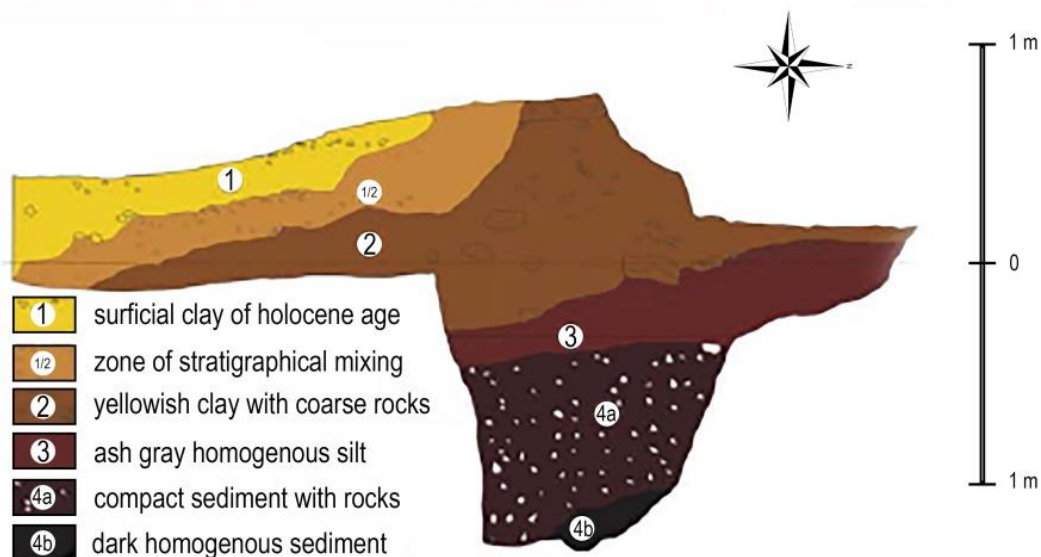


Figure 1.3 – Stratigraphy of the Baranica cave (Jovanović 2005): Layer 1. The humus surface layer is located in the southern part of the excavation and is the only one of Holocene age. There is a mixing zone (1/2) between it and the second layer; Layer 2 - Yellowish clay with large scraps and remains of large mammals and small vertebrates. Within this layer, two horizons can be distinguished: 2a - light yellow clay with coarse debris, 2b - dark yellow clay with coarse scraps. Layer 3 - Gray siltstone with rare remains of small mammals. This deposition is ash-gray in color and homogeneous in composition. It was discovered in the northern part of the excavation below the second layer. The upper part of the layer (3a) contains rare remains of small mammals, and the lower part (3b) is free of fossil remains. Layer 4 - Dark brown clay siltstone with coarse grains. Two horizons can also be distinguished in this sediment: 4a - compact sediment with scraps, 4b - sediment without crumb (Mihailović, personal communication).

The Archeological excavations provided only a few lithic artifacts, mostly finished tools made of diverse, high quality raw materials, a pattern that suggests transitory use of the site (Mihailović and Mihailović 2014; Mihailović et al. 2011).

Remains of fauna and flora from this cave have been described in several works (Argant and Dimitrijević 2007, Bogićević 2004, Brunet-Lecompte et al. 2001, Dimitrijević 1997b, 2004, Forsten and Dimitrijević 2004, Krantić 1997, Salčin 1996, Dimitrijević 2011). The majority of the remains of rodents are described in the master's thesis of a colleague (Jovanović 2005),

a doctoral dissertation (Bogićević 2008), and several publications (Bogićević et al. 2011, 2012). Herpetofaunal remains have been described by Đurić (Đurić et al. 2016, 2017) and (Đurić, 2019). The list of taxa identified in Baranica has been synthesized in Table 1.1.

Layer	AMPHIBIA	REPTILIA	MAMMALIA	MICROMAMMALIA
2	<i>Pelophylax</i> cf. <i>ridibundus</i>	<i>Viper</i> asp. <i>Lacertidae</i> gen. et sp. indet.		<i>Spermophilus citelloides</i> , <i>Sicista subtilis</i> , <i>Cricetus cricetus</i> , <i>Mesocricetus newtoni</i> , <i>Cricetulus migratorius</i> , <i>Clethrionomys glareolus</i> , <i>Arvicola terrestris</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Chionomys nivalis</i> , <i>Lagurus lagurus</i> , <i>Dicrostonyx</i> sp., <i>Apodemus sylvaticus</i> , <i>Spalax leucodon</i>
3	<i>Bufotes</i> ex gr. <i>viridis</i>			<i>Mesocricetus newtoni</i> , <i>Arvicola terrestris</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Lagurus lagurus</i> , <i>Spalax leucodon</i>
4	<i>Pelophylax</i> cf. <i>ridibundus</i> <i>Pelophylax</i> sp. <i>Rana</i> sp. <i>Pelobates</i>	<i>Lacerta agilis</i> <i>Lacerta</i> sp. <i>Anguis fragilis</i> <i>Coronella austriaca</i> <i>Zamenis</i> cf. <i>longisimus</i> <i>Elaphe quatuorlineata</i> <i>Natrix</i> sp. <i>Vipera berus</i> group <i>Vipera ammodytes</i> <i>Vipera</i> sp.	<i>Crocuta spelaea</i> <i>Bos/Bison</i> <i>Mustela nivalis</i> <i>Dicerorhinus</i> sp <i>Equus caballus</i> <i>Panthera</i> sp. <i>Panthera</i> sp. <i>Canis lupus</i> <i>Vulpes vulpes</i> <i>Capra ibex</i>	<i>Spermophilus citelloides</i> , <i>Sicista subtilis</i> , <i>Cricetus cricetus</i> , <i>Mesocricetus newtoni</i> , <i>Cricetulus migratorius</i> , <i>Clethrionomys glareolus</i> , <i>Arvicola terrestris</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Chionomys nivalis</i> , <i>Lagurus lagurus</i> , <i>Dicrostonyx</i> sp., <i>Apodemus sylvaticus</i> , <i>Spalax leucodon</i> , <i>Dryomys nitedula</i> , <i>Muscardinus avellanarius</i>

Table 1.1 – Faunal list recovered from the late Pleistocene site of Baranica (east Serbia).

1.2 HADŽI PRODANOVA CAVE (southwest Serbia)

The cave Hadži Prodanova is located in western Serbia, in the valley of the Raščanska River, about 40 meters above the floor of the valley. The entrance of the cave lies at an altitude of 630 meters above sea level. Nearby is Raščići quarry, and the closest town is seven kilometers away (Ivanjica) (Fig. 1.1) (Lješević 2002). The area is located in a picturesque valley surrounded by the mountain ranges and mountain tops: Golija, Javor, Mučanj, Čemerna and Radočelo. Mountains are the dominant form of landscape, and by their origin and geological composition, they are associated with the Dinaric Alps. Golija has been awarded a status of the “Nature Park” and has been placed under protection in order to preserve the values of forest ecosystems, the diversity of landscapes and the extraordinary beauty of the landscape, cultural goods and their surroundings, durability and quality of basic natural resources (water, and vegetation), biological diversity (rare, endemic and relict species), geoheritage(represented by unusual and attractive landforms and numerous water bodies and phenomena in the form of springs of mountain watercourses and lakes). It is mostly covered with dense forest. Beech forests are especially represented. Some parts of these forests are remote and unaffected by human activity. Southern slopes are overgrown with vast meadows and pastures. In spruce forests, peatlands have been preserved as specific and sensitive ecosystems. Golija is also a refuge of Tertiary flora in Serbia and is important as a center of genetic, species, and ecosystem diversity in the Balkans and Europe. The floristic biodiversity of Golija contains about 900 taxa of the plant world, of which 729 species of vascular fungi, 40 species of moss, 117 species and varieties of algae. Of particular importance in the flora are endemic and relict species, as well as species that have become endangered (<https://srbijasume.rs/zasticena-podrucja/pregled-zasticenih-podrucja/parkovi->

priode). The climate is influenced by surrounding mountains, but the mean annual temperature is not very cold (10°C). Geographically the area is located in a temperate continental zone, with relatively high mean annual precipitation (897 mm). Summers are moderately warm and winters are cold, typically with snowfall.

Although forest habitat is common in the area, the immediate proximity of the cave is a dry rocky quarry creating a microhabitat suitable for reptiles that endure dry rocky conditions (*Lacerta viridis*, *Coronella austriaca*, *Podarcis muralis*, and *Vipera ammodytes*). A broader area allows favorable conditions for a larger diversity of species. Nearby water sources gather “water–edge” species (*Natrix natrix*, *Natrix tessellata*, *Bombina bombina*, *Rana graeca*, *Rana dalmatina*, *Rana temporaria*, and *Pelophylax ridibundus*) (Figure 1.4). Other small vertebrate species that can be found in the area are: *Bombina variegata*, *Bufo bufo*, *Bufo viridis*, *Salamandra salamandra*, *Darevskia praticola*, *Lacerta agilis*, *Zamenis longissimus*, *Dolichophis caspius*, *Vipera berus*, *Testudo hermanni*, *Sorex araneus*, *Talpa europaea*, *Myodes glareolus* (formerly *Clethrionomys glareolus*), *Microtus arvalis*, *Apodemus flavicollis*, *Apodemus sylvaticus*, *Glis glis*, and *Muscardinus avellanarius*.

The small vertebrate remains from Hadži Prodanova cave have been recovered in 2003 and 2004 during the archeological excavations of the cave (Mihailović and Mihailović 2006). Five geological layers were isolated on the open profile (Figure 1.5) (Bogićević et al. 2016; Bogićević et al. 2017).

Rodent remains have been described (Bogićević et al. 2017) and herpetofaunal remains have been described in (Đurić 2019) (Table 1.2). Hadži Prodanova contains clearly perceived activities of the Paleolithic communities. Over a hundred chipped stone artifacts with cultural attribution. Some of them are described in the publication (Mihailović, 2008).



Figure 1.4 – Natural habitats and associated herpetofauna in the vicinity of Hadži Prodanova cave.

Layer	AMPHIBIA	REPTILIA	MAMMALIA	MICROMAMMALIA
3		<i>Anguis fragilis</i> , <i>Lacerta</i> sp., <i>Lacerta agilis</i> , <i>Zamenis longissimus</i> , <i>Vipera</i> cf. <i>berus</i>	<i>Ursus spelaeus</i> , <i>Capra ibex</i> , <i>Canis lupus</i> , <i>Rupicapra rupicapra</i> , <i>Cervus elaphus</i> , <i>Lynx lynx</i> ,	Layer 3: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys glareolus</i> , <i>Mesocricetus newtoni</i> , <i>Apodemus</i> cf. <i>sylvaticus</i> , <i>Sicista subtilis</i> , <i>Muscardinus avellanarius</i>
4	Ranidae indet.	<i>L. agilis</i> , Lacertidae indet.,	<i>Crocuta spelaea</i>	Layer 4: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Arvicola</i> cf. <i>terrestris</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys glareolus</i> , <i>Mesocricetus newtoni</i> , <i>Apodemus</i> cf. <i>microps-maastrichtensis</i> , <i>Apodemus</i> cf. <i>uralensis</i>
5	Anura indet., Ranidae indet., <i>Rana</i> sp.	<i>Anguis fragilis</i> , <i>Lacerta viridis</i> , <i>Lacerta agilis</i> , <i>V.</i> cf. <i>ammodytes</i> , <i>Vipera</i> cf. <i>berus</i>		Layer 5: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys glareolus</i> , <i>Spermophilus citelloides</i>
				Horizont 5a: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Arvicola</i> cf. <i>terrestris</i> , <i>Clethrionomys glareolus</i> , <i>Chionomys nivalis</i> , <i>Spermophilus citelloides</i> , <i>Sicista subtilis</i> , <i>Murinae</i> indet.
				Horizont 5b: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys glareolus</i> , <i>Spermophilus citelloides</i> , <i>Spalax leucodon</i> , <i>Apodemus</i> cf. <i>microps-maastrichtensis</i>
				Horizont 5c: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Clethrionomys glareolus</i> , <i>Mesocricetus newtoni</i> , <i>Sicista subtilis</i> , <i>Spalax leucodon</i> , <i>Apodemus</i> cf. <i>sylvaticus</i>
				Horizont 5d2: <i>Microtus arvalis/agrestis</i> , <i>Microtus subterraneus</i> , <i>Clethrionomys glareolus</i>

Table 1.2 – Faunal list recovered from the late Pleistocene site of Hadži Prodanova cave (southwest Serbia).

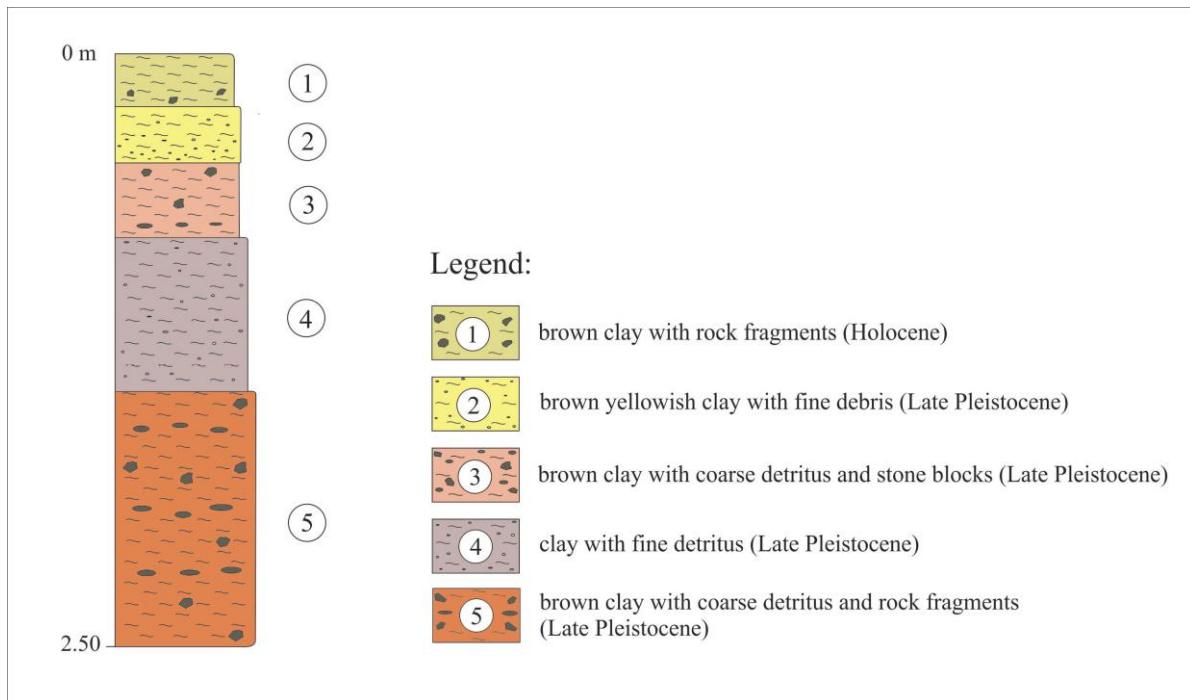


Figure 1.5 – Geological layers of Hadži Prodanova cave: level 1 - gray clay with pieces of rock (Holocene), level 2 - brown-yellow clays with fine debris, level 3 - brown clay with coarse debris, level 4 - brown clay with fine debris, level 5 - dark brown clay with coarse debris (from Bogićević et al. 2017, Đurić 2019, modified).

1.3 PEŠTURINA CAVE (east Serbia)

The cave Pešturina is located on the northern slope of Suva planina near the village of Jelašnica (Figure 1.1). The entrance to the cave is located at a rocky hill facing west, about 330 m above sea level, making the surroundings a perfect habitat for a large diversity of reptiles that thrive in the rocky ground (*Lacerta viridis*, *Coronella austriaca*, *Podarcis muralis*, and *Vipera ammodytes*) (Figure 1.6). The cave is located in the karstic limestone area of Jelašnica gorge, which formed due to intensive cutting of the river flow into the limestone rock mass of Suva Planina mountain slopes (Anđelković 1982; Rakić and Dimitrijević 1973; Vujisić and Navala 1980; Majkić et al. 2017). In the close proximity of the cave, a small Studena river flows creating a permanent water source and habitat for “water–edge” species (*Natrix natrix*, *Natrix tessellata*, *Bombina bombina*, *Rana graeca*, *Rana*

dalmatina, *Rana temporaria*, and *Pelophylax ridibundus*) (Figure 1.6). The karstic topography accumulates water and humidity in various places therefore creating a suitable habitats for amphibians (*Bufo viridis*, *Hyla arborea*, *Lissotriton vulgaris*, *Triturus macedonicus*, and *Salamandra salamandra*) (Figure 1.6). Other small vertebrate species that can be found in the area are *Bombina variegata*, *Bufo bufo*, *Darevskia praticola*, *Lacerta agilis*, *Zamenis longissimus*, *Dolichophis caspius*, *Vipera berus*, *Testudo hermanni*, *Sorex araneus*, *Talpa europaea*, *Crocidura suaveolens*, *Myodes glareolus* (formerly *Clethrionomys glareolus*), *Microtus subterraneus*, *Chionomys nivalis*, *Spalax leucodon*, *Apodemus flavicollis*, *Apodemus sylvaticus*, *Glis glis*, and *Dryomys nitedula*.

Today this area is in a humid continental climate zone. The average annual temperature is 11.7 °C. July is the warmest month of the year, with an average of 22.5 °C. The coldest month is January, averaging at 0.6 °C. The average annual rainfall is 580.3 mm. On average, there are 134 days with rain and snow cover lasts for up to 41 days.

Archeological excavations in the cave have been carried out since 2006 with occasional intermissions (Mihailović and Milošević, 2012), and are still being carried out today. Pešturina is an ongoing archeological site conducted by Professor Dušan Mihailović. During the excavations hundreds of Middle Paleolithic and Upper Paleolithic chipped stone artifacts have been discovered, some of them are discovered in the publication (Mihailović and Milošević, 2012) Small vertebrate remains (Table 1.3) are still being collected and fauna lists are preliminary but presented in chapter IV. Herpetofaunal remains are described in the unpublished thesis (Đurić, 2019). Large mammal remains are described in an unpublished manuscript (Dimitrijević, under review).



Figure 1.6 – Natural habitats in the vicinity of Pešturina cave and associated herpetofauna.

The explored layers in the cave reach a depth of 5 m. Four layers were described (**Figure 1.7**), and the fauna was found in layers 2, 3, and 4. A detailed chronology of the cave is explained in Chapter III.

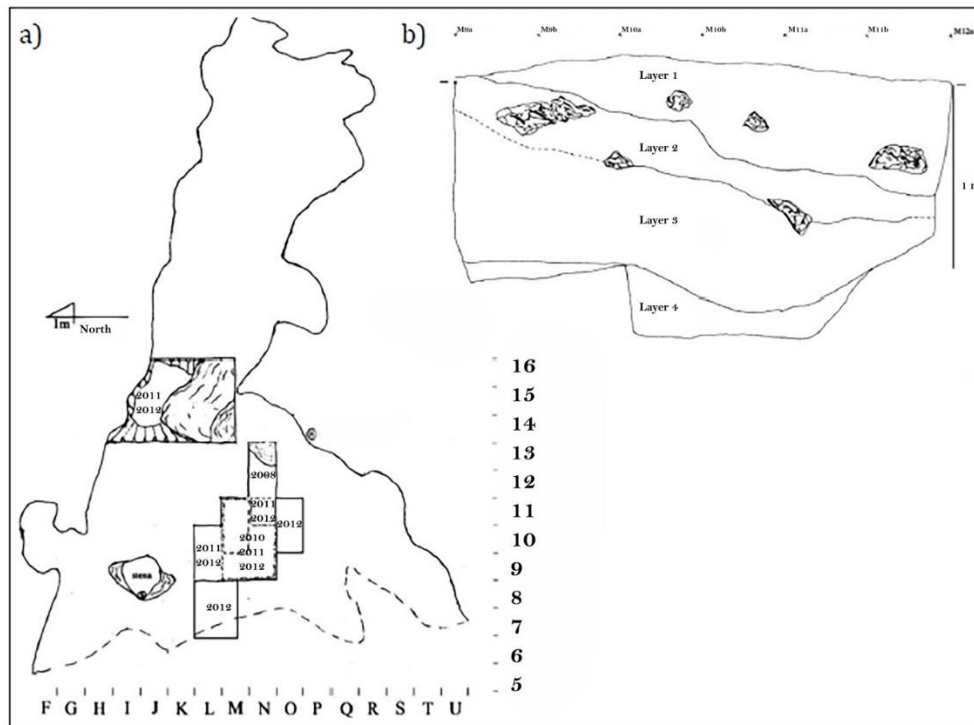


Figure 1.7 – The main excavation plan of Pešturina cave (a), vertical excavation profile (b) (modified after Mihailović and Milošević 2012).

