Taphonomy of the alpine marmot (*Marmota marmota*) remains from the Late Pleistocene deposits of the East Brina Cave, Croatia

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Abstract

The Late Pleistocene deposits of the East and West Brina Caves near Drniš have yielded one of the largest collections of alpine marmot (*Marmota marmota* LINNAEUS, 1758) remains in Croatia. A total of 425 skeletal remains were recovered, with 411 originating from the East Brina Cave. Taphonomic analysis of this assemblage reveals that multiple factors influenced the accumulation and preservation of marmot remains. While natural mortality, most probably, was the primary cause, secondary agents such as predation by small carnivores, particularly martens and foxes, played a significant role. Additionally, a small number of bones bear cut marks, suggesting the occasional human exploitation of alpine marmots by Palaeolithic hunters. Bone surface modifications indicate that many remains were exposed before burial. These finds provide insights into the Late Pleistocene alpine marmot ecological dynamics, and human subsistence strategies in southeastern Europe.

1. INTRODUCTION

The Brina Caves (Pećine u Brini), including the East, West and the Small Cave, located 4 km east of Drniš, yielded one of the largest collections of alpine marmot (*Marmota marmota* LINNAEUS, 1758) bone remains in Croatia, with the East Brina Cave being the largest site in the Dalmatian part of Croatia. The alpine marmot skeletal remains were collected from the Late Pleistocene deposits in the Brina Caves during excavations conducted by Mirko Malez from 1960 – 1961, and from 1968 – 1970 (MALEZ, 1963a, 1963b, 1970, 1971a, 1971b, 1975). Besides alpine marmot remains, abundant Late Pleistocene vertebrate skeletal and dental material was recovered, along with the first Palaeolithic artifacts found in the Dalmatian area (MALEZ, 1963a).

Marmots are the largest members of the Sciuridae family and the second largest representative of Rodentia after beavers. Of the 15 species in the genus *Marmota*, nine are found in Europe and Asia, while the remaining six species inhabit North America (ARMITAGE, 2013). The evolution of *Marmota* began during the Late Miocene, about 10 million years ago in North America, and spread into Eurasia afterwards (ERBAJEVA & ALEXEEVA, 2009). During the Pliocene, Eurasia became a centre for marmot diversification (MENÉNDEZ et al., 2023), extending their range into Eastern Europe by the end of the Pliocene (ERBAJEVA & ALEXEEVA, 2009). In the Early Pleistocene, marmots were extremely rare in Europe and were seldom recorded at fossil sites, such as those in France (CLOT, 1975), Austria (MAUL, 1990), Georgia (TAPPEN et al., 2002), and Croatia (MALEZ & RABEDER, 1984; PAUNOVIĆ & RABEDER, 2000). The only exception is Sierra de Atapuerca in Spain (ESTRAVIZ-LÓPEZ et al., 2021). During the Middle Pleistocene, there was a slight increase in the occurrence of marmot remains in Spain and France, although they were still rare compared to other rodents (ESTRAVIZ-LÓPEZ et al., 2021), as well as in Italy and Romania (PALEOBIOLOGY DATABASE, 2025).

The habitat of Late Pleistocene *Marmota marmota* was widespread across Europe. Their fossils have been found as far west as the Cantabrian Mountains in Spain, across France and northern Belgium, and as far south as Italy, Slovenia, Croatia and Montenegro. They also expanded eastward through Slovakia, Hungary, and Moldova (MALEZ, 1972; ZIMINA & GERASIMOV, 1973; RAMOUSSE & LE BERRE, 1993; TOŠKAN, 2007; BORIĆ et al., 2014; NOW DATABASE, 2023).

In Croatia, the Late Pleistocene marmots have been discovered at 17 different localities, including the continental parts of the country: northwestern Croatia, Gorski kotar, and Lika, as well as the coastal areas of Istria and Dalmatia (MALEZ, 1972). Although this would suggest a widely distributed habitat during the Pleistocene, the amount of fossil remains is relatively low and fragmented at most localities (MALEZ, 1995). The exceptions are the localities such as Vindija, representing one of the richest marmot assemblages in Southern Europe, as well as the Klek Cave, Šaftica Cave, Šandalja II site, and the East Brina Cave, which is studied herein (MALEZ, 1995; PAUNOVIĆ et al., 2001; MAUCH LENARDIĆ & KLEPAČ, 2009). At present, marmots are not part of the recent Croatian fauna, and it is assumed that they disappeared from this area either at the end of the Late Pleistocene or at the beginning of the Holocene (MAUCH LENARDIĆ & KLEPAČ, 2009).

Although abundant literature exists on the ecology, morphology, and other aspects of marmots, taphonomic studies are still relatively rare. The purpose of this paper is to provide a taphonomic analysis, and to elucidate accumulation factors and post-depositional processes that affected the marmot fossil remains from the Brina Caves.

1.1. The Brina Caves

The Brina Caves comprise three separate small caves (East, West, and Small Cave) and are located on the right-hand side of the Čikola River 4 km southwest of the city of Drniš (43°51'23"N, 16°06'29"E; Fig. 1). The Drniš area belongs to the North Dalmatian hinterland. It is a karstic area surrounded by the Promina mountains (1148 m a.s.l.) to the north, Svilaja (1509 m a.s.l.) to the east, Moseć (839 m a.s.l.) to the south, and the Krka River to the west (HODŽIĆ & ŠORIĆ, 2011). Today, the Brina caves are located 25 km from the coast, while during MIS 2 the distance was 40 km (Fig. 1). During the Late Pleistocene, the karstic hinterland was characterized by exposed karst and stands of trees, in contrast to the Great Adriatic Plain (PAUNOVIĆ et al., 2001; MAUCH LENARDIĆ et al., 2018; PILAAR BIRCH & VANDER LINDEN, 2018).

The entrances to the Brina Caves face south and are located at 250 m a.s.l. They were formed in thickly layered, light yellowish rudist limestones from the Late Cretaceous period (MALEZ, 1963a). The largest of the three caves is the East Cave, which is approximately 20 m in length and represents the central location within this cave complex (Fig.

