



LATE NEANDERTHAL SUBSISTENCE AT SAN BERNARDINO CAVE (BERICI HILLS - NORTHEASTERN ITALY) INFERRED FROM ZOOARCHAEOLOGICAL DATA.

Gabriele Terlato^{1,2}, Valentina Lubrano², Matteo Romandini^{2,3}, Ana B. Marín-Arroyo^{1,4},
Stefano Benazzi^{3,5}, Marco Peresani^{2,6,7*}

¹ Grupo de I+D+i EVOADAPTA, Dpto. Ciencias Históricas, Universidad de Cantabria, Spain.

² Dipartimento degli Studi Umanistici, Sezione di Scienze Preistoriche e Antropologiche, Università degli Studi di Ferrara, Italy.

³ Dipartimento di Beni Culturali, Università di Bologna, Italy

⁴ Department of Archaeology, University of Cambridge, UK

⁵ Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Germany.

⁶ Istituto di Geologia Ambientale e Geoingegneria, CNR, Italy.

⁷ Accademia Olimpica, Vicenza, Italy.

Corresponding author: M. Peresani <marco.peresani@unife.it>

ABSTRACT: North-eastern Italy is a key region for the study of Neanderthal way of life over a wide timeframe, as attested by over 20 Middle Palaeolithic multi-layered sites in caves, rock shelters and at open-air sites. Here we contribute to increase our understanding of Neanderthal subsistence strategies through the study of the faunal assemblage of Unit II dated to the first half of Marine Isotopic Stage 3 (MIS3), from San Bernardino Cave. The site is located in the Berici Hills, at low altitude near the edge of a karstic plateau dissected by valleys and delimited by the alluvial lowland. Zooarchaeological and taphonomic analyses suggest that Neanderthal groups were the primary agent for the accumulation of mammal remains, and that hunting mainly focused on ungulates, such as *Cervus elaphus* and *Capreolus capreolus*. Forested environment sustained by mild climatic conditions is also inferred by micromammals evidence. Our data suggest a selective transport of the prey - even for the roe deer - which might have implied a long distance transportation from the site. Also, it might have been related to the age of the prey or to multiple preys hunted in a single episode. The Bayesian method applied to the analysis of skeletal profiles shows a high level of attrition at the site and a greater degree of processing appendicular skeleton. Neanderthals used San Bernardino Cave as a place where carcasses processing was finalized, after an initial process at the kill-site, and then prepared for consumption. Also, discarded bones were used for lithic manufacturing. The San Bernardino evidence can be compared with productive systems for exploiting available ungulate game from other regional-scale MIS 3 Middle Palaeolithic sites.

Keywords: Neanderthal subsistence, Middle Paleolithic, MIS 3, Northeastern Italy, Zooarchaeology.

1. INTRODUCTION

One of the main issues to fully understand how Neanderthals were able to survive for more than 250,000 years across Eurasia is the reconstruction of their diet and subsistence strategies. Studying the fauna remains helps to determine anthropogenic behaviour and to accurately understand the subsistence and adaptation patterns used to exploit different ecological niches (Stiner, 1994; Bocherens, 2009; Ready, 2010; Gaudzinski-Windheuser & Roebroeks, 2011; Morin et al., 2016; Jaouen et al., 2019). However, subsistence behaviour presents specific differences and adaptations between geographical areas and sites, highlighting the importance of the availability and richness of nearby biotopes as much as the functionality of the settlements. Zooarchaeological evidence attests, for example, the exploitation of small game, birds, and aquatic resources (Brown et al., 2011; Cortés-Sánchez et al., 2011; Blasco & Fernández Peris, 2012; Cochard et al., 2012; Blasco

et al., 2013; Fiore et al., 2016; Gómez-Olivencia et al., 2018; Nabais, 2018; Morin et al., 2019; Marín et al., 2019; Zilhão et al., 2020; Guillaud et al., 2021 among others), alongside with the predation and consumption of bears (Romandini et al., 2018a). Despite this broad diet spectrum, the Neanderthals' main animal protein sources were medium and large-sized herbivores. In general, in late Middle Paleolithic contexts, undisputable records had proven how Neanderthals targeted, butchered and consumed a wide variety of ungulates (Patou-Mathis, 2000; Fiore et al., 2004; Costamagno et al., 2006; Rendu, 2010; Rosell et al., 2012; Ready, 2013; Salazar-García et al., 2013; Yravedra & Cobo-Sánchez, 2015; Sanz et al., 2019).

Such scenario does not exclude continental and peninsular Italy, where, in recent years, new information about late Neanderthal groups' subsistence behaviour and mobility has been acquired (Boscato et al., 2011; Peresani, 2011; Romandini et al., 2014, 2018a, 2018b, 2020a; Fiore et al., 2016; Boscato, 2017; Holt et al.,

2019; Moroni et al., 2019; Terlato et al., 2019; Spagnolo et al., 2020; Peretto et al., 2020), thus providing more data on these issues. Notably, in the North of Italy archaeologists uncovered a considerable number of rock shelters and caves yielding evidence of human occupation during Middle and Late Pleistocene (Peresani, 2011; Margaritora et al., 2020). These sites are settled within the ecological corridor bounded by the Apennine, Alpine and Dalmatian mountain ranges and the Adriatic Sea. Such a peculiar geographic location is crucial for the understanding of regional differences in mammals' acquisition and exploitation by Neanderthals. Despite the abundance of archaeological sites, only few of them yielded animal bones. Moreover, not all of them have been analysed with a consistent zooarchaeological approach to assess everywhere the taphonomy, mortality patterns, skeletal profiles, carcass transport, carnivore activities, and so on (Fiore et al., 2004; Miracle, 2005; Thun-Hohenstein, 2006; Romandini et al., 2014, 2018a, b, 2020a; Thun-Hohenstein et al., 2018; Terlato et al., 2019). This lack of data limits analytical comparisons of Neanderthal strategies at a regional and at a larger scale. Thus, within such a discontinued and fragmented framework, new zooarchaeological studies are crucial to provide new data on Neanderthal groups' subsistence.

To further contribute to the diet and subsistence patterns achieved by Neanderthals in southern Alps foreland during late MIS3, we present the analysis of the faunal assemblage of Unit II of San Bernardino cave. This cave was excavated during 1960 and 1986-95 and displayed a cultural sequence rich in lithic implements and faunal remains. We have focused on taxonomical representation, prey selection, skeletal part representations and carcass processing in order to define the site functionality and to compare it with other sites from the regional context.

2. SAN BERNARDINO CAVE IN THE MIS 3 LANDSCAPE

2.1. The subalpine area of the southeastern Alps: physical and ecological setting

San Bernardino Cave lies in the foreland of the eastern Italian Alps. This mountain range represents a physical and environmental threshold where ice fields and alpine glaciers developed during cold stages of the Middle and Late Pleistocene, and where temperate vegetation restored during warm phases. The Alpine foreland is a vast alluvial plain originated since the Middle Pleistocene from the Po and Adige rivers, other minor waterways, and the ones of the Friulian-Venetian Plain (Fontana et al., 2014). Concerning this latter, the area also includes hills of different geological origins, like the Berici Hills and the cone-shaped volcanic reliefs of the Euganean Hills, which were separated by the spreading outwash of the plain. The Berici Hills are a karstic plateau with a maximum altitude of 440 m a.s.l., a honeycomb of sinkholes and depressions shaping an extremely uneven topography, scattered by rock peaks and blocks affected by surface dissolution. The plateau is dissected by depressed systems (e.g., the Fimon, Liona, and Calto valleys) characterised by pocket-valleys where ephemeral streams produced swampy

environments and fed historic mills. The slopes are steep all around. To the east, a steep slope with rock cliffs connects the plateau to the alluvial lowlands that were occupied by marshes and swamps during the Pleistocene and most of the Holocene (Monegato et al., 2011). To the west, the plateau gradually connects to the plain.

Ecological conditions during the first half of MIS3 recorded the presence of open birch-conifer forests, xerophytic scrubs and steppe. Episodes of conifer forests contraction and steppe communities expansion were documented, in alternation with mixed conifer (*Pinus* and *Picea*) - *Betula* forests (Pini et al., 2009, 2010) and with reduced warm-temperate component (*Tilia*) which however persisted up to ca. 40 ka (Pini et al., 2010; Badino et al., 2020). Rainfall and humid conditions in the southeastern Alpine foreland favored by the glaciated Alps have also been confirmed by micromammal assemblages in the Berici Hills at Broion Cave and San Bernardino Cave and in the Monti Lessini area at Fumane Cave (López-García et al., 2015, 2017, 2019).

2.2. San Bernardino Cave

San Bernardino Cave is situated on the eastern slope of the Berici at 135 m above sea-level, facing the alluvial plain of Bacchiglione river and the western side of the Euganean Hills (Fig. 1). Besides San Bernardino, other Middle Palaeolithic caves and shelters open in the same area: Broion Cave and Broion Rockshelter (Peresani et al., 2019; Romandini et al., 2020b), De Nadale Cave (Jéquier et al., 2015; Livraghi et al., 2021), Paina Cave (Bartolomei et al., 1987-88). San Bernardino Cave is 41 m long, 7 m wide and 9 m high and originated from the widening of deep, SE-NW oriented fractures produced by thermoclastic processes and chemical dissolution. The natural morphology of San Bernardino has been modified along time. The cave was used as a hermitage since Medieval times and settled by members of the Franciscan Order. During the Late Middle Ages - or even afterwards - prehistoric deposits were partly dismantled by the construction of a wall sealing the entrance of the cave, as also attested by a modern human tooth dated to 1420-1480 cal AD (Benazzi et al., 2014a). All along the Modern Age, the inner cavity was almost totally emptied from the quarrying of the infill. After the discovery of Pleistocene bones (Fabiani, 1902-03), the first phase of archaeological investigations was coordinated by P. Leonardi in the sixties in the medieval wall facing area. The excavations uncovered a Pleistocene sequence with faunal remains and lithic industries (Leonardi, 1958-1959; Leonardi & Broglio, 1960-1961). A second phase in the excavation was coordinated by A. Broglio and M. Peresani between 1986 and 1995, allowing to re-examine the stratigraphic series from the inner and the outer zones (Peresani, 1995-1996).

The deposit is a complex sedimentary body shaped like an elongated prism, extending from inside to partly outside the cave. It is a remnant of the lower part of the sediments that originally filled the cave. At present, the sedimentary sequence is 4.5 m thick and includes eight stratigraphic units with sub-horizontal bedding, which gradually bend outside the cave (Fig. 2). These record the succession of three main paleoclimatic

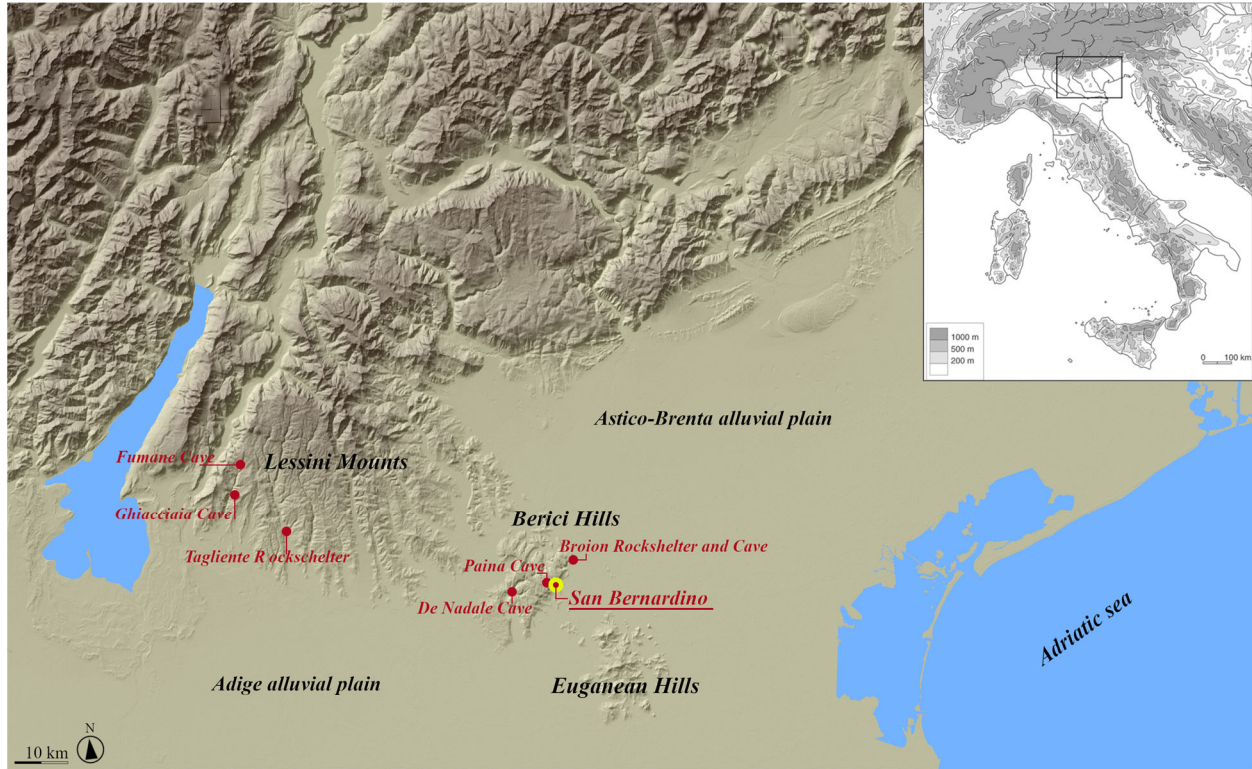


Fig. 1 - Geographical location of San Bernardino Cave in north-eastern Italy.

cycles shifting from temperate to dry/cold conditions: cycle 1 (MIS 7c/b - MIS 6, Units VIII to VII); cycle 2 (MIS 5d and b - MIS 4, Units V to IV) and cycle 3 (MIS 3 - MIS 2? Units III to I) (Cassoli & Tagliacozzo, 1994; López-García et al., 2017). U/Th and ESR dates range from the Middle/Late Pleistocene (Units VIII-VII, ca. 214 and 154 ka; Gruppioni, 2003; Picin et al., 2013) to the Late Pleistocene for Unit II: 52 ± 5 ka BP, 38 ± 5 ka BP and 33 ± 5 ka BP (Peresani, 2001). In addition to a first radiocarbon date at >40 ka BP produced in the Nineties (Peresani, 2001), two new dated bones, one of a *Bos/Bison* (SB42) and another one of a large Cervidae (*Alces/Megaloceros*) (SB918), both with anthropogenic marks from Unit II, yielded >48.6 ka BP (OxA-40121) and 45.9 ± 2900 ka BP (OxA-40203) (Tab. 1). Thus, they confirmed that the archaeological content is not younger than the first half of MIS 3. A OSL dating program is ongoing to support the chronological layout of the sedimentary sequence from Unit VIII up to Unit IV.