Layer	AMPHIBIA	REPTILIA	MAMMALIA	MICROMAMMALIA
2	Anura indet.	<i>Anguis fragilis</i> , Lacertidae indet., <i>Lacerta</i> sp. <i>L. agilis</i> , <i>Lacerta</i> cf. <i>viridis</i> <i>Podarcis</i> sp, <i>P. cf. muralis</i> cf. <i>Zootoca vivipara</i> <i>Zamenis</i> <i>longissimus</i> . <i>Vipera</i> cf. <i>berus</i>	<i>Lepus europaeus</i> , <i>Canis lupus</i> , <i>Vulpes vulpes</i> , <i>Ursus spelaeus</i> , <i>Panthera spelaea</i> , <i>Crocota spelaea</i> , <i>Equus ferus germanicus</i> , <i>Sus scrofa</i> , <i>Cervus elaphus</i> , <i>Bison priscus</i> , <i>Bos s. Bison</i> , <i>Capra ibex</i> , <i>Rupicapra rupicapra</i>	<i>Apodemus</i> ex gr. <i>sylvaticus-flavicollis</i> , <i>Microtus arvalis</i> & <i>agrestis</i> , <i>Microtus subterraneus</i> , <i>Sicista subtilis</i> , <i>Spalax leucodon</i> , <i>Spermophilus citelloides</i> , <i>Glis glis</i> , <i>Clethrionomys glareolus</i> , <i>Lagurus lagurus</i>
3	<i>Ranidae</i> indet. <i>Pelophylax/Rana</i> (os cruris)	<i>Anguis fragilis</i> Lacertidae <i>Podarcis</i> sp. / <i>Lacerta</i> sp. <i>Zamenis longissimus</i> <i>Coronella austriaca</i>	<i>Lepus europaeus</i> , <i>Canis lupus</i> , <i>Vulpes vulpes</i> , <i>Meles meles</i> , <i>Ursus spelaeus</i> , <i>Felis silvestris</i> , <i>Crocota spelaea</i> , <i>Coelodonta antiquitatis</i> , <i>Equus ferus germanicus</i> , <i>Megaloceros giganteus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i> , <i>Capreolus capreolus</i> , <i>Bison priscus</i> , <i>Bos s. Bison</i> , <i>Capra ibex</i> , <i>Rupicapra rupicapra</i>	<i>Apodemus</i> ex gr. <i>sylvaticus-flavicollis</i> , <i>Microtus arvalis</i> & <i>agrestis</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys glareolus</i> , <i>Lagurus lagurus</i> , <i>Spalax leucodon</i> , <i>Spermophilus citellus</i> , <i>Glis glis</i>
4	<i>Rana</i> cf. <i>temporaria</i> <i>Pelobates</i> sp.	<i>Anguis fragilis</i> Lacertidae indet. <i>Lacerta agilis</i> <i>Podarcis</i> sp. <i>Zamenis longissimus</i> <i>Coronella austriaca</i> <i>V. cf. ammodytes</i> <i>Vipera</i> cf. <i>berus</i> <i>Natrix</i> cf. <i>tessellata</i>	<i>Lepus europaeus</i> , <i>Canis lupus</i> , <i>Vulpes vulpes</i> , <i>Ursus spelaeus</i> , <i>Ursus arctos</i> , <i>Panthera spelaea</i> , <i>Felis silvestris</i> , <i>Crocota spelaea</i> , <i>Mammuthus</i> sp., <i>Coelodonta antiquitatis</i> , <i>Equus ferus germanicus</i> , <i>Equus hydruntinus</i> , <i>Sus scrofa</i> , <i>Megaloceros giganteus</i> , <i>Cervus elaphus</i> , <i>Dama dama</i> , <i>Capreolus capreolus</i> , <i>Bison priscus</i> , <i>Bos s. Bison</i> , <i>Capra ibex</i> , <i>Rupicapra rupicapra</i>	<i>Apodemus</i> ex gr. <i>sylvaticus-flavicollis</i> , <i>Microtus arvalis</i> – <i>agrestis</i> , <i>Arvicola mosbachensis/amphibius</i> , <i>Chionomys nivalis</i> , <i>Clethrionomys glareolus</i> , <i>Lagurus lagurus</i> , <i>Spalax leucodon</i> , <i>Spermophilus citellus</i> , <i>Glis glis</i> , <i>Microtus (Terricola) subterraneus</i> , <i>Muscardinus avellanarius</i> , <i>Castor fiber</i>

Table 1.3 – Faunal list recovered from the late Pleistocene site of Pešturina (east Serbia)

1.4 SMOLUĆKA CAVE (southwest Serbia)

Smolućka Cave is located about 15 kilometers northeast of the town of Tutin, in the area of the village of Crkvine in south-eastern Serbia (Figure 1.1). The entrance to the cave is at an altitude of 945 meters above sea level and is located at the end of a small canyon cut through Triassic limestones by the Smolućka river (Kaluđerović, 1985, 1986, 1987, 1993). Mountains are the dominant form of landscape, and by their origin and geological composition, they are associated with the Dinaric Alps. The landscape of the region is characterized by plateaus, hills, numerous mountain areas, gorges, valleys, sinkholes, caves, and rivers with a several of smaller tributaries. Plainland is rare.

The region where the cave is located has a humid continental climate typical of the hilly Raška region. It is generally among the coolest regions in Serbia. The mean annual temperature is 8.9°C. Winters are usually very cold due to altitude (900 - 1200 m above sea level). The lowest average temperatures in the year occur in January when it is around -1.7°C. The warmest month of the year is August, with an average temperature of 18.4°C. The driest month is August, with 66 mm of rainfall. The highest amount of precipitation occurs in November, with an average of 100 mm (<https://en.climate-data.org/europe/serbia/crkvine/crkvine-274272/>).

The abundant amount of rainfall creates favorable conditions for hydrophilic vegetation. Today about one-third of the area is covered with forest. In addition to forest vegetation,

meadow-pasture vegetation is pronounced with fragrant grass and white clover on pastures. This nature of floristic habitats are characteristic for lower altitude, and *Nardetum stricta* (60%), *Festuca rubra falax*, *Poa alpina*, *Plantago carinata* and others are characteristic of higher mountain meadows and pastures.

Presently, the area is inhabited by a great variety of small vertebrate species. During the summer months, a permanent and inexhaustible spring appears at the bottom of the canyon just below the cave, creating a permanent water source and habitat for “water-edge” species (*Natrix natrix*, *Natrix tessellata*, *Bombina variegata*, *Rana dalmatina*, *Rana temporaria*, and *Pelophylax ridibundus*) (Figure 1.8). A rocky soil is not extensively distributed but on occasional bare rocks there are microhabitats suitable for reptiles that endure dry rocky conditions (*Lacerta viridis*, *Coronella austriaca*, *Podarcis muralis*, and *Vipera ammodytes*) (Figure 1.8). Other small vertebrate species that can be found in the area are: *Hyla arborea*, *Bufo bufo*, *Bufo viridis*, *Salamandra salamandra*, *Lacerta agilis*, *Zamenis longissimus*, *Vipera berus*, *Sorex minutus*, *Sorex araneus*, *Talpa europaea*, *Myodes glareolus* (formerly *Clethrionomys glareolus*), *Arvicola amphibius*, *Microtus subterraneus*, *Spalax leucodon*, *Microtus arvalis*, *Apodemus flavicollis*, *Apodemus sylvaticus*, *Glis glis*, and *Muscardinus avellanarius*.

From 1984 to 1987, the Archeological Institute of Belgrade organized excavations in Smolučka cave (Kaluderović 1985, 1986, 1987, 1993). The site yielded over 200 Middle Paleolithic artifacts that were found in the Pleistocene layers. Unfortunately most of them are not preserved until today, yet some descriptions can be found in publications (Kaluderović 1985, 1986, 1987, 1993; Šarić 2013). Numerous small vertebrate remains are described in a number of papers. Descriptions of the rodents from the late Pleistocene of Smolučka cave have been done in a preliminary publication (Dimitrijević 1991), and then completed in an unpublished Ph.D. dissertation (Bogićević 2008). A list of herpetofaunal remains is published

(Paunović and Dimitrijević 1990). Unfortunately, this publication features uncompleted stratigraphical distribution of the remains, and the material has since been lost. Nevertheless, the results are shown in Table 1.4.

The position of the cave could have been attractive to the Middle Paleolithic people. 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, which must have surrounded the cave also during Middle Paleolithic, were certainly a genuine blessing and enormous importance in the process of choosing the habitation location (Šarić 2013).

Late Pleistocene small vertebrates, sharing habitats with humans

It has long been proven that the Balkans was inhabited by different hominin species in the past. Neanderthals have been confirmed as descendants of Western European Middle Pleistocene hominins who spread northwards and eastwards in a pulsing fashion dictated by

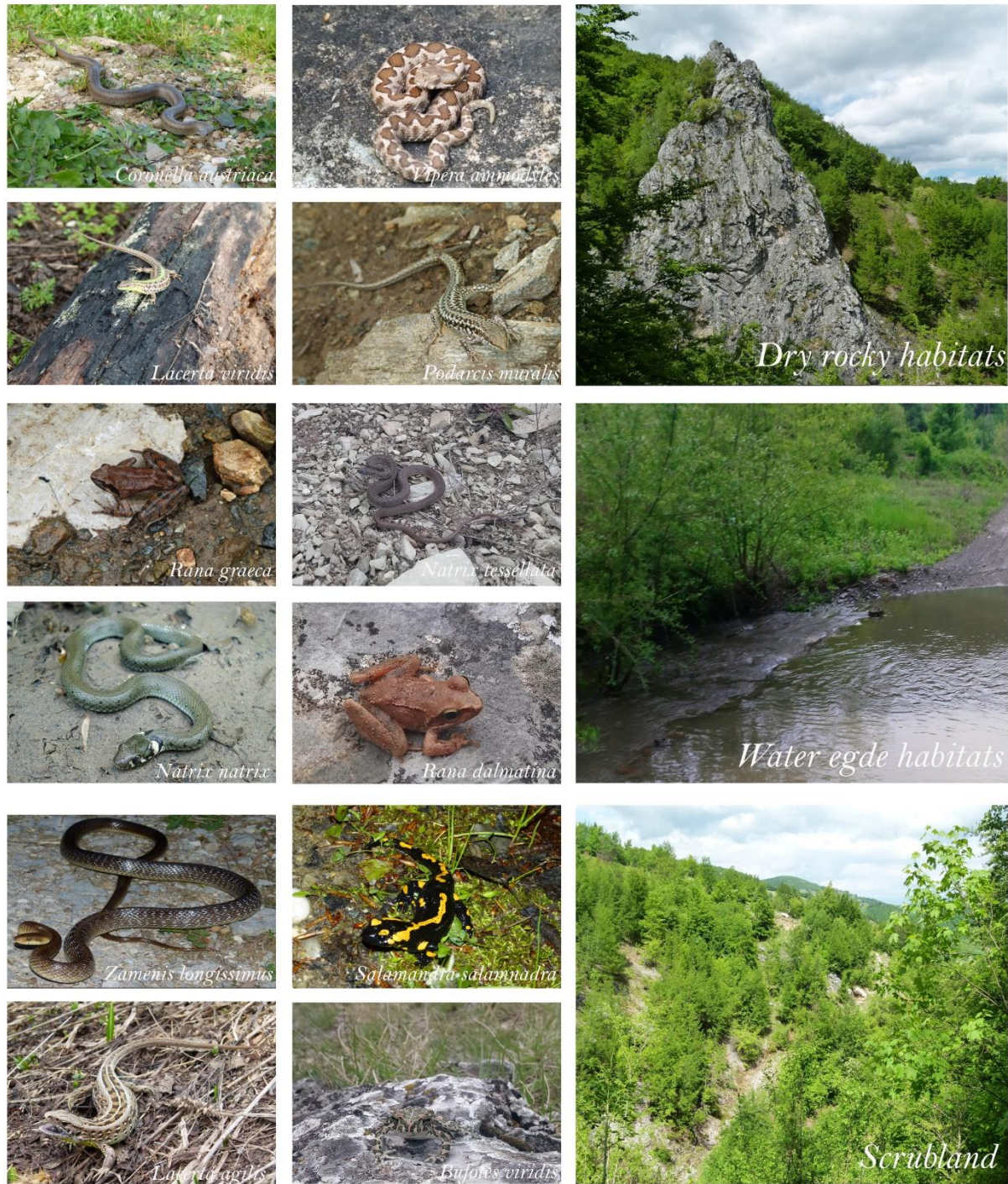


Figure 1.8 – Natural habitats in the vicinity of Smolučka cave and associated herpetofauna.

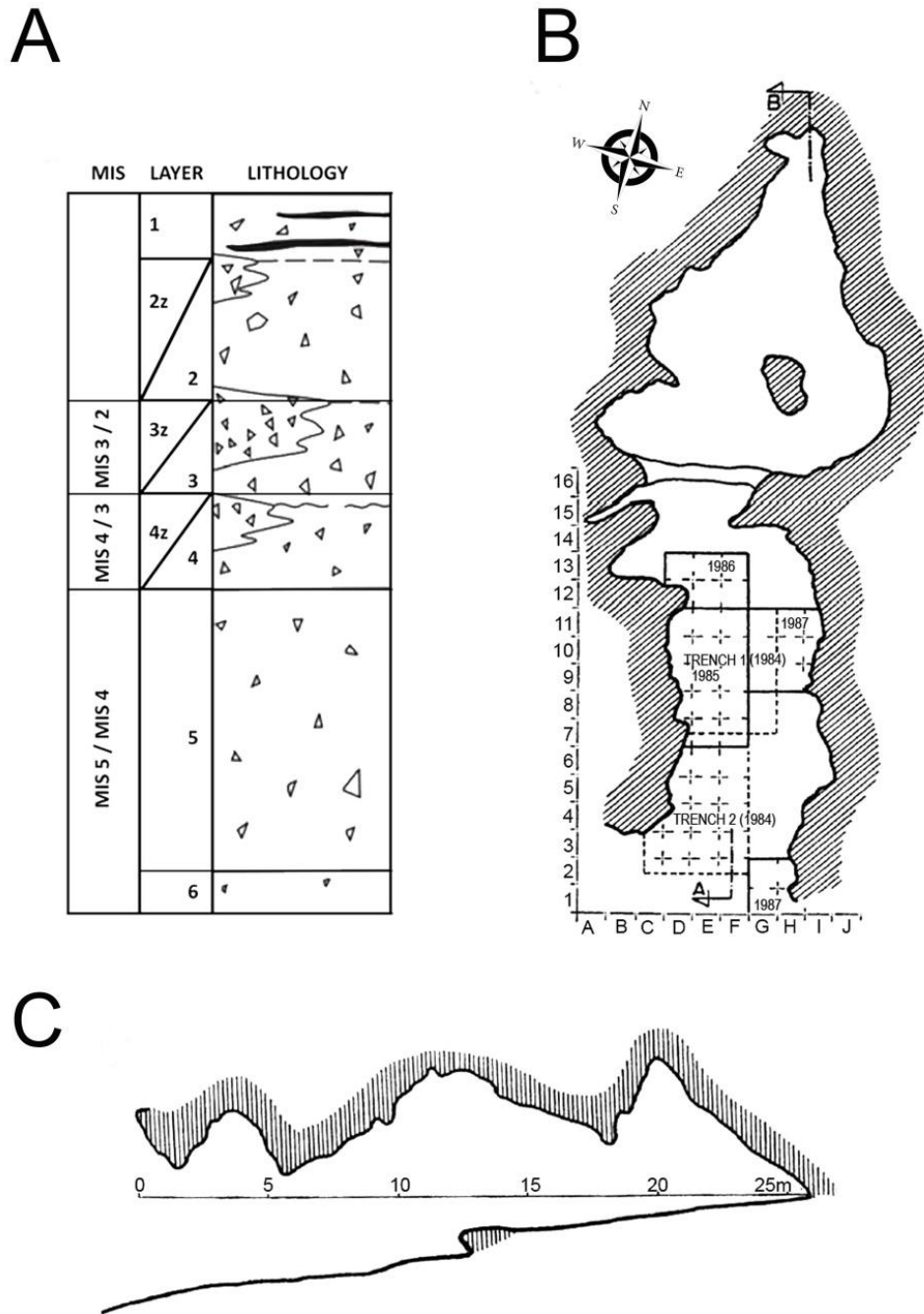


Figure 1.9 – Map of the excavation sectors and trenches inside the cave; A-C; A: Stratigraphical profile from trench 1 (1985 excavation), adapted after Dimitrijević (1991) and Kaluđerović (1985). Layer 1 - light brown clay with remains of pottery and domestic animals; Layer 2 - light brown to brown clay with scraps, remains of pottery and domestic animals; Layer 2z - light brown clay with many fragments but without fossils; Layer 3 - brown to dark brown clay with Paleolithic artifacts; Layer 3z - brown clay with a lot of scraps; Layer 4 - gray-greenish clay with fine debris and Paleolithic artifacts; Layer 4z - reddish-brown clay with a lot of scraps; Layer 5 - dark brown to black clay with fine debris and Paleolithic artifacts; Layer 6 - yellow clay with small fragments and Paleolithic artifacts. B: Ground plan. C: Longitudinal selection. (modified from Kaluđerović 1985).

Layer	AMPHIBIA	REPTILIA	MAMMALIA	MICROMAMMALIA
3z	<i>Rana temporaria</i> , <i>Rana arvalis</i> , <i>Rana esculenta</i> , <i>Bombina variegata</i> , <i>Pelobates fuscus</i> , <i>Salamandra salamandra</i> , <i>Bufo bufo</i> , <i>Bufo viridis</i> , <i>Hyla arborea</i> ,	<i>Anguis fragilis</i> , <i>Pseudopus panonicus</i> , <i>Lacerta agilis</i> , <i>Lacerta viridis</i> , <i>Zamenis longissimu</i> , <i>Coronella austriaca</i> , <i>Natrix natrix</i> , <i>Vipera berus</i> , <i>Vipera ammodytes</i>	<i>Vulpes vulpes</i> , <i>Ursus spelaeus</i> , <i>Rupicapra rupicapra</i>	<i>Sorex araneus</i> , <i>Talpa europaea</i> , <i>Spermophilus citelloides</i> , <i>Muscardinus avellanarius</i> , <i>Dryomys nitedula</i> , <i>Sicista subtilis</i> , <i>Spalax leucodon</i> , <i>Apodemus sylvaticus</i> , <i>Cricetulus migratorius</i> , <i>Mesocricetus newtoni</i> , <i>Clethrionomys glareolus</i> , <i>Arvicola terrestris</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Chionomys nivalis</i> , <i>Ochotona pusilla</i>
3			<i>Canis lupus</i> , <i>Ursus spelaeus</i> , <i>Crocota crocuta spelaea</i> , <i>Panthera pardus</i> , <i>Capra ibex</i>	<i>Spalax leucodon</i> , <i>Cricetulus migratorius</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Chionomys nivalis</i> , <i>Ochotona pusilla</i>
4			<i>Canis lupus</i> , <i>Vulpes vulpes</i> , <i>Ursus spelaeus</i> , <i>Mustela ermine</i> , <i>Meles meles</i> , <i>Cervus elaphus</i> , <i>Capra ibex</i>	<i>Sicista subtilis</i> , <i>Apodemus sylvaticus</i> , <i>Mesocricetus newtoni</i> , <i>Clethrionomys glareolus</i> , <i>Arvicola terrestris</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Chionomys nivalis</i> , <i>Ochotona pusilla</i>
5			<i>Vulpes vulpes</i> , <i>Ursus spelaeus</i> , <i>Cervus elaphus</i> , <i>Bison</i> , <i>Rupicapra rupicapra</i> , <i>Capra ibex</i>	<i>Spermophilus citelloides</i> , <i>Hystrix sp.</i> , <i>Spalax leucodon?</i> , <i>Microtus subterraneus</i> , <i>Microtus arvalis/agrestis</i> , <i>Chionomys nivalis</i> , <i>Ochotona pusilla</i>
6			<i>Ursus spelaeus</i> , <i>Mustela erminea</i> , <i>Rupicapra rupicapra</i> ,	<i>Sorex minutus</i> , <i>Spermophilus citelloides</i> , <i>Myoxus glis</i> , <i>Arvicola terrestris</i> , <i>Microtus arvalis/agrestis</i> , <i>Ochotona pusilla</i>

Table 1.4 – Faunal list recovered from the late Pleistocene site of Smolučka cave (southwest Serbia).

retreating glaciers (Dennell et al. 2011). Since there were no significant geographic barriers between the Balkans during either glacial or interglacial times, the Pleistocene population could have had reduced isolation from South West Asian populations and they could be examined as a single geographic entity (Roksandic et al. 2018). The Middle Pleistocene fossil record plays a crucial role in understanding later human evolution, as well as changes in the behavioral repertoire (Ruff et al. 1997, Roebroeks 2001, Rightmire 2004, 2013). The only documented Middle Pleistocene hominin fossil from Serbia is the BH-1 mandible from the Middle Pleistocene cave of Mala Balanica (Roksandic et al. 2011, Skinner et al. 2016). This finding suggested an interesting possibility that human populations in this part of the continent were not subject to the process of Neanderthalization observed in the west (Roksandic et al. 2018).

The climate in the middle Pleistocene on the territory of Serbia has been studied through exploration of loess sediments, mostly on the territory of Vojvodina (e.g. Marković 2000, 2001, Marković et al. 2003, 2004, 2005, 2006), but have not been properly connected with the central Balkans as small vertebrate studies of the middle Pleistocene are not very common, but are currently in progress through the processing of Mala Balanica sediments at the Paleontological Laboratory in the Faculty of Mining and Geology (Belgrade, Serbia).

Between 52-3 kya, modern humans colonized Europe. The Balkan Peninsula, with river valleys used as migratory routes for humans and other animals in prehistoric as well as historical times, represents the most direct corridor between Asia Minor and Europe. This route was no doubt of extreme importance for Paleolithic migrations (Mihailović 2009, Dennell et al. 2011). It can be assumed that Middle Paleolithic industries were made by

Neanderthals and the Early Upper Paleolithic industries were made by modern humans. Although the sites experienced considerable stratigraphic mixing, the dates of human-modified indicate that humans were present in the Balkan Peninsula at some point between 52-39 kcalBP and 34-28 kcalBP. It is most likely that Middle Paleolithic peoples were present between 52-39 kcalBP and Gravettian people between 34-28 kcalBP. Considering the full chronology of the Balkans and adjacent areas, it appears that, transitional Early Upper Paleolithic industries occurred between 45-40 kcalBP, but in distinct geographic zones. Upper Paleolithic modern humans spread into Europe along both the Danube Corridor and Mediterranean coast (Conard and Bolus 2003, Mellars 2006a), while Middle Paleolithic Neanderthals could persisted in the central/western mountains (Bar-Yosef 2011). The interrelatedness of these biological and cultural processes is greatly debated (Mellars et al. 2007, Bar-Yosef 2002). Genetic evidence shows that Neanderthals and modern humans likely interbred between 60-50 ka in Southwest Asia (Fu et al. 2014) and ~40 ka in Europe (Fu et al. 2015). By 30,000 years ago, only Anatomically Modern Humans, or *Homo sapiens*, were extant (Alex 2016).

Archeological units, variably referred to as industries, traditions, or technocomplexes, are defined based on assemblages of distinct and frequently associated technologies and artifact types. When an archeological unit is found in association with human remains of a particular type, it is often assumed that wherever that archeological unit is found, that particular human type was once present. In this way the Mousterian has long stood as a proxy for European Neanderthals (Higham et al. 2014, Bordes 1961). The Aurignacian technocomplex, widespread throughout Europe after 35 ka, is traditionally seen as the first fully Upper Paleolithic tradition produced by European modern humans (Hublin 2015, Mellars 2006b). In the broadest sense, Aurignacian assemblages have shared features of systematic production of

blade and bladelets, bone and antler tools, and diverse personal ornaments (Teyssandier 2008, Bar-Yosef and Zilhão 2006). The Gravettian is a European Upper Paleolithic technocomplex characterized by distinctive backed blades/bladelets, diverse organic artifacts, and extensive use of symbolic objects including ornaments and figurines, which exhibit strong stylistic similarities across Europe (Svoboda 2012). It has been proposed that the Gravettian arose in Danubian Central Europe, from Protoaurignacian traditions in the Mediterranean, or from other backed-blade traditions outside of Europe, such as the Ahmarian (Kozłowski 2015, Svoboda 2012). Gravettian traditions appeared widely across Europe by 30 ka (Talamo et al. 2014) and have been found with modern human skeletal remains (Trinkaus et al. 2000).

It has long been argued about the causes of Neanderthal extinction. Possibilities include: violence from encountering anatomically modern humans (e.g., Hortolà and Martínez-Navarro, 2013), pathogens or parasites spread from anatomically modern humans (e.g., Greenbaum et al. 2019), slight competitive advantage on the part of modern humans (e.g., Wynn et al. 2016), interbreeding and hybridization with early modern humans (e.g., Dan 2007), and most importantly for the topic of this thesis, climate change or a natural catastrophe. This topic will briefly be resumed in chapter III.

