Foreword

Contrary to most of the Palaeolithic projects done through significant side grants and direct PhD funds, this one is a real praise of good will. Fundings received per annum for the entire project „Cultural changes and population dynamics in the Palaeolithic and Mesolithic of the Central Balkans“, funded by Serbian Ministry of Education and Science (ON 177023) would not suffice to even pay a rent for archaeological team of 10 people to spend a month of archaeological excavations in most of the countries of European Union. This research is an ultimate praise to good will and scientific devotion to all people who were engaged in it. In the shaping of my scientific comprehension of Palaeolithic archaeology I owe the most to dr Dušan Mihailović, professor of Palaeolithic archaeology at Faculty of Philosophy at Belgrade University and leader of the project under which this research was conducted. His devotion to pursue research by all means improved Palaeolithic research in Serbia in last 15 years. Regarding specialistation in archaeozoology nothing of this would be possible without the engagement of my mentor during my MA and PhD studies, dr Vesna Dimitrijević, to whom I am indebted for transferring her knowledge, ideas, and discussion, but also for meeting me with fellow archaeozoologists, some of which greatly helped this study. One of the most important colleagues I received my training from is dr Ana Belen Marín-Arroyo from Cantabria University in Santander, and her instructions in taphonomic perspectives greatly influenced this study. I am greatly indebted to dr Zlatozar Boev from Natural History Museum in Sofia, Bulgaria, and dr Sheila Hamilton-Dyer from Bournemouth University for their immense help with avian remains from the Pešturina and Hadži-Prodanova caves. Good looking images in this work are thanks to John Meenely from Belfast Univeristy for his work on 3D scan at Pešturina, dr Nikola Vuković working as technician at SEM-EDS laboratory of Faculty of Mining and Geology, Belgrade University, and archaeologist Irina Kajtez for GIS data. I need not mention that this was done from their side to support me and for the love of science, without a single coin taken. The shaping of the thesis, control of data and flow of work owes thanks to dr Sonja Bogdanović, dr Marko Porčić and dr Boban Tripković who were immediate members of my PhD defense committee, and dr Bridget Alex who read it independently as a researcher also engaged on this project. During the PhD I was engaged in research on other projects than the one resulting in this book. Some of experiences acquired there greatly influenced this study. For those experiences I would like to specially thank dr Aleksandar Kapuran, dr Aleksandar Bulatović, dr Dragan Milanović, dr Petar Milojević, dr Bridget Alex, dr Ana Majkić, dr Jelena Bulatović, dr Aitor Ruiz-Redondo, Gordan Janjić, dr Bojana Mihailović, Danica Mihailović, and dr Dušan Borić. I thank all colleagues from Laboratory of Bioarchaeology at Faculty of Philosophy, Belgrade University for all their help about uncertainties with the material. Lectorship and language support for the first edition of PhD profited immensely from suggestions by Danica Vukićević-Milošević and Jasmina Živković. I owe thanks to the BAR proofreader for this volume.

The most important credits however must go to my immediate family, especially parents Olivera and Predrag Milošević. Their support throughout my entire life and the liberty I had in choices while being raised enbled me to find a life-long interest in archaeology. Not being angry with me in turning over family attics and drawers, and experimenting with daring, dangerous, and stupid childhood ideas undoubtedly influenced the choice of this profession. I credit my father for the cover of this book and beyond-imagination he had in capturing the point of this study in one illustration. Immense thanks to my fiancee Jelena for all her care and support during my long mind-absent hours at home while working to shape this study. Same goes for my closest and best friends, who were sometimes forced to listen about Palaeolithic perhaps against their will, I know they will recognize themselves in this sentence.

1

Introduction

Since it studies the human past, archaeology strives to create a relevant image of past human societies. As we experience archaeology through different materials from the past, which are not directly related to the phenomenon we study, we build up interpretations of research results to access various aspects of past human lives, but limited to what we are able, or what we think we are able, to observe. For that reason it is crucial to observe past remains from different perspectives – societies, various aspects of natural environment and landscapes which they inhabited, and, from the point of individuals and various social constructs, so that we can understand and interpret them more comprehensively, while still respecting the interpretation limits imposed by the archaeological data and materials we study. This is especially complicated for the Palaeolithic period, because it is not possible to draw any direct analogies between Palaeolithic and contemporary hunter-gatherers, not only with respect to aspects of material culture, but also behavioural and cognitive execution of different life tasks. With the emergence of processual archaeology there was a positive way of looking into the analogies with contemporary hunter-gatherers, and various anthropological and archaeological data created from that period onwards helped in selecting criteria that are measurable and comparable. Nonetheless, the boundary between interpretation and generalizing the Palaeolithic into a universal narrative remains very thin when accessing these analogies with any human being and society in recent history and present-day world.

1.1 Aims of the study

This research studies human subsistence strategies and lifestyles tied with food procurement in various past ecosystems, and mechanisms that influenced them in the Last Interglacial and Glacial environment, within Late Middle and Upper Palaeolithic of the Central Balkans, primarily, but not exclusively, based upon archaeozoological analysis, within the broader context of the Balkans and European Palaeolithic. In order to understand the faunal record it is necessary to examine Neanderthals and modern humans more closely – their lifestyles in Europe from the beginning of Last Interglacial to the Last Glacial Maximum (MIS 5-2), or until the beginning of Epipalaeolithic. Corresponding to time range geological units from the sites presented here, Last Interglacial to the Last Glacial Maximum (approx. 130.000 – 22.000 years BP) are periods that witnessed the evolution of archaic humans into anatomically distinct modern humans in Africa and Neanderthals in Eurasia, among others. The term evolution refers to series of changes in human behaviour, and a greater degree of diversity in human skeletal morphology due to nature of diathonic contact and long isolation between differen palaeodemes at certain times. According to the traditional archaeological periods it can be divided, in Europe, into the Late Middle Palaeolithic corresponding to the material culture of Neanderthals, and Upper Palaeolithic, corresponding to the material culture of modern humans which emerged as they spread out of Africa. The biggest interest, in terms of both physical and cultural anthropology, surrounds "the big transition", the last known cohabitation of different forms of humans on Earth, which, in Europe, happened roughly between 45 and 30 kya BP and ended with the extinction of Neanderthals. Although there are many hypotheses about the possible causes for Neanderthal extinction – climate change, rigid subsistence and settlement strategies, weak ties between the individuals and societies leading to weaker technological exchanges and social learning, violence, diseases, etc. (D'Errico and Sánchez-Goñi 2003; Horan *et al*., 2005; Jiménez-Espejo *et al*., 2007; Banks *et al*., 2008; Underdown 2008), it is still inconclusive what happened over the course of the transitional period.

