

Late Neanderthal “menu” from northern to southern Italy: freshwater and terrestrial animal resources

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ABSTRACT

One of the unanswered questions in Palaeolithic studies is how Neanderthals adapted their subsistence strategies by changing their diet at such a late stage of their existence. Zooarchaeological and taphonomic studies are critical to determine anthropogenic behaviour and to accurately understand the strategies used to exploit different ecological niches. In this line of research, the present paper aims to provide a thorough assessment of the unpublished faunal assemblages from two Late Mousterian Italian sites: Riparo del Broion (northern Italy) and Roccia San Sebastiano cave (southern Italy). These two sites occupy two distant and different areas of Italy, however providing late Neanderthals coeval occupations dated between 50,000–44,000 cal BP.

In this study we analysed more than 27,000 remains following a multidisciplinary approach that combines taxonomical, anatomical and taphonomic investigations. Moreover, an experimental study that supports the instrumental use of valve fragments of *Anodonta* sp. is also presented for Riparo del Broion. Strontium isotope analysis of cervid remains, the most exploited prey in both sites, provides useful information to explore selection of available animals, the mobility of human groups, and the composition of animal herds.

In general, the characteristics of the territory of the two sites highlight the exploitation of different resources that could vary from almost specialized small game (Riparo del Broion) to selective ungulates (Roccia San Sebastiano) hunting strategies. At Riparo del Broion, the main exploitation of red deer was accompanied by beaver hunting, fishing, and shellfish gathering from freshwater lake environments. On the contrary, human groups at Roccia San Sebastiano cave hunted almost exclusively red deer, despite the sea was not far from the cave. The absence of shellfish and fish remains is remarkable. In addition, the transformation and use of diaphyseal bone flakes as retouchers at both sites and the presence of a probable “bone awl” at Roccia San Sebastiano, further confirm an extended capacity in the use of a large range of materials for different subsistence activities.

Present results consist of the first zooarchaeological comparison of the Late Mousterian levels of Roccia San Sebastiano cave and Riparo del Broion. These allowed us to detail environments, and subsistence strategies of two Neanderthal groups that inhabited different ecological niches of the Italian territory and provide important data to disentangle possible changes in faunal exploitation strategies, butchering, processing, and cultural behaviours during the Middle to Upper Palaeolithic transition in Italy.

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1. Introduction

Behaviour and adaptive strategies of humans changed consistently throughout the MIS 3 (ca. 60–30 ky BP) in Europe, mainly driven by recurrent changes in paleoenvironmental conditions. The different response of Neanderthals and Sapiens to changes in the underlying climatic conditions have been of particular interest in various contexts of continental and Mediterranean Europe (among others: Arrighi et al., 2020a; Benazzi et al., 2011, 2015; Blasco and Fernández Peris, 2012; Brown et al., 2011; Cochard et al., 2012; Conard and Prindiville, 2000; Costamagno et al., 2006; Fiore et al., 2004, 2016; Gómez-Olivencia et al., 2018; Grayson and Delpech, 2002; Guillaud et al., 2021; Hublin et al., 2020; Kuhn and Bietti, 2000; Marciani et al., 2020; Milliken, 1999–2000; Morin et al., 2019; Mussi, 2001; Nabais, 2018; Peresani, 2009, 2011; Rendu, 2010; Romandini et al., 2016, 2018a,b, 2020a; Slimak et al., 2022; Stiner, 1994; Texier et al., 2005; Zilhão et al., 2020). One of the questions for which answers are still tentative is how Neanderthals managed resource exploitation and subsistence strategies (e.g., changing and adapting their diet) at a time period that witnessed the arrival of Sapiens in Europe.

Zooarchaeological and taphonomic analysis are key to determine anthropogenic behaviour and to understand the subsistence and adaptation strategies used to exploit different ecological niches. Following recent studies, it is now clear that Neanderthal's subsistence and site function are strongly tied to local conditions (Bocherens, 2009; Gaudzinski-Windheuser and Roebroeks, 2011; Morin et al., 2016; Nava et al., 2020; Ready, 2010; Rendu, 2022; Rivals et al., 2022; Romandini et al., 2018b, 2020a; Sanchis et al., 2019) which also kindle capabilities (e.g., cognitive, technological), in some contexts, to exploit “non-ungulate animals” as a food resource (Blasco et al., 2022; Hockett and Haws, 2005; Fiore et al., 2016; Romandini et al., 2018a, b; Stiner, 2001; Stiner and Munro, 2002, 2011). Indeed, despite Neanderthals' main animal protein sources were medium- and large-sized herbivores (Boscato et al., 2011; Costamagno et al., 2006; Fiore et al., 2004; Morin and Ready, 2013; Patou-Mathis, 2000; Rendu, 2010; Salazar-García et al., 2013; Sanz et al., 2019; Terlatto et al., 2019; Yravedra and Cobo-Sánchez, 2015), in various parts of Europe the exploitation of small game, birds, and aquatic resources is also attested (Blasco and Fernández Peris, 2012; Blasco et al., 2013; Brown et al., 2011; Cochard et al., 2012; Cortés-Sánchez et al., 2011; Fiore et al., 2016; Gómez-Olivencia et al., 2018; Guillaud et al., 2021; Morin et al., 2019; Nabais, 2018; Romandini, 2012; Romandini et al., 2014a, 2016, 2018b; Villa et al., 2020; Zilhão et al., 2020 among others), alongside with the predation and consumption of ursids (Romandini et al., 2018a), confirming the large versatility of the Neanderthal's diet.

Despite the increasing amount of data on Neanderthal's behaviour and mobility, we still have little information concerning their subsistence strategies in the period that records the arrival of Sapiens in Europe, i.e., ca. 50–40 ky, ultimately preventing analytical comparisons at a regional and macroregional scale.

Thus, within such a discontinued and fragmented framework, new multidisciplinary zooarchaeological studies, are crucial to provide new data on Neanderthal groups' subsistence.

The present paper aims to provide zooarchaeological information on the unpublished faunal assemblages retrieved from two late Mousterian sites (ca. 50–44 ky BP) located in different ecological niches of the Italian peninsula: Riparo del Broion (north-east Italy) and Rocca San Sebastiano cave (south-west Italy). These two contexts are of paramount relevance because Mousterian deposits are directly associated to Neanderthal remains in both sites, and the deciduous tooth of Rocca San Sebastiano currently represents the most recent Neanderthal fossil of the Mediterranean area (Oxilia et al., 2022; Romandini et al., 2020b). Accordingly, the faunal assemblages of Riparo del Broion and Rocca San Sebastiano are decisive to infer the subsistence activities developed by the last Neanderthals in two different ecological niches just before their definitive demise, which chronologically corresponds to the arrival

of Sapiens in Europe, and Italy in particular (Benazzi et al., 2011; Higham, 2011; Hublin et al., 2020; Moroni et al., 2013, 2018; Peresani, 2011; Peresani et al., 2016, 2019; Slimak et al., 2022; Stringer and Crété, 2022; Villa et al., 2020).