2. DESCRIPTION OF THE OVERALL AIMS

This work is focusing on reconstructing climate and environments of the past. Using small vertebrates as a proxy, the postulate is that all animals in the past lived in their natural environments, also known as habitats. Some of the species we find in the fossil record went extinct, however high percentage of late Pleistocene small vertebrates survive until today. Therefore we know about their climate and habitat preferences, and consequently we use them as a proxy for reconstructing paleoclimate and paleoenvironments.

In order to do the paleoclimatic and paleoenvironmental reconstructions properly, it was necessary to appropriately prioritize the objectives. The final goal is to create a picture as clear as possible about the conditions in which the Neanderthals lived in the Balkans, from the time when they thrived to the time they disappeared. I have chosen this time period because it represents an important milestone in human history, and Serbian late Pleistocene sites have provided good data for reconstructions of paleoclimate and paleoenvironment. Chronologically this time period covers approximately 100 thousand years from 120 kya to 20 kya. Other objectives derived from the main goal as a necessity or a logical precursor for accomplishing the main objective.

In order to achieve the aims of this thesis, I organize chronologically a plan of action consisting of:

- (1) to perform as complete as possible bibliographical review of the study about Pleistocene small-vertebrates in Serbia
- (2) to try to visit as much sites as possible in order to document their exact location, and surrounding landscape and fauna;
- (3) to participate in ongoing archeological excavations in Serbia and abroad in order to increase the amount of small-vertebrate remains available for this study;

(4) to learn the different existing paleoclimatic and paleoenvironmental reconstruction methods and apply them to the Serbian small-vertebrate record.

2.1 Multidisciplinary bibliographical review

This thesis is a multidisciplinary study based in the field on modern paleontology and archeology, but introducing more studies necessary to produce a more complete picture in paleoenvironmental and paleoclimatic reconstructions. In this work all relevant publications of late Pleistocene small vertebrate remains will be considered as sources for providing data in the context of this research. Scientific publications from the field of archeology will be reviewed for chronological context of small vertebrates recovered from the archeological sites. Older publications are in process of digitalization and if digitized can be found on the internet, but in some cases it will be necessary to search for them in university libraries as well as researchers' personal libraries. There are three main libraries containing publications of interest: the Library at the Archeological faculty, the Library at the Paleontological department in the Faculty of Mining and Geology, and The Belgrade University Library Svetozar Marković. In addition, various other data from different studies will be considered, such as present climate, ecology, faunal studies, geology, geography, botany, palynology, loess sediments studies, and others.

2.2 Field research

Then, taking into account all the information recovered during the bibliographical review, it will be necessary to conduct a field research in order to gather more information, personally experiencing the aspects described in various literature (Figure 2.1).

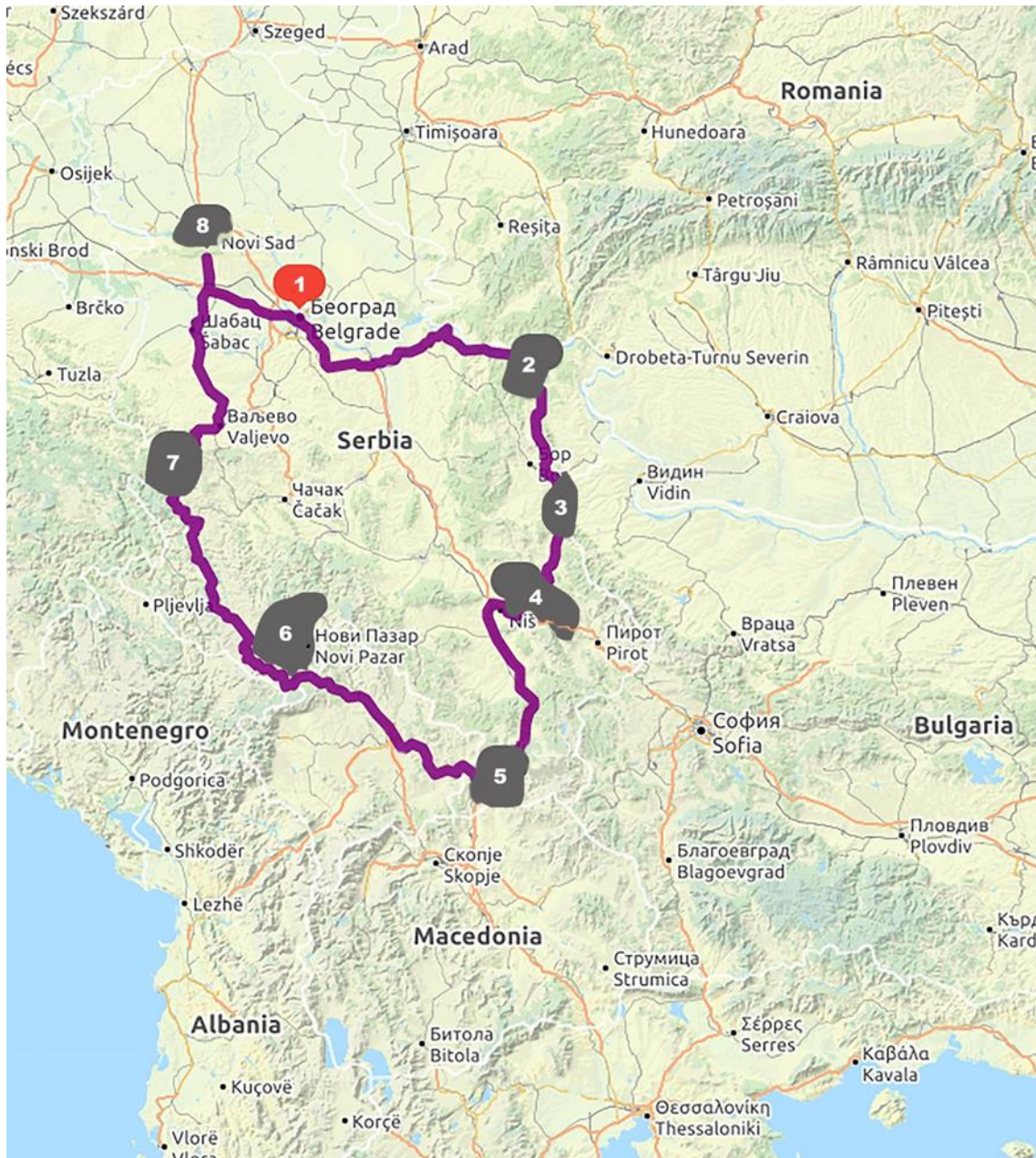


Figure 2.1 – Field research map of areas and distance covered: 1 Starting point – Belgrade – trip planning, searching for herpetofauna at the Avala mountain; 2 - Đerdap gorge – searching for herpetofauna; 3 - East Serbia - documenting the environment and associated herpetofauna around Baranica cave and herpetofaunal hotspots; 4 Southeast Serbia - documenting the environment and associated herpetofauna around Pešturina, Mala Balanica and Velika Balanica; 5 - South Serbia (Pčinja river valley) - documenting the environment and associated herpetofauna; 6 - Southwest Serbia - documenting the environment and associated herpetofauna around Hadži Prodanova and Smolučka caves; 7 - National park Tara - searching for herpetofauna; 8 - Fruška Gora National Park - searching for herpetofauna.

I plan to conduct a field research with some other colleagues visiting the studied sites, six caves: Baranica, Hadži Prodanova, Pešturina, Velika Balanica and Mala Balanica; and five locations considered to be faunal hotspots (Đerdap gorge, Pčinja river valley, National park Tara, Fruška Gora National Park and Avala mountain). The main focus is on understanding the karstic morphology (especially entrance) and how it can affect the archeological and faunal content recovered in this caves and if possible having access to the stratigraphical sections, documenting surrounding landscapes in the vicinity of the caves, and implement an actualistic herpetological field approach.

2.3 Ongoing excavations

At the present time the ongoing Paleolithic excavations of interest in the Serbian archeological sites are Pešturina, Mala Balanica, and Velika Balanica. These three sites are in very close proximity to each other. Pešturina has been excavated for the long time and the most persistent. Therefore the sediments have already been dry-sieved, washed, and sorted to a certain extend.

After learning the different methodologies on sieving-washing archeological sediments in two very different contexts (karstic and lacustrine) in excavations leaded by my host institution IPHES, my aim is to join the Velika and Mala Balanica teams in order to help with the sieving and sorting of the small vertebrates as the late Pleistocene caves of Velika and Mala Balanica, are available for being included in my thesis. For more than a decade these two caves provided tons of sediments that were transported and stored in the Archeological faculty in Belgrade.

2.4 Paleoenvironmental and paleoclimatic reconstructions based on small vertebrates

A number of methods for reconstructing paleoclimate and paleoenvironment have already been applied on the small vertebrate assemblage from Serbian sites. Most commonly they are: Minimum number of individuals, Habitat types (Popov, 1994), and Taxonomical habitat indexes (Evans et al., 1981). These methods are usable only for small mammal remains, since they are not adapted for the use on herpetofauna.

The aim is to revisit these reconstructions, reevaluate the methods and introduce new methods that have been developed, such as: Bioclimatic analysis (Hernández-Fernández, 2001a, b; Hernández-Fernández and Peláez-Campomanes, 2005; and Hernández-Fernández et al., 2007), Mutual Ecogeographic Range (Blain et al., 2009, 2016) and Habitat weightings (Blain et al., 2008).

Depending on results of already established methods the aim should be to improve them, adapt them for use in Balkan peninsula and possibly create a new, relatively easy and reliable method for reconstructing paleoenvironments all across Europe. When all the work will be done the result should be an ecological list of all the species of modern herpetofauna showing their habitat preferences, area and age that can be applicable for paleoenvironmental reconstructions, and broadly available.

3. Pleistocene herpetofaunal studies in Serbia (Balkan Peninsula, SE Europe): state of the art and perspectives

3.1 Introduction

Serbia is located in south-eastern Europe on the southern Pannonian Plain and in the centre of the Balkan Peninsula. Northern Serbia comprises the southern part of the Pannonian Basin, formed after the retreat of the Pannonian Sea (Paratethys) during the Miocene, with rich, fertile plains and dominated by the Danube River. In central Serbia, the relief includes hills, with low and medium-high mountains interspersed with numerous rivers and creeks. Eastern Serbia is dominated by the limestone ranges of the Balkan Mountain range and the Serbian Carpathians, while in the west, the mountains become gradually higher towards the southwest, but do not form real ridges.

During the Miocene, the Balkan Peninsula was subjected to strong tectonic activity which resulted in the formation of two main mountain ranges, the Carpatho-Balkan belt in the east, and the Dinaric Alps in the west (Figure 3.1). The relief of this newly formed terrain, with high mountains and natural barriers, often enabled autochthonous species to find refuge in isolated areas, preventing their extinction.

The remarkable biodiversity of the Balkan Peninsula has long been recognised (Simroth, 1907; Gaston and David, 1994; Džukić and Kalezić, 2004). The retreat of Paratethys resulted in a large plain that allowed species from the Eastern European plains to migrate south and

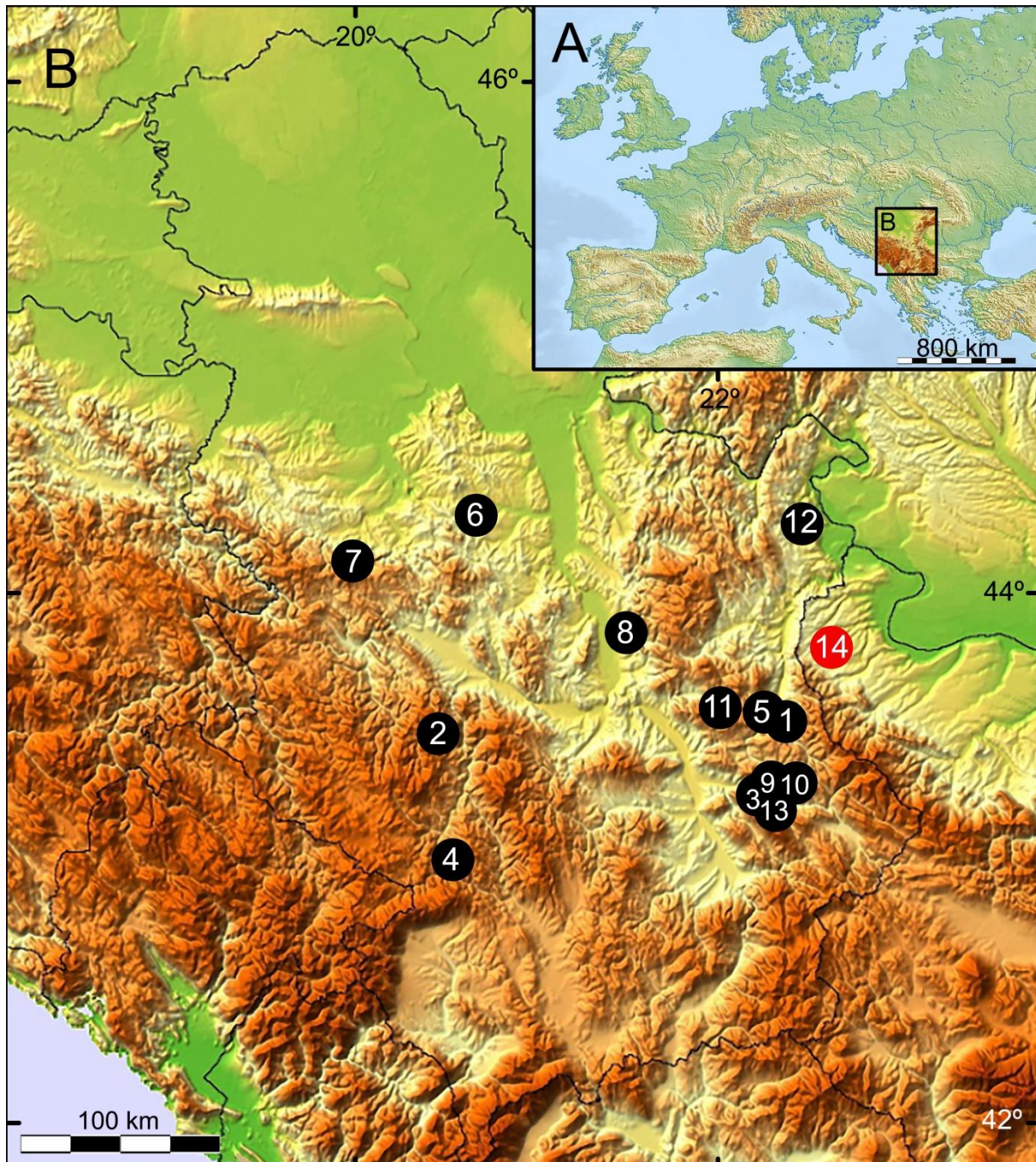


Figure 3.1 – Geographical location of the small vertebrate bearing localities in Serbia and Bulgaria used in this study. 1, Baranica cave; 2, Hadži Prodanova cave; 3, Pešturina cave; 4, Smolučka cave; 5, Vasiljska cave; 6, Venčac; 7, Petnička cave; 8, Miralovska cave; 9, Velika Balanica cave; 10, Mala Balanica cave; 11, Peručki rock; 12, Canetova cave; 13, Vrelska cave; 14, Magura cave (Bulgaria).

populate the Balkans, contributing to the richness and diversity of the Balkan fauna. Fossil evidence documenting faunal mixing during the Miocene is scarce, although it is widely accepted that some of the species currently living in Serbia migrated to the Balkan Peninsula during that period. It would be very difficult to confidently identify all the species that made this migration, as the fossil records are incomplete. During the Pleistocene, the Balkan Peninsula was not as isolated by mountain barriers from the European mainland, unlike the Iberian and Apennine peninsulas. This resulted in an open space for migration in front of the ice sheet (Džukić and Kalezić, 2004). The importance of the Balkan peninsula as a refugium during the Pleistocene has been confirmed by molecular and phylogenetic analyses. (Hewitt, 1999; 2001). The results show that the genomes of Balkans species are much more dominant in modern central and northern European fauna than those of the Iberian and Apennine peninsulas (Hewitt, 2004). This is, generally, the consequence of rapid colonisation from Balkan refugia during the last post glacial warming period (Hewitt, 2000; 2004).

Serbia's position in the central part of the Balkan Peninsula has contributed to the diversity of its herpetofauna. A significant number of endemic and relict taxa are observed, in addition to marginality and distribution fragmentation (Džukić and Kalezić, 2004; Tomović et al., 2014; Vukov et al., 2013). The list of amphibians in Serbia includes 21 native species: eight species from the Caudata clade, and 13 species from the order Anura (Vukov et al., 2013). This species diversity ranks Serbia second among the Balkan countries, just behind Greece, which has 22 native amphibian species (Valakos et al., 2008). There are also 24 species of native reptile in Serbia: three chelonians, 11 lizards, and 10 snakes (Tomović et al., 2014). The Balkan biodiversity is still inadequately understood and is characterised by outstanding levels of endemism, particularly in caves and ancient lakes. Positioned at the crossroads of Europe

and Asia, this region is also renowned as a focus of Pleistocene glacial refugia (Griffiths et al., 2004).

In Serbia, caves are usually formed in the plentiful Mesozoic limestone of the Carpatho-Balkan mountain belt in the east, and the Dinaric Alps in the west (Figure 3.2). Cave deposits usually date from the Pleistocene to Holocene, and, when properly interpreted, are a valuable source of information about the conditions in the area (Table 3.1). Caves in the same zone are usually in close proximity to one another (see Figure 3.1).

The aim of this paper is to present a review of herpetofaunal findings in Serbia, and analyse the collected data. Taken alone, this information is often insufficient for paleoreconstructions, so we also introduced small mammal data to help in the interpretation of the herpetofaunal assemblages.

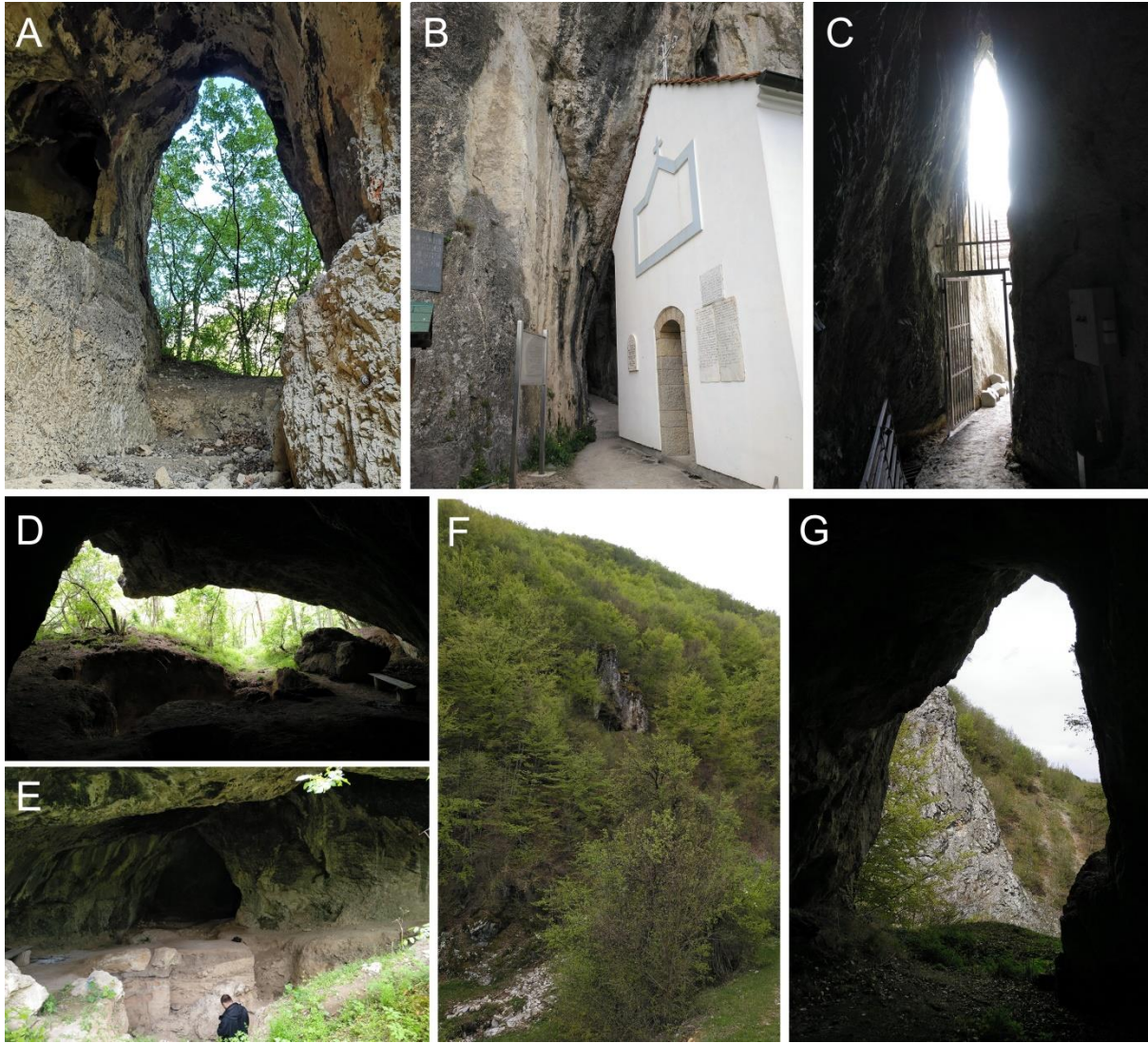


Figure 3.2 – Views of some Serbian caves that have produced the small vertebrate remains included in this study. A, Baranica; B-C, Hadži Prodanova; D-E, Pešturina; and F-G, Smolučka. On picture B, the entrance of the cave is visible behind the early 20th century Church (*St. Archangel Michael*) that once stood right in front of the cave's entrance. On picture F, the entrance of Smolučka cave is visible in the middle of the woodlands. Credits: J.F. Bisbal-Chinesta (A); H.-A. Blain (B-G).

Sites	Geographical affiliation	Datings	Small vertebrates	Large vertebrates	Archeological artefacts
1. Baranica	Carpato-Balkan mountain range	Yes	Yes	Yes	Yes
2. Hadži Prodanova cave	Dinarids mountain range	Yes	Yes	Yes	Yes
3. Pešturina	Carpato-Balkan mountain range	Yes	Yes	Yes	Yes
4. Smolučka	Dinarids mountain range	Yes	Yes	Yes	Yes
5. Vasiljska cave	Carpato-Balkan mountain range	No	Yes	Yes	No data
6. Venčac	Dinarids mountain range	No	Yes	Yes	No
7. Petnička cave	Dinarids mountain range	No data	Yes	Yes	
8. Mirilovska cave	Carpato-Balkan mountain range	No	Yes	Yes	Yes
9. Velika Balanica	Carpato-Balkan mountain range	Yes	Yes	Yes	Yes
10. Mala Balanica	Carpato-Balkan mountain range	Yes	Yes	Yes	Yes
11. Peručki kamen	Carpato-Balkan mountain range	No	Yes	Yes	Yes
12. Canetova cave	Carpato-Balkan mountain range	No	Yes	Yes	No data
13. Vrelska cave	Carpato-Balkan mountain range	No	Yes	Yes	No

Table 3.1 – Basic information on small-vertebrate bearing archeological sites in Serbia.