Earlier interpretation that early modern humans (EMH) colonized Europe in sort of a "big transition", by bringing in lamellar technology, complex worked bone technology, manufacture of personal ornaments and other forms of symbolic behaviour such as the appearance of rock art, is now contested (Mellars 1998a, 1999; Gamble 1999; Marean and Henshilwood 2003). Aurignacian, the first techno-cultural complex, which emerged in Europe or in the Near East, is primarily thought to have EMH origins, but various factors that led to its genesis have not yet been essentially understood. As a lithic industry, it is partly preceded by, and is partly contemporaneous with a number of different stone tool industries, so called "Transitional type industries", which differ from the Mousterian Middle Palaeolithic by having a larger proportion of various Upper Palaeolithic techno-typological indices and an elevated lamellar index. These industries are highly variable spatially and temporally, and have been found in the Near East, lower course of Don river, southern European peninsulas (Iberian, Apenine, Balkans), Moravia, south-west and west-central France (Djindjan *et al*., 2003; Kuhn 2003; Otte and Kozłowski 2003; Svoboda 2003; Bon 2006). Pre 40 kya (kilo-year age) BP Aurignacian in Europe, or Protoaurignacian, is defined by the presence of carinated core technology, the production of twisted and Dufour bladelets, and split-base antler points with complex worked bone technology (Gaudzinski 1999; d'Errico *et al*., 2003, 2011; Soressi *et al*., 2013), and is contemporaneous with several Transitional industries: Châtelperonnian, Uluzzian, Bachokirian and Bohunician (Moncel and Voisin 2006; Zilhão and d'Errico 2006) (Fig. 1). It is still debated whether these industries represent a Neanderthal

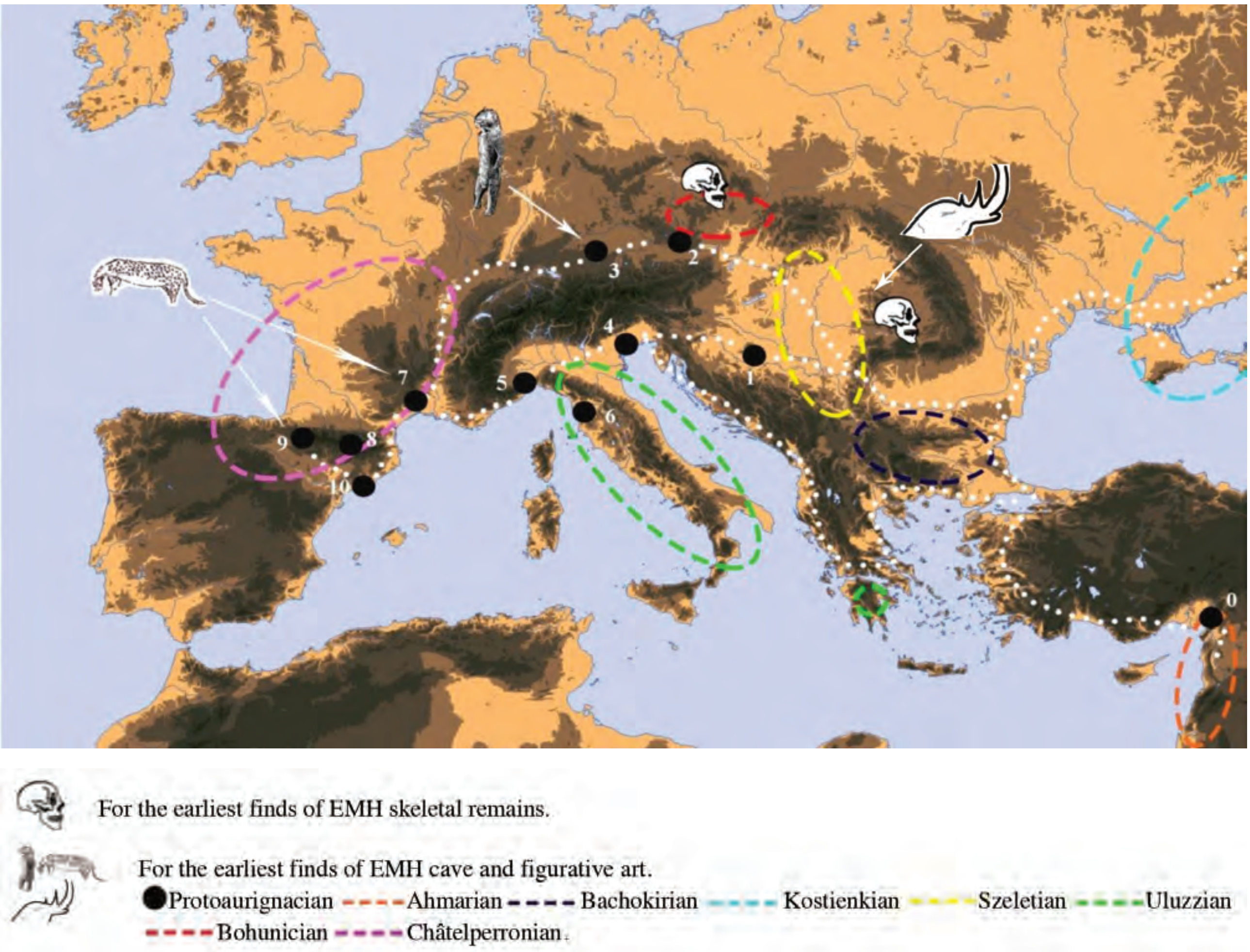

Figure 1. Distribution of various Transitional type industries and Proto-Aurignacian in Europe (45-38 kya BP). Sites: 0. Üçağızlı, 1. Vindija, 2. Senftenberg, 3. Geißenklösterle, 4. Fumane, 5. Riparo Mocchi, 6. Grotta della Fabrica, 7. Esquicho-Grapau, 8. Isturitz, 9. Gatzarria, 10. Abric Romani/L'Arbreda. Dotted routes represent paths of initial spread of EMH.

acculturation to certain Protoaurignacian elements, EMH traditions parallel with the Protoaurignacian, or an exclusively Neanderthal innovation, since it is now widely recognized that archaic humans were able to produce lamellar technology much before the transitional period (Bordes 2003; Chabai 2003; Svoboda 2003; Fernández *et al*., 2004; Kozłowski 2006; Rigaud and Lucas 2006; Tsanova 2012).

Timing the arrival of EMH in Europe is hard to define, both on the basis of archaeological material and anthropological finds. It is still not possible to define a material culture which can be unequivocally attributed to the Neanderthals or EMH during the initial period of their arrival at some point between 50-45 kya BP. Moreover, because of the high skeletal diversity of both types of humans at that time, differences in skeletal morphology can only be studied on better preserved skeletal elements, making highly fragmented remains difficult to discern between late Neanderthals and EMH without a well-defined context (Harvati *et al*. 2004). The oldest EMH anthropological remains in Europe have been recovered at the sites of Peştera cu Oase (40 kya BP), Peştera Muierii (30 kya BP), Peştera Cioclovina (29 kya BP) (Trinkhaus *et al*. 2003; Soficaru *et al*. 2006, 2007; Alexandrescu *et al*. 2010) in Romania, and Mladeč (31 kya BP) (Wild *et al*. 2005), Vogelherd (31 kya BP) (Churchill and Smith 2000) in Central Europe (Fig. 1). Except the Oase individuals, these EMH specimens, correspond to the period when the Aurignacian already became widespread, so they are not typical anthropological representatives of the initial EMH groups in Europe.

Already towards the end of Transitional industries and when Aurignacian became widespread, we witness appearance of the Gravettian, the genesis and origins of which are still being sought in Eurasia. It appears over the vast area from Europe to Central and Northern Asia. What distinguishes the Gravettian from other Palaeolithic periods is the fact that for the first time humans continually settled all climatic belts and landscapes, except the parts covered by the ice sheets. The origin and rapid spread of Gravettian over a vast territory of Eurasia remains an unsufficiently understood phenomenon (Kozłowski 2014). According to traditional Perigordian periodization, it was assumed that origin of Gravettian is local and based on cultural traits which evolved from the Aurignacian, but accumulated data suggest that the the Gravettian was more likely part of a second, maybe larger, migration of EMH (Svoboda 2004). Early Gravettian (30-25 kya BP) appeared over the area of Central and Eastern Europe and could coincide with appearance of variant I of Y chromosome halpogroup in European populations, the appearance of which is estimated at 24±7,1 kya BP (Rootsi *et al*., 2004). Results of MtDNA studies also presented a significant mix of local European and new gene alleles at 20 kya BP (Pala *et al*., 2012).