Unit II, the focus of this paper, is situated at the entrance of the cave and was totally excavated over an area of 20 sqm extending below the medieval wall as well. Unit II (Fig. 2) thickens up to 40 cm, it includes

different sublayers named 1, 2, 3, 4a, 4b and 4c, and it records an increase in the density of anthropogenic evidence - faunal remains, lithic artefacts, and hearths - in comparison with the underlying Units III, IV and V. A previous taxonomic study of the macromammal association (Cassoli & Tagliacozzo, 1994) showed the presence of a broad variety of mammal species such as roe deer, red deer, moose, wild boar and bovines (Terlato et al., 2019), while cave bear was the most abundant carnivore. Taphonomic analysis of a restricted sample of large ungulate bones, revealed traces of disarticulation, defleshing and the use of bone fragments as retouchers (Malerba & Giacobini, 1998).

Lithic industry in Unit II is featured by intensive exploitation of local and exogenous chert, responsible for reduction in size of cores, flakes and retouched tools. Flake-manufacture was based on the exclusive application of recurrent unidirectional and centripete Levallois modalities (Peresani, 1996; Porraz & Peresani, 2006). Moreover, although many tools were shaped at the cave, a significant number of them had been introduced at different stages of reduction. It has been hypothesized that such exploitation might be linked to long-term

ID	Square	Unit	Sub-unit	Species	Anatomical element	Anthropogenic marks	Sample nr	Age (^{14}C yr BP)	Yield	%Yeld	%C	$\delta 13\text{C}$	$\delta 15\text{N}$	C:N
SB42	526 a	II	4a	<i>Bos/Bison</i>	Femur	PM	OxA-40121	$>48,600$	2.89	0.6	44.7	-20.4	2	3.3
SB918	517a	II	4b	<i>Alces/Megaloceros</i>	Metatarsal	CM	OxA-40203	$45,900 \pm 2,900$	19.52	3.3	42.3	-20.2	4.7	3.2

Tab. 1 - New radiocarbon dates from Unit II of San Bernardino Cave. PM: percussion marks; CM: cut marks.

human occupations (Peresani, 1995-1996). Most of these artefacts were made of finely textured chert collected in the surroundings (1-5 km), together with chert of similar quality supplied from farther sources (15-20 km) in the Euganean Hills up to the central-western Monti Lessini (80 km) (Peresani, 1996). Levallois end- and by-products were shaped in a wide range variety of retouched tools, like simple, double and convergent scrapers, while transverse scrapers were made from cortical, centripetal Levallois flakes and other flakes (Peresani, 1995-1996). Denticulates and points sorted in different forms and sizes (Peresani, 1995-1996; Picin et al., 2010, 2013), in contrast, are rare. The attribution of Levallois technology and/or Mousterian tools to Late Neanderthals exploiting this region during MIS 3 is proven by the association with human remains from Fumane Cave (Benazzi et al., 2014b), Broion Rockshelter (Romandini et al., 2020b) and Tagliente Rockshelter (Arnaud et al., 2016).

3. MATERIALS AND METHODS

Our analysis concerned the bone assemblage from Unit II. The remains were recovered during fieldwork carried on in 1959-1964 (Bartolomei, 1960) and 1986-1995 (Broglio & Peresani, 1992), using a main grid of one square meter divided in nine smaller squares. Sediments were wet sieved through superimposed mesh from 5 to 0.5 mm. The faunal remains were systematically recovered in situ during the excavation process and after wet-sieving the sediments. Following Cassoli & Tagliacozzo's taxonomical study (1994) and a preliminary taphonomical observation (Malerba & Giacobini, 1998), a zooarchaeological re-examination of bovids remains and a first analysis of small mammal bones were performed by Terlato et al. (2019) and Romandini et al. (2018b) respectively. Each of these works used the same methodological approaches for taphonomy studies to evaluate the whole assemblage. Overall, 9,429 faunal remains were scrutinized for this analysis. The complete Alpine fauna reference collection of the Section of Prehistoric and Anthropological Science at University of Ferrara and Barone's (1976) reference were used for taxonomic identification and for anatomical nomenclature, respectively. In order to include in the study bones that could not be identified taxonomically by any diagnostic landmark, all the remains have been grouped into four weight sizes classes, based on the modification of the criteria proposed by Bunn (1986): (1) small-sized mammals weighing <20 kg (Lagomorphs, Rodents and small carnivores); (2) medium-sized animals weighing between 20 and 100 kg (i.e. Caprids, *Capreolus capreolus*, *Sus scrofa*, *Canis lupus*); (3) medium-large sized animals weighing between 100 and 300 kg (i.e. *Cervus elaphus*, *Ursidae*; *Panthera pardus*); (4) large animals weighing >300 kg (i.e. *Alces alces*, *Megaloceros giganteus*, large bovids).

The identified elements were quantified using the following measures: NR (Number of Remains); NISP (Number of Identified Specimens) (Grayson, 1984); MNE (Minimum Number of Elements) - has been counted considering side, body size and ontogeny (Klein &

Cruz-Urbe, 1984; Binford, 1984); MNI (Minimum Number of Individuals) (Klein & Cruz-Urbe, 1984; Grayson, 1984; Lyman, 1994) and MAU (Minimum Animal Units) (Binford, 1984). %MAU was calculated by dividing each MAU by the highest MAU value of the assemblage. A 100% representation of all body parts would infer the presence of complete animal bodies.

The assemblage diversity was then examined through the Inverse of Simpson's Index. This index measures both the richness (N-types) and evenness (proportionality) of the kind of prey characterizing the diet (Simpson, 1949). The lower the resultant value, the more the assemblage involved is dominated by a single taxon and a narrow diet (Magurran, 1988). For regional comparison of hunting preferences, correspondence analysis was employed.

To evaluate the prey transport strategies and the intensity of the subsequent attrition, bivariate correlations between %MAU and different indices (Binford, 1978; Metcalfe & Jones, 1988; Marín-Arroyo, 2009a; Morin & Ready, 2013) were applied: %MAU and MGUI (Modified General Utility Index - Binford, 1978), FUI (Food Utility Index - Metcalfe & Jones, 1988), CFUI (Corrected Food Utility Index - Morin & Ready 2013) to define strategies employed in the use or transport of animal carcass; %MAU and maximum bone density (Lam et al., 1999) to assess the influence of destructive processes in the faunal assemblage. In order to determine if the bone breakage patterns were the result of marrow extraction, correlations between %MAU and the Marrow Index (Binford, 1978) were calculated. In addition, %MAU of the high survival elements was correlated with the unsaturated marrow index (UMI) proposed by Morin (2007). Spearman's coefficient of correlation was used to test the quantitative validity of these correlations and to determine the level of statistical significance (p) thereof. Furthermore, to overcome the limitations of previous indices to evaluate the skeletal profiles and attrition at the site, a Bayesian approach was applied (Marín-Arroyo & Ocio, 2017). This method considers two parameters, alpha (α) and beta (β), that are active during the formation of the assemblage. The former, transport preference (α), can take any value between -1 (>axial contribution) and 1 (>appendicular contribution) based on butchering efficiency in skeletal elements. The latter, degree of attrition (β), which follows the definition established by Rogers (2000 a, b), and relates the survivorship of bone element to their maximum bone density. This method aims specifically to overcome the problem of equifinality in skeletal profile interpretations, analysing two factors simultaneously.

Animals' age at death was estimated on the basis of the time of eruption, the replacement of teeth, and the degree of dental wear, as well as the stage of the bone epiphyseal fusion. Habermehl (1961), Aitken (1974), Mariezkurrena (1983), Azorit et al (2002), D'Errico & Vanhaeren (2002) and Tomé and Vigne (2003) were used for calculating the age of *Cervus elaphus* and *Capreolus capreolus*. Once the age at death was determined, individuals were grouped into five age groups: I (Infant - animals with deciduous teeth), J (Juvenile - lightly worn deciduous teeth and erupted M1); subAd (sub-Adult - animals with moderately worn deciduous

teeth and erupted M2); Ad (Adult - all erupted permanent teeth with any or moderate wear); S (old Adult or Senile - very advanced wear on most of the crown). The type of cortical tissue (compact in adults or more porous in young animals) was also used on the isolated diaphysis fragments.

To determine the effects of biostratigraphical (both hominins and carnivores) and postdepositional processes, breakage type and surface modification were treated at both macroscopic and microscopic level. When necessary, microscopic analyses of bone surfaces were carried out using a Leica S6D Greenough stereomicroscope with 0.75-70X magnification range, also employed for capturing images.

For each faunal remain, we systematically recorded the different taphonomic alterations, including those made by rodents, carnivores or hominins, as well as climatic and edaphic modifications (water abrasion, concretion, root marking, trampling, chemical corrosion and manganese oxide coating. For the purpose of identifying these main taphonomical modifications we used the criteria established by Behrensmeyer (1978), Binford (1981), Lyman (1994), Blumenshine et al. (1996), Fernández-Jalvo & Andrews (2003, 2016) (among others). Trampling marks were distinguished from butchering marks using the works of Blasco et al. (2008) and Domínguez-Rodrigo et al. (2009). Evidence of anthropogenic modification observed on the faunal remains includes cut-marks, intentional bone breakage and burning. Cut-marks have been recognised and grouped into incisions and scraping marks (Binford, 1981; Potts & Shipman, 1981; Shipman, 1981; Shipman & Rose, 1984; Lyman, 2008; Galán et al., 2009; Vettese, 2014). The analysis of cut-marks took into account the number of striations, their location and distribution (isolated, clustered, crossed) and orientation (longitudinal, transverse and oblique) on the bone. By using these cut-marks criteria, it was possible to interpret the specific butchering activities (Binford, 1981; Fisher, 1995; Nilssen, 2000). The causes of fractures were investigated analysing the type and the angle of fracturing (fresh-green or old-dry) (Villa & Mahieu, 1991) together with structural and surface damage, such as percussion notches, pits, impact flakes and adhering flakes (Blumenshine & Selvaggio, 1988; Capaldo & Blumenshine, 1994; Pickering & Egeland, 2006; Galán et al., 2009; Pickering et al., 2013; Vettese

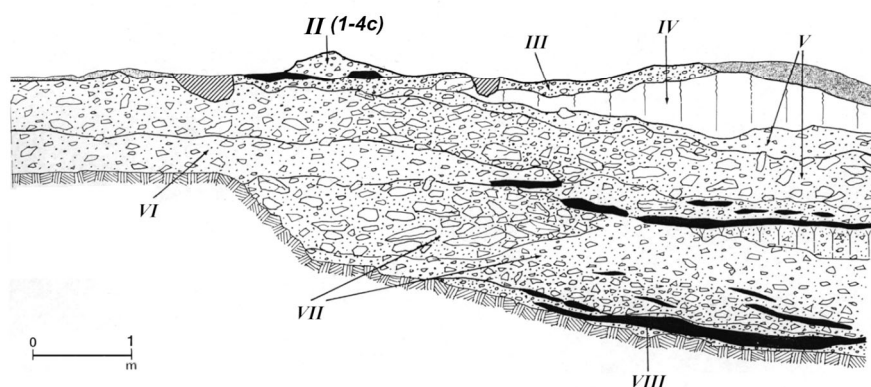
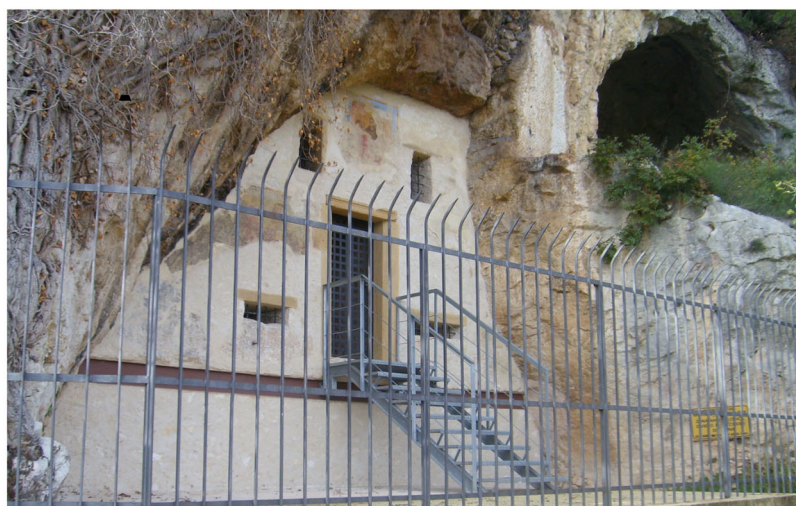


Fig. 2 - Above: today's entrance of the cave after the restoration. Below: Stratigraphic section. Unit II visible on the section is a remnant of the layer extended over the cave entrance and completely excavated during the 1959-1964 and 1985-1993 fieldworks.

et al., 2017, 2020). Impact flakes have been defined and distinguished by those made by carnivores (Coil et al., 2020) according to diagnostic characteristics: ventral face with point of detachments and bulb; greater breadth than length; absence or reducing of cortical surface. Burnt damages were recorded in terms of presence/absence (naked eye) and into three colour stages (Stiner et al., 1995): mainly brown (lightly burnt), black (carbonized), grey to white (calcinated). Carnivore marks were classified as follows: pits, scores, punctures, furrowing, gnawing and corrosion of gastric acid (Fisher, 1995; Domínguez-Rodrigo & Piqueras, 2003; Domínguez-Rodrigo & Barba, 2006). Finally, the study of bone retouchers was carried out following Mallye et al. (2012) and Mozota Holgueras (2012).

4. RESULTS

4.1. Bone assemblage

The analyzed assemblage consists of 9,421 remains of mammals, three of fish and five of birds, which correspond to 52 different individuals and 22 taxonomic

<i>Taxa</i>	NR	NISP	MNI	MNI by age				
				I	J	subAd	Ad	S
<i>Stephanorinus</i> sp.	1	1	1				1	
Cfr. <i>Rhinoceros</i>	1	1	1		1			
<i>Bos primigenius</i>	1	1	1				1	
<i>Bos/Bison</i> sp.	31	31						
<i>Megaloceros giganteus</i>	9	9	2				2	
<i>Alces alces</i>	19	19	3				3	
<i>Cervus elaphus</i>	143	143	5				4	1
<i>Capreolus capreolus</i>	253	253	9		2	1	4	2
Cervidae medium/large size	132	132						
<i>Capra ibex</i>	3	3	1				1	
<i>Rupicapra rupicapra</i>	54	54	3		1		2	
Caprinae indet.	8	8						
<i>Sus scrofa</i>	38	38	4		1	1	1	1
Ungulata indet.	517	517						
Total Ungulata	1210	1210	30		5	2	19	4
<i>Ursus arctos</i>	3	3	1				1	
<i>Ursus spelaeus</i>	101	101	6	1	1	1	1	2
<i>Ursus</i> sp.	100	100						
<i>Canis lupus</i>	3	3	1				1	
<i>Vulpes vulpes</i>	9	9	1				1	
<i>Felis silvestris</i>	3	3	2				2	
<i>Lynx lynx</i>	5	5	2		1		1	
<i>Panthera pardus</i>	1	1	1		1			
<i>Mustela putorius</i>	2	2	1				1	
<i>Martes</i> sp.	1	1						
Carnivora indet.	7	7						
Total Carnivora	235	235	15	1	3	1	8	2
<i>Lepus</i> sp.	3	3	1				1	
<i>Marmota marmota</i>	18	18	2		1		1	
<i>Castor fiber</i>	29	29	4		2		2	
Total Lagomorpha and Rodentia	50	50	7		3		4	
Birds	5	5						
Fishes	3	3						
Mammal small size	48							
Mammal medium size	1937							
Mammal medium-large size	699							
Mammal large size	212							
Mammal indet. size	5030							
Total	9429	1503	52	1	11	3	31	6

Tab. 2 - Total Number of skeletal Remains (NR), Number of Identified Specimens (NISP) and Minimum Number of Individual (MNI) found in San Bernardino II.