Inferences about paleoclimate and ecological settings are based on well-established links among ungulates-rodents-carnivores families/avifaunal group/freshwater resources and on the specific environmental settings to which they were and still are adapted. These considerations are supported by detailed regional palaeoenvironmental reconstructions based on palaeoecological analysis (Badino et al., 2020b). We focused on taxonomical representation, prey selection, skeletal representation, and carcass processing to define each site's use and to compare it with other sites from the Mediterranean context.

Finally, preliminary insights on change in animal exploitation strategies and butchering processes are presented through taphonomic analysis, a qualitative-comparative experimentation based on shells from Riparo del Broion, and isotopic analysis on cervids from both sites.

2. Environmental and sites contexts

In northern Italy, palaeoecological records from Lake Fimon and Azzano Decimo (north-eastern Alpine foothills; Badino et al., 2020a, Badino et al., 2023; Monegato et al., 2011; Pini et al., 2009, 2010, 2022), document short-to long-term environmental dynamics during MIS 3. During the first half of the Middle Würm, cool-mixed temperate forests expanded after MIS 4 contraction, composed of *Pinus sylvestris/mugo* and *Picea* with broad-leaved trees (*Alnus* cf. *Incana* and tree *Betula*), the latter particularly favoured by local fires (Badino et al., 2023). A gradual reduction of warm-temperate elements took place between 60 and 40 ka (e.g., *Tilia* in Lake Fimon record). Interestingly, peaks of *Tilia* pollen have been identified in layers preserving Mousterian artifacts and dated to 40.6–46.4 ka 14C BP from cave deposits at the Riparo del Broion (Cattani and Renault-Miskovsky, 1983–84; Leonardi and Broglio, 1966).

Despite evidence of afforestation persisting at a long-term scale south of the Alps during MIS 3, dry and other grassland types expanded steadily from 44–43 ka, peaking at HS 4 (40.2–38.3 ka; Cheng et al., 2021). During the following millennia and up to 27 ka, the Berici Hills were covered by steppe, desert-steppe and open dry boreal forests expanded during interstadial intervals (Badino et al., 2023). In this framework, xerophytic steppe and semi-deserts (e.g., *Artemisia* and *Chenopodiaceae*) increased mostly during GS 5.1-HS3 (30.6–28.9 b2k; Rasmussen et al., 2014; Badino et al., 2020a).

Such drier and colder stadial conditions likely favoured the presence of Alpine ibex, chamois, and marmot at low altitudes (in the Colli Berici), as well as the presence of micromammals from steppic environments, and the diffusion of boreal bird species. The Po alluvial valley was, in contrast, inhabited by woolly rhinoceros, mammoth, and bison (Sala, 1990).

In southern Italy, Lago Grande di Monticchio (Monte Vulture, Basilicata) provides a mid-to-high resolution record of millennial-scale changes in vegetation through the last glacial between open/forested environments. Woody taxa, including deciduous *Quercus*, *Abies* and *Fagus* (up to 30–60% AP) expanded during Greenland Interstadials (Allen et al., 1999), with maximum increase between ca. 55–50 ka (i.e., GI 14; Allen et al., 1999; Badino et al., 2020a, b; Fletcher et al., 2010). *Artemisia*-dominated steppe/wooded steppe environments mainly occurred between 45 and 30 ka with major expansions during GS9-HS4 and GS 5.1-HS3 (39.9–38.2 and 30.6–28.9 b2k, Rasmussen et al., 2014). Recently, seven tephra layers, including Campanian Ignimbrite (CI), have been used to improve the age-depth model between 50 and 30 ka (Wutke et al., 2015), allowing a more effective comparison with N-Italian records.

While Monticchio record provides a unique palaeoenvironmental framework for the inner southern regions, faunal assemblages coming from MIS3-aged stratigraphic sequences along the coasts highlight

different climatic trends between Tyrrhenian (south-western) and Ionian (south-eastern) contexts (Romandini et al., 2020a) due to an almost persistent moisture availability on the former, mainly generated by the orographic uplift of air charged with moisture from the Tyrrhenian Sea, and to Balkan influence on the latter. The Ionian area is characterised by open environment taxa (e.g., *Bos primigenius*) while the Tyrrhenian one shows an abundance of forest species (cervids).

2.1. Riparo del Broion

Riparo del Broion is located on the eastern slope of the Berici Hills (Municipality of Longare, Vicenza) at 135 m a.s.l., up a steep cliff face that connects the peak of Mount Brosimo (327 m a.s.l.) to the Friulian-Venetian plain (Fig. 1). The rock shelter – which is 10 m long, 6 m deep,

and 17 m high, whose filling sediments seem to extend for a total of about 85 m² of surface – was formed by a rock collapse along a major ENE-WSW oriented fault that developed because of thermoclastic processes and chemical dissolution (Dal Lago and Mietto, 2003; Sauro, 2002). Stratified deposits were dated to the Late Pleistocene and include evidence for the Middle-to-Upper Palaeolithic transition. A detailed overview of the geographical and paleoecological setting, as well as of the archaeological excavation and sedimentary sequence uncovered at Riparo del Broion, was recently published (Peresani et al., 2019). Excavations spanning from 1998 to 2021 led archaeologists to identify 19 stratigraphic units (for a total thickness of about 2.8 m), among which unit 1 was split into seven subunits (layers), from 1a to 1 g.

The sedimentary deposits of Riparo Broion were partially dismantled in historical times by shepherds with use to store hay and wood. Further