Local origins are also less probable because Gravettian chipped stone technology, based on blade production from narrow faced core, is temporarily overlapping with Aurignacian chipped stone assemblages. Gravettian chipped stone industry is most similar to Levantine Ahmarian (Skrdla 1997), in which the production sequence is charaterized by unipolar exploitation of blades from narrow faced core. Some authors are of the opinion that chipped stone industries appearing in Eastern Europe between 34-31 kya BP, notably in layer VII of Kozarnika cave and layer 3g of Temnata dupka in Bulgaria, layer III of Buran Kaya on the Crimean peninsula, and Kostienki 8 in the Don river valley contain these basic elements in chipped stone technology (Tsanova 2006; Prat *et al*., 2011) that define Gravettian. Others (Pessese 2008, 2010) see a link between final Aurignacian and initial Gravettian, but also agree that it is perhaps too simplistic to readily assign some of final Aurignacian techno-types, such as Font-Yves bladelets and points, to either Aurgnacian or Gravettian.

Research questions of this study are aligned in several different, but contextually integrated paths divided between the Late Middle Palaeolithic and Gravettian, corresponding to results of paleoecological, taxonomic, taphonomic, and spatial analyses of different levels at the studied sites:

- Did humans and large carnivors target the same prey? What is the difference in ecological patch choice in the Central Balkans between Neanderthals, modern humans, and carnivores when targeting large herbivores? What is the level of biodiversity across MIS 5-2 span and availability of herbivores to Neanderthals, modern humans, and large carnivores within the same site?
- What is the difference in skeletal parts representation and processing strategies of humans and carnivores? Is it possible to identify and discern activity zones of humans and carnivores on the basis of spatial distributions of different sets of finds?
- Was there a competition between humans and carnivores for large herbivores preferring different ecological patches, or intra-site competition?

1.2 Chronological and biological framing of Upper Pleistocene humans, and their socio-economic behaviour

Separation of two distinctive forms of *Homo sapiens* sub-species – Neanderthals and modern humans, is a consequence of the emergence and spread of their common ancestor *Homo erectus* out of Africa, followed by long periods of isolation between the populations. The emergence of skeletal morphologies typical for both human forms is subject to debate. According to palaeoanthropological data acquired so far, there is now growing evidence that they are the consequence of multiregional local evolution of the common ancestor (Wolpoff *et al*., 2000), but with occasional gene flow between some of these populations (de Castro and Martignón-Torres 2013). Pre-Neanderthal skeletal forms are defined on the basis of palaeoanthropological material recovered at the sites of Sima de Los Huesos, Arago-Tautavel, Petralona, Apidima, Steinheim, and Mauer, to which the Mala Balanica hominin from Central Balkans temporally corresponds, while the archaic forms of anatomically modern humans are defined on the basis of the remains recovered at the sites of Kabwe, Bodo, Omo 2, Ndutu and Elandsfontein (Rightmire 2007, 2008). These sites roughly fall into the period between 600 and 300 kya BP, and human remains recovered at them clearly show derived morphology of *Homo erectus*, and are classified globally as *Homo heidelbergensis*. The assumption is strengthened when the individuals that lived temporarily close, but spatially very distant from one another are compared, such is, for example, a striking geomorphometric similarity between Kabwe and Petralona skulls (Van Vark 1995; Rightmire 2008; Harvati 2009).

Besides skeletal morphology, the multiregional evolution model is supported by DNA studies. According to the molecular clock and ancient DNA analyses combined, it is possible to establish that the split between African and European human lineages happened between 700 and 500 kya BP (Prüfer *et al*., 2014, 2017). From that time and the next large-scale contact between these two populations around 100 kya BP, ones that lived out of Africa acquired around 3% of new gene alleles through gene flow and mutation (Green *et al*., 2006: 334). The point of these data is not to show that there was a considerable genetic difference between African and outside African populations, but that rather occasional gene flow happened within both of them, which led to the existence of the variety of temporal and spatial allotaxons, or palaeodemic variations. This is best seen on the example of ancient DNA fragments obtained from Denisova hominins, an archaic human population that lived in Central Asia 130-40 kyA BP, showing that it diverged from the population of *Homo erectus* even earlier than European population, between 1000 and 500 kya BP (Krause *et al*., 2010; Sawyer *et al*., 2015). Comparison of the ancient DNA fragments with human genomes worldwide made a big step in understanding of these variations. It is established that the maximum DNA difference, at the level of alleles, between Neanderthals and modern humans is always between zero and three per cent, and that the difference is always bigger outside of Africa (up to 3.7%) than within it (up to 1.7%). Such a result points that, at the level of DNA alleles, Neandertals are more closely related to contemporary Eurasian than African populations (Green *et al*., 2010: 713). Finally, the analysis of ancient DNA recovered from the oldest known skeletal remains of modern humans in Europe, the Oase 1 individual from Peştera cu Oase, showed that it holds 10% of DNA allele similarity with the Neanderthals, more than twice the value of contemporary populations, which strongly suggests that Oase 1 had a Neanderthal ancestor not more than four to six generations before (Fu *et al*., 2015). This discovery seals the debate about the Neandertals being regarded as a different species from modern humans, as the oldest known modern human in Europe had itself Neanderthal admixture (Harvati and Roksandic 2016). In terms of biological similarity, their genomes were compatible and could produce fertile hybrids that could carry them on, at least in some instances as shown in Oase 1 individual.

In comparison to the earlier periods of the Pleistocene, the Upper Pleistocene is characterized by abrupt and frequent climate changes on a global scale with two peaks – the Last Interglacial or marine isotopic stage (MIS) 5e around 130 kya BP, and the Last Glacial Maximum at the boundary of MIS 3 and 2 around 22 kya BP. The Last Interglacial, encompassing MIS 5e-5a, and the Last Glacial, encompassing MIS 4, 3 and 2, do not represent the periods of constant warm or cold climate. They both have shorter warmer and colder oscillations, with shorter cold oscillations during the interglacial climate and shorter warm oscillations during the glacial climate (Boroughs 2005; Sánchez Goni 2007). Futhermore, climatic conditions in Europe should not be assessed in general since they differ between Western Europe, where climate is influenced by the Atlantic Ocean, Northern Europe, where it is influenced by Scandinavian and Alpine ice sheets, Eastern Europe, with climate influenced by the “mammoth steppe” – the largest continuous steppe that existed on Earth in the Upper Pleistocene, and southern European peninsulas with climate influenced by the Mediterranean (Kukla *et al*., 2002; van Kolfschoten 2002). Because of that, expansion and contraction of various ecosystem types happened at different paces within given European regions.