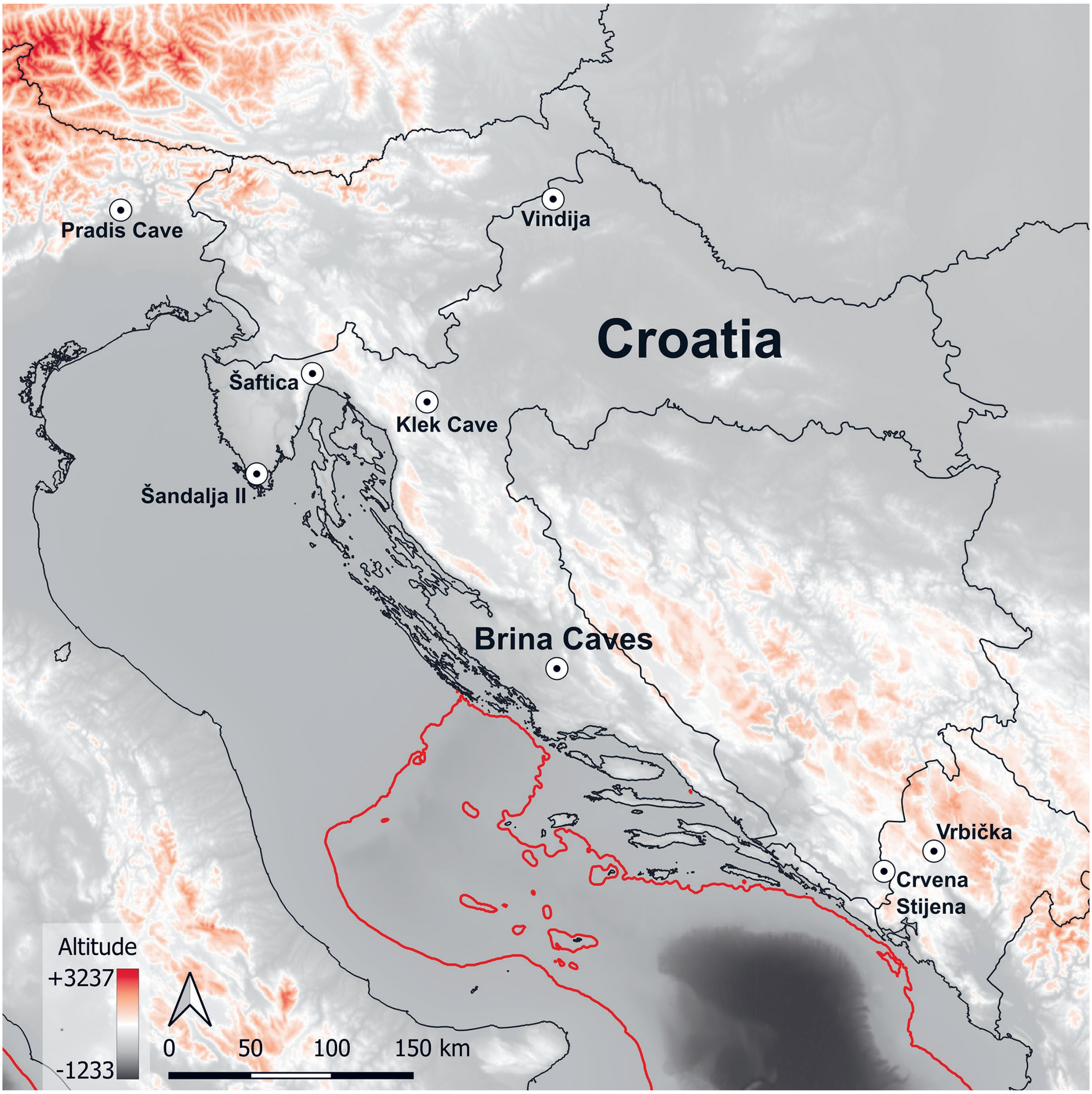

Figure 1. Map showing the location of the Brina Caves near Drniš, Croatia, along with some known localities where Late Pleistocene marmot remains have been identified. Red line represents sea level during MIS 2.

2a, b). In the middle of the East Cave, MALEZ (1963b, 1975) logged a detailed profile (Fig. 2c), recording the following stratigraphy: layer a – humus (5 – 15 cm thick), layer b – finely laminated yellow flowstone (10 – 15 cm), layer c – brown porous clay with scattered rock fragments (40 – 50 cm), layer d – red compact illite (15 – 20 cm), and layer e – olive green to dark grey illite (25 – 30 cm) (Fig. 2c). Within the layer e, a marmot burrow was detected during the excavations (Fig. 2c, marked by "m"). In the topmost layer, rare recent bones from sheep and goats were recovered, along with the ceramic fragments of so-called "gradinska keramika". The flowstone covers fossiliferous illite layers, representing the oldest Quaternary deposits in the cave. In layers d and e, evidence for the presence of Late Pleistocene humans was found, represented by charcoal, charred bones, and flint tools. According to MALEZ (1975), all the collected artefacts belong to the Upper Palaeolithic, and the sediments were formed during the Würm Glacial. According to PAUNOVIĆ et al. (2001), layer a is of Holocene age, and layers b – d belong to the OIS 2 (Würm 3) (PAUNOVIĆ et al., 2001; after MALEZ, 1963a, b, 1975). Based on the faunal assemblages, Malez dated the East Brina Cave's layers c – e and West Brina Cave layers d – e to the Late Pleistocene age (PAUNOVIĆ et al., 2001; after MALEZ, 1975). This was confirmed by radiometric dating (^{14}C) on bison bone from the upper part of layer d in the West Brina Cave, that yielded an age of 18,388 years BP (MALEZ, 1975).

The fossiliferous Late Pleistocene layers (c, d, and e) comprise abundant fossil material, including: *Erinaceus* sp. LINNAEUS, 1758, *Crocidura* sp. WAGLER, 1832, *Lepus timidus* LINNAEUS, 1758, *Oryctolagus cuniculus*

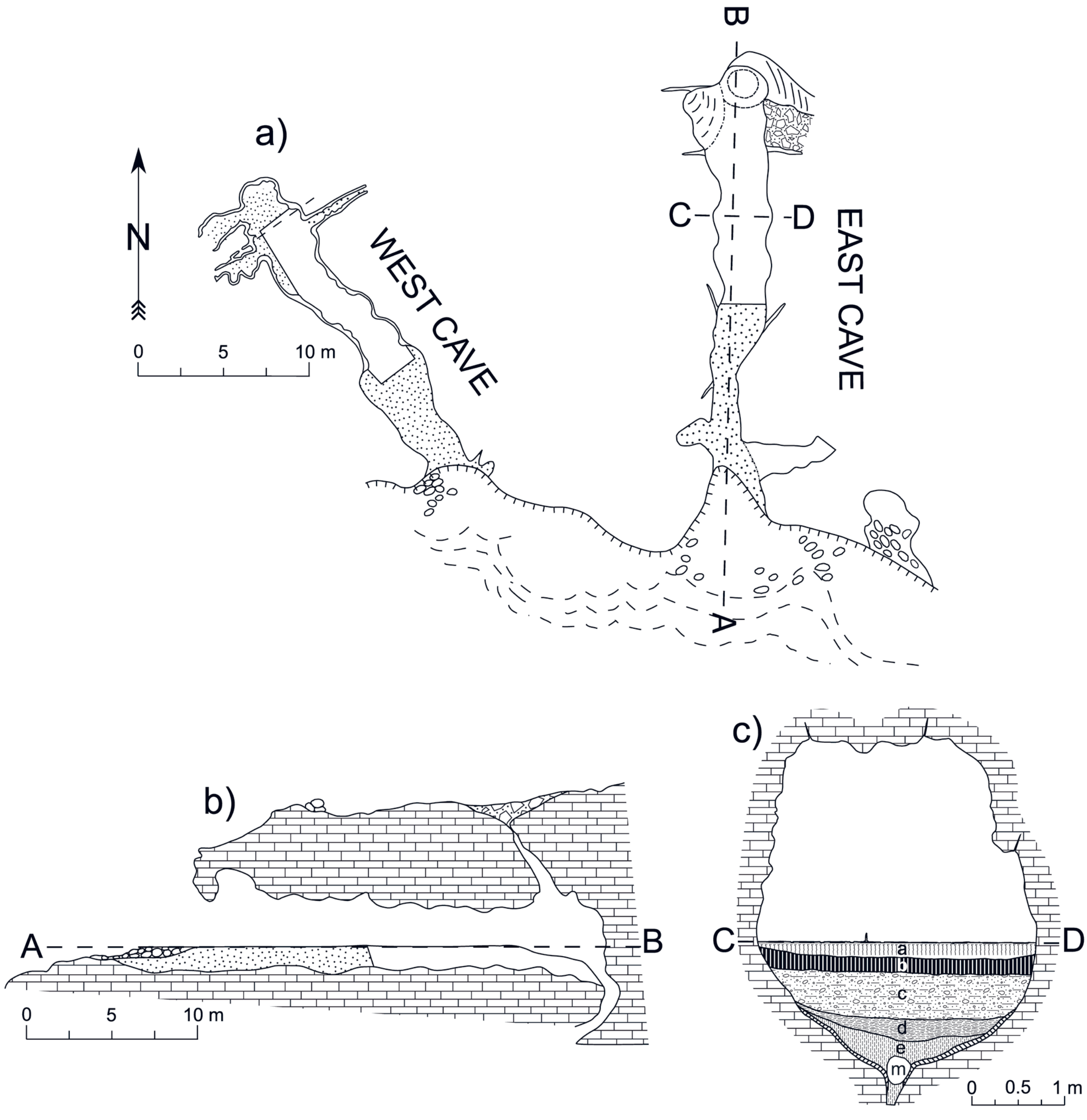

Figure 2. The Brina Caves plan **(a)** with detailed profile **(b)** and transect **(c)** of the East Cave (after MALEZ, 1975).

