

Velika Pećina: Zooarchaeology, taphonomy and technology of a LGM Upper Paleolithic site in the central Balkans (Serbia)

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ABSTRACT

The Last Glacial Maximum (MIS 2) was a period of rapid and extreme environmental change, prompting remarkable human adaptive responses across the world. While large parts of the temperate zone were uninhabitable during this interval, other areas served as refugia for plant, animal and human populations. The Balkans region is identified as a biotic refugium zone for many species during high glacial intervals, but until recently there has been little archaeological evidence that it was also a refugium for Paleolithic human populations. This paper reports archaeological findings from the cave site of Velika Pećina (Zagubica, Serbia), which preserves evidence for multiple episodes of human presence between 24,000 and 20,500 cal BP. Species combinations within the macro- and microfaunas attest to a mosaic environment with high habitat and species diversity over relatively small areas in the periods leading into, during, and following the LGM. Humans hunted a wide spectrum of large mammals, birds, and small carnivores while occupying Velika Pećina. Other mammalian and avian carnivores used the cave when humans were not present. Lithic and osseous artifact assemblages indicate that a range of manufacturing activities took place in the cave, despite the relatively low density of occupational debris. The late Upper Paleolithic groups used the cave as a residential base during a series of brief, probably seasonal visits. Human populations were small in the study area, but their presence was not diminished during episodes of extreme variation in global climate.

1. Introduction

Archaeological sites dating to the Last Glacial Maximum (LGM) are comparatively rare throughout much of Eurasia. Even in areas with rich archaeological records pre- and post-dating this interval, the LGM often corresponds with a decline or even a gap in human presence. The extreme cold and corresponding drop in terrestrial productivity that defines this climate phase at middle and upper latitudes may have been especially challenging for humans, resulting in demographic declines. However, many estimates of human population size have exaggerated the extent of depopulation during peak glaciation by relying too heavily on known site distributions. Gaps in the archaeological record corresponding to the LGM in some areas may be explained by limited archaeological survey and/or patterns of erosion and low sedimentation that worked against site preservation. Recent climate-envelope modeling based on paleoclimate data and hunter-gatherer demographic projections suggests that around 36% of the European continent remained unfragmented, human-habitable land throughout

the LGM (Tallavaara et al. 2015).

If large parts of the European landmass were uninhabitable during the LGM, there is also the question of where hunter-gatherer populations persisted (see Gautney and Holliday 2015; Klein et al. 2021; Ray and Adams 2001; Wren and Burke, 2019, among others). Archaeological evidence indicates that humans, along with numerous other taxa, continued to thrive in refugia within southwestern Europe (Banks et al. 2011; Cascalheira et al., 2021; Ducasse et al. 2019; Maier et al. 2016; Reade et al., 2020), the Urals-Siberia (Kuzmin and Keates 2018; but see Buvit et al. 2015), and in areas of eastern Europe and the Balkans (e.g., Boev and Milošević 2020; Kulakovska et al. 2021; Mihailović 2014; Pinhasi et al. 2014).

The Balkans present both a fascinating example and a natural laboratory for addressing questions about refugia and human responses to the LGM. Though the region is less intensively researched than southwestern Europe, recent archaeological work has focused on establishing presence-absence of archaeological sites through continued survey and excavation to gain a more complete picture of human presence there

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during the Paleolithic. A variety of Middle and Late Pleistocene archaeological sites have been discovered in the Central Balkans (Serbia), for example, including some that date to the LGM (Alex et al. 2019; Dimitrijević et al. 2018; Kuhn et al. 2014; Mihailović 2014). Faunal and botanical records meanwhile point to the existence of ecological refugia in this region (e.g., Connor et al. 2013; Dogandžić et al. 2014). The scale and heterogeneity of favorable ecological zones and their constituent species remain poorly understood, however, making the relationship between refugia and human migration corridors largely a matter of conjecture. Fine-scale data on human presence during glacial periods is sorely needed.

The rugged limestone karst lands of the Central and Eastern Balkans seem to preserve relatively sparse archaeological records throughout much of the Pleistocene, but abundant carnivore (especially bear) records (e.g., Gamble 1986; Cvetković and Dimitrijević 2014; Dimitrijević 1997; Dimitrijević 1998; Heffter 2021; Kuhn et al. 2014). Yet the archaeological evidence suggests that some parts of the rugged interior experienced unique microclimates and local ecosystems that responded differently than expected to intervals of extreme global climate.

This research reports results from the archaeological excavations at Velika Pećina¹, one of several recently investigated cave sites in Serbia that preserve LGM-aged components (Fig. 1). Velika Pećina (VP) is a relatively small site that yielded a notable diversity of anthropogenic remains. Here we present results of radiocarbon dating as well as analyses of artifacts and faunal remains. The site was visited repeatedly by Upper Paleolithic foragers between roughly 24.5 k and 19.6 k cal BP,

with the bulk of the occupations dating to between 24.5 k and 20.5 k cal BP.

2. Background to Velika Pećina

Velika Pećina (VP) occurs within a typical karst landscape of rugged uplands and deeply incised drainages (Fig. 1c). The local peaks rise to 1500 masl, and elevations increase eastward and southward into the Carpatho-Balkanid mountain belt. This landscape opens onto the Danube corridor to the north and west, which defines the rim of the Panonian lowland before cutting into the Carpatho-Balkanids. The Morava river and its tributaries drain areas west of VP, flowing north to meet the Danube (Fig. 1b). Together with the Vardar/Axios river valley, the Morava forms a long north-south corridor that links the Danube and Panonia hinterland to the southern Balkans, and ultimately to the northern Mediterranean rim. The extreme topographic relief in this part of the world channeled the movements of people and animals through corridors such as these for millennia.

The cave of VP is situated within a narrow canyon of the Crna Reka (Black river), a tributary of the Tisnica river (Fig. 1c), and it lies 5–6 km southeast of a basin occupied by the modern town of Žagubica. The cave opens near the bottom (ca. 446 masl) of the winding canyon, roughly mid-way between the basin (downstream to the west, ca. 320 masl) and higher plateau lands upstream (southeastward, ca. 700–800 masl). As such, the site was well-positioned to exploit a variety of habitats while also enjoying a somewhat sheltered location.

The cave itself is a small but complex karstic cavity that opens near the base of a tall, near-vertical limestone falaise on the north bank of the Crna Reka. The central chamber, where the main excavation took place, is an open, high-ceilinged cavity roughly 7 m wide and 8 m deep (Fig. 2b). The entrance faces southeast, and the floor at the entrance lies about 10 m above the modern riverbed. A substantial terrace has formed outside the cave mouth, but this may have been created during construction of a road through the gorge. Two narrow, tubular chambers, emanating from the northwest and northeast, enter the main chamber at the rear of the cave. The western chamber is roughly 10 m long, and its floor rises gently. The eastern cavity is much wider and longer, extending back >25 m, and it rises steeply and irregularly into the bedrock. There is a small natural deposit of red ochre near the back of this eastern cavity.

VP was excavated during three field seasons in 2013, 2015, and 2016 as part of a collaborative project between Belgrade University and the University of Arizona. The excavation trench was 11 m² in area within the main chamber and reached bedrock in most units (Fig. 2). The excavation followed procedures typical for Paleolithic projects in the region, including 3-D plotting of finds *in situ* and systematic dry sieving through 5 mm upper and 2 mm lower meshes. Selected sediment samples were also wet-sieved through 2 mm mesh to check recovery effectiveness for small bladelet fragments and microfauna remains. Wet-sieved samples contained only non-diagnostic microfauna and small bone fragments, so we are confident that the samples of artifacts and identified faunal remains are representative.

3. Stratigraphy and dating

The intact sedimentary infilling of Velika Pećina varies between 1.2 and 1.75 m in thickness, depending on location within the excavation trench. The stratigraphic sequence consists of four main units, each of which was subdivided based on variations in color, induration, sediment composition, and anthropogenic content. Layer 1 is a loose, dry surface layer that contains a mixture of Paleolithic and more recent artifacts; this layer has been extensively reworked by recent human and animal activities. Layer 2 is defined by reddish clayey sediments with variable amounts of angular limestone debris (SI Fig. 1); initially subdivided into 2a and 2b based on differences in color and compaction, these subunits were later recombined because the boundary between them is diffuse or

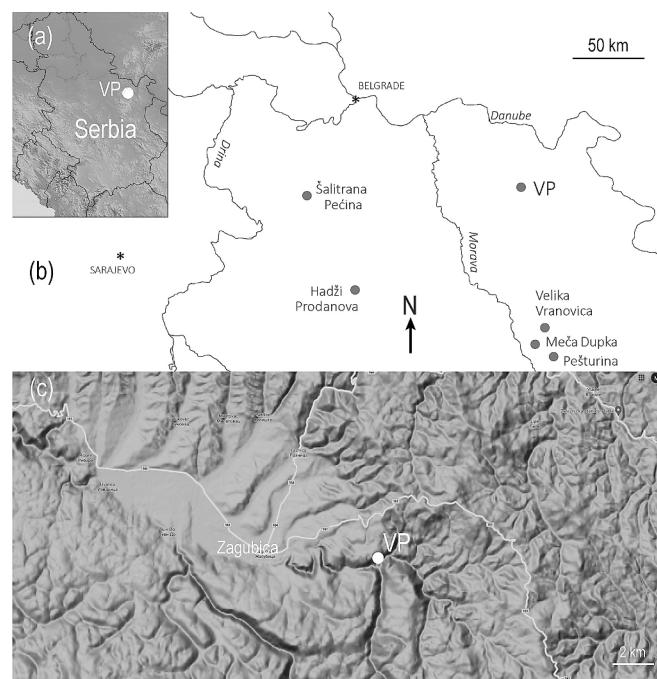


Fig. 1. (a) Location of Velika Pećina (VP) in southeastern Serbia; (b) location of VP and other sites with LGM components in the study region; (c) local topography in the area of VP, including basin to the west where the modern town of Žagubica is situated. Topographic base map .
adapted from <https://www.google.com/maps/place/Crna+Reka,+Serbia/>

¹ Velika Pećina (“large cave”) is a common local toponym throughout the territory of the former Yugoslavia. At least one well-known Paleolithic site in northern Croatia, with Mousterian, Aurignacian and Gravettian components, shares this name (Mary Malez, 1979). In Serbia, there is also at least one other cave with Pleistocene deposits with the same name (Dimitrijević et al., 2002).

