



Contents lists available at ScienceDirect

Journal of Archaeological Science: Reports

journal homepage: www.elsevier.com/locate/jasrep

Hunting game: New data on the subsistence strategies during the Uluzzian in Italy

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ARTICLE INFO

Keywords:

Zoarchaeology
Taphonomy
Middle-Upper Palaeolithic
Uluzzian
Italy

ABSTRACT

In this study we present the results of the archaeozoological and taphonomic analysis of the macromammal assemblage from the Uluzzian levels of three Italian sites: Uluzzo C Rock Shelter, Rocca San Sebastiano cave, and Riparo del Broion. Our archaeozoological data outlined several common elements and differences between sites sharing this culture. The most abundant taxon registered at Rocca San Sebastiano cave is *Cervus elaphus*; for Riparo del Broion we registered mostly *Ursus* sp., but we found anthropogenic modifications on different bones of *Cervus elaphus*. At Uluzzo C, the most abundant taxon is *Vulpes vulpes* and the most hunted is *Cervus elaphus*. Anthropogenic modifications are observed mostly on limb bones (long bones, phalanges, and sesamoids) attesting the practice of marrow extraction. We outlined hunting strategies against carnivore species in particular for northern Italy (Riparo del Broion). In southern Italy, the fauna exploitation is focused mostly on cervids and equids, as attested for several coeval Italian sites (Castelcivita, Grotta del Cavallo, Grotta della Cala, and Grotta La Fabbrica). The data obtained provide new relevant information about animal resource exploitation and allow us to improve and complete our understanding of the Uluzzian hunting and subsistence strategies in the Mediterranean area.

1. Introduction

The Middle to Upper Palaeolithic in western Eurasia is one of the most important periods in recent human evolution. Although several aspects of the arrival of early modern humans and the disappearance of Neanderthals have been better understood in recent years (Benazzi et al., 2011, 2015; Harvati et al., 2019; Higham et al., 2014; Hublin, 2020; Hajdinjak et al., 2018; Mylopotamitaki et al., 2024; Morin et al.,

2019; Peresani et al., 2019; Romandini et al., 2020, 2023) some new data on the ecological, behavioural, and cognitive spheres of these human groups can contribute to shed light to this pivotal moment. During the transition from the Middle to Upper Palaeolithic in Europe, the archaeological record presents evidence of a shift in material culture and technology across the continent, albeit varying spatially and temporally (Arrighi et al., 2020; Benazzi et al., 2011; Hublin, 2015; Hublin et al., 2020; Marciari et al., 2020), sparking ongoing debates

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<https://doi.org/10.1016/j.jasrep.2024.104575>

Received 21 November 2023; Received in revised form 10 March 2024; Accepted 1 May 2024

Available online 18 May 2024

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regarding the number and timing of Late Pleistocene *Homo sapiens* migration(s) into Europe (Hublin et al., 2020) and the assignment of different techno-complexes to various *Homo* species (Bar-Yosef, 2007; Benazzi et al., 2011; Hoffecker, 2009; Hublin, 2015; Marciani et al., 2020; Moroni et al., 2018; Slimak et al., 2022). Different cultures, such as Châtelperronian, Bachokirian, Bohunician, and Protoaurignacian emerged during this transitional period, although there is uncertainty about their origin (Roebroeks, 2008). In the South of Europe, this transitional phase is known, in terms of cultural complexes, as the Uluzzian, which stretches along the central edge of the Mediterranean from the Italian Peninsula to the southern Balkans (see references in Moroni et al., 2018; Douka et al., 2019; Peresani et al., 2014; Peresani

et al., 2019; Collina et al., 2020; Carvalho and Bicho, 2022) approximately between 41.7 to 30.3 ka cal BP (Hedges et al., 1998; Higham et al., 2009, 2014; Peresani, 2012; Wood et al., 2012; Douka et al., 2014). Currently, the Uluzzian is one of the oldest known cultural expressions associated with modern human skeletal remains in western Eurasia (Benazzi et al., 2011; Douka et al., 2014; Peresani et al., 2019; Zanchetta et al., 2018).

Italy provides a unique perspective for investigating differences and similarities between Neanderthals and first modern humans in human-environment interactions, as it encompasses a variety of climates and ecosystems (for reference see Marciani et al., 2020; Badino et al., 2023; Romandini et al., 2020; Arrighi et al., 2020), with differences in the

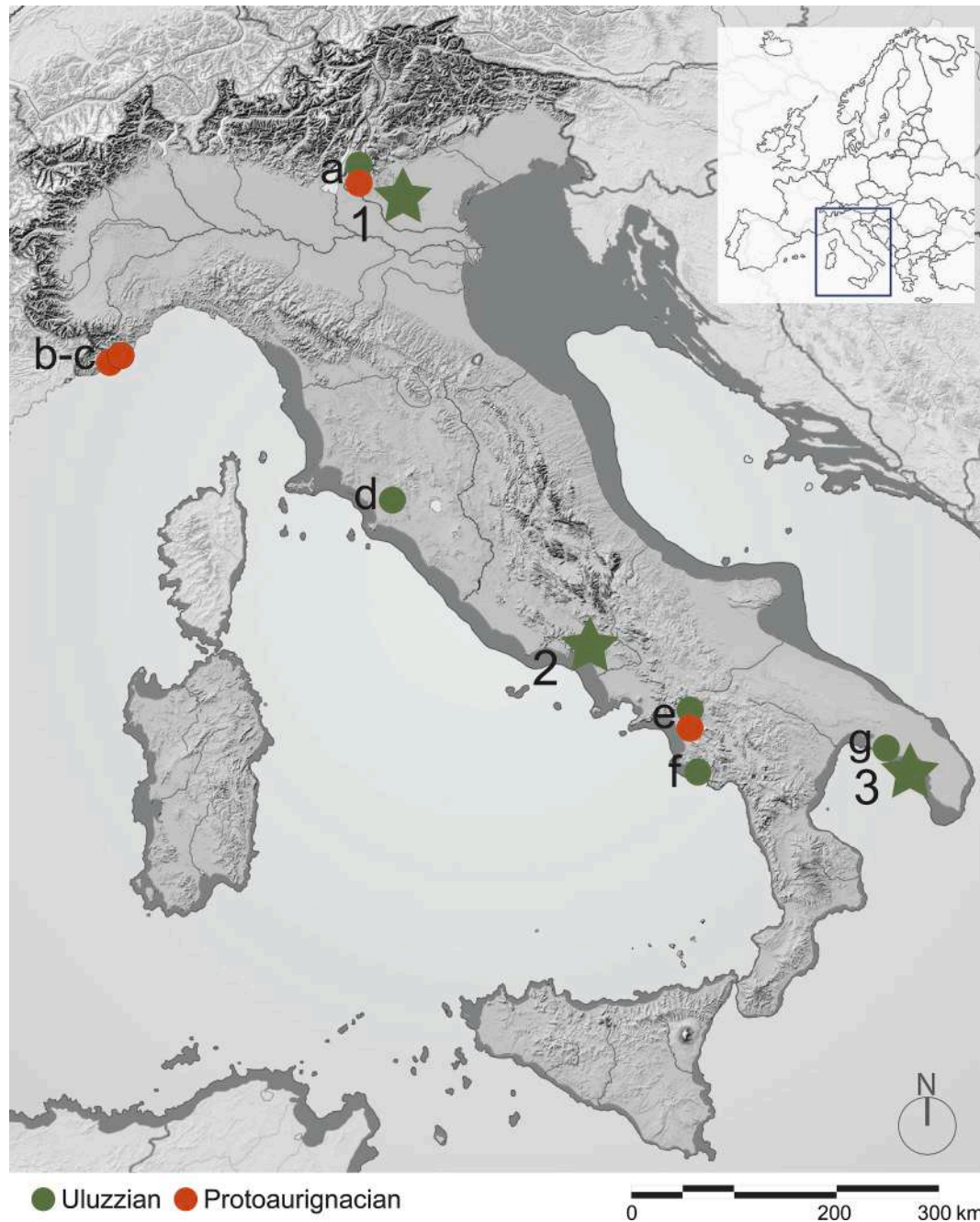


Fig. 1. MIS 3 map of Italy (modified from Moroni et al., 2018) with the geographic location of the sites analysed in this study (stars) and the sites with previously published faunal assemblages mentioned in this work (points). For each site the colours represent the presence of levels, SUs and/or layers chronologically and technologically linked respectively to the Uluzzian (green) and Protoaurignacian (orange). 1. Riparo del Broion; 2. Roccia San Sebastiano; 3. Uluzzo C; a. Grotta di Fumane; b. Riparo Bombrini; c. Riparo Mochi; d. Grotta la Fabbrica; e. Grotta di Castelcivita; f. Grotta della Cala; g. Grotta del Cavallo.

faunal assemblages (for review see Romandini et al., 2020). Research at Riparo del Broion (Peresani et al., 2019) and Grotta di Fumane (Peresani et al., 2016) in northern Italy have expanded our understanding of the Uluzzian, by showing that previously ‘believed-to-be’ southern-specific assemblages were also present elsewhere. These data are key because many sites in north-western Italy and on the southern and eastern margins of Italy’s Po Valley show a lack of comparable diagnostic evidence for this culture (Peresani, 2011; Karavanić et al., 2018; Riel-Salvatore and Negrino, 2018). However, only a limited number of Uluzzian contexts provide the chance to compare various contexts, shedding light on the transition from the Middle to Upper Palaeolithic through analyses of faunal remains, material cultures, and chronologies available only for a few sites in Italy, namely: Grotta di Fumane, Riparo del Broion, Grotta La Fabbrica, Grotta di Castelcivita, Grotta della Cala, and Grotta del Cavallo. For all of these sites archaeozoological studies, faunal exploitation patterns and related palaeoecological frameworks have been published (Tagliacozzo et al., 2013; Romandini et al., 2020; Marín-Arroyo et al., 2023; Masini and Abbazzi, 1997; Benini et al., 1997; Boscato and Crezzini, 2012). However, the published information is relatively scarce, especially considering the number of remains and the proportion of sites in relation to a territory as large and diversified as the Italian Peninsula.

Here, we present new archaeozoological data of three Italian sites with Uluzzian layers: Riparo del Broion (Longare), Roccia San Sebastiano cave (Mondragone) and Uluzzo C Rock Shelter (Nardò). The main goal is to provide new data on the economic behaviour of the human populations present at these sites and to understand their adaptation to the different biotopes available in the Italian Peninsula. We present new data on the taxonomic composition but also on carcass processing and resources exploitation and consumption, having in mind previous palaeoecological publications (Gurioli et al., 2006; Bell et al., 2018; Romandini et al., 2018; 2020; Peresani et al., 2019; Silvestrini et al., 2021; Silvestrini et al., 2022). Finally, we outlined several common elements and differences between sites sharing this culture, providing new relevant information about Uluzzians’ animal resource exploitation.

2. Regional setting

The sites included in this work are located in three different areas of Italy: Uluzzo C Rock Shelter in the south-eastern (Ionian area), Roccia San Sebastiano cave in the south-western (Tyrrhenian Area), and Riparo del Broion in the north (southern Alps) (Fig. 1).

Uluzzo C Rock Shelter (Fig. 1) is situated in Nardò, a municipality within the province of Lecce in southern Italy, on the western side of the Apulian Coast facing the Ionian Sea. During archaeological investigations, which covered an area of approximately 6 m², the stratigraphic sequence discovered includes five layers (from top to bottom): a Romanellian, a sterile, two Uluzzians and one thick Mousterian layer. A detailed overview of this context was published recently by Silvestrini et al. (2021) and Spinapolice et al. (2021). Here, we took into consideration for the archeozoological analysis the Uluzzian SUs 3, 15 + 17, 21, 22, 23 and 25 dated to 40.6 ± 1.4 ka (Spinapolice et al., 2021).