3.2 Material and methods

3.2.1 Bibliographical research on small vertebrates

It was important to systematise the extent of small vertebrate studies (mainly on amphibians, reptiles, and rodents) in Serbia. To do this we undertook a literature review of herpetofaunal and small mammal findings in Serbia, and later analysed the collected data. The literature search included all the relevant scientific journals, carried out in the two main libraries in the Faculty of Mining and Geology in Belgrade as well as researchers' personal libraries, in addition to using the major internet search engines (primarily Google and Bing). Oral and written communication with Serbian researchers in the field of archaeology and archaeozoology, ecology, paleontology, and geology also comprised an important part of the review.

3.2.2 Statistical analyses of the herpetofaunal fossil record in Serbia

Hierarchical clustering was selected for the statistical analysis, as this generates a dendrogram that reveals the similarity and difference relationships between the associations of species concurring in the archaeopaleontological levels included in the data matrix. The aim was to investigate whether the resulting herpetofaunal groups are based on chronostratigraphic criteria whose origins are related to possible diachronic biogeographical changes. In addition, the Jaccard similarity index was applied, since this is recommended for clustering binary data as it gives more importance to joint concurrences in the assemblages (Hammer et al., 2001). Also, the “unweighted pair-group average” was applied to the data matrix, resulting in the grouping in the dendrogram, with different groups created based on

the average distances between members. Correspondence Analysis (CA) was used to support the results of the hierarchical clustering. CA is the recommended method for comparing associations (assigned to columns) with the total count of taxa, or identifying taxa (assigned to rows) through associations (Greenacre, 2010). The aim of this part of the research was to define the proximity relationships between taxa from different associations, grouping them closely, in contrast to more atypical taxa, which appear in an eccentric position in relation to the rest of the set. The paleontological statistics program (PAST3) was used for all the statistical approaches (Hammer et al., 2001).

3.2.3 Paleoenvironmental and paleoclimatic quantitative reconstructions applied to the small mammal fossil record from Serbia

To interpret the analyses of amphibian and reptile data, due to the scarcity of both the fauna itself and amphibian and reptile studies, it was not possible to use quantitative methods. Several methods were applied to the corresponding small-mammal assemblages to reconstruct environments and climate, as a complementary proxy to help interpret the herpetofaunal assemblages.

In this research, only one rodent species, *Spermophilus* cf. *citelloides*, has become extinct (Kowalski, 2001). Some species no longer live in in Serbia (*Cricetus cricetus*, *Mesocricetus newtoni*, *Cricetulus migratorius*, *Lagurus lagurus*, *Dicrostonyx* sp., and *Hystrix* sp.) but they are still present in other parts of the world. Consequently, the modern ecology of these extant species can be used to extrapolate paleoenvironmental and paleoclimatic conditions.

3.2.3.1 Habitat types

Every small mammal species has different environmental requirements. The species can therefore be divided into ecological groups of similar recent ecological preferences. This method use the current distribution of the 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, 1994).

For this purpose, and in accordance with the primary objective of this research, the rodents have been divided into five groups, according to their main habitat preferences (Bogićević, 2008):

A – Woodland species (*Clethrionomys glareolus*, *Apodemus* ex gr. *sylvaticus-flavicollis*, *Dryomys nitedula*, *Muscardinus avellanarius*)

B – Species inhabiting moist meadows (*Arvicola amphibius*, *Microtus subterraneus*, *Microtus agrestis*)

C – Mountain inhabitants and petrophilous species (*Chionomys nivalis*)

D – Xero-mesophilous species (*Spermophilus* cf. *citelloides*, *Mesocricetus newtoni*, *Microtus arvalis*, *Spalax leucodon*)

E – Steppe and semi-arid species (*Sicista subtilis*, *Cricetulus migratorius*, *Cricetus*, *Microtus gregalis*, *Lagurus lagurus*)

3.2.3.2 Taxonomic habitat index

This method was introduced by Evans et al. (1981). It recognises that not all species live in just one type of environment, and that a species lives in different biotopes but has a preferred habitat. This method is used to assess habitat preferences. This is the so-called taxonomic habitat index (THI; Evans et al., 1981), which takes into account the fact that the vast majority of mammal species inhabit several biotopes. The affinity for a particular kind of habitat is expressed as a number from 0 to 1 (0 if it never lives in the mentioned habitat; 1 if it lives exclusively in that habitat). This method provides relatively precise data, since the distribution of small mammals in nature is complex and it is hard to assign a single habitat type to each species. For example, although many species of small mammals tend to live in coniferous (boreal) forest, none of them is considered an indicator of that habitat, for which reason coniferous forests remain “hidden” in environmental analyses (Andrews, 1990).

Information on small mammal distribution preferences is taken from Andrews (1990) and adopted in accordance with the objectives of this research. The indexes used for calculating the presence of paleohabitats are presented in Table 3.2.

3.2.3.3 Bioclimatic analysis

The bioclimatic model postulates that there is significant correlation between the climate and mammal communities. According to Hernández-Fernández (2001a, b), Hernández-Fernández and Peláez-Campomanes (2005), and Hernández-Fernández et al. (2007), any mammal assemblages can be included within ten climate types, which can be distributed using the Climatic Restriction Index ($CRI_i = 1/n$, where “n” is the number of climate zones where the

Species/distribution	PES/L 4	PES/L 3	PES/L 2	Tu	B	D	M	S	FS	A	Tr	Mo
<i>Apodemus ex gr. sylvaticus-flavicollis</i>	+	+	+	0	0	2	2	2	2	2	0	0
<i>Arvicola mosbachensis/amphibius</i>	+	-	-	2	3	2	0.5	1	1	0	0	0.5
<i>Chionomys nivalis</i>	+	+	-	0	0	0	0	1.5	0.5	0	0	8
<i>Clethrionomys glareolus</i>	+	+	+	0	4	4	0	0	1	0	0	1
<i>Lagurus lagurus</i>	+	+	+	0	0	0	0	6	1.5	1	0	1.5
<i>Microtus arvalis-agrestis</i>	+	+	+	0.5	1	1.5	0.7	1.3	0.8	1.4	0.1	2.7
<i>Microtus (Terricola) subterraneus</i>	+	-	+	0	0	1.5	2.3	2	0	0.5	0	3.7
<i>Muscardinus avellanarius</i>	+	-	-	0	0	7	3	0	0	0	0	0
<i>Sicista subtilis</i>	-	-	+	0	0	0	0	7	2	0.5	0	0.5
<i>Spalax leucodon</i>	+	+	+	0	0.5	1	0	7	1	0	0	0.5
<i>Spermophilus citelloides</i>	+	+	+	0	0	0	0	9	1	0	0	0
<i>Glis glis</i>	+	+	+	0.5	0.5	6	1	0.5	1	0	0	0.5

Table 3.2 – Indexes used for calculating the presence of paleohabitats in the layers in Pešturina cave. Indexes for species: *Apodemus ex gr. sylvaticus-flavicollis*, *Arvicola mosbachensis/amphibius*, *Microtus arvalis* and *M. agrestis*, *Microtus (Terricola) subterraneus*, and *Muscardinus avellanarius* are adapted from Andrews (1990). Indexes for species: *Chionomys nivalis*, *Lagurus*, *Sicista subtilis*, *Spalax leucodon*, *Spermophilus citelloides*, and *Glis glis* 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 is represented and “i” is the climate 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 climate group, the bioclimatic component (BC; representation by level of each of the available climates) can be calculated using the following formula:

$$BC_i = (\sum CRI_i) \times 100/S,$$

where S is the number of species per unit. From the BC, a mathematical model has been elaborated using a multiple linear regression (Hernández-Fernandez and Peláez-Campomanes, 2005) which allows, by means of a series of functions, various climate parameters to be estimated. Based on this method, two climate factors have been estimated: the mean annual temperature (MAT) and the mean annual precipitation (MAP).

3.3 Results and comparison between different proxies

3.3.1 Review of small vertebrate studies in Serbia

The first historical mention of small vertebrates in Serbia was done by Stevanović (1939), who described a few fossil elements of a water vole as “*Arvicola* sp.”. Extensive research on fossil small vertebrates in Serbia only started in the 1980s. The largest numbers of small vertebrate remains have been found in late Pleistocene cave sediments.

Herpetofaunal and bird remains did not receive significant attention in older publications, as the importance of these fossils had not yet been recognised. The most notable publication describing fossil bird remains from Smolučka cave is Malez and Dimitrijević (1990). The herpetofaunal remains from Smolučka cave are described in Paunović and Dimitrijević (1990). The complete analysis of this material was published in a paper on Smolučka cave (Dimitrijević, 1991). In her doctoral dissertation on Pleistocene mammals, Dimitrijević described all the fossil rodents that had been described from Serbian caves up to that time:

Vrelska, Vasiljska, Petnička, Prekonoška, and Popšićka caves, as well as Risovača cave (Dimitrijević, 1995; 1997). The material from Vrelska cave was further elaborated in special reports (Pavlović and Marković, 1991; Marković and Pavlović, 1991). Findings from Pećurski kamen have also been published (Malez and Salković, 1988; Medved, 1994). Intensive archeological work at Paleolithic sites led to the discovery of rodents in further Serbian caves: Mirilovska (Dimitrijević and Jovanović, 2002); Hadži Prodanova; Baranica (Krantić, 1997; Jovanović, 2005); Velika Balanica and Mala Balanica (Bogićević, 2008).

In his article on the Pleistocene rodents of Europe, Kowalski (2001) describes four localities in Serbia (Mol, the caves of Risovačka, Smolučka, and Vrelska), giving a brief description of the geographical location of each site, the paleontological content, a list of the types of rodents found, relevant literature, and an assessment of its stratigraphic age. An article on Pleistocene subterranean voles (subgenus *Terricola*) from Serbia and Montenegro analysed the remains from the Smolučka, Vrelska, and Vasiljska caves, from Baranica and Pećurski kamen (Brunet-Lecomte et al., 2001). The remains of Pleistocene cricetids from the Vasiljska, Vrelska, Petnička, and Smolučka caves, as well as from Venčac, were the subject of a Master's thesis (Marković, 1997).

Recent studies of small vertebrate remains have focused on several sites: Baranica (Djurić et al., 2016, 2017; Bogićević, 2004; Jovanović, 2005, Bogićević, 2008; Bogićević et al., 2011, 2012; Jovanović, 2016); Hadži Prodanova (Bogićević et al., 2017); Pešturina (Djurić, 2019); Velika Balanica and Mala Balanica (Bogićević, 2008; Djurić, 2019). Sites where the predominant fossil record involves small mammal remains (Vrelska cave, Vasiljska cave, Venčac, Petnička cave, Mirilovska cave, Canetova cave, Pećurski kamen, Prekonoška cave,

Popšička cave, Risovača, Susek, Bridge Sremska Kamenica, Serbian Crnja, Mol, Palace Albanija, and half-cave Jerinin grad) are described in a thesis by Bogićević (2008).

3.3.2 Dating

Fossiliferous layers containing small vertebrates have been organised chronologically using numerical dating. Dates from Serbian cave deposits have been collected and adapted for this purpose (Figure 3.3).

Baranica is a composite cave, and in this locality two sites have been excavated (Baranica I and Baranica II). Only the findings from Baranica I were selected for analysis. Two dates were obtained through AMS dating of bone and teeth samples, at the Oxford laboratory: 25.9-25.5 kcal BP 2 for Layer 2 and 39.2-37.7 kcal BP for Layer 4 (Pacher and Stuart, 2009; Dimitrijević, 2011).

The dates for Hadži Prodanova cave range from $18,730 \pm 80$ 14C yr BP to beyond the background. Age increases with depth, but certain samples deviate from this pattern, indicating that materials in Hadži Prodanova were subjected to stratigraphic mixing (Alex, 2016). Not all the samples have been included in Figure 3.3, as the purpose of this figure is to produce a chronological context for the layers within the late Pleistocene, rather than illustrate all the dates. For Layer 2, two samples were chosen: RTD7274, dated as 30-29 kcal BP; and RTD7271, dated as 29 kcal BP. For Layer 3 we used only sample RTD7277, dated as 35-36 kcal BP. Two samples were assigned to Layer 4: RTD7273 (39-37 kcal BP); and RTD7276 (41-39 kcal BP). Samples RTD7270 (44-43 kcal BP) and RTD7482 (52-45 kcal BP) (adapted from Alex, 2016).

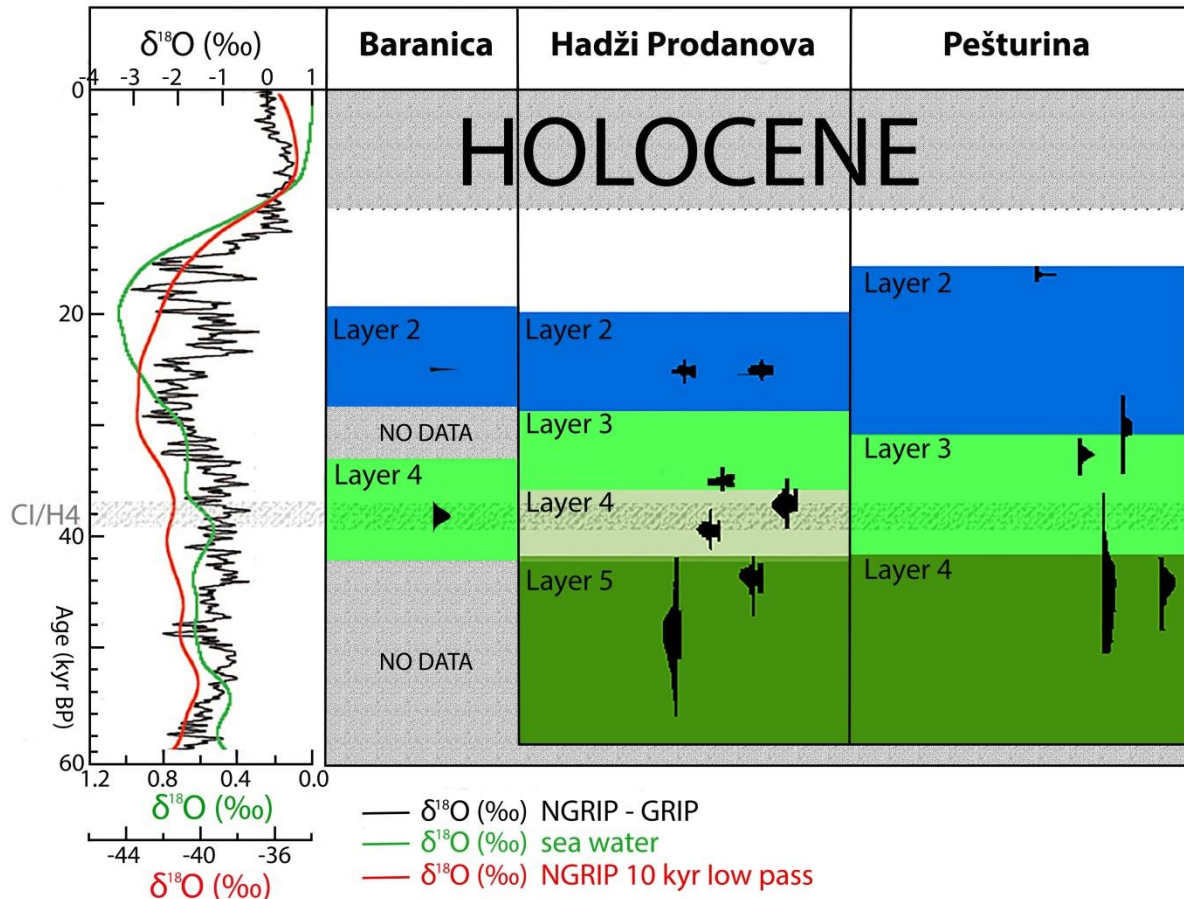


Figure 3.3 – Age and chronology of the caves of Baranica, Hadži Prodanova, and Pešturina, simplified for the purpose of this research. This figure shows only chosen samples dated by various authors (as explained in the text). The colours are associated with plausible human cultural contexts: Mousterian (dark green); Aurignacian (light green); and Gravettian (blue). In Hadži Prodanova Layer 4, the human cultural context could not be determined and it is assigned to the Mousterian-Aurignacian. The temperature deviation curve has been adapted from Andersen et al. (2004).

The same principle was used for Pešturina cave, and only certain samples were selected for Figure 3.3. The dates from Pešturina were published in detail in Alex and Boaretto (2014), Blackwell et al. (2014), and Alex et al. (2019). Samples from Layer 2 range from $>37,800$ ^{14}C yr BP to $13,440 \pm 60$ ^{14}C yr BP; samples from Layer 3 range from $40,230 \pm 3600$ ^{14}C yr BP to $28,680 \pm 180$ ^{14}C yr BP; and the one sample from lithostratigraphic Layer 4 (RTD7149) was dated as $40,500 \pm 590$ ^{14}C yr BP. Generally, the samples demonstrate increasing age with depth. However, stratigraphic mixing is evident at the transition between

Layers 2 and 3 (Alex and Boaretto, 2014). To stratigraphically position the layers in Figure 3.3, we used samples RTD7148 and RTK6446 for Layer 2, samples RTD7231B and RTK6449 for Layer 3, and sample RTD7149 for Layer 4 (adapted from Alex, 2016).

3.3.3 Statistical analyses of the herpetofaunal fossil record and comparison with the associated small mammal fossil record

For the analysis, it was necessary to collect all available data on osteological finds. Although the data from Pešturina cave is still preliminary (Tables 3.3 and 3.4), we were able to incorporate these data in our analyses. After completing the analysis, statistical methods were applied to nine layers from three Serbian caves that passed the selection criteria. As mentioned above, a principal criterion was the presence of identified small vertebrate remains in a chronological context.

Sites/species	Baranica	Smolučka	Hadži Prodanova	Pešturina	Vasijska	Venčac	Petnička	Mirilovska	Velika Balanica	Mala Balanica	Peručki kamen	Canetova	Vreška
Amphibians													
<i>Salamandra salamandra</i>	-	+	-	-	-	-	-	-	-	+	-	-	-
<i>Bombina variegata</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Paleobates fuscus</i>	?	+	-	-	-	-	-	-	-	-	-	-	-
<i>Pelobates</i> sp.	+	?	-	-	-	-	-	-	-	-	-	-	-
<i>Bufo bufo</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
Bufoinae indet.			-	-	-	-	-	-	-	-	-	-	-
<i>Bufo</i> ex gr. <i>viridis</i>	+	+	-	-	-	-	-	-	-	-	-	-	-
<i>Hyla arborea</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Rana temporaria</i>	?	+	-	+	-	-	-	-	-	-	-	-	-
<i>Rana arvalis</i>	?	+	-	-	-	-	-	-	-	-	-	-	-
<i>Pelophylax</i> kl. <i>esculentus</i>	?	+	-	-	-	-	-	-	-	-	-	-	-
<i>Pelophylax ridibundus</i>	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pelophylax</i> sp.	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rana</i> sp.	+	?	-	+	-	-	-	-	-	-	-	-	-
Ranidae indet.	?	?	+	+	-	-	-	-	-	-	-	-	-
Anura indet.	?	?	-	-	-	-	-	-	-	-	-	-	-
Reptiles													
<i>Lacerta viridis</i>	?	+	+	+	-	-	-	-	-	+	+	-	-
<i>Lacerta agilis</i>	+	+	+		-	-	-	-	-	-	-	-	-
<i>Lacerta</i> sp.	?	?	+	+	-	-	-	-	-	-	-	-	-
Lacertidae indet.	?	?	-	+	-	-	-	-	-	-	-	-	-
<i>Podarcis</i> sp.	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Zootoca vivipara</i>	-	-	+	+	-	-	-	-	-	-	-	-	-
<i>Pseudopus panonicus</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
<i>Anguis fragilis</i>	+	+	+	+	-	-	-	-	-	+	-	-	-
<i>Elaphe quatuorlineata</i>	-	-	-		-	+	-	-	-	-	-	-	-
<i>Zamenis longissimus</i>	+	+	+	+	-	-	-	-	-	+	-	-	-
<i>Coronella austriaca</i>	+	+	-	+	-	-	-	-	-	-	-	-	-
<i>Natrix natrix</i>	+	+	-	-	-	-	-	-	-	-	-	-	-
<i>Natrix tessellata</i>	?	-	-	+	-	-	-	-	-	-	-	-	-
<i>Natrix</i> sp.	+	?	-	-	-	-	-	-	-	-	-	-	-
<i>Vipera berus</i>	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Vipera berus</i> group	?	?	+	?	-	-	-	-	-	-	-	-	-
<i>Vipera ammodytes</i>	+	+	-	?	-	-	-	-	-	-	-	-	-
<i>Vipera</i> sp.	+	-	-	+	-	-	-	-	-	-	-	-	-
Ophidia indet.	+	+	-	-	-	-	-	-	-	-	-	-	-
Small-mammals													
Eulipotyphla													
<i>Sorex araneus</i>	-	+	-	-	-	?	-	-	-	-	-	-	+
<i>Sorex minutus</i>	-	+	-	-	+	?	-	-	-	+	-	-	+