LINNAEUS, 1758, *Ochotona pusilla* PALLAS, 1769, *Marmota marmota* LINNAEUS, 1758, *Cricetus cricetus* LINNAEUS, 1758, *Arvicola scherman* SHAW, 1801, *Microtus* sp. SCHRANK, 1798, *Ursus spelaeus* ROSENMÜLLER-HEINROTH, 1794, *Mustela nivalis* LINNAEUS, 1758, *Crocuta spelaea* GOLDFUSS, 1823, *Equus caballus fossilis* LINNAEUS, 1758, *Asinus hydruntinus* GRAY, 1824, *Sus scrofa* LINNAEUS, 1758, *Cervus elaphus* LINNAEUS, 1758, *Alces alces* LINNAEUS, 1758, Bovidarum gen. et spec. indet., *Capra ibex* LINNAEUS, 1758, as well as abundant bird, amphibian, and snail finds (MALEZ, 1963b). Marmot burrows were recorded in the lowermost stratum e, which irrefutably proves that they lived in the East Brina Cave.

2. MATERIALS AND METHODS

A total of 425 skeletal remains were collected from the Brina Caves, of which 411 (96.7%) were found in the East Brina Cave (Tables 1, 2). Hence, we present here a taphonomic analysis of the East Brina Cave marmot assemblage, while the number of samples (14 remains) from the West Cave is insufficient to offer statistically significant results. The material is stored at the Institute for Quaternary Palaeontology and Geology of the Croatian Academy of Sciences and Arts in Zagreb. Taxonomic identification and metrical analysis for long bones and skulls were already undertaken for 219 skeletal remains by TUKŠA (2019). However, during the preparation of the master's thesis by one of the authors (ŠANJEK, 2023), an additional 192 marmot skeletal remains were found in the Institute's collection.

There are no available data about the excavation and sampling methods, and the bone remains do not have any provenance data, except that they were stored separately for the East and West Caves. MALEZ (1963a, 1975) recorded that the most of the marmot remains in the East Cave were collected in the upper part of layer c, just below the flowstone (layer b). The remains included abundant limb bones, and two complete skulls, among other skeletal elements (Table 2). Based on the absence of small bone fragments and considering the site was excavated in the 1960s, we can presume that most of the skeletal remains were manually collected.

Skeletal analysis involved the detailed examination of each skeletal fragment and the documenting of anatomical, taxonomic and taphonomic information. Anatomical and taxonomic identifications were made using a recent osteological reference collection of the Institute for Quaternary Palaeontology and Geology of the Croatian Academy of Sciences and Arts.

The preservation category was based on the percentage of preserved bone compared to the original complete bone. The assessment was rounded to the closest percentage category: 10%, 25%, 50%, 75%, 90%, 95%, or 100%. Poorly preserved bones were those below 75%, while bones with 75% or more preservation were considered well preserved.

Table 1. Most highly represented skeletal elements in the East Brina Cave and marmot age classes.

Element	NISP	MNE	Adult	Juv	Very Juv	MNI
Mandible	30	27	3 sin, 9 dex	7 sin, 4 dex	/	16
Ulna	29	29	2 sin, 2 dex	5 sin, 6 dex	5 sin, 9 dex	17
Femur	29	24	4 sin, 2 dex	7 sin, 11 dex	/	15
Tibia	31	25	1 sin, 2 dex	4 sin, 1 dex	8 sin, 8 dex	14

Table 2. Identified skeletal elements of marmots in the East Cave. NISP – number of identified specimens, MNE – minimum number of elements, RA – relative abundance, FI – Fragmentation Index.

	NISP	%NISP	MNE	%RA	FI
Cranium	12	2.9	5	29.4	0.4
Mandibula	30	7.3	27	79.4	0.9
Tooth	55	13.4	-	-	-
Atlas	1	0.2	1	5.9	1
Axis	1	0.2	1	5.9	1
Cerv. v.	8	1.9	5	5.9	0.6
Thorac. v.	15	3.6	13	6.4	0.9
Lumb. v.	27	6.6	20	19.6	0.7
Sacrum	2	0.5	2	11.8	1
Caud. v.	10	2.4	7	2.2	0.7
Sternum	1	0.2	1	5.9	1
Rib	23	5.6	23	11.3	1
Clavicula	8	1.9	8	23.5	1
Scapula	11	2.7	10	29.4	0.9
Humerus	23	5.6	19	55.9	0.8
Radius	13	3.2	13	38.2	1
Ulna	29	7.1	29	85.3	1
Metacarpus	13	3.2	13	15.3	1
Pelvis	36	8.8	13	76.5	0.4
Femur	29	7.1	22	64.7	0.8
Tibia	31	7.5	25	73.5	0.8
Fibula	2	0.5	1	2.9	0.5
Calcaneus	3	0.7	3	17.6	1
Astragalus	2	0.5	2	11.8	1
Metatarsus	13	3.2	13	15.3	1
Phalanx	13	3.2	13	15.3	1
Total	411	100	289		

The relative age of the bones and teeth in the mandibles was determined by the criteria described in TOMÉ (1998). Based on the bone size, epiphysis fusion, teeth type and teeth wear, the remains were determined as being very juvenile (cub born in the spring of the same year), juvenile (cub from the previous year), and adult (3 years old and older).

Taphonomic analyses included careful bone examination under a 10x magnification hand lens and with a binocular microscope with camera (XTL-3400D, magnification up to 136.6x, camera Dino-Eye AM4023X), followed by interpretation based on the intensity and weathering type, mineral coating, burn marks, bite marks, gnawing, and cut marks. The types of taphonomic modifications were defined following BEHRENSMEYER, 1978; BEHRENSMEYER et al., 2003; LYMAN, 1987, 2008; FERNÁNDEZ-JALVO & ANDREWS, 2016; INDRA et al., 2022; NANNINI et al., 2022; ROMANDINI et al., 2012; ROMANDINI et al., 2018; MARQUES et al., 2018.

Since the purpose of this study was to determine the factors affecting the accumulation of marmots in the East Brina Caves, we separated taphonomic modifications into two categories: weathering marks and predatory markings, to simplify the factors affecting accumulation. To achieve this, it was necessary to differentiate between marks obtained during predation and those developed during deposition. This approach also accounts for additional biotic markings (non-related to predation or scavenging), including etching by plant roots, algae, fungi, or bacteria, along with abiotic modifications such as mechanical processes associated with deposition and possible post-mortem transport, as well as diagenesis (e.g. mineral coatings). Bacterial corrosion occurs as pitting and usually has an irregular distribution, while soil corrosion affects a wider area of the bone, usually at one end, and creates a rough surface. Digestive corrosion, on the other hand, usually affects the entire bone and produces smooth edges.

Predation marks include carnivore tooth marks, scratching (represented by a series of three or four parallel shallow striations), corrosion caused by digestion, cut marks, and possibly burned bones. Weathering includes cracking, splitting, flaking, erosion, abrasion, and chemical etching. Mechanical weathering typically occurs while the bone is still on the surface, whereas chemical etching occurs when the bone is buried. Recent modifications caused by excavations or laboratory processing are included in the category of mechanical weathering.

The relative abundance (RA) for each element of the skeleton was calculated using the formula by DODSON & WEXLER (1979):

$$\%RA = (MNE / (MNI * E)) * 100,$$

where MNE represents the minimum number of skeletal elements, MNI is the minimum number of individuals, and E is the number of specific elements present in one skeleton. MNI was calculated based on the most abundant skeletal element, based on a body side and age.