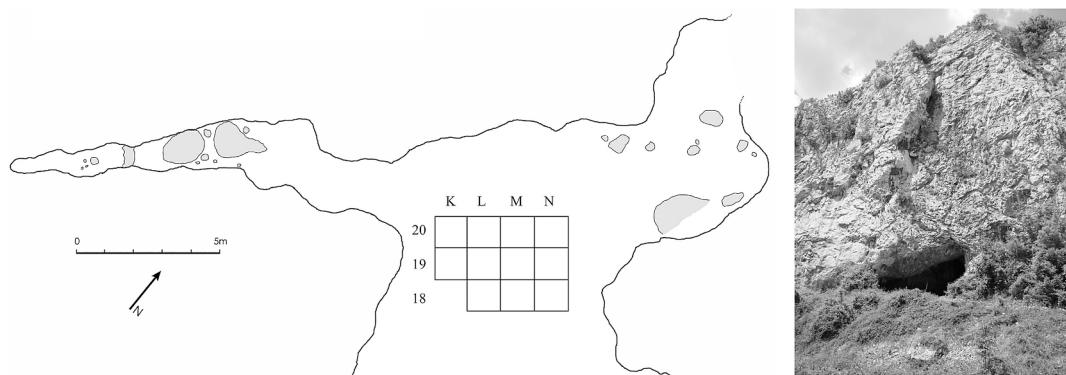


Fig. 2. Schematic plan of VP and excavation trench inside the main chamber (1×1 m grid squares); and photograph of cave entrance at right.

unclear in some parts of the trench. Layer 2 yielded a moderate number of late Upper Paleolithic artifacts and bones. The sediments of Layer 3 are also rich in clay but include larger amounts of sand and fine gravel than Layer 2. Layer 3 was subdivided as follows: 3a is reddish and relatively rich in clay and includes a few ash lenses; 3b is distinctive for its gray color and very high sand content, probably of aeolian origin, as well as richness of artifacts and bones and presence of some combustion products; 3c is somewhat sandy but includes more red clay than 3b. Layer 3 yielded the largest samples of bones and lithics, mostly from 3b and 3c. Finally, Layer 4 is a thin, rocky deposit immediately overlying the limestone bedrock; what little cultural material exists in this layer likely originates from Layer 3b-c. Our study emphasizes material from well-defined stratigraphic units in Layers 2 and 3. The contents of transitional or dual stratigraphic designations (2/3, 3a/3b, etc.) are treated separately.

A total of 15 ^{14}C dates were obtained from VP (Fig. 3), Table 1. Twelve dates are on collagen extracted from vertebrate bones and teeth. With the exception of *Ursus* remains, all of the dated skeletal samples bore traces of human actions (e.g., cut marks). Three other dates were obtained from pine wood charcoal. It is readily apparent from Table 1 that the bones of *Ursus spelaeus* (cave bear) yield infinite ^{14}C ages and thus clearly pre-date the human occupations by > 20 ky. The single brown bear specimen from Layer 2 dates to less than 1000 years before present. All three of the *Ursus* samples are from the northeast edge of the trench, near the mouth of the larger tubular side chamber.

The remaining eleven ^{14}C dates reflect Paleolithic human occupations of the cave. One date from Layer 2 is substantially younger than the others at 17,118–16,816 cal BP and may represent one or more brief late Upper Paleolithic occupations. The other ages associate with MIS 2, the Last Glacial Maximum *sensu lato*. The central calibrated ages span roughly 24,000 to 20,000 years cal BP, and these may resolve into two clusters. Two overlapping ages on collagen of very large ungulates from Layer 3b have central values between 23,950 and 24,250 cal BP. The remainder of the age determinations from Layers 3b, 3a and 2 appear substantially younger, with central values between 20,450 and 21,950 cal BP. One other charcoal date from Layer 3b is intermediate to these two groups.

The most parsimonious interpretation for the spread of dates from Layers 2, 3a and 3b is that they reflect a series of sporadic human occupations during MIS 2, mainly the later part of the LGM between 20,450 and 21,950 cal BP. The two substantially older dates on very large ungulate bones (one is probably of *Megaloceros*) may refer to a separate, somewhat earlier occupation event or series of events.

4. Lithic assemblages

A total of 492 lithic artifacts were collected from the VP excavations. Roughly two-thirds of these artifacts (308) come from Layer 3 (Fig. 4), Table 2. The artifacts were manufactured from a range of raw materials,

but crypto-crystalline silica rocks that include radiolarite and chalcedony predominate (ca. 65%). We lack information on local flint sources in the study area.² However, preserved cortical surfaces on the artifacts are evenly distributed among heavily altered (pebble), moderately altered (rolled nodule) and unaltered (nodule) categories. This tells us that the raw materials were collected from primary outcrops as well as from secondary, alluvial sources. The pebbles and nodules exploited were relatively small. Unbroken cores from the site average 52.3 mm in maximum dimension ($sd = 22.5$). Removing two unusually large specimens (each > 100 mm long) from the sample reduces the mean length of cores to 45.0 mm ($sd = 13.1$). The fracture surfaces of the stone artifacts show no signs of abrasion or rounding from water transport, indicating that the assemblage was not reworked by fluvial action before or after being deposited in the cave.

A variety of raw materials other than crypto-crystalline silica rocks are also present in the artifact sample, including silicified limestone, limestone, metaquartzite, vein quartzite, and indeterminate igneous rocks. Silicified limestone is the most abundant among these materials at 18.75% of the total assemblage, and it is most abundant in Layer 3 (SI Table 1), where about one-quarter of artifacts are made from it. Silicified limestone is represented almost exclusively as unmodified blanks and debris; only one core and one retouched tool are made from this material. Overall, flint and other varieties of crypto-crystalline silica were strongly preferred for retouched tools (94.1%) and cores (77.8%). The difference in representation of crypto-crystalline silica rocks among the retouched tools and unshaped blanks is statistically significant ($\chi^2 = 13.511$, $df = 1$, $p = 0.0002$).

A full spectrum of débitage products and byproducts, including cortical flakes and core trimming elements (primary and secondary crested blades, platform tablets), is present in the larger assemblages from VP (Table 3). Roughly one-third of blanks (152/464) and 85% of cores (24/28) preserve some dorsal cortex, indicating that early stages of core reduction occurred on site. The frequency of cortex is likely elevated in part by the small sizes of the raw material packages used by the VP tool makers.

The lithic assemblages from Layers 2, 3b and 3c are generally similar. Laminar blanks (blades and bladelets) are more common than flakes throughout this sequence, and bladelets typically outnumber blades,

² V. Bogosavljević Petrović from the National Museum in Belgrade organized a detailed survey of raw-material sources in this part of Serbia and succeeded in identifying many chert sources (as yet unpublished), but nothing similar to the material commonly used at Velika Pećina. A 2016 presentation entitled “Raw Materials Exploitation at Belovode: Sourcing, Processing and Distribution” describes of the survey results, which were part of the larger project *Origin, Interpretation and Distribution of the Stone Raw Materials in Prehistory of Serbia*, sponsored by the National Museum in Belgrade. (Belovode 2016 - Arheološka istraživanja šire okoline lokaliteta Belovode Narodnog muzeja u Beogradu. Narodni muzej u Beogradu, Beograd).

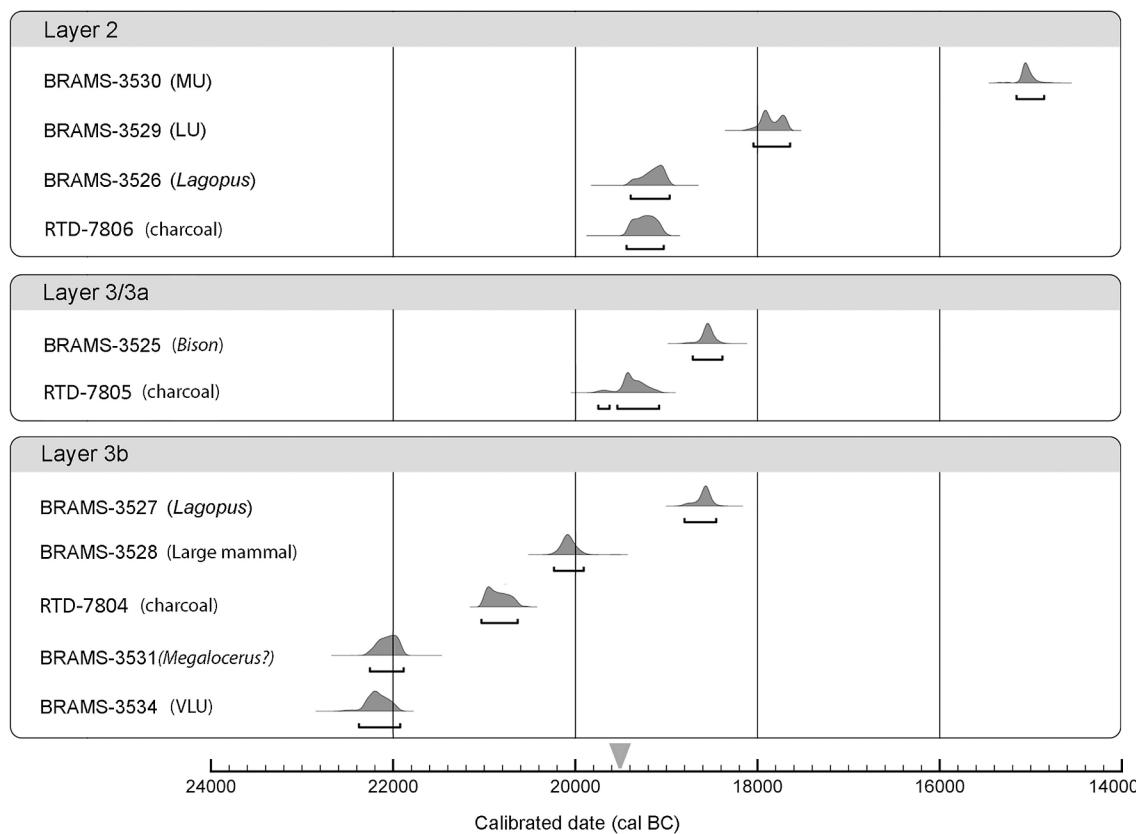


Fig. 3. Radiocarbon dating results for VP by layer group as calibrated BC. Taxon or charcoal identification appears alongside date number and sample source: (MU) medium ungulate; (LU) large ungulate; (VLU) very large ungulate; (*Lagopus*) ptarmigan. BRAMS-3532 sample is probably *Megaloceros* (giant deer), and BRAMS-3534 sample represents an ungulate in the same body size range. Approximate lowest temperature point indicated by inverted triangle on the horizontal axis, based on Greenland ice core records. (BRAMS-) Bristol Radiocarbon AMS Facility, UK; (RTD-) D-REAMS Radiocarbon Laboratory, Weizmann Institute of Science, Israel (Dr. Bridget Alex). Calibrated using OxCal version 4.4, IntCal 20 curve.

Table 1
Radiocarbon dating results on bone collagen and charcoal for VP by layer and taxon.