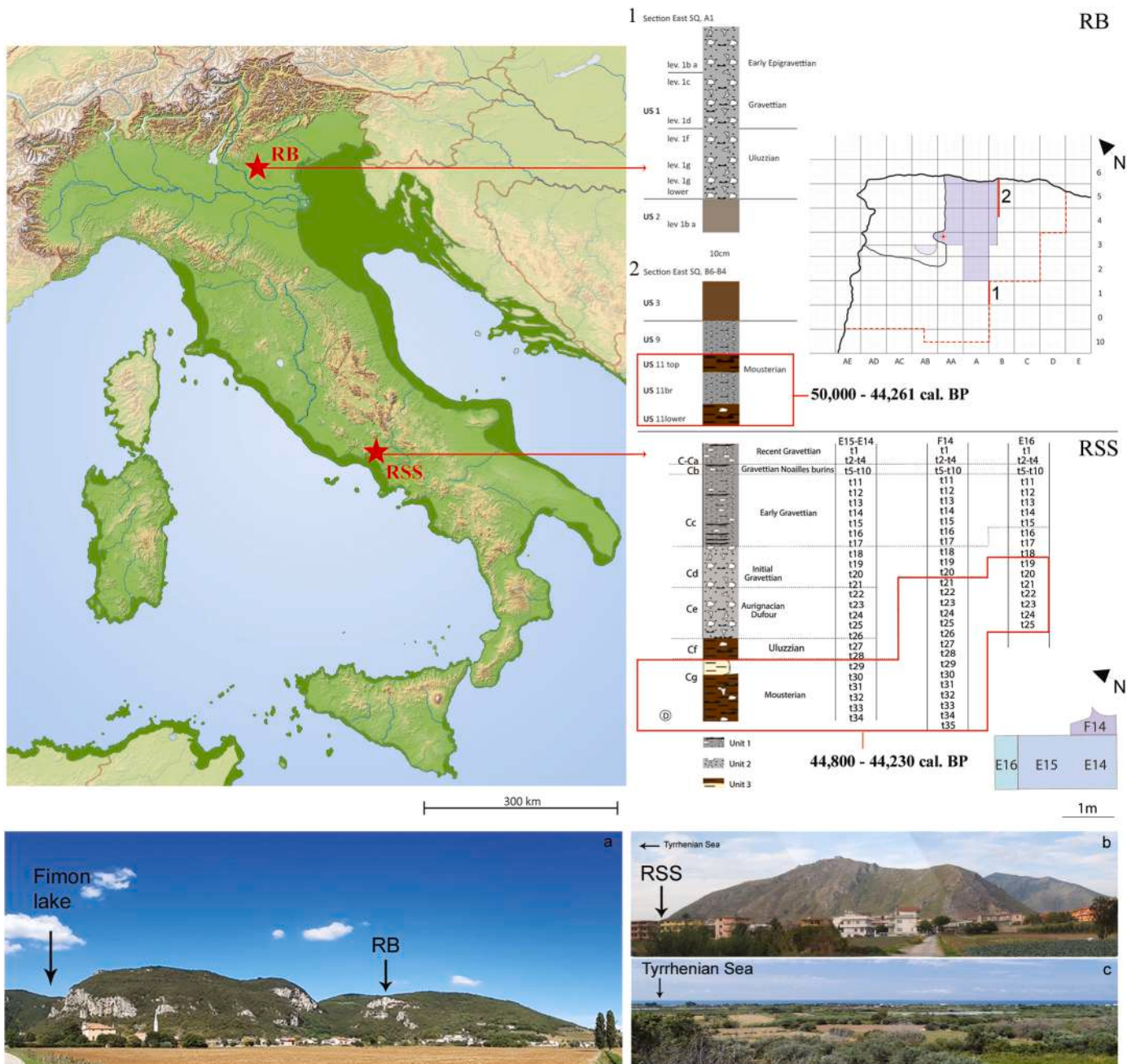


Fig. 1. Localization of the Riparo del Broion (RB) and Roccia San Sebastiano cave (RSS) (left) and the particular of the stratigraphic sequence correlation, lithological column, planimetry of the excavated areas and cultural domain (highlighted in red, the Late Mousterian levels). a) picture with the Riparo del Broion and Fimon lake position; b-c) picture with the Roccia San Sebastiano cave and its relationship with the current Tyrrhenian Sea level.

damage occurred in 1984 when unauthorized excavators removed sediments from pits and trenches on a total area of 14 sqm down to 2 m at the deepest. Archaeological excavations were initially directed by Alberto Broglio (1998–2008) and by two of us (M.R. and M.P., 2015–2021) on a 40 sqm area bounded to north and west from the rock walls. The work focused for the most part on the Upper Palaeolithic levels (investigated in extension) and only in the last four years on the lower middle part of the deposit linked to repeated Neanderthal frequentations. The bedrock has not yet been reached. Sediments are mostly small stones and gravel with large prevalence on loams.

Currently 11 of these stratigraphic units have been totally or partially studied. The studied stratigraphy displays the following cultural sequence: Early Epigravettian (layers 1a–1b); Gravettian (1c–1d); Uluzzian (1e–1f–1g); and Late Mousterian (units 4 + 7, 9, and 11), with the latter being separated by the others by units 2 and 3, which present no evidence of anthropic activity (De Stefani et al., 2005; Gurioli et al., 2006; Peresani et al., 2019; Romandini et al., 2012a, 2020b). In this work we analysed the zooarchaeological remains from the in situ late Mousterian stratigraphic unit 11. This unit, whose thickness varies between 50 and 60 cm, contains lithic Mousterian artifacts still under study and faunal remains. This unit has a dark-brownish colour that clearly differentiates it from others. This coloration is also due to the presence of numerous (currently about ten) hearths of various sizes. This evidence together with the abundant number of lithic artifacts and faunal remains suggest palimpsests of occupations probably repeated over a long time. Apart from some isolated bioturbation linked to plant roots, the entire stratigraphic unit and relative materials do not appear to have undergone significant post-depositional alterations. Geomorphological and micromorphological studies of the sediment are currently in progress.

The human tooth uncovered in US 11, square AA3a (Nava et al., 2020; Romandini et al., 2020b) was recovered from the top of this latter cultural phase, for which this contribution aims to detail the archeozoological analysis. Morphological information, morphometric analysis, and ancient DNA analysis show that the Riparo Broion 1 tooth belongs to a Neanderthal child, which lived in north-eastern Italy in a period close to the arrival of *Homo sapiens* in southern Europe (Romandini et al., 2020b).

For Late Mousterian stratigraphic units 9 and 11, radiocarbon dating results (Romandini et al., 2020b) are consistent. The posterior probability distribution assigned by the Bayesian age model to unit 9 ranges from 44,261 to 42,716 cal BP, while for unit 11 it ranges from 50,000 to 44,261 cal BP (95% confidence interval). With the same model, the Uluzzian layers present a chronological range from 42,716 to 41,783 cal BP (Peresani et al., 2019; Romandini et al., 2020b).

The Uluzzian attribution of the lithic assemblage uncovered in levels 1f–1g confirmed the presence of this early Upper Palaeolithic culture in northern Italy (Peresani, 2008; Peresani et al., 2016, 2019). Uluzzian faunal assemblages from layers 1f+1 g stratigraphically close to the Late Mousterian levels US 9 and US 11 (the latter analyzed in this study) display a richness of taxa due to the different environments of the surroundings. Alongside the presence of marmot, hare, chamois, ibex, bison and possibly aurochs, the number of red deer and roe deer bones, as well as the abundance of wild boar remains, suggest the existence of humid woodlands located in the alluvial plain to the east of Mount Brosimo (Peresani et al., 2019). The Uluzzian layer was analyzed in our recent work with the integration of ZooMS (Zooarchaeology by Mass Spectrometry), which improved the faunal composition of the site by confirming the taxa identified by morphological analysis, providing further details about the climatic and environmental conditions (Silvestrini et al., 2022).

2.2. Roccia San Sebastiano cave

Roccia San Sebastiano cave (Municipality of Mondragone, Caserta) is a tectonic-karstic cavity that opens at the foot of the southern slope of

Mt. Massico (Fig. 1). The cave is placed at 40 m a.s.l. And, at the time of the Neanderthal presence in the site, around, at 13 km from the seacoast (today 5 km).