In addition to the relative abundance, the proportion of skeletal elements was calculated after NANNINI et al. (2022), using anatomical indices based on ANDREWS (1990), LLOVERAS et al. (2008, 2016), and the normalized ratios modified by PELLETIER et al. (2020). The following skeletal elements were grouped together to calculate the ratios mentioned above: postcranial elements (PCTR), cranial elements (CR), limb elements (PCRAP), postcranial long bones (PCRLB), autopodia (AUT), zygopodia (Z), stylopodia (E), anterior limb (AN) and posterior limb (PO).

3. RESULTS

The analyzed samples include most of the skeletal elements present in the marmot skeleton, with a total NISP of 411 (*Number of Identified Specimens*; Table 1). Bones (including mandibles with tooth rows) make up 86.6% (NISP = 356) of the samples from the East Cave, while the isolated teeth account for 13.4% (NISP = 55). The bone samples exhibit varying degrees of preservation. The majority (NISP =256, 71.9%) of the bones (excluding teeth) from the East Cave are well-preserved (with more than 75% of the bone's original structure intact), and almost half of these well-preserved bones are completely intact (NISP = 126, 49.2%). Poorly preserved bones account for 28.1% (NISP = 155) of the bone sample from the East Cave.

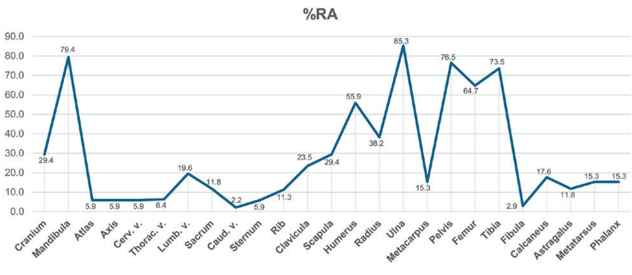

Figure 3. Chart showing the relative abundance (RA) of the alpine marmot skeletal elements in the East Brina Cave.

Based on the determined relative ages of the four most represented skeletal elements in the assemblage, and the side of the body to which the bone belongs, the minimum number of individuals (MNI) was calculated (Table 1). The highest MNI is based on the ulna and includes a minimum of 17 individuals: 2 adults, 6 juvenile and 9 very juvenile.

3.1. Anatomical representation

The anatomical composition of the identified remains (Table 2) shows that the most frequent elements are isolated teeth (13.4% NISP), pelvis (8.8% NISP), tibia (7.5% NISP), and mandible (7.3% NISP), while smaller elements including the atlas, axis and sternum show the lowest values. This can probably be explained by the excavation process, particularly overlooking the smaller bones during the primary excavation. The relative abundance shows a mean value of 28.4% (Table 2, Fig. 3) which is characterized as low, and is indicative that the sample was affected by the significant loss of some skeletal elements. Based on the relative abundance, the ulna is the most represented bone in the assemblage (85.3%), followed by mandible (79.4%), pelvis (76.5%), tibia (73.5%) and femur (64.7%). The lowest relative abundance is calculated for caudal vertebrae (2.2%) and the fibula (2.9%), respectively.

Ratios between skeletal elements shown in Table 3 are indicative of a deficiency in the numbers of postcranial remains compared to the cranial ones with PCRT/CR of 28.5% and PCRAP/CR of 30.3%. Only when cranial remains are compared with long bones does the PCRLG/CR index show a relatively balanced proportion of 72.4%. While comparison of the lower to upper limb elements shows the dominance of upper limbs (AUT/ZE = 4.8%), the Z/E index of 40% shows a decrease in the abundance of stylopodia over zygopodia. Similar numbers are derived in comparison between the posterior and anterior limb elements, showing a loss of the latter (AN/PO = 38.2%).

Table 3. Ratios between the different parts of the marmot skeleton from the East Brina Cave.

INDEX	%
PCTR/CR	28.5
PCRAP/CR	30.3
PCRLB/CR	72.4
AUT/ZE	4.8
Z/E	40
AN/PO	38.2

3.2. Bone surface modifications

3.2.1. Weathering

In the analyzed material, mechanical weathering was more dominant (NR = 262; 63.8%) than chemical weathering (NR = 133; 32.4%), while 16 bone remains (3.9%) were not affected by weathering (Table 4). Among mechanical weathering, erosion was the most dominant type (45.5%), followed by fine line fractures and/or spalling (17.3%), while trampling (2.9%) and abrasion (1%) were rare. Damage caused by recent manipulation (i.e. excavation) is recorded at 19 bones (4.6%). Pitting, caused by bacterial corrosion, was by far the most prevalent type of chemical weathering (NR = 110; 26.7%), followed by root etching (NR = 21; 5.2%), while soil corrosion was identified on four bones (1.0%). It was very common for a single bone to exhibit multiple weathering marks, including multiple types of mechanical weathering, multiple types of chemical weathering, or a combination of both.

3.2.2. Animal and Predation Marks

A total of 98 remains (23.8%) displayed animal-origin surface modifications (Fig. 4, Pl. 1), with gnawing marks from small carnivores being predominant (NR = 58; 14.1%) compared to only 18 remains (4.3%), that display possible anthropogenic marks (Table 5, Fig. 5). Samples with only animal-origin marks predominate, while a combination of animal and anthropogenic marks was recorded on eight specimens. The identified animal-origin marks include rodent gnawing (3.4%), gnawing of unknown origin (6.8%), small animal scratchin (6.31%), small carnivore bite marks (10.0%), a combination of rodent gnawing and small carnivore bite marks (4.1%), and bite marks of unknown origin (6.8%). Anthropogenic-origin marks include cut marks (1.2%; Fig. 5), possible cut marks (1.2%), and possible burning (1.9%).

4. DISCUSSION

4.1. Preservation and Representation of Skeletal Elements

The long limb bones are very well preserved making up 30.9% (NISP = 127, Table 2) of the NISP. Besides being the largest bones, they are also among the most dense bones in the skeleton (LYMAN et al., 1992) which likely accounts for their high preservation potential and representation in the sediment. The same criterion can be applied to the lower jaws that are also relatively well represented in the sample (7.3% NISP); however, the same cannot be applied to pelvic bones (8.8% NISP) that are among the least dense marmot bones. Therefore, it can be assumed that their relative frequency is related to their size and collection bias. The samples studied also contain a significant number of isolated teeth (13.4%), but since teeth are the most resistant part of the skeleton due to their composition, their abundance can be expected. However, 69% (NISP = 38) of NISP isolated teeth are incisors, which are the largest marmot teeth and were therefore the easiest to notice and handpick during the excavation.

When considering values of different anatomical indices (Table 3), it can be inferred that there is a balanced proportion

Table 4. Bone modification – weathering on alpine marmot skeletal remains from the East Brina Cave. Abbreviations: NR – number of remains, FFS – fine line fractures and spalling, CHE – chemical etching, RE – roots etching and bacterial pitting, AB – abraded, water-worn, ER – eroded, TR – trampling, MI – mineral and $CaCO_3$ coating, BS – black staining.