Riparo del Broion (Fig. 1) is located in the municipality of Longare (Vicenza), at the edge of the Berici Mounts karst plateau at 135 m asl. For a detailed description of the site and the excavations at Riparo del Broion, see Peresani et al. (2019) and Romandini et al. (2023). During the archaeological excavations, which covered an area of approximately 40 m², at least 20 units have been identified. Unit 1 is split in 7 levels numbered from 1a to 1g and contains the following sequence of lithic assemblages: Early Epigravettian (levels 1a-1b), Gravettian (1c-1d) and Uluzzian (1e-1f-1g), preceded by Mousterian (units 4 + 7, 9 and 11). For this site, we studied all the bone remains not included in Peresani et al. (2019) and Romandini et al. (2020), deriving from the Uluzzian level radiocarbon dated to 44,42–41,872 (95.4 %) ky cal BP (Peresani et al., 2019).

Roccia San Sebastiano cave (Fig. 1) is located in the municipality of

Mondragone, south-western Italy. Here we focused our attention on the Uluzzian sub-units which correspond to an area of 3 m² pits 27–28 in the E14-E15 trench; pits 18-t20 in F14 trench and pits 16-t18 in E16 trench. For more information about the context and the stratigraphic sequence see Collina et al. (2020) and Romandini et al. (2023). The latest dating of the Uluzzian layer (trench F14 t19) yields a chronology between 42,640 and 42,380 BP (Oxilia et al., 2022).

3. Materials and methods

We conducted a morphological and taphonomic study of the macrofaunal remains collected from the Uluzzian level of these three sites. The total number of remains studied was 22,532 from Riparo del Broion (n = 12,160), Roccia San Sebastiano cave (n = 2,264) and Uluzzo C Rock Shelter (n = 8,108). For Roccia San Sebastiano, the materials come from the excavation of trench F14 which covered an area of 1 × 1 m, whereas trench E16 covered an area of 30 × 50 cm. The sub-units were excavated in artificial pits of 5–7 cm depth, following the slope of layers and other physical markers such as archaeological features or the presence of archaeological materials. The sediment was screened with a mesh of 0.2 cm. Moreover, the taxonomic determinations obtained with ZooMS in a previous study (Silvestrini et al., 2022) were integrated in our analysis and some new indeterminate fragments were incorporated in the final sample count. For this paper, we analysed only mammal remains, thus birds were excluded.

3.1. Taxonomic and anatomical analysis

Taxonomic and skeletal identification was based on the reference collection stored at the Laboratory of Osteoarchaeology and Palaeo-anthropology (Bones Lab) of the Department of Cultural Heritage of the University of Bologna (Ravenna, Italy). All bone fragments were counted and grouped by size (0.2–1 cm, 1–2 cm, 2–3 cm, 3–4 cm, 4–5 cm, >5 cm) and by body size class (large, medium-large, medium, medium-small, and small) based on cortical bone thickness and fragment size (Romandini, 2012). Faunal remains were classified as determinate (taxonomical and anatomical identification) and indeterminate (solely anatomical identification or not even that). Age-at-death was established by bone epiphyseal fusion, tooth eruption and dental wear (Barone, 1976; Hillson, 2005; Silver, 1963). The individuals were classified in five categories: foetus, juvenile, young/adult, adult and senile (Azorit, 2011; Barone, 1976; Hillson, 2005; Mariezkurrena, 1983; Silver, 1963). To evaluate species abundance, we considered the number of identified specimens (NISP), the minimum number of individuals (MNI), the minimum number of elements (MNE), and the standardised minimal animal units (%MAU) (Binford, 1984; Brain, 1981; Lyman, 2008). Only for Roccia San Sebastiano cave, we could apply correlation between % MAU and bone density of the most abundant prey (*Cervus elaphus*), to assess the transport strategies and the attrition processes. Moreover, we correlated the %MAU with other indices to evaluate the transport and exploitation decisions: MGUI (Modified General Utility Index, Binford, 1978), FUI (Food Utility Index, Metcalfe and Jones (1988), Marrow Index, and UMI (Unsaturated Marrow Index, Morin, 2007). We applied the Spearman’s correlation coefficient to all these indices. For the other contexts, we could not obtain this information because the number of remains for each taxon is much lower than the minimum required for the calculation to be statistically significant (Faith and Gordon, 2007).

The assemblage diversity was examined through the Simpson’s Diversity Index (1-D) (Simpson, 1949). This index scores between 0 and 1. The higher the value, the greater the diversity of the assemblage (Magurran, 1988). For regional comparison, the Simpson’s Diversity Index with NISP was estimated, whenever possible.

3.2. Taphonomic analysis

The bone surface was investigated with a Leica stereomicroscope

(Leica S9i Greenough stereomicroscope with 0.61–55) to identify fractures, biotic modifications and diagenetic alterations. First, the percentage of complete vs fragmented bones and the proportion of epiphyses/diaphyses were calculated. Second, the origin of the fractures was established as fresh, dry and indeterminate (Villa and Mahieu, 1991) and also following the specific morphotypes describes by Real et al. (2022). Moreover, due to the great number of indeterminate remains –mainly in Riparo del Broion–, the length and its relation to the thermal alterations were considered to calculate the fragmentation percentage and the possible use of bones as fuel (Costamagno et al., 1999,2005; Thery-Parisot et al., 2005).

Cut-marks, percussion marks (notches, stigmas and flakes) and burnt bones were registered as anthropogenic modifications (e.g., Binford, 1981; Blumenschine, 1995; Galan et al., 2009; Pérez Ripoll, 1992; Potts and Shipman, 1981; Shipman and Rose, 1983; Vettese et al., 2020). Burnt remains were recorded according to their colouration by two groups: brown/black-charred and grey/white-calcined (Stiner et al., 1995). Different types of modifications caused by the dental action of carnivores and digestion corrosion were considered according to the definition proposed by Binford (1981), Brain (1981), Haynes (1980, 1983), Sala et al. (2012) and Sala and Arsuaga (2018). Lastly, diagenetic alterations such as weathering, concretion, erosion, manganese, trampling and roots were registered (Fernandez-Jalvo and Andrews, 2016; Lyman, 1994) to assess the state of preservation of the assemblages.

4. Results

4.1. Riparo del Broion

4.1.1. Taxonomic and anatomical composition

The analysed assemblage from this site comprises 12,160 bone remains (Table 1).

Of these, only 2.3 % were taxonomically and anatomically determined, the rest are size class (0.7 %), but mainly indeterminate remains (99.1 %). Most of them correspond to cranial and limb bones (Fig. 2). Bones classified as ungulate without further taxonomic identification are abundant (42.4 %). All of them are fragments of the skull and of limb bones (Fig. 2).

The most represented taxon is *Ursus* sp. (11.1 %) (NISP = 32). Moreover, 2.8 % of the remains have been identified as *Ursus spelaeus* and 1 % as *Ursus arctos*. The fragments of *Sus scrofa* (4.9 %), and *Cervus elaphus* (2.8 %) are also relatively abundant. Moreover, we registered Cervidae (9 %) and indeterminate carnivores (17.7 %). On the contrary, caprines and mustelids are scarce. The most represented skeletal parts of *Ursus* (considering all the bone fragments identified as *Ursus* sp., *Ursus arctos* and *Ursus spelaeus*) are cranium, hemimandible and in general the limb bones (radius, ulna and femur in particular) (Fig. 3; Suppl. Table 1).

Sesamoids, teeth, metacarpals, metatarsals and phalanges are less abundant. Regarding the most abundant ungulates registered in the assemblage (Suppl. Table 2), *Sus scrofa* is represented mainly by teeth, whereas *Cervus elaphus*, *Capreolus capreolus* and Cervidae by metapodial fragments (Fig. 3, Fig. 4). We attest in this cervid group, other main elements such as humerus, radius and femur.

4.1.2. Age-at-death

A total of 21 MNI, 12 ungulates, 8 carnivores and 1 *Lepus* sp. were calculated, based on epiphyseal fusion, dental pattern and MNE (Table 2). In this context, we identified mainly adult individuals for the different species. For *Ursus* sp., *Sus scrofa*, *Canis lupus* and *Felis silvestris* we recorded young individuals (for *Ursus* sp. also a foetal one). These elements point to spring-summer seasonality, near the time of their birth.

4.1.3. Fragmentation

The fragmentation of the assemblage is very high (Suppl. Table 3);

Table 1

Taxonomic composition for the Uluzzian level of Riparo del Broion, Roccia San Sebastiano and Uluzzo C.

Site	RB		RSS		UC	
	1g, 1e, 1f		F14 t.18, 19, 20 E16 t.16, 17, 18		3, 15 + 17, 21 + 22 + 23 + 25	
Taxa	NISP	% NISP	NISP	% NISP	NISP	% NISP
<i>Lepus</i> sp.	1	0.3	2	0.4	11	1.7
Total Lagomorpha	1	0.3	2	0.4	11	1.7
<i>Felis</i> sp.	1	0.3				
<i>Felis silvestris</i>					3	0.5
<i>Lynx lynx</i>					1	0.2
<i>Vulpes vulpes</i>	3	1.0	2	0.4	39	6
<i>Canis lupus</i>	2	0.7	1	0.2	5	0.8
<i>Mustela nivalis</i>					1	0.2
<i>Meles meles</i>	1	0.3			2	0.3
<i>Martes</i> sp.					1	0.2
Mustelidae					4	0.6
<i>Ursus spelaeus</i>	8	2.8				
<i>Ursus arctos</i>	3	1.0				
<i>Ursus</i> sp.	32	11.1				
Carnivora indet.	51	17.7			9	1.4
Total Carnivora	101	35	3	0.5	65	10
<i>Equus ferus</i>			16	2.8	21	3.2
<i>Equus</i> sp.			4	0.7		
<i>Sus scrofa</i>	14	4.9	18	3.2	17	2.6
<i>Megaloceros giganteus</i>	2	0.7	1	0.2		
<i>Alces alces</i>	2	0.7				
<i>Cervus elaphus</i>	8	2.8	117	20.6	37	5.7
<i>Dama dama</i>			2	0.4		
<i>Capreolus capreolus</i>	6	2.1	23	4.1	8	1.2
Cervidae	26	9.0	26	4.6	20	3.1
<i>Bison priscus</i>	1	0.3				
<i>Bos primigenius</i>			4	0.7		
<i>Bos/Bison</i>	3	1.0	39	6.9	9	1.4
Bovidae					3	0.5
<i>Capra ibex</i>	2	0.7				
<i>Rupicapra</i> sp.			4	0.7	3	0.5
Caprinae			3	0.5	6	0.9
Ungulata	122	42.4	305	53.8	449	69.2
TOTAL Ungulata	186	64.6	562	99.1	573	88.3
TOTAL DET.	288	2.3	567	25	649	8
Small sized mammals	12	0.1	42	2.5	38	0.5
Small-medium sized mammals	2	0	40	2.4	40	0.5
Medium sized mammals	3	0	179	10.5	42	0.6
Medium-large sized mammals	41	0.3	571	33.6	63	0.8
Large sized mammals	38	0.3	19	1.1	23	0.3
Indet. sized mammals	11776	99.1	846	49.9	7253	97.2
TOTAL INDET.	11872	97.6	1697	75	7459	92
TOTAL NR	12160		2264		8108	