The cave opens into Cretaceous limestone rocks which are attributable to the paleo-geographic units of Mt. Matese - Mt. Maggiore and that form the main part of Mt. Massico. The surrounding landscape of this Mount is characterised by two plains that originate since the Late Quaternary: the first one (to the NW) is called the Garigliano River alluvial plain, whilst the second one (to the SE) is the Campanian Plain and includes the Volturno River mouth. These zones are enclosed by the high-morphostructural carbonate relief of Mt. Massico (Aiello et al., 2018; Collina et al., 2020). Alluvial plain deposits that characterise these plains consist of Pleistocene–Holocene reworked pyroclastic and fluvial-marine sediments (Aiello et al., 2018). Between the Upper Pliocene and the Lower Pleistocene, a marine and/or brackish sedimentation occurred in the graben, during the previous tectonic phase. This sedimentary process lasted until the Middle Pleistocene, also due to subsequent tectonic phases which formed a low-morphostructural landscape. Subsequent tectonic phases of marginal reliefs caused the eastward gradual migration of the shoreline until the beginning of the Upper Pleistocene (Aiello et al., 2018). The present-day morphological features of the overall area are markedly influenced by the violent Campanian Ignimbrite eruption (40Ar/39Ar age: 39.85 ± 0.14 ka; Giaccio et al., 2017) of the Phlegraean Fields occurred after the disappearance of Neanderthals from the territory. The event generated a vast marine gulf that opened to the northwest, and that was gradually filled by river and marine sediments as well as volcanic debris that came from the erosion of the surrounding hills (Aiello et al., 2018). During the marine regression a wide coastal plain emerged and the coastline in the Mondragone area was located some tens of kilometres westward (Aiello et al., 2018). Geomorphological and paleoenvironmental data (Aiello et al., 2018) indicate that the plain of Mondragone was characterised by the presence of persistent freshwater environments mostly after the deposition of CI, ~39 kyr BP.

The entrance to the cave is located near an abandoned limestone quarry. The cave is divided into two distinct parts: 1. The shelter, about 12 m in length and 3 m in depth; and 2. The cave (whose dimensions have not yet been ascertained since it is still partially obstructed by reworked sediments), for a total of about 50 m² of surface. The shelter was filled with a thick succession of fine-grained and coarse-grained deposits (allochthonous sediments) and large debris (i.e., autochthonous sediments deriving from the collapse of the ceiling of the cave) (Collina et al., 2020). Because of these rock collapses and the presence of huge boulders that obstructed the entrance of the cave and part of the inner surface, the excavation work required a great deal of effort and a prolonged - slowed down - timeline.

The excavations highlighted a thick sedimentary sequence that can be broadly subdivided into two parts. The upper part is composed of coarse-grained sediments and debris, containing a mixture of Palaeolithic and historical artifacts. The lower part, consisting of reddish sandy sediments, is characterized by the archaeological deposits in situ, rich in faunal and lithics remains (Collina et al., 2020).

Roccia San Sebastiano cave was discovered in 1999 by C. Collina and M. Piperno during a systematic surveying project promoted by the University of Naples 'Federico II', the Museo Civico Biagio Greco of Mondragone and the Soprintendenza Archeologia Belle Arti e Paesaggio di Salerno e Avellino, Benevento e Caserta. From 2001 to 2010, the systematic excavations led by MP allowed the removal of the reworked sediment inside the cave, the excavation of an extended Gravettian level over an area of 6 m² and the dig of a deep test trench 2 × 1 m in square E14–E15 to understand the potential of the cave's cultural sequence. The trench is 2.8 m deep and stops at a sterile layer. In this trench, the in-situ units and sub-units (Fig. 1) consist in: Unit 1, including sub-units C–Ca (recent Gravettian), Cb (Gravettian with Noailles burins), and Cc (Early Gravettian); Unit 2, including the sub-units Cd (Initial Gravettian) and Ce (Aurignacian with Dufour bladelets), with a large block of collapsed

limestone separating the two subunits; Unit 3 including sub-units Cf (Uluzzian) and Cg (Final Mousterian) (Collina et al., 2020; Collina and Gallotti, 2007; Collina and Piperno, 2011; 2018). Each sub-unit was excavated with artificial pits labeled with the letter “t” and numbered consecutively.

From 2011 to 2019, the campaign led by CC excavated two further trenches, one in square F14 (1 × 1 m), and the other in square E16 (30 × 50 cm), which is still being dug. In this work we investigate the zooarchaeological remains from the in situ Late Mousterian layers of these two new trenches, investigated in the last two years of excavation: US3 sub-unit Cg: specifically, from pits t21 to t39 of trench F14, and from pits t19 to t25 of trench E16, for a thickness respectively of about 95 cm and 50 cm. The sediment in these trenches consists mainly of dark sandy, silty deposits, rich in organic matter (Collina et al., 2020). For these levels the presence of post-depositional processes was not documented during the excavation, however the material comes from two trenches and a detailed spatial analysis. The detailed lithic materials study is still in progress. At the current state of research, the Late Mousterian occupations were intense, repeated and rich in materials in excellent condition.

In the rich deposit of Roccia San Sebastiano two human teeth were found: one from sub-unit Cf, pits t16, trench E16 which was attributed to a *Homo sapiens*, and the other from sub-unit Cg, pits t34, trench E15-E14 which was identified as a deciduous tooth of a Neanderthal child (Oxilia et al., 2022). The latter, alongside the deciduous tooth from Riparo del Broion, is one of the latest pieces of fossil evidence for Neanderthal presence in Italy. Specifically, the tooth was found in a more recent layer than the one with Mousterian lithic industry (trench F14, spit t39) dated between 44,800–44,230 cal BP (ETH-99085.1.1) (Oxilia et al., 2022). The chronological range 42,640–42,380 cal BP (ETH-99090.1.1) from sub-unit Cf, trench F14, spit t19, on the other hand, documents the earliest presence of Uluzzian groups in the Tyrrhenian side of the Italian Peninsula (Oxilia et al., 2022). In Aiello et al. (2018), the oldest date for the Mousterian deposit (R_Date Rome-2111) is 43,6–0–42,190 (68.2%) cal BP – 44,740–41,700 (95.4%) cal BP, based on a bone fragment collected in sub-unit Cg-t29-34 (Final Mousterian). The most recent date (R_Date Rome-2447) is 23,8–0–23,320 (68.2%) cal BP – 24,070–23,020 (95.4%) cal BP based on a bone collected in sub-unit Ca-t1-4 (Recent Gravettian). Published faunal studies are scarce and are currently relative only to the Gravettian layer C from the 2001 fieldwork (Collina et al., 2008). The best-represented species are *Equus caballus*, *Equus hydruntinus* and *Bos primigenius*, but other ungulates such as *Cervus elaphus*, *Rupicapra* sp., *Sus scrofa*, and carnivores (*Canis lupus* and *Vulpes*) are also present. Anthropogenic modifications, including percussion notches, flakes, and cut-marks were identified. Gravettian human groups exploited the prey to consume the marrow and meat.

3. Material and methods

3.1. Materials and methods of excavation

At Riparo del Broion, 23,817 mammal remains, 16 birds, 7 fish and 105 freshwater shells from the Late Mousterian stratigraphic Unit 11 were unearthed during the 5 excavation campaigns, which interested approximately a 7 m² area. The position of all specimens that were at least 5 cm long or identifiable was recorded during the excavations using an electronic theodolite. Sediment was water-screened using superimposed meshes (from 5 to 0.2 mm) and all the bone fragments were recovered after sieving and considered for this study.

At Roccia San Sebastiano cave, 3623 mammal remains and 7 birds from Late Mousterian sub-unit Cg from trench F14, including t21 to t39, and trench E16, including t19 to t25, were unearthed during the excavation campaigns carried out between 2011 and 2019. The materials come from the excavation of the two trenches: trench F14 covered an area of 1 × 1 m, whereas trench E16 covered an area of 30 × 50 cm. The deposit of each sub-unit was excavated in artificial pits of 5–7 cm in

depth, following the slope of the layers, the presence of archaeological features and/or the location of archaeological materials. The sediment was screened with a mesh of 0.2 cm.