	NR	CM	PM	CM+PM	%BM	Ret.	B	C	Car.
Cfr. Rhinoceros	1						1		
<i>Bos/Bison</i> sp.	31	5	3		25.8	3	2	1	
<i>Megaloceros giganteus</i>	9	2		1	33.3		3		1
<i>Alces alces</i>	19			1			1		2
<i>Cervus elaphus</i>	143	12	5	5	15.3	1	32	2	1
<i>Capreolus capreolus</i>	253	8	2	1	4.5		86	3	3
Cervidae medium large/size	132	10		1	8.3	6	19		1
<i>Capra ibex</i>	3						1		
<i>Rupicapra rupicapra</i>	54	2			3.7		14		5
Caprinae indet	9						3		
<i>Sus scrofa</i>	38	1					4	1	2
Ungulata indet.	517	17	31	3	9.8		128	7	6
<i>Ursus spelaeus</i>	101	2	1		2.9		6		11
<i>Ursus</i> sp.	100			1			4		2
<i>Panthera pardus</i>	1								1
<i>Marmota marmota</i>	18								3
<i>Castor fiber</i>	29	3			10.3		4	1	1
<i>Lepus</i> sp.	3							1	
NISP	1503	62	42	13	7.8	10	308	16	39
Mammals small size	48	2	1		6.2		31	5	
Mammal medium size	1937	5	13		0.9		1170	179	3
Mammal medium-large size	699	2	6		1.1	1	292	8	10
Mammal large size	212	9	5	3	8		31	4	6
Mammal indet. size	5030	1				1	2933	470	
Total	9429	81	67	16	1.7	12	4765	682	58

Tab. 3 - Number of mammals remains showing butchering marks, thermal-alterations and carnivore marks. CM: cut-marks; PM: percussion marks; CM+PM: cut-marks + percussion marks; % BM: % butchering marks; Ret.: retouchers; B: burned-black/brown bones; C: calcined-grey/white bones; Car.: carnivore marks.

groups (Tab. 2). Among them, 15.9% were identified anatomically and taxonomically. 84.1% were determined as generic mammals and sorted into weight size classes (Tab. 2). A considerable amount of remains (NR=5,030, 53.3%) results to be indeterminate anatomically, taxonomically and by weight size class.

Five mammal Orders including Perissodactyla, Artiodactyla, Carnivora, Lagomorpha, Rodentia have been identified. Ungulates (80.5% of NISP) are the most numerous one, represented by *Stephanorinus* sp., *Megaloceros giganteus*, *Alces alces*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, *Capra ibex*, *Rupicapra rupicapra* and *Sus scrofa*. Carnivores remains (NISP=235, 15.6%) correspond to *Ursus arctos*, *Ursus spelaeus*, *Canis lupus*, *Vulpes vulpes*, *Panthera pardus*, *Lynx lynx*, *Felis silvestris*, *Mustela putorius*, *Martes* sp. Lagomorphs and rodents (NISP=50, 3.3%) are repre-

sented by *Lepus* sp., *Marmota marmota* and *Castor fiber* (Tab. 2). These data confirm previous results obtained by Cassoli & Tagliacozzo (1994). Due to the high fragmentation and the massive presence of diaphysis, it was challenging to precisely distinguish amongst the genera *Bos* and *Bison* and the species *Alces alces* and *Megaloceros giganteus*. For this reason, most of the remains were generically assigned to the category *Bos/Bison* sp. and in a broad group of medium/large Cervidae, which is also the case for many other contemporaneous sites. According to the NISP and MNI data, the faunal assemblage is clearly dominated by cervids with *Capreolus capreolus* and *Cervus elaphus* as the most representative. Since the roe deer represents most of the identified remains (NISP=253), it is not surprising that non identifiable bone remains assigned to medium sized animals are also the most abundant (NR=1,937, 20.5%) (Tab. 2).

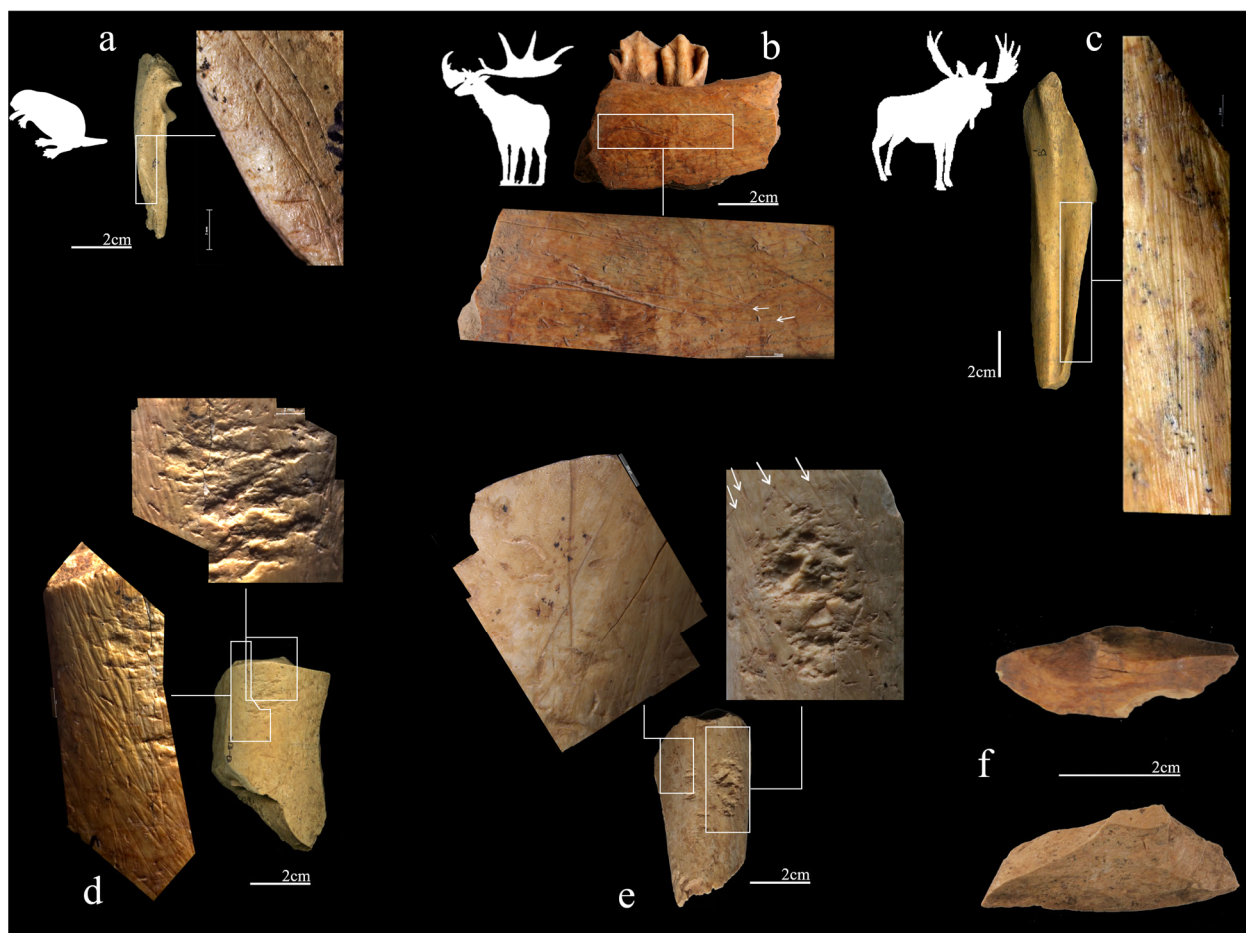


Fig. 3 - Position and details of anthropogenic traces: (a) right ulna of *Castor fiber* with skinning marks; (b) right mandible of *Megaloceros giganteus* with cut-marks on the medial side; (c) metatarsal of *Alces alces* with scraping marks; (d and e) femur diaphysis of cervids with scraping marks and close-up of the area used as a retoucher; (f) isolated flakes produced by percussion activity.

The estimation of the age at death of the ungulates indicates a predominance of adult individuals (MNI=19, 63.3%), followed by juveniles (MNI=5, 16.6%) and old individuals (MNI=4, 13.3%) (Tab. 2). Based on the analysis of dental eruption and replacement sequences, it was possible to estimate the season of death of young individuals; no foetal remains were preserved. This involves two roe deer and one wild boar. For *Capreolus capreolus* one germin of M2 (erupt around 6-8 months - Habermehl, 1961) allows us to define the season of death during the end of autumn. On the other hand, two decidual premolar (one dp_3 and one dp_2) with marked wear attest that one individual died in spring. In the same way, seasonality indicates that the wild boar died in autumn.

We identified a variety of species among the carnivore remains (Tab. 2). Ursids are the most abundant, while *Ursus spelaeus* (NISP=101) is better represented than *Ursus arctos* (NISP=3). For a total of 100 remains (*Ursus* sp.), mostly fragments of isolated teeth and extremities of limb bones, it was not possible to precisely ascribe their taxonomy to either *Ursus arctos* or *Ursus spelaeus*. Cave bear is represented with at least one

individual for each age range, from infant to senile (Tab. 2).

Data concerning the sex identification of animal remains are scarce, due to the high fragmentation that limited the presence of sexual diagnostic elements and the acquisition of characteristic biometric data. Despite a general lack of diagnostic skeletal part, a few observations can be made. The presence of two antler fragments of roe deer suggests at least that one male is present in the assemblage. We applied the criteria proposed by d'Errico & Vanhaeren (2002) to three upper canines of *Cervus elaphus* to distinguish the age and sex. However, due to the high fragmentation of remains it was not possible to determine the sex. Finally, the presence of a bear's *baculum* shows that one male individual is present.

4.2. General taphonomic observations

Assemblage from San Bernardino Cave is highly fragmented (98.1%). Complete elements are extremely rare (1.9% of the whole assemblage is complete) and they mostly correspond to isolated teeth (16.8%) and small fat bearing bones (70.6%) such as carpals, tar-

sals, sesamoids and phalanges. Low-density bone portions (ribs, sternum, vertebra fragments, scapula) and teeth are scarce (4.7% and 4.8%) and related to long-shaft fragments, which play a significant role altogether (38.5%). Epiphyses are underrepresented (1.3%), and spongy bone fragments (<1%) are also scarce. Ungulates remains are complete in only 7% of cases. Crania, mandibles and long bones are always fragmented. The fractures analysis shows that long bones of over 3 cm mostly were broken when green, and especially by oblique, curved and smooth fractures. 28.9% of carnivore remains are complete. All the complete elements, namely teeth, metacarpals, metatarsals, and phalanges belong to bears, red fox and lynx. Lagomorpha and Rodentia remains are complete in 36% of cases, mostly represented by metatarsals and phalanges of beaver and marmot.

Overall, we observed an excellent preservation of the bone surface. Among the biostratigraphic modifications, we identified trampling abrasion (14.9%), root marks (9.7%), and micro-fissures from weathering and/or weathering cracks (1.9% of the total). 83% of the bones displays diagenetic alterations and manganese dendrites, while some remains show concretion (2.9%) and rare chemical corrosion (0.2%). Rodents gnawing marks were detected only on 0.2% of the bones. Carnivore modifications are extremely scarce and only affect 0.6% (NR=58) of the specimens (Tab. 3). Pits, scores and gnawing tooth marks on the diaphysis of large-sized animals are the main alterations. No corrosion attacks made by carnivore digestion were detected. Only one cave bear bone shows furrowing traces that could be related to canids activity.

In terms of taxa, bear bones recorded the highest rate of tooth marks (22.4%), followed by chamois (8.6%). The frequency of remains with carnivore marks by weight class shows that medium-large and large sized animals were the most affected (17.2%; 10.3%). Carnivore marks were observed only on few medium animals' remains (NR=3).

4.3. Anthropogenic modifications

Anthropogenic modifications observed in the sample include several butchering traces, bone breakage, cut-marks (1.7% of NR) and burn damage (57.7% of NR) (Tab. 3).

83 remains (50.6% of NR with human traces) pre-

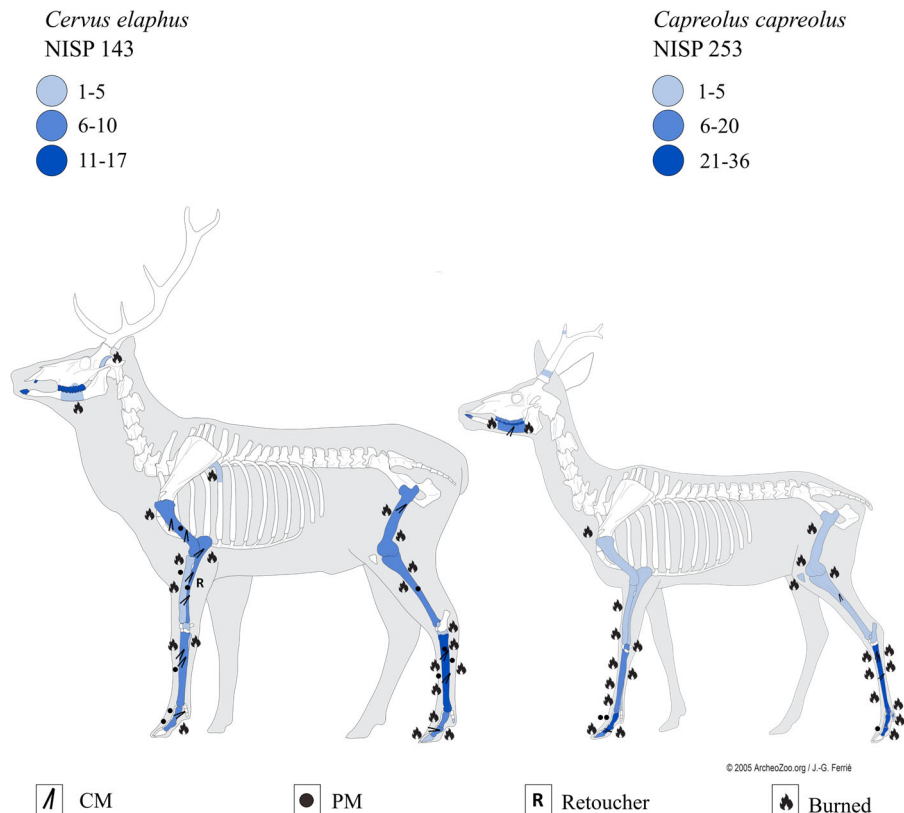


Fig. 4 - Frequency of skeletal elements of *Cervus elaphus* and *Capreolus capreolus* and distribution of anthropogenic modifications.

sent percussion marks (PM) from intentional anthropogenic breakage (Tab. 3). These are mainly percussion notches and impact flakes, whereas percussion pits are rare and peeling was not recorded. We identified only one adhering flake on a giant deer bone. The damaged elements are mainly the long bones of generic Ungulates and red deer. Within the indeterminate bone assemblage, percussion marked remains are mostly observed on large- and medium- sized animals.