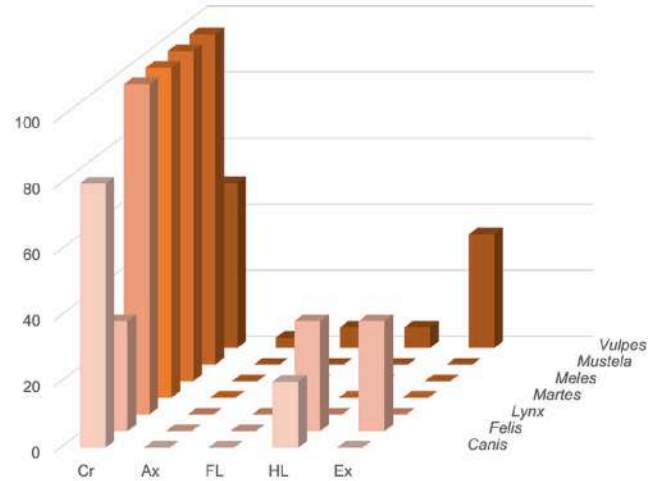
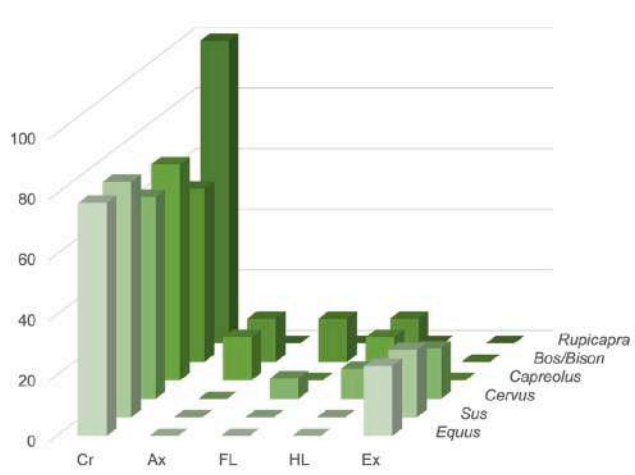
only 21 are complete bones and 96.9 % of the fragmented bones are less than 3 cm. If we analyse the size of the remains, the number of determinate specimens per length interval is evenly distributed from 0 to 1 to > 5 (Fig. 5). The indeterminate remains, however, are concentrated on less than 1 cm (64.2 %) or between 1–2 cm (28.7 %).

Considering the determinate remains, the complete bones are teeth, sesamoids, and phalanges mainly of *Ursus*. Fresh fractures are abundant and represented by diaphyses of long bones without complete circumference (Fig. 6; Suppl. Table 4). Metapodia are almost represented by fragmented diaphyses too and, phalanges are characterised mainly by fragmented epiphyses.

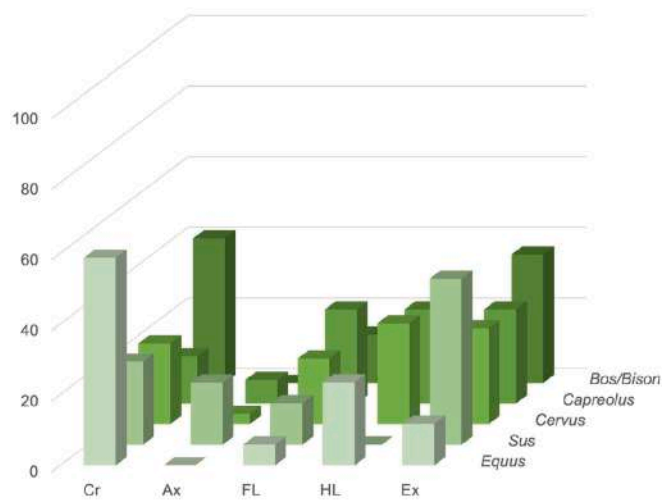
4.1.4. Modifications

Diagenetic alterations affect around 50 % of the assemblage and include mainly manganese (30 %) and concretions (23.5 %) (Table 3).

Riparo del Broion



Roccia San Sebastiano



Uluzzo C

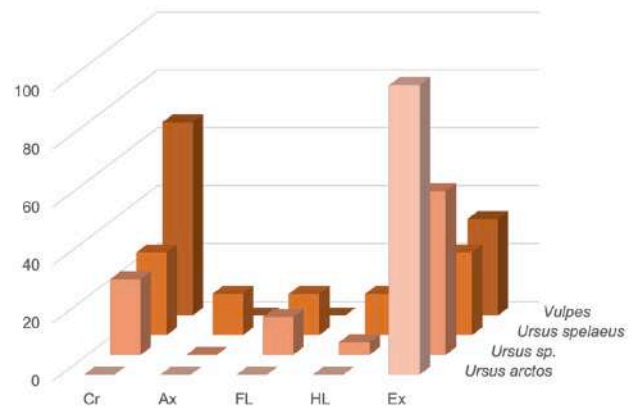
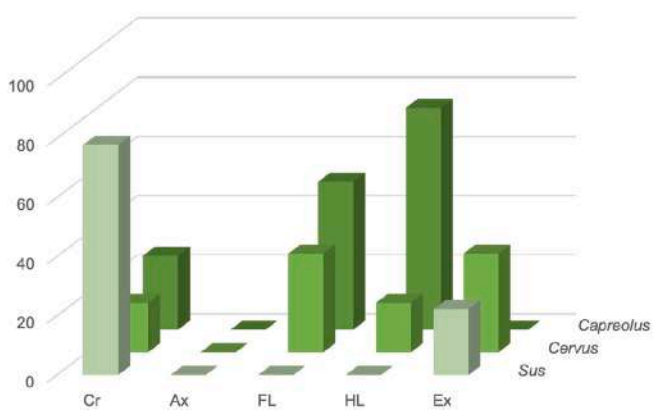


Fig. 2. Anatomical representation of all the determined species of Riparo del Broion, Roccia San Sebastiano and Uluzzo C. Abbreviation: cranial (Cr), axial (Ax), forelimbs (FL), hindlimbs (HL) and extremities (Ex).

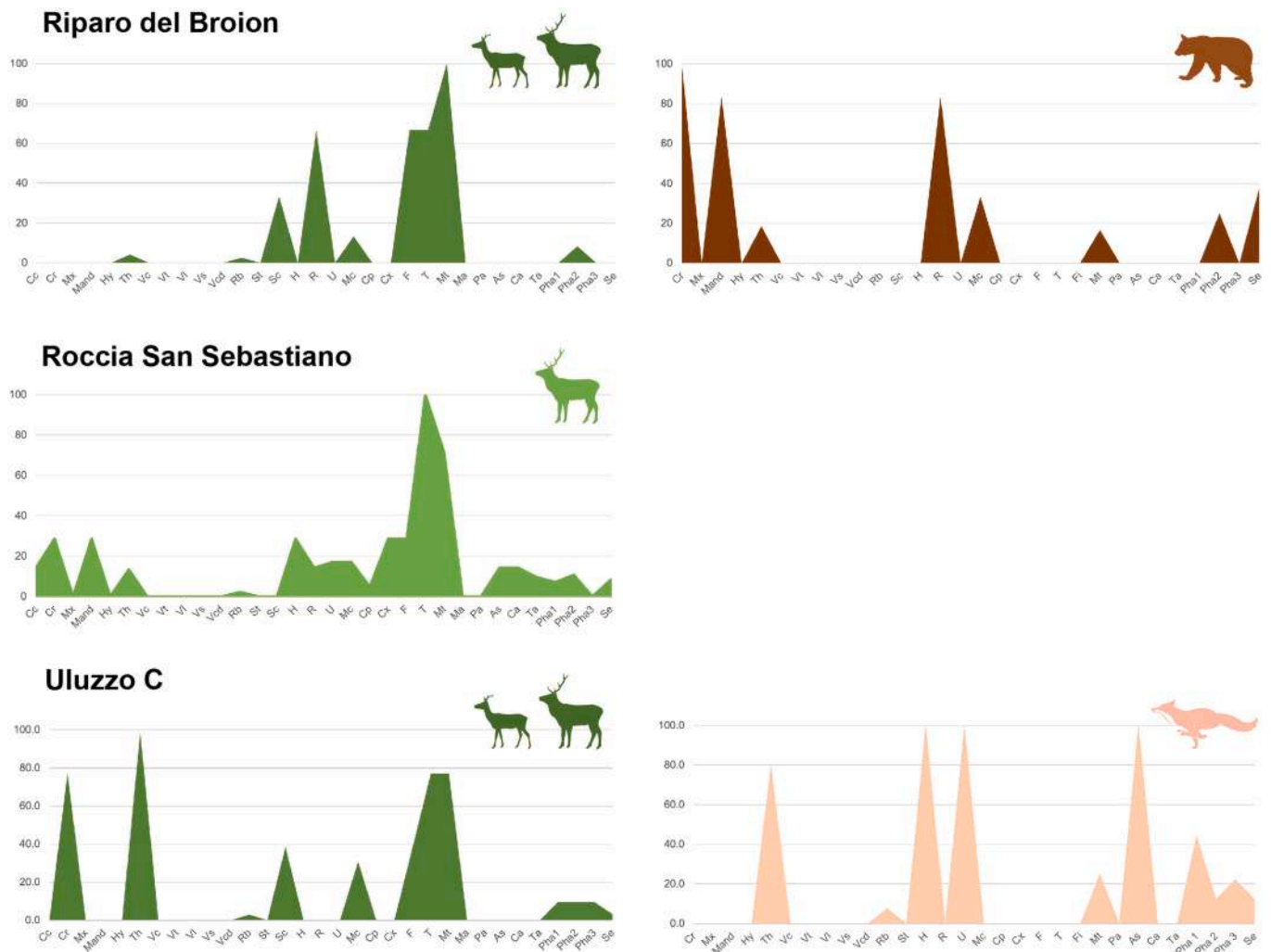


Fig. 3. Anatomical representation of the main taxa in the sites based on %MAU. Abbreviation: Cc (Antler/Horn), Cr (cranium), Mx (maxilla), Mand (mandible), Hy (Hyoid), Th (Teeth), Vc (cervical vertebra), Vt (thoracic vertebra), Vl (lumbar vertebra), Vs (sacrum vertebra), Vcd (caudal vertebra), Rb (rib), St (Sternum), Sc (scapula), H (humerus), R (radius), U (ulna), Mc (metacarpal), Cp (carpal), Cx (coxal), F (femur), T (tibia), Fi (Fibula), Mt (metatarsal), Ma (malleolus), Pa (patella), As (astragalus), Ca (calcaneus), Ta (tarsal), Pha (phalange), Se (sesamoid).

Modifications are documented on 4,067 bone remains (33.6 %) (Table 4), all of them have an anthropogenic origin.

After thermal alterations, we recognised mainly percussion flakes on indeterminate and ungulate bones (42) and very few percussion marks (7). We identified a percussion mark on the diaphyses of *Alces alces* humerus (Fig. 7), Cervidae tibia and metapodial, and *Ursus* sp. radio.

Regarding cut-marks (16), we found striae on several Cervidae diaphyses (7). There are also slicing marks on diaphyses of ungulate and on a rib of a carnivore. These modifications could be related to e.g. defleshing.

Burnt bones are very abundant in this context (NR = 4,001) (Table 5). This alteration affects almost entirely indeterminate remains (33.7 %). Charred degree (19.5 %) is the best-represented, although in this context we recorded a similar percentage of calcination (13.4 %).