According to distribution of Late Middle Palaeolithic sites in Europe it has been established that Neanderthals preferred to settle in mosaic ecosystems – that is to have availability to choose between diferent ecological patches both in mountainous and lowland landscapes, in order to have better access to various economic resources (Wenzel 2007). As such, Neanderthals had their own histories of population bottlenecks and isolations in Western Europe, Mediterranean and sub-Mediterranean Europe through glacial periods, population expansions to Central and Eastern Europe (and the Middle East/Central Asia) and migrations, as ecolological patchiness increased or decreased between these regions (Pathou-Matis 2000; Dennell *et al*., 2011). This means that the cold climate would not necessarily lead to a demographic decline of European Neanderthals, but rather to their redistribution with higher concentration in the regions of Europe with milder climate conditions that enable a wider choice of ecological patches. Archaeological data about Neanderthal subsistence shows that they hunted large mammals in open, lowland habitats (such as horses, bison, reindeer), while often exploiting medium-sized mammals in mountainous habitats (deer, ibex and chamois), as they were adaptive to the local game availability within an ecosystem. Subsistence is rarely tied to one species, but in those cases it can be more readily defined as animal foraging of the most productive species from the set of available habitats comprising the ecosystem (Stiner 1991, 1992, 2004b; Boyle 2000; Hoffecker and Cleghorn 2000; Mussi 2001: 152–154; Fiore *et al*., 2004; Valensi and Psathi 2004; Miracle 2007; Daujeard and Moncel 2010; Daujeard *et al*., 2012). Studies that synthetize Neanderthal subsistence in different regions always emphasize the fact that large game hunting is nearly always focused on adult animals, which is confirmed at least at 31 Middle Palaeolithic sites from La Cotte de Saint Brelade in Bretagne up to Teshik Tash and Aman Kutan in Uzbekistan (Gaudzinski 2006). These sites dominated by a single species are most probably just one of the faunal exploitation strategies within a settlement strategy in a wider area, rather than hunting specialization. Such assumption is strengthened by the fact these locations were not visited repetitively and seasonally and represent remains of one or several random herd hunting events, based on lithic assemblages encountered there. In other words, these sites were stations where prey was mass hunted, butchered, and brought out (Fairzy *et al*., 1994; Stiner 1994; Boyle 2000: 343; Gaudzinski 2000, 2004). Recent studies have shown that, besides being well-organized foragers (Adler and Bar-Oz 2009), Neanderthals were also top ecological opportunists, since their subsistence included small mammals, such are rabbit/hare (Cochard *et al*., 2012; Fa *et al*., 2013), birds (Blasco and Fernandez 2009) tortoises (Stiner *et al*., 2000; Blasco 2008; Starkovich 2012), marine mammals and shellfish (Cortés Sánchez *et al*., 2011; Stringer *et al*., 2008), as well as a narrow variety of plants (Henry *et al*., 2010). Stable isotope analyses, which reveal the origin of proteins in diet on one hand, and position in the food chain on the other, suggests that Neanderthals were predators at the top of the food chain, so that almost all of their diet was based upon protein originating from terrestrial mammals (Drucker and Bocherens 2004; Richards and Trinkhaus 2009; Dobrovolskaya and Tiunov 2011).

Several independent lines of evidence from various sites, such as occupation stress and trauma markers at Krapina and Moula Gercy, stone tool technology (universal over the vast area of Eurasia) and wooden spears (Lehringen), indicate that Neanderthals hunted large mammals from close quarters. At the sites of Krapina and Moula Gercy, which contained the largest numbers of Neanderthal individuals found at one place and as such present the largest available samples, the outline of humerus cortical bone at 35% of its length from the distal end shows that the diaphysis was remodelled mainly by the pressure of flexor muscles (Churchill *et al*., 1996). Antero-posterior depth of trochlea humeri in relation to longitudinal humeral axis, which marks the maximum extension angle of the forearm (Hambücken 2012), as well as the optimal angle of reaction force transferred from the forearm to humerus, is positioned at an average optimal angle of 101º. Schmitt *et al*., 2003: 104, Table 1, shown that this is the optimal position of the arm for reaction force transfer when thrusting a spear. The asymmetry of these parameters between left and right humerus is around 16.5%, which is generally low and also suggests a thrusting arm movement. Stress markers characteristic of throwing would be opposite to these, because throwing engages arm extensor muscles which cause lateral torsion of the distal end, and the alignment of trochlea axis with the longitudinal axis of humerus (observed in lateral norm), since the longer movement enhances the javelin speed at the moment of release and gives higher propulsion force to the projectile (Rhodes and Churchill 2009). In the period of the initial human settlement in Europe, during Aurignacian, we do not encounter any larger sample of complete human remains. But, remains of hunting technology encountered at Aurignacian sites such as antler split base points (Tartar and White 2013; Tejero 2016) might suggest the appearance of projectile technology. Gravettian populations in Europe, represented by a larger sample of well-preserved human remains (such as Sungir for e.g. Trinkhaus *et al*., 2014), show twice more stress marker asymmetry between left and right humerus (around 31.7%), but the evidence for thrown weighted atlatls, javelins and harpoons made of bone and antler is also abundant (Goutas 2016).

Traces of physical trauma on more complete Neanderthal skeletons show that almost every individual had at least one sprained joint or a broken bone, and that most of these injuries affected hands, feet, head and neck (Berger and Trinkhaus 1995). These accumulated traumas on Neanderthals skeletons which point to repetitive bruises caused by running and falling under a heavy physical activity or on rough terrain add to the hypothesis of close quarters hunting, as hunting injuries may have been perceived as routine (Pettitt 2000). A similar conclusion can be reached by closer examination of their hunting tool kit. Neanderthal chipped stone spear points were of standardized production, designed and conceptualized to be curated and resharpened several times before refusal, which is also a sign of a well-structured behaviour tied to the manufacture and use of hunting tool kit (Lazuen 2012). Techniques of tipping the spears and other chipped stone tools with adhesives such as bitumen (Böeda *et al*. 1996; Koller *et al*., 2001; Cărcuimaru *et al*., 2012) and tar obtained from birch bark by oxygen reduction (Mazza *et al*., 2006; Pawlik and Thissen 2011) are observed through the chemical analysis of their residues on the artefacts themselves, but were not implied to be used as collated lithic segments for a potential sort of projectile.

In rare cases, remains of wooden hunting equipment have been found. At the site of Lehringen in NE Germany, dated to the Last Interglacial, a wooden spear split in several pieces but preserved in almost its entire length has been recovered, with an estimated length around 2,20-2,40 m, and was found together with elephant bones (Schmitt *et al*., 2003). The considerable length also means that Neanderthals could keep themselves at a safer distance when hunting large mammals from close quarters (Ruff *et al*., 1997). Direct evidence of Neanderthal close quarters hunting is also sometimes observed on fauna. A mesial fragment of a Levallois point was found embedded in a cervical vertebra of a wild donkey at the site of Umm el Tlel in Syria (Böeda *et al*., 1999), this suggests that Neandertals had exquisite knowledge of critical points when hunting, and aimed to bring their prey with one fatal blow, since wounded prey could easily flee.

Data represented by archaeozoological research, stress markers on Neanderthal skeletons, and crafting technology and use of chipped stone implements reveals a well-structured behaviour, but also tremendous versatility concerning hunting activities. This pattern implies manufacture of specific tool kits and applying different

Table 1. Published C14 and ESR dates for different layers of Pešturina.

layer	laboratory sign		dates				
			C14 years BP	ESR			
	C14	ESR		EU γ	SD	LU γ	SD
layer 2	RTD7148	/	16271±58	/	/	/	/
	RTK6446	/	30888±622	/	/	/	/
layer 3	RTD7231	AT23	33129±176	34300	± 1900	38900	± 2500
	RTK6449	/	47608±3597	/	/	/	/
layer 3/4	RTK6450	/	42921±2171	/	/	/	/
layer 4	RTD7149	AT22	44599±591	86100	± 4500	92900	± 5200
	/	AT32	/	95200	± 3500	101900	± 3800

C14 cal. BP ultrafiltration at 68% confidence; SD – standard deviation; EU – early uptake, LU – linear uptake. C14 dates from Alex and Boaretto (2014), Alex *et al*., (2019), ESR dates from Blackwell *et al*., (2014).

tactics and handling of prey, depending on animal species, surrounding landscapes and ecosystems, as they were able to hunt ungulates of quite different sizes, agilities, aggressiveness, living solitary or in herd, and in different ecological settings.