Layer	Material	Taxon	Element	Lab no.	^{14}C yearsBP	Calibrated BP 2 σ range
2	bone	<i>Ursus arctos</i>	mandible	BRAMS-3532	927 ± 25	915–775
2	bone	Medium ungulate	mandible	BRAMS-3530	13975 ± 41	17118–16816
2	bone	Large ungulate	indet long bone	BRAMS-3529	16433 ± 49	19994–19594
2	bone	<i>Lagopus</i> sp.	metatarsal	BRAMS-3526	17475 ± 54	21338–20911
2?	charcoal	<i>Pinus</i> sp.	na	RTD-7806	17540 ± 50	21382–20977
3/3a	bone	<i>Bison priscus</i>	tibia	BRAMS-3525	16966 ± 51	20658–20335
3b1	bone	<i>Lagopus</i> sp.	ulna	BRAMS-3527	16999 ± 52	20749–20402
3b	charcoal	<i>Pinus</i> sp.	na	RTD-7805	17650 ± 50	21493–21036
3b1	bone	Large mammal	indet long bone	BRAMS03528	18074 ± 57	22186–21861
3b/3c	charcoal	<i>Pinus</i> sp.	na	RTD-7804	18865 ± 50	22969–22573
3b3	bone	<i>Megaloceros</i> ?	femur	BRAMS-3531	19997 ± 68	24204–23835
3b1	bone	Very large ungulate	rib	BRAMS-3534	20177 ± 70	24204–23951
3c	bone	<i>Ursus spelaeus</i>	fibula	BRAMS-3533	>43256	>45309
3	tooth	<i>Ursus spelaeus</i>	dentin	AA-109327	>38,200	>42221
3	tooth	<i>Ursus spelaeus</i>	dentin	AA-109328	>40,000	>42892

Notes: (BRAMS-) Bristol Radiocarbon AMS Facility, UK; (AA-) Arizona Radiocarbon AMS Laboratory, USA; (RTD-) D-REAMS Radiocarbon Laboratory, Weizmann Institute of Science, Israel (Dr. Bridget Alex). Calibrated using OxCal version 4.4, IntCal 20 curve.

especially among the retouched pieces. Among all blanks, the relative abundances of blades and flakes do not vary between Layers 2 and 3 (Fisher's exact test $p = 0.653$). There are more blades than bladelets in the Layer 2 assemblage, while the reverse is true in Layer 3, but these differences are not statistically significant (Fisher's exact test $p = 0.161$).

The small assemblage of cores from VP (SI Table 2) contains a large proportion (11/28) of informal or lightly worked specimens that can be described as tested and amorphous types. The next most abundant categories are prismatic blade/bladelet cores ($n = 8$) and uni- and bi-

directional flake/blade cores ($n = 6$). Blade/bladelet cores are mostly unidirectional (6/8). Although quantities are small, each of these three core categories suggests a preference for certain raw materials. Eight of the 11 amorphous and tested cores were made of a coarse-grained gray and tan flint, whereas only three of the more formal cores were made from this material (Fisher's exact test $p = 0.006$). A fine-grained mottled tan flint was used to make five of the eight prismatic blade/bladelet cores, and no other core forms were produced on this material (Fisher's exact test $p = 0.0006$). Three of the four uni/bidirectional flake cores are

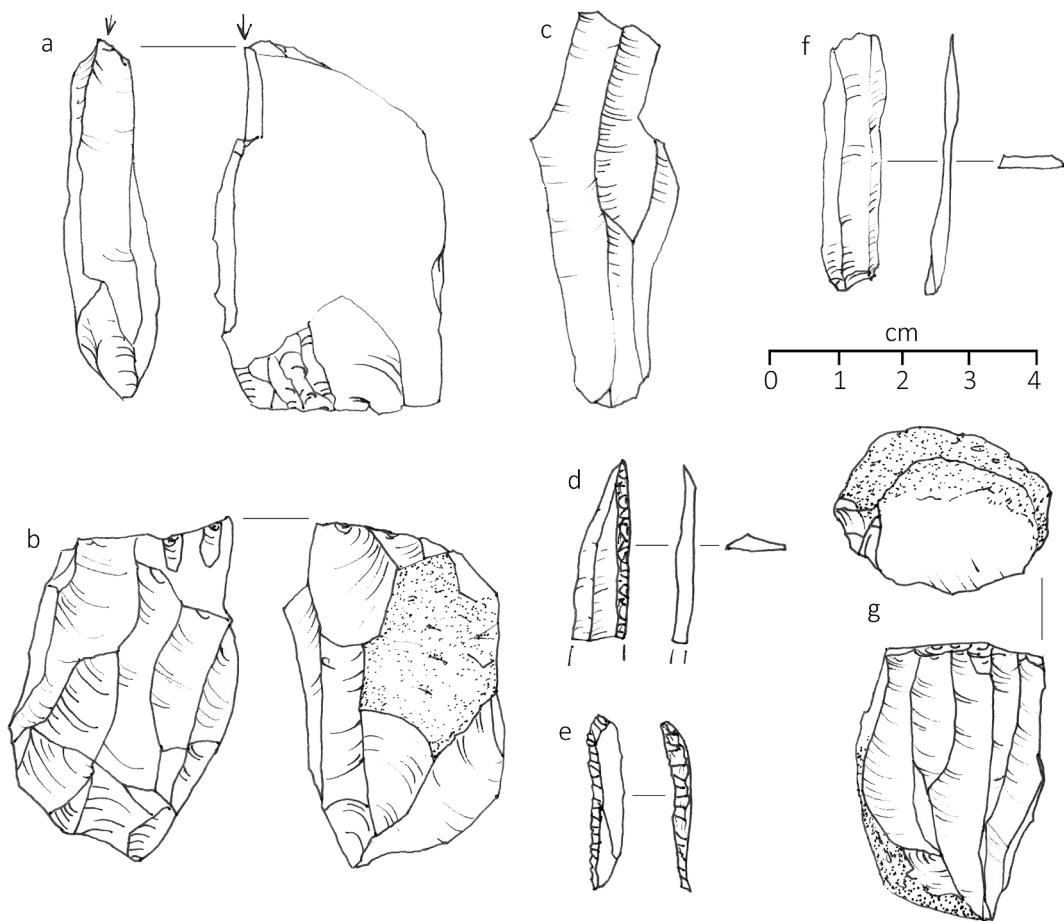


Fig. 4. Examples of lithic artifacts from VP: (a) burin, (b, g) cores, (c, f) unretouched blade and bladelet respectively, and (d-e) backed bladelets. Images redrawn by M.C.S. from originals by I. Sanchez-Morales (a, b, e, g) and D. Mihailović (c, d, f).

Table 2
Artifact classes by layer in VP.

ARTIFACT CLASS	Layers:	2	2/3	3	3c/4	4	Indet.	Total
Flakes, blades, etc.	13	75	37	163	1	8	6	303
Retouched tools	2	8	8	31	1	0	1	51
Cores	0	2	6	15	2	2	1	28
Chips	9	15	5	39	2	0	0	70
Chunks	1	3	2	29	5	0	0	40
Total	25	103	58	277	11	10	8	492

made from a fine-grained, light brown translucent flint, a material that was used for just one of the other 21 cores (Fisher's exact test $p = 0.011$).

These observations are difficult to interpret in the absence of information about raw material distributions in the surrounding area. We can hypothesize that the coarse-grained grey and tan flint was obtained locally, based on its preferential use in informal and brief reduction sequences. The finer-grained tan flint was used preferentially for cores that were more elaborately worked. This material may have come from a greater distance from VP, or it may have been scarcer in local secondary deposits and thus reserved for more demanding procedures.

Blades and bladelets from VP are predominantly straight or lightly concave ventrally. Bladelets with markedly twisted profiles are absent. Production of bladelets appears to have been by unipolar method almost

Table 3
Blank types by layer in VP, retouched and unretouched pieces.

BLANK TYPE	Layers: 1	2	2/3	3	3c/4	4	Indet.	Total
>50% cortical blade	0	2	1	4	0	0	0	7
>50% cortical flake	1	5	6	9	0	1	0	22
Plain blade	1	19	7	28	1	1	1	58
Plain bladelet	4	16	7	46	0	0	4	77
Plain flake	4	25	15	46	1	2	1	94
Burin spall	0	0	0	1	0	0	0	1
Core trimming elem.	0	6	3	12	0	3	1	23
Indeterminate	5	10	7	48	0	1	0	71
Pebble fragment	0	0	0	1	0	0	0	1
Chip	9	15	5	39	2	0	0	70
Chunk	1	3	2	28	5	0	0	40
Core	0	2	6	15	2	2	1	28
Total	25	103	58	277	11	10	8	492

exclusively. Dorsal scars that originate from the distal ends of bladelets tend to be short, and likely arose from adjusting the distal convexity of the face of detachment rather than resulting from blank detachment. A few larger blades and one core do show signs of true bidirectional production.

The Velika Pećina lithic assemblages correspond with the early Epigravettian in southeastern Europe (Kozłowski 1999; Mihailović and Mihailović, 2007). However, the small collection of shaped tools ($n = 51$) lacks diagnostic artifact forms such as microgravettes and shouldered points. The assemblage is dominated by backed and retouched bladelets, which account for about half of the total sample, but the proportions of bladelet tools are higher in the Layer 3 collection (61%, Table 4). Large tools include two large, pointed retouched blades (from Layer 3), five burins, and two endscrapers (one from an indeterminate context). Retouch on bladelets is mostly abrupt (true backing) or semi-abrupt; fine marginal retouch is present on only 4 of 35 modified bladelet edges. Retouch scars originate from the ventral surface on almost all backed pieces; the single exception shows bipolar backing. Most of these artifacts are simple backed or retouched bladelets, although the sample from Layer 3 includes two straight-backed pointed bladelets.

5. Osseous artifacts

The sample of osseous artifacts from VP is small but varied both in forms and the raw materials used (ivory, bone, teeth, antler, Figs. 5–8). Worked specimens include mammoth ivory fragments along with sections of at least two bone needles or fine awls. The needle-like artifacts are broken and neither preserves an eye (Fig. 7e-f). Also present are one point-base (probably of antler) and various debris from bone, antler and ivory working. One unifacial “mega-polisher” made from a bison distal metatarsal shows extensive wear from prolonged rubbing on a soft gritty material (Fig. 6c); no other specimens from VP show this kind of damage.

We assume that the proboscidean ivory is from mammoth. The ivory does not appear to be fossilized and thus may be contemporary to the anthropogenic layers, but this is not certain. One large ivory fragment is extensively worked and has deep axial incisions (Fig. 5), another one is burned, and most specimens display conchoidal fractures (Fig. 7c-d). At least two of the ivory fragments derive from the tusk tip, which typically has finer, straighter growth rings than mature ivory (Fig. 7d). This tissue, called mantle ivory, forms before the process of dentine formation becomes more constrained or circumferentially crowded as the animal ages and has tree-like growth rings for this reason (see Raubenheimer

Table 4
Tool forms by layer in VP.