4.2. Roccia San Sebastiano cave

4.2.1. Taxonomic and anatomical composition

The analysed assemblage is composed of 2,264 remains. Of these, 25 % were taxonomically and anatomically determined, and 75 % remained undetermined (Table 1). The most represented taxon is *Cervus elaphus* (20.3 %) (NISP = 117); relatively abundant are also the fragments of *Bos/Bison* (6.8 %), *Capreolus capreolus* (4 %), and *Sus scrofa*

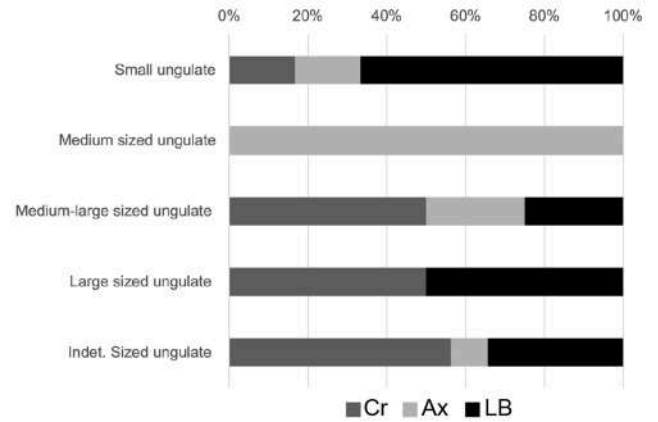
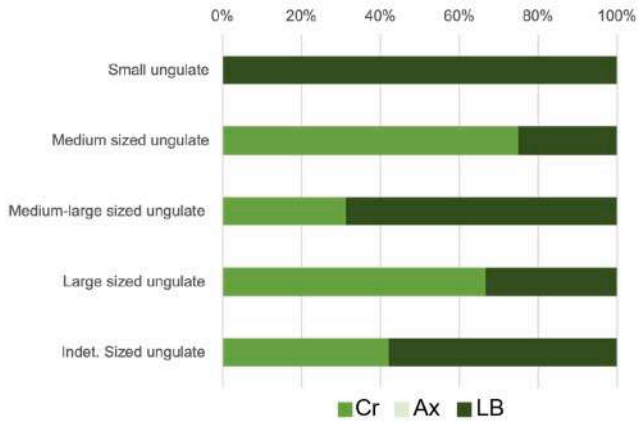
(3.1 %). On the contrary, caprines, carnivores and small taxa are scarce. Carnivores are only represented by an ulna of *Canis lupus* and a rib and a tarsal of *Vulpes vulpes*. A tibia and a vertebra correspond to *Lepus* sp.

In the case of red deer, hind limbs, extremities and the cranial skeleton (mainly teeth) are the best-represented groups, between 23–29 % (Fig. 2). On the other hand, as the %MAU shows, tibia, hemimandible, humerus and metatarsal are prominent (Fig. 3). Radius, ulna, metacarpal and phalanges are less abundant, while vertebrae, maxilla and sternum are totally absent. The %MAU and the bone density of *Cervus elaphus* show a significant correlation (Table 6). Thus, post-depositional processes could explain the absence of different groups or anatomical elements. We also compared the %MAU with other utility indices (Table 6) and, there is a positive correlation with the Marrow index and the Unsaturated Marrow Index (UMI).

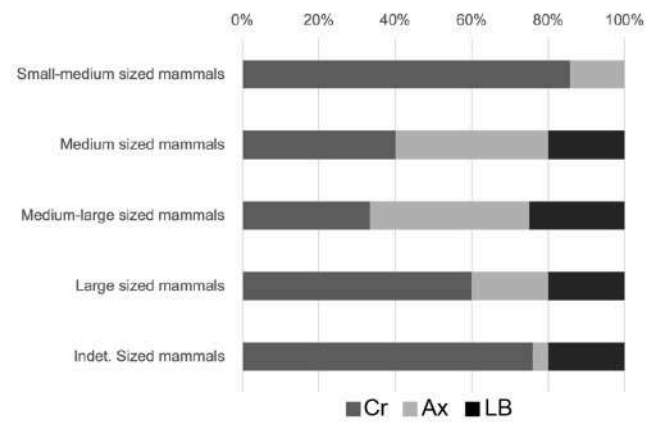
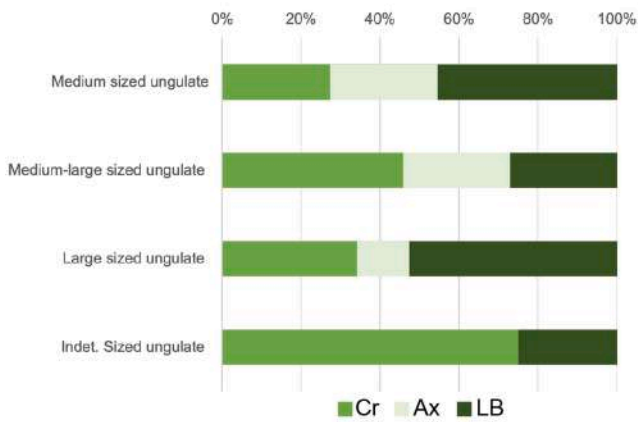
Regarding the other most abundant species registered in the assemblage, *Sus scrofa* and *Bos/Bison* are represented mainly by teeth, hemimandibles and indeterminate phalanges, whereas for *Capreolus capreolus* we identified several bones belonging to the posterior limbs (metatarsals and tibias) (Fig. 2; Suppl. Table 5).

The bones classified as ungulate without further taxonomic identification are abundant (53 %). Most of them are fragments of cranial and limb bones (Fig. 4). The indeterminate remains are represented mainly by fragments of indeterminate animals (49.9 %) and bones from

Riparo del Broion



Roccia San Sebastiano



Uluzzo C

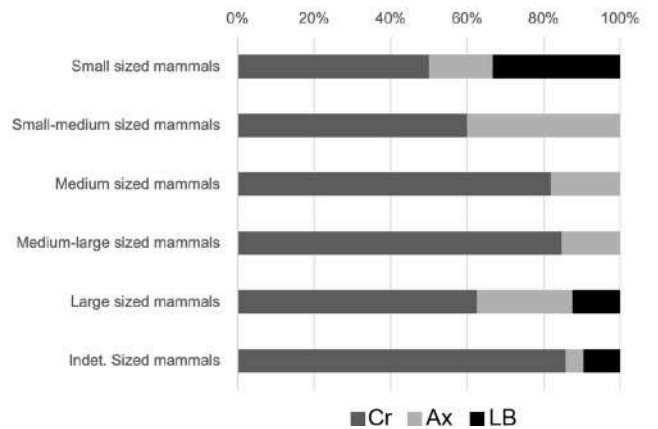
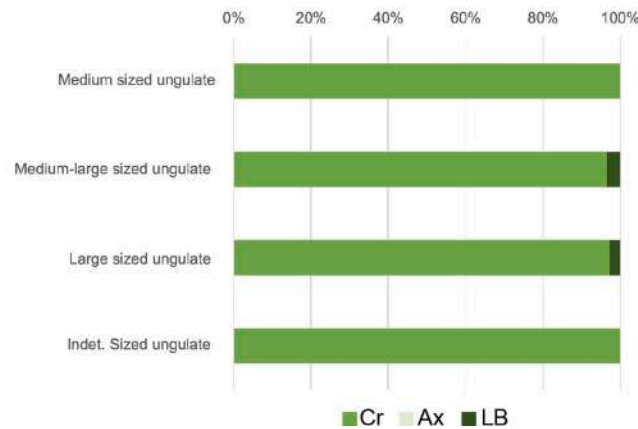


Fig. 4. Anatomical representation of indeterminate ungulates (green column) and indeterminate sized mammals (grey column). Abbreviation: cranial (Cr), axial (Ax), long bones (LB).

medium-large-sized animals (33.6 %) and medium-sized animals (10.5 %). Most of them correspond to cranial and axial groups (Fig. 5).

4.2.2. Age-at-death

We counted a total of 21 MNI: 12 ungulates, 8 carnivores and 1 lagomorph (Table 2), following the methods outlined above. Adults stand out in the case of red deer and roe deer. We recorded senile individuals only for *Cervus elaphus* and *Equus ferus*. Juvenile individuals

are represented by epiphyses of unfused long bones such as tibia or radius in the case of *Capreolus capreolus* and of deciduous teeth for *Equus ferus*. This evidence suggests that the site was seasonally frequented during summer.

4.2.3. Fragmentation

The fragmentation of the assemblage is high; only 1.2 % are complete bones, mainly teeth and sesamoids (Suppl. Table 6), and 77.1 % of

Table 2

MNI and age estimation for all the determined species from Riparo del Broion, Roccia San Sebastiano and Uluzzo C. Abbreviation: Foetus (F), Juvenile (J), Young/Adult (Y-A), Adult (AD), Senile (S).

	RB MNI	RSS MNI	UC MNI
<i>Lepus</i> sp.	1AD	1	3AD
<i>Felis</i> sp.	1Y		
<i>Felis silvestris</i>			2: 2AD
<i>Lynx lynx</i>			1
<i>Vulpes vulpes</i>	1AD		7: 2Y, 4AD, 1S
<i>Canis lupus</i>	2: 1Y, 1AD	1AD	3: 1AD, 1Y-A, 1S
<i>Mustela nivalis</i>			1
<i>Meles meles</i>	1		2: 1AD, 1S
<i>Martes</i> sp.			1Y
<i>Ursus spelaeus</i>	2: 2AD		
<i>Ursus arctos</i>	1AD		
<i>Ursus</i> sp.	2: 1F, 1Y		
<i>Equus ferus</i>		2: 1G, 1AD-S	5: 1Y, 1Y-A, 3AD
<i>Sus scrofa</i>	4: 2Y, 1Y-A, 1AD	3: 1Y-A, 1Y, 1 AD	4: 1Y, 1Y-A, 2AD
<i>Megaloceros giganteus</i>	1AD		
<i>Alces alces</i>	1AD		
<i>Cervus elaphus</i>	2: 1Y, 1AD	5: 1Y, 1S, 3AD	8: 5AD, 2Y-A, 1Y
<i>Dama dama</i>		1	
<i>Capreolus capreolus</i>	2: 2AD	3: 1Y, 2AD	2: 1AD-S, 1Y
<i>Bison priscus</i>	1		
<i>Bos/Bison</i>	1AD	2: 1Y, 1AD	4: 3AD, 1Y
<i>Capra ibex</i>	2: 2AD		
<i>Rupicapra</i> sp.		1AD	2: 1Y-A, 1AD
Total	25	18	45

the fragmented bones are less than 3 cm. Most of the determinate ungulate species are between 2–3 and 1–2 cm of length, and between 2–3 and 3–4 cm in the case of indeterminate ungulate bones. Regarding the remains classified by size, 1–2 and 2–3 cm of length are the main intervals, with a higher predominance of 1–2 cm among indeterminate sized mammals (Fig. 5).

Fresh fractures are present mainly on long bones and metapodia (Suppl. Table 7). For *Cervus elaphus*, the proportion of anatomical parts shows a predominance of diaphyses without complete circumference, as well as few distal parts of the humerus and radius/ulna and proximal parts of the femur (Fig. 6). Phalanges are characterised mainly by epiphyses, but also fragments of diaphyses in the case of the first phalanx.

4.2.4. Modifications

Regarding diagenetic alterations, 27.8 % of the remains are characterised by a manganese coating, only 0.5 % have concretions and 2.9 % have root furrows on the bone surface (Table 3). We therefore had no difficulties with the analysis of bone surfaces.

Modifications are documented on 842 bone remains (Table 4). Anthropogenic modifications are the only type of marks registered and include cut-marks (12.1 %), percussion marks (9 %), and burnt bones (78.9 %). Regarding cut-marks, the majority is concentrated on the diaphyses of indeterminate bones (58), ungulate (19) and on red deer (14). Noteworthy, most of the slicing marks on *Cervus elaphus* are concentrated on long bones (humerus, femur and tibia) and metapodia, as a result of the defleshing process (Fig. 8). There are also two small slicing marks on the ilium and, on the exterior zone of a mandible, perhaps related to the skinning phase. We also identified cut-marks on a first phalanx and a coxal bone of *Sus scrofa*, on the ilium and an ulna of *Rupicapra* sp., on a metacarpal and a radius of *Bos/Bison* (Fig. 8), on a metatarsal of *Capreolus capreolus* and on the distal epiphyses of the tibia of *Equus ferus*.

In relation to the percussion marks, we reported 17 notches and 59 percussion flakes mainly on indeterminate remains, ungulate, and *Cervus elaphus* remains. In the case of red deer, the notches are on diaphyses of long bones (femur, radius and metapodial) (Fig. 8), and the

percussion flake on a metacarpal diaphyses.