3.2. Zooarchaeological analysis of mammal remains

At the current state of research, zooarchaeological analyses were carried out on the whole osteological sample, including bones and teeth recovered from the above-mentioned sites. All were studied and classified from the taxonomic and taphonomic point of view.

Taxonomic and anatomical identifications made in this study are based on the Alpine fauna reference collection of the Department of Cultural Heritage at the University of Bologna with the help of the well-established literature (Davis, 1987; France, 2009; Lyman, 1994; Reitz and Wing, 2008).

Indeterminate remains were grouped primarily on the basis of morphological characteristics into long bones, flat bones and articular bones (Cáceres, 2002). Then, all remains were grouped into weight size classes (as adults), following the modification of the criteria proposed by Bunn (1986): very small, <20 kg (i.e. lagomorphs, Mustelidae, *Vulpes*); small, 20–100 kg (i.e. *Capreolus*, *Capra ibex*; *Rupicapra rupicapra*, *Canis lupus*); medium, 100–200 kg (i.e. *Sus scrofa*, *Cervus elaphus*); large, 200–300 kg (i.e. *Alces alces*, Ursidae); very large, >300 kg (i.e. *Megaloceros giganteus*, Bovinae).

Age-at-death was established based on modern animal birth, teeth eruption, dental wear, and epiphyseal fusion patterns (Aitken, 1974; Azorit, 2011; Azorit et al., 2002; Barone, 1976a,b; d'Errico and Vanhaeren, 2002; Hillson, 2005; Mariezkurrena, 1983; Silver, 1963; Tomé and Vigne, 2003) and the individuals were classified in five categories: neonatal (deciduous teeth in eruption), infantile (complete deciduous teeth and permanent teeth germs), juvenile (deciduous teeth with different wear stage and some permanent teeth), adult (permanent teeth with different wear stage) and senile (permanent teeth with heavy degree of wear) (Blasco, 2011).

Taxonomically identified specimens were used to evaluate species abundance through the number of identified specimens (NISP) and the minimum number of individuals (MNI) (Bökönyi, 1970; Grayson, 1984). The minimum number of elements (MNE), the standardised minimal animal units (%MAU) and fragmentation indexes (Binford, 1981, 1984; Brain, 1981; Klein and Cruz-Urbe, 1984; Lyman, 1994) were calculated to evaluate the skeletal representation of different animals and the skeletal survival rate. To assess transport strategies and attrition processes, the correlation between %MAU and bone density was applied only for the *Cervus elaphus* (Kreutzer, 1999) assemblage from Roccia San Sebastiano cave because the number of remains for the other species is much lower than the minimum required to be statistically significant (Faith and Gordon, 2007).

All bone surfaces were evaluated both at a macroscopic (using a hand lens at 10x magnification) and at a microscopic (Leica S9i Greenough stereomicroscope with 0.61–55) level to identify bone surface alterations. Furthermore, bone industry was analysed using a metallographic microscope Zeiss Axioscope 7 mounted with an Axiocam 305 colour.

To distinguish among anthropogenic and non-anthropogenic modifications, trampling abrasion, and modern mechanical modifications produced by excavation tools, taphonomic literature was used as reference (Binford, 1981; Brain, 1981; Blumenschine, 1995; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Domínguez-Rodrigo and Piqueras, 2003; Fernández-Jalvo and Andrews, 2016; Fisher, 1995; Shipman, 1981).

Evidence of anthropogenic modification is based on the presence of cut-marks, percussion marks and burnt bones. Cut-marks were distinguished between slicing marks and scraping marks (Binford, 1981; Lyman, 2008; Potts and Shipman, 1981; Shipman, 1981; Shipman and Rose, 1983, 1984). A slicing mark is defined as a striation with a linear outline, a V-shaped section and (frequently) internal microstriations, whereas a scraping mark is a shallow sub-parallel cut-mark caused by a

stone tool dragged transversally along the length of the bone (Bromage and Boyde, 1984; Noe-Nygaard, 1989; Shipman and Rose, 1983, 1984). We recorded the following characteristics for each modification: number of striations, location, distribution on the bone, orientation, intensity, and shape (length, width, depth); and we compared them to several experimental and ethnological studies on medium/large prey (e.g. Costamagno and David, 2009; Galán and Domínguez-Rodrigo, 2013; Soulier et al., 2014; Soulier and Costamagno, 2017; Soulier and Morin, 2016) to hypothesize the performed action (skinning, evisceration, dismemberment, disarticulation, defleshing, removal of tendons, removal of the periosteum).

Anthropogenic traces caused during bone breakage for marrow extraction were analysed and divided into three categories: percussion marks, percussion stigmas and flakes (Blumenschine and Selvaggio, 1988, 1991; Capaldo and Blumenschine, 1994; Vettese et al., 2020). Intentional bone breakage to access marrow was recognized by analysing the shape and texture of the edge of the bone fracture (Blumenschine, 1995; Coil et al., 2017; Fisher, 1995; Outram, 2001; Villa and Mahieu, 1991).

The thermal alteration was documented following the methodology developed by the well-established literature and burnt bones were divided into two different categories: charred (200–500 °C, black/brown) and calcined (Costamagno et al., 2005; Shipman et al., 1984; Stiner et al., 1995; Théry-Parisot et al., 2004).

The identification of non-anthropogenic modifications followed classic criteria (e.g. Andrews, 1990; Binford, 1981; Domínguez-Rodrigo and Piqueras, 2003; Fernández-Jalvo and Andrews, 1992; Sala et al., 2012; Yravedra, 2006). We distinguished between tooth marks (pits, punctures, gnawing) and digestive corrosion.

3.3. Isotope analysis of mammal remains

The strontium isotope ratio ($^{87}\text{Sr}/^{86}\text{Sr}$) of the enamel of eight cervid teeth ($n = 3$ individuals from Riparo del Broion and $n = 5$ individuals from Rocca San Sebastiano cave) was determined. About 5 mg of tooth enamel were sampled using a dentist drill and processed for Sr chemistry at the Geochemistry Lab of the Department of Chemical and Geological Science, UNIMORE. Samples were digested using 6 M suprapure® nitric acid, dried down and then re-dissolved in 3 M nitric acid. Sr separation was performed through 30 µl columns filled with Eichrom Sr resin. Sr isotope analyses were run on a Neptune MC-ICPMS housed at the Centro Interdipartimentale Grandi Strumenti, UNIMORE (see e.g. Argentino et al., 2021; Lugli et al., 2017). Background and interference correction followed previous works (Lugli et al., 2017). Repeated measures of the NBS987 reference material yielded an $^{87}\text{Sr}/^{86}\text{Sr}$ ratio of 0.710246 ± 0.000019 (2 SD; $n = 8$). All values were reported to an NBS987 accepted value of 0.710248. Total laboratory Sr blanks did not exceed 180 pg.