Skeletal element	NISP	FFS NR	FFS %	CHE NR	CHE %	RE NR	RE %	AB NR	AB %	ER NR	ER %	TR NR	TR %	MI NR	MI %	BS NR	BS %
Cranium	12	0	0.0	0	0.0	2	0.0	0	0.0	3	25.0	0	0.0	7	58.3	9	75.0
Mandibula	30	6	20.0	0	0.0	12	13.3	0	0.0	13	43.3	0	0.0	12	40.0	21	70.0
Lower I1	11	9	81.8	0	0.0	4	0.0	0	0.0	3	27.3	2	18.2	5	45.5	9	81.8
Upper I1	27	8	29.6	0	0.0	12	0.0	0	0.0	3	11.1	2	7.4	14	51.9	24	88.9
P3 4 to M3	17	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Vertebrae	62	4	6.5	0	0.0	18	3.2	0	0.0	36	58.1	1	1.6	42	67.7	27	43.5
Sacrum	2	0	0.0	0	0.0	2	0.0	0	0.0	2	100.0	0	0.0	0	0.0	2	100.0
Sternum	1	0	0.0	0	0.0	1	100.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Rib	23	0	0.0	0	0.0	5	115.0	1	4.3	4	17.4	0	0.0	1	4.3	18	78.3
Clavicula	8	1	12.5	0	0.0	2	0.0	0	0.0	2	25.0	1	12.5	5	62.5	8	100.0
Scapula	11	2	18.2	0	0.0	3	33.0	1	9.1	4	36.4	0	0.0	2	18.2	8	72.7
Humerus	23	4	17.4	1	4.3	10	13.0	0	0.0	13	56.5	2	8.7	10	43.5	14	60.9
Radius	13	3	23.1	0	0.0	1	0.0	0	0.0	6	46.2	0	0.0	6	46.2	10	76.9
Ulna	29	11	37.9	0	0.0	4	0.0	0	0.0	11	37.9	0	0.0	19	65.5	24	82.8
Metacarpus	13	0	0.0	0	0.0	9	69.2	1	7.7	5	38.5	0	0.0	5	38.5	10	76.9
Pelvis	36	6	16.7	0	0.0	13	5.6	0	0.0	19	52.8	1	2.8	19	52.8	30	83.3
Femur	29	11	37.9	2	6.9	10	0.0	0	0.0	17	58.6	2	6.9	10	34.5	19	65.5
Tibia	31	5	16.1	0	0.0	4	0.0	0	0.0	26	83.9	0	0.0	6	19.4	20	64.5
Fibula	2	0	0.0	0	0.0	1	0.0	0	0.0	0	0.0	0	0.0	0	0.0	2	100.0
Calcaneus	3	0	0.0	0	0.0	2	33.3	0	0.0	3	100.0	0	0.0	0	0.0	1	33.3
Astragalus	2	0	0.0	0	0.0	0	0.0	0	0.0	2	100.0	0	0.0	0	0.0	0	0.0
Metatarsus	13	1	7.7	0	0.0	6	15.4	0	0.0	9	69.2	0	0.0	3	23.1	13	100.0
Phalanx	13	0	0.0	1	7.7	10	76.9	1	7.7	6	46.2	1	7.7	4	30.8	13	100.0
Total	411	71	17.3	4	1.0	131	31.9	4	1.0	187	45.5	12	2.9	170	41.4	282	68.6

Table 5. Bone modification – animal and predation marks on the alpine marmot skeletal remains from the East Brina Cave. Abbreviations: NR – number of remains, CM – cut marks, CM? – possible cut marks, PB – possible burning, RG – rodent gnawing, SCG – small carnivore gnawing, RCG – rodent and small carnivore gnawing, UG – gnawing of the unknown origin, SSA – scratching from the small animals.

Skeletal element	NISP	CM NR	CM %	CM? NR	CM? %	PB NR	PB %	RG NR	RG %	SCG NR	SCG %	RCG NR	RCG %	UG NR	UG NR%	SSA NR	SSA %
Cranium	12	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	8.3	0	0.0
Mandibula	30	0	0.0	0	0.0	1	3.3	0	0.0	12	40.0	2	6.7	5	16.7	8	26.7
Lower I1	11	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	9.1	1	9.1
Upper I1	27	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	3.7	0	0.0
P3 4 to M3	17	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Vertebrae	62	0	0.0	1	1.6	0	0.0	0	0.0	0	0.0	0	0.0	1	1.6	0	0.0
Sacrum	2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Sternum	1	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Rib	23	0	0.0	0	0.0	1	4.3	1	4.3	0	0.0	0	0.0	0	0.0	0	0.0
Clavicula	8	0	0.0	0	0.0	0	0.0	0	0.0	2	25.0	0	0.0	0	0.0	0	0.0
Scapula	11	0	0.0	0	0.0	0	0.0	0	0.0	4	36.4	0	0.0	2	18.2	1	9.1
Humerus	23	0	0.0	0	0.0	0	0.0	1	4.3	5	21.7	2	8.7	0	0.0	1	4.3
Radius	13	1	7.7	0	0.0	1	7.7	0	0.0	7	53.8	1	7.7	2	15.4	0	0.0
Ulna	29	2	6.9	2	6.9	1	3.4	5	17.2	3	10.3	4	13.8	1	3.4	3	10.3
Metacarpus	13	0	0.0	0	0.0	0	0.0	0	0.0	1	7.7	0	0.0	1	7.7	0	0.0
Pelvis	36	0	0.0	0	0.0	2	5.6	1	2.8	4	11.1	1	2.8	6	16.7	0	0.0
Femur	29	1	3.4	1	3.4	2	6.9	4	13.8	1	3.4	4	13.8	4	13.8	5	17.2
Tibia	31	1	3.2	1	3.2	0	0.0	2	6.5	2	6.5	3	9.7	2	6.5	7	22.6
Fibula	2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Calcaneus	3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Astragalus	2	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Metatarsus	13	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Phalanx	13	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0	1	7.7	0	0.0
Total	411	5	1.2	5	1.2	8	1.9	14	3.4	41	10.0	17	4.1	28	6.8	26	**6.3**

between the front (AN/PO% = 38.2%) and hind limbs (Z/E% = 40%). Slightly less balanced proportions can be noted in the ratios between the cranial (PCTR/CR% = 28.5%) and postcranial regions (PCRAP/CR% = 30.3%), suggesting a decrease in autopodial elements as well as the vertebrae. A very low anatomical index of AUT/ZE%, representing the ratio between the autopodial and long bones, of only 4.8% suggests the absence of paws, corresponding to the results of the analysis by NANNINI et al. (2022), AUT/ZE% = 6.5%. However, the PCRLB/CR% ratio, in which paws are excluded,