In the other ungulates, direct fractures are also present on the tibia, mandible, and coxal. Moreover, a percussion notch associated with two flakes has been registered on the distal part of the diaphyses of an *Equus* tibia (Fig. 7).

Burnt bones are abundant (NR = 665), present almost on 30 % of the assemblage (Table 4) and more frequently present as indeterminate remains. This alteration on determinate bones affects mainly ungulates and Cervidae species. Charred degree (24.8 %) is the best-represented, although calcination (4.5 %) is also present among indeterminate remains (Table 5).

4.3. Uluzzo C Rock Shelter

4.3.1. Taxonomic and anatomical composition

The total analysed assemblage from this site comprises 8,108 remains (Table 1). Of these, 8 % were taxonomically and anatomically determined. The most represented taxon is *Vulpes vulpes* (6 %) and slightly less abundant are the fragments of *Cervus elaphus* (5.7 %). The remains of *Equus ferus* (3.2 %), and *Sus scrofa* (2.6 %) are more scarce. Owing to the conspicuous presence of *Vulpes vulpes*, *Canis lupus*, *Felis silvestris*, *Lynx lynx*, and undetermined Carnivora, the carnivorous component of the site is considerable. Moreover, we identified some remains of mustelids (NISP = 8). *Capreolus capreolus*, *Bos/Bison* and *Rupicapra* sp. are also attested.

We calculate the anatomical composition for the ungulates and carnivores, and all are represented mainly by teeth and phalanges (Fig. 2; Suppl. Tables 8 and 9), even the indeterminate ungulate (Fig. 4).

In the case of red fox, as showed by the %MAU, teeth are prominent; the humerus, ulna and astragalus are abundant, as are metatarsals and phalanges (in particular I) (Fig. 3). Among the ungulates, the Cervidae family is the main represented group (10.02 %), but the anatomical groups are poorly represented, showing only cranial fragments and hindlimbs (femur, tibia and metatarsal) (Fig. 3).

The indeterminate remains (92 %) are represented mainly by fragments of indeterminate animals (97.2 %). Among the size class, medium-large and medium are better represented mostly by fragments of cranial elements (Fig. 4).

4.3.2. Age-at-death

All age groups/categories are represented in this context, mainly adult and juvenile individuals (Table 2). In the case of adults, we counted 25 MNI of ungulates, 10 of carnivores and 3 of *Lepus* sp. *Cervus elaphus* (NMI = 8) represents the most abundant species in this context together with *Vulpes vulpes* (NMI = 7). Senile individuals were registered for a few taxa (*Vulpes vulpes*, *Canis lupus*, *Capreolus capreolus* and *Meles meles*). We also identified some young individuals for *Capreolus capreolus*, *Cervus elaphus*, *Bos/Bison* and *Vulpes vulpes*, pointing to a possible seasonality of the occupations during spring-summer.

4.3.3. Fragmentation

The fragmentation of the assemblage is very high; only 0.6 % are complete bones and 98.3 % of the fragmented bones are less than 3 cm. If we consider the determinate remains, the complete bones are mainly phalanges and teeth (Suppl. Table 10). The range of length of determinate remains (determinate ungulates and carnivores) is 1–2 and even 2–3; but 73.7 % of the indeterminate ungulates are less than 1 cm (Fig. 5). In the case of indeterminate remains, they are mainly less than 1 cm.

Fresh fractures are the most abundant type in the determinate remains and we recognised them mainly on fragmented diaphyses of long bones, e.g., femur and tibia (Fig. 6; Suppl. Table 11). Metatarsals and metacarpals are almost all represented by fragmented diaphyses and distal epiphyses. Phalanges are characterised mainly by epiphyses with part of diaphyses. In the case of cervids, however, fragments correspond



Fig. 5. Length variability for determinate remains (ungulates and carnivores) and indeterminate remains (sized and indeterminate-sized mammals) of Riparo del Broion, Roccia San Sebastiano and Uluzzo C.

entirely to diaphyses.

4.3.4. Modifications

Regarding diagenetic alterations, bone surfaces are characterised by two main agents: manganese (67.7 %) and concretions (71.6 %) (Table 3). These alterations have hampered the identification of the biotic modifications on the surface of the bones. Modifications are documented on 1,144 bone remains and are all from an anthropogenic origin (Table 4). Fire alteration is the most common modification recorded on the assemblage (NR = 1,121) and it affects almost entirely indeterminate remains (Table 5). Charred degree (13.6 %) is the best-represented, thus calcinate bones are only 0.2 % of the assemblage.

We also registered percussion flakes on indeterminate and ungulate bones (14) and only one percussion notch on an indeterminate specimen (Table 4). Regarding cut-marks (8), we identified other butchering traces (in addition to Silvestrini et al., 2021), on the fragment of a tibia and a metacarpal of *Cervus elaphus* and on the diaphyses of an indeterminate bone of an ungulate.

5. Discussion

5.1. Riparo del Broion, Roccia San Sebastiano and Uluzzo C: Comparison of the exploitation patterns

The Uluzzian levels of the southern Italy sites examined in this study (Roccia San Sebastiano cave and Uluzzo C) show similar taxonomic spectra. The most represented taxa in Uluzzo C are red fox (6 %) and red deer (5.7 %). Unlike Roccia San Sebastiano, the carnivorous component is significant in this context. At Uluzzo C, the few recognized butchering traces are concentrated mainly on the diaphyses of long bones of red deer. Thus, we considered that the economic activity of the human groups in this level was focused on this animal. The data obtained from the anatomical composition outlined a prominent presence of teeth for all the species. This could be related to the greater resistance of dental enamel to taphonomic and diagenetic factors than bone (Hillson, 2005; Scott, 2008). For Roccia San Sebastiano, where the taphonomic conditions of bone surfaces are better, the exploitation of red deer (20.6 %) is

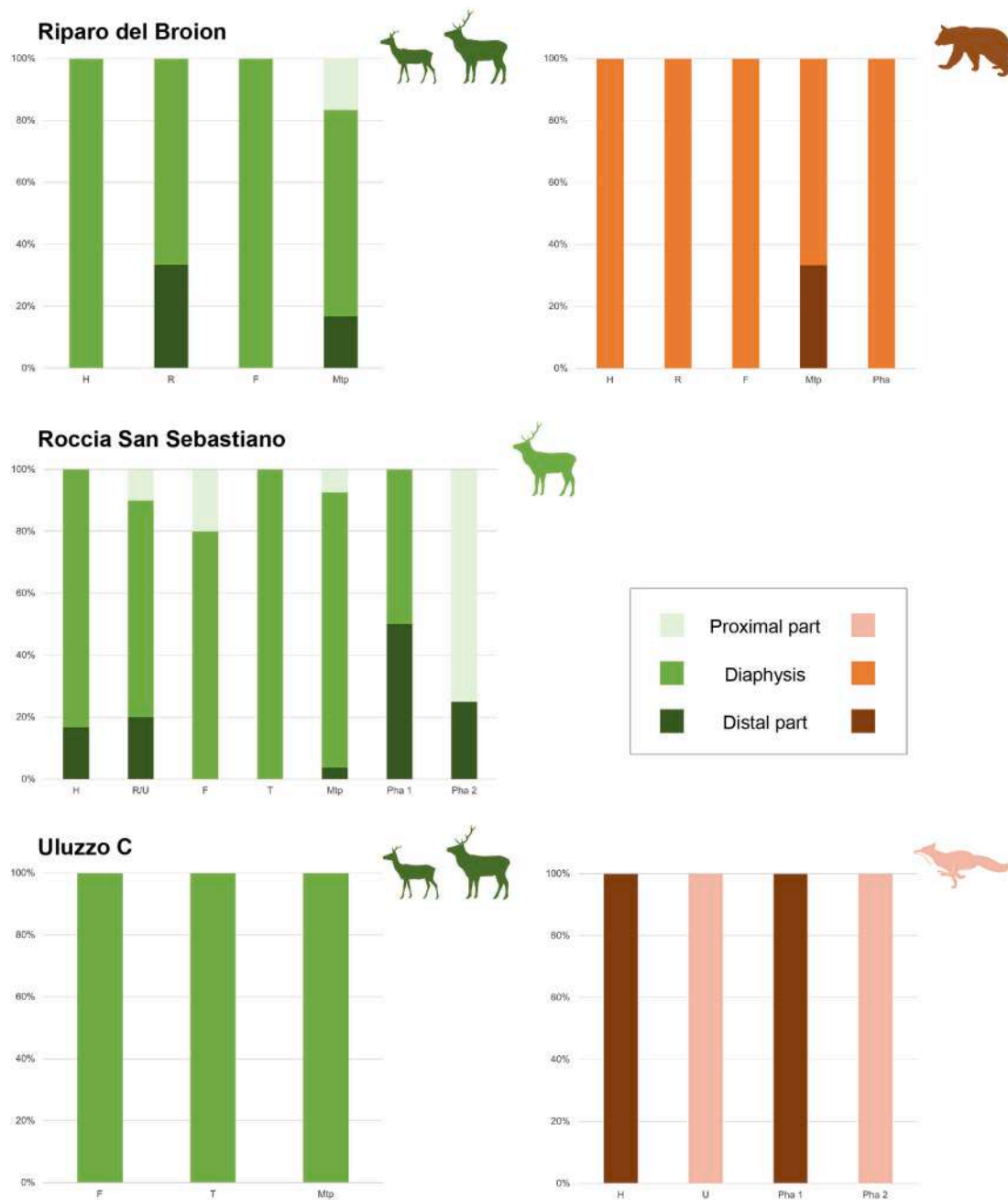


Fig. 6. Anatomical parts of long bones, metapodials and phalanges of the main species of Riparo del Broion, Roccia San Sebastiano and Uluzzo C. For bones abbreviation see Fig. 3.

Table 3
Diagenetic alterations registered at Riparo del Broion, Roccia San Sebastiano and Uluzzo C.

Site	RB		RSS		UC	
	NISP	%NISP	NISP	%NISP	NISP	%NISP
Roots	116	1.0	66	2.9	24	0.3
Corrosion	192	1.6	3	0.1	25	0.3
Exfoliation	7	0.1	21	0.9	9	0.1
Flutiation	7	0.1	4	0.2	8	0.1
Manganese	3647	30.0	629	27.8	5487	67.7
Concretions	2861	23.5	11	0.5	5802	71.6
Trampling	2	0.0	3	0.1	10	0.1
Wethering	–	–	1	0.0	6	0.1

predominant compared to the other ungulates. In this context, the carnivorous component is almost absent. We reported anthropogenic modifications (cut-marks and percussion marks) generally on long bones of medium-large sized ungulates. Based on these modifications, as well as on the fresh fractures recorded, the hunting of these animals is likely associated with the exploitation of meat and marrow of long bones and metapodia. There is also evidence of marrow exploitation from other elements with smaller medullary cavities such as mandibles or phalanges. First and second phalanges from red deer (90 %) but also from all ungulates (94.8 %) were splintered systematically for marrow extraction, as these elements are rich in unsaturated grease acids (Morin, 2007). Slicing marks indicate that at least not only red deer but also other ungulates (wild boar, equids, chamois) were skinned, disarticulated and defleshed.

A different pattern of faunal composition and exploitation are

Table 4
Anthropogenic modifications by taxa of Riparo del Broion, Roccia San Sebastiano and Uluzzo C.

