

The palaeoecological significance of the Pleistocene mammalian fauna from Veternica Cave, Croatia. Revision of the lagomorpha, canidae, mustelidae and felidae



Preston T. Miracle¹ and Dejana Brajković²

¹ Department of Archaeology, University of Cambridge, Cambridge CB2 3DZ, UK; (ptm21@cam.ac.uk; tel: +44(0)1223-333-532, fax: +44(0)1223-333-503)

² Institute for Quaternary Geology and Paleontology, Croatian Academy of Sciences and Arts, A. Kovačića 5, 10000 Zagreb, Croatia; (zpgkvartar@hazu.hr)

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ABSTRACT

Revision of Upper Pleistocene lagomorph, canid, mustelid, and felid remains from Veternica Cave, Croatia, eliminates previously-identified “cold-adapted” taxa like mountain hare (*Lepus timidus*), arctic fox (*Alopex lagopus*), and wolverine (*Gulo gulo*), and “steppe-adapted” animals like pika (*Ochotona* sp.) from the faunal assemblage. Our revision does not support an interpretation of significant climatic oscillations during the deposition of layers associated with MIS 2, 3, and 4. The removal of “cold-adapted” taxa suggests that either remains were deposited only during more temperate periods within MIS 3 and 2 or that cold oscillations were not strongly expressed in northern Croatia. The large mammal fauna is remarkably stable in composition over time. A wide range of environments – open, forested, wetland, and rocky – were usually present in the area surrounding Veternica, and conditions in the region appear to have been broadly temperate. This apparent stability could be owing to one or more of the following factors: A) hominins and other animals preferentially used specific sites or the region during warm phases, B) sedimentation and erosion have created a bias for warm phases, C) climatic oscillations in the region were less marked than previously thought, D) local factors of microclimate and topography buffered faunal communities from climatic oscillations, and E) animals had wider temperature/precipitation tolerances than previously thought.

Keywords: Pleistocene, Mammal, Croatia, Neandertal, Palaeoecology, Veternica Cave

1. INTRODUCTION

The Balkan Peninsula has served as a stage for meetings, contacts, movements, and exchanges since well back in the Neogene to the present day, regardless of whether the elements under consideration are tectonic plates, weather systems, vegetation communities, animal species, human cultures, or religions. Our

interest here is in the intersection between changing climates and mammalian communities. In studies of faunal changes during the Pleistocene, these themes have been variously pursued in terms of when and from whence new populations and species have evolved and migrated into or within Europe (KURTÉN, 1968; GUÉRIN & PATOU-MATHIS, 1996).

The Balkans have been recognized as a key region for examining faunal changes during the Pleistocene owing to the fact that they were an important glacial refugium for plant and animal species (BENNETT et al., 1991; TABERLET et al., 1998; HEWITT, 2000; SOMMER & NADACHOWSKI, 2006). They sit on one of the major routes in and out of Europe, and straddle a region of significant changes between climatic-vegetation regions to the north and south. It is well established that during periods of climatic amelioration, taxa expanded from the Balkans to the north. Likewise, during glacial periods there was an expansion of more open environments supporting steppic vegetation, although some woodland remained in the region (WILLIS & van ANDEL, 2004). With the expansion of more open environments came mammals adapted to more open environments; there is a repeated pattern of incursions of “Asiatic” taxa into Europe during glacial periods (KAHLKE, 1999; KURTÉN, 1968; SALA et al., 1992). During periods of glacial advance cold-adapted taxa such as mammoth (*Mammuthus primigenius*) and reindeer (*Rangifer tarandus*) are commonly found in refugia of southern Europe where they co-exist with temperate elements like roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), aurochs (*Bos primigenius*), boar (*Sus scrofa*), and red fox (*Vulpes vulpes*) (SOMMER & NADACHOWSKI, 2006, p. 258). Recent work on Pleistocene faunas in Iberia has shown that cold-adapted taxa first appeared on the peninsula during MIS 6, and that they became more common during distinct pulses in MIS 3 and MIS 2 (ÁLVAREZ-LAO & GARCÍA, 2010). These results are in broad agreement with other palaeoclimatic proxies in the region (*idem*).

The situation in the Balkans, however, is less clear. MALEZ (1972) registered the presence of many “cold-adapted” taxa in the region of former Yugoslavia and gave particular emphasis to shifts in faunal composition at the cave sites of Veternica (MALEZ, 1963), Velika pećina (MALEZ, 1986), and Vindija (MALEZ & RUKAVINA, 1979). The faunal lists from these sites were used to correlate different assemblages, determine their relative ages, and reconstruct ice age climates. From these results MALEZ (1979a) reconstructed a series of oscillations between colder and warmer conditions during the Upper Pleistocene in the region. We lack, however, adequate absolute dates to confirm these associations and sequences of change. Furthermore, revision of ungulate assemblages from Veternica (MIRACLE & BRAJKOVIĆ, 1992) and Velika pećina (BRAJKOVIĆ & MIRACLE, 1995) suggests that the originally published determinations should be treated with caution. The primary purpose of this paper is to help clarify the picture of Upper Pleistocene faunal change in the Balkans by revising the lagomorph and smaller carnivore assemblages from Veternica cave. We have focused in particular on “cold-adapted” taxa. The present contribution is thus part of a larger project of revision and re-dating of the existing faunal assemblages from the Croatian Zagorje (MIRACLE et al., 2010).

This revision of the Veternica mammalian assemblages is used to address several questions as a step toward a better understanding of the pattern and nature of late Pleistocene faunal changes in the Balkans.

1. How common were cold-adapted taxa in the region during the Upper Pleistocene (MIS 5–2), and how do these mammalian records compare to other proxies of climatic change?
2. Did the Balkans serve as a refugium for mammals during cold events during the Upper Pleistocene?

2. VETERNICA CAVE

Veternica is a significant and well-known speleological, palaeontological, and archaeological site in the Croatian Zagorje. The Croatian Zagorje is crucial to studies of the Pleistocene of the region owing to the long stratigraphic sequences and important fossil remains contained in its numerous cave sites. Among these sites are Krapina (GORJANOVIĆ-KRAMBERGER, 1906; FRAYER, 2006), Vindija (VUKOVIĆ, 1954; MALEZ et al., 1980), Velika pećina (MALEZ, 1986), and Veternica (MALEZ, 1963). The first two sites are particularly significant because of their large collections of Neanderthal fossils.

Veternica is located about 9 km west of the centre of Zagreb, Croatia, on the southwestern slope of Medvednica. The southeastern-facing entrance is about 8 m wide and 4 m high, and beyond it is an entrance chamber (15 x 7 m), “left hall” (14 x 3–7 m) followed by several kilometres of passageways and canals (MALEZ, 1963, 1965; BOŽIČEVIĆ, 1995). Quaternary sediments were excavated over an area of approximately 207 m² by MALEZ from 1951–1955 and in 1970 in trenches in front of the cave, in the entrance chamber, and in the left hall (MIRACLE & BRAJKOVIĆ, 1992).

In the most complete profiles (excavated to a depth of ca. 8 m) 11 geological layers were identified. Layer k was sterile. Layer j probably dates to the last interglacial (MIS 5) on the basis of the associated faunal assemblage (MALEZ, 1963; MIRACLE & BRAJKOVIĆ, 1992). Layers h, i, j contained evidence of hominin occupation from frequent Mousterian lithic artefacts and hearth features; charcoal from a hearth in layer i was radiocarbon dated at >43,200 BP (GrN-4984) (MALEZ, 1979a, 218). Layer g consisted mostly of large rock rubble and was found primarily in front of the cave and in the entrance chamber; it was sterile of archaeological or palaeontological remains except for a few cave bear bones near the contact with level h (MALEZ, 1965, 207). Layers d, e, and f contained few archaeological and palaeontological finds other than the abundant remains of cave bears. Several non-diagnostic stone tools were found in layer f (MALEZ, 1979b, 269), and layer d contained a few lithic artefacts and a hearth (MALEZ, 1965, 203). Overlying these sediments was layer c, a dripstone radiocarbon dated to the mid-Holocene to late Pleistocene (MALEZ, 1979a, 218). The uppermost layers, a and b, were rich in organic material, faunal remains, and artefacts from the Neolithic to Medieval periods.

3. METHODS

Our methods are similar to those used in an earlier revision of the Pleistocene ungulate remains from Veternica (MIRACLE & BRAJKOVIĆ, 1992). Identifications were made in

the first instance using the extensive recent comparative collections curated at the Institute for Quaternary Palaeontology and Geology of the Croatian Academy of Sciences and Arts, Zagreb (ZPGK). Comparative measurements on recent specimens were made by MIRACLE on collections housed in the Cambridge University Museum of Zoology (CUMZ), the Cambridge University Clark Laboratory for Zooarchaeology (CUCLZ), and the University of Michigan Museum of Zoology (UMMZ). Considerable use was also made of large palaeontological and zooarchaeological collections from sites such as Šandalja II (MIRACLE, 1995, 1996, 2007a), as well as relevant literature (e.g. carnivores: BONIFAY, 1971; POPLIN, 1976; ARGANT, 1996; DÖPPES, 2001; ALTUNA, 2004; lagomorphs: KOPY, 1959, 1960; CHALINE, 1966; POPLIN, 1976; DONARD, 1981; STAMPFLI, 1983; SUÁREZ & MEIN, 2004). Unless otherwise indicated, all measurements are after DRIESCH (1976) and were made using digital calipers (rounded to 0.1 mm).

The Pleistocene assemblages from Veternica are dominated by the remains of cave bear (ca. 75% of NISP), and we have not studied these remains. Likewise, we have not considered the Holocene assemblages from layers b and a beyond measuring the remains of hare (*Lepus europaeus*) for comparative purposes.

4. PALAEOLOGICAL REVISION OF THE VETERNICA ASSEMBLAGES

4.1. Lagomorpha

4.1.1. Leporidae

Lepus timidus

Material¹: layer d: a fragmentary skull with P³-M² left and P³-M² right (VTR. 220)²; a right I¹ (VTR. 221); a left I¹ (VTR. 222); a left mandible with I₁, P₃-M₂ (VTR. 218); a right I₁ (VTR. 223); a right M₂ (VTR. 224); a right M₃ (VTR. 225)³; a left M₁ (VTR. 226); a left M₂ (VTR. 227); a left M₃ (VTR. 228); an atlas (VTR. 217); 2 right humeri (VTR. 203, VTR. 204); a right radius (VTR. 205); a right metacarpal III (VTR. 213); a right tibia (VTR. 229); 2 left tibiae (VTR. 230, 231); a right metatarsal II (VTR. 215); a right metatarsal III (VTR. 214); layer e: a left innominate (VTR. 212); a left radius (VTR. 206); layer f: a right mandible with I₁, P₃-M₃ (VTR. 219)⁴.