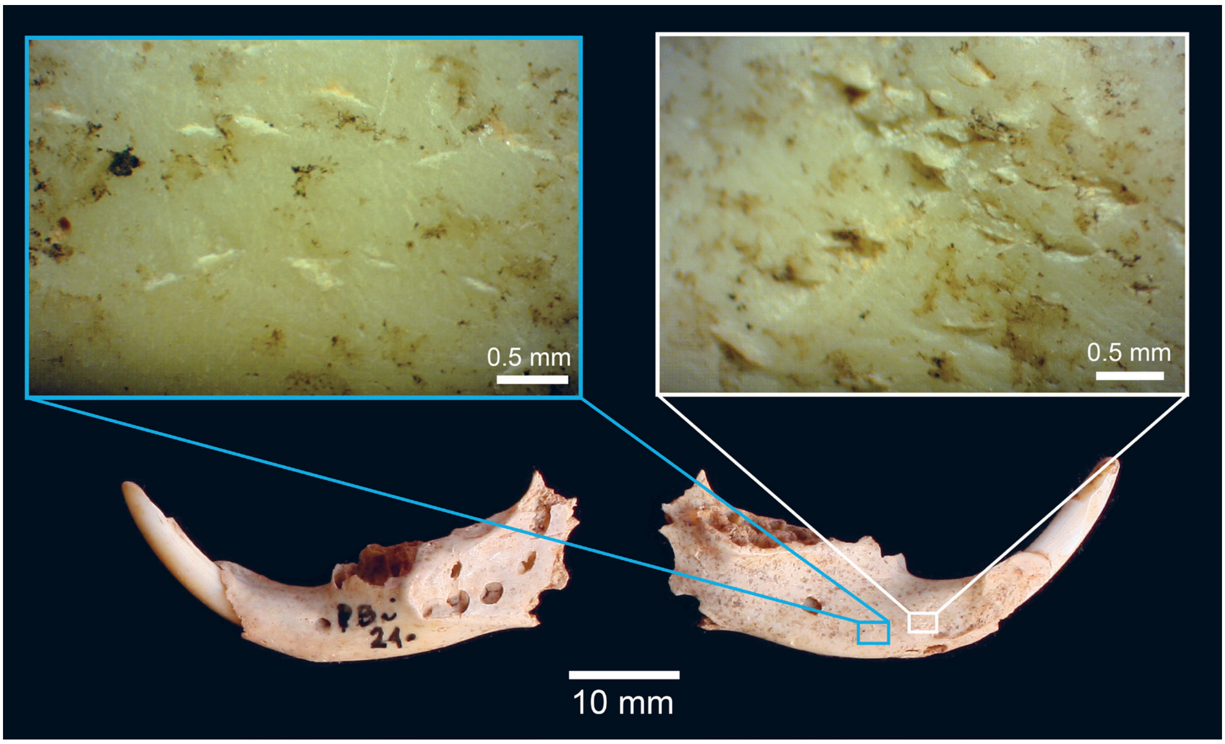

Figure 4. Specimen PBi 21 – left mandible of alpine marmot, lateral and medial views, showing small carnivore (fox) tooth marks, and delicate tooth marks (blue and white squares) of an unknown small animal, possibly from a fox cub.

is on the other hand, showing the highest value of 72.4%. Considering all the ratios, it can be concluded that the high proportion of almost complete skeletons is indicative of complete marmots whether they lived and died *in situ* or were transported into the East Cave by predators. Another correlation with the study of NANNINI et al. (2022) can be made in the low percentages of vertebrae and ribs. However, in the current study, the main reason for this is suggested to be the sampling method, since samples were collected in the 1960's, when the focus was on larger fauna. Additionally, the absence of paw and tail elements (Fig. 3) might also be related to the same reason, caused by inadequate sampling. As noted before, the indices of relative abundances could be correlated with NANNINI et al. (2022), as well as therein mentioned references, all focusing on the Late Glacial anthropogenic accumulations, but also reporting the presence of complete skeletal remains.

It should be noted that the majority of bones from the East Cave are well preserved with only minimal signs of weathering, which can be due to the alkaline environment of the carbonate bedrock but also a taphonomic (collection) bias. It is also evident that a large part of the sample consists of juvenile (and very juvenile) marmot bones, which show no signs of predation and/or only minimal weathering. Since marmot burrows were found in the East Cave (Fig. 2c; MALEZ, 1963a), this could indicate that these juvenile individuals died from natural causes, most likely during their first hibernation when they are in their most vulnerable life stage because of lower body weight and body fat percentage (MANN et al., 1993). Considering that adult individuals leave the natal colony upon reaching sexual maturity (KRYŠTUFEK, 1991), it can be concluded that, over the years, multiple generations of alpine marmot colonies chose the Brina Caves as their habitat.

4.2. Animal Traces

The gnawing and bite marks from small carnivores such as martens and foxes are the most dominant taphonomic traces of animal origin (14.1%) within the studied samples (Fig. 6). Since excellent impressions of nearly complete predator bites have been preserved on certain specimens (PBi 21, PBi 100; Fig. 4, Pl. 1), a comparison with jaws from the recent comparative collection allowed for the precise identification of the predators as martens and foxes (Pl. 1). Although their bones were not found in the Brina Caves, according to MALEZ (1979) both species lived in the area during the Upper Pleistocene. Predator bite marks were also found on the lower jaws of juvenile individuals, whose permanent teeth had just begun to emerge, indicating that marmot pups, only a few months old, served as easy prey for predators. In the Sciuridae family (squirrels), permanent teeth typically emerge at around 3–4 months of age (CARDINI & THORINGTON, 2006), which would mean that predators hunted marmot pups in late summer or early autumn. During this period, as they prepare for hibernation, adult marmots have their highest body weight and fat content, making it logical that they, too, were more frequently preyed upon during this time.

4.3. Anthropogenic Traces

One of the premises of this study was an attempt to find evidence of human hunting of marmots, considering that the Upper Pleistocene hunters from the area, and similar sites in Montenegro, such as Vrbička and Crvena stijena, have been documented (BORIĆ et al., 2014; MIHAILOVIĆ, 2017). Large hunting camps specialized in hunting alpine marmots have also been documented in northern Italy (NANNINI et al., 2022; ROMANDINI et al., 2012, 2018). Although a complete taphonomic analysis of alpine marmot bones in Croatia is still

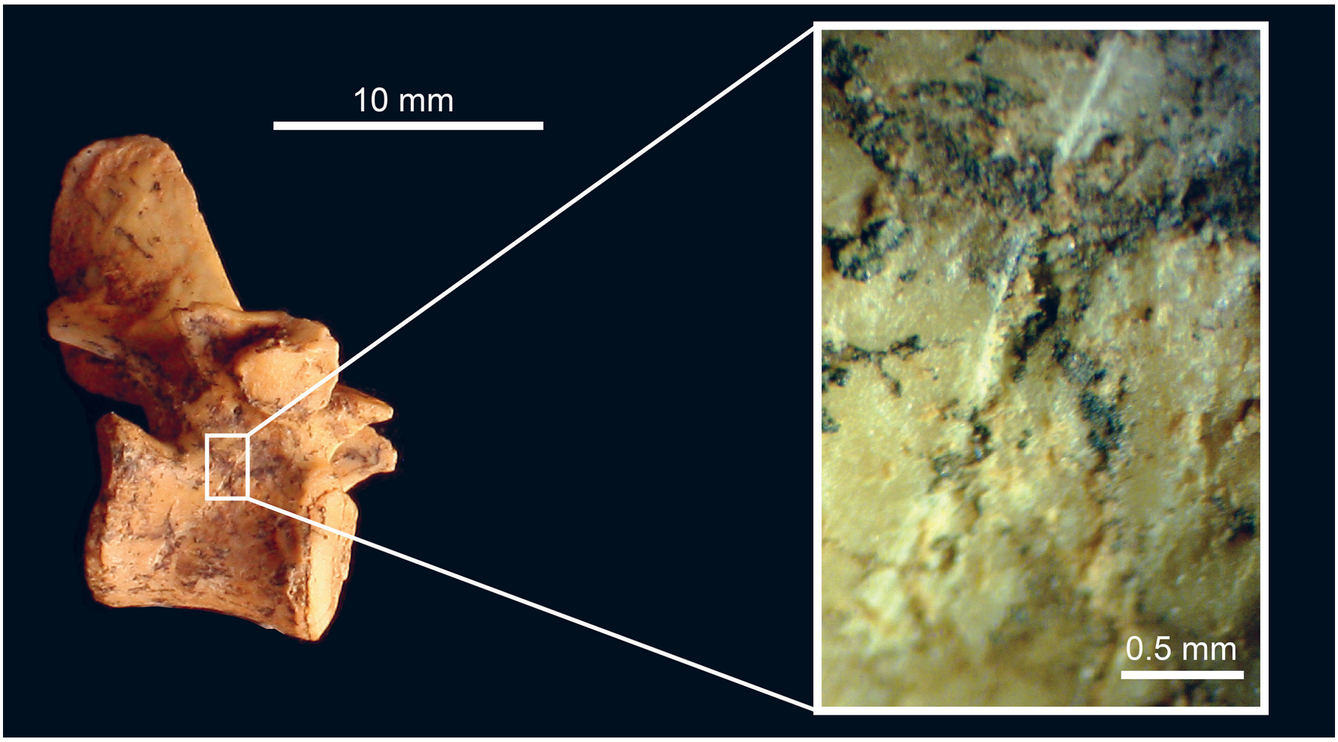

Figure 5. Specimen PBi 278 – thoracic vertebra showing fine line fractures, erosion, black staining and cut marks (white square).

missing, MIRACLE (2007) mentions a single alpine marmot bone with a cut mark in his monograph on the Hušnjakovo Neandertal site near Krapina.