The distribution, orientation and types of cut-marks (CM) provide evidence of different butchering activities. The most common types of cut-marks were incisions indicating skinning, disarticulation, defleshing and periosteum removal. In addition, scraping marks related to periosteum removal were also identified.

The taxonomic groups showing cut-marks are beaver, bears and all the main ungulate species, accounting for 4.1% (NR=62) of the total NISP. Three bones of *Castor fiber* bear cut-marks (Fig. 3a); Romandini et al., 2018b). One right ulna shows three longitudinal incisions suggesting possible skinning (Fig. 3a). Clustered, short, and oblique incisions on III and V metatarsals could be related to the removal of tendons of the hindlimb and the recovering of the hide. Amongst carnivores, only *Ursus spelaeus* and *Ursus* sp. present remains with anthropogenic modifications. Butchering traces have been observed on two portions of fibula and one portion of femur and could be related to defleshing and disarticulation. All

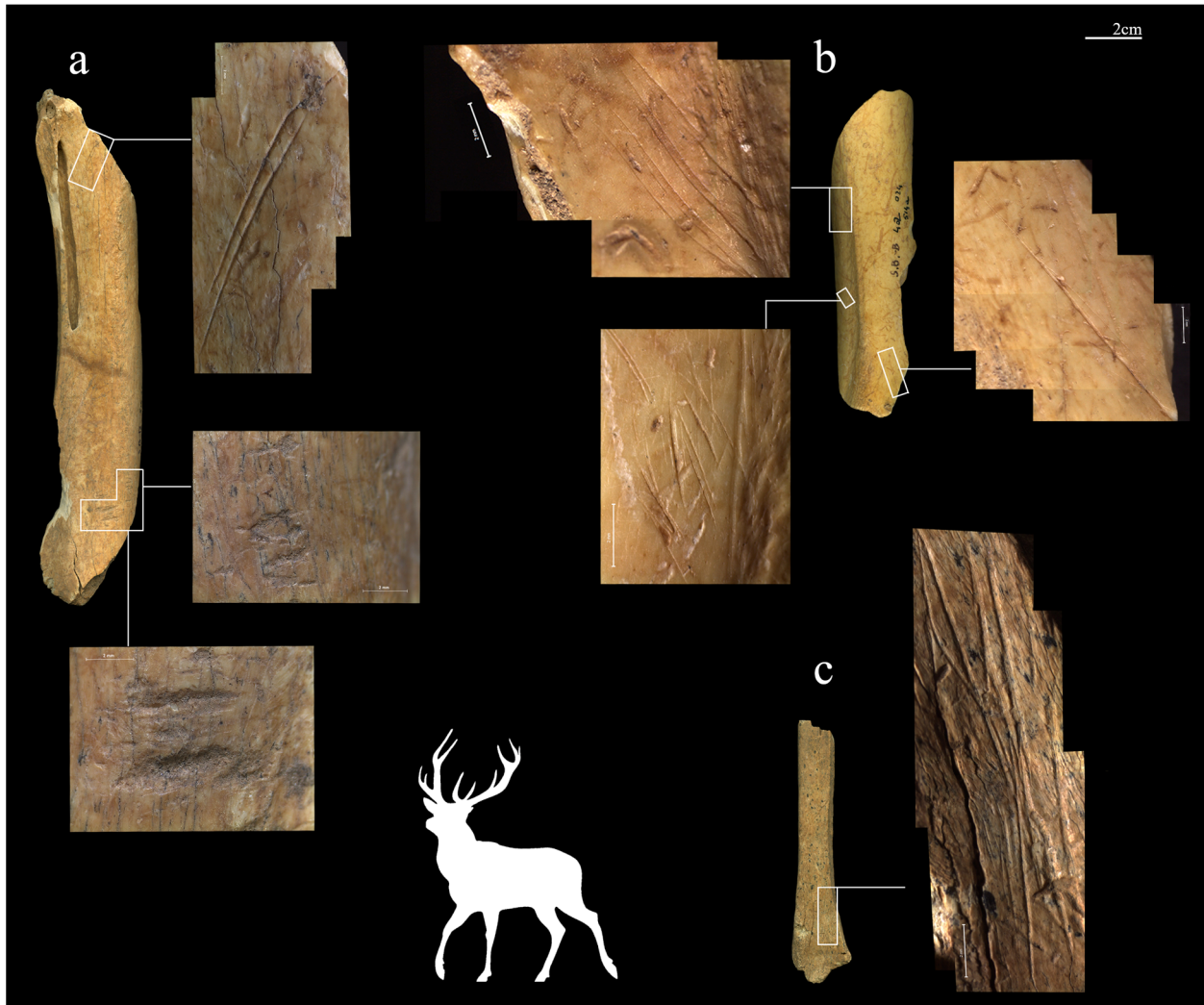


Fig. 5 - Position and details of anthropogenic modifications on some skeletal elements of *Cervus elaphus*: (a) left radius/ulna with incisions marks and pits produced during knapping on diaphysis; (b) right femur with close-up of different cut-marks; (c) left metapodial with scraping marks.

the main ungulate species have been processed (Tab. 3; Fig. 3) and provide the best record for inferring human subsistence at San Bernardino Unit II. Anthropogenic traces were found mostly on cervids, but also on large bovids (Terlato et al., 2019), caprids and wild boar remains. Cut-marks are preserved on three bones of *Megaloceros giganteus*. One hemi-mandible fragment bears longitudinal and oblique incisions. These are located on the medial side, under the second and third molars, and could be associated with the dismembering or removal of the tongue (Fig. 3b). Incisions aiming to meat procurement, together with percussion notches and adhering flake were recognized on one tibia. Finally, one radius/ulna shows long and longitudinal incisions which might be related to defleshing. Evidence of *Alces alces* skinning is suggested by one metatarsal fragment, which also present scraping marks for periosteum removal and percussion notch for marrow extraction (Fig. 3c). *Rupicapra rupicapra* remains include one metatarsal fragment with skinning marks and one tibia shaft

fragment with short, repeated, and oblique incisions that might hint at defleshing. Only one first phalanx of *Sus scrofa* yields cut-marks.

Cervus elaphus and *Capreolus capreolus* are the taxa bearing most of the Neanderthal induced modifications. Despite the non-homogeneous presence of their skeletal parts, the exploitation of these animals is attested for all the anatomical elements in the assemblage (Fig. 4). Traces of human activities ascribed to dietary and non-nutritional purposes can be observed over all the anatomical parts.

For *Cervus elaphus*, 17 remains are characterized by butchering traces (Tab. 3, Fig. 4). Each long bone of the limbs shows cut-marks, with the forelimbs (humerus, radius and metacarpal) being more intensely subjected to these human modifications, whereas only the first and the second phalanges of the extremities of the limbs present traces of this kind of alterations. Cut-marks suggest defleshing (long, sparse, oblique and longitudinal incisions and scrapings, Fig. 5a, c) and the cutting off of

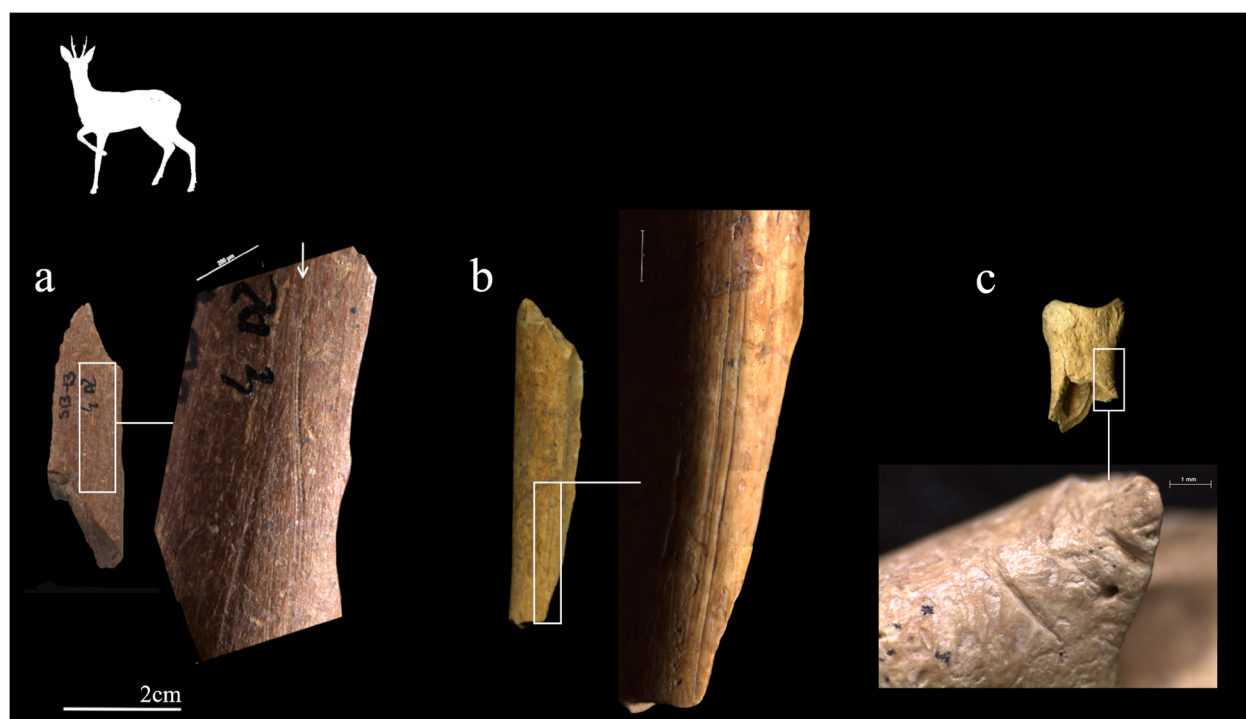


Fig. 6 - Position and details of anthropogenic modifications on some skeletal elements of *Capreolus capreolus*: a-b) metatarsal with longitudinal cut-marks; (c) left second phalange with close-up of skinning incision.

insertions of muscles and tendon (short, repeated, transverse and/or slightly oblique incisions, Fig. 5b). Both these actions mostly affected the diaphysis of the long bones. Skinning (longitudinal, oblique, isolated and/or clustered) is equally well documented on the phalanges (first and second). Often, different anthropogenic modifications can be observed on the same bone. For instance, one radius/ulna of *Cervus elaphus* shows cut-marks related to defleshing and scraping aimed to the removal of the periosteum, before the bone was used for retouching (Fig. 5a).

Concerning *Capreolus capreolus* remains, cut-marks have been recorded on 8 bones (Tab. 3, Figs. 4 and 6) and they are gathered mainly on the extremities of the hindlimb: 4 metatarsal, 2 phalanges and 1 tibia. Cut-marks on the metatarsal and phalanges are associated with skinning (Fig. 6). The latter is also suggested by oblique cut-marks on buccal surface of one mandible. One tibia fragment bears short and transverse incision ascribed to filleting.

For both species intentional bone breakage is attested by a series of percussion marks, including notch marks and percussion pits. Following the analysis of percussion marks, we can observe that marrow access activity is more intense in red deer limbs. However, it is noteworthy that not only long bones were broken but even phalanges (both first and second) were exploited to get access to the marrow. Deliberate fragmentation has been inferred on five phalanges of *Cervus elaphus* and on three of *Capreolus capreolus*. In most of them, we observed longitudinal breakage pattern as well.

Modifications caused by fire concerned more than half of the total specimens (57.7%): 50.6% were affect-

ed by moderate combustion (brown/black), while 7.1% were calcinated (grey/white) (Tab. 3). The burnt specimens account for 21.5% of NISP and include elements from all anatomical regions and ungulate categories. Roe deer is the most affected taxon by burn damage (35.1% of roe deer NISP), followed by red deer (24.4% of red deer NISP). In both cases, burnt autopodium elements outnumber other anatomical elements (Fig. 4).

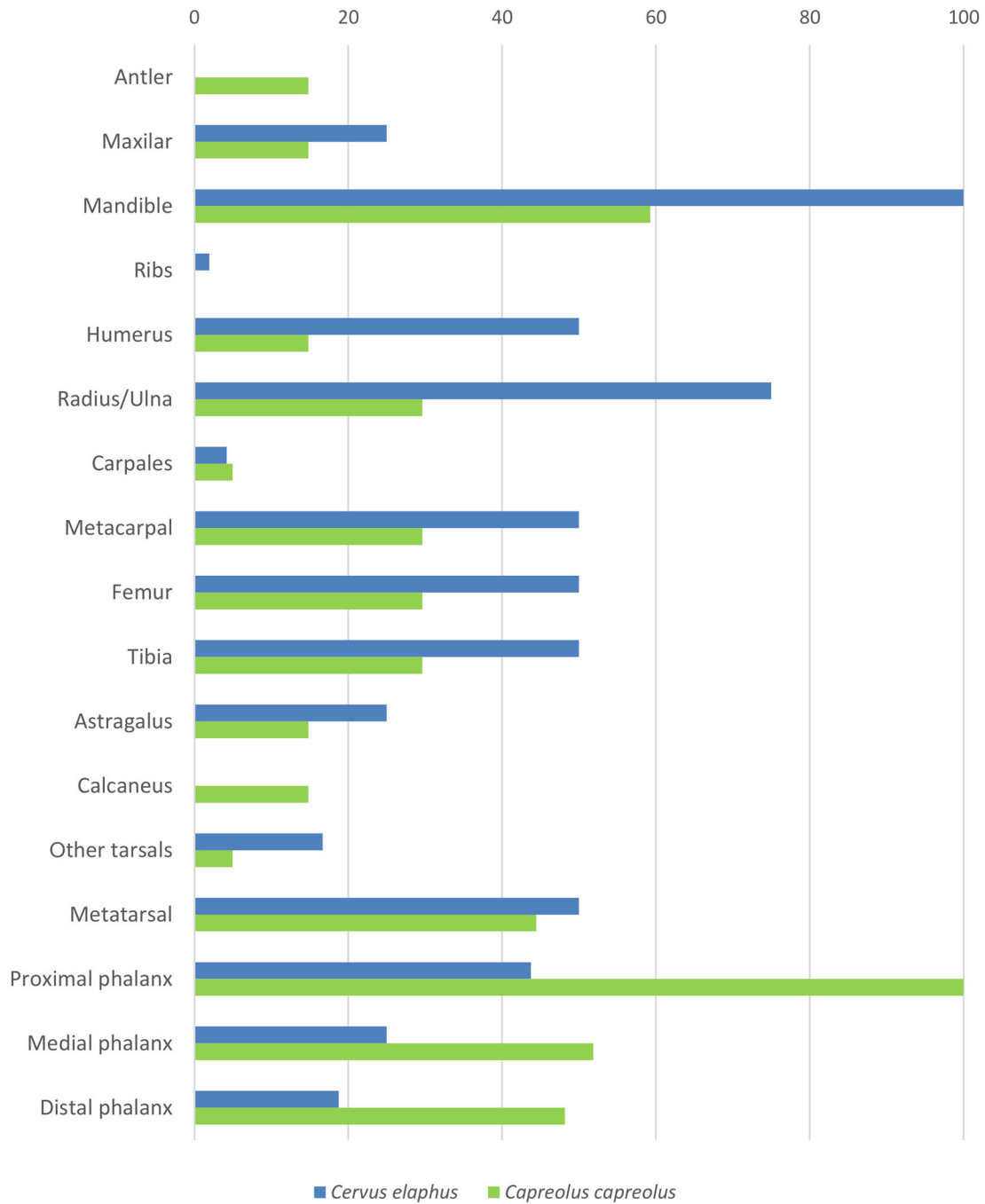
Finally, within the whole assemblage, twelve bone shafts were used as hammers for retouching flint artifacts. The retouchers were manufactured from metapodials, radius, femurs and tibia. Most of them show traces of cut-marks and they belonged to large-sized herbivores, likely medium/large cervids (Figs. 3d, 3e, 4 and 5a; Terlato et al., 2019).