3.4. Avifaunal analysis

The fossil avifauna comes from both sites. The taxonomic analysis relied on the comparison with modern specimens from two bird skeletal collections: the one stored at the Laboratory of Zooarchaeology and Taphonomy (L.A.T.) of the Prehistoric and Anthropological Sciences Section of the University of Ferrara and the “Marco Pavia Ornithological Collection” (MPOC) stored at the Dipartimento di Scienze della Terra of the University of Torino. For the systematics we followed Del Hoyo et al. (2014, 2016). The taphonomic analysis was carried out using a 30 × magnifying glass, in raking or reflected artificial light, and a 0.75–70 × Leica S6D Greenough stereomicroscope, available at the L. A. T. at the University of Ferrara.

3.5. Shell and fish analysis

The study of the malacological assemblage includes taxonomic, taphonomic and experimental analysis. For taxa identification, private

malacological collections and the *Atlante delle conchiglie terrestri e dulciacquicole italiane* (Cossignani and Cossignani, 1995) were consulted. The validity of the nomenclature applied in this analysis refers to the online checklist World Register of Marine Species (WoRMS; www.marinespecies.org).

The experimental work focused mainly on the identification of possible technical and practical properties of freshwater shells and their possible instrumental use by human groups. Current samples of both *Unio* sp. and *Anodonta* sp. were collected near the site, as these taxa seem to be more taxonomically related to the archaeological finds. Both alive (called ‘fresh’) and dead (called ‘dry’) mollusk shells were selected to observe any differences in the efficacy of the raw material. These samples were then tested on soft and medium-hard plant material in various ways, including cutting and scraping. The main aim of these initial experimental approaches was to test the effective instrumental capacity of this type of shell on relatively easy-to-handle materials.

Fish remains were determined by comparing specimens to a reference collection at the Bones Lab of the Department of Cultural Heritage of the University of Bologna.

The detailed taphonomic observation of both archaeological and experimental material, and the acquisition of photographs and digital images in multi-focus mode were carried out with a Fujifilm X-T3 digital camera with a Fujinon 80 mm macro lens, a Leica S9i stereomicroscope provided by the Bones Lab of the University of Bologna and, a Hirox KH-7700 3D digital microscope with MXG-10C body equipped with OL-140II lenses (140x-480x) provided by the University of Siena.

4. Results

4.1. Riparo del Broion assemblage

The faunal assemblage from Riparo del Broion is composed by 23,817 remains of macro and mesomammals, as well as 16 birds, 7 fish and 105 freshwater shell remains (Table 1).

4.1.1. Mammals taxonomic and anatomical data

Amongst the macro and mesomammals remains, 629 (2.6%) were taxonomically and anatomically identified, and 23,188 (97.4%) are indeterminate (Table 1). Most of the indeterminate remains are fragments less than 20 mm of length that could not be identified anatomically (98.2%).

Four families of ungulates (Equidae, Bovidae, Cervidae, Suidae) which represent 54.6% of the determinate remains, four of carnivores (Ursidae, Hyaenidae, Canidae, Felidae) representing 7.3% and three among rodents and lagomorphs (Castoridae, Sciuridae, Leporidae) corresponding to 37.9% of the determined remains are present in the assemblage (Fig. 2).

Amongst the ungulates, *Cervus elaphus* (19%) is the most abundant species, although represented by a few bones: mainly tibias and femurs, and some teeth (Table 2; Fig. 3). There are other species of cervids: *Megaloceros giganteus* (11%), also represented mainly by tibias; *Alces alces* (2%) by two phalanges; and *Capreolus* (5%) by some teeth and phalanges and a fragmented radius (Suppl. Table 1). In addition, the cervid group (37%) comprises bones of cranial and appendicular skeleton that could not be identified with a specific taxon. Caprinae (8%) includes three bones of *Rupicapra rupicapra* (teeth and a first phalange) and some elements that could correspond to the same species. Moreover, there are two fragments of tibia and a tooth of Equidae (3%); a rib and two metapodials of *Bos/Bison* (3%); and 11 fragments of teeth of *Sus scrofa* (11%).

We also classified 244 remains as Ungulate based on size categories, among which 27.5% are from medium-large-sized, 25% from small-medium-sized, and 20.1% from medium-sized animals. Most of these remains are fragments of long bones and cranial elements.

Regarding carnivores, *Ursus* (37%) is the main species (Fig. 2), including *Ursus arctos* and *Ursus spelaeus*. Most of the elements are teeth,

Table 1

Riparo del Broion (stratigraphic unit US11) e Rocca San Sebastiano cave (stratigraphic unit US3 sub-unit Cg): Late Mousterian taxonomic faunal composition by NISP, %NISP and MNI.

	RB			RSS		
	NISP	% NISP	MNI	NISP	% NISP	MNI
<i>Equus ferus</i>	2	0.6	2			
<i>Equus</i> sp.	1	0.3	1			
<i>Bos primigenius</i>				4	0.3	1
<i>Bos/Bison</i>	3	0.9		4	0.3	
<i>Capra ibex</i>				2	0.2	1
<i>Rupicapra rupicapra</i>	3	0.9	1	3	0.2	1
Caprinae	5	1.5		7	0.5	
<i>Megaloceros giganteus</i>	11	3.2	1			
<i>Alces alces</i>	2	0.6	1			
<i>Alces-Megaloceros</i>	1	0.3				
<i>Cervus elaphus</i>	19	5.5	2	81	6.3	4
<i>Capreolus capreolus</i>	5	1.5	2	36	2.8	3
Cervidae	37	10.8		79	6.1	
<i>Sus scrofa</i>	11	3.2	3	2	0.2	2
Ungulate very large	1	0.3				
Ungulate large	41	11.9		16	1.2	
Ungulate medium-large	67	19.5		38	2.9	
Ungulate medium	49	14.2		147	11.4	
Ungulate medium-small	61	17.7		557	43.1	
Ungulate small	10	2.9		117	9	
Ungulate indet.	15	4.4		200	15.5	
Total Ungulates	344	54.7	13	1293	99.9	12
<i>Ursus arctos</i>	3	6.5	2			
<i>Ursus spelaeus</i>	5	10.9	1			
<i>Ursus</i> sp.	9	19.6	1			
<i>Crocota crocuta</i>	2	4.3	1	1		1
<i>Canis lupus</i>	7	15.2	3	1		1
<i>Vulpes</i>	5	10.9	1			
<i>Cf. Alopex lagopus</i>	1	2.2	1			
<i>Panthera spelaea</i>	1	2.2	1			
<i>Felis silvestris</i>	1	2.2	1			
Carnivora indet.	12	26.1				
Total Carnivores	46	7.3	12	2	0.1	2
<i>Castor fiber</i>	236	98.7	6			
<i>Marmota marmota</i>	1	0.4	1			
<i>Castor/Marmota</i>	1	0.4	1			
<i>Lepus europaeus</i>	1	0.4	1			
Total Rodents-	239	38	9			
Lagomorpha						
Total NISP	629	100	34	1295	100	14
Large size	115	0.5		6	0.26	
Medium-large size	80	0.3		33	1.4	
Medium size	25	0.1		68	2.9	
Small-medium size	65	0.3		441	18.9	
Small size	129	0.6		39	1.7	
Very small size	9	0.04		5	0.2	
Indeterminate	22,765	98.2		1736	74.6	
Total indeterminate	23,188			2328		
Total meso/macrofauna	23,817			3623		
Birds	16			7		
Fishes	7					
Freshwater shells	105					
Total remains	23,945			3630		

but there are also some vertebrae, radius, femurs, and second phalanges. *Canis lupus* (15.2%) and *Vulpes* (10.9%) are also relevant. Other species including hyena and lion, are represented by less than five remains from the cranial skeleton (Suppl. Table 2).