The majority of the lagomorph remains from Veternica were identified by MALEZ (1963, 20–24) to mountain hare, *Lepus timidus*. The basis of this determination was the shape

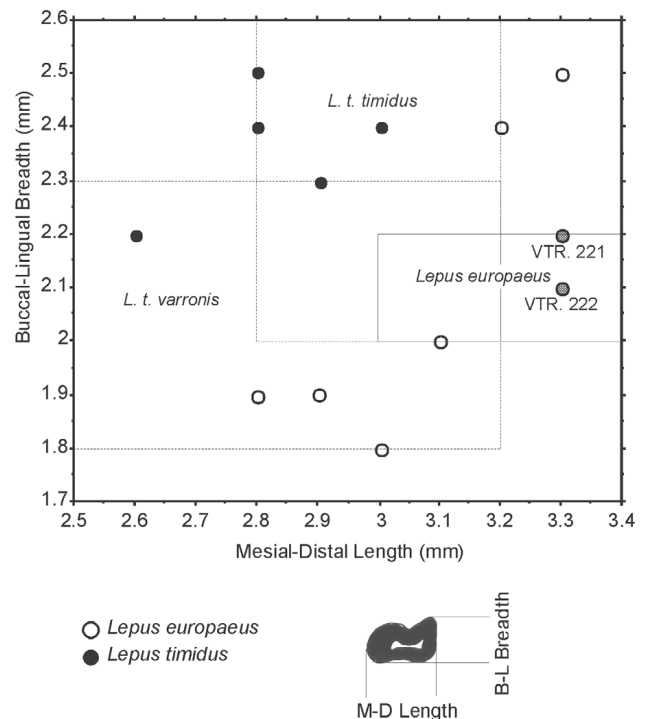


Figure 1: Length (L, mesial-distal, at occlusal surface) against breadth (B, buccal-lingual, at occlusal surface) of I¹ from Veternica compared to recent remains of *Lepus europaeus* (ZPGK) and *Lepus timidus* (CUCLZ) and fossil remains of *L. europaeus* (Holocene layer b at Veternica; Betalov spodmol, RAKOVEC, 1959; Šandalja II, MIRACLE, 1995) and *L. timidus* (Betalov spodmol, RAKOVEC, 1959; Šandalja II, MIRACLE, 1995). The boxes show the range of variation proposed by KOPY (1959, 37). Measurements on recent material from Croatia extend the range of variation of *L. europaeus*.

and morphology of the I¹; the remainder of the hare remains from layers d and e were also identified to *L. timidus* on the basis of the determination of the incisors.

The conclusive identification of lagomorph remains depends on the morphology and dimensions of the upper and lower incisors, the morphology of the P², and the relative length of the frontal to the nasal bones (KOPY, 1959, CORBET, 1966, 182–183). Of these characters, the morphology and dimensions of the incisors are particularly useful; these teeth are commonly preserved and the contrasts in dimensions are easily shown with simple, bivariate plots. *L. timidus* has incisors with a quadratic cross section while in *L. europaeus* incisors have a more rectangular cross section (KOPY, 1959, 1960; POPLIN, 1976; STAMPFLI, 1983). This contrast can be clearly presented in a bivariate plot of incisor length (mesial-distal) against breadth (buccal-lingual)⁵. In Fig. 1 we compare these dimensions for the upper incisors from Veternica to the established range of variation

¹ A right M³, right P³, and left metatarsal I reported by MALEZ (1963, 20) were not found.

² Right and left P² and left M³ reported by MALEZ (1963, 20) were not found.

³ VTR. 224 and VTR. 225 were found among the lagomorph remains identified to *Lepus timidus* from layer d, but were not included in the monograph (MALEZ, 1963).

⁴ VTR. 219 is reported to have come from layer e (MALEZ, 1963, 21). The associated stratigraphic label was “layer f”, and this specimen may account for the indicated presence of *Lepus timidus* in layer f on the summary table of faunal changes (MALEZ, 1963, table 33).

⁵ These dimensions are measured as cross-sections near the occlusal surface.

of different hare species as established by KOBY (1959), as well as to Pleistocene and recent comparative specimens. The dimensions of the Veternica I¹ are well within the range of *L. europaeus* (Fig. 1). Measurements on recent comparative material of *L. europaeus* from Croatia show that the range of variation is considerably wider than that proposed by KOBY (1959). Nonetheless, upper incisors from *L. timidus* continue to have broader occlusal surfaces for their lengths (Fig. 1). Turning to morphology, both incisors are closer to *L. europaeus* than to *L. timidus*. In both cases the furrow on the buccal surface of the incisor is not filled with dental cement; such an infilling is commonly present in *L. timidus* and is not found in *L. europaeus* (CHALINE, 1966, 406; DONARD, 1981). Furthermore the furrow on the buccal surface forms a wide “v” in cross-section, which is more similar to *L. europaeus* than *L. timidus* (CHALINE, 1966, 406; DONARD, 1981). Thus, based on both the cross-sectional dimensions of the incisors as well as their morphology, we have revised the identification of these specimens from *L. timidus* to *L. europaeus*.

Lower incisors of *L. timidus* and *L. europaeus* vary in their dimensions in a manner similar to that of the upper incisors. The cross-sectional dimensions of lower incisors identified to *L. timidus* by MALEZ (1963) are plotted in Fig. 2. VTR. 219 and 223 both lie within the range of variation for *L. europaeus* proposed by KOBY (1959). The revision of these teeth from *L. timidus* to *L. europaeus* is straightforward. Although VTR. 218 is slightly smaller than the range of variation for *L. europaeus* proposed by KOBY (1959), its relatively great occlusal length relative to breadth aligns it with the distribution of measurements of *L. europaeus*. We thus have revised all of the lower incisors identi-

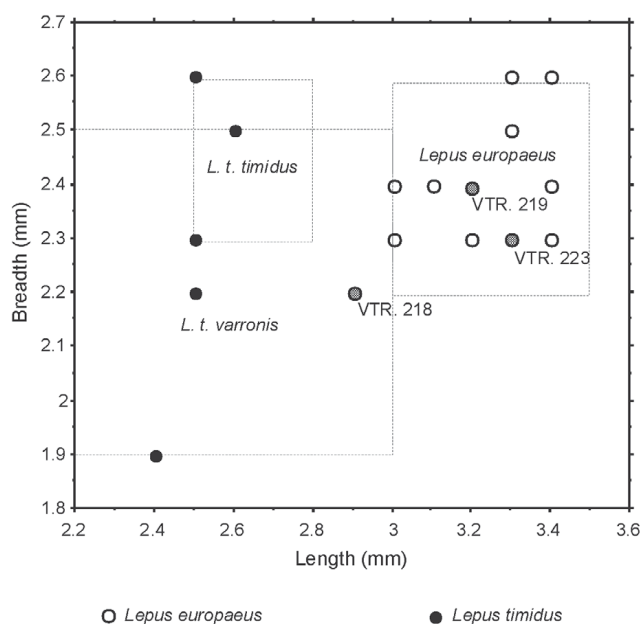


Figure 2: Length (L, mesial-distal, at occlusal surface) against breadth (B, buccal-lingual, at occlusal surface) of lower first incisors from Veternica compared to remains of *L. europaeus* and *L. timidus* from recent comparative material (*L. europaeus*), Holocene layer b at Veternica (*L. europaeus*) and late glacial layers at Šandalija II (*L. europaeus* and *L. timidus*, MIRACLE, 1995). The boxes show the range of variation proposed by KOBY (1959, 37).

Table 1: Long bone dimensions (GL = greatest length) of recent *Lepus europaeus* (ZPGK; POPLIN, 1976) and *Lepus timidus* (CUCLZ; POPLIN, 1976), and fossil *L. europaeus* (Table 2) and *L. timidus* (Abri Pataud, BOUCHUD, 1975).

Element, measurement	<i>Lepus timidus</i>			<i>Lepus europaeus</i>		
	Mean	Range (mm)	N	Mean	Range (mm)	N
Humerus, GL	98.4	93.5–104.5	8	107.5	102–113	12
Radius, GL	103.2	98.1–108.4	7	115.1	112.7–117.9	6
Femur, GL	126.5	121–134	4	134.9	127–140	9
Tibia, GL	143.6	136.5–154.3	6	153.6	143–158.8	9

fied to *L. timidus* to *L. europaeus*. Therefore, the most characteristic lagomorph elements have been shown to come from *L. europaeus* rather than *L. timidus*.

KOBY (1959, 41) observed that alpine variable hares tend to be smaller in body size than brown hares, but cautioned that the dimensions of individual bones are not diagnostic to species. The situation is further complicated by the large size attained by arctic variable hares, apparently in accordance with Bergmann’s rule, which is comparable to that of brown hares. On the other hand, the Pleistocene remains of variable hares that KOBY (1960, 168–170) studied had smaller limb bone lengths than those of recent brown hares. Comparison of long bone lengths of recent and fossil samples of *L. europaeus* and *L. timidus* confirms Koby’s observations (Table 1).

Despite the overlapping ranges of variation, it is still possible in some cases to identify individual long bones to species. A right humerus (VTR. 204) from layer d has a greatest length (GL) of 110.1 mm; it is not only larger than two humeri from layer b (Table 2) identified by MALEZ (1963, 9), but it lies beyond the range of *L. timidus* (Table 1). We have revised it from *L. timidus* to *L. europaeus*. A right radius (VTR. 206) from layer e with GL = 117.5 is beyond the range of *L. timidus*, while a left radius (VTR. 205) from layer d with GL = 114.5 is at the very top end of the range of *L. timidus* (Table 1). We have revised both specimens from *L. timidus* to *L. europaeus*. Only two bones, tibiae VTR. 229 and VTR. 230 from layer d, have GL (140.3 mm and 140.4 mm, respectively) smaller than the range of variation for *L. europaeus* (Table 1). These tibiae are likely from the same individual (MALEZ, 1963, 23). Given the positive identification of *L. europaeus* from the same layer, we think that they were more likely from an unusually short-legged *L. europaeus* rather than from *L. timidus*. Given the uncertainties around these specimens, we assign them to *Lepus* sp. We have not revised the identification of undiagnostic hare remains assigned by Malez to *Lepus* sp., although we note that the dimensions of these specimens are similar to those of recent *L. europaeus*. We thus have revised specimens identified to *L. timidus* by MALEZ (1963, 20–24) to either *L. europaeus* or to *Lepus* sp. (Table 3).

Lepus sp.

Material: layer h: right distal humerus (VTR. 208); right distal radius (VTR. 207); right distal femur (VTR. 210); layer i: left innominate (VTR. 211); right distal tibia (VTR. 209).

Table 2: Measurements on remains identified to *L. europaeus* and *Lepus* sp. from Veternica. Measurements on incisors are as defined in Fig. 1; other measurements are as defined in DRIESCH (1976).