4.4. Skeletal part representation of *Cervus elaphus* and *Capreolus capreolus*

Carcass transport strategy was only inferred for *Cervus elaphus* and *Capreolus capreolus*, as they yielded the most abundant data (Tab. 4, Fig. 7). %MAU shows a clear predominance of the limbs over the axial skeleton elements (Tab. 4). The anatomical distribution is characterized by a significant presence of phalanges and sesamoids followed by frontal and hind limbs bones (humerus, radius/ulna, metacarpals, femur, tibia and metatarsals). Cranium is mainly represented by isolated teeth and fragmented parts of the mandible, maxilla and antler. The axial skeleton is almost absent, with only one portion of red deer's rib. The two species do not present any considerable difference between forelimbs and hindlimbs representation. Conversely, some dissimilarities can be detected in terms of NISP between the limb

<i>Cervus elaphus</i>					<i>Capreolus capreolus</i>			
	NISP	MNE	MAU	%MAU	NISP	MNE	MAU	%MAU
Antler					2	1	0.5	14.81
Maxilla	1	1	1	25	1	1	0.5	14.81
Upper Teeth	13	3			14			
Mandible	4	4	2	100	6	4	2	59.26
Lower Teeth	13	4			31			
Tooth indet.	18				8			
Hyoid	1	1	1					
Tot. cranium	50	13			62	6		
Rib	1	1	0.04	1.92				
Tot. axial skeleton	1	1						
Humerus	6	2	1	50	2	1	0.5	14.81
Radius/Ulna	3	3						
Radius	4	1	1.5	75	3	1	1	29.63
Ulna	4	3			2	2		
Carpals	1	1	0.08	4.17	9	2	0.17	4.94
Metacarpal	10	2	1	50	9	2	1	29.63
Metacarpal rudim.	1	1			5	5		
Tot. forelimb	29	13			30	13		
Femur	7	2	1	50	3	2	1	29.63
Patella					1	1		
Tibia	7	2	1	50	4	2	1	29.63
Calcaneum					1	1	0.5	14.81
Astragalus	1	1	0.5	25	1	1	0.5	14.81
Tarsals	2	2	0.33	16.67	1	1	0.17	4.94
Metatarsal	12	2	1	50	27	3	1.5	44.44
Tot. hindlimb	29	9			38	11		
Metapodial	4				16			
First phal.	9	7	0.88	43.75	35	27	3.38	100
Second phal.	9	4	0.5	25	24	14	1.75	51.85
Third phal.	3	3	0.38	18.75	13	13	1.36	48.15
First phal. rudim.					4	4		
Second phal. rudim.					7	7		
Third phal. rudim.	3				5	5		
Sesamoid	6				19			
Tot. indet. limb	34	14			123	70		
Tot.	143	50			253	100		

Tab. 4 - NISP (Number of Identified Specimens), MNE (Minimum Number of Elements), MAU and %MAU (Minimum Animal Unit) of *Cervus elaphus* and *Capreolus capreolus*.

Fig. 7 - Percentage of Minimum Anatomical Units of *Cervus elaphus* and *Capreolus capreolus*

Taxa	%MAU/MGUI		%MAU/FUI		%MAU/CFUI		%MAU/Meat		%MAU/Grease		%MAU/Marrow		%MAU/UMI		%MAU/Bone density	
	Spearman	p	Spearman	p	Spearman	p	Spearman	p	Spearman	p	Spearman	p	Spearman	p	Spearman	p
<i>Cervus elaphus</i>	-0.03	0.88	-0.15	0.54	-0.06	0.81	-0.23	0.29	0.47	0.03	0.67	0.003	0.81	0.00	0.55	0.01
<i>Capreolus capreolus</i>	-0.29	0.17	0.11	0.65	0.15	0.54	-0.53	0.01	0.41	0.06	0.61	0.001	0.31	0.31	0.45	0.03

Tab. 5 - Correlation between %MAU and MGUI (Modified General Utility Index), FUI (Food Utility Index), CFUI (Corrected Food Utility Index), UMI (Unsaturated Marrow Index), Grease, Meat, Marrow and Bone density Indices of *Cervus elaphus* and *Capreolus capreolus*.

Site	Cultural	Unit	Species	α parameter		β parameter		Zooarchaeological data			
				Median	95% credibility interval	Median	95% credibility interval	MNE	MNI	Total Adults	Total Juvenile
San Bernardino	Mousterian	II	<i>Cervus elaphus</i>	0.33	-0.39 - 0.9	6.43	0.83 - 9.83	143	5	4	
			<i>Capreolus capreolus</i>	0.35	-0.37 - 0.9	6.34	0.78 - 9.82	253	9	4	2

Interpretation of different transport strategies corresponding to α parameter									
	-1	-0.75	-0.5	-0.25	0	0.25	0.5	0.75	1
Head									
Neck									
Trunk									
Pelvis+ Sacrum									
Forelimb									
Hindlimb									
Feet									
Type of transport	>Axial				Complete			Appendicular	

Interpretation of degree of attrition corresponding to β parameter					
β	0	1	2	3	4
Survival (%)	100	50	26	15	8

Tab. 6 - Alpha parameter (skeletal transport) and beta parameter (attrition) of *Cervus elaphus* and *Capreolus capreolus*, and interpretation of the Bayesian model.

bones, among which metacarpals and metatarsals are always the most represented elements (Tab. 4).

The results of the differential transport strategies adopted by Neanderthal groups for *Cervus elaphus* and *Capreolus capreolus* are presented in Tab. 5. Considering red deer, the bivariate correlations between %MAU with MGUI, FUI and CFUI are negative ($\rho=-0.03$, $\rho=-0.15$, $\rho=-0.06$) and not significant ($p=0.88$, $p=0.54$, $p=0.81$). With regard to roe deer, the correlation between %MAU with MGUI is negative ($\rho=-0.29$) and not significant ($p=0.17$); with the Food Utility indexes (both FUI and CFUI) the correlations are positive ($\rho=0.11$ and $\rho=0.15$) and not significant ($p=0.65$ and $p=0.54$). %MAU and meat index is negative for both cervids ($\rho=-0.23$ and $\rho=-0.53$), however it is not-significant for red deer ($p=0.29$) and significant for roe deer ($p=0.01$). For both species, %MAU with grease, marrow and UMI indexes are positively ($\rho=0.47$, $\rho=0.67$, $\rho=0.81$ - $\rho=0.41$, $\rho=0.61$, $\rho=0.31$ respectively) and significantly correlated ($p<0.05$), except for roe deer's UMI that is not significantly correlated ($p>0.05$). %MAU with bone density is

positively and significantly correlated for both species ($\rho=0.55$, $\rho=0.45$ and $p<0.05$). Finally, no significant correlations were found between the bone density and utility indexes for both species. Transport decision privileged anatomical parts rich in grease and marrow (mainly long bones, including metacarpals and metatarsals) to exploit them at the site (Fig. 8). The results of the Bayesian model for the evaluation of the prey transport strategies (α) are 0.33 and 0.35 for *Cervus elaphus* and for *Capreolus capreolus*, and the attrition at the assemblage (β) (Fig. 9, Tab. 6) are 6.43 and 6.34, respectively. These data indicate carrying prey strategy for both taxa of the appendicular skeleton (α - median values) and very high attrition at the level (β - median values). The β median index with values of 6, implies that more than 95% of the original record would have disappeared (Tab. 6). The high attrition would explain the imperceptible representation of low dense elements. The results of correspondence analysis, in addition to a significant level of attrition, attest a greater degree of appendicular skeleton processing for both species.

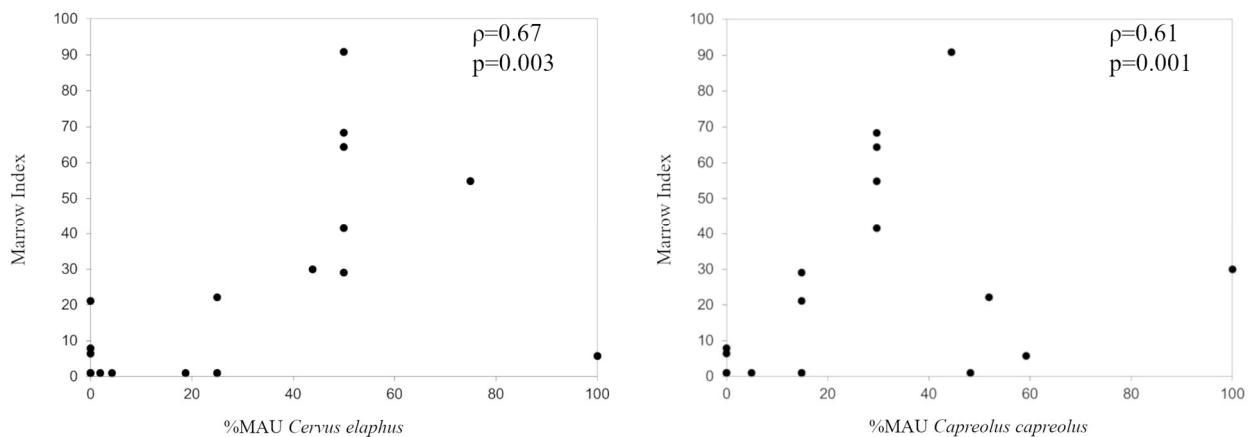


Fig. 8 - Correlation between % MAU and Marrow Index of *Cervus elaphus* and *Capreolus capreolus*.

5. DISCUSSION

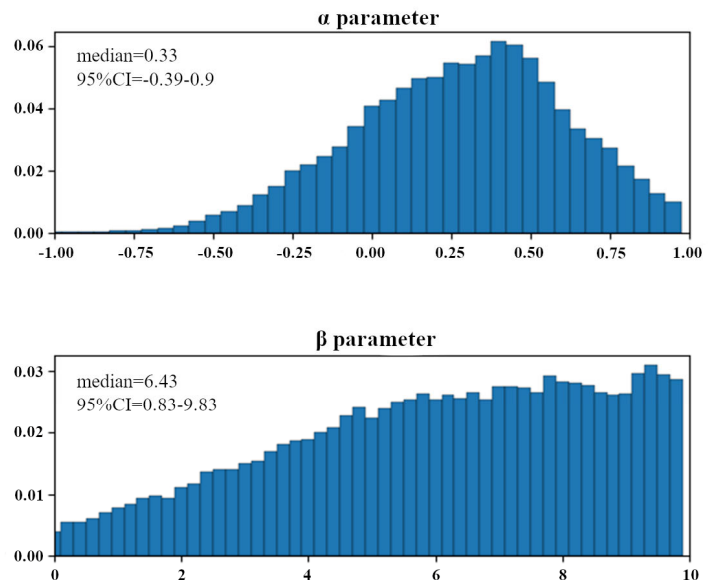
The zooarchaeological data acquired through our analysis allow the reconstruction of Neanderthal subsistence economy and ecological exploitation during the first half of MIS 3 at San Bernardino Cave. The taxonomic consistency of the faunal remains, dominated by the ungulates, especially cervids, as well as the taphonomic bone modifications and its association with lithic tools (Peresani, 1996), support the anthropic origin of the assemblage, occasionally disturbed by biological agents other than humans.

5.1. Palaeoenvironmental implications from macromammals

The faunal spectrum shows the presence of a broad variety of species, mostly represented by ungulates such as large bovids, large and medium-sized cervids, caprids, and wild boar, but also some carnivores, leporids and rodentia, associated with scant remains of fish and birds.

Regarding the ecological context, the faunal assemblage from San Bernardino II is representative of diverse past environments inhabited by humans. In fact, the site surroundings consisted of close and open forests with transitive and discontinuous Alpine grasslands or sparse vegetation on carbonate rocks, completed by a humid environment and watercourses. The dominance of red deer and roe deer over other taxa may reflect that forests were commonly the Neanderthals' most exploited hunting environment. However, caution is needed in declaring this assumption given the ecological plasticity of these kind of deers, which can live in different ecosystems. The roe deer primary habitat is forest clearings, hedges, and woodland edge (Danilkin, 1996). Furthermore, red deer can inhabit variable environments, from open steppe to close temperate forest (Geist, 1999). Besides, the wild boar remains reveal the existence of woodlands close to San Bernardino Cave. Moreover, the exploitation of large bovids is representative of ecological conditions diversity, spanning from dense forests with wetlands and small streams ecologically, more attractive to *Bos primigenius*, to hilly grasslands and plains populated by bison (Terlato et al., 2019). Still, rhinoceros, moose, beaver

Ratio of acceptance=0.448



Ratio of acceptance=0.449

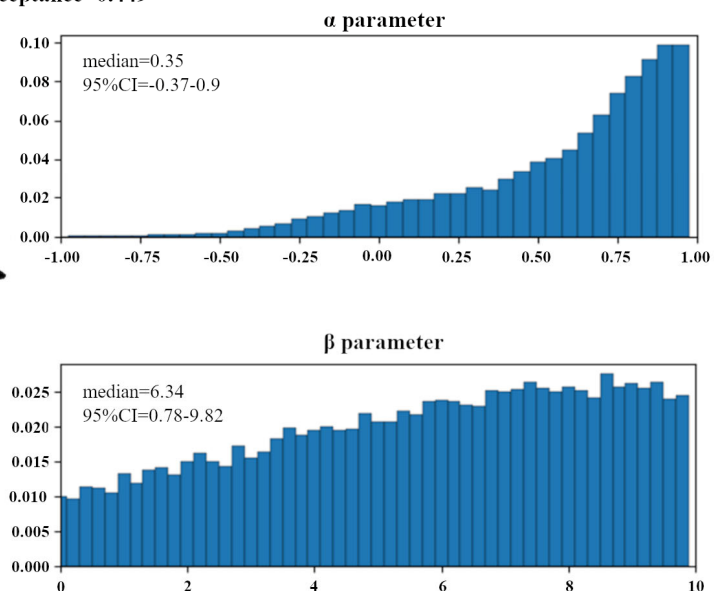


Fig. 9 - α and β parameters from *Cervus elaphus* and *Capreolus capreolus*

and the few remains of fishes and birds (ducks and geese) (Cassoli & Tagliacozzo, 1994; Fiore et al., 2004) suggest humid environments and watercourses in the proximity of the site. Finally, the importance of *Castor fiber* remains is given by the peculiar environmental conditions it lives in, always associated with flowing water. These data are consistent with a recent study of the micromammal associations, which highlights the

presence of *Microtus agrestis* and *Apodemus gr. sylvaticus-flavicollis* as the most abundant species in Unit II, thus demonstrating mild and humid conditions in a landscape dominated by woodland formations (López-García et al., 2017).