Although there is no evidence that Neanderthals made early art parallel to Chauvet, Altxerri B, Coliboaia, and bone and ivory figurines found at the sites of Swabian Jura (Conrad and Bolus 2006; Clottes *et al*., 2012; González-Sainz *et al*., 2013), they were able to express symbollic behaviour through the use of pendants and colourants much earlier than the Transitional period. Mineral processing to obtain colourants is evidenced already in early Neanderthals, as observed at the site of Bečov in Moravia (MIS 7), where porcelanite chunks, fired to obtain different colours, were found beside a quern with traces of the pigment both on the grindstone and the quern itself (Šajnerová *et al*., 2006). Two caves in eastern Spain – cova Aviones and cova Anton contained shell caps perforated in the umbo region, while one contained traces of pigment and solder, and the layers in which they were found are older than 45kya BP (Zilhão *et al*., 2009). Neanderthal personal ornaments from the transitional period are rich in their variety of forms, although they appear as such only in regions where the presence of transitional type industries is strong: Châtelperronian, Bachokirian, Uluzzuan (d'Errico *et al*., 1998; Arnaud *et al*., 2016; Fabbri *et al*., 2016), so that some of the authors also contest their Neanderthal origin (Caron *et al*., 2011). Besides, it has been recently observed that Neanderthals butchered birds for feathers, probably used to garment or decorate themselves (Peresani *et al*., 2011; Finlayson *et al*., 2012).

The timing of EMH arrival in Europe and demise of Neanderthals also coincides with climatic deterioration. Although mild glacial climatic conditions prevailed in MIS 3, glacial maximums, or Heinrich events, were too brief to severely change biotopes in Europe. However, between 46 and 38 kya BP, Heinrich events 5 and 4 occured temporarily close, and led to a much drier climate (Boroughs 2005; Sánchez Goni 2007). A similar, yet more pronounced climatic occurence happened with Heinrich events 3 and 2, leading to the LGM. Thus, Heinrich events 5 and 4 must had an impact on the demise of distribution of animal and human populations in Europe during the transitional period. Modelling demographic advancement of EMH in Europe and the replacement of Neanderthals predicts Neanderthal population compression and an increase in population density in milder regions of Europe, rather than population decline, which might have enabled EMH to settle in. Even if EMH had greater demographic rise, it would not suffice, without Neanderthal population admixiture itself, to demographically outcompete them (Morin 2008; Excoffier and Currat 2011; French 2011; Mellars and Dogandžić, McPherron 2013).

It was earlier stated that the Middle to Upper Palaeolithic transition was marked by a shift in human subsistence from opportunistic to specialized hunting (Mellars 1992, 1996, 1998b, 2004). As shown on the example of south-western France and northern Spain, EMH specialized in reindeer hunting, the remains of which are usually the most numerous at Proto- and Early Aurignacian sites. They specialized not only by species selection but also through an original hunting gear (Teyssandier 2002; Liolios 2006; Soulier 2013). Holding that true, it should be stated that increase in reindeer subsistence has also been observed in late Neanderthals and was already a dominant prey type before, even during MIS 4 at some of the sites in Western Europe such as Combe Grenal and Jonzac (Chase 1989; Niven *et al*., 2012). More recently, it was demonstrated that species selection at early EMH sites in the region was mostly due to ecologial conditions (Grayson *et al*., 2001; Grayson and Delpech 2002, 2006). Besides, butchery and transport strategies were not essentially different between Neanderthals and EMH (Chase 1989; Stiner 1994; Burke 2000; Costamagno *et al*., 2006; Grayson and Delpech 2008; Niven *et al*., 2012) not only in SW Europe but elsewhere, and use of small prey by Neanderthals has also been observed (Blasco and Fernández Peris 2009, 2012; Blasco *et al*., 2016). Contrary to Mellars' theory, it is now accepted that main response of EMH in ecological competition was not species specialization, but broadening of diet (O'Connel 2006; Lloveras *et al*., 2016) to more often include species from a wider array of ecological sets than the Neanderthals.

In comparison to the Aurignacian, larger differences are observed in subsistence and settlement strategies in the Early Gravettian, since it is, above all, characterized by large mammoth bone hut settlements at the bands of large rivers – Morava, Danube, and Don. They subsist on large mammals living in herds: before all mammoths, but also horses, bison and reindeer (Svoboda *et al*., 2005; Bosch 2012; Nikolskiy and Pitulko 2013; Brugère 2014), and hunt small carnivores for fur (Wojtal *et al*., 2012). Existence of composite chipped stone armatures which minimize damage to the fur when hunting/trapping is also evidenced, and bone eyeneedles point to the existance of tailored clothes (Brühl 2005), which would have been thermodynamically much more efficient than interconnected patches of fur (Gilligan 2007). Gravettian societies traded raw materials and shells over longer distances than in previous periods, and show cohesion in ritual and burial behaviours (Henry-Gambier 2008; Trinkhaus et al. 2014). Some of these open-air sites were settled year round (Fišáková 2013). The use of symbollic objects in the Early Gravettian is quite complex, with a great variety of forms, from personal ornaments to antropomorphic and zoomorphic figurines carved in bone, teeth, ivory, stone, and for the first time from baked clay (Svoboda 1995; Trinkhaus and Svoboda 2006). Late Gravettian, after 25 kya BP, is characterized by a certain degree of cultural and population dispersal towards valleys between the Dniepr and Don rivers, which represents the period of the so called Eastern Gravettian (Sinitsyn 2007), with culmination in numbers and size of open air settlements such as Kostienki and Avdeevo. In other parts of Europe, in the Mediterranean and Sub-Mediterranean climatic belt, cave and rockshelter sites are more numerous, with subsistence orientated towards large mammals represented in milder climate and mixed steppe-forest habitats, notably bison, horses, red deer, and ibex, and small mammals and birds as well (Boscato 2007; Starkovich 2012; Stiner et *et al*., 2012; Tagliacozzo *et al*., 2012; Vacca *et al*., 2012; Starkovich 2017), but also small mammals (Condrad *et al.* 2013). Chipped stone (steeply gravette retouched bladelets, blades and their segments) and osseous technology is used for production of composite and projectile implements. Rare remains of organic matter document the existence of nets and traps (Adovasio *et al*., 1996) used in fishing and fowling (Bochenski *et al*., 2009). Gravettian was the start of the ultimate adaptation of human hunter-gathereres to every environment type of Ice Age of Europe. Their societies are socially, culturally and technologically highly organized and geared for settling different ecosystems year-round. The settlement pattern is mainly residential-logistic or residential-cyclic, which is observed, beside the existence of year-round settled locations, on the numerous sites showing pronounced seasonality of human subsistence activities at some locations and regions.

There are the first indications of humans intentionally changing the landscape such as killing off large predators in resident territories to lessen their pressure on the common ungulate prey, competition for shelter, fur, or even food (Kitagawa *et al*., 2012; Bocherens *et al*., 2014; Demay *et al*., 2015; Wilczyński *et al*., 2015; Wojtal *et al*., 2015; 2018). Various human deposited contexts containing almost exclusively carnivore remains, and remains of carnivores containing cutmarks are more numerous than in previous periods. The evidence of possible early animal taming (not to be confused with domestication process) comes from the Early Gravettian site of Předmosti, where geometric morphometric studies of canine skulls has shown, although on a small sample, reduction of the teeth row lenghth, and difference in skull morphology between wolves and wolf-dog hybrids, which were, besides, uncovered in a „domestic space“ or inside of the dwelling structures (Germonpré *et al*., 2012; Germonpré *et al*., 2015). This suggests that if interaction of humans and wolves existed, wolves and bastard-dogs were not kept separate by humans in order to domesticate them.