TOOL FORM	Layers: 1	2	2/ 3	3	3c/ 4	indet	Total
Backed blade	0	0	0	1	0	0	1
Truncated backed blade	0	1	0	0	0	0	1
Backed bladelet	0	2	1	3	0	0	6
Backed bladelet frag.	0	0	1	9	0	0	10
Backed point	0	0	0	2	0	0	2
Truncated backed bladelet	0	0	1	0	0	0	1
Retouched bladelet	0	1	0	5	0	0	6
Burins	0	1	2	2	0	0	5
Endscraper	0	0	1	0	0	1	2
Truncation	1	1	0	0	0	0	2
Percoir	0	0	0	1	0	0	1
Micro-percoir	0	1	0	0	0	0	1
Pointed blade	0	0	0	2	0	0	2
Raclette	0	0	1	0	0	0	1
Retouched blade	0	0	0	3	1	0	5
Retouched flake	0	0	1	1	0	0	1
Partially backed piece	0	0	0	1	0	0	1
Fragment	1	1	0	1	0	0	3
Total	2	8	8	31	1	1	51

et al. 1998). Possibly also linked to early tusk development are the porous, netted surfaces on two of the ivory fragments (Fig. 5 and 6a).

Certain other ungulate bone fragments may have served as informal retouchers. Apart from one specimen, these occurrences are difficult to assess because the VP inhabitants also frequently cracked large marrow bones by striking them on rough limestone anvils or hammers (see below). Multiple pitted surfaces on some bones indicate that multiple blows were needed to break them open, a pattern consistent with expedient use of local rocks.

The lone ornament recovered from VP Layer 3 was made from a lower incisor of *Alces* (Fig. 8). The tooth root was pierced bi-directionally, and the perforation shows rounding (polish) from use. The specimen is nearly complete. Our taxonomic identification of the incisor is based on the shape and width of the crown, its relatively long root, and the overall straightness of the tooth (see SI Fig. 2 and associated text).

6. Results on the vertebrate faunal remains

The VP faunal assemblages are rather small but contain rich arrays of mammal and bird species (summary diversity statistics provided in SI Tables 3–4). A total of 160 identified vertebrate remains (NISP) were retrieved from secure contexts in Layer 2, and 1221 NISP from Layer 3. The range of species (Appendix A) testifies to a complex environment that included grassy steppe, rocky uplands, patches of woodland, streams, and ponded water, all within a relatively small area.

6.1. Species composition and environmental correlates

Small vertebrate remains are comparatively abundant in VP, especially in Layer 3 (375 NISP, 85 identified to species; see Appendix A, SI Table 5). Identified remains in Layer 2 are too few for reliable comparison. The Layer 3 small vertebrate assemblage is dominated by rodents, along with rare remains of insectivores, small reptiles, amphibians, and fish. Of the nine rodent species identified, six are voles (*Arvicolidae*), two are cricetids, and one is the blind molerat, *Nannospalax leucodon*. The predominance of voles and cricetids, and the absence of murids, attest to generally cold dry conditions. The rodent assemblage contains no extinct species, but the Romanian hamster (*Mesocricetus newtoni*), gray dwarf hamster (*Cricetulus migratorius*), and narrow-headed vole (*Stenocranius gregalis*) no longer exist in Serbia. The common/field vole (*Microtus arvalis/agrestis*), Romanian hamster and blind molerat are typical inhabitants of xero-mesophilous environments, and these taxa constitute two-thirds of the identified rodent species. However, a wider range of local habitats are suggested by the presence of other species, including steppe and semi-arid conditions (dwarf hamster and narrow-headed vole), moist meadows and riverbanks (water vole, *Arvicola terrestris*; pine vole, *Terricola subterraneus*), alpine terrain (European snow vole, *Chionomys nivalis*), and rarely forest (bank vole, *Myodes glareolus*). Also present are hare (*Lepus europaeus*), steppe pika (*Ochotona pusilla*), and hedgehog (*Erinaceus roumanicus*). The presence of pika confirms a prevalence of steppe vegetation, as does the rodent fauna. The recent distribution of this lagomorph is confined to the temperate steppes of Central Asia.

Large herbivores in Layer 3 are dominated by ibex (*Capra ibex*), an upland herbivore, and steppe bison (*Bison priscus*). There are scant remains of rhinoceros, proboscidean (presumably *Mammuthus primigenius*), horse (*Equus ferus*), red deer (*Cervus elaphus*), and giant deer (*Megaloceros giganteus*). Chamois (*Rupicapra rupicapra*) is present but rare. The mammalian carnivores in VP include cave bear (*Ursus spelaeus ingressus*), brown bear (*Ursus arctos*), wolf (*Canis lupus*), red fox (*Vulpes vulpes*), lynx (*Lynx lynx*), leopard (*Panthera pardus*), and three mustelid species at very low frequencies (*Meles meles*, *Martes martes*, *Mustela erminea*).

The bird species in Layers 2 and 3 are particularly varied (see SI Table 4) and again testify to considerable environmental heterogeneity



Fig. 5. Worked ivory specimen (left) and detail of natural surface texture and grooves (right).

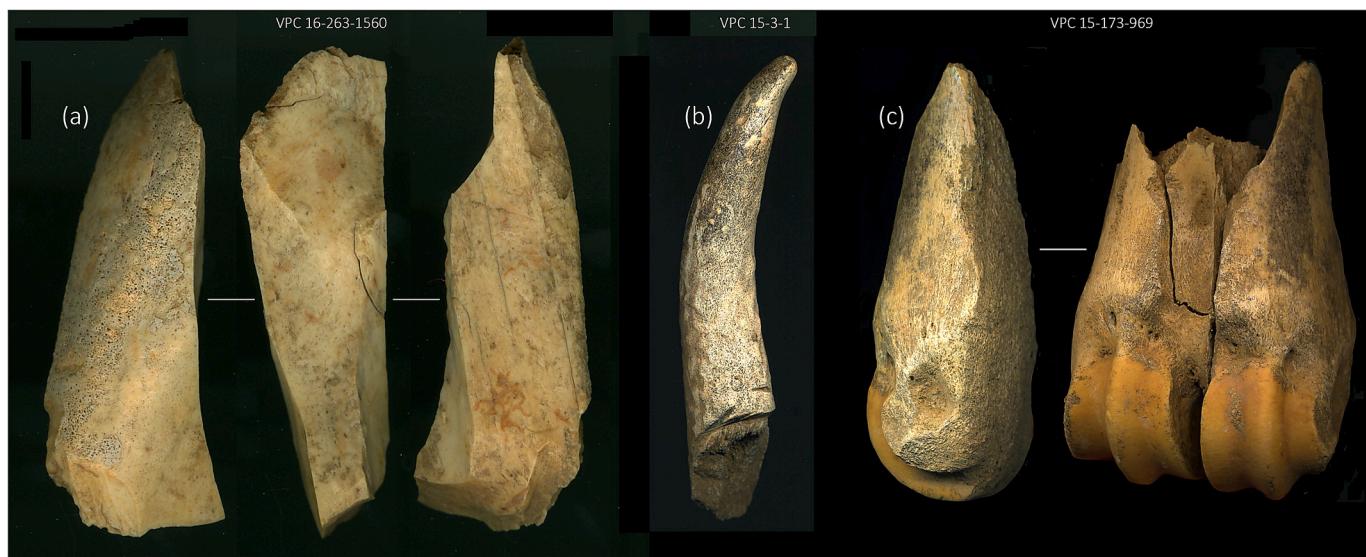


Fig. 6. Worked osseous artifacts made from different raw materials: (a) three views of fractured mantle ivory from mammoth, specimen length 66 mm; (b) red deer antler tine detached by groove-and-snap method, length 112 mm; (c) bison distal metatarsal, posterior face of which was used as a polisher or abrader, length 95 mm.

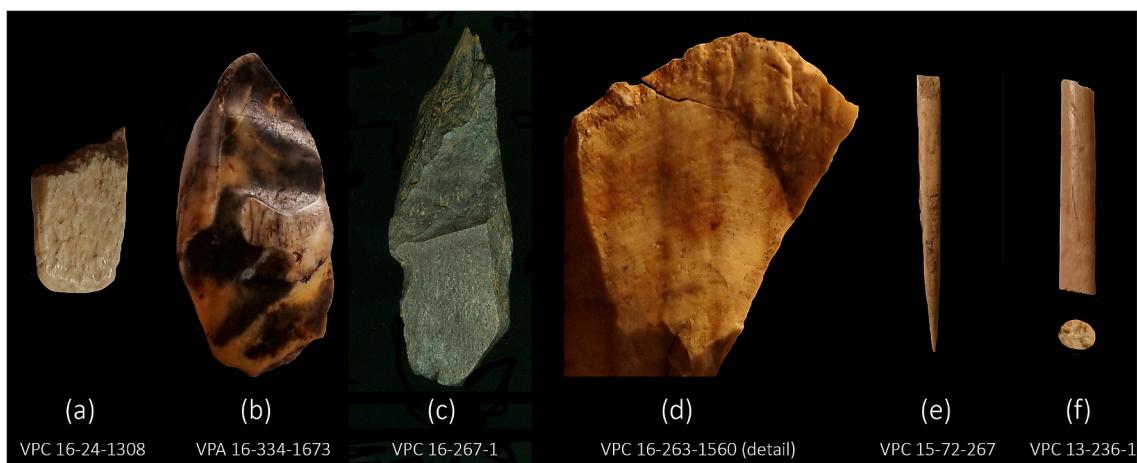


Fig. 7. Smaller osseous artifacts (not to same scale): (a) probable point base (possibly antler), specimen length 16 mm; (b) cave bear lower canine fragment with conchoidal fracture, possibly modified by humans, length 28 mm; (c) mammoth ivory with conchoidal fracture and burning damage, length 40 mm; (d) detail of mammoth mantle ivory cross-section from Fig. 6; (e) probable bone needle, length 32 mm; (f) heavy needle or fine point shaft and cross-section, from Layer 2–3 interface, length 15 mm.



Fig. 8. European elk (*Alces alces*) incisor ornament with drilled root from VP Layer 3: (a) detail of modified root tip; (b) multiple views of the entire specimen; (c) modern *Alces* incisor for comparison (courtesy K. Mannermaa of the Helsinki Museum of Natural History). The total length of the VP incisor from the root apex to the top of its lightly worn crown is 51.0 mm, and the occlusal length of the crown is 11.5 mm. The basal width of the crown (bucco-lingual dimension) is 10.8 mm, and the basal length (mesio-distal) is 7.6 mm.

within the study area (see also Boev and Milošević 2020). The avifauna is dominated by land fowl (galliform birds), especially ptarmigans (willow ptarmigan, *Lagopus lagopus*; rock ptarmigan, *L. muta*), but also black grouse (*Tetrao/Lyrurus tetrix*), grey partridge (*Perdix perdix*), and the migratory common quail (*Coturnix coturnix*). Four species of duck (*Anas crecca*, *A. acuta*, *A. platyrhynchos*, and *A. querquedula*) and an undetermined species of goose (*Branta* sp.) were also identified in Layer 3. The ducks are dabbling types that frequent shallow water and water edges, and these co-occur with water rail (*Rallus aquaticus*), coot (*Fulica atra*) and an undetermined species of crake (*Porzana* sp.).