#	Layer	Element	Species	GL	GB	BFcr	BFcd	GLF	LAD	#	Layer	Element	Species	L	B					
VTR. 217	d	atlas	<i>Lepus</i> sp.	15.7	33.7	18.2	14.9	13.5	7.8	VTR. 221	d	I ¹	<i>L. europaeus</i>	3.3	2.1					
#	Layer	Element	Species	GL	Dp	Bd									VTR. 222	d	I ¹	<i>L. europaeus</i>	3.3	2.2
VTR. 203	d	humerus	<i>Lepus</i> sp.	104.5	20.6	12.6									VTR. 218	d	I ₁	<i>L. europaeus</i>	2.8	2.3
VTR. 204	d	humerus	<i>L. europaeus</i>	110.1	17.3	12.5									VTR. 219	f	I ₁	<i>L. europaeus</i>	3.2	2.4
VTR. 208	h	humerus	<i>Lepus</i> sp.			12.6									VTR. 223	d	I ₁	<i>L. europaeus</i>	3.3	2.3
VTR. 235	b	humerus	<i>L. europaeus</i>	104.6	12.7										VTR. 232	b	I ₁	<i>L. europaeus</i>	3.1	2.4
VTR. 236	b	humerus	<i>L. europaeus</i>	106.4	12										VTR. 233	b	I ₁	<i>L. europaeus</i>	3	2.4
VTR. 237	b	humerus	<i>L. europaeus</i>			12.8									VTR. 234	b	I ₁	<i>L. europaeus</i>	3.2	2.3
#	Layer	Element	Species	GL	Bp	Bd	#	Layer	Element	Species	L P3-M3									
VTR. 205	d	radius	<i>L. europaeus</i>	114.5	9.5	10.7	VTR. 220	d	maxilla	<i>Lepus</i> sp.	18									
VTR. 206	e	radius	<i>L. europaeus</i>	117.5	9.9		VTR. 220	d	maxilla	<i>Lepus</i> sp.	18.3									
VTR. 207	h	radius	<i>Lepus</i> sp.			11.6	VTR. 218	d	mandible	<i>L. europaeus</i>	19									
VTR. 238	b	radius	<i>L. europaeus</i>	117.9	9.1	9.6	VTR. 219	f	mandible	<i>L. europaeus</i>	21.2									
#	Layer	Element	Species	GL	Bp	DC	Bd	VTR. 232 <td>b</td> <td>mandible</td> <td><i>L. europaeus</i></td> <td>19.2</td> <td colspan="4"></td>	b	mandible	<i>L. europaeus</i>	19.2								
VTR. 210	h	femur	<i>Lepus</i> sp.			20.6		VTR. 233	b	mandible	<i>L. europaeus</i>	17.7								
VTR. 241	b	femur	<i>L. europaeus</i>	135.3	29.9	9.8	20.5	VTR. 234	b	mandible	<i>L. europaeus</i>	18.9								
VTR. 242	b	femur	<i>L. europaeus</i>	136.1	28.7	10.2	20	#	Layer	Element	Species	LA								
VTR. 243	b	femur	<i>L. europaeus</i>			10.7	20.8	VTR. 211	i	innominate	<i>Lepus</i> sp.	12.1								
VTR. 244	b	femur	<i>L. europaeus</i>			28.9	10	20.4	VTR. 212	e	innominate	<i>Lepus</i> sp.	12.7							
#	Layer	Element	Species	GL	Bp	Bd	Dd	VTR. 246 <td>b</td> <td>innominate</td> <td><i>L. europaeus</i></td> <td>12.1</td> <td colspan="4"></td>	b	innominate	<i>L. europaeus</i>	12.1								
VTR. 209	i	tibia	<i>Lepus</i> sp.			20.8		#	Layer	Element	Species	GL								
VTR. 229	d	tibia	<i>Lepus</i> sp.	140.3	21.2	16.9	10.3	VTR. 213	d	metacarpal III	<i>Lepus</i> sp.	33.4								
VTR. 230	d	tibia	<i>Lepus</i> sp.	140.4	21.4	17	10.4	VTR. 252	b	metacarpal III	<i>L. europaeus</i>	39.7								
VTR. 231	d	tibia	<i>Lepus</i> sp.			16.1	10.5	VTR. 247	b	metatarsal II	<i>L. europaeus</i>	59.7								
VTR. 239	b	tibia	<i>L. europaeus</i>	154.8	20.6	15.6	10.2	VTR. 248	b	metatarsal II	<i>L. europaeus</i>	53.6								
VTR. 240	b	tibia	<i>L. europaeus</i>	153.9	21.6	16.4	10.5	VTR. 249	b	metatarsal II	<i>L. europaeus</i>	58.3								
VTR. 245	b	tibia	<i>L. europaeus</i>	158.8	21.4	16.7	10.6	VTR. 250	b	metatarsal III	<i>L. europaeus</i>	61.2								
								VTR. 214	d	metatarsal IV	<i>Lepus</i> sp.	52.2								
								VTR. 251	b	metatarsal IV	<i>L. europaeus</i>	53.6								

Hare remains recovered from layers h and i at Veternica were considered not to be sufficiently characteristic for specific determination; hence MALEZ (1963, 24) identified them only to genus. We agree with these determinations, and have not changed any of them. Measurements for these specimens are presented in Table 2 for comparative purposes.

4.1.2. Ochotonidae

Ochotona sp.

Material: layer f⁶: right I¹ (VTR. 269)

MALEZ (1963, 24–25) assigned a single right I¹ to *Ochotona* sp. (pika) on the basis of its anatomical-morphological characteristics and proportions, although he noted

that its dimensions were somewhat greater than a specimen identified to *O. pusilla* from Ukraine. A lateral view and cross-section of the incisor were published several years later (MALEZ, 1966, 6; MALEZ, 1968, 148). The morphology of this tooth differs considerably from *Ochotona* in lateral view (Fig. 3). In *Ochotona* the occlusal surface extends much further down the lingual side of the tooth than is the case in *Lepus*; VTR. 269 is similar to *Lepus* and differs from *Ochotona*. Comparison of a cross section of the crown to recent and fossil specimens of *Ochotona*, *Oryctolagus* (rabbit), and *Lepus* (hare) shows that the morphology of the tooth is similar to *Lepus* and very different from *Ochotona* (Fig. 4). Furthermore, in Leporidae the mesial face of the I¹ of juvenile specimens is slightly rounded and becomes more rounded in

⁶ The material is labelled “layer f”, while in the literature it is assigned to “layer e” (MALEZ, 1963, 24). We consider the original label to be more reliable than the publication, and hence assign the incisor to layer f.

Table 3: Revision of lagomorpha from Veternica.

#	Element	Layer	Malez (1963)	Revised
VTR. 269	I ¹	f	<i>Ochotona</i> sp.	<i>Lepus</i> sp.
VTR. 221	I ¹	d	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 222	I ¹	d	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 218	mandible with I ₁ , P ₃ – M ₂	d	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 223	I ₁	d	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 204	humerus	d	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 205	radius	d	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 206	radius	e	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 219	mandible with I ₁ , P ₃ –M ₃	f	<i>L. timidus</i>	<i>L. europaeus</i>
VTR. 220	fragmentary skull	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 226	M ₁	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 227	M ₂	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 228	M ₃	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 217	atlas	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 203	humerus	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 213	metacarpal III	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 229	tibia	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 230	tibia	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 231	tibia	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 215	metatarsal II	d	<i>L. timidus</i>	<i>Lepus</i> sp.
VTR. 214	metatarsal III	d	<i>L. timidus</i>	MT IV, <i>Lepus</i> sp.
VTR. 212	innominate	e	<i>L. timidus</i>	<i>Lepus</i> sp.

adults, while in Ochotonidae the mesial face is straight in juveniles and adults. Another indication that this tooth is from a juvenile is the thinness of the enamel and the restriction of dentine in the tooth to the region near the occlusal surface. Finally, enamel is present on the mesial side of I¹ in Leporidae, while it is missing in Ochotonidae (SUÁREZ & MEIN, 2004, S120).

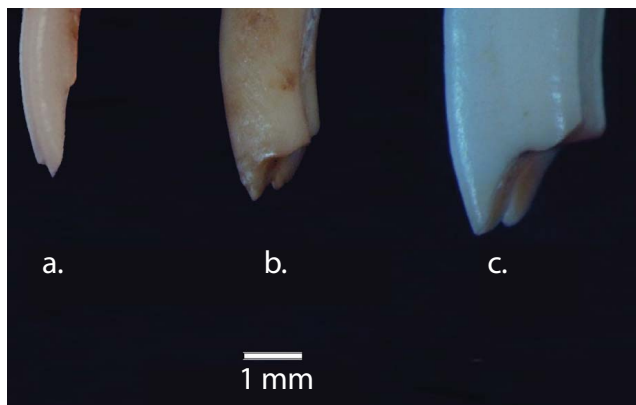


Figure 3: Revision of I¹ (VTR. 269), lateral view: a) *Ochotona pusilla* (CUMZ), b) VTR. 269, c) *L. europaeus* (ZPGK).

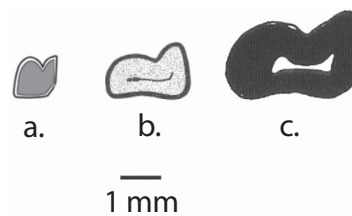


Figure 4: Revision of I¹ (VTR. 269), occlusal view: a) *Ochotona* sp. (after HILLSON, 2005, fig. 1.77), b) VTR. 269 (after MALEZ, 1966, fig. 1A), c) *L. europaeus* (after DONARD, 1981, fig. 1).

A bivariate plot of mesial-distal length (L) against buccal-lingual breadth (B) shows that this tooth is indeed larger than *Ochotona*, while smaller than adult specimens from *Oryctolagus* and *Lepus* (Fig. 5). Lagomorph incisors, however, grow continuously and deciduous teeth are not replaced by permanent incisors; incisors are small in juveniles and increase in both mesial-distal length and buccal-lingual breadth until maturation (SUÁREZ & MEIN, 2004, S120). VTR. 269 is larger than juvenile specimens of *Oryctolagus*; furthermore the cross-sectional dimensions increase from L = 2.00 mm, B = 1.33 mm at the occlusal surface⁷ to L = 2.64 mm, B = 1.76 mm just above the break on the tooth, which is already at the lower end of the range of variation for adult *Lepus* (Fig. 5). Hence, this I¹ would have grown much larger in an adult, and based on size and morphology, we have revised it from *Ochotona* sp. to *Lepus* sp.

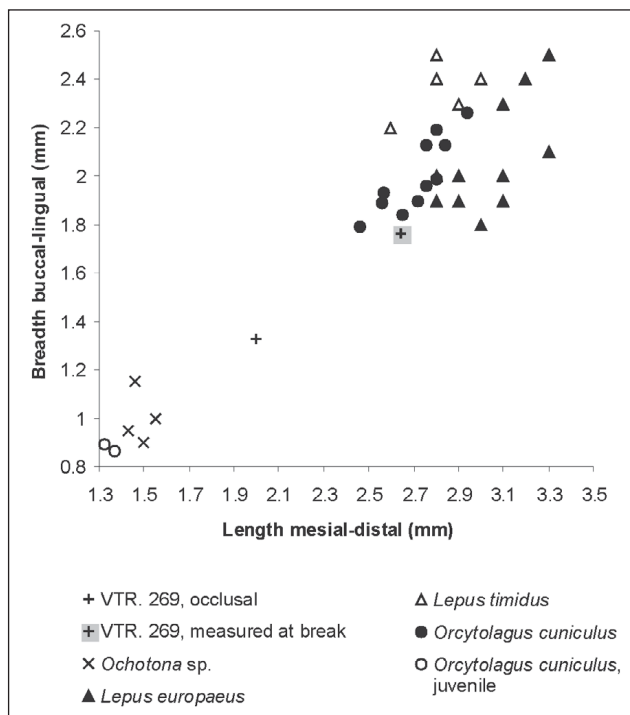


Figure 5: I¹ mesial-distal length vs. buccal-lingual breadth in Lagomorpha compared to VTR. 269. Comparative measurements from comparative material and sources as follows: *Ochotona* (CUMZ; MALEZ, 1963, p. 25; SUAREZ & MEIN, 2004, fig. 5); *L. europaeus* (CUMZ; ZPGK); *L. timidus* (CUMZ; RAKOVEC, 1959; MIRACLE, 1995); *Oryctolagus* (CUCLZ; SUAREZ & MEIN, 2004, fig. 5).