1.3 Spatial framework of the study

The area of this study is the Central Balkans, the geographical boundaries of which are to the north Kupa, Sava, and Danube rivers, and Mediterranean and Black Sea from other cardinal points. The Central Balkans covers about one sixth of the Balkan peninsula. It is defined mostly by larger geographic barriers – river valleys of the Sava and Danube to the north, Drina river basin to the west, Rhodopian and Balkan mountain chains to the east, and the Dinaric and Šar-planina mountains to the south, south-west (fig. 2). The main feature of the Central Balkans, in terms of physical geography, is the existence of series of mostly lowland basins, but sometimes highland plateaus, separated by canyons, gorges, or mountains. Such a geographic position made this area relatively open to climatic influences from the north and east of Europe along the Sava, Danube, and upper course of Morava river basins, but relatively closed to the climatic influences of sub-Mediterranean and Atlantic climates, and separated from Mediterranean and Atlantic with high mountain chains with glaciers: the Dinaric Alps, Prokletije, and Šar-planina. Contemporary climatic factors on the Central Balkans are complex, but are characterized by mild continental climate type, and continental climate at the heights above 1000 m a.s.l., while its easternmost lowland parts are under the influence of a sub-tropical climatic type from the Black Sea shores (Savić and Obuljen 1979). However, it is not possible to discuss what key climatic factors were represented through the Upper Pleistocene in the Central Balkans, largely because it lacks such a holistic and interdisciplinary study. For that reason, it is unknown at what pace biomass changed in regard to a warm/cold and wet/dry climate. Although it contains lowland corridors along larger rivers, with altitudes below 200 m, the Central Balkans is mostly a hilly-montane region with altitudes between 300-500 m, but as high as 2.600 m. Considering the relief and human settlement, it is worth asking what was the physical boundary in altitude as well. In the southern part of the Central Balkans, Palaeolithic sites were discovered at higher altitudes, such as Crvena Stijena (700 m), and Smolućka pećina (945 m), and it is possible that smaller mountain glaciers never dropped below 700 to 1000 m during the Upper Pleistocene, and even during the LGM (Đurović 2012). Variations in oxygen isotope ratios, oxygen isotope in ostracod shells from bental sediments of lake Ohrid in North Macedonia show that during the last 140 kya the climate was subtropical-Mediterranean and corresponds to oxygen isotope ratios from ostracods in Ioannina (Epirus, Greece), Monticchio (Campania, Italy), Corchia (Liguria, Italy), and core MD01-2444 in the Atlantic Ocean, approximately 100 km from the shores of Alentego (Portugal) (Belmecheri *et al*., 2012). Across the east-west axis, the Central Balkans is less accessible, with fewer natural communication routes. It is important to establish whether there were connections between lowland ecosystems as well on this axis, between the river basins of Timok and the Nišava, and Velika and Zapadna Morava rivers, which would have made possible the movement of large migrating herbiovore species between them.

1.4 History of research and archaeological data on the Palaeolithic in Serbia

Systematic research of the Palaeolithic period in Serbia has a long tradition, but is characterized by large pauses in exploration. A brief review is presented here, since detailed history of Palaeolithic research in Serbia and Central Balkans was given already in several publications (Mihailović 2009; Mihailović *et al*., 2011; Mihailović 2014). The earliest Palaeolithic research conducted was the field and test trench surveys of Đoka Jovanović (Јовановић 1892, 1893) and Jovan Cvijić, who first excavated in the Prekonoška cave near Svrljig according to methodological standards at that time and published the

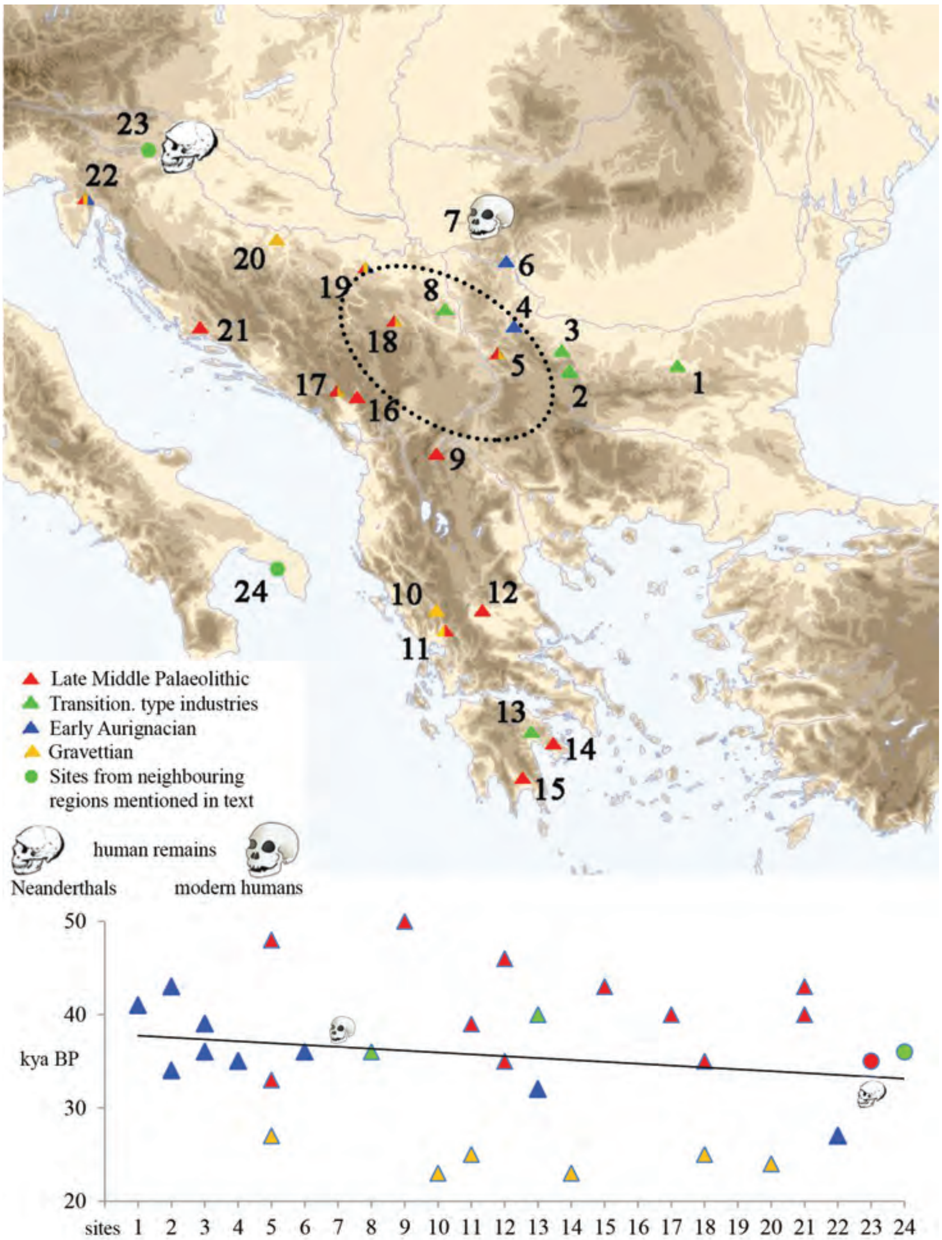

Figure 2. Late Middle and Upper Palaeolithic sites on the Balkans studied in detail, and some sites in surrounding regions which are of importance for this study: 1. Temnata dupka, 2. Bacho Kiro, 3. Kozarnika, 4. Baranica, 5. Pešturina, 6. Tabula Traiana cave, 7. Peştera cu Oase, 8. Risovača, 9. Golema pesht, 10. Kastritza, 11. Asprochaliko, 12. Theopetra, 13. Klisoura, 14. Franchti, 15. Lakonis, 16. Bioče, 17. Crvena stijena, 18. Hadži-Prodanova cave, 19. Šalitrena cave, 20. Kadar, 21. Mujina cave, 22. Šandalja, 23. Vindija, 24. Grotta de Cavallo. Regression line shows gradual replacement and demise of the Neanderthal societies in Balkans between 38-33 kya BP.