Lastly, Rodentia includes mainly remains of *Castor fiber* (98.7%). All anatomical groups are present (Table 3; Fig. 3), but the cranial skeleton, the stylopodia and zeugopodia are the most abundant parts. Phalanges and axial elements, except for the ribs, show a lower percentage of preservation.

Regarding the MNI and the age-at-death, based on tooth wear and MNE, there are two adult individuals of *Ursus arctos* of different sizes and three individuals of *Canis lupus* (one juvenile and two adults). Among the ungulates, three individuals of *Sus scrofa* (one infantile, one juvenile and

one adult), two individuals of *Cervus elaphus*, two individuals of *Capreolus* (one senile and one adult) and two individuals of *Equus ferus* were calculated. Furthermore, six individuals of *Castor fiber* (two juveniles and four adults) were registered. The other species of ungulates, lagomorphs and carnivores are represented by only one individual.

4.1.2. Mammals taphonomic data

Only 40 bones (0.2%) are complete, so the assemblage is very fragmented (99.8%). The complete bones are small bones, like teeth, carpals, phalanges, some caudal vertebrae and non-fused epiphyses. The fragmented remains are mostly less than 10 mm (64.6%), and only 0.5% are more than 50 mm.

The assemblage is altered by diagenetic processes such as concretion (33.9%) and manganese (5.5%). However, only for a few fragments with high concretion it was challenging to examine the surface of the bones.

Moreover, we recorded 12,756 remains with modifications, 99.9% are anthropogenic (cut-marks (0.45%), percussion marks (0.65%) and thermal alterations (98.7%) and 0.03% are from carnivores (tooth marks and digestion) (Table 4; Suppl. Table 3). Cut-marks, including slicing and scraping, were identified on ungulate, carnivore and rodent bones, as well as on a high number of diaphyses of long bones from indeterminate ungulates and indeterminate animals. Among cervids, there are oblique, short and simple slicing marks on a tibia and a metatarsal, and a simple, longitudinal one on another tibia of *Cervus* (Fig. 4; Fig. 5); oblique, short and multiple slicing marks on a tibia and a metapodial of *Megaloceros*; as well as on a femur and a tibia of cervid, all linked to defleshing and the removal of muscles. A radius fragment of *Ursus arctos* presents a transverse short slicing mark (Fig. 4C) on the diaphysis, parallelly to the edge of the green bone fracture (Fig. 4C).

Regarding the percussion marks, flakes ($n = 77$) are the most abundant. They are present mainly on long bones of large- and medium-large sized animals. Moreover, we identified notches on the diaphysis of a tibia of *Cervus*, a radius of cervid, a tibia of *Alces-Megaloceros*, and on other long bones of indeterminate animals. Thermal alterations are present on 15.3% of the determinate remains (including herbivores (NR:50), carnivores (NR:12), and rodents (NR:34) and 53.9% of the indeterminate (Table 5). Modifications classified as charred (81.6%) are more abundant than calcinate (18.4%).

Regarding the beaver bones, traces of post-depositional modifications are registered on 9.7% of the remains which have concretions and 26.6% are characterised by a manganese coating. Moreover, anthropogenic modifications (Fig. 4D; Fig. 5) were identified on 15 bones of this large rodent (6.6% of the NISP). Cut-marks were detected mainly on ribs (10), coxal (1), phalanx I (1), metatarsals (2), and tibia (1). Cut-marks are primarily skinning –slicing marks on a proximal dorsal diaphysis of rib (RB27) and a metatarsal (RB315), but there also signs of defleshing. Moreover, this last anatomical element (RB315) has a brown colouring, attributable to burning activities (Fig. 4E). In total, among the analysed beaver remains, 13.3% are burned and all are brown or black in colour (burning temperature c. 200–400 °C) (Costamagno et al., 2005; Stiner et al., 1995).

Carnivore modifications (Table 4) are present only as tooth marks on two indeterminate bones of large-sized animals and on one indeterminate remain and, as digestion corrosion on a Caprinae metapodial distal epiphysis that measured 10–20 mm of length.

4.1.3. Bone retouchers

We identified eight bones used as retouchers. The most relevant are on a femur and a metatarsal of *Cervus*, and on a radius and a femur of cervid (Fig. 6). These bones show trihedral impressions, that in some cases have longer and linear impressions with the same orientation. Other four indeterminate long bones from large-sized animals and indeterminate also present this type of marks.