Several species of the crow family (Corvidae) are also present, namely the Eurasian jay (*Garrulus glandarius*), spotted nutcracker (*Nucifraga caryocatactes*), jackdaw (*Coloeus/Corvus monedula*), possibly magpie (*Pica* sp.), and two species of chough (red-billed *Pyrrhocorax pyrrhocorax*, alpine *P. graculus*). The corvid species associate with a variety of habitats. The nutcracker's main food source is nuts from pine, spruce and hazel, whereas Eurasian jays prefer mixed woodland but associate most strongly with oak and beech trees. The smaller-bodied alpine chough, true to its name, breeds at high elevations and utilizes barren rocky areas. The red-billed chough prefers rocky cliffs and caves, and the cliff above VP would have provided good nesting sites for them.

The presence of both rock and willow ptarmigans in Layers 2 and 3 is not unexpected, since they are reported at certain other Upper Paleolithic sites that formed during glacial conditions and/or occur at high elevations (Smith et al. 2013; Smolučka Cave in Serbia, Malez and Dimitrijević 1990; Rio Secco Cave in the Italian Alps, Carrera et al. 2018; La Vache Cave in the French Pyrenees, Laroulandie, 2005). At VP, ptarmigans co-occur with partridges, the latter of which prefer lower latitudes/altitudes. Because the slightly smaller grey partridge is common throughout modern Europe, the relationship between ptarmigans and partridges at VP is important to understanding the climate and environmental background to the Paleolithic occupations there. We used metric comparisons and morphological features to distinguish among two species of ptarmigan (*Lagopus*) and grey partridge (*Perdix*) in the assemblages. The results, presented in SI Tables 6-7 and SI Fig. 3, confirm the presence of both grey partridge and ptarmigans in the archaeological assemblages, with ptarmigans being much more common than partridges. Moreover, measurements of tarsometatarsals indicate that rock ptarmigan, which is adapted to open rocky uplands, is much more abundant than willow ptarmigan at VP.

The prevalence of voles and cricetids, which prefer open-lands and steppe, is typical for the glacial stadials of the Late Pleistocene in Serbia (Dimitrijević 1997, 1998; Bogićević, 2008). The VP assemblages are unique, however, for their very poor representation of woodland taxa (only one bank vole specimen), complete absence of glirids, high incidence of boreal narrow-headed vole (*Stenocranius gregalis*), and presence of mountain-dwelling snow vole. The faunal spectra of Layer 2 and Layer

3 both point to sub-arctic to cold-temperate conditions. Ptarmigans, for example, associate with very cold habitats and no longer exist in Serbia. But many more taxa in these layers are typical of cold temperate conditions. Given that the radiocarbon dates for Layer 3 are fairly constrained in time (Table 1, Fig. 3), it seems that boreal, steppe and arctic types coexisted in the study area around the time of the LGM.

In sum, the diversity of habitats suggested by the VP faunal assemblages is striking. Layer 3 contains wetland birds alongside alpine birds and mammals (choughs, rock ptarmigan, ibex, and chamois). The most important mammal species in both archaeological layers is ibex (*Capra ibex*), typical of upland areas, but the second most important mammal, the steppe bison (*Bison priscus*), requires grasslands. A diverse suite of open-land grazers and browsers are represented by willow ptarmigan, black grouse, horse, steppe bison, red deer, giant deer, rhinoceros, and mammoth. This diversity is partly explained by the steep altitudinal gradients in the landscape around the site, but also by the relatively fine-scaled habitat patchiness of the region overall.

6.2. Human and non-human agents of bone accumulation and modification

The VP assemblages are extensively fragmented in the manner typical of European Upper Paleolithic faunas for generally. Otherwise, the quality of macroscopic preservation is very good. Most of the fractures occurred when the bones were fresh and their collagen structure intact. Specimens in anatomical connection are very rare, on the other hand, due to some combination of colluviation, surface scattering, and some bioturbation. Weathering damage is common in Layer 2 (33% of total NISP), indicating a slow rate of burial, but rare in Layer 3 (5%, Table 5). The extent of weathering damage is uniformly mild where it occurs and is limited to fine surface cracking (see Behrensmeyer 1978). Importantly, weathering damage is much more prevalent on large mammal bones than on the other vertebrate remains in each layer (Table 5). This result implies that larger specimens may have rested on the ground surface for longer periods inside the cave.

The multiplicity of bone accumulating agents was another factor that contributed to species diversity in the VP faunas. The majority of larger faunal remains in VP relate to human activity at the site. However, certain carnivorous mammals and birds also visited the cave, most importantly bears, wolves, foxes, and large owls. Bones and teeth of cave bears (*Ursus spelaeus ingressus*) are numerous in Layer 3, and some are also found Layer 2. Radiocarbon dates indicate that the cave bears are significantly older than, and brown bear significantly younger than, the human occupations at VP (Table 1). Cave bears declined in western and central Europe after 30,000 years ago, and intensive dating programs have demonstrated that the last populations went extinct around the end of the Gravettian culture period (e.g., Baca et al. 2017; Gretzinger et al. 2019). The cave bear remains concentrate in squares N19-20, near the opening of the larger interior chamber on the eastern end of the excavation grid (Fig. 9). Their bones are more mineralized and darker in color than the other faunal remains. They lack tool marks and were heavily gnawed by large predators. It seems that the cave bear remains were redeposited into the main chamber from deeper cavities in the cave system. A similar depositional scenario applies to the recent brown bear remains. All the bear remains likely stem from mortality associated with winter dens.

The cave also attracted other carnivorous animals on a seasonal basis and/or in alternation with the human occupations. Non-ursid carnivore remains show no bias in their horizontal distributions, but human-modified bones (burned and/or with impact damage) concentrate in the western end of the excavation grid (Fig. 9) where hearth traces were also identified. Bird remains are widely scattered in Layer 3 (not shown, but see SI Fig. 4), but corvid distributions generally differ from those for land fowl (galliforms) in Fig. 9. Microfauna remains are common throughout Layer 3 but most abundant in the area where corvid remains are also most common (squares M18-N18, Fig. 9).

Table 5

Summary of the frequencies of taphonomic alterations to identified specimens from VP by level and general animal categories.

Taxon/Size class	Total NISP	NISP tool-marked %	NISP worked (tech) %	NISP gnawed/punctured %	NISP burned %	NISP weathered %	NISP with impact damage %
Layer 2:							
Pisces	1	0	0	0	0	0	0
Small mammals	18	*	0	*	0	*	0
Medium mammals	12	0	0	*	0	*	*
Large mammals	6	*	?	*	0	*	0
Large herbivores	58	21	?	14	5	28	31
Carnivores	31	?	0	23	0	45	8
Birds	24	?	0	4	0	0	0
All taxa combined	150	10	1	12	2	33	13
Layer 3:							
Pisces	0	0	0	0	0	0	0
Small mammals	49	0	0	18	0	0	10
Medium mammals	92	9	2	14	2	3	1
Large mammals	77	8	1	6	12	3	1
Large herbivores	523	22	1	13	8	37	33
Carnivores	155	3	0	17	1	7	4
Birds	221	2	0	2	1	0	0
All taxa combined	1117	12	1	11	5	5	17

Notes: (?) possibly present but not certain; (*) small sample size, damage is present but percentage calculation suspect; (tech) osseous artifact or manufacturing debris. NISP in this table combines taxon-specific and body class-based identifications.

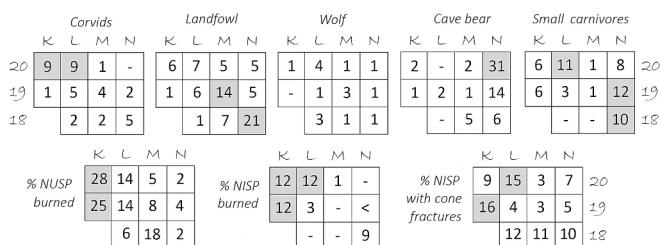


Fig. 9. Horizontal distributions of key taxa and bone damage types (burned or cone fractured) in VP Layer 3 by 1 × 1 m horizontal excavation units: (top row) NISP counts for corvids, landfowl, cave bears, small carnivores, and wolf; (bottom row) percent NUSP burned, percent NISP burned, and percent NISP with cone fractures for all micromammal remains. Shading highlights highest frequencies as relevant. Burned bone frequencies (%) by square are given separately for the identified (NISP) and unidentified (NUSP) material. Because our approach to recording burning damage is conservative (following Stiner et al. 1995), the frequencies are minimum estimates. Cone fracture and/or impact-notched percentages are based on NISP only, and include specimens identified only to body size classes for ungulates and carnivores.

The sources of bird and small mammal remains in VP are not altogether clear. Very few bird bones are tool-marked, burned, or gnawed by carnivores (Table 5). We find mild digestive erosion on some of the small mammal and bird bones, and a few with fine angular perforations from a large beak of the sort typically produced by eagle owls (Bochenksi and Tomek 2020). Rare eagle-owl (*Bubo bubo*) remains are present in Layer 3, and this large owl is noted for consuming an exceptionally wide range of prey, especially rats, voles, hamsters, hedgehogs, and lagomorphs (Web source 1). Indeed, the species composition in a large sample of modern eagle-owl pellets from Romania (Sándor and Ionescu 2009) is similar to the combined sample of microfauna, birds and small mammal components from Layer 3 (SI Table 8), except for the higher frequencies of land fowl and corvids in VP. Body part representation for the VP land fowl and waterfowl (SI Fig. 5, SI Table 9) also contrasts with human-hunted ptarmigans from the Upper Paleolithic site of La Vache in France, where many cut marks were identified on coracoids, scapulae and upper limb bones (Laroulandie, 2005: Tab. 2). A few cut marks are found on the VP land fowl bones (Table 5), so at least some of these birds were exploited by humans.

Damage to hare and steppe pika mandibles follows a single pattern of mild rounding of break edges from saliva or digestive acids, with the posterior parts of the mandibular rami broken away (SI Fig. 6). The

extent of digestive erosion could indicate a large owl and/or canid (compare Andrews 1990; Schmitt and Juell 1994; Stiner 1994), but breakage to the mandibles is most consistent with large owls. Experimental studies show that owls favor juvenile hares and rabbits, whereas human hunters tend to take adult animals (Hockett 1991). The age-able scapulae of hares in VP are fused, but 75% of proximal humeri and tibias are unfused, indicating juvenile individuals. The rodents can also be linked to owl predation (pellets). Cranial remains are mostly mandibles (NISP 100), with no complete skulls preserved and just a few partial maxillae (NISP 4). The damage to rodent mandibles is strikingly uniform, with horizontal rami usually intact, and the vertical rami partly or completely broken.