⁷ MALEZ (1963, 25) reported these dimensions as mesial-distal L = 1.9 mm, lingual-buccal B = 1.35 mm.

4.2. Carnivora

4.2.1. Canidae

Alopex (cf.) *lagopus*

Material: layer f: left ulna (VTR. 255)

A left ulna (VTR. 255, layer f) was attributed by MALEZ (1963, p. 64–66) to arctic fox, *Alopex* cf. *lagopus*. This specimen is well preserved and complete except for the distal end, which is missing (Fig. 6). MALEZ (1963, 64) noted that the general morphology of the ulna was like that of recent representatives of *Vulpes vulpes*, but that VTR. 255 was much smaller and differed in specific morphological details from *V. vulpes* ulnae. The primary criteria that MALEZ (1963, 65) used to identify the ulna to *A. lagopus* were 1) the morphology of the volar face of the proximal end and 2) the cross-sectional morphology of the diaphysis. MALEZ (1963, 64) suggested that the key morphological criterion for taxonomic determination was the angle between the posterior part of the olecranon and the ridge on the volar edge of the ulna; this angle is smaller in *Alopex* compared to *Vulpes*; VTR. 255 is described as having an angle similar to that in



Figure 6: Revision of ulna (VTR. 255): a) *Vulpes vulpes*, b) VTR. 255, c) *Alopex lagopus*. Comparative specimens are from ZPGK. The arrow indicates the angle between the posterior part of the olecranon and the ridge on the volar edge of the ulna.

Alopex (Fig. 6). GROMOVA (POMOBA 1950, 182) gave a more precise definition of this difference; this angle is $< 140^\circ$ in *Alopex*, while in *Vulpes* it is usually $> 130^\circ$. Measurements on a small sample of recent comparative material confirm Gromova's observations; an *Alopex* ulna has an angle of 138° , while two *Vulpes* ulnae have angles of 150° and 160° . VTR. 255 has an angle of 150° and by this criterion is clearly from *Vulpes*. Turning to the cross-sectional morphology of the shaft, Malez, following GROMOVA (ГРОМОБА, 1950, 182), suggested that in *Alopex* the diaphysis is flattened in the middle portion, while in *Vulpes* the same portion is circular in cross section. Furthermore, based on his own observations on recent material, MALEZ (1963, 65) suggested that muscle attachments, in particular the *crista interossea*, are more developed in *Alopex* than in *Vulpes*. The diaphysis of VTR. 255 is circular in cross section, and thus more similar to *Vulpes* than *Alopex*. Furthermore, our own observations on recent material indicate that the degree of development of muscle attachments is indicative of age at death and is not taxonomically indicative.

Metric analysis of the proximal end shows that, contrary to Malez's description, VTR. 255 is considerably larger than recent specimens of *A. lagopus* and that it instead falls well within the distribution of *V. vulpes* (Fig. 7, Tables 4–5). Hence, on the basis of both morphological and metric comparisons, we have revised VTR. 255 from *A. cf. lagopus* to *V. vulpes*.

Vulpes vulpes

Material: layer d: left mandible with P_1 - M_3 (VTR. 831/car), right metacarpal II (VTR. 834/car), left metacarpal III (VTR. 836/car), right metacarpal IV (VTR. 835), left femur shaft (VTR. 266); layer h: right upper C (VTR. 842/car), caudal vertebra (VTR. 837/car); layer i: right proximal radius (VTR. 265), left calcaneus (VTR. 832/car)

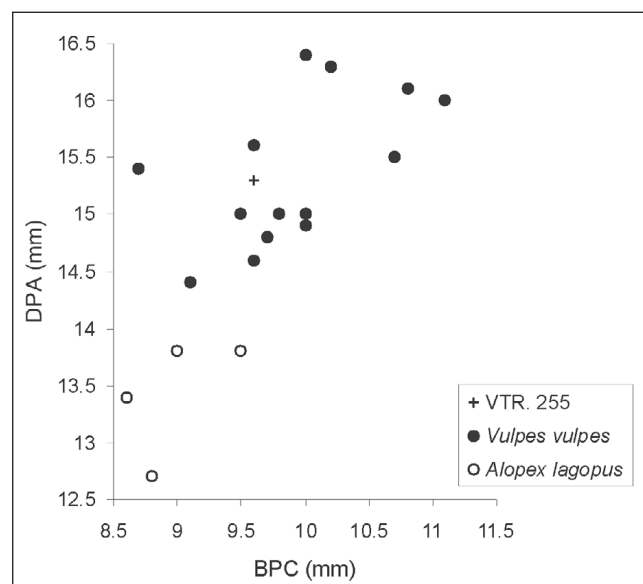


Figure 7: Fox proximal ulna dimensions (depth of the olecranon [DPA] against breadth across the coronoid process [BPC]) from Veternica compared to recent comparative material of *V. vulpes* and *A. lagopus*. Measurements as defined by DRIESCH (1976).

Table 4: Measurements on a proximal fox ulna from Veternica (VTR.255) compared to recent specimens of *A. lagopus* (UMMZ; ZPGK) and *V. vulpes* (CUCLZ; UMMZ; ZPGK).

	<i>Alopex lagopus</i>			<i>Vulpes vulpes</i>			
	VTR. 255	mean	range	N	mean	range	N
BPC	9.6	9.0	8.6–9.5	4	10.1	8.7–11.2	17
DPA	15.3	13.4	12.7–13.8	4	15.7	14.4–17.6	17

We confirm the identification of remains previously assigned to *V. vulpes* (MALEZ, 1963, 66–70). To these we add a left proximal ulna from layer f (VTR. 255) that was previously identified as *A. cf. lagopus* and a left metatarsal V from layer d/h/i (VTR. 262) that was previously identified as *Felis lynx pardina* (= *Lynx pardinus*). Measurements on these remains are presented in Table 5. The mandible (VTR. 831/car) is complete except for the coronoid process and the symphysis anterior to the canine alveolus; these parts are missing and appear to have been damaged at the time of excavation. The mandible is not otherwise modified. The distal ends of ulna VTR. 255 and radius VTR. 265 appear to have been broken when the bones were still fresh. These breaks are smooth and spiral-shaped. These bones are not otherwise modified. Although the femur shaft (VTR. 266) suffered

Table 5: Measurements on remains identified to *V. vulpes* from Veternica. All measurements as defined in DRIESCH (1976); numbers in parentheses for mandibular measurements refer to DRIESCH (1976, fig. 23a).

#	Layer	Element	(8)	(10)	(11)	(19)	(20)
VTR. 831/car	d	mandible	58.7	27.2	32.8	13.6	12.0
#	Layer	Element	L	B			
VTR. 842/car	h	upper C	6.4	4.3			
VTR. 831/car	d	P ₃	8.8	3.6			
VTR. 831/car	d	P ₄	9.5	4.2			
VTR. 831/car	d	M ₁	15.6	5.9			
VTR. 831/car	d	M ₂	8.3	5.7			
#	Layer	Element	BPC	DPA	SDO		
VTR. 255	f	ulna	9.6	15.3	12.6		
#	Layer	Element	Bp	Dp	SD		
VTR. 265	i	radius	12.4	7.8	8.4		
VTR. 266	d	femur			14.2		
#	Layer	Element	GL	Bd			
VTR. 834/car	d	metacarpal II	45.7	6.9			
VTR. 836/car	d	metacarpal III	51.0	5.9			
VTR. 835/car	d	metacarpal IV	45.8	6.8			
VTR. 262	d, h, i	metatarsal V	57.3	6.3			
VTR. 832/car	i	calcaneus	34.8				

(8) length of cheek teeth P₁-M₃ at alveoli

(10) length of molar row at alveoli

(11) length of premolar row at alveoli

(19) height of mandible behind M₁ on buccal side

(20) height of mandible in front of P₃ on buccal side

slight excavation damage to proximal and distal ends, there is evidence of light carnivore gnawing (shallow furrows and pitting) on the posterior side of the distal shaft and the distal end was probably removed by gnawing. The remainder of the remains are complete and do not show any surface modifications.

4.2.2. Mustelidae

Mustela erminea

Material: layer h: left proximal tibia (VTR. 719/car); layer i: left innominate (VTR.720/car)

We confirm the identifications of *M. erminea* (MALEZ, 1963, p. 76). The proximal tibia (VTR. 719) is slightly damaged on the postero-lateral edge of the proximal articulation and the distal end has been removed by a recent break. The innominate (VTR. 720/car) has been broken on the shafts of the ilium and pubis. These remains are not otherwise modified.

Mustela putorius

Material: layer d: left femur (VTR. 723/car); layer h: cranium with left P³-M¹ and right P⁴-M¹ (VTR. 721/car); layer i: left mandible with P₂-M₂ (VTR. 722/car), right femur missing proximal end (VTR. 724/car)

We confirm the identifications of *M. putorius* (MALEZ, 1963, p. 76–81). The cranium (VTR. 721/car) is missing the occipital, left petrous, and most of the cranial base from an old break. The mandible (VTR. 722/car) is broken at the canine alveolus. The left femur (VTR. 723/car) is complete. The right femur (VTR. 724/car) is missing the proximal end on an old break. On both femora, localized patches of spongy bone have been exposed, probably from digestion by an owl. These remains are not otherwise modified.

Martes martes

Material: layer h: right humerus (VTR. 717/car); layer i: left mandible with P₃ and M₁ (VTR. 716/car).

We confirm the assignment of the left mandible to *M. martes* on the basis of the relatively large distance (7.3 mm) between the two mandibular mental foramina (ANDERSON 1970, p. 34; GRUNDBACHER 1992; MALEZ, 1963, p. 81). The mandible (VTR. 716/car) shows minor post-depositional damage to the coronoid process and symphysis. The broken roots of the P₂ are still in the alveoli. The mandible is not otherwise modified.