<i>Sorex sp.</i>	?	?	+	+	-	+	-	-	-	+	-	-	-
<i>Talpa europaea</i>	-	+	-	-	+	-	+	-	-	-	-	-	-
<i>Talpa sp.</i>	-	-	-	+	-	+	-	-	-	-	-	-	-
<i>Crocidura leucodon</i>	-	-	-	-	+	?	-	-	-	-	-	-	+
<i>Neomys sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	+
Rodentia													
<i>Apodemus epimelas</i>	-	-	-	?	-	-	-	-	+	+	-	-	-
<i>Microtus gregalis</i>	+	-	-	-	-	-	-	-	?	-	-	?	-
<i>Microtus (Tericola) subterraneus</i>	+	+	+	+	+	-	-	-	?	+	+	?	-
<i>Hystrix sp.</i>	-	+	-	-	-	-	-	-	-	-	-	-	-
Murinae indet.	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Sciurus vulgaris</i>	-	-	-	-	+	-	-	-	-	-	-	-	-
<i>Apodemus ex gr. sylvaticus-flavicollis</i>	+	+	+	+	+	+	+	-	+	+	-	+	+
<i>Arvicola mosbachensis/amphibius</i>	+	+	+	+	+	+	?	-	-	?	-	-	+
<i>Chionomys nivalis</i>	+	+	+	+	+	-	-	-	-		+	-	+
<i>Clethrionomys glareolus</i>	+	+	+	+	+	+	+	-	-	?	-	+	+
<i>Cricetulus migratorius</i>	+	+	-	-	+	+	-	-	-	+	-	-	+
<i>Cricetus cricetus</i>	+	-	-	-	-	+	-	+	-	-	-	-	+
<i>Dryomys nitedula</i>	+	+	-	-	+	-	+	-	+	+	-	-	+
<i>Lagurus lagurus</i>	+	-	-	+	-	?	-	-	-	?	-	-	+
<i>Mesocricetus newtoni</i>	+	+	+	-	+	+	+	+	+	+	-	-	+
<i>Microtus arvalis-agrestis</i>	+	+	+	+	+	?	+	-	?	+	+	?	+
<i>Muscardinus avellanarius</i>	+	+	+	+	+	-	+	-	-	-	-	-	+
<i>Sicista subtilis</i>	+	+	+	+	-	-	-	-	+	-	-	-	+
<i>Spalax leucodon</i>	+	+	-	+	-	-	-	+	-	-	-	-	+
<i>Spermophilus citelloides</i>	+	+	+	+	-	+	-	-	-	?	-	-	+
<i>Spermophilus sp.</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Glis glis</i>	-	+	-	+	+	?	+	-	?	-	-	+	+
<i>Apodemus cf. microps-maastrichtensis</i>	-	-	+	-	-	+	-	-	-	-	-	-	+
<i>Apodemus mystacinus</i>	-	-	-	-	-	-	-	-	+	+	-	-	+
<i>Microtus nivaloides</i>	-	-	-	-	-	+	-	-	?	-	-	?	-
<i>Lagurus sp.</i>	-	-	-	+	-	+	-	-		+	-	-	-
<i>Mus musculus</i>	-	-	-	-	-	+	-	-		-	-	-	-
<i>Glis sackdiligensis</i>	-	-	-	-	-	+	-	-	?	-	-	-	-
<i>Arvicola sp.</i>	-	-	-	-	-	-	+	-		+	-	-	-
<i>Microtus sp.</i>	-	-	-	-	-	-	-	-	+	+	+	+	-
<i>Mesocricetus</i>	-	-	-	+	-	-	-	-	+	-	-	-	-
<i>Clethrionomys sp. Juv</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Castor fiber</i>	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Apodemus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
Lagomorpha													
<i>Lepus sp.</i>	+	+	-	-	+	+	+	+	-	-	+	-	+
<i>Ochotona pusilla</i>	+	+	-	?	+	+	-	+	-	-	-	-	+
<i>Ochotona sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ochotona</i>	-	-	-	+	-	-	-	-	-	-	-	-	-
<i>Lepus cf. timidus</i>	-	-	-	-	-	-	-	+	-	-	-	-	-
Chiroptera													

<i>Rhinolophus ferrumequinum</i>	-	-	-	-	+	-	-	-	?	?	?	?	-
<i>Rhinolophus euryale</i>	-	-	-	-	+	-	+	-	?	?	?	?	-
<i>Rhinolophus sp.</i>	-	-	-	-	-	-	-	-	?	?	?	?	+
<i>Rhinolophus hipposideros</i>	-	-	-	-	-	-	+	-	?	?	?	?	+
<i>Rhinolophus mehelyi</i>	-	-	-	-	-	-	-	-	-	-	-	-	+
<i>Myotis myotis</i>	-	-	-	-	-	-	+	-	?	?	?	?	+
<i>Myotis blythii</i>	-	-	-	-	-	-	+	-	?	?	?	?	-
<i>Miniopterus schreibersii</i>	-	-	-	-	-	-	+	-	?	?	?	?	-

Table 3.3 – Summary of small vertebrate findings documented from Serbian caves. Symbol "+" means confirmed presence, "-" means not found, "?" means possible (unconfirmed) presence.

	MIS 4				MIS 3				MIS 2			uncertain	TODAY			
	PES/L4	HPP/L5	PES/L3	BAR/L4	HPP/L4	BAR/L3	PES/L2	HHP/L3	BAR/L2	SMP	SMP/AC	HHP/AC	BAR/AC	PES/AC		
<i>Salamandra salamandra</i>	-	-	-	-	-	-	-	-	-	+	+	+	+	+		
<i>Bombina variegata</i>	-	-	-	-	-	-	-	-	-	+	+	+	+	+		
<i>Pelobates gr. fuscus</i>	+	-	-	+	-	-	-	-	-	+	-	-	-	-		
<i>Bufo bufo</i>	-	-	-	-	-	-	-	-	-	+	+	+	+	+		
<i>Bufo ex gr. viridis</i>	-	-	-	+	-	+	-	-	-	+	+	+	+	+		
<i>Hyla arborea</i>	-	-	-	-	-	-	-	-	-	+	+	+	+	+		
<i>Rana temporaria</i>	+	-	-	-	-	-	+	-	+	+	+	+	+	+		
<i>Rana arvalis</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-		
<i>Pelophylax esculentus</i>	-	-	-	-	-	-	-	-	-	+	-	-	+	+		
<i>Pelophylax ridibundus</i>	-	-	-	+	-	-	-	-	+	-	+	+	+	+		
<i>Lacerta viridis</i>	-	+	-	-	-	-	+	-	-	+	+	+	+	+		
<i>Lacerta agilis</i>	+	+	-	+	+	-	+	+	-	+	+	+	+	+		
<i>Podarcis muralis</i>	-	-	-	-	-	-	+	-	-	-	+	+	+	+		
<i>Zootoca vivipara</i>	-	-	-	-	-	-	+	-	-	-	+	-	-	-		
<i>Pseudopus pannonicus</i>	-	-	-	-	-	-	-	-	-	+	-	-	-	-		
<i>Anguis fragilis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+		
<i>Zamenis longissimus</i>	+	-	+	+	-	-	+	+	-	+	+	+	+	+		
<i>Coronella austriaca</i>	+	-	+	+	-	-	-	-	-	+	+	+	+	+		
<i>Natrix natrix</i>	-	-	-	+	-	-	-	-	-	+	+	+	+	+		
<i>Natrix tessellata</i>	+	-	-	-	-	-	-	-	-	-	+	+	+	+		
<i>Vipera ammodytes</i>	+	+	-	+	-	-	-	-	-	+	+	+	+	+		
<i>Vipera berus</i>	+	+	-	+	-	-	+	+	+	+	+	+	+	+		

Table 3.4 – Herpetofaunal chronological biogeography showing the chronological distribution of species in geographical settings in Serbia.

The statistical analysis showed that when analysing only herpetofaunal remains, layers of similar ages have a low similarity index (Figure 3.4A). This is most likely due to the

incomplete nature of the fossil record, as in most layers very few taxa have been identified. The small mammal data is much more complete, but when this is added to the analysis the similarity index between layers of similar ages remains low. In order to fix this problem, we incorporated the list of modern herpetofauna living in the vicinity of the cave (Figures 3.4A and 3.4B: BAR/AC, HPP/AC, PES/AC), and typical herpetological faunal associations for Pleistocene climate cycles in Central Europe (modified from Böhme, 1996, 2000). This approach solved the problem of the low similarity index. Unfortunately, we were unable to perform a correspondence analysis on the small mammal assemblages because typical small mammal faunal associations for Pleistocene climate cycles in Central Europe have not been established as such; for this reason, other methods were chosen for analysing the rodent remains.

When implementing the hierarchical clustering method, it is important to consider that the surroundings of the caves selected for this analysis do not have the same biogeographical properties, so this may influence the results. Baranica and Pešturina Caves are relatively close to one another (approximately 40 km apart), both are located in a river valley (but of different rivers), they are within the Carpato-Balkan mountain belt, and are from an approximately similar altitude. Smolučka and Hadži Prodanova caves are significantly different in terms of biogeographical properties. They are located within the Dinaric Alps, they are from a notably higher altitude than the previous two caves, and the area is generally much more secluded in comparison to the previous two caves, which are surrounded by more open areas.

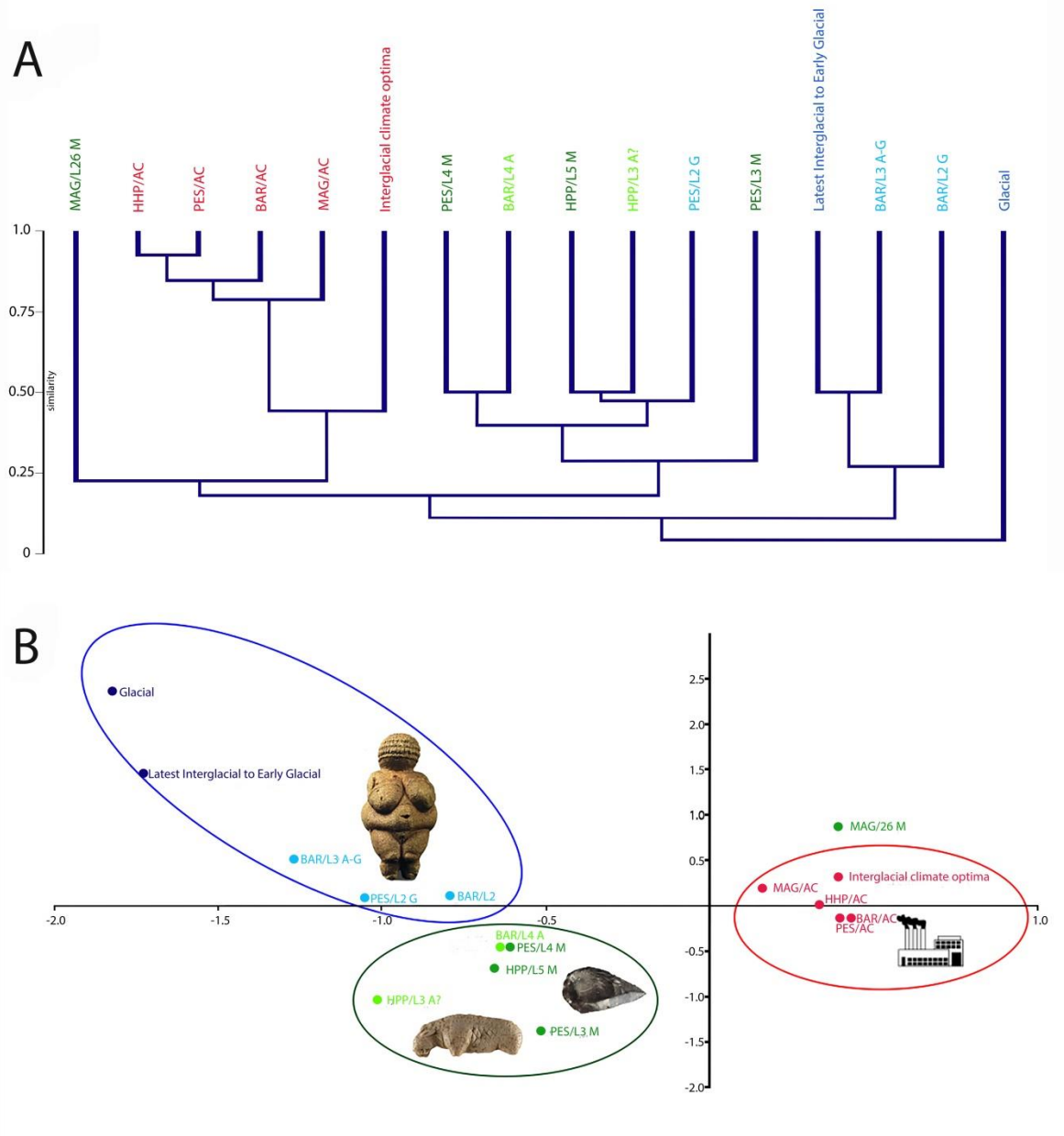


Figure 3.4 – Statistical analyses of the herpetofaunal fossil record in Serbia. **A.** Dendrogram created by cluster analysis using the Jaccard similarity index, showing herpetofaunal groups based on chronostratigraphic criteria whose origins are related to possible biogeographic changes. Typical Central European herpetofaunal assemblages for interglacial climate optima, Latest interglacial to Early glacial, and Glacial periods are modified from Böhme (1996, 2000). **B.** Graphic presentation of the correspondence analysis for herpetofaunal assemblages during the Mousterian-Aurignacian-Gravettian succession: Mousterian (dark green); Aurignacian (light green); Gravettian (blue); and modern (red).

The amphibian and reptile bone remains from the caves of Baranica, Hadži Prodanova, and Pešturina, represent at least 14 taxa, as shown in Table 3.3. The herpetofaunal remains from these three caves document toads, frogs, lacertid lizards, and several snakes, but interestingly no tortoises, newts, or salamanders.

Some species recorded on the faunal lists and used in the Paleontological Statistics (PAST3) analysis are considered osteologically too similar to distinguish from incomplete fossils, and, for that reason, have been listed within the same group (*Triturus cristatus/macedonicus*, *Pelobates fuscus/syriacus*, *Lacerta viridis/trilineata*). Two anuran species: *Rana arvalis* and *Epidalea calamita* have been removed from the data matrix as there is no evidence that they have ever lived in the vicinity of these caves, although *R. arvalis* is recorded in the fossil record from Smolučka cave, but with an uncertain stratigraphic position (Paunović and Dimitrijević, 1990). The most common species in our fossil record is *Vipera berus*, which is present in 7 of the 9 layers studied (63%; PES/L4, HPP/L5, BAR/L4, BAR/L3, PES/L2, HPP/L2, BAR/L2). *V. berus* prefers Eurosiberian open woodland and shrubland, and is sometimes found in rocky habitats. *V. berus*, like *Lacerta agilis* and *Zootoca vivipara*, can be considered among the most cold-tolerant taxa, since in modern times this species survives at altitudes of up to 2600 m. (Gasc et al. 1997, Andersson 2003, Carlsson 2003). It has probably survived in non-Mediterranean refugia, such as the Carpathian Basin (Jogger et al. 2007). This snake is currently rare in Serbia, and its presence in the close vicinity of these three caves is doubtful. According to Tomović et al. (2014), Hadži Prodanova and Pešturina caves are within the potential range of *V. berus*, while Baranica is not. The species *L. agilis*, *Anguis fragilis*, and *Zamenis longissimus* appear together in our fossil record in 4 of the 9 layers (36%; PES/L4, BAR/L4, PES/L2, HPP/L3), and all three are currently present in Serbia (Tomović et al. 2014). The concurrence of these three species indicates sunny (at least in the

central months of the year), but certainly humid conditions, with the presence of scrubland and woodland. The record of *Rana temporaria*, which is present in PES/L4 and PES/L2, together with *L. agilis*, *A. fragilis* (in most of Europe and north-eastern Iberia *R. temporaria* lives in the same habitats as *A. fragilis* and *L. agilis*), and *Z. longissimus*, could be interpreted as a cold-tolerant assemblage, with a Eurosiberian origin but with Mediterranean influence due to the presence of *Z. longissimus*. In central Europe, *R. temporaria* is usually the only anuran associated with full glacial cold stages, but curiously in the Serbian context it appears with other herpetofaunal taxa. This is very similar to the scenario in the Iberian Peninsula, where *R. temporaria* was the dominant species in the northern regions during the late Pleistocene, although it appeared in concurrence with other cold-tolerant generalist species (Bisbal-Chinesta and Blain 2018). *R. temporaria* is not very widespread in Serbia due to competition with other ranid species, but it does survive through both colder and warmer climate phases at higher altitudes.

3.3.3.1. MIS 5/4? to early MIS 3 (Mousterian) layers

The oldest layer included in this research is Pešturina Layer 4. For our analysis, this layer is considered to be older than 45 ky but with an undetermined limit, and it is plausible that at least part of the deposit originated from MIS 4 and possibly even MIS 5. This layer contains diverse herpetofauna. Our analysis included 9 taxa. The herpetofauna composition indicates an intermediate climate, with relatively humid conditions, and the presence of wet grassland, shrubland, and woodland (*L. agilis*, *A. fragilis*, *Z. longissimus*, and *V. berus*), and rocky areas (*Coronella austriaca*, and *V. ammodytes*) with water points (*Natrix tessellata*). The small mammal assemblage is also very diverse. It includes one typical woodland inhabitant (*Apodemus* ex gr. *sylvaticus-flavicollis*); species inhabiting moist meadows (*Arvicola*

amphibius and *Microtus (Terricola) subterraneus*); montane and petrophilous species (*Chionomys nivalis*); xero-mesophilous taxa (*Spermophilus cf. citelloides*, *Microtus arvalis* and *M. agrestis*, and *Spalax leucodon*); and only one steppe and semi-arid species (*Lagurus lagurus*). Compared to Layer 2 and Layer 3 from Pešturina cave, Layer 4 has the highest number of potential woodland inhabitants. In archeological context, this means that the Mousterian had a warm climate and high precipitation rate (Table 3.5), according to the increase of woodland habitats (Figure 3.5).

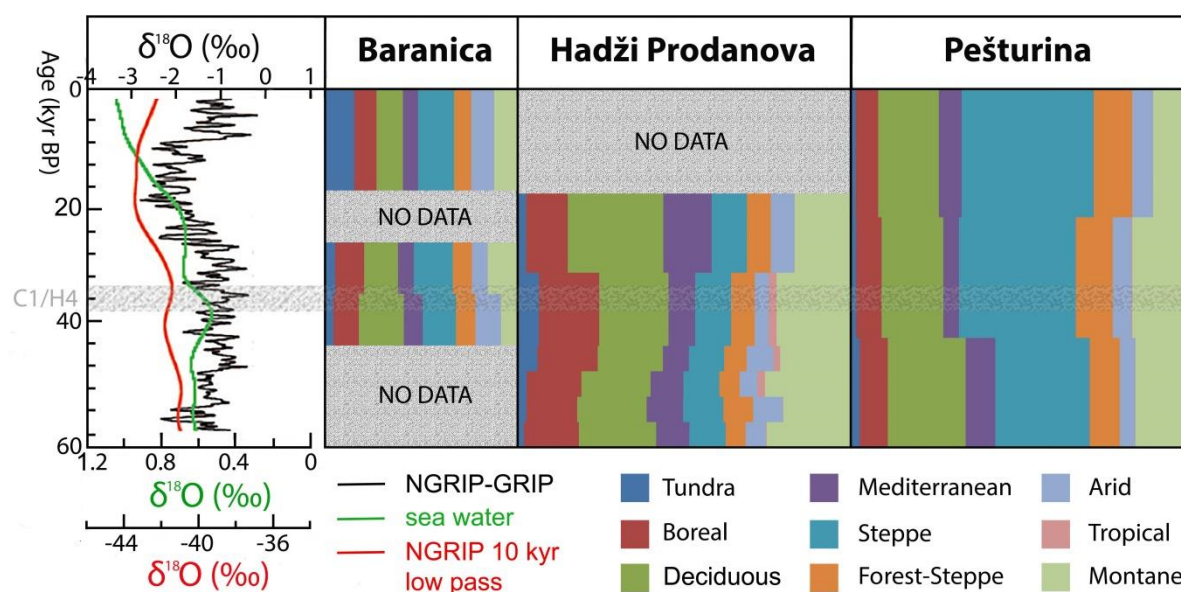


Figure 3.5 – Distribution of taxonomic habitat indexes: tundra (dark blue); boreal forest (red); deciduous forest (light green); Mediterranean regions (purple); steppe (light blue); forest-steppe (orange); arid regions (dark grey); tropical regions (pink); mountains (light grey). The temperature deviation curve has been adapted from Andersen et al. (2004).

The oldest deposits from Hadži Prodanova cave yielding herpetofaunal remains are designated Layer 5. This layer contained the most herpetofaunal remains in the cave. The presence of *A. fragilis*, *L. agilis*, *L. viridis*, *V. ammodytes* and *V. berus* indicate a relatively humid mixed grassland-shrubland habitat with rocky areas. Within this layer are 4 horizons: HPP/L5a, HPP/L5b, HPP/L5c, and HPP/L5d (Bogićević et al. 2017). These horizons

probably record slight climate changes within the layer but, unfortunately, they have not yet been dated, and their chronological position is uncertain. For paleoecological reconstructions this layer must be regarded as a single unit. Dated as being more than 43 ky old, it is considered to have been deposited in MIS 3. The small mammal assemblage indicates a humid temperate climate. The faunal list reveals a predominance of voles, typical representatives of a cold climate (Bogićević et al. 2017). A bioclimatic analysis of rodent remains (Table 3.5) shows a cold but humid climate with a mean annual temperature 4°C lower than today, and precipitation 209 mm higher than at the present.

3.3.3.2. MIS 3 (Aurignacian or Early Upper Paleolithic) layers

From the dating results, Hadži Prodanova Layer 4 is assigned chronologically to the Aurignacian cultural context for the purpose of this research. This layer is chronologically comparable to Pešturina Layer 3 and Baranica Layer 4 (confirmed Aurignacian) (Figure 3.3). This layer contains very few herpetofaunal remains; the only species that has been positively identified is *L. agilis*, which is a generalist species and could be considered one of the most cold tolerant, although it does need significant levels of insolation in the spring and summer. This layer also produced some frog remains (Ranidae indet.) as well as a few lacertid vertebrae that could not be identified. The bioclimatic analysis of the rodent remains (Table 3.5) shows that the climate was probably dryer than at present, but not extremely cold during the deposition of the layer. The mean annual temperature was just 2°C lower than today. In addition to this, the THI revealed a very high presence of woodland, both boreal and deciduous, along with a high index of mountain elements.

According to the dating, Pešturina Layer 3 is estimated to have been deposited roughly between 32-45 ky (Figure 3.3), during MIS 3. This layer records multiple climate fluctuations in terms of the age range, although in Central Europe and the Balkans, the climate was more stable in MIS 3 than MIS 2. Because the osteological results are still preliminary, only three herpetofaunal taxa were included in the analysis (*A. fragilis*, *C. austriaca*, and *Z. longissimus*). Anuran remains were not identifiable, and there were also some unidentified lacertid remains. The small mammal fauna is similar to Layer 2, but the climate was probably drier (*Microtus (Terricola) subterraneus* is absent), and presence of *Chionomys nivalis* indicates a greater presence of the mountain biotype. The THI results show a high presence of steppe and deciduous forest (Figure 3.5). The bioclimatic analysis showed the mean annual temperature to be, on average, lower than at present (4.8°C less) and the climate was humid, but less so than in Layer 4 (Table 3.5).

LAYERS:	PES-L4	HPP/L5	PES/L3	BAR/L4	HPP/L4	BAR/L3	PES/L2	HHP/L 3	BAR/L2
MAT (in °C)	8.2	6.0	6.9	8.7	8.0	10.5	7.5	7.8	6.7
Today	11.7	10.0	11.7	11.2	10.0	11.2	11.7	10.0	11.2
Delta	-3.5	-4.0	-4.8	-2.5	-2.0	-0.7	-4.2	-2.2	-4.5
MAP (in mm)	1305.9	1106.1	1052.4	993.7	861.6	824.8	1328.04 1	1225.1	811.2
Today	595.0	897.0	595.0	605.0	897.0	605.0	595.0	897.0	605.0
Delta	710.9	209.1	457.4	388.7	-35.4	219.8	733.0	328.1	206.2

Table 3.5 – Results of the bioclimate analysis are based on the correlation between the climate and mammal communities. By means of a series of functions (as explained in the text), two climate factors have been estimated: the mean annual temperature (MAT) and the mean annual precipitation (MAP).