In contrast to rodents, some birds of the crow family (corvidae) may have entered the deposits through attrition from nests. Juvenile bird remains occur in both layers, with one nestling element in Layer 2 (4% of bird NISP) and 17 nestling elements in Layer 3 (7% of bird NISP). These remains are from medium-sized corvids, probably red-billed choughs. Choughs prefer to nest on cliffs or in caves, and immature individuals probably fell or were predated from nests above or near the cave entrance.

Wolves and foxes were the main sources of gnawing and digestion damage on ungulate and carnivore remains (Table 5). Gnawing traces include small and large punctures, salivary rounding, “crenulation”, outward peeling of compact bone tubes, and tooth drag marks (SI Fig. 7). A small number of compression (cone) fractures on the carnivore bones probably resulted from direct pressure from wolf jaws rather than from human tools; these fractures tend to be irregular in diameter and form, and they co-occur with obvious gnawing traces (and thus were quantified as gnawing damage). Several other specimens were digested by wolf-sized carnivores and entered the deposits as fecal bone (SI Fig. 8). The few remains of chamois in VP were deposited in this way, almost certainly by wolves. There is good evidence that wolves and foxes were also scavenging from humans' refuse middens in the cave. At least ten specimens in Layer 3 have cut marks over-printed by carnivore gnawing damage (minimally 8% of cut-marked specimens), and one other specimen was identified in Layer 2 (Table 6). Fig. 10 shows one example of an ungulate limb shaft fragment that were first cut marked by human tools and then digested or extensively gnawed by a large carnivore.

There is no clear evidence for denning by wolves or foxes in VP. The wolf remains are from one sub-adult and possibly another adolescent. Fox remains include one cub along with parts of two adolescent/young adult individuals. These remains might indicate young raised in the cave, but it is equally possible that they were brought in by other

Table 6

Summary of cut mark properties by layer in VP.

Cut mark properties	Layer 2N specimens	%	Layer 3N specimens	%
Perpendicular cuts	4	29	31	25
Diagonal cuts	7	50	73	60
Axial cuts	2	14	15	12
Axial scrapes	1	7	3	2
Multi-grooved cuts	6	43	14	11
Gnawing overprinted	1	7	10+	8+
Total specimens with cut marks	14		122	

Notes: (*) Data exclude chop and hack marks from human tools. Cut mark orientations are classified relative to the main axis of the bone. Unidentified fragments with cut marks but no morphologically defining qualities are omitted from the comparison. "Gnawing overprinted" refers to specimens for which cut marks occurred first and carnivore gnawing or digestion occurred afterwards. (+) Minimum estimate, excludes ambiguous specimens.

predators; the fragile innominate fragment from the fox cub, for example, could have been dropped by a large owl.

6.3. Human modifications and carcass processing

Tool marks are common on the remains of the large herbivores from VP. Carcass processing traces attributed to humans include burning damage, cut marks, axial scrapes, hack marks, and impact damage from stone hammers and anvils (Table 5). Double or multiple grooves occur within several of the main cut mark incisions on bone surfaces (Fig. 11), Table 6, usually in short diagonal or perpendicular strokes. About 43% of all cut-marked specimens in Layer 2 are multi-grooved, but only 11% in Layer 3 are multi-grooved.

Cut mark orientations were recorded relative to the main anatomical axis of the bone specimen. Diagonal and perpendicular cut marks, often aligned in clusters (Fig. 12 b-c), are typical of basic butchering routines of the Middle and Upper Paleolithic periods, and these comprise 79% and 85% of all cut-marked specimens in Layer 2 and Layer 3, respectively (Table 6). Long axial cuts and axial scrapes are present at lower frequencies (21% in Layer 2, 14% in Layer 3). Most of these are long axial incisions (Fig. 12d) that indicate filleting of masses of tissue from the upper limbs of large herbivores. One dramatic example of filleting can be seen on the anterior shaft of a giant deer femur in Fig. 13. Axial scrapes (also in Fig. 12d) are comparatively rare and indicate occasional use of flint scrapers or knives to remove periosteum or other tough connective tissues from bone surfaces.

The majority of cut marks occur on ungulate bones. Most of these are found on limb shafts—especially of the femur, humerus, and metapodials—but also on scapulae, vertebra, skull fragments, and the proximal-dorsal surfaces of ribs. Table 7a presents counts of bone specimens from Layer 3 with cut marks by anatomical region and major prey group. Table 7b presents the same data but standardized to total MNE (NISP/MNE) for each region and prey group. The latter statistic corrects for differential fragmentation and the fact that some body parts are simply better represented than others in the VP assemblages. Mean NISP/MNE cut mark values for small-medium and large-very large ungulates are high at 0.74 and 1.32, respectively (Table 7b). Most, or all, of

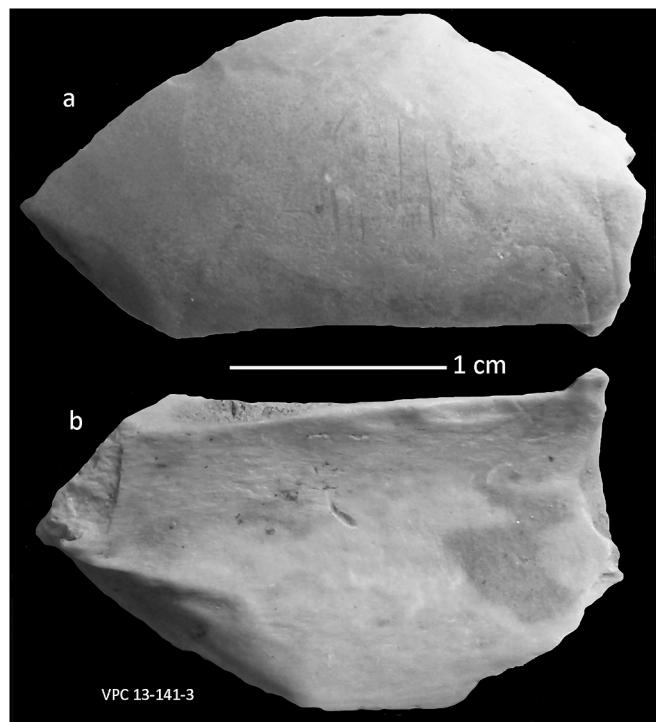


Fig. 10. An example of a cortical limb bone fragment from a medium-sized ungulate from VP with cut marks from human tools, which subsequently was gnawed and/or digested by a large carnivore, probably wolf. The cut marks are partly eroded by digestive acids but still visible, specimen length 28 mm.

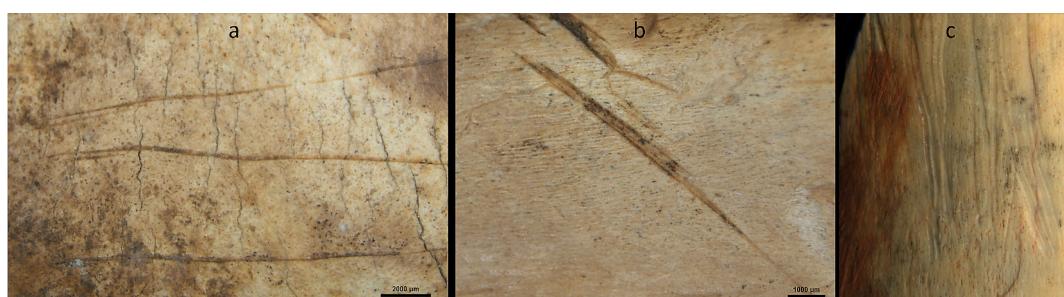


Fig. 11. Detailed views of cut marks, showing tendency for multiple grooves in each stroke on (a) lumbar vertebra and (b) rib of medium-sized ungulate; (c) axial scraping on bison metatarsal.

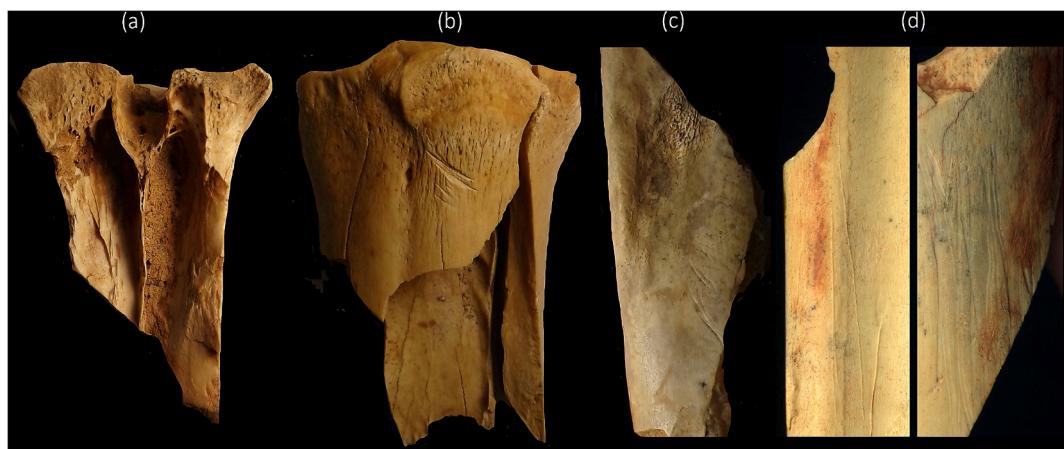


Fig. 12. Examples from VP of (a) opposing impact cones on bison metatarsal (specimen length 75 mm); (b) short deep perpendicular cuts on the anterior face of the proximal metacarpal of ibex (length 55 mm); (c) deep angled cuts on humerus shaft of medium-sized ungulate (length 48 mm); (d) two different faces of same bison metatarsal fragment with long axial cut marks at left and multiple axial tracks from a scraping tool at right (length 94 mm).



Fig. 13. Large fragment of the anterior femoral shaft of a very large deer with multiple axial cuts that indicate defleshing (filleting). The cut mark tracks are highlighted with black lines in the lower image, while the upper image provides a closer view of some of these marks. The position of the nutrient foramen (f) on the upper anterior shaft excludes large bovid species but is typical of deer. The large size of the bone (specimen length is 190 mm) indicates an exceptionally large deer in the body size range of *Megaloceros*.

the elements that were carried to the site were also marked by cutting tools at some point. The standardized data also reveal that cut marks are disproportionately abundant on head parts, ribs, humeri, scapulae, femurs (small-medium ungulates only), and tibias and metatarsals (larger ungulates).