The humerus (VTR. 717/car) is complete and unmodified. It is relatively long (GL = 70.4 mm) compared to its proximal depth (Dp = 12.9) and distal breadth (Bd = 15.1 mm, BT = 10.4 mm). A small recent sample of *M. martes* (N = 2) and *M. foina* (N = 3) humeri available in Zagreb (ZGPK) suggests that this bone is more gracile (longer relative to the depth/breadth of the articular ends) in *M. martes* than in *M. foina*. The relative dimensions of VTR. 717/car are more similar to *M. martes* than *M. foina*. The small size of our comparative sample and the absence of other diagnostic mor-

phological features, however, prevent us from determining this humerus to species level with certainty. Hence we assign this humerus to *Martes* sp.

Martes foina

Material: layer d: cranium with left P²–M¹ and right P², P⁴–M¹ (VTR. 718/car)

We confirm the identification of cranium VTR. 718/car as *M. foina* on the basis of the orientation of the external auditory meatus, the form of the infraorbital foramen, the morphology of the P³, and the morphology of the M¹ (HANS & STEINER, 1986; MALEZ, 1963, p. 83–84). The cranium has suffered minor damage to the zygomatic processes and left occipital condyle, most likely at the time of excavation. The specimen is in excellent condition and is not otherwise modified.

Gulo gulo

Material: layer f: left I³ (VTR. 267) and right I³ (VTR. 268)

A right and a left upper third incisor were identified by MALEZ (1963, p. 85–86, pl. XVI, fig. 3a–b) as wolverine (VTR. 267 and VTR. 268, both level f). It is worth noting that in the absence of recent comparative material, Malez based this identification on comparisons with photographs from the palaeontological literature. MALEZ (1963, 85) observed that both teeth were worn to an equal degree, and that given their similar dimensions, that they probably came from the same individual. Our measurements at the crown base of length (mesial–distal) and breadth (buccal–lingual) are somewhat greater than those reported by Malez (Table 6). These dimensions are almost identical to those of a recent female wolf (Fig. 8); wolf I³ appear to be elongated mesio–distally compared to wolverine.

The morphology of VTR. 267 and VTR. 268 is also closer to comparative specimens of wolf than wolverine. The cingulum is more pronounced in wolverine than wolf, forming a distinct bulge on the mesial–buccal side of the tooth (Fig. 9; DÖPPES, 2001, fig. 9). The axis of the crown (a tangent joining the mesial and distal ridges) is oriented anterior–posteriorly in alignment with the canine in wolf, whereas in wolverine the axis of the crown is oriented medial–laterally in alignment with the other upper incisors (Fig. 9). In wolf,

Table 6: Measurements on I³ from Veternica compared to recent specimens of *Canis lupus*, *C. familiaris*, *Gulo gulo*, and fossil remains of *C. lupus* from Šandalja and Velika pećina.

Specimens	L	min–max (N)	B	min–max (N)
VTR. 267	7.1		8.8	
VTR. 268	7.0		8.8	
<i>Canis lupus</i> , male	7.6	7.6 (2)	10.05	9.9–10.2 (2)
<i>Canis lupus</i> , female	7.05	7–7.1 (2)	9.0	8.9–9.1 (2)
<i>Canis lupus</i> , fossil	8.34	7.7–9.4 (5)	10.72	10.2–11.3 (5)
<i>Canis familiaris</i>	6.5	6–7 (2)	8.45	7.6–9.3 (2)
<i>Gulo gulo</i>	5.1		8.5	

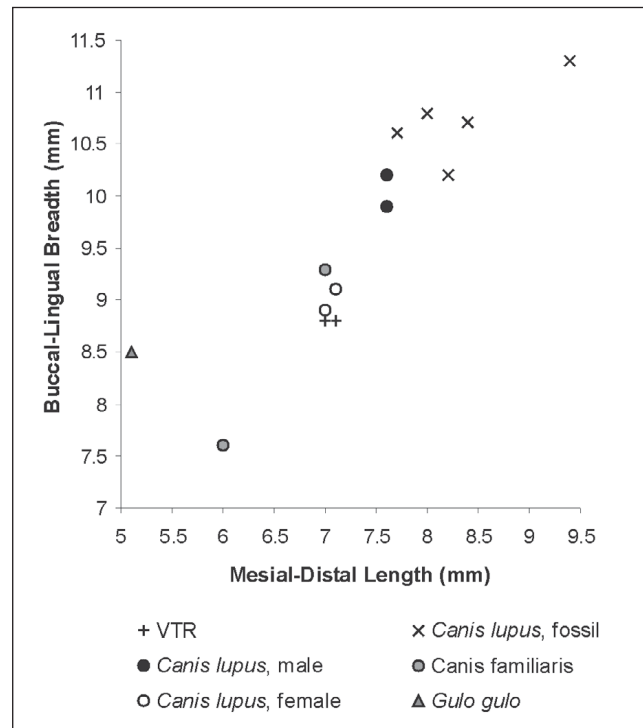


Figure 8: I³ mesial–distal length vs. buccal–lingual breadth (both measured at crown base) in VTR. 267, 268 compared to recent specimens of *Canis lupus* (ZPGK), *C. familiaris* (ZPGK), *Gulo gulo* (CUMZ), and fossil specimens of *C. lupus* from Šandalja and Velika pećina.

the root has a triangular cross section and is relatively larger relative to the crown, whereas in wolverine the root has an oval cross section and is relatively small relative to the crown. In all of these characters VTR. 267 and VTR. 268 are similar to wolf and different from wolverine.

Meles meles

Material: layer d: cranium with left I², upper C, P⁴ and right P⁴–M¹ (VTR. 726/car), maxilla with M¹ (VTR. 730/car), right mandible with I₂–M₂ (VTR. 723/car), left mandible

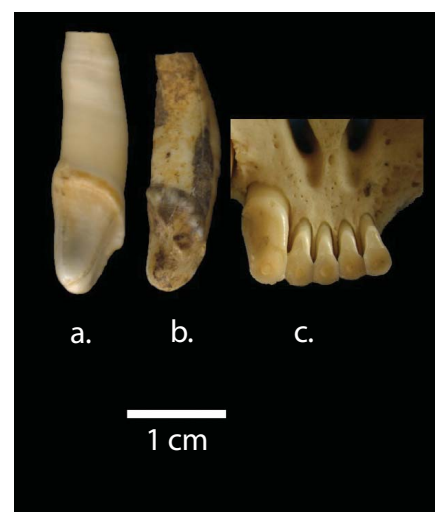


Figure 9: Revision of I³ (VTR. 267): a) *C. lupus*, b) VTR. 267, c) *G. gulo*.

with lower C, P₄–M₂ (VTR. 727/car), left articular condyle of a mandible (VTR. 728/car), atlas (VTR. 731/car), right humerus (VTR. 733/car), right ulna (VTR. 734/car), right radius (VTR. 735/car), left femur (VTR. 738/car), two right tibiae (VTR. 736/car and VTR. 737/car), left calcaneus (VTR. 739/car); layer i: left proximal humerus (VTR. 740/car), left ulna (VTR. 741/car)

We confirm the identifications of *M. meles* by MALEZ (1963, p. 86–92), with the exception of the left proximal humerus from layer i (VTR. 740), which we have reassigned to *F. silvestris*. To the badger remains we have added a left distal tibia from layer d (VTR. 260) that was originally identified as *F. Lynx pardina* (MALEZ, 1963, p. 97).

Starting with the proximal humerus (VTR. 740/car), although the greater tubercle is damaged on the specimen, it is much less developed than is the case in *M. meles*. As a result, the proximal end is relatively narrower (medial-lateral) relative to its depth (anterior-posterior). Finally, the extension of the deltoid crest onto the lateral surface of the proximal shaft is much less pronounced in VTR. 740/car than is the case in *M. meles*; this situation is much closer to the case in *F. silvestris* (Fig. 10). We conclude that VTR. 740/car is from a wild cat, although it is considerably larger than recent specimens. As discussed in greater detail below, the large size of Pleistocene wild cat remains from Veternica fits the pattern observed by KURTÉN (1965, p. 16) for Pleistocene wild cats in Europe and the Levant.

Turning to the remains confirmed as *M. meles* from layer d, the cranium (VTR. 726/car) is complete except for recent damage to the cranial base and occipital. The teeth are very

heavily worn, indicating that the cranium came from a very old individual. The complete mandibles (VTR. 727/car and VTR. 729/car) are in excellent condition and are not otherwise modified. Wear on the M₁ is moderate, suggesting that both mandibles came from prime-aged adults. The mandibles differ enough in size to indicate that they came from different individuals. The third mandibular fragment (VTR. 728/car) preserves only the articular condyle; it was broken post-depositionally, possibly at the time of excavation. The atlas (VTR. 731/car) has suffered slight post-depositional damage to the wings, but is otherwise unmodified. All of the long bones (VTR. 733, 734–738) are complete and unmodified other than slight abrasion to some of the articular ends and two small cut marks on the medial shaft of tibia VTR. 736/car. The calcaneus (VTR. 739) is complete and unmodified.

We confirm the presence of badger in layer i from a single ulna (VTR. 741/car). Other than very minor damage to the olecranon process, this bone is unmodified.

4.2.3. Felidae

Felis silvestris

Material: layer d: left femur (VTR. 264); layer h: right mandible with P₃–M₁ (VTR. 713/car), left proximal radius (VTR. 263); layer i: left lower C (VTR. 714/car), distal metapodial (VTR. 715/car)

We confirm the existing determinations of *F. silvestris* at Veternica (MALEZ, 1963, p. 94–96). To these we add the following elements revised from *L. pardinus* (MALEZ, 1963, p. 96–97): a left distal humerus from layer i (VTR. 256), a right metatarsal II from layer d (VTR. 261), a left proximal metatarsal IV from layer h (VTR. 257), a left metatarsal IV from layer h (VTR. 258), and a left proximal metatarsal IV from layer i (VTR. 259). We have also added a left proximal humerus from layer i (VTR. 740/car) revised from *M. meles*. We have also identified as *F. silvestris* a distal metapodial without stratigraphic information (VTR. 715/car). Measurements are presented in Table 7. The lower canine (VTR. 714/car) shows little wear; its tip is broken by a recent break. The mandible (VTR. 713/car) is complete except for slight excavation damage to the ascending ramus; it is not otherwise modified. The distal humerus (VTR. 256) is broken near the mid-shaft; the edges of the break are in places rough and stepped and parts of the break appear to have followed existing fractures in the bone. This break thus appears to have been post depositional but prior to excavation. The radius (VTR. 263) is broken by a recent break near the distal end. The femur (VTR. 264) is complete. The metatarsal II (VTR. 261) is complete. Considering the fourth metatarsals, VTR. 257 is unbroken but missing an unfused distal epiphysis; VTR. 258 is complete, and VTR. 259 is broken mid-shaft by an old, transverse (dry bone) break. The distal metapodial fragment (VTR. 715/car) is broken near the distal end by an old, dry-bone break; although it is too incomplete to measure, it would have come from a large-sized animal. None of the postcranial elements of wild cat have been otherwise modified.