In Baranica Layer 4 there is a significant increase in woodland habitats compared to Layer 2. The presence of three species together, *L. agilis*, *A. fragilis*, and *Z. longissimus*, indicate insolated/sunny but certainly humid conditions, with the presence of wet grassland and

woodland. They appear in the record with the toad *Bufo viridis*, which is typical of open environments in grassland, steppe or forest-steppe conditions, also for rocky areas, and not very sensitive to aridity, warmth, or the cold (Blain et al. 2014; Ratnikov 2009, 2016). The THI results show that deciduous forests dominated the landscape. Closer observation of the horizons within Layer 4, shows that horizon 4a is dominated by steppe elements, with a high proportion of deciduous and coniferous forest taxa, as well as mountain species. Horizon 4b predominantly contains inhabitants of deciduous forests, although elements of steppe, coniferous forests, and arid areas are fairly well represented (Bogićević 2008). The bioclimatic analysis results (Table 3.5) also show that this layer was deposited in a relatively warm period during MIS 3, as the mean annual temperature calculated is just 2.5°C lower than at present, and the mean annual precipitation is 389 mm higher than today. Baranica Layer 4, Pešturina Layer 3, and Hadži Prodanova Layer 4 were deposited at a similar time, but any analysis of the faunal lists should be done with caution, as the bioclimatic conditions in these three caves (elevation, mountain range, terrain configuration, and wind) were different, and the deposition duration of the layers is likely to have been significantly different.

The youngest deposit from Hadži Prodanova cave that we have included in this research is Layer 3. Herpetofaunal remains are not very abundant, although the quartet of species (*L. agilis*, *A. fragilis*, *Z. longissimus* and *V. berus*) representing insolated/sunny and humid conditions with meadows and woodlands is present. The small mammal assemblage shows a very high exemplification of woodland. The most numerous inhabitants are from deciduous forests (Bogićević 2008). The bioclimatic analysis (Table 3.5) shows a slightly lower mean annual temperature than today (2.2°C lower), but significantly higher precipitation during the deposition of this layer (328 mm higher than at present). This layer is chronologically

comparable to Baranica Layer 3, for which, unfortunately, we have insufficient information to undertake this kind of analysis.

3.3.3.3 MIS 2 (*Gravettian*) layers

Taking into account the dating of Pešturina Layer 2 (Figure 3.3), it is estimated that this layer may have been deposited over a period possibly lasting more than 15,000 years, in MIS 2. This covers multiple climate fluctuations before the glacial maximum. According to Musil (2010), a relatively warm climate in Central Europe has been recognised at 31,500, 30,000, 27,500, 26,000 and 21,000; while relatively cold periods existed at 32,000, 31,000, 29,000-27,500, 25,000-21,500 (all data are in calibrated years BP). This layer could contain the signature of all these fluctuations, and any paleoreconstruction would correspond to the entire early to full glacial at this locality. Although both the herpetofauna and small mammal lists for Pešturina cave are still preliminary, seven herpetofaunal taxa have been identified, and we were able to include these in the analysis. Three species (*Vipera* cf. *berus*, *Zootoca vivipara* and *Rana* cf. *temporaria*, representing 43% of the whole association) are typical herpetological Latest Interglacial to Early Glacial faunal associations for Pleistocene climate cycles in Central Europe. Another species (*L. agilis*) is known to be typical for the Latest Interglacial to Early Glacial in the Balkans (Jogger et al. 2007). *Podarcis* cf. *muralis* is a cold-tolerant generalist species that lives in a variety of habitats, but especially in rocky environments, while another two species (*Z. longissimus* and *A. fragilis*) are clearly species better suited for sunny conditions that either survived for some time after MIS 3, or repopulated the area during the interstadials and Heinrich events. By analysing the small mammals, we were able to divide the taxa into ecological groups: woodland species (*Apodemus* ex gr. *sylvaticus-flavicollis*), steppe and semi-arid species (*Lagurus lagurus*),

xero-mesophilous taxa (*Spermophilus* cf. *citelloides*, *Microtus arvalis*, and *Spalax leucodon*), and species inhabiting moist meadows (*Microtus (Terricola) subterraneus*). The THI also revealed a variety of different habitats, a consequence of the wide age range of the layer (Figure 3.5). As expected, (considering this layer was deposited during MIS 2), the bioclimate analysis revealed a cold climate (4.2°C lower than today), but which was unexpectedly humid in comparison to other caves, MIS 2 in Central Europe, and today's local climate. These results probably represent only a short period during the deposition of the entire layer, and do not reflect the average of the whole unit.

The fauna of Baranica Cave is characterised by the presence of some "cold" elements in Layer 2, representatives of both large and small mammal fauna, and also herpetofauna (cf. *R. temporaria* and *V. berus*). In Figure 3.5 THI from Baranica Layer 2 is characterised by the prevalence of steppe elements, with a high number of tundra and deciduous forest elements, and only slightly fewer arid environment and mountain elements; warm ("tropical") elements are practically absent. This evidence supports the idea that the area had a rather cold climate and an environment dominated by open habitats (Bogićević 2008). This agrees with the bioclimate analysis results obtained from small mammals (Table 3.5), which reveal that the mean annual temperature during the deposition of this layer was 6.7°C, 4.5°C lower than today.

3.4. Discussion

The stratigraphic position of the layers we have studied in this work represents an interesting change in human history. In a cultural context, the layers described were deposited during the Mousterian-Aurignacian-Gravettian succession.

3.4.1 The Middle to Upper Paleolithic transition

Some authors have studied the archeological remains from the layers in Serbian caves (Alex 2016; Mihailović 2009, 2014, etc.), but studying small vertebrate remains introduces an opportunity to reconstruct climate conditions during this transition. Correspondence analysis has only been performed on herpetofauna (Figure 3.4B) groups from MIS 4 and MIS 3 (Mousterian and Aurignacian) layers together, and no significant difference in the herpetofaunal assemblage has been recognised. This suggests that during MIS 3 the climate was somewhat stable, but clearly separate from that recorded in MIS 2 (Gravettian) layers, where there was a change in the composition of the herpetofaunal assemblage, linked to a change in climate during MIS 2. To create a picture of climate conditions in MIS 4 we have added a faunal list from Magura cave Layer 26 (Mousterian), a site very near Baranica and Pešturina caves, but located in Bulgaria, published by Ivanova (Ivanova et al. 2016). Curiously, both hierarchical clustering (Figure 3.4A) and correspondence analysis (Figure 3.4B) recognise greater similarity with extant fauna than with Mousterian layers, indicating a warm spell during the deposition of Layer 26.

The different synchronic associations of herpetofauna, and the diachronic changes in the fossil record, also show an evolution of the landscape in accordance to the Late Pleistocene glacial cycle (Figure 3.6). The concurrence of reptiles and amphibians ascribed to the Mousterian phase indicate the existence of a varied landscape in temperate conditions, which remain slightly cooler and wetter during the Aurignacian. It is during the levels assigned to the Gravettian phase that the coldest conditions are manifested, with the presence of herpetofauna characteristic for cold mountain conditions and capable of resisting even sub-boreal conditions (concurrence of *R. temporaria*, *L. agilis*, *Z. vivipara* and *V. berus*), although the continued presence of *Z. longissimus* is also indicative of the persistence of humid deciduous woodlands in the landscape surrounding the caves.

An event considered critical for understanding population histories in the Balkans is the Campanian Ignimbrite (CI or Y5) eruption, one of the largest known volcanic eruptions in the Quaternary. The most widely used age estimate for this event, based on $^{40}\text{Ar}/^{39}\text{Ar}$ dating, is $39,280 \pm 110$ yr BP (de Vivo et al., 2001; Bronk Ramsey et al., 2015). Based on sulphate concentrations in the Greenland ice core record, the eruption may have caused global cooling of 1-2°C (Costa et al., 2012) or 3-4°C (Fedele et al., 2008) for a period of 2-3 years. The CI eruption coincided with the onset of Heinrich Event 4 (H4), a millennial-scale period of cooling within the milder interglacial conditions of Oxygen Isotope Stage 3 (OIS-3 or MIS 3) (Hemming, 2004). The impact of the CI eruption on the environment and human populations has been widely debated (e.g., Lowe et al., 2012; Costa et al., 2012; Fedele et al., 2008). Some mammal assemblages seem to have remained stable throughout this period (Miracle et al., 2010). In our study, this event chronologically best matches Hadži Prodanova layer 4 (HPP/L4). Analysis of our small mammal assemblage suggests that the CI eruption did not



Figure 3.6 – Actualistic interpretation of the different landscapes documented in Baranica, Hadži Prodanova and Pešturina caves for the chronocultural phases of the Mousterian, Aurignacian and Gravettian (MIS3 to MIS2) based on modern main herpetological species concurrences. The Gravettian phase presents the lowest diversity of species, coinciding with the Last Glacial Maximum, together with the appearance of species more typical of alpine and cold open environments, such as mountain prairies accompanied by coniferous forests (A: Tara mountains, Kršanje municipality). However, the diachronic presence throughout the

sequence of *Zamenis longissimus*, a snake adapted to humid deciduous forests (B: Avala forest, Voždovac municipality), indicates the survival of wooded areas even in the coldest moments of the Late Pleistocene. During the Aurignacian, the concurrences indicate a cooling of the climate and a high degree of environmental humidity, which generates a landscape dominated by humid grasslands with scrub associations (C: Fruška Gora, Banoštor municipality) and by deciduous humid forests (D: Serbian Carpathians, Reka municipality). The herpetological record associated with the Mousterian shows temperate conditions, comparatively warmer in comparison with the later ones, with varied open and wooded environments (E: Kozjak mountains, Bujanovac municipality), but also sunny and humid (F: Gamzigrad hills, Zaječar municipality). Credits: H.-A. Blain (A); J.F. Bisbal-Chinesta (B-F and herpetological photos).

critically impact the local environment; in fact, woodland elements remain very high and fairly stable in comparison to the older Layer 5. A good herpetological record for the time of this event would certainly enable a reconstruction of the impact CI had on the environment in the Balkans, but unfortunately our herpetological record is very poor, in fact HPP Layer 4 is the poorest layer in terms of herpetological remains. The transition from Layer 4 to Layer 3 in Pešturina cave is very uncertain (Alex 2016) and for this reason cannot be compared with the CI eruption. Nevertheless, our results do not contradict the claim that centennial-scale pollen records show a marked increase in grasses and a decline in tree taxa (Müller et al. 2011; Tzedakis 2002). The bioclimate analysis reveals a significant drop in precipitation in Layer 3, and the THI shows a significant decrease in woodland habitats in the transition from Layer 4 to Layer 3. It is possible that Baranica Layer 4 (BAR/L4) was also coeval with the CI eruption, but we cannot claim this with certainty, as the dates from this layer appear to be slightly younger. Correspondence analysis of the herpetofaunal assemblage shows very high degree of similarity between Pešturina Layer 4 (PES/L4) and BAR/L4, suggesting that at least part of BAR/L4 could have been deposited prior to the CI eruption and H4 event, while PES/L3 was drier (e.g., the aquatic snake *Natrix cf. tessellata* is absent), but not dry *per se*. It is possible that the ecological impact of the CI eruption and H4 varied across the Balkans due to local topography and precipitation patterns (Alex 2016). This is also a possible reason for

such clear differences between western Serbia (Hadži Prodanova cave) and eastern Serbia (Baranica and Pešturina caves). To obtain more detailed information about these events, it is necessary to add more excavation sites, but currently there is only acceptable information available for these three sites.

The period of archeological diversity ended by 39 kcal BP at the time of the CI eruption, after which there is no convincing evidence for Mousterian industries. This absence of evidence does not prove the disappearance of Neanderthals in the Balkans post 39 kcal BP, although there may have been a substantial reduction or local extinction of human groups after the CI eruption. The reduction or disappearance of human groups may have left a relatively open landscape for later groups of dispersing humans. With the dates available, the duration of Neanderthal-modern human overlap cannot be precisely determined. Regardless of its length, the period of potential overlap indicates segregation. It seems that coexistence was characterised by avoidance and territoriality, as proposed by Mihailović (2004). This proposal is in coincidence with the conclusion drawn for Western Europe (Higham et al. 2014). However, in Western Europe the timing and nature of the overlap has been studied more intensively.

Neanderthals are thought to have survived longest in southern European regions, such as the Balkans, Italy, and Iberia (Carrión et al. 2011; Dennell et al. 2011). Faunal and botanical records suggest that the Balkans may have been buffered from severe climate oscillations, offering a refugium for humans during glacial periods (Miracle et al. 2010; Tzedakis 2002). Even so, there is no archeological evidence for Neanderthals living in the Balkans after 39 kcalBP, while on the Iberian Peninsula, archeological evidence suggests that Neanderthals inhabited Gorham's Cave possibly as late as 28,000 years ago (Finlayson et al. 2006). Iberia

was an important glacial refuge for Neanderthal populations (Stringer 2000; Finlayson et al. 2006, 2008; Carrión et al. 2008, 2011). As a part of the eastern Mediterranean area, the Balkans could have followed different evolutionary and population trajectories compared to Western Europe (Roksandić et al. 2018).

Paleoclimate reconstructions from the time of disappearance of the last Neanderthal populations reinforce the theory that climate did not play the main role in the demise of the Neanderthals. Blain et al. (2013) concluded that during the latest Pleistocene (late MIS3 and MIS2), the reconstructed climate in the vicinity of Gorham's Cave, and the southern Iberian peninsula in general, was warm and had a wide atmospheric temperature range. The summers were warm and the winters were mild, but the atmospheric temperature range was higher during the latest Pleistocene than today, mainly due to the current mild winter temperatures.

Another site on the Iberian Peninsula documenting the transition from the Middle Paleolithic to Upper Paleolithic is Cueva del Conde. Studies carried out on the microvertebrates of Cueva del Conde also seem to support the hypothesis that the climate was not the decisive factor triggering the extinction of the Neanderthals and their replacement by groups of modern humans, and that other factors, possibly of a social nature involving competition between groups of hominids or territorial organisation, may provide a more plausible explanation for the changes that occurred in the transition in this time interval (López-García et al. 2011a).

There seems to be a general consensus between researchers that climate itself could not have been the decisive factor in the demise of the Neanderthals on the Iberian Peninsula, but it may have contributed by reducing woodland areas, as Neanderthals have been associated with woodland habitats (see for example López-García et al. 2008, 2011a, 2011b; 2012a, 2012b; Burjachs et al. 2012; among others). The disappearance of large tracts of forest may have made them vulnerable, except in some small refuges in southern Iberia (e.g., the Rock of Gibraltar). Generally, data from the Iberian Peninsula suggests that the paleoenvironment during MIS 3 was dominated by open woodland formations, with the highest proportion of woodland in Gorham's Cave. According to the small-vertebrate assemblage from Cova Eirós the paleotemperatures were lower and the paleoprecipitation was higher than at present, meaning the extinction of the Neanderthal populations would have resulted from a combination of different factors, and cannot be explained by paleoenvironmental and paleoclimate conditions alone. (Rey-Rodríguez et al. 2016). Similar conditions seem to have been present in the Apennine Peninsula at that time, where in MIS 3 Neanderthals were associated with landscapes dominated by woodland formations in mild climate conditions (López-García et al. 2019).

3.4.2 The late Pleistocene to Holocene transition and the establishment of the modern herpetofaunal biodiversity in central Balkans

Zoogeographic analysis has classified contemporary Serbian amphibians and reptiles into ten chorotypes (Vukov et al. 2013; Tomović et al. 2014): 1. Eastern-Mediterranean, 2. Southern-European, 3. Centralasiatic-Europeo-Mediterranean, 4. Turano-Mediterranean, 5. Turano-Europeo-Mediterranean, 6. Europeo-Mediterranean, 7. European, 8. Turano-European, 9. Central-European, and 10. Euro-Siberian. Serbian reptiles have representatives in eight chorotypes, while amphibians have representatives in six chorotypes. A further criterion is

used to classify amphibians and reptiles at the regional level. Within Serbia there are three clearly distinguishable zones of species diversity according to biogeography, altitude, and latitude: Pannonian, Peripannonian, and Mountain-valley. Some species are found within only one zone (*Bombina bombina*, *Pelobates fuscus*, and *Pelobates syriacus*), but most species are widespread across two or three zones. Refugia are mostly typical for reptiles and these can be within a single zone (*Algyroides nigropunctatus*, *Zootoca vivipara*, *Podarcis erhardii*, *Elaphe quatuorlineata*, *Platycephalus najadum*, and *Testudo graeca*) or, in one case, within two zones (*Vipera berus*). By analysing the distribution patterns, individual species can be assigned to 6 regional chorotypes comprising the zones mentioned above: Chorotype 1 (Mountain-valley), Chorotype 2 (Peripannonian and Mountain-valley), Chorotype 3 (Pannonian, Peripannonian and Mountain-valley), Chorotype 4 (Pannonian and Peripannonian), Chorotype 5 (Pannonian), Chorotype 6 (Peripannonian) (adapted from Vukov et al., 2013, and Tomović et al., 2014).

In the fossil record from Serbian caves, 23 herpetofaunal species have been identified (Table 3.4), representing around 50% of the species living in Serbia today. The taxa that are missing from the fossil record are newts, salamanders (only one documented finding in Smolučka), turtles, and tortoises (undocumented findings), in addition to many species that are too similar for osteological differentiation in the fossil record (*Pelobates syriacus* and *Podarcis tauricus*). Nine species have been found only in Smolučka cave, but due to the uncertain stratigraphic position of the findings we were unable to incorporate this cave into other analyses. Considering that this is not a crucial factor, we are able to make some comments on the paleobiogeography of the species from Smolučka cave (Table 3.4). The most dominant chorotype in this faunal list is Southern-European with 4 species (22%). Interestingly, a high percentage (3 species, or 17% of the whole association) belongs to the Euro-Siberian

chorotype, comprising the most cold-tolerant species: *Rana arvalis*, *Vipera berus*, and *Lacerta agilis*, with *R. arvalis* being possibly completely absent from extant Serbian faunal assemblages, as it is better suited to cold open habitats that are no longer present in Serbia. It is noticeable that the extinct species *Pseudopus pannonicus* is present; this must be revised as this species is considered to have been extinct since the Pliocene or Early Pleistocene (see, for example, Bailon and Blain 2007; Blain et al. 2016). Smolučka cave is located in the Dinaric Alps in southern Serbia — today this zone is assigned to the Mountain-valley regional chorotype. With regard to the regional distribution of species, notable appearances include *Pelobates fuscus* and *Pelophylax klepton esculentus*. Currently, *P. kl. esculentus* is distributed across more than 50% of Serbia, but prefers Pannonian and Peripannonian chorotypes, while *P. fuscus* is considered a rare species with fragmented distribution and is found mostly in Pannonian chorotypes and along the Morava River. Curiously, Smolučka cave is located 1000 m above sea level (Paunović and Dimitrijević 1990), which is 190 m outside the upper elevation limit for *P. fuscus* (Zavadil et al. 1995; Kuzmin 1999; Beškov and Nanev 2002). Today, these amphibians mostly inhabit Pannonian and Peripannonian chorotypes while fossil evidence suggests that in the past they thrived in the Mountain-valley regional chorotype. This phenomenon is not seen with reptiles, as there are no reptiles that inhabit exclusively Pannonian or Peripannonian chorotypes. All the amphibians and reptiles found in the fossil record of Baranica, Hadži Prodanova, and Pešturina caves from MIS 3 and MIS 2 are still present in these areas, except for, occasionally, *V. berus*, and *R. temporaria*, which are considered “glacial relicts” from Pleistocene fauna (Paunović and Dimitrijević 1990), and have been in decline since the Pleistocene. Although these taxa are often found in the fossil record (especially *V. berus*), the distribution of this species is very fragmented and limited to refugia.

3.5. Conclusions

This paper is a review of Pleistocene herpetofaunal findings in Serbia. For the moment it includes only herpetofauna from late Pleistocene sites that have been published in either English or Serbian. Changes in the faunal composition have been recognised in relation with the successive cultural contexts of the last 60,000 years (the Mousterian-Aurignacian-Gravettian succession). Within the Balkan Peninsula, Serbia can be considered an interesting place to study the transition between the late Pleistocene and Holocene, contributing to our knowledge of the formation of the current biodiversity in the central Balkans. The most common problem encountered while gathering data from Serbian fossil sites for this work, is that, in many cases, small vertebrate findings cannot be directly associated to a particular cultural/chronological context due to a lack of dating. For a more complete picture of the climate in the Balkan Peninsula during the Mousterian-Aurignacian-Gravettian succession, it is necessary to expand this research, adding new sites into the analysis and possibly including older and younger layers. Often deeper layers are not investigated, but they may contain valuable information about the climate in MIS 4 or MIS 5. Similarly, small vertebrate records from the Holocene are generally not preserved due to stratigraphic mixing, but in cases where it is possible to distinguish early Holocene layers, these might contain very valuable information on the species that survived the Last Glacial Maximum, or the complex repopulating of the Balkan Peninsula by amphibians and reptiles.

4. New paleoclimatic and paleoenvironmental reconstructions for the Late Pleistocene from Smolucka cave

4.1. Introduction

The climate system is dynamic and variable, made up of a maze of connected components and subsystems (Tierney et al., 2020). Since it is such a complex system, its modelling is very difficult. Examining the results of various climate models requires a large amount of data on past climates (Kohfeld and Harrison, 2000). In the last decades of the 20th century, two of the most important paleoclimatic discoveries have been 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, 2007), 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 Bond cycles, and Heinrich events (Bond et al., 1992; Dansgaard et al., 1993; Bond and Lotti, 1995). In the meantime, the specific patterns of short relative warm intervals known as Greenland Interstadials (GI) became a stratigraphic standard for the last glacial period (Björck et al., 1998; Blockley et al., 2012).

Serbia is occupying the territory of central and northern part 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 (Carpatho-Balkan belt in the east, and

the Dinaric Alps in the west). As a consequence of the variance in 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 analysing small vertebrates (Đjurić 2019; Đjurić et al., 2016, 2017; Bogićević, 2004, 2008; Bogićević et al., 2011, 2012, 2017; Jovanović, 2016; Jovanović et al., 2020), large mammal fauna (e.g., Dimitrijević, 1995, 1997a, 1997b) and occasionally by pollen analysis (Argant and Dimitrijević, 2007). These remains are mainly found in the cave sediments since both mountain ranges are very favourable for the creation of limestone caves. Another approach in reconstructing the Late Pleistocene climate is analysing malacofauna from loess sequences of North Serbia (e.g. Marković, 2000, 2001; Marković et al., 2003, 2004, 2005, 2006).

The mammalian faunas from the Balkans have been synthesized by Musil (2003) and Stewart et al. (2003) which improved the understanding of climatic, vegetational, and faunal changes during the period of MIS 3 in Europe. Since small mammals 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., 2005; López-García et al., 2010). The aim of this study is to apply the Bioclimatic Analysis method (Hernández-Fernández, 2001a, b; Hernández-Fernández et al., 2005, 2007) and the Taxonomic Habitat Index (Evans et al., 1981) on the Late Pleistocene rodent assemblages from Smolučka 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.