As with the land fowl remains, small carnivore bones rarely have tool marks on them (Table 5). Mean NISP/MNE cut mark values for carnivores and birds are 0.13 and 0.05, respectively. The available sample is small, but the cut marks seem to concentrate on the limb bones of the small carnivores (fox and lynx, Table 7b), and the upper wing bones of the birds (consistent with human-generated patterns; see Laroulandie, 2005; Lazar 2021).

Cone fractures occur at high rates on the ungulate remains from VP—31% in Layer 2 and 33% in Layer 3 (see Table 5; Fig. 12a). This pattern is consistent with humans rather than carnivores being the main agent of production (Stiner 1994: 130–132). Paired cones confirm the use of hammer and anvil in some cases. In addition to producing cone fractures, hammer-and-anvil techniques can result in massive crushing and coarse pitting of bone surfaces, especially if rough stones are used. This was indeed the situation at VP (SI Fig. 9b). However, as noted

above, a few bones may instead have been used as “retouchers” or “percussors” (SI Fig. 9a).

In summary, there is widespread evidence for butchering and marrow extraction activities by humans at VP. Marrow processing relied on cold extraction methods only and focused on medullary marrow of the major limb elements and mandibles of ungulates. Fig. 14 illustrates the positions of cut marks and cone fractures on ibex and bison mandible fragments, which suggest a process of cutting and peeling away the cheek muscles and removal of the tongue; associated cone fractures reflect subsequent opening of the large marrow cavity of the horizontal ramus. SI Fig. 10 illustrates the distribution of cut marks on the limb shafts of small carnivores and ibex. Pelt removal is the likely explanation for some of the cut marks on fox and lynx. The cut marks on the ibex tibia may relate to muscle removal (SI Fig. 10d); this specimen is also an example of human processing (cuts and large cone fracture) followed by intensive gnawing of the proximal end by a small to medium-sized carnivore.

Burning damage on bones is uncommon in Layer 2 (2% of total NISP) and Layer 3 (5% of total NISP) alike. Darkened bone surfaces were noted throughout the VP assemblages, but much of this alteration relates

Table 7

Comparison of the incidence of cut-marked specimens by anatomical region for small-medium ungulates, large-very large ungulates, small carnivores, and game birds in Level 3 based on (a) NISP and (b) cut marked rate as NISP/MNE. (a) Cut-marked NISP counts:

Anatomical region	Constituent elements	Small-medium ungulates	Large-very large ungulates	Smallcarnivores	Gamebirds
Head	cranium, mandible	4	7	–	–
Neck	atlas, axis, cervical vertebrae	1	1	–	–
Rib cage	ribs	12	13	–	–
Other axial elements	post-cervical vertebrae, pelvis	4	2	–	–
Upper front limb	scapula, humerus, coracoid*, sternum*	7	6	2	3
Lower front limb	radius, ulna, metacarpal	6	4	–	1
Upper hind limb	femur	4	2	–	–
Lower hind limb	tibia, metatarsal	9	8	1	1
Feet	1st, 2nd, 3rd phalanges	–	–	–	–
Undetermined limb	shaft fragments and splinters	10	10	–	–
	Total NISP with cut marks	57	45	3	4+

(b) Cut-marked rate as NISP corrected to MNE (NISP/MNE):

Anatomical region	Constituent elements	Small-medium ungulates	Large-very large ungulates	Smallcarnivores	Gamebirds
Head	cranium, mandible	0.67	2.33	0	0
Neck	atlas, axis, cervical vertebrae	0.50	0.50	0	0
Rib cage	ribs	0.86	6.50	na	na
Other axial elements	post-cervical vertebrae, pelvis	0.50	0.33	0	0
Upper front limb	scapula, humerus, coracoid*, sternum*	1.75	2.00	1.00	0.21
Lower front limb	radius, ulna, metacarpal	0.46	0.80	0	0.04
Upper hind limb	femur	2.00	0.50	0	0
Lower hind limb	tibia, metatarsal	0.69	1.60	0.50	0.05
Feet	1st, 2nd, 3rd phalanges	0	0	0	0
	NISP/MNE mean with cut marks	0.74	1.32	0.13	0.05

Notes: (*) region includes coracoid and sternum for birds. Specimens with “possible cut marks” are omitted from this table. A low value indicates low incidence of cut marks for the specified anatomical region, higher values indicate the opposite. (na) not applicable.

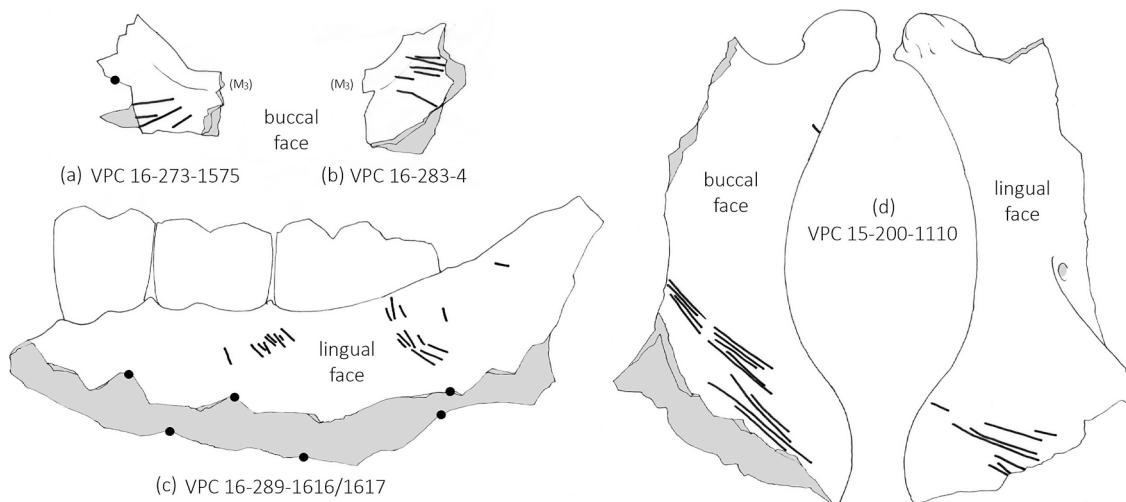


Fig. 14. Locations of cut marks (lines) and cone fractures (black points) on ungulate mandible fragments from VP: (a-b) two ibex mandible fragments (R and L sides, specimen lengths 45 mm and 43 mm, respectively), each with cut marks on the posterior buccal face of the horizontal ramus, behind the lower third molar; (c) bison right mandible fragment with cut marks on lingual face of the horizontal ramus, below the lower second and third molars, and with three pairs of cone fractures along the edge of the marrow cavity, specimen length 180 mm; (d) bison left posterior mandible fragment with long cut marks on buccal and lingual faces, the latter probably from tongue removal, specimen length 142 mm.

to mineral staining. The burning damage occurs mostly on ungulate remains (Table 5), whereas carnivore and bird bones are burned at rates of 1% of total NISP in Layer 3. The extent of burning damage on specimens is consistently light. Partial or complete calcination is extremely rare in Layer 3 (less than 1% of burned specimens), and absent in the small sample from Layer 2. However, one large jugal fragment from a bison cranium in Layer 3 is partly calcined, and there are many short, deep perpendicular cut marks on its posterior margin, along with a separate set of longer cutting and scraping marks on the lateral surface. This specimen is interpreted as evidence of roasting the cranium on hot coals.

6.4. Body part representation and age structures

The study sample from VP is small, and so general patterns of body part representation can be discussed only for Layer 3 (SI Fig. 11 and SI Table 10). Body part representation for medium (ibex) and large to very large ungulates (bison, possibly aurochs, red deer, rare giant deer, and horse) follows the typical pattern for Paleolithic shelter faunas with good bone preservation (e.g., Stiner 2005). The representation of heads and major limb bones is well-balanced, whereas vertebrae and other axial elements and phalanges are under-represented. To the extent that ungulate axial bones are present, these are dominated by ribs that tend to have perpendicular cut marks on their proximal-dorsal surfaces.

Carnivore body part representation (SI Fig. 11) is difficult to interpret due to the small number of remains, but head parts are uniformly common even though tooth elements were not used to estimate head part abundance.

Because the large mammal remains from VP originate from few individuals, and more than one collection agent was involved, we have little to say about prey mortality patterns or seasonality. In connection to the human occupations, dental data and infantile remains (cranial fragment, and unfused and underdeveloped 1st phalanx) indicate the presence of one ibex kid (ca. 1 month old) in addition to two adults.

7. Discussion

Velika Pećina is positioned intermediately to upland and lower elevation habitats, within a short but steep valley that linked several ecozones. The site likely served as a small residential camp for seasonal or periodic hunting of ungulates and small carnivores. VP was also a brief waystation at different times for wolves, foxes, owls, and bears. This “revolving-door” dynamic was common in karstic regions of southern Europe during the Pleistocene. Apart from the bears, carnivore activity at VP is not accompanied by clear evidence of denning. Rare remains of chamois at VP occur in the form of fecal (digested) bone from a large canid (presumably wolf). The kinds of damage on the cave bear bones are typical of hibernation-related mortality in paleontological sites (Andrews and Turner 1992; Kurtén 1958, 1976; Stiner et al. 1996), but these materials greatly antedate the human occupations. The presence of at least one cub is consistent with use of the cave as a hibernation den. Some individuals were attacked or scavenged by other bears and wolves in this context.

Hunting seems to have been the purpose for humans visiting VP, but the occupants also engaged in a wider variety of activities on site that included hide preparation, hide working, and osseous tool production, along with carcass butchering and marrow extraction. The patterns of tool damage on the ungulate bones indicate several butchering stages. Initial dressing of carcasses probably took place at the kill sites, where many of the axial bones and some of the toe bones were discarded. Heads and limbs were then carried to the cave for further processing. The butchering methods included filleting of large muscle masses. The medullary cavities of all major limb bones and mandibles of ungulates were opened for marrow, using expedient cold-extraction techniques.

The osseous artifact assemblage from Layer 3 is small but contains an impressive variety of tool types and raw materials—ivory, bone, teeth, and antler—along with some manufacturing debris. Unfortunately, osseous industries are under-published in the Balkans, making nearly every find seem unique. At least one possible needle fragment was found in Layer 3, but the specimen lacks its proximal end. Eyed bone needles and fine awls are reported in northeastern Romania with the onset of the UP (Bistrițioara-Lutărie III; Anghelini et al. 2017), but all other fine pointed tools that could have functioned as needles in the Balkans date to the LGM and after, such as at Badanj near the Adriatic coast (Borić et al. 2021) and at sites on the Mani peninsula in Greece (Darlas and Psathi 2017). These kinds of artifacts are also known from the Mesolithic of the Iron Gates area (Vitezović 2011). The large unifacial polisher made from the distal end of a bison metapodial from VP Layer 3 resembles examples from sites of various ages and regions, including the forager-farmer transition site of Aşağı Höyük in Turkey, where micro-wear traces indicated forceful rubbing against thick wet hide (Stiner et al. 2018: Fig. 17). While the abraded bison metapodial may point to some hide preparation at VP, we note that stone scraping tools are rare.