	Anthropogenic modifications		percussion mark		percussion flake		burnt bones	
	NISP	%NISP	NISP	%NISP	NISP	%NISP	NISP	%NISP
Riparo del Broion 1g,1e,1f								
<i>Ursus</i> sp.			1	3.1			2	6.3
Carnivora	1	3.9						
<i>Sus scrofa</i>							1	7.1
<i>Alces alces</i>			1	50				
<i>Capreolus capreolus</i>							1	16.7
Cervidae	7	26.9	2	7.7				
Ungulata	2	1.6			12	9.8	1	0.8
TOTAL DET	10	3.5	4	1.4	12	4.2	5	1.7
Small sized mammals	1	8.3					1	8.3
Small-medium sized mammals	1	50					1	50
Medium sized mammals								
Medium-large sized mammals					2		6	
Large sized mammals			1	2.6	6	15.8		
Indet. sized mammals	4	0.03	2	0.02	22	0.2	3988	33.9
TOTAL INDET	6	0.04	3	0.03	30	0.3	3996	33.7
TOTAL REMAINS	16	0.1	7	0.1	42	0.3	4001	32.9
Roccia San Sebastiano F14 t.18, 19, 20 E16 t.16, 17, 18								
<i>Equus ferus</i>	1	6.3	1	6.3	1	6.3		
<i>Sus scrofa</i>	2	11.1					2	11.1
<i>Cervus elaphus</i>	14	12	4	3.4	1	0.9	19	16.2
<i>Dama dama</i>							1	50
<i>Capreolus capreolus</i>	2	8.7	1	4.3			4	17.4
Cervidae	2	7.7					1	3.8
<i>Bos primigenius</i>								
<i>Bos/Bison</i>	2	5.1	2	5.1			3	7.7
<i>Rupicapra</i> sp.	2	50						
Ungulata	19	6.2	5	1.6	6	2	54	17.7
TOTAL DET	44	7.7	13	2.3	8	1.4	84	14.6
Small sized mammals								
Small-medium sized mammals					1	2.5	32	80
Medium sized mammals	4	2.2			6	3.4	63	35.2
Medium-large sized mammals	18	3.2	1	0.2	12	2.1	181	31.7
Large sized mammals	2	10.5	1	5.3	3	15.8	4	21.1
Indet. sized mammals	34	4	2	0.2	29	3.4	300	35.2
TOTAL INDET	58	3.4	4	0.2	51	3	580	34.2
TOTAL REMAINS	102	4.5	17	0.8	59	2.6	664	29.3
Uluzzo C 3, 15+17, 21+22+23+25								
<i>Lepus</i> sp.	1	9.1					2	18.2
Carnivora							1	11.1
Bovidae	1	33.3						
<i>Sus scrofa</i>							1	5.9
<i>Cervus elaphus</i>	2	5.4						
Cervidae							1	5
Ungulata	3	0.7			3	0.7	14	3.1
TOTAL NISP	7	1			3	0.4	19	2.9
Small sized mammals							4	10.5
Small-medium sized mammals			1	2.5	1	2.5	6	15
Medium sized mammals							3	7.1
Medium-large sized mammals	1	1.6			1	1.6	6	9.5
Large sized mammals							2	8.7
Indet. sized mammals					9	0.1	1081	14.9
TOTAL INDET	1	0	1	0	11	0.1	1102	14.8
TOTAL REMAINS	8	0.1	1	0.01	14	0.2	1121	13.8

outlined for Riparo del Broion. In this study we considered all the faunal data examined here and in previous studies (Peresani et al., 2019; Romandini et al., 2020), obtaining the most complete picture of the Uluzzian faunal assemblage of this site to date (Table 7).

Furthermore, using ZooMS (Silvestrini et al., 2022), it was possible to increase the NISP of this context. Comparing the available results, the trend outlined in the first studies is confirmed, but we also identified some new taxa: e.g., *Ursus arctos* (NISP = 3), *Canis lupus* (NISP = 2) and

Meles meles (NISP = 1). Indeed, in the present study, the percentage of carnivorous species in the Uluzzian levels has increased. We identified here only one *Lepus* bone, unlike what was previously reported, as well as few remains of marmot (NISP = 3) and beaver (NISP = 1). On the other hand, the percentage of bovids within the context remains low, while the presence of wild boar is more conspicuous. Among ungulates, *Rupicapra rupicapra* is the only species not attested in our recent study, which is instead registered in Romandini et al. (2020) and Peresani et al.

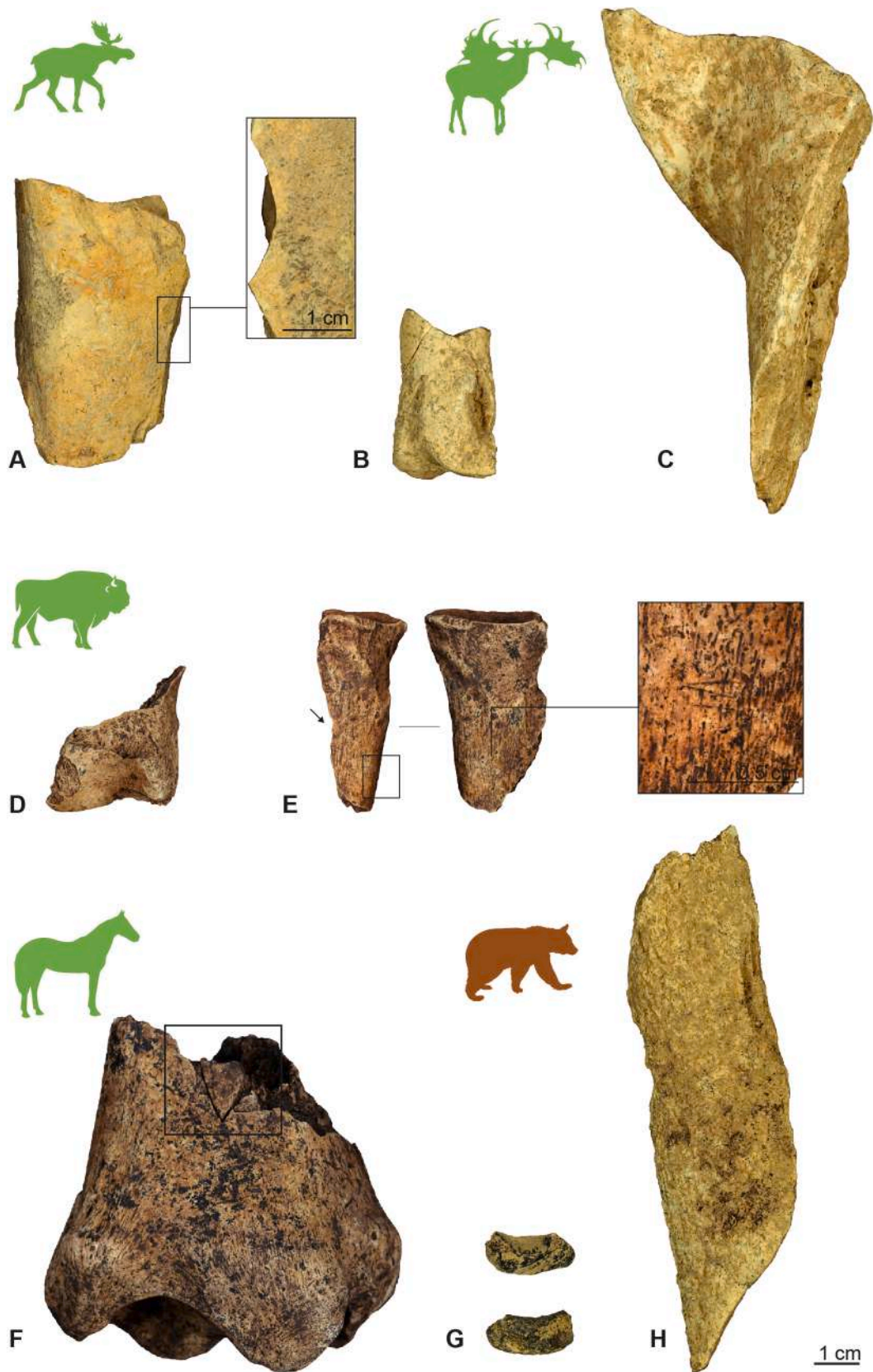


Fig. 7. Anthropogenic modifications on *Alces alces* (A, B), *Megaloceros giganteus* (C), *Bos/Bison* (D, E), *Equus ferus* (F) and *Ursus* sp. (G, H) from Riparo del Broion and Roccia San Sebastiano.

Table 5

Burnt bones of Riparo del Broion, Roccia San Sebastiano and Uluzzo C classified by the colour (charred: black-brown, calcined: grey-white).

	Charred		Calcined		TOTAL	
	NISP	% NISP	NISP	% NISP	NISP	%
Riparo del Broion 1 g, 1e, 1f						
<i>Ursus</i> sp.	2	6.3			2	6.3
<i>Sus scrofa</i>	1	7.1			1	7.1
<i>Capreolus capreolus</i>			1	16.7	1	16.7
Ungulata	1	0.8			1	0.8
TOTAL DET	4	1.4	1	0.3	5	1.7
Small sized mammals	1	8.3			1	8.3
Small-medium sized mammals	1	50			1	50
Medium sized mammals						
Medium-large sized mammals	4	9.8	2	4.9	6	14.6
Large sized mammals						
Indet. Sized mammals	2364	20.1	1624	13.8	3988	33.9
TOTAL INDET	2370	20	1626	13.7	3996	33.7
TOTAL	2374	19.5	1627	13.4	4001	32.9
Roccia San Sebastiano F14 t.18, 19, 20 E16 t.16, 17, 18						
<i>Sus scrofa</i>	2	11.1			2	11.1
<i>Cervus elaphus</i>	19	16.2			19	16.2
<i>Dama dama</i>	1	50			1	50
<i>Capreolus capreolus</i>	4	17.4			4	17.4
Cervidae	1	3.8			1	3.8
<i>Bos/Bison</i>	3	7.7			3	7.7
Ungulata	54	17.7			54	17.7
TOTAL DET	84	14.8			84	14.8
Small-medium sized mammals	32	80			32	80
Medium sized mammals	61	34.1	2	10.1	63	35.2
Medium-large sized mammals	133	23.3	48	8.4	181	31.7
Large sized mammals	2	10.5	2	10.5	4	21.1
Indet. Sized mammals	250	29.4	50	5.9	300	35.3
TOTAL INDET	478	28.2	102	6	580	34.2
TOTAL	562	24.8	102	4.5	664	29.3
Uluzzo C 3, 15 + 17, 21 + 22 + 23 + 25						
<i>Lepus</i> sp.	2	18.2			2	18.2
Carnivora	1	11.1			1	11.1
<i>Sus scrofa</i>	1	5.9			1	5.9
Cervidae	1	5			1	5
Ungulata	14	3.1			14	3.1
TOTAL DET	19	2.9			19	2.9
Small sized mammals	4	10.5			4	10.5
Small-medium sized mammals	6	15			6	15
Medium sized mammals	3	7.1			3	7.1
Medium-large sized mammals	5	7.9	1	1.6	6	9.5
Large sized mammals	2	8.7			2	8.7
Indet. Sized mammals	1065	14.7	16	0.2	1081	14.9
TOTAL INDET	1085	14.5	17	0.2	1102	14.8
TOTAL	1104	13.6	17	0.2	1121	13.8

(2019) (NISP = 4). The most represented taxon is *Ursus* sp. (11.2 %); relatively abundant are also wild boar (8.7 %) and *Ursus spelaeus* (7.2 %). Red deer (3.2 %) is registered but is not so abundant as in the other contexts included in our study, although if we consider all the Cervidae remains together this could increase the relative importance of red deer as hunted prey (%NISP of Cervidae: 9.7 %). The total absence of horse remains emphasises a marked difference in climate and palaeoenvironment (with more closed and wooded spaces) available to Uluzzo human groups in north-eastern Italy compared to those in the south.