results (Цвијић 1891). The first systematic, archaeological and paleontological excavations were conducted in the 1950s at the cave of Risovača near Aranđelovac (Гавела 1988). These were followed by excavations in the 1980s – in the Smolućka cave near Novi Pazar (Калуђеровић 1985), At an open air Aurignacian site near Vršac (Radovanović 1986), Pećurski kamen cave near Sokobanja (Malez and Salković 1988), and systematic surveys in gorges of Resava and Suvaja rivers (Вучковић 1985; Ђуричић 1990). During the first half of the 1990s, several surveys with test trenches were conducted: the Prekonoška cave near Svrljig (Калуђеровић 1992), the Markova and Pećurski kamen caves near Sokobanja (Kaluđerović 1993), the Baranica cave near Knjaževac (Сладић and Јовановић 1995; Михаиловић *et al.*, 1997), Mirilovska cave near Paraćin (Ђуричић 1996), Drenaićka cave near Valjevo (Калуђеровић and Јеж 1996), and Kremenac, a flint raw material source near Niš (Калуђеровић 1996). In the last decade, systematic archaeological excavations of Palaeolithic sites occurred at the Hadži-Prodanova cave near Ivanjica (Михаиловић and Михаиловић 2006), the Šalitrena cave near Mionica (Mihailović 2008), Velika and Mala Balanica in the Sićevo gorges (Михаиловић 2009; Roksandic *et al.*, 2011) and the Pešturina cave in Jelašnica near Niš (Михаиловић and Милошевић 2013). Sites studied in more detail are presented in fig. 3. Several surveys and systematic excavations of Palaeolithic sites are currently underway in eastern Serbia and the Morava river basin.

A hominin mandible dated to around 500 kya BP recently discovered at the Mala Balanica cave represents the earliest evidence of archaic human settlement in the Central Balkans and, as already said, belongs to a small group of human fossils from pre-Neanderthal period in Europe. Some of them are characterized by derived skull morphology features that are absent in so called „neanderthalization" (gradually acquiring typical Neanderthal skull landmark features). The mandible of this individual does not posses typical anatomical landmarks for pre-Neanderthals (*Homo heidelbergensis* sensu lato in Western/Central Europe) (Roksandic *et al*., 2011; Roksandic 2016), similar to more recent interpretation of Apidima 1 cranium from Greece (Harvati *et al*., 2019). This opens the question of timing of that process across various palaeo populations in Europe, and might point to multiple dispersals of modern humans from Africa at least in this part of Europe (Ivanova 2016; Spasov 2016).

Mihailović gives, on multiple occasions, comprehensive studies of technological variability, similarities, and problems in connecting Middle and Upper Palaeolithic chipped stone industries of the Central Balkans with other parts of the Balkans and Europe (Mihailović 2009; Mihailović *et al*., 2001; Mihailović 2014; Mihailović and Bogićević 2016), so only the most important features of it will be presented here. From the techno-cultural point of view, the Central Balkans represents one of the areas which witnessed an early appearance of Charentian type Mousterian (Михаиловић 2009), and according to finds from the sites of Velika Balanica and Crvena stijena in Montenegro, they can be related to Protocharentian assemblage from the site of Karain in Anadolia, which came from layers dated to 330-280 kya BP (Kozłowski 2002), with such assemblages also appearing further in the Near East. There is a large temporal gap in Charentian technological tradition between the Balkans and the Near East, and Western and Mediterranean Europe where it appears around MIS 5/4 boundary (around 90-80 kya BP). On the other hand, the technological tradition in the Mediterranean zone of the Balkans is different, and is based on cores and flakes produced from smaller cores, or perhaps nodules, and intensive exploitation of them, which in the pre-refusal stage is done with centripetal knapping. This technology, named Micromousterian, appears at the sites of Bioče in Montenegro, Asprochaliko, Teopethra, and Klissoura in Greece, and the Mujina cave in Croatia (Dogandžić and Đuričić 2017; Karavanić and Bilich-Kamenjarin 1997; Darlas 2007; Mihailović 2014; Vujević *et al*., 2017), but tools of small size appear as well in Central Italy (Kuhn 1995). The authors who studied this technological phenomenon argued that it has to do with high moblity of late Neanderthal societieties within these regions, which prevented them from visiting the best raw material sources in the region frequently. Technological variability between the Central Balkans and other European (Fig. 4) and Near Eastern regions may suggest population continuity and continuity of techno-cultural ideas, or population isolation.

The beginning of the Middle to Upper Palaeolithic transitional period in the Balkans temporally corresponds to a natural catastrophe – a volcanic eruption which happened in Campi Flegreii in Campania, Italy. Layers of volcanic ash and pyroclastic ignimbrites were identified in stratigraphic sequences at Crvena stijena, Franchthi, Klissoura, Golema pešt, the cave above Tabula Traiana and Temnata dupka (Lowe *et al*., 2012), and provide an indication of the scale of this eruption. Such a natural catastrophe could be one of the triggers influencing the demise of Neandethal populations in the Central Balkans, but also one of the reasons why we currently lack Early Upper Palaeolithic sites in this region, as well as in western Adriatic (Hoffecker *et al*., 2008; Fitzsimmons *et al*., 2013).

The evidence for Early Upper Palaeolithic settlement in the Central Balkans is sparse, and documented just with several chipped stone artefacts in the cave above Tabula Traiana (34 kya BP, Borić *et al*., 2012) and Baranica (36 kya BP, Mihailović *et al*., 2011), which is relatively late compared to dates of EUP layers at the sites of Bačo Kiro and Klissoura, and human remains from Peştera cu Oase, in surrounding areas. The context and technology of Late Aurignacian finds from At may be connected with open-air Aurignacian sites in Romania – Tinçova, Koşava, and Romaneşti-Dumbraviţa (Mihailović *et al*., 2011: 94), and probably to Šalitrena cave in western Serbia, where it is dated to around 32 kya BP, while the Middle Palaeolithic layer there, dated to 38 kya BP, has among the latest Neanderthal occupation ages in the Central Balkans (Mihailović and Mihailović 2012). The apparent lack of the Early Upper Palaeolithic seems to indicate that a large part of the Balkans, from the Mujina cave (Rink *et al*., 2002) on the Adriatic to the west, to the lower Morava river basin to the east, and Thessaly to the south, was not inhabited by EMH between 41-39 and 34-28 kya BP (fig. 2), as indicated by Alex *et al*., (2019). Contrary to the north-western parts of the Balkans and Danube corridor, which withnessed Early Aurignacian and Transitional industries periods, this area starts to be colonized by modern humans in the Early Gravettian, as observed at the sites of the Šalitrena cave, Kozarnika, and Temnata dupka (Mihailović 2008; Tsanova *et al*., 2012). Although it is apparent that Gravettian assemblages from the Danube corridor belong to the same technological group as the Central European Gravettian, the nature of Gravettian in the interior of the Balkans remains unresolved. The most recently published research on the Central Balkans Paleolithic will be presented in the discussion of results, especially in context of this study.