5.2. Subsistence economy

It must be mentioned that, despite the varied environmental range that existed around the cave, which were the habitat of the prey species, the inhabitants of the site may not have spent equal time foraging in these different patches. Taxonomic data demonstrate that the majority of mammals remains carried to the site belonged to prey typical of woodlands, valley bottoms and lowlands. The paucity of large prey types within the assemblage, might be explained with a lower encounter rates than red deer and roe deer's one, or, perhaps, they were disregarded when the hunters' success rate were lower than the ones for smaller prey species (Bird et al., 2009). On the other hand, while small/medium ungulates, like chamois and ibex, might have a higher rate of capture due to their marked attitude for living in herds - compared to wild boar or roe deer's ones for instance-, they were less frequently encountered than red deer and roe deer (Marín-Arroyo, 2009b; Romandini et al., 2014). It is also possible that ungulates typical of rocky landscapes or highlands were in part excluded from the diet but used as an alternative food source when the higher-ranked game was less abundant. Furthermore, it seems that mountain habitat areas were not widespread nearby the cave.

San Bernardino is not a unique example of Neanderthal subsistence, as other late Middle Palaeolithic settlements in the fringe of sub-Alpine area show similarities with it. This is the case of Tagliente Rockshelter (Thun-Hohenstein & Peretto, 2005; Thun-Hohenstein, 2006) and Fumane Cave (Cassoli & Tagliacozzo, 1991; Fiore et al., 2004; Romandini et al., 2014, 2020a; Peresani et al., 2017). Qualitative and quantitative data reveal that the types of hunted ungulates at each site are compliant with their respective environmental and climatic conditions. At Tagliente, layers 35-37, the most common species to have been brought into the site are roe deer and red deer, while ibex and chamois are less common. At Fumane, Units A5-A6 and A9, hunting targeted different species, primarily red deer, roe deer and large cervids of all age classes, with a lesser incidence of chamois, ibex, large bovids (Peresani et al., 2011; Romandini et al., 2014) and to birds (Fiore et al., 2016; Romandini et al., 2016). To further analyse the diet breadth in terms of diversity, we measured the inverse

of Simpson's Index, which takes into account both richness and evenness, as shown in Tab. 7. San Bernardino, Fumane unit A9 and Tagliente share a similar pattern for hunted species. The NISP values are quite lower in relation to animal. On the other hand, MNI index is higher and it identifies the diversification of species consumption. Hence, this framework confirms that selective hunting was undertaken by humans in order to target game availability in the surroundings of the site.

5.3. Hunting strategies and site functionality

At San Bernardino cave, humans were the principal agents of the faunal assemblage. Occasionally, other predators scavenged Neanderthals' leftovers, as attested by the low percentage of carnivore gnawing marks found on bone surfaces. This situation suggests a secondary access to the remains for carnivores, which therefore did not significantly contribute to bone accumulation after or before human activities.

Hunting practices targeted different species. In particular, clear traces of anthropogenic intervention have been documented on three remains of Castor fiber's bones, related to fur recovering (Romandini et al., 2018b). Nevertheless, cave bear is the only carnivore species presenting few remains with anthropogenic modifications. Infant or very young and senile cave bears show a differentiated occupation of the cave by humans and bears, as also recorded in late Middle Paleolithic sites in northern Italy, such as Fumane Cave, Rio Secco Cave among others (Romandini et al., 2018a). As a matter of fact, ungulates were the most exploited animals. Cervids, mostly deer and roe deer adult specimens, were the most hunted animals. Yet, the presence of two young, one sub-adult, four adult and two senile individuals of *C. capreolus* reflects the age structure of natural populations, thus confirming the hypothesis for the exploitation of whole herds. Seasonality information inferred by roe deer hunting season, allowed to esteem that the site occupation likely occurred during summer and autumn. On the other hand, the absence of fetal and neonatal individuals suggests that the site was not frequented in spring. Nevertheless, seasonality studies are still lacking a more complete documentation. For this reason, the acquisition of more detailed data based on isotopes, microwear analysis and cemento chronology is needed to provide further information.

The Neanderthals used San Bernardino as a place where, after an initial preparation at the kill-site, carcasses processing and consumption activities were carried out; still, discarded bones were used for lithic manufacturing. This is revealed by the skeletal profile analyses achieved with the correlation indices and the Bayesian method for *Cervus elaphus* and *Capreolus capreolus*. As a matter of fact, it seems that Neanderthal groups carried to the site appendicular body parts, by selecting the anatomical parts with higher nutritional content (both marrow and meat) and economic values, even for roe deer with a smaller body size than red deer. Hence, the high significant statistical correlations between %MAU and Grease, Marrow and UMI likely identifies a preference for bones transportation related to their grease and marrow content, except for roe deer, for which no statis-

Cave	Unit	1/D NISP	1/D MNI
San Bernardino	II	3.5	7.6
Fumane ^a	A9	3.1	6.5
Tagliente ^b	37-35	2	5.8

Tab. 7 - San Bernardino, Fumane and Tagliente ungulates diversity results based on the Inverse of Simpson's Index (1/D) according to NISP values. ^a Data from Romandini et al., 2014; ^b Data from Thun-Hohenstein 2006.

tical correlation with unsaturated marrow index (UMI) was detected.

Cut-marks, scraping, burning, percussion marks and fresh fractures are present, without any significant difference in both animals. Moreover, the correlation between the fracture degree and the Marrow index has confirmed the intense exploitation of within-bone nutrients, even in the case of phalanges. In fact, phalanges exploitation for marrow extraction is due to its taste and soft texture. The marrow present in the phalanges is known for its better taste because of its high content of unsaturated fatty acids, compared to other long bones (Morin, 2007). We demonstrated that the extremely high attrition of the bones in this cave could be related to the selective transport of the prey and to the intensive human activity. The latter consisted in the above-mentioned process and the employ of butchering refuse, rich in fats, used as fuel for fires or living floor maintenance (Costamagno et al., 2009, 2010; Morin, 2010). The absence of vertebrae and ribs, together with other low-survival elements could also be due to such reasons (Marín et al., 2017).

Considering the differential carcass transport, even though a considerable attrition within the assemblage affected less dense skeletal elements, it might be inferred that Neanderthal groups maximized the caloric input of the hunted prey brought to the cave. Such decisions might depend on several factors, including the weight of both red deer and roe deer carcass portions, the distance between the kill/prime butchering site and the camp base, the daytime of the hunting episode, the number of hunters involved, and so on (Mnahan, 1998; Marín-Arroyo, 2009a; Schoville & Otárola-Castillo, 2014). Moreover, the number of hunted animals and the competition with other carnivores in the environment, must not be excluded either.

San Bernardino Cave's topographic location - low altitude, close to the edge of a karstic plateau dissected by deep valleys and delimited by the alluvial lowlands - supported the exploitation of the prey recognized. At the same time, its position required significative efforts to cover distance in the landscape. Likely, carrying patterns of red deer and roe deer did not exceed 5-7 km from the site, underpinning an intentional focus on local resources. Additionally, knappable raw materials for stone tools were available in the surroundings. Nevertheless, large bovids' remains and the presence of exogenous raw materials also suggest that longer-distance movements did occur (Peresani, 1996).

6. CONCLUSION

Zooarchaeology and taphonomic analyses, thanks to their capability of characterising human economic behaviour and its relationship between human-animal and environmental exploitation, is currently one of the most widely used approaches to understand human strategies. Macrofaunal data from San Bernardino Cave provide new insights regarding animal exploitation and butchering practices during the late Middle Palaeolithic in continental Italy. The faunal spectrum reveals that site occupation generally occurred with temperate conditions, suggesting a forest landscape interspersed with

clearings and wetlands. Still, our results have shown that, despite the high attrition of the assemblage, Neanderthal subsistence strategies at San Bernardino Cave were mostly based on ungulates exploitation, especially red deer and roe deer, whereas the procurement of large ungulate and small chamois was sporadic. Neanderthal groups adopted a notable degree of energetic efficiency in carcasses processing, with a quite selective transport of red deer and roe deer. All this evidence highlights additional aspects of Neanderthal landscape use, hunting strategies and mobility in north-eastern Italy, where Eastern Italian Alps' ecosystems and forelands offered a wide range of opportunities in terms of animal resources, to sustain Neanderthal populations approaching the edge of their demise.

ACKNOWLEDGEMENTS

Excavations and studies at San Bernardino Cave are coordinated by the University of Ferrara (M.P.) and supported by the Ministry of Cultural Affairs and Tourism and Veneto Archaeological Superintendency (SABAP-Verona, Vicenza and Rovigo), public institutions (Veneto Region - Department for Cultural Heritage, Province of Vicenza, Municipality of Mossano). Author contributions: M.P. conceived research; V.L., G.T. and M.R. analysed data; A.B.M.A. supported new radiocarbon dating; S.B. and M.R. are supported by the ERC-CoG Horizon 2020 project SUCCESS (Ref 724046 - website: <http://www.erc-success.eu/>); G.T. and M.P. wrote the paper with inputs from A.B.M.A., M.R. and S.B. The authors want to acknowledge Lucía Agudo Pérez for graphic support. Radiocarbon dating has been funded by the ERC-CoG Horizon 2020 project SUBSILIENCE (Ref 818299 - website: <https://www.subsilience.eu/>) led by A. B. Marín-Arroyo.

REFERENCES

- Aitken R.J. (1974) - Delayed implantation in roe deer (*Capreolus capreolus*). Journal of Reproduction and Fertility, 39, 225-233.
- Arnaud J., Peretto C., Panetta D., Tripodi M., Fontana F., Arzarello M., Thun Hohenstein U., Berto C., Sala B., Oxilia G., Salvadori P.A., Benazzi S. (2016) - A reexamination of the Middle Paleolithic human remains from Riparo Tagliente, Italy. Quaternary International, 425, 437-444.
- Azorit C., Analla M., Carasco R., Calvo J.A., Muñoz-Cobo J. (2002) - Teeth eruption pattern in red deer (*Cervus elaphus hispanicus*) in southern Spain. Anales de Biología, 24, 107-114.
- Badino F., Pini R., Ravazzi C., Margaritora D., Arrighi S., Bortolini E., Figus C., Giaccio B., Lugli F., Marciani G., Mongato G., Moroni A., Negrino F., Oxilia G., Peresani M., Romandini M., Ronchitelli A., Spinapolice E., Benazzi S. (2020) - An overview of Alpine and Mediterranean palaeogeography, terrestrial ecosystems and climate history during MIS 3 with focus on the Middle to Upper Palaeolithic transition. Quaternary International, 551, 7-28.
- Barone R. (1976) - Anatomie comparée des mammifères domestiques. Tome 1: Ostéologie. Vigot,

- Paris. Italian Edition, pp. 690.
- Bartolomei G. (1960) - Nota preliminare sulla fauna della Grotta Maggiore di San Bernardino nei Colli Berici (Vicenza). *Annali Università Ferrara*, III (7), 119-125.
- Bartolomei G., Broglio A., Cattani L., Cremaschi M., Lanzinger M., Leonardi P. (1987-88) - Nuove ricerche nel deposito pleistocenico della Grotta di Pina sui Colli Berici (Vicenza). *Atti dell'Istituto Veneto di Scienze, Lettere e Arti*, CXLVI, 112-160.
- Benazzi S., Peresani M., Talamo S., Fu Q., Mannino M.A., Richards M.P., Hublin J.J. (2014a) - A reassessment of the presumed Neandertal human remains from San Bernardino Cave, Italy. *Journal of Human Evolution*, 66, 9-94.
- Benazzi S., Bailey S.E., Peresani M., Mannino M.A., Romandini M., Richards M.P., Hublin J.J. (2014b) - Middle Paleolithic and Uluzzian human remains from Fumane Cave, Italy. *Journal of Human Evolution*, 70, 61-68.
- Behrensmeyer A.K. (1978) - Taphonomic and ecologic information from bone weathering. *Paleobiology*, 4 (2), 150-162.
- Binford L.R. (1978) - *Nunamiut Ethnoarchaeology*. Academic Press, New York, pp. 530.
- Binford L.R. (1981) - Bones, ancient men and modern myths. Academic Press, New York, pp. 320.
- Binford L.R. (1984) - Faunal Remains from Klasies River Mouth. Academic Press, New York, pp. 305.
- Bird D.W., Bliege Bird R., Codding B.F. (2009) - In pursuit of mobile prey: Martu hunting strategies and archaeofaunal interpretation. *American Antiquity*, 74, 3-29.
- Blasco R., Rosell J., Fernández Peris J., Cáceres I., Vergès J.M. (2008) - A new element of trampling: an experimental application on the level XII faunal record of Bolomor Cave (Valencia, Spain). *Journal of Archaeological Science*, 35(6), 1605-1618.
- Blasco R., Fernández Peris J. (2012) - A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quaternary International*, 252, 16-31.
- Blasco R., Rosell J., Fernández Peris J., Arsuaga J.L., Bermúdez de Castro J.M., Carbonell E. (2013) - Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quaternary Science Reviews*, 70, 124-144.
- Blumenschine R.J., Selvaggio M.M. (1988) - Percussion marks on bone surfaces as a new diagnostic of hominid behavior. *Nature*, 333, 763-765.
- Blumenschine R.J., Marean C.W., Capaldo S.D. (1996) - Blind tests of interanalyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *Journal of Archaeological Science*, 23, 493-507.
- Bocherens H. (2009) - Neanderthal dietary habits: review of the isotopic evidence. In: *The evolution of hominid diets: integrating approaches to the study of Palaeolithic subsistence* (Ed. by Hublin J.J., Richards M.). Springer, New York, 241-250.
- Boscato P. (2017) - Ambienti ed economia nel Paleolitico medio della Puglia: lo studio delle faune. In: *Preistoria e Protostoria della Puglia* (Ed. by Radina F.). *Studi di Preistoria e Protostoria* 4, 119-124.
- Boscato P., Gambassini P., Rinaldo F., Ronchitelli A. (2011) - Management of Paleoenvironmental resources and raw materials exploitation at the Middle Paleolithic site of Oscuruscio (Ginosa, Southern Italy): Units 1 and 4. In: *Neanderthal Lifeways, Subsistence and Technology - One Hundred Fifty Years of Neanderthal Study* (Ed. by Conard N.J., Richter J.). *Vertebrate Paleobiology and Paleoanthropology Series*, Springer, New York, 87-98.
- Broglio A., Peresani M. (1992) - Grotta di San Bernardino (Comune di Mossano, Vicenza). *Rivista di scienze preistoriche* XLIV, 234-235.
- Brown K., Fa D.A., Finlayson G., Finlayson C. (2011) - Small Game and Marine Resource Exploitation by Neanderthals: The Evidence from Gibraltar. In: *Trekking the Shore. Interdisciplinary Contributions to Archaeology* (Ed. by Bicho N., Haws J., Davis L.). Springer, New York, 247-272.
- Bunn H.T. (1986) - Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *Journal of Human Evolution*, 15, 673-690.
- Capaldo S.D., Blumenschine R.J. (1994) - A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *American Antiquity*, 59, 724-748.
- Cassoli P.F., Tagliacozzo A. (1991) - Considerazioni paleontologiche, paleoeconomiche e archeozoologiche sui macromammiferi e gli uccelli dei livelli del Pleistocene superiore del Riparo di Fumane (VR) (Scavi 1988-91). *Bollettino Museo Civico Storia Naturale Verona*, 18, 349-445.
- Cassoli P.F., Tagliacozzo A. (1994) - I resti ossei di macromammiferi, uccelli e pesci della Grotta Maggiore di San Bernardino sui Colli Berici (VI): considerazioni paleoeconomiche, paleoecologiche e cronologiche. *Bollettino di Paleontologia*, 85, 1-71.
- Cochard D., Brugal J.P., Morin E., Meignen L. (2012) - Evidence of small fast game exploitation in the Middle Paleolithic of Les Canalettes Aveyron, France. *Quaternary International*, 264, 32-51.
- Coil R., Yezzi-Woodley K., Tappen M. (2020) - Comparisons of impact flakes derived from hyena and hammerstone long bone breakage. *Journal of Archaeological Science*, 120, 105167.
- Cortés-Sánchez M., Morales-Muñoz A., Simón-Vallejo M.D., Lonzano-Francisco M.C., Vera-Peláez J.L., Finlayson C., Rodríguez-Vidal J., Delgado-Huertas A., Jiménez-Espejo, F.J., Martínez-Ruiz F., Martínez-Aguirre M.A., Pascual-Granged A.J., Bergadà-Zapata M.M., Gibaja-Bao J., Riquelme-Cantal J., López-Sáez J.A., Rodrigo-Gámiz M., Sakai S., Sugisaki S., Finlayson G., Fa D.A., Bicho N.F. (2011) - Earliest Known Use of Marine Resources by Neanderthals. *PLoS One*, 8 (12), e81476.
- Costamagno S., Meignen L., Cédric B., Bernard V., Bruno M. (2006) - Les Pradelles (Marillac-le-Franc,