At Riparo del Broion, we identified very few anthropogenic

Table 6

Spearman's rank correlation analysis for *Cervus elaphus* in Roccia San Sebastiano. Spearman correlations are calculated between %MAU and bone density and the following indices: Meat, Marrow, MGUI (Modified General Utility Index), FUI (Food Utility Index), UMI (Unsaturated Marrow Index) and Meat storage. Spearman correlation coefficients and *p*-values are reported. Significant results are highlighted in bold ($p < 0.001$).

<i>Cervus elaphus</i> Indices	Spearman	<i>p</i>
Density	0.7917	0.000016
Meat	-0.015	0.472428
Marrow	0.6891	0.000098
(S)MGUI	0.0766	0.357384
FUI	0.2387	0.1948195
UMI	0.8961	0.000094
Meat-storage	-0.657	0.007353

modifications, also due to the high fragmentation of the remains (82.4 % of the fragments are less than 1 cm- see [Suppl. Table 12](#)) and the presence of concretions on the bone surface, making the characterisation of the carcass treatment more challenging. Apart from burned bones, evidence of anthropic actions is very scarce (also by [Romandini et al. \(2020\)](#) only 16 remains were documented with cut-marks and 11 with percussion marks). For example, when examining red deer, we found evidence of butchering only on a tibia and a metacarpal. Nevertheless, we can highlight the Broion assemblage for the large number of burned remains ($n = 4001$) compared to Uluzzo C ($n = 1102$) and Roccia San Sebastiano cave ($n = 665$). Thermal alterations affect 45.4 % of the Broion remains and most of them are indeterminate fragments. This quantity added to the high proportion of calcinate fragments (20 %) (see [Suppl. Table 13](#)) and the very small size (0.2–1 cm) of both determinate and indeterminate remains, may suggest that they could be used as fuel ([Costamagno et al., 1999, 2005](#); [Mentzer, 2009](#); [Thery-Parisot et al., 2005](#)). In fact, in the layer 1 g, two hearths (S2 and S3) have been discovered. Their presence is marked by tiny fragments of charcoal chunks of burnt bones and thermally weathered flint artefacts ([Peresani et al., 2019](#)). In one of the two cases (S3) the hearth is surrounded by stones to delimit its perimeter. Furthermore, the hypothesis of bones being used as fuel is supported by [Badino et al. \(2023\)](#), who highlighted that between 44–38 ka years ago, at Riparo del Broion, climatic conditions were dry enough to promote fires, but the high degree of landscape openness resulted in a very limited or absent local fuel availability for fire propagation.

On the other hand, the number of carnivores in Riparo del Broion is quite elevated. *Ursus* –including *arctos* and *spelaeus*– is well-represented and fractures and burnt bones were identified on different elements. However, we point out this evidence is not sufficient to determine the origin of the whole accumulation, natural or mixed.

Regarding the evaluation of the transport and exploitation of the carcasses, although anatomical composition was calculated for all the taxa recorded in the sites, only Roccia San Sebastiano had enough MNE to apply the different indices. Based on the bone density, we conclude that post-depositional processes should be at least one of the reasons for the absence of different groups or anatomical elements of the red deer. On the other hand, the correlation with the utility indices reveals that at least the exploitation of marrow was relevant in the subsistence of Roccia San Sebastiano. This result is consistent with the proportion of epiphyses/diaphyses and the high fragmentation values.

5.2. Hunting strategies of different modern human groups

Regarding coeval sites, it is possible to highlight similarities in the exploitation of ungulates at Grotta del Cavallo (45–43 ky cal BP, [Romandini et al., 2020](#)), situated in the same bay as Uluzzo C. Cut-marks are concentrated on the limb bones of medium-large sized ungulates, mainly wild horse, auroch and red deer, and are attributable to the

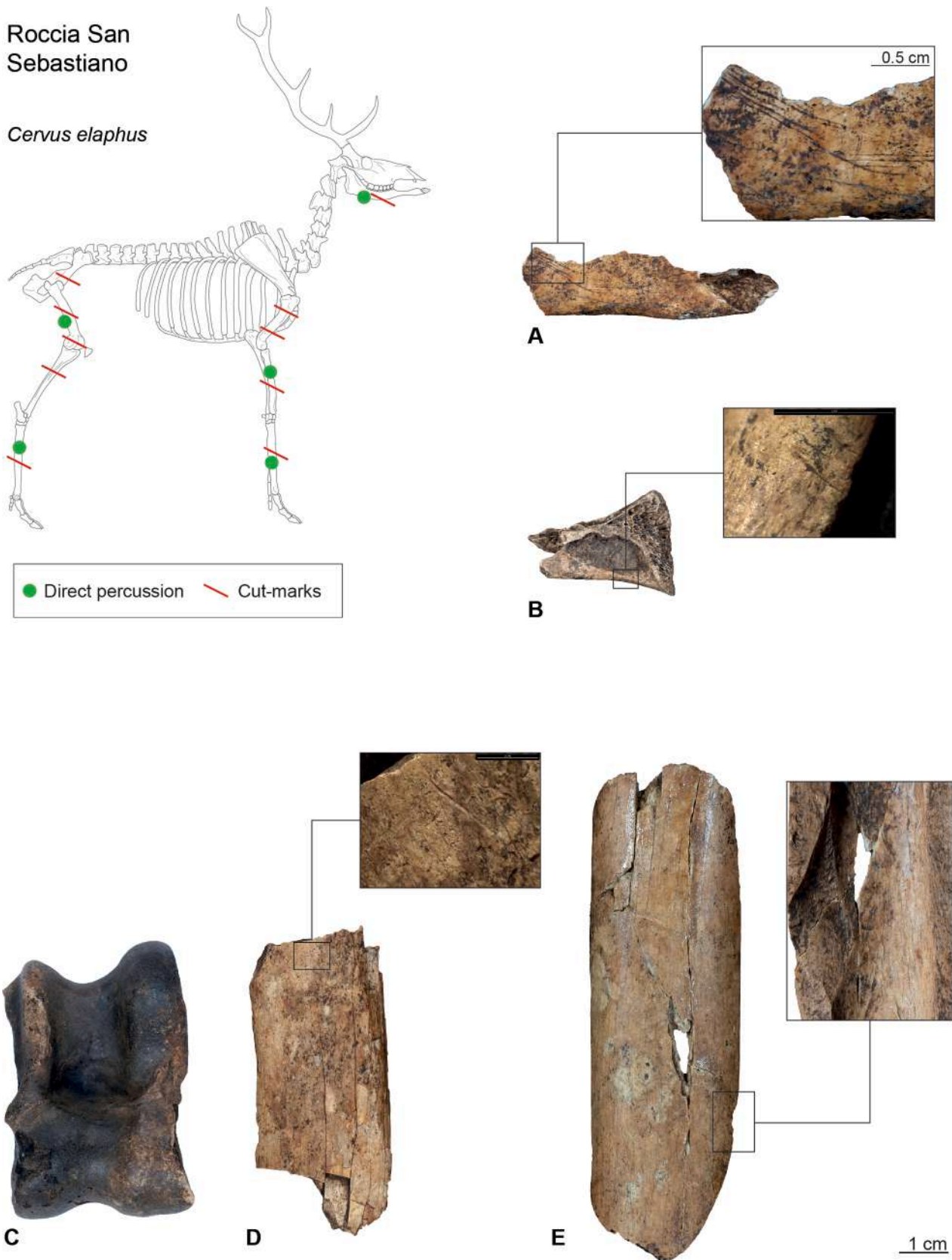


Fig. 8. Examples of anthropogenic modifications' localizations on *Cervus elaphus* of Roccia San Sebastiano: A. mandible with percussion notches and cut-marks; B. coxal with cut-marks; C. thermo-altered astragal; D. tibia with cut-marks; E. radius with percussion notch.

Table 7

Taxonomic composition of the Uluzzian layer of Riparo del Broion considering all the data available: present study and previous studies (Peresani et al., 2019; Romandini et al., 2020).

Technocomplex	UL		UL		UL	
Site/SU-Level	RB 1e,1f,1g (Romandini et al., 2020; Peresani et al., 2019)		present study		Total	
Taxa	NISP	%	NISP	%	NISP	%
<i>Lepus</i> sp.			1	0.3	1	0.2
<i>Lepus</i> cfr. <i>timidus</i>	2	1.8			2	0.5
<i>Marmota marmota</i>	3	2.7			3	0.7
<i>Castor fiber</i>	1	0.9			1	0.2
Total Lagomorpha and Rodentia	6	5.3	1	0.3	7	1.7
<i>Felis</i> sp.	1	0.9	1	0.3	2	0.5
<i>Felis silvestris</i>	2	1.8			2	0.5
<i>Vulpes vulpes</i>	4	3.5	3	1.0	7	1.7
<i>Canis lupus</i>			2	0.7	2	0.5
<i>Meles meles</i>			1	0.3	1	0.2
<i>Martes martes</i>	1	0.9			1	0.2
<i>Ursus spelaeus</i>	21	18.6	8	2.8	29	7.2
<i>Ursus arctos</i>			3	1.0	3	0.7
<i>Ursus</i> sp.	13	11.5	32	11.1	45	11.2
Carnivora undet.	6	5.3	51	17.7	57	14.2
Total Carnivora	48	42.5	101	35	149	37.2
<i>Sus scrofa</i>	21	18.6	14	4.9	35	8.7
<i>Megaloceros giganteus</i>	2	1.8	2	0.7	4	1.0
<i>Alces alces</i>	3	2.7	2	0.7	5	1.2
<i>Cervus elaphus</i>	5	4.4	8	2.8	13	3.2
<i>Capreolus capreolus</i>	3	2.7	6	2.1	9	2.2
Cervidae	13	11.5	26	9.0	39	9.7
<i>Bison priscus</i>	1	0.9	1	0.3	2	0.5
<i>Bos primigenius</i>	1	0.9			1	0.2
<i>Bos/Bison</i>	1	0.9	3	1.0	4	1.0
<i>Capra ibex</i>	1	0.9	2	0.7	3	0.7
<i>Rupicapra</i> sp.	4	3.5			4	1.0
Caprinae	4	3.5			4	1.0
Ungulata			122	42.4	122	30.4
Total Ungulata	59	52.2	186	64.6	245	61.1
TOTAL DET	113	0.3	288	2.4	401	0.8
Indeterminate mammals	37277	99.7	11872	97.9	49149	99.2
TOTAL NR	37390		12160		49550	

disarticulation of carcasses with the aim of acquiring meat (Boscato and Crezzini, 2012). Impact traces and fractures are mainly distributed on the limb elements. These traces are related to the breakage of long bones for marrow extraction. At Grotta di Castelcivita (Salerno), the Uluzzian sequence (pits 32–34, 18 and upper-15- dated to 41,846–40,952 cal. BP – Wood et al., 2012) is characterised by higher frequencies of horse and large bovids and a decrease in the frequency of fallow deer (Masini and Abbazzi, 1997; Romandini et al., 2020). Fragments mostly consist of cranial and autopodium fragments (metacarpals and metatarsals, phalanges, and sesamoids). A fair number of bones with gnawing marks (7.7 %) is registered in this layer, unlike Uluzzo C. At Grotta della Cala (Salerno), the Uluzzian layer (radiocarbon dated to 33,923–32,548 cal BP- Martini et al., 2018) is characterised by a conspicuous presence of Cervidae, particularly fallow deer, and this layer exhibits an increasingly higher percentage of phalanges and sesamoids (Benini et al., 1997). In addition, the faunal composition of Grotta La Fabbrica (Grosseto) is mostly represented by equids (*Equus caballus* and *Equus hydruntinus*), red deer, and aurochs. Less abundant are wild boar, fallow deer, roe deer, and chamois (Pitti et al., 1976). As also noted in the other context of southern Italy, carnivore remains are very scarce (Romandini et al., 2020). For the northern sites, in the Uluzzian stratigraphic unit A3

(dated to 44–42 ka cal BP, Sinet-Mathiot et al., 2019) at Grotta di Fumane (Verona) red deer and ibex were the most hunted species, but the giant deer, roe deer, bison, and chamois were also pursued (Sinet-Mathiot et al., 2019; Tagliacozzo et al., 2013). In the same unit, carnivores like wolf, fox and brown bear were hunted for the recovery of fur, as suggested by the traces of skinning, and probably their meat was also consumed (Tagliacozzo et al., 2013).