4.2 Smolučka Cave

Smolučka Cave is located about 15 kilometers northeast of the city of Tutin, in the area of the village of Crkvine (Figure 4.1). The entrance to the cave is at an altitude of 945 meters above sea level and is located at the end of a small canyon cut through Triassic limestones by the Smolučka river. In front of the cave is a rather small platform, a so-called talus, from which the path descends to the bottom of a canyon created by the Smolučka River (Kaluderović, 1985, 1986, 1987, 1993). Sediments deposited inside the cave formed a total of six layers. It is assumed 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.

During the excavations, numerous bones and Middle Paleolithic (Mousterian) chipped stone artifacts have been collected. Description of the chipped stone artifacts has been presented by Kaluderović (1987, 1993) and Šarić (2013). Paleontological examination and identification have been performed on around 1200 mammal bone and teeth remains, of which 554 were identified as small mammals, and 644 belonged to large mammals (Dimitrijević, 1991). These remains findings were published in numerous papers (Dimitrijević, 1985, 1988, 1991, 1993, 1995, 1997a; Marković, 1997; Bogičević 2008). Fish, amphibian, and reptile remains have also been found, and 120 fossilized remains were identified (Paunović and Dimitrijević, 1990), but stratigraphical distribution has not been consistently recorded. Bird remains have

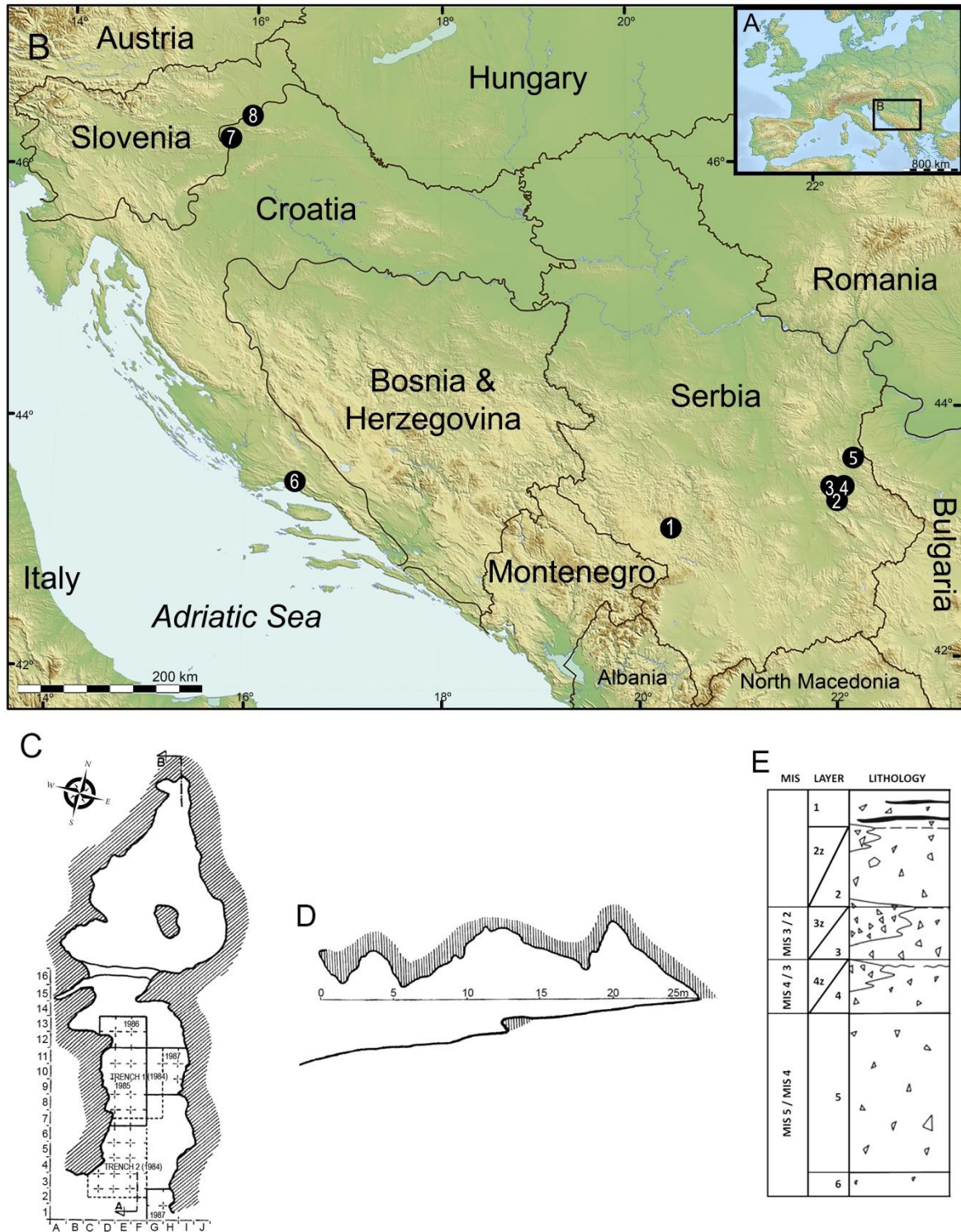


Figure 4.1 – A-B: Geographical location of the Smolučka site and other north Balkans cave sites, cited in this study. 1, Smolučka (Serbia); 2, Pešturina (Serbia); 3, Velika Balanica (Serbia); 4, Mala Balanica (Serbia); 5, Baranica (Serbia); 6, Mujina (Croatia); 7, Krapina (Croatia); 8, Vindija (Croatia); **C:** Map of the excavation sectors and trenches inside the cave; **D-E:** Stratigraphical profile from trench 1 (1985 excavation), adapted after Dimitrijević (1991) and Kaluđerović (1985).

also been found (Malez and Dimitrijević, 1990). Palynological samples have been negative (Dimitrijević, 1991). Fossiliferous layers containing small vertebrates have been organized chronologically using numerical dating. First dating done on material from Smolućka cave have been described in Hedges et al. (1990). The results came from AMS dating bone on charcoal from Layer 5 and showed age older than 38.000 years. Alex (2016) 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 54900 ± 3800 ($>49700\text{calBP}$), RTD7229B 60200 ± 6000 ($>54700\text{calBP}$); and four samples from layer 5: RTD7224 >39170 , RTD7225 >39170 , RTD7226B 53900 ± 2300 ($>50000\text{calBP}$), RTD7227 >39170 .

The position of the cave is very interesting and could have been appealing to the Middle Paleolithic groups. 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, which must have surrounded the cave also during Middle Paleolithic were certainly a genuine blessing and enormous importance in the process of choosing the habitation location (Šarić, 2013).

The region where the cave is located has a humid continental climate typical of the hilly Raška region. It is generally among the coolest regions in Serbia, but with hydrophilic vegetation. The landscape of the region is characterized by plateaus, hills, numerous mountain areas, gorges, valleys, sinkholes, caves, and rivers with a number of smaller tributaries. Plainland is rare.

4.3 Material and methods

4.3.1 Faunal list

Descriptions of the rodents from the late Pleistocene of Smolučka cave have been done in a preliminary publication (Dimitrijević, 1991), more complete descriptions can be found in Dimitrijević (1995), and then completed in an unpublished PhD dissertation (Bogićević, 2008). Most of complementary data concerning other Serbian caves have been collected from previous publications (Jovanović et al., 2020), checked, and updated for this research. Faunal lists used in this research are presented in Table 4.1.

Species/distribution	Layer 6		Layer 5		Layer 4		Layer 3		Layer 3z	
	MNI	%	MNI	%	MNI	%	MNI	%	MNI	%
<i>Apodemus sylvaticus</i>	-	-	-	-	1	2.6	-	-	2	2.3
<i>Arvicola mosbachensis/amphibius</i>	1	20	-	-	1	2.6	-	-	5	5.7
<i>Chionomys nivalis</i>	-	-	1	12.5	4	10.5	2	16.7	7	8
<i>Clethrionomys glareolus</i>	-	-	-	-	?	?	-	-	2	2.3
<i>Cricetulus migratorius</i>	-	-	-	-	-	-	1	8.8	4	4.6
<i>Glis glis</i>	1	20	-	-	-	-	-	-	-	-
<i>Hystrix sp.</i>	-	-	1	12.5	-	-	-	-	-	-
<i>Mesocricetus newtoni</i>	-	-	-	-	3	7.9	-	-	9	10.3
<i>Microtus arvalis/agrestis</i>	2	40	2	25	22	57.9	6	50	37	42.5
<i>Microtus subterraneus</i>	-	-	2	25	6	15.8	2	16.7	12	13.8
<i>Muscardinus avellanarius</i>	-	-	-	-	-	-	-	-	1	1.1
<i>Dryonomys nitedula</i>	-	-	-	-	-	-	-	-	1	1.1
<i>Sicista subtilis</i>	-	-	-	-	1	2.6	-	-	5	5.7
<i>Spalax leucodon</i>	-	-	1	12.5	-	-	1	8.3	1	1.1
<i>Spermophilus cf. citelloides</i>	1	20	1	12.5	-	-	-	-	1	1.1
Shannon diversity index	1.33		1.73		1.33		1.36		1.92	

Table 4.1 – Faunal rodent lists from Smolučka cave (Serbia) with distribution within layers expressed in Minimum Number of Individuals (MNI), percentage within the total assemblage (%), and Shannon diversity index.

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, 1967). 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, 1978; Andrews et al., 1979; Artemiou, 1984; Bonis et al., 1992; Andrews, 1995). This assumption is based on the fact that climate imposes a series of habitats which, in turn, impose structure on the community (Walter, 1970; Blondel, 1986; Currie, 1991; Kerr and Packer, 1997; Shepherd, 1998). 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, 1967; Fleming, 1973; Weerd and Daams, 1978; Legendre, 1986; Kay and Madden, 1997). 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, 1978; Daams and Meulen, 1984; Sesé, 1991; Meulen and Daams, 1992) and quantitative (Montuire, 1996; Montuire et al., 1997).

4.3.2 Bioclimatic Analysis

The Bioclimatic Analysis is used to reconstruct Pleistocene paleoclimate. This method is first introduced by Hernández Fernández two decades ago, and later developed to be applicable on Pleistocene sites (Hernández-Fernández et al. 2007, Royer et al. 2020). Bioclimatic model is based in the hypothesis that a significant correlation between the climate and the mammals communities exists. According to Hernández-Fernández (2001a, b), Hernández-Fernández and Peláez-Campomanes (2005) and Hernández-Fernández et al. (2007), any mammal assemblages can be included in ten climatic types, that can be distributed using the Climatic Restriction Index ($CRI_i = 1/n$, 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*; III *Transition tropical semiarid*; IV *Subtropical arid*; V *Subtropical semiarid*; VI *Subtropical arid*; VII *Subtropical semiarid*; VIII *Subtropical arid*; IX *Subtropical semiarid*; X *Subtropical arid*.

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 4.2), the Bioclimatic Component (BC; representation level by level of each of the available climates) can be calculated using the following formula:

$$BC_i = (\sum CRI_i) \times 100/S,$$

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, 2005) which allows, by means of a series of functions, to estimate various climatic parameters.

Four climatic variables have been calculated for each of the Smolučka 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) (Table 4.4). Distribution Indexes used for calculating these climatic variables are presented in Table 4.2.

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.

For larger taxonomic categories, like *Arvicola cantiana/terrestris* (here adapted to recent nomenclature as *Arvicola mosbachensis/amphibi* and *Hystrix* sp. (as listed in Dimitrijević, 1991), it was necessary to consider their taxonomical position in order to establish their CRI.

	I	II	II/III	III	IV	V	VI	VII	VIII	IX
<i>Apodemus sylvaticus</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.50 0	0.00 0	0.50 0	0.00 0	0.00 0	0.00 0
<i>Arvicola mosbachensis/amphibi</i> <i>us</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.25 0	0.00 0	0.25 0	0.25 0	0.25 0	0.00 0
<i>Chionomys nivalis</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.25 0	0.00 0	0.25 0	0.00 0	0.25 0	0.25 0
<i>C. glareolus</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.50 0	0.00 0	0.50 0	0.00 0
<i>Cricetulus migratorius</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.33 3	0.00 0	0.33 3	0.33 3	0.00 0	0.00 0
<i>Dryonomys nitedula</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.33 3	0.00 0	0.33 3	0.33 3	0.00 0	0.00 0
<i>Glis glis</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	1.00 0	0.00 0	0.00 0	0.00 0
<i>Hystrix</i> sp.	0.33 3	0.33 3	0.00 0	0.00 0	0.00 0	0.33 3	0.00 0	0.00 0	0.00 0	0.00 0
<i>Mesocricetus newtoni</i>	0.00 0	0.00 0	0.00 0	0.00 0	1.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0
<i>M.arvalis/ agrestis</i>	x	x	x	x	x	x	x	x	x	x
<i>Microtus subterraneus</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	1.00 0	0.00 0	0.00 0	0.00 0
<i>Muscardinus avellanarius</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	1.00 0	0.00 0	0.00 0	0.00 0
<i>Sicista subtilis</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.50 0	0.00 0	0.50 0	0.00 0
<i>Spalax leucodon</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.00 0	0.50 0	0.50 0	0.00 0	0.00 0
<i>Spermophilus citelloides</i>	0.00 0	0.00 0	0.00 0	0.00 0	0.33 3	0.00 0	0.33 3	0.33 3	0.00 0	0.00 0

Table 4.2 – Distribution Indexes used for calculating paleoclimatic reconstruction based on the Bioclimatic analysis. The values are used from Hernández-Fernández (2001a, b) and adapted in accordance with this research from Hernández-Fernández et al. (2007).

Koenigswald and Kolfshoten (1996) consider *Arvicola cantianus* as a subspecies of the current *A. terrestris*, in contrast to other authors (Chaline and Sevilla, 1990; Cuenca-Bescós et al., 1995; Rekovets and Nadachowski, 1995). 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) (Hernandez-Fernandez et al., 2007). 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, 1994). For this reason, the assignment of current analogues will be made based on belonging to any of the current subgenus (Weers, 1994). *Hystrix primigenia* (Wagner, 1848) and *H. refossa* Gervais, 1852: they belong to the subgenus *Hystrix* to which three of the current species belong (*H. africae australis*, *H. cristata* and *H. indica*) that, together, occupy climatic zones I, II, II / III, III, IV, V, and VII. *Hystrix vinogradovi* Argyropulo, 1941 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 (1991), no skeletal remains of the crested porcupine were currently found in Smolučka 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 teeth of any other rodent. This is typical behaviour for *H. cristata* as it commonly chews on bones for calcium and to sharpen its incisors (Nowak, 1999). However, a recent discovery of *Hystrix vinogradovi* in Pešturina cave layer 4 (Dimitrijević, under review) implies that without osteological findings teeth marks on the long bone of a large mammal from layer 5 Smolučka cave (Dimitrijević, 1991) cannot be assigned to a certain species.

4.3.3 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, 1994). For this purpose, and in accordance with the primary objective of this research, the rodents have been divided into five groups, according to their main habitat preferences (Bogićević, 2008):

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 arvalis* and *agrestis*, *Spalax leucodon*)

E – Steppe and semi-arid species (*Sicista subtilis*, *Cricetulus migratorius*, *Cricetus cricetus*)

4.3.4 Taxonomic Habitat index

This method has been first introduced by Evans et al. (1981), 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. 1981), 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 1990).

Data on small mammal distribution preferences are used from Andrews (1990) and adopted in accordance with this research. Indexes used for calculating are presented in Table 4.3.

Species/distribution	Tu	B	D	M	S	FS	A	Tr	Mo
<i>Apodemus sylvaticus</i>	0	0	0.2	0.2	0.2	0.2	0.2	0	0
<i>Arvicola mosbachensis/</i> <i>amphibius</i>	0.2	0.3	0.2	0.05	0.1	0.1	0	0	0.05
<i>Chionomys nivalis</i>	0	0	0	0	0.15	0.05	0	0	0.8
<i>Clethrionomys</i> <i>glareolus</i>	0	0.4	0.4	0	0	0.1	0	0	0.1
<i>Lagurus lagurus</i>	0	0	0	0	0.6	0.15	0.1	0	0.15
<i>Microtus</i> <i>arvalis/agrestis</i>	x	x	x	x	x	x	x	x	x
<i>Microtus subterraneus</i>	0	0	0.15	0.23	0.2	0	0.05	0	0.35
<i>Muscardinus</i> <i>avellanarius</i>	0	0	0.7	0.3	0	0	0	0	0
<i>Sicista subtilis</i>	0	0	0	0	0.7	0.2	0.05	0	0.05
<i>Spalax leucodon</i>	0	0.05	0.1	0	0.7	0.1	0	0	0.05
<i>Spermophilus</i> <i>citelloides</i>	0	0	0	0	0.9	0.1	0	0	0
<i>Glis glis</i>	0.05	0.05	0.6	0.1	0.05	0.1	0	0	0.05
<i>Mesocricetus newtoni</i>	0	0	0	0	0.8	0.15	0	0	0.05
<i>Cricetulus migratorius</i>	0	0	0	0.1	0.3	0.1	0.5	0	0
<i>Dryonomys nitedula</i>	0	0.2	0.4	0	0	0.2	0	0	0.2

Table 4.3 – 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*, *Glis glis* are from Jovanović et al. (2020). Indexes for species: ***Mesocricetus newtoni*** and ***Dryonomys 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.

4.3.5 Species diversity and richness

The number of species in a community is called the species richness. According to Rapoport's rule (Stevens, 1989, 1992) the number of species decreases with increasing latitude and altitude. However, this can only be taken globally and regarding the overall fauna. The richness of the species 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., 1998).

It is most often calculated as follows:

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

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

4.4 Results

4.4.1 Rodent assemblages from Smolučka 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 presence of this taxa is not accounted in Table 4.2 and Table 4.3. Most representatives in the rodent assemblage from Smolučka cave (seven species: *Cricetulus migratorius*, *Mesocricetus newtoni*, *Arvicola mosbachensis/amphibius*, *Chionomys nivalis*, *Microtus arvalis/agrestis*, *Microtus (Terricola) subterraneus*, *Clethrionomys glareolus*) are cricetids (*Cricetidae*). One species (*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 Hystriidae (*Hystrix* sp.) (Table 4.1). 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, 2001), now representatives of this species live only in Romania and Bulgaria (Wilson and Reeder, 2005). *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., 2008). As taxonomical position of the member of a genus *Hystrix* is explained above. Distribution of *Hystrix* sp. today can be attributed to Italy, North Africa, and sub-Saharan Africa (Cabrera, 1932; Corbet and Jones, 1965; Ranck, 1968; Smit and Wijngaarden, 1981; Niethammer, 1982). 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., 2019). 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.

4.4.2 Paleoclimatic reconstructions

The south Raška region features is characterized by continental mountainous climate. The landscape is mostly 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.

Past climatic parameters were obtained by applying the Bioclimatic analysis method to the fossil rodent assemblages (Table 4.4). 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, 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 4.1, Figure 4.2). 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 Smolučka 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 levels are continuously high, slightly dropping in Layer 4 but with no real indications of dry climate (Figure 4.2, Table 4.4).

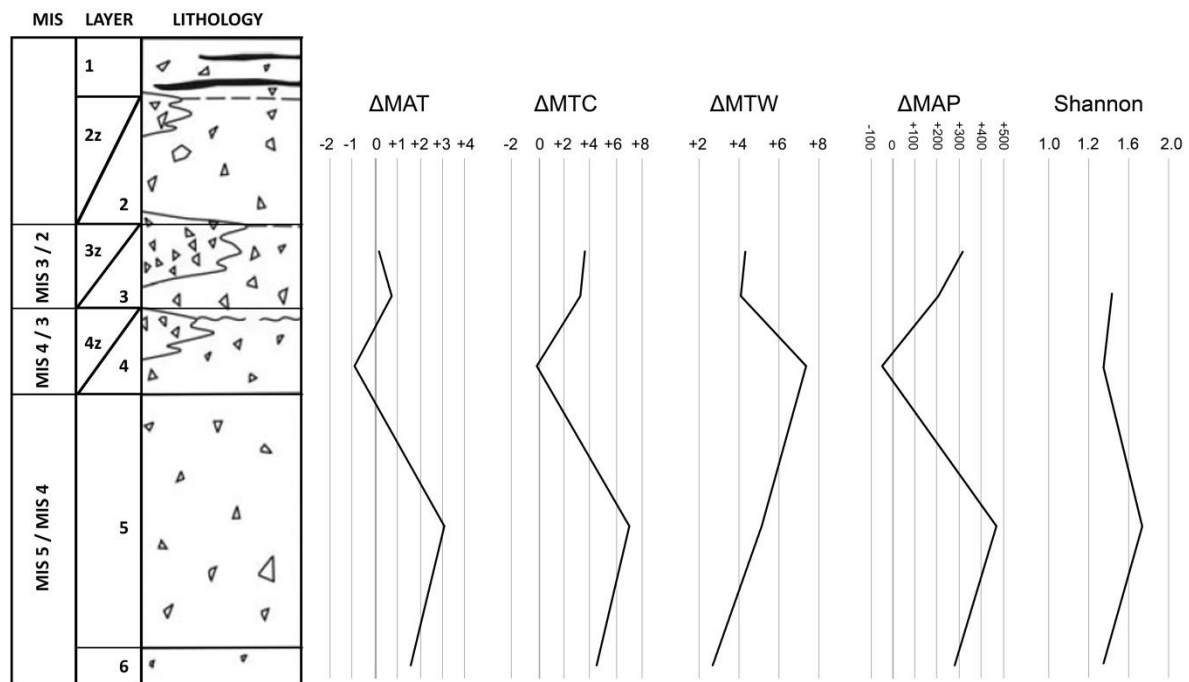


Figure 4.2 – Paleoclimatic and biodiversity reconstructions for the Late Pleistocene of Smolučka cave (Serbia). Graphical representation showing climatic parameters: Δ MAT (difference between estimated and modern mean annual temperature in °C), Δ MTW (difference between estimated and modern mean temperature of the warmest month in °C), Δ MTC (difference between estimated and modern mean temperature of the coldest month in

°C), Δ MAP (difference between estimated and modern mean annual precipitation in mm), and Shannon diversity index.

	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
Δ MAT	+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
Δ MTW	+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
Δ MTC	+4.5	+7.0	-0.1	+3.2	+2.4
MAP (in mm)	1247	1431	924	1178	1277
Today	965	965	965	965	965
Δ MAP	+282	+466	-41	+213	+312

Table 4.4 – 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).

4.4.3 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 (Figure 4.3, Table 4.5). 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 aquatic environments such as *Arvicola mosbachensis/amphibius*. Mountain elements are also highest in Layer 5, coincidentally 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. In general environment while these layers formed was slightly more humid and warmer and the representation of real forests is low.