- France): A mousterian reindeer hunting camp? *Journal of Anthropological and Archaeology*, 25, 466-484.
- Costamagno I., Théry-Parisot I., Castel J.C., Brugal J.P. (2009) - Combustible ou non? Analyse multifactorielle et modèles explicatifs sur des ossements brûlés paléolithiques. In: *Gestion des combustibles au Paléolithique et au Mésolithique: nouveaux outils, nouvelles interprétations* (Proceedings of workshop 21, XV Congress luspp, Lisbonne, 2006) (Ed. by Théry-Parisot I., Costamagno S., Henry A.). BAR International Series 1914, Archaeopress, Oxford, 65-84.
- Costamagno S., Théry-Parisot I., Kuntz D., Bon F., Mensan R. (2010) - Impact taphonomique d'une combustion prolongée sur des ossements utilisés comme combustible. In: *Taphonomie des résidus organiques brûlés et des structures de combustion en milieu archéologique* (Ed. by Théry-Parisot I., Chabal L., Costamagno S.). *Palethnologie*, 2, 173-187.
- D'Errico F., Vanhaeren M. (2002) - Criteria for identifying red deer (*Cervus elaphus*) age and sex from their canines. Application to the study of Upper Palaeolithic and Mesolithic ornaments. *Journal of Archaeological Science*, 29, 211-232.
- Danilkin A. (1996) - Behavioural ecology of Siberian and European roe deer. Chapman & Hall, London, pp. 300.
- Domínguez-Rodrigo M., Piqueras A. (2003) - The use of tooth pits to identify carnivore taxa in tooth-marked archeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *Journal of Archaeological Science*, 30, 1385-1391.
- Domínguez-Rodrigo M., Barba R. (2006) - New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid-carnivore hypothesis failed. *Journal of Human Evolution*, 50, 170-194.
- Domínguez-Rodrigo M., de Juana S., Galán A.B., Rodríguez M. (2009) - A new protocol to differentiate trampling marks from butchery cut marks. *Journal of Archaeological Science*, 36, 2643-2654.
- Fabiani R. (1902-03) - La fauna fossile della Grotta di San Bernardino nei Colli Berici. *Atti Istituto Veneto SS.LL.AA.*, LXII, 657-671.
- Fernández-Jalvo Y., Andrews P. (2003) - Experimental effects of water abrasion on bone fragments. *Journal of Taphonomy*, 1, 147-163.
- Fernández-Jalvo Y., Andrews P. (2016) - Atlas of Taphonomic Identifications. *Vertebrate Paleobiology and Paleoanthropology*. Springer, Dordrecht, pp. 372.
- Fiore I., Gala M., Tagliacozzo A. (2004) - Ecology and subsistence strategies in the Eastern Italian Alps during the Middle Palaeolithic. *International Journal of Osteoarchaeology*, 14, 273-286.
- Fiore I., Gala M., Romandini M., Cocca E., Tagliacozzo A., Peresani M. (2016) - From feathers to food: Reconstructing the complete exploitation of avifaunal resources by Neanderthals at Fumane cave, unit A9. *Quaternary International*, 421, 134-153.
- Fisher W.J. (1995) - Bone surface modifications in zooarchaeology. *Journal of Archaeological Method and Theory*, 2, 7-68.
- Fontana A., Mozzi P., Marchetti M. (2014) - Alluvial fans and megafans along the southern side of the Alps. *Sedimentary Geology*, 301, 150-171.
- Galán B., Rodríguez M., de Juana S., Domínguez-Rodrigo M. (2009) - A new experimental study on percussion marks and notches and their bearing on the interpretation of hammerstone-broken faunal assemblages. *Journal of Archaeological Science*, 36, 776-784.
- Gaudzinski-Windheuser S., Roebroeks W. (2011) - On Neanderthal subsistence in last interglacial forested environments in Northern Europe. In: *Neanderthal Lifeways, Subsistence and Technology - One Hundred Fifty Years of Neanderthal Study* (Ed. by Conard N.J., Richter J.). *Vertebrate Paleobiology and Paleoanthropology Series*, Springer, New York, 61-71.
- Geist V. (1999) - *Deer of the World*. Swan Hill Press, Shrewsbury, England, pp. 432.
- Gómez-Olivencia A., Sala N., Núñez-Lahuerta C., Sanchis A., Arlegi M., Rois-Garaizar J. (2018) - First data of Neanderthal bird and carnivore exploitation in the Cantabrian Region (Axlor; Barandiaran excavations; Dima, Biscay, Northern Iberian Peninsula). *Scientific Reports*, 8, 10551.
- Grayson D.K. (1984) - *Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas*. Academic Press, Orlando, pp. 202.
- Gruppioni G. (2003) - Datation par les méthodes Uranium-Thorium (U/Th) et Résonance Paramagnétique Electronique (RPE) de deux gisements du Paléolithique moyen et supérieur de Vénétie: la Grotta de Fumane (Monts Lessini - Verone) et la Grotte Majeure de San Bernardino (Monts Berici - Vicence). Ph.D. dissertation, University of Ferrara.
- Guillaud E., Béarez P., Daujeard C., Defleur A.R., Desclaux E., Roselló-Izquierdo E., Morales-Muñiz A., Moncel M.H. (2021) - Neanderthal foraging in freshwater ecosystems: A reappraisal of the Middle Paleolithic archaeological fish record from continental Western Europe. *Quaternary Science Reviews*, 252, 106731.
- Habermehl K. H. (1961) - *Die Altersbestimmung bei Haustieren, Pelztieren und beim jagdbaren Wild*. Paul Parey Verlag, Berlin, 223 pp.
- Holt B., Negrino F., Riel-Salvatore J., Formicola V., Arellano A., Arobba D., Boschian G., Churchill S.E., Cristiani E., Di Canzio E., Vicino G. (2019) - The Middle-Upper Paleolithic transition in Northwest Italy: new evidence from Riparo Bombrini (Balzi Rossi, Liguria, Italy). *Quaternary International*, 508, 142-152.
- Jaouen K., Richards M.P., Le Cabec A., Welker F., Rendu W., Hublin J.J., Soressi M., Talamo S. (2019) - Exceptionally high $\delta^{15}\text{N}$ values in collagen single amino acids confirm Neanderthals as high-trophic level carnivores. *PNAS*, 116, 4928-4933.
- Jéquier C., Peresani M., Romandini M., Delpiano D., Joannes-Boyau R., Lembo G., Livragi A., López-García J.M., Obradovic M., Nicosia C. (2015) - The De Nadale Cave, a single layered Quina Mousterian

- an site in the North Italy. *Quartär*, 62, 7-21.
- Klein R.G., Cruz-Urbe K. (1984) - The Analysis of animal bones from archaeological sites. University of Chicago Press, Chicago, pp. 304.
- Lam Y.M., Chen X., Pearson O.M. (1999) - Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *American Antiquity*, 64(2), 343-362.
- Leonardi P. (1958-1959) - Risultati della prima campagna di scavo della stazione musteriiana di S. Bernardino nei Colli Berici (VI). *Atti Istituto Veneto SS.LL.AA.*, 117, 387-402.
- Leonardi P., Broglio A. (1960-1961) - Le Paléolithique de la Vénétie. *Annali Università di Ferrara*, 15(1), 1-118.
- Livraghi A., Fanfarillo G., Dal Colle M., Romandini M., Peresani M. (2021) Neanderthal ecology and exploitation of cervids at the onset of MIS4: A study on De Nadale cave, Italy. *Quaternary International*, 586, 24-41.
- López-García J.M., dalla Valle C., Cremaschi M., Peresani M. (2015) - Reconstruction of the Neanderthal and Modern Human landscape and climate from the Fumane cave sequence (Verona, Italy) using small-mammal assemblages. *Quaternary Science Reviews*, 128, 1-13.
- López-García J.M., Luzi E., Peresani M. (2017) - Middle to Late Pleistocene environment and climatic reconstruction of human occurrence at Grotta Maggiore di San Bernardino (Vicenza, Italy) through the small-mammal assemblage. *Quaternary Science Reviews*, 168, 42-54.
- López-García J.M., Berto C., Peresani M. (2019) - Environmental and climatic context of the hominin occurrence in northeastern Italy from the late Middle to Late Pleistocene inferred from small-mammal assemblages. *Quaternary Science Reviews*, 216, 18-33.
- Lyman R.L. (1994) - Vertebrate taphonomy. Cambridge University Press, Cambridge, pp. 552.
- Lyman R.L. (2008) - Quantitative Paleozoology. Cambridge University Press, Cambridge, pp. 348.
- Magurran A.E. (1988) - Ecological Diversity and its Measurement. Princeton University Press, Princeton, pp. 192.
- Malerba G., Giacobini G. (1998) - Les restes fauniques du Paléolithique moyen de la Grotte de San Bernardino (Vicenza, Italie nord-orientale): analyse micromorphologique des surfaces osseuses. *Proceedings XIII International Congress of Prehistoric and Protohistoric Sciences*, 203-208.
- Mallye J.B., Thiébaud C., Mourre V., Costamagno S., Claud É., Weisbecker P. (2012) - The Mousterian bone retouchers of Noisetier Cave: experimentation and identification of marks. *Journal of Archaeological Science*, 39(4), 1131-1142.
- Margaritora D., Dozio A., Chelidonio G., Turrini M.C., Peresani M. (2020) - The Lower and Middle Palaeolithic settlements in the Baldo-Lessini mountains. Results from a GIS investigation. *Alpine and Mediterranean Quaternary*, 33(1), 115-132.
- Mariezcurrera K. (1983) - Contribución al conocimiento del desarrollo de la dentición y el esqueleto post-craneal de *Cervus elaphus*. *Munibe*, 35, 149-202.
- Marín J., Saladié P., Rodríguez-Hidalgo A., Carbonell E. (2017) - Ungulate carcass transport strategies at the Middle Palaeolithic site of Abric Romaní (Capellades, Spain). *Comptes Rendus Palevol*, 16, 103-121.
- Marín J., Rodríguez-Hidalgo A., Vallverdú J., Gómez de Soler B., Rivals F., Rabuñal J.R., Pineda A., Chacón M.G., Carbonell E., Saladié P. (2019) - Neanderthal logistic mobility during MIS3: zooarchaeological perspective of Abric Romaní level P (Spain). *Quaternary Science Reviews*, 225, 106033.
- Marín-Arroyo A.B. (2009a) - Exploitation of the Montane zone of Cantabrian Spain during the Late Glacial: faunal evidence from El Mirón cave. *Journal of Anthropological Research*, 65, 69-102.
- Marín-Arroyo A.B. (2009b) - The use of optimal foraging theory to estimate late glacial site catchment areas from a central place: The case of eastern Cantabria, Spain. *Journal of Anthropological Archaeology*, 28, 27-36.
- Marín-Arroyo A.B., Ocio D. (2017) - Disentangling faunal skeletal profiles. A new probabilistic framework. *Historical Biology*, 30(6), 720-729.
- Metcalfe D., Jones K.T. (1988) - A reconsideration of animal body part utility indices. *American Antiquity*, 53, 486-504.
- Miracle P. (2005) - Late Mousterian subsistence and cave use in Dalmatia: The Zooarchaeology of Mujina Pečina, Croatia. *International Journal of Osteoarchaeology*, 15, 84-105.
- Monahan C.M. (1998) - The Hadza carcass transport debate revisited and its archaeological implications. *Journal of Archaeological Science*, 25, 405-424.
- Monegato G., Pini R., Ravazzi C., Reimer P., Wick L. (2011) - Correlating Alpine glaciation with Adriatic Sea-level changes through lake and alluvial stratigraphy. *Journal of Quaternary Science* 26, 791-804.
- Morin E. (2007) - Fat composition and Nunamiut decision-making: a new look at the marrow and bone grease indices. *Journal of Archaeological Science*, 34, 69-82.
- Morin E. (2010) - Taphonomic implications of the use of bone as fuel. In: *The Taphonomy of Burned Organic Residues and Combustion Features in Archaeological Contexts* (Ed. by Théry-Parisot I., Chabal L., Costamagno S.). *Palethnologie*, 2, 215-223.
- Morin E., Ready E. (2013) - Foraging goals and transport decisions in western Europe during the paleolithic and early Holocene. In: *Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene* (Ed. by Clark J.L., Speth J.D.). Springer, Dordrecht, 227-269.
- Morin E., Speth J.D., Lee-Thorp J. (2016) - Middle Palaeolithic Diets: a critical examination of the evidence. In: *The Oxford Handbook of the Archaeology of Diet* (Ed. by Lee-Thorp J., Katzemberg M.A.). Oxford University Press, Oxford, 1-37.