In the Uluzzian landscape, we must take into consideration the Greek contexts of Kephalaria (layer F1&F2) and Klissoura cave (layer V- dated to ~ 39 ka cal BP) (Starkovich, 2012, 2017; Starkovich and Ntinou, 2017). In Kephalaria, humans hunted mostly small and fast-moving animals (hares and partridges). Ungulates such as aurochs, ibex, fallow deer and chamois are documented but in smaller quantities. In Klissoura cave, carnivores were rare in the assemblages and only 0.2 % of the entire bone assemblage displayed carnivore damage, as we also observed in our contexts. The large game found in the Klissoura assemblage included European wild ass (*Equus hydruntinus*), red deer, wild boar, and ibex. In general, hominins processed first phalanges more often than second and third phalanges, as in our sites. This behaviour reflects differences in nutritional return since first phalanges contain more marrow than terminal phalanges (Starkovich, 2017). In summary, during the Uluzzian phase in this area the most abundant taxon is fallow deer. In addition, an increase in the exploitation of small game like European hare and tortoise is also registered, unlike in the Italian Peninsula, where for this chronological period the lagomorphs are scarce in the assemblages (Starkovich, 2012).

According to Benazzi et al. (2011) and Benazzi et al., (2015) and Oxilia et al. (2022), modern humans are associated with Uluzzian and Protoaurignacian assemblages in the Palaeolithic context of Mediterranean Europe. The Protoaurignacian and Uluzzian occupations are contemporaneous, ranging from 41,7 to 30,3 ka cal BP (Hedges et al., 1998; Higham et al., 2009, 2014; Peresani, 2012; Wood et al., 2012; Douka et al., 2014). Thus, to explore the behaviour of different early modern human groups, we considered the subsistence patterns found in our contexts with those of the Protoaurignacian levels of Grotta di Fumane (A1-A2- dated to 41–38 ka cal BP, Sinet-Mathiot et al., 2019). In this cave, among herbivores, ibex and chamois are the most abundant taxa, followed by red deer and roe deer. Anthropogenic modifications like butchering activities, deliberate breakage activities (percussion marks- mainly impact flake- and percussion notches) and thermal alterations (37.1 %) were identified on herbivores (ibex and red deer), and there is evidence for the exploitation of marrow and grease (Marín-Arroyo et al., 2023), as for Rocca San Sebastiano. At Riparo Bombrini (Protoaurignacian level A1, 40,2 ky cal BP; and A2, 38 to 36 ka cal BP) the most represented taxon is red deer, followed by bison. Considering the bone flakes and percussion marks on long bone shafts and the high percentage of burnt bones, the authors hypothesize that marrow extraction and the use of bones as fuel took place in Bombrini (Pothier Bouchard et al., 2020). Some of these aspects are also found at Broion such as the exploitation of red deer (Fumane) and a very high percentage of burnt bone fragments (Bombrini and Fumane). A clear difference is the absence of bear in the faunal assemblage. Another context to consider is the site of Riparo Mochi, in particular unit G, associated with the Protoaurignacian (39,520–39,076 cal BP, Frouin et al., 2022). Ungulates dominate the faunal assemblage, while carnivores are rare. *Cervus elaphus* is the most hunted species, with a selection of specific anatomical elements (posterior appendicular skeleton-tibiae and metapodials). Interestingly, in this unit, alpine taxa such as *Capra ibex* and *Rupicapra rupicapra* are more abundant, probably because first modern humans began to hunt prey at higher altitudes than Neanderthals (Perez et al., 2022).

Considering a southern site, in the Protoaurignacian levels of Castelcivita (10 upper-8 and 7-top sequence) the most represented taxa are equids, wild boar, chamois and red deer. Specimens mostly consist of cranial and limb bones, but the frequency of small limb bones (phalanges, sesamoids, carpals, and tarsals) is also high, a pattern we

evidenced also for other southern sites. Anthropogenic modifications have not been identified in the Protoaurignacian assemblage. Carnivore gnawing marks are fewer in the Protoaurignacian layers (2.6 % of total material) and more abundant in the Uluzzian (7.7 %) layers (Romandini et al., 2020).

It has been suggested by Boschin et al. (2022), that southern Italy could be considered a refugium for the last Neanderthals and early modern humans, as it has been also pointed out for the three southern European peninsulas (Iberian, Italian and Balkans) (Carvalho and Bicho, 2022). The concept of refugia and its meaning, however, could vary based on its characteristics, for example the number of species (single-species or multi-species) or the scale of refugia (macro-refugia, micro-refugia, refugia-within-refugia or sub-refugia) among others (Jones, 2021; see also Roditi et al., 2024). To assess this line of research, we calculated the Simpson's Diversity Index (see Suppl. Table 14), and we obtained that southern Italian contexts (mean S 1-D: 0.78) are richer in terms of species diversity compared to the northern sites (mean S 1-D: 0.69) considered in this study. Uluzzo C (S 1-D: 0.85) and Castelcivita (S 1-D: 0.85), are the most diverse contexts in terms of biodiversity. The lower value obtained for Roccia San Sebastiano (S 1-D: 0.7) is influenced by the almost exclusive predation towards a single animal (red deer). Furthermore, there is a slight increase in diversity within the Uluzzian faunal assemblages (mean S 1-D: 0.72) when compared with those of the Protoaurignacian (mean S 1-D: 0.69). These results, with values close to one that are recorded in the Italian Peninsula, are also reflected in archaeological records from the Middle Palaeolithic to the Upper Palaeolithic in the Iberian Peninsula (Real et al., 2022). The region of central-eastern Iberian Mediterranean is suggested as a refugium due to its notable concentration and long-term persistence of biodiversity, which may also account for the abundance of Palaeolithic sites. As previously mentioned, also the Balkans and the riparian area of the Danube basin are believed to have acted as refuges given the occurrence of various animal, plant, and hominin species over an extended period, despite the scarcity of Palaeolithic sites in those areas (Borić et al., 2022).

In general, the Uluzzian groups have adapted to different palaeoclimatic and biotic conditions in Italy, as other early modern human groups elsewhere in Europe. On the one hand, they exploited the available animal resources, with a highly diverse taxonomic spectrum but focusing primarily on red deer. Moreover, although in some sites there is evidence of red foxes (Fumane A3), leporids (Uluzzo C) and wild cat (Castelcivita) exploitation, the scarcity of evidence of an important small prey game such as lagomorphs, tortoises or birds stands out in comparison to other areas, such as Greece (Starkovich, 2012; Starkovich and Ntinou, 2017), or even other Early Upper Palaeolithic periods in the Iberian Peninsula (e.g. Lloveras et al., 2016; Sanchis et al., 2016; Villaverde et al., 2019). On the other hand, they have adapted to coexisting and confronting other predators of different sizes, such as wolves and bears and in some cases, they have even taken advantage of them.

Finally, the age-at-death data on ungulate taxa point out a marked seasonal occupations centre in spring-summer at our three sites. Furthermore, human occupations seem to be as short and sporadic as is already described for the Early Upper Palaeolithic (e.g. Marín-Arroyo et al., 2023; Smith et al., 2021; Villaverde et al., 2021).

6. Conclusions

The archaeozoological data collected here allow us to improve and refine our understanding of the Uluzzian in the Mediterranean area, outlining a series of common elements and differences between sites sharing this culture. Cervids (e.g., red deer) are the most abundant mammals, linked to the human exploitation, in all Uluzzian levels considered. At Roccia San Sebastiano, based on the anthropogenic modifications recorded, the hunting of red deer is aimed at the exploitation of meat and marrow. We also point out that not only red deer, but also other ungulates (wild boar, equids, chamois) were skinned,

disarticulated and defleshed at this site. Moreover, the presence of fresh fractures suggests that Uluzzian populations exploited animal carcasses with the aim of extracting bone marrow, as suggested in Romandini et al. (2020). For Riparo del Broion, it is challenging to define the carcass treatment, but we have recorded a high fragmentation and quantity of burnt bones that we can assume were used as fuel.

Only in Uluzzo C and Riparo del Broion carnivore bones have been recorded, whereas at Roccia San Sebastiano carnivores are almost absent. Anthropogenic modifications on carnivore bones are scarce at these sites, although they are observed on some (fractured and burnt) bear remains at Broion. Therefore, we are not able to assert that all carnivores were hunted or exploited by humans, unlike in other assemblages like Grotta di Fumane (Tagliacozzo et al., 2013; Romandini et al., 2016; Romandini et al., 2020; Romandini, 2012).

In summary, the data obtained from this study outlines hunting strategies against carnivore species for the North (Riparo del Broion), and the exploitation of cervids and equids for the South of Italy (Roccia San Sebastiano and Uluzzo C), as documented also for Castelcivita, Grotta del Cavallo, Grotta della Cala, and Grotta La Fabbrica. The hunting of medium sized ungulates and the scarce presence of carnivores in the faunal assemblage are attested also in Protoaurignacian Italian sites. The spectra of the exploited fauna do not exhibit distinctive features indicative of *Homo sapiens* subsistence practices when compared to those of the last Neanderthals. Instead, the absence of evidence about the consumption of fish and other small animals suggests a reduction in the diversity of prey species exploited during the Uluzzian period.

CRedit authorship contribution statement

Sara Silvestrini: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Cristina Real:** Investigation, Formal analysis, Data curation, Conceptualization, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Federico Lugli:** Investigation, Validation, Writing – review & editing. **Davide Delpiano:** Investigation, Validation, Writing – review & editing. **Katerina Harvati:** Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing. **Carminé Collina:** Writing – review & editing, Resources, Validation. **Marco Peresani:** Resources, Validation, Writing – review & editing. **Enza Elena Spinapolice:** Validation, Writing – review & editing. **Matteo Romandini:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Stefano Benazzi:** Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Declaration of competing interest

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

Data availability

Data will be made available on request.

Acknowledgements

This study and related field activities carried out between 2017 and 2019 received funding from the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no. 724046 – SUCCESS); this study received funding from the European Research Council (ERC) under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement no. 101019659- FIRSTSTEPS); research at Riparo Broion is coordinated by the University of Bologna (M.R.) and the University of

Ferrara (M.P.) with the support of the Italian Ministry of Culture, Veneto Archaeological Superintendency SAPAB, the Municipality of Longare, Leakey Foundation (Spring 2015 Grant), and Istituto Italiano di Preistoria e Protostoria. Cristina Real was the beneficiary of an APOSTD2021/143 grant from the Generalitat Valenciana and she is part of the PID2021-122308NA-I00 project funded by MCIN/AEI/10.13039/501100011033/ and FEDER Una manera de hacer Europa; research at Rocca San Sebastiano cave was carried out thanks to the support and funding of the Municipality of Mondragone. Research is coordinated by Museo Civico Archeologico Biagio Greco (C.C.), Mondragone, Caserta, which provided funding, logistic support and welcomed the researchers since 1999 with the support of Archaeological Superintendency SAPAB of Salerno e Avellino, Benevento e Caserta. Research at Uluzzo C is supported by Leakey Foundation (Spring 2015 Grant). Authors are grateful to MiBACT that release the permits to excavate and investigate materials and to the Museo della Preistoria di Nardò, the Soprintendenza Archeologia, Belle Arti e Paesaggio per le province di Brindisi, Lecce e Taranto, and the Gruppo Speleologico Neretino. K.H. is also supported by the Deutsche Forschungsgemeinschaft (DFG FOR 2237; Gottfried Wilhelm Leibniz Prize 2021).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2024.104575>.

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