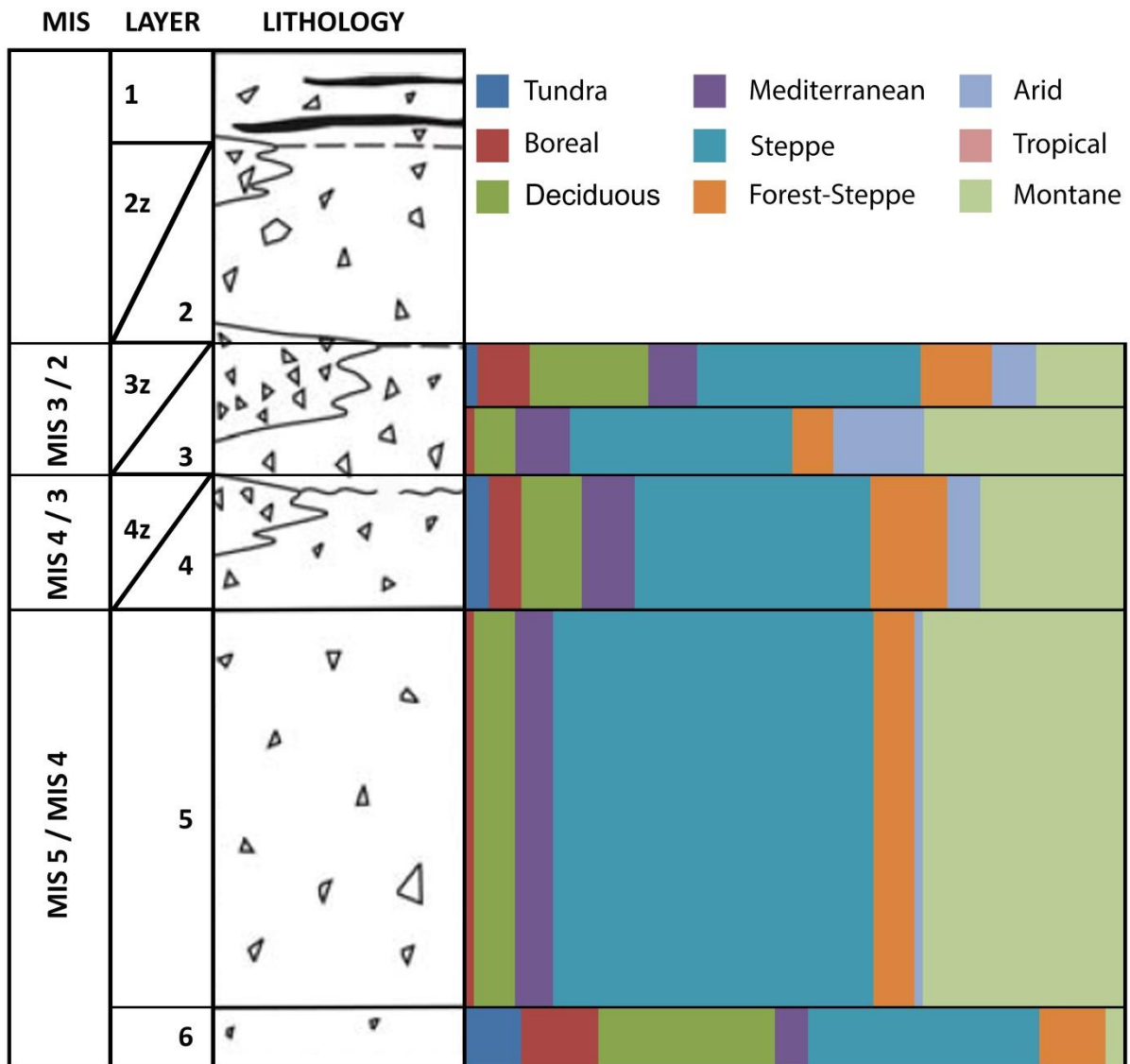


Figure 4.3 – Paleoenvironmental reconstruction for the Late Pleistocene of Smolučka cave (Serbia) based on the Taxonomic Habitat Indexes.

	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

Table 4.5 – Distribution of habitats obtained by calculating indexes from Table 4.3, presented in percentage (%).

4.4.4 Biodiversity

The vicinity of Smolučka cave is a complex system of mosaic habitats with extraordinary environmental heterogeneity. High altitude, fertile plains, abundant water, exposure to sunlight, therefore supports 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, 1992).

Throughout the different archeological layers, rodents showed various patterns of appearances and disappearances (Table 4.1). The value of the Shannon diversity index is highest in Layer 5. The value of the index in the other layers is approximately the same. But if in the chart instead of values for Layer 3 we set the value for 3z, we get significant growth in diversity, therefore, a significant 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.

4.5 Discussion

4.5.1 Comparison with different proxies (Insectivores and large mammals)

The mammalian fauna from Smolučka cave consists of 42 different species. Arvicolins are the most represented group in the Smolučka cave, but Insectivores (Eulipotyphla) are also quite common, especially in the lower layers, while in the higher layers their number decreases (the climate becomes 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, the most frequent and present in all layers, is the cave bear (*Ursus spelaeus*) who regularly used the cave for habitation. The cave bears prefer to avoid open plains, instead they search for caves close to the forested or forest-edged terrains (Bieder, 2005). Other carnivores could have also used the cave as a shelter or occasionally bring their prey 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. In layer 5 is recorded presence of a large bovid (*Bos* or *Bison*), certainly associated to steppe environments.

4.5.1 Chronological context of Smolučka cave

The oldest layers in these analyses from Smolučka cave are layers 5 and 6. The proposed age of Layer 6 according to its superposition corresponds to the “first Wurmian stadial”

(Dimitrijević, 1991). Layer 6 did not provide identifiable material except a small number of osteological finds. This layer is probably deposited during the early MIS 5. Layer 5 is possibly comparable to Pešturina Layer 4. This layer has recently been thoroughly explored since the discovery of the first Neanderthal specimen from Serbia (Radović et al., 2019), but without new datings from Smolučka 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 Smolučka layer 5 are also present in Pešturina layer 4, suggesting that these two layers were probably at least partially deposited at the same time. Pešturina layer 4 has been thoroughly dated using the ESR method (Blackwell et al., 2014). 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, under review). Sedimentological features and mammalian remains of Layer 5 indicate interstadial character of this deposition. According to the (Dimitrijević, 1991), this layer is deposited after the “first Wurmian stadial”, when warm climate species disappeared from central Europe, and probably the Balkans. After the macroscopic analysis of sediments from Layer 5, Šarić (2013) 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 is almost certain that it has been deposited during the MIS 5.

Layer 4 contains osteological material and chipped stone artifacts, the chronology of this layer remained insufficiently defined (Šarić, 2013). According to Dimitrijević (1991), Layer 4 probably belongs to “second Würmian stadial” stage. Macroscopic analysis of sediments confirmed that layer 4 dates from “interstadial Würm 2/3” (Šarić 2013). 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 we conclude that this layer is deposited during the MIS 4 and possibly late MIS 5.

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, two cold species of the genus *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, 1991). Among the rodent remains, Layer 3 holds the most “cold elements” compared to other layers (Figure 4.3), *Spermophilus* cf. *citelloides*, *Mesocricetus newtoni*, and *Chionomys nivalis* are more common in layer 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 Figures 4.1 and 4.2). The superposition of the sublayer is uneven which makes establishing the age of the sublayer difficult without dating (Dimitrijević, 1991).

The two uppermost (Layers 1 and 2) of Smolučka 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.

4.5.2 Paleoclimatic and paleoenvironmental evolution during the Late Pleistocene in Serbia

4.5.2.1 Marine Isotope Stages 5

In Layer 6, THI shows a notable rise of Boreal forest inhabitants compared to Layer 5 (Figure 4.3), this suggests that climate was probably slightly colder than during the deposition of

Layer 5 and this is supported by Bioclimatic analysis results. Habitat surrounding the Smolučka cave during the early MIS 5 was probably Boreal Forest-Steppe.

The most striking layer in Smolučka cave is Layer 5. It's very abundant 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, personal communication), with findings in caves: Praška Grobina in Slovenia (Rakovec, 1961), Veternica in Croatia in the layer assigned to MIS 5 (Miracle et al., 2010), 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, 1982). 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 (Figure 4.3). Such climate pattern is consistent with an interglacial period, but it is poorly understood in Northwestern Balkans and rarely put in context with small vertebrate remains.

4.5.2.2 Marine Isotope Stage 5 or 4

Deposition of Layer 4 probably represents long-lasting climate shifts during the late MIS 4, as such, it records both warm and cold climate periods. As the exact age of this layer is still undetermined, and 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 (Cserkés et al., 2009). Compared to other layers in Smolučka cave, Layer 4 has the lowest index for the diversity of species, but not much lower than Layers 5 and 6 (Bogićević, 2008). A Low index can indicate disappearance of species that could not adapt in new living conditions (López Antoñanzas and Cuenca-Bescós, 2002; Williams et al., 2002). The difference in climate between Layer 5 and Layer 4 can be determined through analysis of the difference in fossil findings, as 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 1-4°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 (Figure 4.3).

4.5.2.3. Marine Isotope Stages 3 or 2

Bioclimatic analysis for Smolučka 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 (Figure 4.3). 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. Maybe 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., 2020). A problem presents a fact that we cannot pinpoint the exact age of the deposition of the MIS 3 Smolučka 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 Smolučka. These results are somewhat unexpected due to Smolučka being located at a higher altitude than the other sites. All of the species represented in Smolučka also are present in other sites.

4.5.2.4 Comparison with other Balkan sites

In Western Balkans, Mujina cave (Croatia) can possibly be correlated with Smolučka layers. Mujina cave, in Western Dalmatia, is the only systematically excavated and well-dated

Middle Paleolithic cave site in the eastern Adriatic. Its stratigraphic sequence covers the period between 45 and 39 uncalibrated ka (Karavanić et al., 2008, Boschian et al., 2017), corresponding to the younger layers from Smolučka (Layers 4, 3 and 3z). Similar to Smolučka 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., 2017). 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., 2017). 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, 2014; Alex, 2016) thus overlapping with Uluzzian and Protoaurignacian industries in Italy (Villa et al., 2018). The Middle Paleolithic sites in Croatia are important because of the association between lithic industries and hominin remains. Probably the stone tools from Smolučka cave could be correlated with most famous sites like Krapina or Vindija in NW Croatia. This is probably what original excavators had in mind when they picked Smolučka in 1985, but unfortunately no hominin fossils were unearthed there.

4.6 Conclusions

Smolučka cave has long been recognized as an important archeological site. Systematic archeological excavations have been organized in the past, but the paleontological importance of this site has been sometimes overlooked in recent years. The excavations in this site

stopped due to the worsening political situation in the country at that time. Smolućka can be considered as one of the richest 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 (Serbia) allows some characterization of environmental change in central Balkans between MIS 5 and MIS 3. MIS 5 (Layer 5) has been characterized as interstadial with 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 did not have 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., 2019), and has been suggested for the Middle Pleistocene layers of the nearby Velika Balanica (Radović et al., 2020; Roksandic et al., 2020). New excavations and multidisciplinary studies currently conducted at Smolućka cave, which include systematic dating via ESR (instead of the ^{14}C AMS method), could advance this work and address numerous problems we have encountered.

5. GLOBAL CONCLUSIONS AND FUTURE PERSPECTIVES

The stratigraphic position of the layers I have studied in this thesis ranges from an interglacial MIS 5, which is an interesting period in the evolution of climate, to another interesting change in human history which is the arrival of anatomically modern humans. In a cultural context, the layers described in this thesis were deposited during the Mousterian-Aurignacian-Gravettian succession. During this approximately 100 ky long period, it is acknowledged that the Balkans, along with the rest of the world, was subjected to multiple climatic changes. Through extensive research of the fossil record using multidisciplinary approach, we can hope to determine their chronology and discover effects on the living world.

5.1. The last major interglacial (before Holocene)

Termed the Eemian (Sub-stage MIS 5e), the last major interglacial period before Holocene, has been established between 124 kya and 119 kya, and reached its peak at 123 kya, when the global mean surface temperatures were at least 2 °C warmer than today. Mean sea level was 4–6 m higher than at present as a consequence of reductions of the Greenland ice sheet (Rohling et al., 2007). Until recently this period has not been extensively studied in the territory of Serbia, but some dates from Pešturina cave Layer 4 obtained using the ESR method (Blackwell et al., 2014) being placed around 120 ky, attract more interest to this sub-stage. Especially interesting is the comparison of this layer with the lower layers from Smolučka cave. Small vertebrate faunal analysis of the Smolučka Layer 5 shows remarkable similarity with Pešturina Layer 4. Another important indicator that lower layers of Smolučka cave may have exhibited interglacial climate conditions, are results of Bioclimatic analysis

(elaborated in Chapter 4), indicating on average 2.3 °C warmer temperature than today. On a global scale, Eemian is followed by a rapid climatic deterioration at about 116 kya (MIS 5d). This was followed by a warmer period at about 100 kya (MIS 5c) (Stone et al., 2012). I am not able to conclude with certainty which of these sub-stages was the last harboring the thermophilic fauna living in northern Balkans. To complete the picture of climate conditions in the northern Balkans during the MIS 5 we need to augment more sites and make the comparisons. Herpetofaunal data from this time period is especially scarce. Potential data may come from Pešturina, Mala Balanica, Velika Balanica, and eventual renewed excavation of Smolučka cave, since the remains described in a publication (Paunović, 1990) are considered lost. Because there are no other sites in Serbia conclusively attributed to the MIS 5 and dated, up to this point, it could be possible to use the data from the sites located in the neighboring countries. Without any intention to exclude any other potentially comparable sites, based on the publications available, potential MIS 5 sites may include: Praška Grobina cave (Slovenia), and Veternica, Vindija, Krapina and Mujina caves (Croatia).

5.2 The Middle to Upper Paleolithic transition

Paleolithic sites containing the Mousterian-Aurignacian-Gravettian succession are numerous across Serbia and Europe; arguably all karstic caves in Serbia with a deposition of sediments have a sequence containing at least a part of this succession.

Some authors have studied the archeological remains from the layers in Serbian caves (Alex, 2016; Mihailović, 2009, 2014, etc.) in an attempt to establish chronology of appearances and disappearance of Neanderthals and arrival of anatomically modern humans on the Balkans.

Sitting at the crossroads of Europe, the Balkan Peninsula represents the connection of several important migration corridors. Rivers such as the Danube cut paths through mountain ranges, making roads for migrating animals and humans to follow (Roksandić, 2016). Presence of

Neanderthals has been recorded in numerous sites (e.g. Alex, 2016; Mihailović, 2009, 2014), but only one Neanderthal tooth has been found in Pešturina cave (Radović, et al., 2018). This site has also been confirmed for presence of anatomically modern humans, but at different times. Regarding the climatic and environmental changes during the Mousterian-Aurignacian-Gravettian succession, according to analyses (elaborated in Chapter 3), there were no significant difference in the herpetofaunal assemblage when Mousterian and Aurignacian assemblages are compared. The analysis performed on rodent assemblage show mild climate, slightly colder than today, but stable. Judging by these results, I propose that climate change was not crucial factor in Neanderthal extinction on Balkans. Neanderthals and anatomically modern humans overlapped for several thousand years in the Balkans (Alex, 2016). During this period of overlap Neanderthals and anatomically modern humans occupied distinct geographic zones, consistent with the models of prolonged coexistence by displacement or avoidance. The period of overlap ended by 39 kya at the time of the Campanian Ignimbrite eruption and onset of the Heinrich Event 4 cold phase (Alex, 2016). However, we have no evidence of Neanderthals in Serbia after the 44 kya (Mihailović, personal communication) and every Neanderthal finding with associated small vertebrate remains represents an interesting opportunity for future studies.

An event considered critical for understanding human history in the Balkans is the Campanian Ignimbrite eruption, one of the largest known volcanic eruptions in the Quaternary. The most widely used age estimate for this event, based on $^{40}\text{Ar}/^{39}\text{Ar}$ dating, is $39,280 \pm 110$ yr BP (de Vivo et al., 2001; Bronk Ramsey et al., 2015). Based on sulphate concentrations in the Greenland ice core record, the eruption may have caused global cooling of $1-2^\circ\text{C}$ (Costa et al., 2012) or $3-4^\circ\text{C}$ (Fedele et al., 2008) for a period of 2-3 years. The Campanian Ignimbrite eruption coincided with the onset of Heinrich Event 4 (H4), a millennial-scale period of cooling within the milder climate conditions in MIS 3 (Hemming,

2004). The impact of the Campanian Ignimbrite eruption on the environment and human populations has been widely debated (e.g., Lowe et al., 2012; Costa et al., 2012; Fedele et al., 2008). In Chapter 3, I have attempted to identify the difference in small vertebrate communities before and after this event. Based on the results, I can consent that some mammal assemblages seem to have remained stable throughout this period (Miracle et al., 2010), and there are no notable changes in the composition of herpetofauna. Nonetheless, the problem represents that the Campanian Ignimbrite eruption has not been recognized physically in the stratigraphy of the sites in the form of a depositional line, and the small vertebrate remains have not been collected relative to this line. Only Pešturina cave has been dated thoroughly enough to the point of firmly establishing it. In the future, other sites (with exception of Hadži Prodanova cave, as stratigraphical profile is permanently buried) can also be excavated with a special attention aimed to the Campanian Ignimbrite deposition and the extinction of the Neanderthals.

In contrast to the mild climate during the MIS 3, clearly there was a change in the composition of the herpetofaunal assemblage, recorded in the Gravettian layers, linked to the change in climate during MIS 2. It is during the levels assigned to the Gravettian phase that the coldest conditions are manifested, with the presence of herpetofauna characteristic for cold mountain conditions and capable of resisting even sub-boreal conditions (concurrence of *Rana temporaria*, *Lacerta agilis*, *Zootoca vivipara* and *Vipera berus*). Unfortunately younger layers are often subjected to the substantial stratigraphical mixing, therefore attracting less consideration within the researchers. According to Clark et al. (2009), and Evans et al. (2014), growth of ice sheets commenced 33,000 years ago, and maximum coverage was between 26,500 years and 19–20,000 years ago, when deglaciation commenced in the Northern Hemisphere, causing an abrupt rise in sea level. Decline of the West Antarctica ice sheet occurred between 14,000 and 15,000 years ago, consistent with evidence for another

abrupt rise in the sea level about 14,500 years ago. According to Musil (2010), a relatively warm climate in Central Europe has been recognized at 31,500, 30,000, 27,500, 26,000 and 21,000; while relatively cold periods existed at 32,000, 31,000, 29,000-27,500, 25,000-21,500 (all data are in calibrated years BP). These climatic fluctuations can be assigned to specific climatic phases for the purpose of establishing typical herpetofaunal assemblages for northern Balkans. This concept is introduced by Böhme (1996, 2000), and phases include: late glacial, early interglacial, interglacial climate optima, late interglacial and interstadial., Latest interglacial to Early glacial, and Glacial periods. In Chapter 3, I have attempted to make comparisons with typical Central European herpetofaunal assemblages (Böhme 1996, 2000), without establishing typical herpetofaunal assemblages for northern Balkans.

5.3 Future perspectives

Traditionally, Paleolithic archeological excavation usually focused on searching for osteological hominine remains, and/or lithic tools and the bones of the large mammals. New approaches in Archaeology is more and more involving additional disciplines and techniques in order to produce multidisciplinary and transdisciplinary studies, especially when hominine remains have been recovered. In this line, Serbian archaeology has been involving paleontologists or zooarchaeologists searching for small vertebrate remains by means of methods of sieving and washing, and producing faunal list usable for precising both chronology (biochronology) and paleoenvironment. In the last decades, studies of small vertebrates have increased notably (see for example Cuenca-Bescós et al., 2016). They are associated with important archeological and paleontological Quaternary sites in Europe. In parallel with these studies on small mammals, an increasing number of researchers have been progressively interested in other groups of small vertebrates such as fish, amphibians, reptiles and birds and the paleoecological data they can furnish.

As a result of their reduced size, small habitat ranges and in most cases low mobility, small vertebrates are known to be more susceptible to regional changes than large mammals and plants, especially in Europe where mountain ranges and sea barriers block their retreat to the south. Among the microvertebrates, rodents are known to be the best tools for biochronological, biostratigraphic and paleoecological reconstructions. Amphibians and reptiles also have an increasing reputation in the context of paleoclimatic and paleoenvironmental analyses (López-García and Blain, 2020).

Little by little, new studies are enlarging the field of work to include new areas of the European continent. In such cases, the main task is the description of the species represented in these fossil assemblages, and there remain many living species still not described osteologically, as it is currently being done in Serbia by researchers as Katarina Bogičević and Dragana Đurić. Taking advantage of synergies with other disciplines, small vertebrate studies are progressively incorporating new methodologies such as ancient DNA extraction, oxygen isotope studies or geometric morphometrics, and introducing computer science and more complex modelling into their analyses (López-García and Blain, 2020). These types of studies very much complement, but do not replace, fundamental methods in osteological and morphometric description. Nevertheless, their main aims are to help with the reconstruction of paleoclimate and paleoenvironment of the different hominine species and replace their activities inside a changing ecological context.

Such a program is obviously very ambitious and would need many years, and funds for studies specialized in different disciplines. But my perspectives of future would be to continue in such a direction.

In this work, I have tried to establish a review of the state of the art on small-vertebrates studies in Serbia, by documenting all available data on small vertebrate remains for Baranica, Hadži Prodanova, Pešturina, and Smolučka caves. Herpetofaunal data from MIS 5 sediments

is especially scarce, and I would intend to continue to produce new data for this time period. Mousterian-Aurignacian-Gravettian succession is better documented. Neanderthals and anatomically modern humans overlapped for several thousand years. *Homo sapiens* survived, while Neanderthals went extinct, and based on paleoclimatic and paleoenvironmental reconstructions, climate change was not a crucial factor in Neanderthal extinction on Balkans. Balkan Peninsula has already been identified as the confirmed route of animal migrations in the Early Pleistocene (O'Regan et al. 2011). Regarding the Middle and the Late Pleistocene it would be very important to establish a pattern of appearances and disappearances of small vertebrates. Such an attempt is presented in this thesis but it is an ongoing process that will be further reinforced by future exploration.

In the autumn of 2020, after I have participated in the excavation of Velika Balanica and Mala Balanica caves and I was presented with the opportunity to process the sediments, some of which from the earlier excavations, even when the famous *Homo* sp. BH-1 mandible was recovered. I was able to begin the processing using the methods of sieving and washing I learned at previous excavations in Spain (Orce and Atapuerca), but unfortunately due to limited time in my doctoral program, these results will be published later, in some other research.

I had the opportunity to learn the methods for the reconstruction of paleoclimate and paleoenvironment, different from the ones that were already applied on Serbian small-vertebrate record, and use them with success. I have acquired substantial quantity of results that were partially presented in Chapters 3 and 4. But significant amount of data is still without context and could not be presented in this thesis, but will be presented in future publications instead.

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