- Morin E., Meier J., El Guennouni K., Moigne A.M. (2019) - New evidence of broader diet for archaic *Homo* populations in the northwestern Mediterranean. *Science Advances*, 5 (3), eaav9106.
- Moroni A., Boschian G., Crezzini J., Montanari-Canini G., Marciani G., Capecci G., Arrighi S., Aureli D., Berto C., Freguglia M., Araujo A., Scaramucci S., Hublin J.J., Lauer T., Benazzi S., Parenti F., Bonato M., Ricci S., Talamo S., Segre A.G., Boschin F., Spagnolo V. (2019) - Late Neandertals in central Italy. High-resolution chronicles from Grotta dei Santi (Monte Argentario - Tuscany). *Quaternary Science Reviews*, 217, 130-151.
- Mozota Holgueras M. (2012) - El utillaje óseo del final del Musteriense en el sector central del norte de la Península Ibérica. Ph.D. dissertation, University of Cantabria.
- Nabais M. (2018) - Neanderthal Subsistence in Portugal: What Evidence? *Archaeology International*, 21 (1), 95-100.
- Nilssen P.J. (2000) - An actualistic butchery study in South Africa and its implications for reconstructing hominid strategies of carcass acquisition and butchery in the Upper Pleistocene and Plio-Pleistocene. Ph.D. Dissertation, University of Cape Town.
- Patou-Mathis M. (2000) - Neanderthal subsistence behaviours in Europe. *International Journal of Osteoarchaeology*, 10, 379-395.
- Peresani M. (1995-1996) - Sistemi tecnici di produzione litica nel Musteriano d'Italia. Studio tecnologico degli insiemi litici delle unità VI e II della Grotta di San Bernardino (Colli Berici, Veneto). *Rivista Scienze Preistoriche*, 47, 79-167.
- Peresani M. (1996) - The Levallois reduction strategy at the Cave of San Bernardino (Northern Italy). In: *Reduction Processes (chaînes opératoires) in the European Mousterian* (Ed. by Bietti, A., Grimaldi, S.). *Quaternaria Nova VI*, Rome, 205-236.
- Peresani M. (2001) - An overview of the Middle Palaeolithic settlement system in North-Eastern Italy. In: *Settlement Dynamics of the Middle Palaeolithic and Middle Stone Age* (Ed. by Conard N.J.). *Kerns Verlag, Tübingen*, 485-506.
- Peresani M. (2011) - The end of the Middle Palaeolithic in the Italian Alps. An overview on Neanderthal land-use, subsistence and technology. In: *Neanderthal Lifeways, Subsistence and Technology - One Hundred Fifty Years of Neanderthal Study* (Ed. by Conard N.J., Richter J.). *Vertebrate Paleobiology and Paleoanthropology Series*, Springer, New York, 249-259.
- Peresani M., Chravzez J., Danti A., De March M., Duches R., Gurioli F., Muratori S., Romandini M., Tagliacozzo A., Trombino L. (2011) - Fire-places, frequentations and the environmental setting of the final Mousterian at Grotta di Fumane: a report from the 2006-2008 research. *Quartär*, 58, 131-151.
- Peresani M., Delpiano D., Duches R., Gennai J., Marazzan D., Nannini N., Romandini M., Aleo A., Cocilova A. (2017) - Il Musteriano delle unità A10 e A11 a Grotta di Fumane (VR). Risultati delle campagne di scavo 2014 e 2016. *FastiOnLine Documents & Research*, 397.
- Peresani M., Bertola S., Delpiano D., Benazzi S., Romandini M. (2019) - The Uluzzian in the north of Italy: insights around the new evidence at Riparo Broion. *Archaeological and Anthropological Science*, 11, 3503-3536.
- Peretto C., Arzarello M., Coltorti M., Bertolini M., Cui Q-Y., De Curtis O., Lebreton V., Lembo G., Marquer L., Pieruccini P., Ravani S., Rufo E., Sala B., Talamo S., Thun Hohenstein U. (2020) - Grotta Reali, the first multilayered mousterian evidences in the Upper Volturno Basin (Rocchetta a Volturno, Molise, Italy). *Archaeological and Anthropological Science*, 12 (3), 67.
- Picin A., Peresani M., Vaquero M. (2010) - Application of a new typological approach to classifying denticulate and notched tools: the study of two Mousterian lithic assemblages. *Journal of Archaeological Science*, 38, 711-722.
- Picin A., Peresani M., Falguères C., Gruppioni G., Bahain J.J. (2013) - San Bernardino Cave (Italy) and the appearance of Levallois technology in Europe: results of a radiometric and technological reassessment. *PloS One*, 8(10), e76182.
- Pickering T.R., Egeland C.P. (2006) - Experimental patterns of hammerstone percussion damage on bones: Implications for inferences of carcass processing by humans. *Journal Archaeological Science*, 33, 459-469.
- Pickering T.R., Domínguez-Rodrigo M., Heaton J.L., Yravedra J., Barba R., Bunn H.T., Musiba C., Basquedano E., Díez-Martín F., Mabulla A., Brain C.K. (2013) - Taphonomy of ungulate ribs and the consumption of meat and bone by 1.2-million-year-old hominins at Olduvai Gorge, Tanzania. *Journal of Archaeological Science*, 40(2), 1295-1309.
- Pini R., Ravazzi C., Donegana M. (2009) - Pollen stratigraphy, vegetation and climate history of the last 215 ka in the Azzano Decimo core (plain of Friuli, north-eastern Italy). *Quaternary Science Reviews*, 28, 1268-1290.
- Pini R., Ravazzi C., Reimer P.J. (2010) - The vegetation and climate history of the last glacial cycle in a new pollen record from Lake Fimon (southern Alpine foreland, N-Italy). *Quaternary Science Reviews*, 29, 3115-3137.
- Porraz G., Peresani M. (2006) - Occupations du territoire et exploitation des matières premières: présentation et discussion sur la mobilité des groupes humains au Paléolithique moyen dans le nord-est de l'Italie. In: *Notions de territoire et de mobilité. Exemples de l'Europe et des premières nations en Amérique du nord avant le contact européen* (Ed. by Bressy C., Burke A., Chalard P., Lacombe S., Martin H.). *ÉRAUL*, 116, 11-21.
- Potts R., Shipman P. (1981) - Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature*, 291, 577-580.
- Ready E. (2010) - Neanderthal man the hunter: a history of Neanderthal subsistence. *Explorations in Anthropology*, 10(1), 58-80.
- Ready E. (2013) - Neanderthal foraging during the late

- Mousterian in the Pyrenees: new insights based on faunal remains from Gatzarria Cave. *Journal of Archaeological Science*, 40, 1568-1578.
- Rendu W. (2010) - Hunting behavior and Neanderthal adaptability in the Late Pleistocene site of Pech-de-l'Aze I. *Journal of Archaeological Science*, 37, 1798-1810.
- Rogers A.R. (2000a) - Analysis of bone counts of maximum likelihood. *Journal of Archaeological Science*, 27, 111-125.
- Rogers A.R. (2000b) - On the values of soft bones in faunal analysis. *Journal of Archaeological Science*, 27, 635-639.
- Romandini M., Nannini N., Tagliacozzo A., Peresani M. (2014) - The ungulate assemblage from layer A9 at Grotta di Fumane, Italy: a zooarchaeological contribution to the reconstruction of neanderthal ecology. *Quaternary International*, 337, 11-27.
- Romandini M., Fiore I., Gala M., Cestari M., Tagliacozzo A., Guida G., Peresani M. (2016) - Neanderthal scraping and manual handling of vulture wing bones: evidence from Fumane cave. *Quaternary International*, 421, 154-172.
- Romandini M., Terlato G., Nannini N., Tagliacozzo A., Benazzi S., Peresani M. (2018a) - Humans and Bears a Neanderthal tale. Reconstructing uncommon behaviors from zooarchaeological evidence in southern Europe. *Journal of Archaeological Science*, 90, 71-91.
- Romandini M., Thun Hohenstein U., Fiore I., Tagliacozzo A., Perez A., Lubrano V., Terlato G., Peresani M. (2018b) - Late Neanderthals and the exploitation of small mammals in Northern Italy: fortuity, necessity or hunting variability? *Quaternaire*, 29(1), 61-67.
- Romandini M., Crezzini J., Bortolini E., Boscato P., Boschini B., Carrera L., Nannini N., Tagliacozzo A., Terlato G., Arrighi S., Badino F., Figus C., Lugli F., Marciani G., Oxilia G., Moroni A., Negrino F., Peresani M., Benazzi S. (2020a) - Macromammal and bird assemblages across the late Middle to Upper Palaeolithic transition in Italy: an extended zooarchaeological review. *Quaternary International*, 551, 188-223.
- Romandini M., Oxilia G., Bortolini E., Peyrégne S., Delpiano D., Nava A., Panetta D., Di Domenico G., Marini P., Arrighi S., Badino F., Figus C., Lugli F., Marciani G., Silvestrini S., Menghi Sartorio J.C., Terlato G., Hublin J.J., Benazzi S. (2020b) - A late Neanderthal tooth from northeastern Italy. *Journal of Human Evolution*, 147, 102867.
- Rosell J., Cáceres I., Blasco R., Bennàsar M., Pilar B., Gerard C., Montserrat E.N., Fernández-Laso M.C., Gabucio J.M., Huguet R., Ibáñez N., Martín P., Rivals F., Rodríguez-Hidalgo A., Saldí P. (2012) - A zooarchaeological contribution to establish occupational patterns at Level J of Abric Romaní (Barcelona, Spain). *Quaternary International*, 247, 69-84.
- Salazar-García D., Power R.C., Sanchis Serra A., Villaverde V., Walker M.J., Henry A.G. (2013) - Neanderthal diets in central and southeastern Mediterranean Iberia. *Quaternary International*, 318, 3-18.
- Sanz M., Rivals F., García D., Zilhão J. (2019) - Hunting strategy and seasonality in the last interglacial occupation of Cueva Antón (Murcia, Spain). *Archaeological and Anthropological Science*, 11, 3577-3594.
- Schoville B.J., Otárola-Castillo E. (2014) - A model of hunter-gatherer skeletal element transport: the effect of prey body size, carrier, and distance. *Journal of Human Evolution*, 73, 1-14.
- Shipman P. (1981) - *Life History of a Fossil. An Introduction to Taphonomy and Paleocology*. Harvard University Press, Harvard, 232 pp.
- Shipman P., Rose J. (1984) - Cutmark mimics on modern fossil bovid bones. *Current Anthropology*, 25, 116-177.
- Simpson E.H. (1949) - Measurement of diversity. *Nature*, 163, 688.
- Spagnolo V., Marciani G., Aureli D., Martini I., Boscato P., Boschini F., Ronchitelli A. (2020) - Climbing the time to see Neanderthal behaviour's continuity and discontinuity. SU 11 of the Oscursciuto Rockshelter (Ginosa - Southern Italy). *Archaeological and Anthropological Science*, 12, 54.
- Stiner M.C. (1994) - *Honor among Thieves. A Zooarchaeology Study of Neanderthal Ecology*. Princeton University Press, Princeton, New Jersey, pp. 448.
- Stiner M.C., Kuhn S.L., Weiner S., Bar-Yosef O. (1995) - Differential Burning, Recrystallization and Fragmentation of Archaeological Bone. *Journal of Archaeological Science*, 22, 223-237.
- Terlato G., Livraghi A., Romandini M., Peresani M. (2019) - Large bovids on the Neanderthal menu: exploitation of *Bison priscus* and *Bos primigenius* in northern Italy. *Journal of Archaeological Science: Reports*, 25, 129-143.
- Thun-Hohenstein U., Peretto C. (2005) - The exploitation of the faunal remains in the Mousterian levels at Riparo Tagliente (Verona, Italy). In: *Les premiers peuplements en Europe: Données récentes sur les modalités de peuplement et sur le cadre chronostratigraphique. Géologique et paléogéographique des industries du Paléolithique inférieur et moyen en Europe* (Ed. by Molines N., Moncel M.H., Monnier J.L.). BAR International Series 1364, Archaeopress, Oxford, 261-268.
- Thun Hohenstein U. (2006) - Strategie di sussistenza adottate dai Neandertaliani nel sito di Riparo Tagliente (Prealpi venete). In: Sala, B., Tecchiati, U. (Eds), *Studi di archeozoologia in onore del Prof. Alfredo Riedel*. Soprintendenza Archeologica del Trentino Alto Adige, Bolzano, 31-38.
- Thun Hohenstein U., Bertolini M., Channarayapatna S., Modolo M., Peretto C. (2018) - Bone retouchers from two north Italian Middle Palaeolithic sites: Riparo Tagliente and Grotta della Ghiacciaia, Verona. In: *The origins of bone tool technologies* (Ed. by Hutson J.M., Garcia-Moreno A., Noack E.S., Turner E., Villaluenga A., Gaudzinski-Windheuser S.). Monrepos, Neuwied, 235-250.
- Tomé C., Vigne J.D. (2003) - Roe deer (*Capreolus capreolus*) age at death estimates: New methods and modern reference data for tooth eruption and wear, and for epiphyseal fusion. *Archaeofauna*, 12,

- 157-173.
- Vettese D. (2014) - Le traitement des carcasses d'ongulés chez les Néanderthaliens de l'Abri du Maras (Ardèche, MIS4)/individualisme ou poids des traditions? Master thesis Erasmus Mundus: Quaternaire et Préhistoire. Muséum national d'Histoire naturelle, Paris, p. 106.
- Vettese D., Daujeard C., Blasco R., Boreal A., Cáceres I., Moncel M.H. (2017) - Neandertal long bone breakage process: standardized or random patterns? The example of Abri du Maras (southeastern France, MIS 3). *Journal of Archaeological Science: Reports*, 13, 151-163.
- Vettese D., Blasco R., Cáceres I., Gaudzinski-Windheuser S., Moncel M.H., Thun Hohenstein U., Daujeard C. (2020) - Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. *Archaeological and Anthropological Science*, 12, 48.
- Villa P., Mahieu É. (1991) - Breakage patterns of human long bones. *Journal of Human Evolution*, 21, 27-48.
- Yravedra J., Cobo-Sánchez L. (2015) - Neanderthal exploitation of ibex and chamois in southwestern Europe. *Journal of Human Evolution*, 78, 12-32.
- Zilhão J., Angelucci D.E., Igreja M.A., Arnold L. J., Badal E., Callapez P., Cardoso J.L., d'Errico F., Daura J., Demuro M., Dechamps M., Dupont C., Gabriel S., Hoffmann D.L., Legoinha P., Matias H., Monge Soares A.M., Nabais M., Portela P., Queffelec A., Rodrigues F., Souto P. (2020) - Last Interglacial Iberian Neandertals as fisher-hunter-gatherers. *Science*, 367(6485), eaaz7943.

Ms. received: March 2, 2021
Accepted: May 5, 2021

Revised: April 30, 2021
Available online: June 29, 2021