The analysis of animal remains was an integral part of archaeological research from the first systematic Palaeolitic excavations in Serbia, at the cave of Risovača (Rakovec 1965). During the 1980s, the analysis of

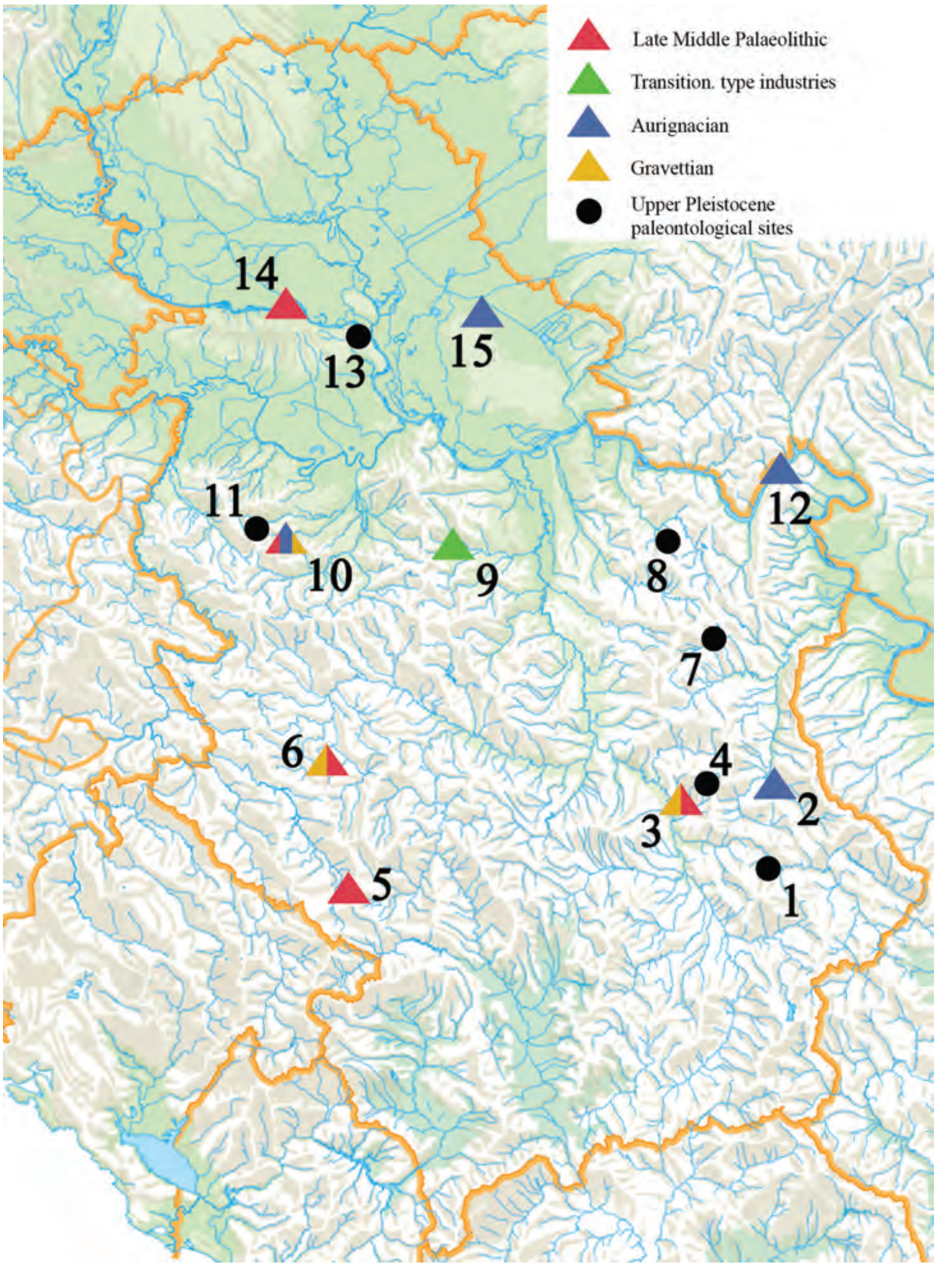

Figure 3. Map of systematically explored Palaeolithic sites in Serbia: 2. Baranica, 3. Pešturina, 5. Smolućka cave, 6. Hadži–Prodanova cave, 9. Risovača, 10. Šalitrena cave, 12. Tabula Traiana cave, 14. Petrovaradin, 15. At; and paleontological sites: 1. Vrelska cave, 4. Prekonoška cave, Pećurski kamen 7. Lazareva cave, 8 Ceremošnja, 11 Petnička cave, Visoka cave, 13 Janda hole.

faunal remains from the Smolućka cave near Novi Pazar (Dimitrijević 1985) and Pećurski kamen near Sokobanja (Malez and Salković 1988) was conducted. These faunal analyses were orientated towards species identification, relative stratigraphic position in absence of absolute dates, and paleoecological reconstruction. On the basis of fauna, Rakovec dates Risovača to MIS 4, while Malez and Salković (1988), and Dimitrijević (1997), assign Pećurski kamen and the Smolućka caves more broadly to Upper Pleistocene. A synthesis of micro and macrofaunal remains from the Upper Pleistocene archaeological and paleontological records in Serbia was conducted by Dimitrijević (1997). Upon those results, the basic picture of the paleoecology of the Central Balkans during the Upper Pleistocene was established. It was concluded that taxa typical for steppe predominate, with lesser presence of taxa inhabiting forests, the smallest proportion being those inhabiting decidous forests. Presence of exclusively boreal species was not confirmed. In lowland parts of the Central Balkans, the landscape was dominated by steppe fauna, typically represented by mammoths, wooly rhino, horses, bison and hyenas (Dimitrijević 2011, 2013). Cave bear sites are quite numerous in this region, mostly in the hilly-montaine areas, but also in lowlands. Remains of cave bears from archaeological and paleontological sites in Serbia are well-studied paleontologically (Михајловић and Павловић 1988; Paunović 1991; Dimitrijević *et al.*, 2002; Cvetković and Dimitrijević 2014). From the paleontological work, the most important conclusions to this research explain their use of caves during winter hibernation. On the basis of the fauna from Upper Pleistocene sites in the Central Balkans the presence of mosaic ecosystems is apparent. Roe deer (*C. capreolus*), wild boar (*S. scrofa*), giant elk (*M. giganteus*), and narrow nosed rhino (*S. hemiotoechus*) are present in the Central Balkans Upper Pleistocene fauna and and are stenotypic faunal elements of a more temperate and humid climate. Contrary to that is the complete absence of cervids adapted to drier and colder climate – reindeer (*R. tarandus*) and elk (*A. alces*). Narrow nosed rhino went extinct in all regions of Europe during MIS 4, except in Italy and the Balkans, where it survived well into MIS 3, and most probably because of the milder climate (Bedetti *et al*., 2005; Pushkina 2007). For a more comprehensive picture about the Upper Pleistocene fauna in Central Balkans, it is important to chronologically integrate archaeological and paleontological (Fig. 3) sites. In this way, it is possible to observe more broadly whether and to what extent climate changes could influence the taxonomic distribution and composition, and whether the Central Balkans was a faunal refugia and if it was where these ecosystems could be found. In some faunal studies, taphonomic agents of bone accumulation were also presented and discussed on the basis of taphonomic traces (Dimitrijević 1993, 1996, 1997; Dimitrijević and Jovanović 2002; Kuhn *et al*., 2014). These studies suggested that all indicated sites contained faunal material deposited mostly by natural and carnivore agents, with little anthropogenic influence, but offered an ecosystem explanation in the form of food web reconstruction. Avifauna from Palaeolithic sites of Serbia are studied only for the Smolućka cave assemblage (Malez and Dimitrijević 1990).

Over the area of Central Balkans, more precisely the territory of Serbia from which the material for this study comes from, there are just a few systematically excavated and published sites, out of which the majority, according to dates obtained, contain Late Pleistocene sediments. However, several Palaeolithic projects are currently undergoing and they shall produce more results which will allow further insight, and in greater detail, into human lifeways through the Late Middle and Upper Palaeolithic in Central Balkans.