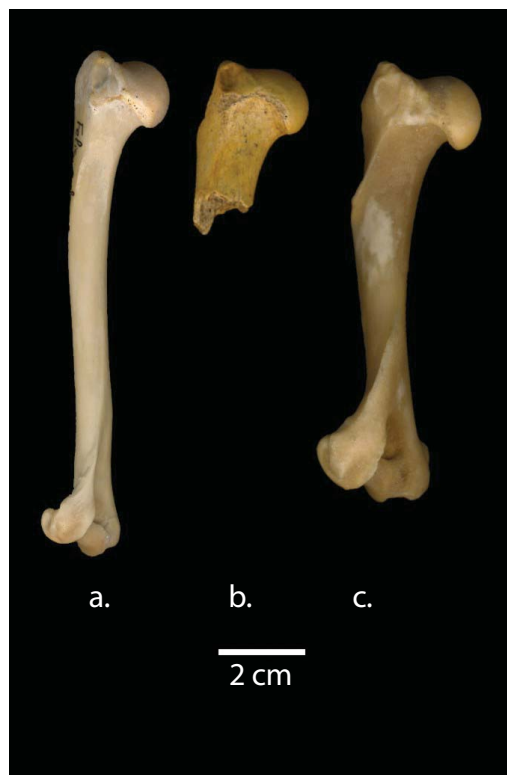


Figure 10: Revision of proximal humerus (VTR. 740/car): a) *Felis silvestris*, b) VTR. 740/car, c) *Meles meles*. Comparative specimens are from ZPGK.

Table 7: Measurements on remains identified to *F. silvestris* from Veternica. All measurements as defined in DRIESCH (1976); numbers in parentheses for mandibular measurements refer to DRIESCH (1976, fig. 24).

#	Layer	Element	(1)	(5)	(7)	(8)	(9)	(10)	
VTR. 713/car	h	mandible	63.3	22.6	29.1	12.4	10.5		
#	Layer	Element	L	B					
VTR. 714/car	i	lower C	6.0	4.7					
VTR. 713/car	h	P ₃	7.3	2.9					
VTR. 713/car	h	P ₄	7.3	2.9					
VTR. 713/car	h	M ₁	8.5	3.9					
#	Layer	Element	GL	Bp	Dp	DC	Bd	BT	SD
VTR. 256	i	humerus					26.9	18.5	11.2
VTR. 740/car	i	humerus			26.8				
VTR. 263	h	radius		9.2	5.3				6.0
VTR. 264	d	femur	104.6	20.1		10.2			8.2
VTR. 261	d	metatarsal II	65.4				7.4		
VTR. 257	h	metatarsal IV		8.1					
VTR. 258	h	metatarsal IV	70.8	8.0			7.2		
VTR. 259	i	metatarsal IV		7.9					

(1) total length = infradentale – condylar process

(5) length of cheek teeth P₃-M₁ at alveoli

(7) length of M₁ at alveolus

(8) height of the vertical ramus = basal point of angular process – coronion

(9) height of mandible behind M₁ on buccal side

(10) height of mandible in front of P₃ on buccal side

Lynx pardinus

Material: layer d: left distal tibia (VTR. 260); right metatarsal II (VTR. 261); layer h: two left metatarsal IV (VTR. 257, VTR. 258); layer i: left distal humerus (VTR. 256); left metatarsal IV (VTR. 259); layer unspecified (d/h/i): right metatarsal V (VTR. 262).

Felid remains from layers d, h, and i were identified to the pardel or Iberian lynx, *L. pardinus*, using the older nomenclature of *Felis lynx pardina* (MALEZ, 1963, p. 96–97). The distal humerus from layer i (VTR. 256) is in morphology clearly from a felid, and MALEZ (1963, p. 96) identified it to *L. pardinus* based on the morphological similarity of the specimen to the excellent illustrations of humeri identified to *F. (Lynx) pardina* (= *Lynx pardinus*) from the sites of Grottes de Grimaldi (BOULE, 1910, p. 271–277, pls. XXXII–XXXIII) and Grotte de l'Observatoire (BOULE & DE VILLENEUVE, 1927, p. 78–80, pls. XVII–XVIII). We are not aware of any morphological differences between wild cat and lynx; hence we rely on metric comparisons to identify the specimen. The humeri from Grottes de Grimaldi and Grotte de l'Observatoire are considerably larger than VTR. 256 (Fig. 11). While the plot of greatest distal breadth (Bd) against the breadth of the trochlea (BT) shows that VTR. 256 is larger than recent comparative material of *F. silvestris* and

considerably smaller than recent material of *Lynx lynx*, it clearly clusters with fossil representatives of *F. silvestris* from Holocene (Viktorjev spodmol) and Pleistocene (Šandalja II) sites in the region (Fig. 11). The left distal tibia (VTR. 260) has a recent break on the distal end (probably excavation damage) that removed the medial malleolus; hence it is not suitable for metric comparisons. Nonetheless, its morphology is identical to recent badger (*M. meles*) tibiae and distinctly different from recent lynx tibiae in the comparative collections of ZPGK (Fig. 12). We have revised this specimen from *L. pardinus* to *M. meles*.

The right metatarsal II (VTR. 261) is in dimensions considerably smaller than the same bone identified by Boule to *L. pardinus* and larger than recent *F. silvestris* (Fig. 13). The dimensions are very similar to a fossil specimen identified by BOULE & DE VILLENEUVE (1927, p. 80) to African wild cat (*F. ocreata*), a taxon that is now accepted as a subspecies of *F. silvestris* (SUNQUIST & SUNQUIST, 2002, p. 84). Hence we also have revised VTR. 261 to *F. silvestris*. Of the three left metatarsal IV, one from layer h is complete (VTR. 258), while the other two preserve only the proximal end (VTR. 257 and VTR. 259). Compared to recent fourth metatarsals, VTR. 258 is much smaller than lynx and larger than wild cat (Fig. 14). Given the very large size of other bones identified to Pleistocene forms of *F. silvestris*, we think that these fourth metatarsals are also most likely from *F. silvestris*. Fossil forms of wild cat are reported to attain very large sizes, sometimes approaching that of a small lynx (ARGANT, 1996, p. 214); hence in all of these cases we are confident that we are dealing with a large-sized wild cat and not with a small-sized lynx. The right metatarsal V (VTR. 262) is complete. Its morphology is identical to red fox and dis-

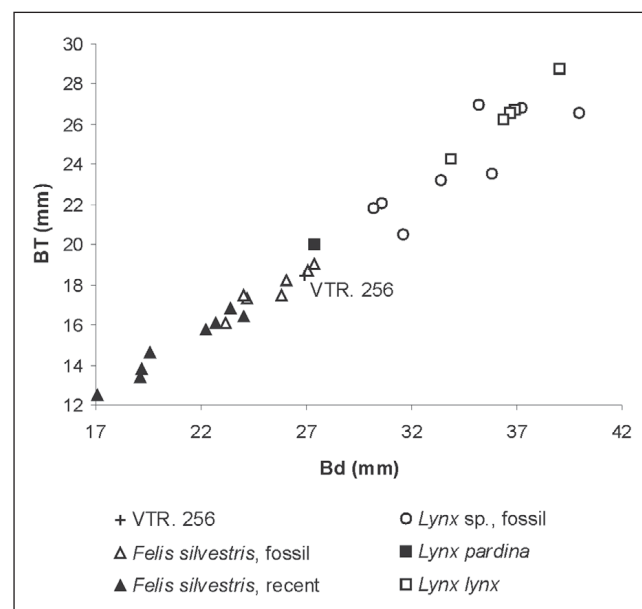


Figure 11: Distal humerus breadth (Bd) vs. breadth trochlea (BT) in VTR. 256 compared to recent specimens of *F. silvestris* and *L. lynx* (CUMZ and ZPGK), and fossil specimens of *F. silvestris* (MIRACLE, 1995; TOŠKAN & DIRJEC 2004; CASSOLI & TAGLIACOZZO, 1994, 168) and *Lynx sp.* (BOULE, 1910, pl. 32; BOULE & DE VILLENEUVE, 1927, pl. XVIII; DEL CAMPANA, 1954, p. 42; BONIFAY, 1971, p. 271; CLOT & BESSON, 1974, p. 165; SARRIÓ, 1978, p. 8; CASSOLI & TAGLIACOZZO, 1994, 176).

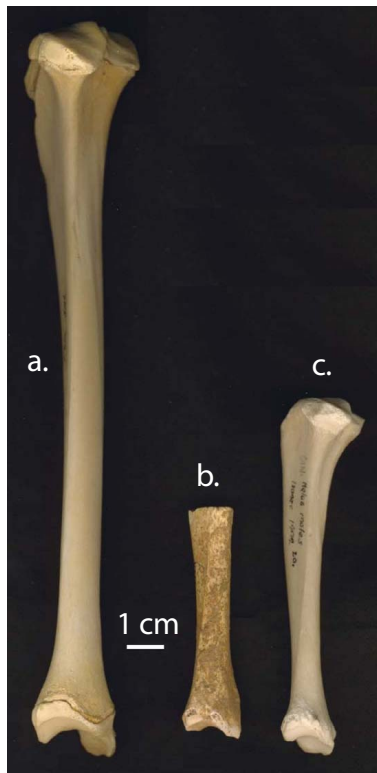


Figure 12: Revision of distal tibia (VTR. 260): a) *Lynx lynx*, b) VTR. 260, c) *Meles meles*. Comparative specimens are from ZPGK.

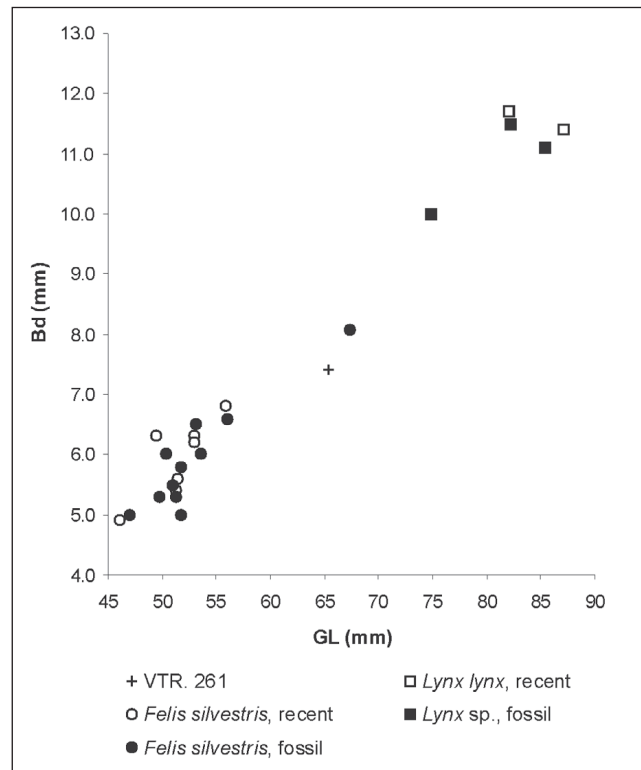


Figure 14: Metatarsal IV greatest length (GL) vs. distal breadth (Bd) of VTR. 258 compared to recent specimens of *F. silvestris* and *L. lynx* (CUMZ and ZPGK), and fossil specimens of *F. silvestris* (BOESSNECK, 1978b) and *Lynx sp.* (CLOT & BESSON, 1974, p. 165).