In the samples studied, five bones have been definitively identified as bearing cut marks, with an additional five potentially exhibiting similar marks (Table 5). However, a challenge in identifying these marks arises from the preservation of the Brina Cave bones in a light colour, as any potential cut marks also appear in a similar light, white shade. Such cut marks were previously considered to be a product of recent manipulation by excavators or curation and were not considered in taphonomic analysis. Nonetheless, recent forensic research (MARIN-MONFORT et al., 2018) has proven that there is no difference in colour between recent and fossil traces on bones. Therefore, some of the incisions, which would otherwise be considered recent, were identified as fossil markings (Fig. 5).

For the five samples with potential cut marks, it could not be determined with certainty whether their characteristics can be classified as incisions, and further detailed research is necessary. When considering the number of specimens with (potential) anthropogenic manipulation, only 2.4% of the bones in the sample bear cut marks. This is four times fewer

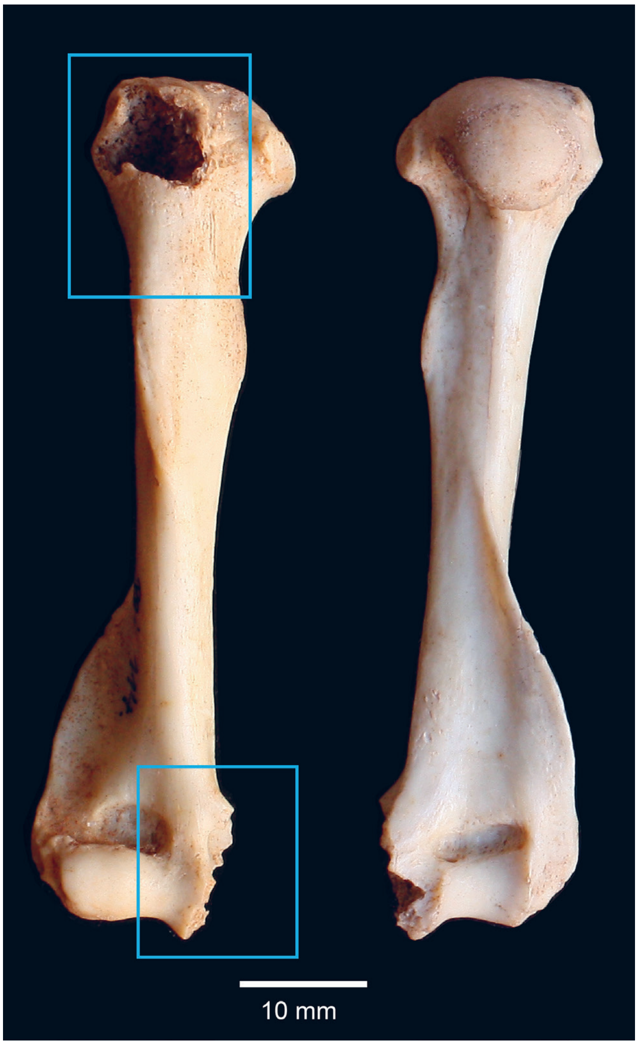

Figure 6. Specimen PBi 114 – right humerus, cranial and caudal view, with small carnivore gnaw marks (blue squares).

than at the Grotte di Pradis site, where a specialized camp for hunting alpine marmots was found in northern Italy (NANNINI et al., 2022).

Burning on eight remains was labeled as potential, as the only criterion by which burning could be determined was the colour of the bones (MARQUES et al., 2018). However, the bones could have also acquired such a colour from the sediment in which they were found since the sediment from layer c, where the majority of the marmot bones were found, was brownish clay (MALEZ, 1963b, 1975), and therefore burning could not be confirmed with certainty. If all samples with potential burning were considered to have been charred, they would make up 1.9% of the bone samples, which is about three times fewer than in Grotte di Pradis (NANNINI et al., 2022).

After the loss of plains during the Late Glacial interstadial warming, humans seasonally exploited high-altitude ecosystems (NANNINI et al., 2022, and references therein). In the Italian pre-Alps, humans exploited and consumed marmots in large numbers; moreover, some sites were specialized camps for marmot exploitation. When comparing the marmot assemblage from Grotta di Pradis (NANNINI et al., 2022) to that of East Brina Cave, excellent bone preservation can be noted at both sites, with no evidence of digested bone and a nearly identical representation of anatomical elements. However, there are striking differences in animal and anthropogenic traces: while anthropogenic modifications, such as cut marks, dominate at Pradis and animal traces are rare, small carnivore gnawing marks are prevalent at East Brina. In both caves, tooth marks correspond to fox and marten tooth-rows. Additionally, in Pradis, adult remains are more prevalent, whereas in Brina, juvenile remains dominate. This difference also suggests distinct accumulation agents: humans in Pradis and carnivores in Brina.

5. CONCLUSIONS

The discovery of numerous skeletal remains of alpine marmots in the East Brina Cave near Drniš provides significant insights into the palaeoecology and taphonomic processes of this species during the Late Pleistocene. A total of 356 bone remains (including mandibles with teeth) and 55 isolated teeth, making up a total of 411 skeletal fragments, were found in the East Cave, representing the highest occurrence of alpine marmot skeletal remains in Dalmatia. These finds suggest that the caves were used either as active burrowing sites or as accumulation areas resulting from predation and natural mortality.

Taphonomic analysis reveals that the preservation and representation of skeletal elements were influenced by a combination of factors, including bone density, collection bias, and environmental conditions. While natural death was the primary cause of bone accumulation, secondary agents such as small carnivores, particularly martens and foxes, played a significant role in modifying the sample. Predation patterns indicate that marmots, especially juvenile individuals, were targeted by predators, primarily during the autumn when they are at their maximum weight, shortly before entering hibernation.

The presence of cut-marked bones provides important, albeit limited, evidence of occasional human interaction with marmots in the region. While the frequency of anthropogenic modifications is lower than at specialized hunting sites in northern Italy, the fossil remains contribute to the broader understanding of Palaeolithic subsistence strategies in southeastern Europe. Although the extent of human exploitation remains uncertain, the combination of natural accumulation, carnivore activity, and occasional human intervention suggests a complex interplay of ecological and cultural factors shaping the entire sample of the Brina Caves.

Further research, including detailed microscopic and geochemical analyses such as environmental SEM analyses of cut marks and EDS analyses of mineral staining and coatings, may help clarify the role of humans in the accumulation of these remains and refine taphonomic interpretations. By integrating these finds with regional studies, the Brina Caves offer valuable data for reconstructing the Pleistocene ecosystems and understanding the dynamic interactions between humans, animals, and their environments in southeastern Europe.