The lithic industries of Layers 2 and 3 could be ascribed to the technologically undifferentiated Gravettian or early Epigravettian, as known from other sites in the Balkans such as Šalitrena Pećina (Layer 3), Pešturina, Hadži Prodanova Pećina, and Meča Dupka in Serbia (Kozłowski 1999; Mihailović and Mihailović 2007; Mihailović and Milošević 2012; Plavšić and Popović 2020). The lithic assemblages lack clear “type fossils,” possibly due to small sample sizes, especially from

Layer 2. The diversity of lithic raw materials, the presence of secondary “pebble” cortex, varied debris and core trimming elements, and the frequencies of cores and cortex-bearing flakes all indicate that in-situ reduction of local raw materials contributed substantially to the assemblages. However, at least some of artifacts, including those made of rarer fine-grained flints, may have been introduced to the site from greater distances. In the absence of comprehensive raw material studies in the area, we cannot determine where such artifacts might have originated.

Multiply grooved incisions on bones, especially in Layer 2 and somewhat less commonly in Layer 3, suggest the use of composite instruments in which two or more small blades were affixed to an armature. We find no bone or antler handles, meaning that such hafts were not discarded at the VP and/or they were made of wood and have since decomposed. Given the great importance of bladelets and blades in the VP toolkits, hafting of small and large stone artifacts may also explain the considerable depth of many of the cut marks on bones from both archaeological layers.

The only ornamental object from VP is a perforated lower first incisor of *Alces*. The attribution to *Alces* is surprising because, while *Megaloceros giganteus* is often represented in Pleistocene deposits in Serbia, *Alces* has not been reported from the hundreds of caves and rockshelters that have been excavated by paleontologists and archaeologists. The tooth most probably was imported into the study area, possibly from the east. Perforated herbivore incisors and canines are reported in Europe during the Upper Paleolithic, but they are uncommon (e.g., Vanhaeren and d'Errico, 2006; Wilczyński et al., 2014). Those manufactured from deer incisors are reported as having come from “large deer” (e.g., Karavančić 2003) or specifically European elk (*Alces*, e.g., Wilczyński et al., 2014). While objects like the VP specimen have not been reported in the southern Balkans previously, a large sample of ornaments made from perforated bison and European elk incisors was found in a Gravettian child burial in Borsuka Cave (layer VI, 28,686–29,685 cal BP) in southern Poland (Wilczyński et al., 2014).

Archaeological traces of human presence across the LGM are often surprising in their content and remind us how little we still understand about this interval of human existence in Eurasia. Why, for example, did populations persist in some areas and not in others at similar latitudes? The Balkans region is unusual in that a combination of middle-latitude temperature regimes and fine-grained structural variation created refugium conditions for European fauna and flora during peak glaciation periods (Griffiths et al. 2004; Hewitt 2000). The Central Balkans, for example, supported patchworks of steppe vegetation, coniferous, deciduous, and mixed forests within relatively small areas during the periods leading into, during and following the LGM. Paleontological and archaeofaunal records from cave deposits generally testify to a high diversity of vertebrate species throughout the karst zone of Serbia (Bogićević 2008; Cvetković and Dimitrijević 2014; Dimitrijević 1997, 1998; Jovanović et al. 2020; Malez and Dimitrijević 1990). At VP, this diversity clearly persisted through the LGM. Some of the species identified no longer occur in southern or central Europe (e.g., pika, willow ptarmigans) and others have gone extinct (e.g., woolly mammoth, rhinoceros, steppe bison, giant deer, cave bear).

An important question is whether the diversity of the VP faunas is the result of (1) a prolonged accumulation time that included significant variations in climate, (2) habitat fragmentation due to fine-scale topographic relief, (3) multiple agents of bone accumulation, (4) patterns of species coexistence that no longer occur today, or (5) some combination of these. The final explanation is the most likely, but we can also rank the relative strength of these distinct influences.

During the roughly 4000 years of human use of the site, palimpsest effects could have amplified our perception of faunal diversity in the environment. Ursids must be excluded from the outset, since the cave bear occupations greatly pre-date the human occupations, and the dated brown bear sample was deposited only ca. 1000 years ago. The relatively constrained time frame of the archaeological layers largely argues

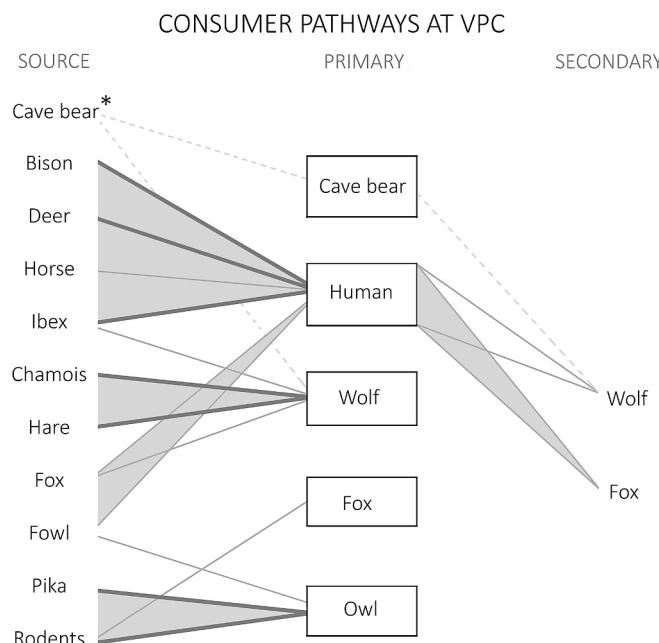


Fig. 15. Schematic summary of documented or likely consumer pathways (primary and secondary access) at VP based on taphonomic observations. Heavy lines and shading indicate the most important consumer connections; fine lines indicate probable or weaker connections. Dashed lines denote carnivore (cave bear and some wolf) interactions that took place earlier in the Late Pleistocene, before humans occupied the cave.

against the influence of different climate regimes, although the uniquely early presence of giant deer may relate to pre-LGM conditions (Table 1). However, the richness of species in the VP assemblages more than anything testifies to topography-driven environmental heterogeneity in the region, conditions that persisted as global climate shifted. Streams and standing water suitable for dabbling ducks, water edges for wading birds, and rocky uplands, grassy steppe, and patches of forest must all have existed within a day's walk of the site during the LGM. In other words, the taxonomic diversity in Layers 2 and 3 for the most part reflects synchronic richness of the ecosystem, including the coexistence of species that have distinct geographic distributions today. Because species tend to respond to climate change individually rather than as species sets, animal community composition of the Holocene generally cannot provide analogs for community structure in the Late Pleistocene (e.g., Baca et al. 2017).

That said, multiple bone collecting agents were active in VP during the Late Pleistocene. With their distinct foraging and digestive adaptations, these agents could greatly enrich the mix of species in a single location. The history of VP is one of light occupation and high turnover among various carnivorous species, with humans exerting the strongest influence on the macrofaunal assemblages. Humans visited the site many times, but they stayed relatively briefly with each visit and thus left many opportunities for foxes, wolves, and predatory birds to visit the cave when humans were not there. Fig. 15 models this complexity of consumer-deposition pathways based on taphonomic observations. The main prey of humans at VP were ungulates, especially ibex and bison, but they also hunted small carnivores, some land fowl, and other animals in low numbers. Carnivore-modified bones are scattered through Layers 2 and 3, but carnivore influences were quite limited apart from occasional scavenging of human refuse. Eagle owls appear to have deposited most of the rodent, pica and hare remains in the cave, greatly enriching the microfauna assemblages with their own hunting waste in the forms of pellets and undigested bones.

8. Conclusion

Human visited VP over a span of about 4000 years, but their use of the cave was greatest during the 2000 years straddling the LGM. We conclude from the totality of archaeological evidence that late Paleolithic humans used Velika Pećina as a short-term campsite and hub for foraging activities. These brief occupations likely involved small numbers of persons. The very low incidence of burning damage on bones, for example, supports the interpretation of short-lived occupations, which effectively reduce the chances of reburning of surface waste (Stiner et al. 1995). The relatively small sizes of the lithic and faunal assemblages corroborate a situation of brief occupations. The late Upper Paleolithic groups nonetheless conducted a range of activities at the site, including the manufacture and use of osseous artifacts. They hunted large herbivores and birds in a variety of local habitats that included rocky uplands, open grassland and wetlands. The products of hunting were butchered, cooked, and consumed in and around the cave, and at least some hides prepared for future use. Filleting cut marks indicate that at least some of the meat was removed from carcasses en masse, possibly to be smoked or dried for storage. Though focused on ungulate prey, the meat diet was relatively broad and included small carnivores and landfowl. Human activities account for only part of the overall diversity of the VP faunal assemblages, however, making it difficult to resolve the full extent of small game use at this site.

Velika Pećina represents only a small part of the land use system of the Paleolithic foragers who occupied it. It is difficult to estimate what the entire mobility and settlement system would have looked like. What we do know is that VP was situated in the rough karst lands 50–60 km south of the Danube and east of the Morava river, and that vast lowlands of the Danube corridor open to the north and west. If tree cover was limited and steppe grasslands extensive in these corridors, these areas would have supported higher ungulate biomass than the karst uplands in which VP is situated. We may therefore expect a highly differentiated pattern of land-use in the larger region, with alternating periods of high and low residential mobility depending on the season. The reticulated topographic interface between the Danube corridor and the first limestone foothills at its southern margin might have offered significant protection from winter winds and storms, along with providing firewood. In this scenario, VP might simply represent a specific kind of warm-season residential camp in the uplands that was utilized by a small group. If, on the other hand, tree biomass was high throughout the region, and patches of grassland small, people might have engaged in high residential mobility year-round (Kelly, 1983; Binford, 2001; Hamilton et al., 2016), thus creating sites of uniform character over a much larger area. In this latter scenario, VP would represent a “modal” kind of occupation. It is not certain that the land use system supported larger aggregation sites in any season. Additional studies of, and comparisons with, other sites are needed to gain a more complete picture of human use of the south-central Balkans during the LGM.

Human persistence in the Central Balkan karst during the LGM nonetheless is striking in that it was thinly but continuously populated (see also Heffter 2021). Species richness was a consistent feature of the regional ecosystem, undiminished and possibly increased slightly across the LGM. Such demographic continuity in humans points to considerable stability in community structure in spite of major climate shifts in the northern hemisphere through the Late Pleistocene. Some of the species combinations may seem disharmonious by recent standards but likely were normal to the region prior to the Holocene.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2021.103328>.

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