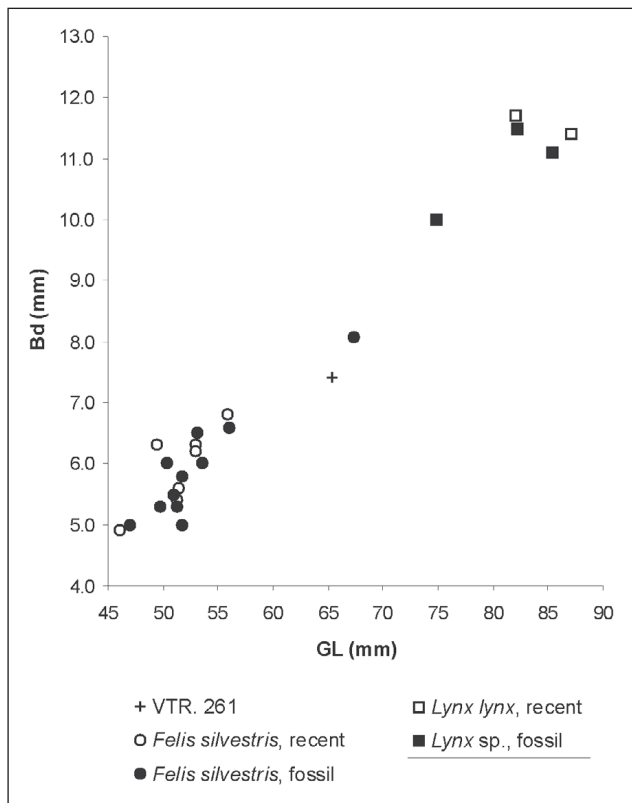


Figure 13: Metatarsal II greatest length (GL) vs. distal breadth (Bd) of VTR. 261 compared to recent specimens of *F. silvestris* and *L. lynx* (CUMZ and ZPGK), and fossil specimens of *F. silvestris* (BOULE & DE VILLENEUVE, 1927, pl. XVIII; BOESSNECK, 1978a, 1978b, 1978c; CASSOLI & TAGLIACOZZO, 1994, 168) and *Lynx sp.* (BOULE & DE VILLENEUVE, 1927, pl. XVIII; CLOT & BESSON, 1974, p. 165; CASSOLI & TAGLIACOZZO, 1994, 176).

tinctly different from lynx fifth metatarsals in the comparative collections of ZPGK (Fig. 15). The dimensions of this specimen show that it is much smaller than lynx and that it falls within the range of variation of recent representatives of red fox (Fig. 16). Morphological and metrical analyses support revising VTR. 262 from *L. pardinus* to *V. vulpes*.

Our revision of remains identified to pardeel lynx removes this taxon from the assemblage. The result is similar to a recent revision of similarly identified canine teeth from Parska golobina, Slovenia (KROFEL et al., 2005). Thus, there is no evidence that the range of the Iberian lynx extended into South-eastern Europe during the Pleistocene. In its place we have evidence for large-sized wild cats (Table 7). This result does not come as a surprise as KURTÉN (1965, p. 16) observed over 40 years ago that “Late Pleistocene forms both in Europe and Palestine are much larger than their living descendants”.

Revision of the canid, mustelid, and felid remains from Veternica thus removes *A. lagopus*, *G. gulo*, and *L. pardinus* from the fauna and increases the frequency of *V. vulpes*, *Canis sp.*, *F. silvestris*, and *M. meles* (Table 8). As with the revision of the lagomorphs, these data have for the most part eliminated cold-adapted taxa and replaced them with taxa with a wider climatic tolerance.

5. DISCUSSION

Layer j at Veternica probably dates to MIS 5, and previous revision of the ungulate assemblages removed many “warm-climate” taxa from the assemblage (Table 9, MIRACLE &



Figure 15: Revision of metatarsal V (VTR. 262): a) *Vulpes vulpes*, b) VTR. 262, c) *Lynx lynx*. Comparative specimens are from ZPGK.

BRAJKOVIĆ, 1992). The current revision does not further change the composition of the faunal assemblage beyond our observation that although MALEZ (1963, p. 98) reported the presence of the cave lion, *Panthera spelaea*, in layer j, none of the remains are so labeled. Although it is likely that cave lion was present in layer j, we cannot verify this from the material. Given that the cave lion is not indicative of particular palaeoenvironmental conditions, the issue of its presence or absence in layer j does not have an impact on our interpretations of the age and palaeoecological conditions in the region at the time of its deposition.

The best comparisons to Veternica layer j are Krapina (MIRACLE, 2007b), dated to MIS 5e, and the lower layers (layer 13 and below, Facies C) at Divje babe I (TOŠKAN, 2007) that are thought to date to MIS 5a–d (TURK, 2007). All of the larger mammals present in Veternica layer j are also present at Krapina. The only differences are in the insectivores and rodents; *Erinaceus europaeus*, *Talpa europaea*, *Arvicola terrestris*, *Microtus cf. agrestis*, and *Hystrix cristata* were found in Veternica layer j (MALEZ, 1963, table 33) and not at Krapina (MIRACLE, 2007b, p. 213). With the exception of the crested porcupine (*H. cristata*), the absence of these taxa at Krapina can be explained by the recovery and curation biases against smaller-sized remains documented at Krapina (MIRACLE 2007b, p. 7–8). Porcupine bones are comparable in size to the abundant beaver remains at Krapina; they would have been recovered if they had been present. Furthermore, the rarity of evidence of rodent gnawing at Krapina (MIRACLE 2007b, p. 237) suggests that porcupines were not active at the rockshelter. The contrast in porcupine representation between these sites is probably related to cave morphology and other local factors that influenced porcupine behavior instead of regional climates and/or age of deposition. The taxa present at Veternica

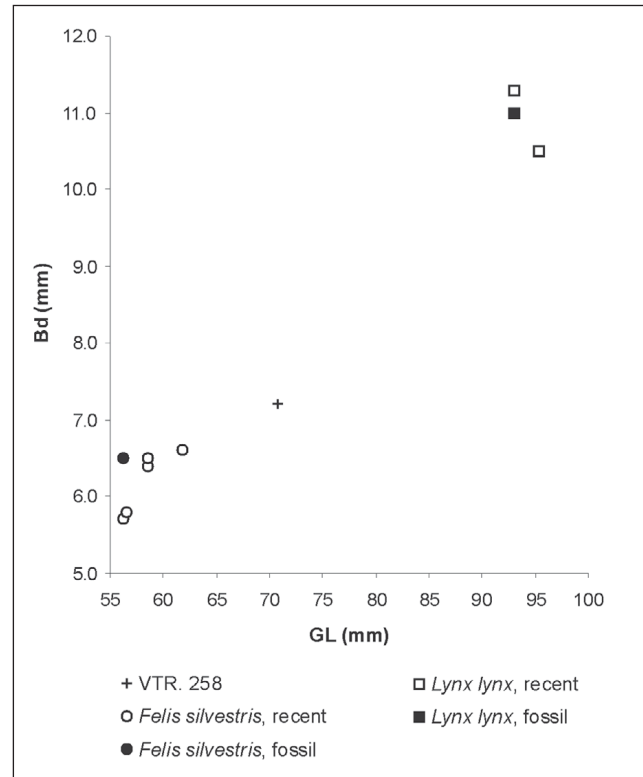


Figure 16: Metatarsal V greatest length (GL) vs. distal breadth (Bd) of VTR. 262 compared to recent specimens of *V. vulpes* and *L. lynx*. Comparative specimens are from ZPGK.

and missing from Krapina are indicative of temperate to warm conditions; none of them are adapted to particularly cool or dry environments. The overall similarities between these assemblages suggest that they accumulated under roughly comparable palaeoecological conditions.

There are important differences between the larger mammal assemblages from Veternica layer j and Divje babe I Facies C. Present at Veternica layer j and missing from Divje babe Facies C are *Castor fiber*, *H. cristata*, *Panthera pardus*, *Stephanorhinus* sp., *S. scrofa*, and *Bison priscus*, while *Lepus* sp., *V. vulpes*, *M. martes*, and *Rupicapra rupicapra* are missing from Veternica layer j and are present at Divje

Table 8: Revision of specimens identified to *Alopex cf. lagopus*, *Gulo gulo*, and *Lynx pardinus*.

#	Element	Layer	MALEZ (1963)	Revised
VTR. 255	ulna	f	<i>A. cf. lagopus</i>	<i>V. vulpes</i>
VTR. 267	∩ ³	f	<i>G. gulo</i>	<i>Canis</i> sp.
VTR. 268	∩ ³	f	<i>G. gulo</i>	<i>Canis</i> sp.
VTR. 740/car	humerus	i	<i>M. meles</i>	<i>F. silvestris</i>
VTR. 256	humerus	i	<i>L. pardinus</i>	<i>F. silvestris</i>
VTR. 260	tibia	d	<i>L. pardinus</i>	<i>M. meles</i>
VTR. 261	metatarsal II	d	<i>L. pardinus</i>	<i>F. silvestris</i>
VTR. 257	metatarsal IV	h	<i>L. pardinus</i>	<i>F. silvestris</i>
VTR. 258	metatarsal IV	h	<i>L. pardinus</i>	<i>F. silvestris</i>
VTR. 262	metatarsal V	d/h/i	<i>L. pardinus</i>	<i>V. vulpes</i>

babe Facies C (MALEZ, 1963, table 33; TOŠKAN, 2007, table 11.14). The first impression is that the Veternica layer j fauna has more of a “full interglacial” (e.g. MIS 5e) character than Divje babe Facies C owing to the presence of taxa including *Castor*, *Hystrix*, *Stephanorhinus*, and *Sus*. Some of these contrasts, however, can be accounted for by the more open setting of Veternica compared to Divje babe. Taxa like forest/prairie rhinoceros and bison might have preferred the wide valley of the Sava on the edge of which Veternica is situated, whereas chamois and pine marten may have favored the relatively steep and narrow Idrija valley in which Divje babe is located. Furthermore, all of these species were present in the region during both interglacial and glacial periods (MIRACLE, 1991; MIRACLE et al., 2010). The contrast in faunal composition between Veternica layer j and Divje babe I Facies C probably reflects local conditions and does not have further palaeoecological or chronostratigraphic importance.

As we previously noted (MIRACLE & BRAJKOVIĆ, 1992, p. 9) the sediments, pollen spectra, and faunal remains from Veternica layer j indicate deposition under relatively warm and wet conditions, at least with regards to the rest of the sequence at Veternica. We previously suggested dating layer j to sub-stages MIS 5c or 5a (c. 100,000 and 80,000 ka, respectively) instead of the full interglacial conditions of MIS 5e. Although the further revision of the Veternica fauna does not change the composition of the layer j assemblage, comparison to other sites in the region, in particular Krapina, suggests that layer j could have also accumulated during MIS 5e.