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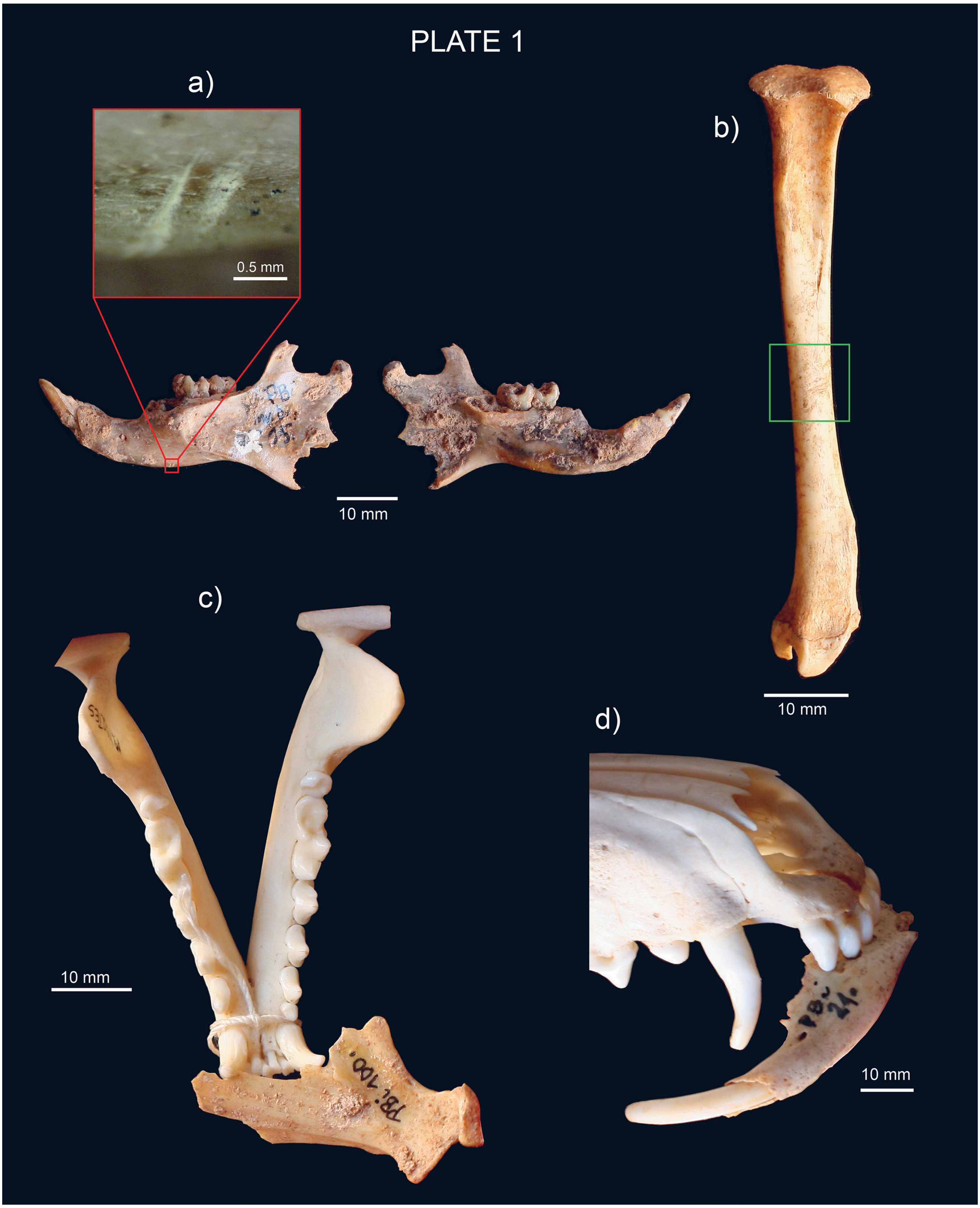

Plate 1. a) Pbi 15 – left mandible, lateral and medial views showing fine line fractures, spalling, rodent tooth marks (red square), mineral coating and black staining; **b)** PBi 221 – left tibia, caudal view, with four cut marks (green square); **c)** PBi 100 – left scapula of an alpine marmot with crenulated edge of the scapula blade and two (puncture) tooth marks that correspond to the lower canines of marten from the recent reference collection; **d)** PBi 21 – left mandible of an alpine marmot with tooth marks that correspond to the upper incisors of fox from the recent reference collection.

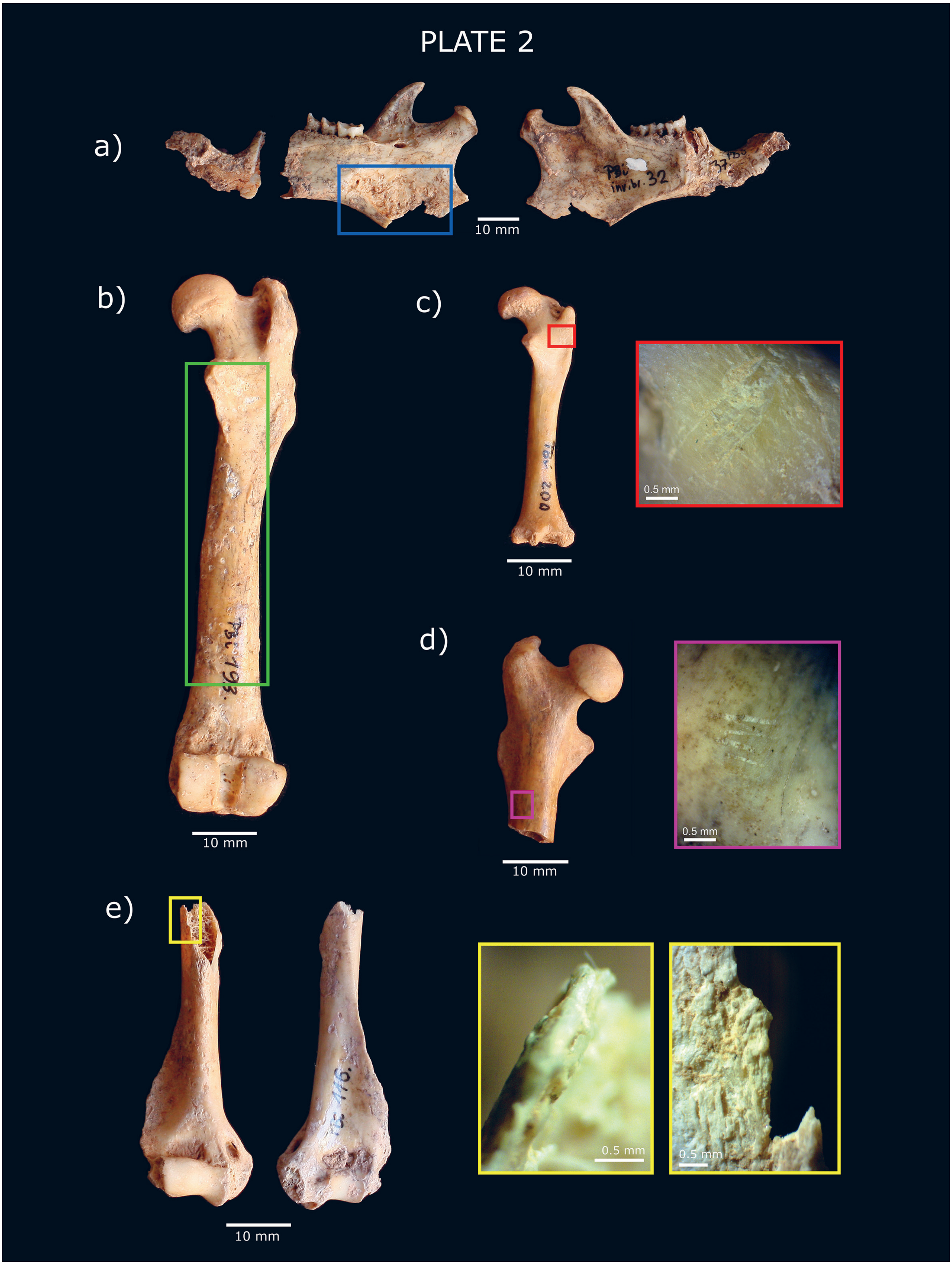

Plate 2. a) Pbi 32 and Pbi 37 – right mandible, medial and lateral views showing bacterial corrosion (blue square) and light-colored mineral coating; **b)** Pbi 193 – right femur, caudal view showing bacterial corrosion (pitting, green square); **c)** Pbi 200 – right juvenile femur, caudal view showing small animal scratching (red square); **d)** Pbi 198 – right femur, cranial view showing small animal scratching (violet square); **e)** Pbi 116 – right humerus, cranial and caudal views showing soil corrosion (yellow squares).