Layers g–i most probably date to MIS 3 and 4; a ^{14}C date of > 43,200 BP on a hearth from layer i confirms layers i and j were deposited before c. 45,000 BP (MIRACLE & BRAJKOVIĆ, 1992). The previous revision of the ungulate fauna removed *Megaloceros giganteus* and *Alces alces* from layer i, and *Bos primigenius* from layers h and i. Our recent analyses of the remainder of the mammal assemblage show that remains identified as *L. pardinus* are from *F. silvestris* (Table 9). These determinations are consistent with the remainder of the assemblage, which includes *Clethrionomys glareolus* (layer i), *Arvicola terrestris*, *C. lupus*, *V. vulpes*, *M. erminea*, *M. putorius*, *M. meles* (layer i), *F. silvestris*, *P. spelaea*, *P. pardus* (layer i), *C. elaphus*, *C. capreolus*, *B. priscus* (layer i), and *R. rupicapra* (layer h) (Table 9; MIRACLE et al., 2010). The disappearance of the crested porcupine (MALEZ, 1963, table 33) and the appearance of elk in layer h correspond with a shift in sediment composition that may indicate relatively cooler and drier depositional conditions (MIRACLE & BRAJKOVIĆ, 1992, p. 9). On the whole, the faunal assemblages from Veternica layers h and i suggest deposition under temperate conditions with some forest cover and wetlands in the region.

Layer g at Veternica contained only sporadic remains of cave bear near the contact with layer h (MALEZ, 1963, p. 154); they were interspersed among a large quantity of rock rubble. This major roof collapse (MALEZ, 1965, 207) prob-

ably occurred during a cooler period in MIS 3, although another interpretation would be that layers h and i were deposited in MIS 5 and layer g was deposited during MIS 4. Whatever the interpretation, the roof collapse in layer g probably closed the entrance to Veternica, causing a major hiatus in cave use by hominins, bears, and other larger mammals.

Layers e and f are placed in MIS 3 based on the disappearance of Mousterian lithic artifacts alongside the continuing presence of a few undiagnostic stone tools. Our previous revision confirmed the presence of *C. elaphus* in both layers, *C. capreolus* and *R. rupicapra* in layer e, removed *Capra ibex* from layer e, and added *S. scrofa* to layer e (MIRACLE & BRAJKOVIĆ, 1992). The current revision replaces *L. timidus* with *L. europaeus*, *Ochotona* sp. with *Lepus* sp., *A. lagopus* with *V. vulpes*, and *G. gulo* with *Canis* sp. We lack adequate comparative material to confirm the identification of a P^1 to *Crocota spelaea* (MALEZ, 1963, p. 92). We can confirm the presence of *P. spelaea* in layer f, but not in layer e. The elimination of *L. timidus*, *Ochotona* sp., *A. lagopus*, and *G. gulo* from layers e and f in conjunction with the addition of *S. scrofa* suggests at most cool to relatively temperate conditions during the deposition of these layers. Therefore we cannot confirm a significant cold oscillation at Veternica during the deposition of layers e and f as originally suggested by MALEZ (1963, p. 151).

Turning to the wider region, the larger mammal assemblages from Velika pećina and Vindija also lack indicators of particularly cold conditions (MIRACLE et al., 2010). Although missing at Veternica, we have confirmed the presence of wolverine (Velika pećina: layers f, g, i, k, and Vindija: layer G upper) and steppe pika, *O. pusilla*, (Vindija: layer G lower). Wolverines may not be as reliable as indicators of cold climates as is commonly thought. In the recent past the range of wolverines extended as far south as northern Germany and Poland (KROTT, 1959, p. 14; NOWAK, 1991, p. 1124–1125), and this range has probably been reduced owing to competition from humans, wolves, and other competitors (KROTT, 1959, p. 96). Finally, wolverines are reported to travel long distances in response to changing conditions (KROTT, 1959, p. 101; NOWAK, 1991, p. 1124–1125). Turning to the wolverine fossils found at Velika pećina and Vindija, only a small number of remains from the head and extremities were found. These bones might have been still attached to pelts that had been transported relatively long distances by past people. For these reasons we are reluctant to use the presence of wolverines to infer very cold climatic conditions in the immediate region of Veternica. The presence of steppe pika and other taxa adapted to relatively open environments suggests that at times such conditions were prevalent in the region. Overall we reconstruct relatively temperate conditions with a range of environments present in the region.

The deposition of layer d is assigned to MIS 2 on the basis of a ^{14}C date ca. 16,740 BP on overlying flowstone from layer c⁸. The revision of the ungulate fauna removed *Ovis* sp.

⁸ This and other radiocarbon dates have been calibrated using “Online CalPal” – quickcal2007 ver.1.5 (<http://www.calpal-online.de/>).

Table 9: The revised Pleistocene mammal assemblage from Veternica Cave. Taxa added to the assemblage are indicated with a "+"; taxa confirmed as present in the assemblage are indicated with a "√"; taxa removed from the assemblage are indicated with a "-". Taxa that could neither be confirmed nor removed are indicated with a "?".

Taxon	N	MIS 2	MIS 3	MIS 3-4			MIS 5
		d	e	f	g	h	i
LAGOMORPHA							
<i>Lepus timidus</i>		-	-	-			
<i>Lepus europaeus</i>	10	+	+	+			
<i>Lepus</i> sp.	22	+		+	√	√	
<i>Ochotona</i> sp.				-			
CARNIVORA							
<i>Canis lupus</i>	146	√	√	√	√	√	√
<i>Canis</i> sp.	5			+		√	
<i>Alopex lagopus</i>				-			
<i>Vulpes vulpes</i>	18	√		+	√	√	
<i>Cuon alpinus</i>	6			√			
<i>Mustela erminea</i>	2				√	√	
<i>Mustela putorius</i>	16	√			√	√	
<i>Martes martes</i>	3				-	√	
<i>Martes foina</i>	9	√					
<i>Martes</i> sp.	1				+		
<i>Gulo gulo</i>				-			
<i>Meles meles</i>	32	√				√	
<i>Crocuta spelaea</i>				?			
<i>Felis silvestris</i>	12	√			√	√	
<i>Lynx pardinus</i>		-			-	-	
<i>Panthera spelaea</i>	53		-	√	√	√	?
<i>Panthera pardus</i>	12					√	√
UNGULATA							
<i>Stephanorhinus</i> sp.	4						√
<i>Sus scrofa</i>	24	√	+				√
<i>Megaloceros giganteus</i>							-
<i>Dama</i> cf. <i>Dama</i>							-
<i>Cervus elaphus</i>	156	√	√	√	√	√	√
<i>Alces alces</i>	2				√	-	
<i>Capreolus capreolus</i>	17	√	√		√	√	√
Cervidae	3		-	√	-	√	√
<i>Bos primigenius</i>					-	-	-
<i>Bison priscus</i>	7					+	+
<i>Bos/Bison</i>	11	+			+	+	+
Bovidae		-					
<i>Capra ibex</i>	3	√	-				
<i>Rupicapra rupicapra</i>	10	√	√		+		
Capridae	1	+					
<i>Ovis</i> sp.		-					

from the assemblage and added *Bos/Bison* (MIRACLE & BRAJKOVIĆ, 1992). The current revision of the lagomorphs and small carnivores confirms the presence of *Lepus* sp., *C.*

lupus, *V. vulpes*, *M. putorius*, *Martes foina*, *M. meles*, *F. silvestris*, removes *L. pardinus* from the assemblage, and replaces *L. timidus* with *L. europaeus*. Many of these taxa (e.g. *S. scrofa*, *C. capreolus*, *L. europaeus*, and *F. silvestris*) are indicative of temperate conditions with some vegetative cover; none of them are indicative of particularly cold conditions.

We can tentatively correlate Veternica layer d with Velika pećina layer d and Vindija layer E (MIRACLE et al., 2010). Although not present at Veternica, there is some evidence of the appearance of cold-adapted taxa at the other sites, in particular *L. timidus* in Vindija layer E/F and *Rangifer tarandus* in Vindija layers E and E/F (MIRACLE et al., 2010, table 3). While Vindija provides some evidence of climatic deterioration with the onset of MIS 2, these cold-climate indicators appear alongside taxa with wide tolerances and/or a preference for more temperate conditions (e.g. *L. europaeus*, *V. vulpes*, *M. putorius*, *M. meles*, *F. silvestris*, *S. scrofa*, *C. elaphus*, *C. capreolus*, and *B. primigenius*). This suite of taxa suggests that conditions were not particularly harsh or cold.

This apparent mix of species with divergent climatic tolerances can also be explained by the close proximity of exposed, open alluvial plains and sheltered valleys in the region. Such a juxtaposition of microhabitats would have provided a diversity of niches for local mammal populations. In any case, individual animals, not communities, populations, or species respond to climatic changes. Hence, in the past as is the case today, faunal "communities" would have been in a constant state of flux. They would have been taken apart and reconstituted as animals (species) came and went through local processes of range shift, migration, and extirpation.

6. CONCLUSIONS

At Veternica there is neither evidence of "cold-adapted" larger mammals like mountain hare, arctic fox, and wolverine nor of "steppe-adapted" animals like pika. Our revision of the Veternica faunal assemblages does not support an interpretation of significant climatic oscillations during the deposition of layers associated with MIS 2, 3, and 4. The absence of "cold-adapted" taxa suggests that either remains were deposited only during more temperate periods within MIS 3 and 2 or that cold oscillations were not strongly expressed in northern Croatia. The large mammal fauna is remarkably stable in composition over time; conditions in the region appear to have been broadly temperate. With rare exceptions (e.g. pika and reindeer at Vindija), there is little evidence of a significant immigration of larger mammals into the region during the Upper Pleistocene. A wide range of environments – open, forested, wetland, and rocky – were usually present in the area surrounding Veternica. Recent revision and study of the larger mammal and micromammal faunas from Velika pećina and Vindija supports this interpretation (MIRACLE et al., 2010). There aren't any dramatic or significant changes in faunal composition over time with the exception of the appearance in Vindija of a few "cold-adapted" taxa associated with the onset of the last glacial maximum (MIS 2) after about 27,000 BP.

Thus, the Croatian Zagorje appears to have supported a fairly diverse and productive mammal fauna; this would have made it a favorable region for hominin settlement during MIS 2–5. There is no evidence of significant changes in faunal composition at the time of the Middle Palaeolithic–Upper Palaeolithic transition (ca. 40,000–30,000 ka, BRAJKOVIĆ & MIRACLE, 2008). Contrary to the suggestion that there was a “substantial evolution” in the mammalian faunas, which were “less stable [in]... Slovenia and Croatia where rather large changes in species composition occurred in the course of the same period” (MUSIL, 2003, p. 182), our revision of the Veternica mammal fauna shows stability and continuity in the assemblages over time. This apparent stability could be due to one or more of the following factors: A) hominins and other animals preferentially used specific sites or the region during warm phases, B) sedimentation and erosion have created a bias for warm phases, C) climatic oscillations in the region were less marked than previously thought, D) local factors of microclimate and topography buffered faunal communities from climatic oscillations, E) animals had wider temperature/precipitation tolerances than previously thought. Explanation of this apparent stability in mammalian faunas requires further revision of existing assemblages and better control over chronology, formation processes, and other lines of palaeoecological evidence.

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