4.1.4. Avifaunal remains

The taxonomic analysis of the bird assemblage allowed the

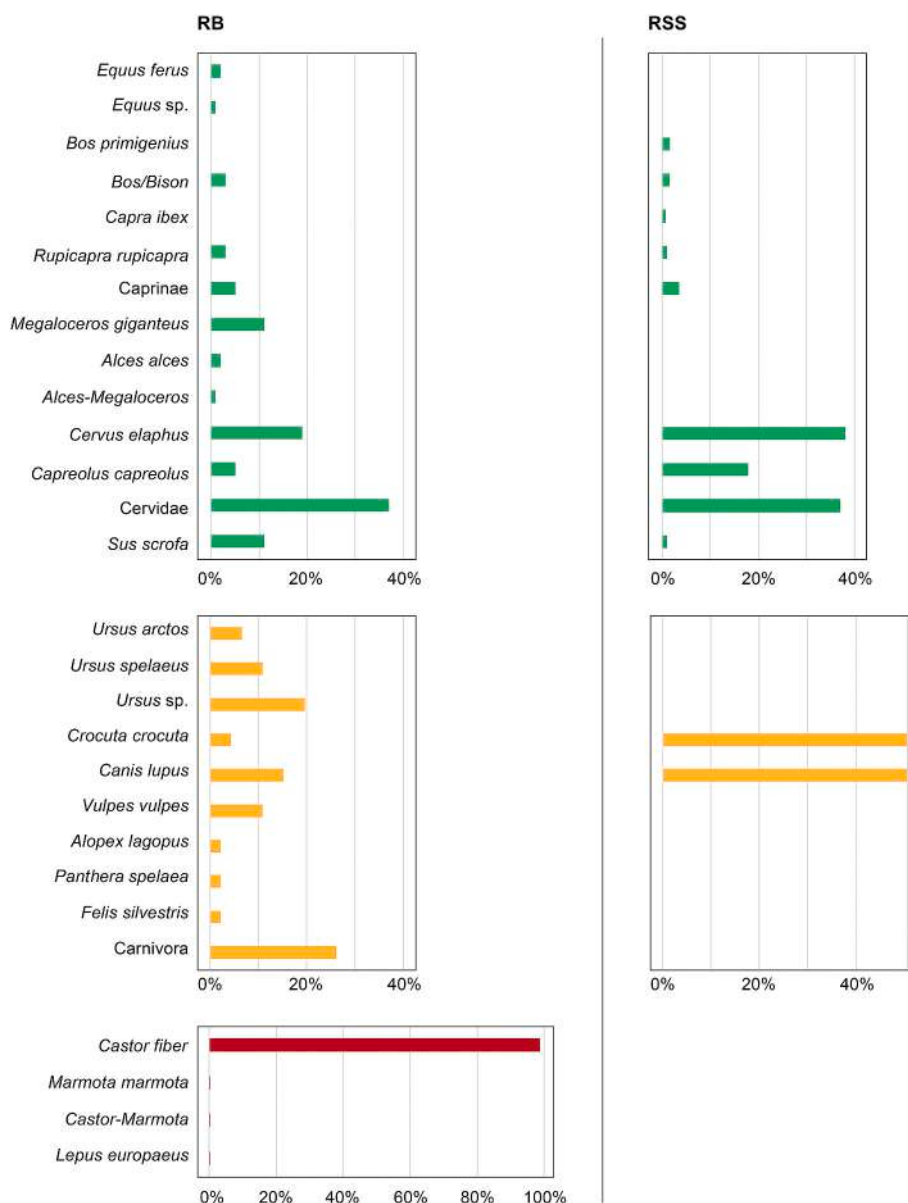


Fig. 2. Species classified by ungulates, carnivores and rodents. %NISP calculated by the total remains from each group from Riparo del Broion (ungulates 344 remains; carnivores 46 remains; rodents 239 remains) and Roccia San Sebastiano cave (ungulates 1293 remains; carnivores 2 remains).

identification of 10 bird taxa, whereas 3 out of 16 bird bones were not identified because too fragmentary (Suppl. Table 4). One tarsometatarsus was tentatively attributed to *Gallinago media*, a species which has rarely been reported in the Italian fossil record, whereas one coracoid was identified as *Scolopax rusticola*. These two Scolopacidae indicate, respectively, the presence of wetlands and woodlands in the surrounding of Riparo del Broion (Cramp, 1998). The presence of wetlands is further supported by the finding of an ulna distal fragment, referred to *Cygnus cygnus*.

A small claw was attributed to a swift (*Apus pallidus/apus*), which could suggest the presence of rocky outcrops and cliffs near the cave (Cramp, 1998). Several species of diurnal and nocturnal raptors are also part of the bird assemblage. An ulna fragment was attributed to a juvenile *Falco* sp., whereas two proximal fragments of ungual phalanges belonged to a large Accipitridae and to an unidentified Strigidae. Moreover, one proximal carpometacarpus has been referred to *Picus canus/Dendrocopos leucotos*, supporting the presence of woodlands around the cave. As for Passeriformes, a proximal epiphysis of a humerus was referred to *Prunella collaris*, which suggests the presence of

rocky outcrops and meadows near the cave, whereas four other small bones belonged to unidentified Passeriformes.

More in general, the hind limb bones are more abundant than the fore limb bones and the axial skeleton. Most of the bird bones are incomplete, with a high fragmentation rate. From a taphonomic perspective, the most abundant natural modifications on bird bones are manganese dioxide staining and root etching, whereas rodent marks and surface corrosion were observed only on a few remains. The slight superficial corrosion observed on the distal *Cygnus cygnus* ulna and on a small Passeriformes remain is likely due, respectively, to the digestion by a carnivore and by a nocturnal raptor (Andrews, 1990). Both possibly participated in the accumulation of the bird bones in the cave.

Three posterior phalanges have combustion traces and, among these, the one referred to a Strigidae is calcined. A potential cut-mark was detected on the tarsometatarsus of cf. *Gallinago media*. This trace is short and longitudinal to the major axis of the element and is located on the dorsal part of the diaphysis (Suppl. Fig. 1).

Table 2

Anatomical composition of the main ungulates of each site: *Cervus elaphus* from Riparo del Broion (stratigraphic unit US 11), and *Cervus elaphus* and *Capreolus* from Roccia San Sebastiano cave (stratigraphic unit US3 sub-unit Cg).

	RB			RSS					
	<i>Cervus</i>			<i>Cervus</i>			<i>Capreolus</i>		
	NISP	MNE	%MAU	NISP	MNE	%MAU	NISP	MNE	%MAU
Cranial	6	6		25	16		6	6	
Mand				7	3	42.9	1	1	20
Teeth	6	6	7.5	18	13	11.6	6	6	7.5
Axial	1	1							
Rb	1	1	1.5						
Fore limbs	2	2		21	17		10	8	
H				4	4	57.1	1	1	20
R				6	6	85.7	4	3	60
U				3	3	42.9	2	2	40
Cp	1	1	3.3						
Mc	1	1	8	8	4	22.9	3	2	16
Hind limbs	10	8		22	16		19	11	
Cx				1	1	14.3	1	1	20
F	2	2	40	4	3	42.9	1	1	20
T	7	5	100	4	4	57.1	4	3	60
As							1	1	20
Ta				1	1	4.8			
Mt	1	1	20	12	7	100	12	5	100
Extremities				13	12				
Mtp				2	1				
Pha1				6	6	21.4			
Pha2				2	2	7.1			
Pha3				1	1	3.6			
Pha3 R				2	2				
Total	19	17		81	61		35	25	

4.1.5. Freshwater resources

We recorded seven fish elements, and 105 fragments of freshwater shellfish remains in level 11 (Table 1 and Suppl. Table 5). All fragments of freshwater shellfish belong to *Unio* sp. Family. Based on the taxonomic spectrum of the assemblage (Table 1), their predation by animals is excluded (Girod, 2015), although the taphonomic analysis did record tooth marks of micromammal gnawing on some finds (Fig. 7, 8-y). Nevertheless, these bivalves, as also indicated by excavation evidence, are clearly associated with anthropogenic levels of habitation and are contextual with flints, animal remains with butchery modifications and, in some cases, with specific combustion structures. Regardless, the observation of the fragmented remains did not identify traces (such as combustion or modifications caused by the opening of the shells) that could confirm their use as food, although it is very likely. However, the small size of the fragments, between 6 and 15 mm, must be considered. Here, the instrumental use of the shells or of portions of them is supported by the presence of polycations and fractures on the edge of some Unionidae fragments (Fig. 7, 7x-9x). Furthermore, the use of shells as tools is attested both by ethnographic sources – such as knives made from *Unio* sp. By the Ainu of Hokkaido Island (Cuenca-Solana et al., 2011) – and by Middle Palaeolithic archaeological evidence – such as the use of *Callista chione* in southern Italy and Greece (Romagnoli et al., 2017; Villa et al., 2020), or of *Glycymeris glycymeris* and *Mytilus galloprovincialis* during the Spanish Upper Palaeolithic (Cuenca-Solana, 2015; Cuenca-Solana et al., 2011, 2021).

The experimentation (Suppl. Fig. 2) carried out on *Unio* sp. and *Anodonta* sp. Shells, indicated a substantial difference in the use of fresh and dry shells for any instrumental operation. The defoliation of the layers of the exoskeleton causes dry shells to break. The scraping operation with fresh shells on soft and medium-hard plant material was successful only when new sharper edges were created. Indeed, the use of the natural edge of the valve does not allow an easy grip, as it breaks easily due to its thinness and does not tolerate prolonged action over time. The creation of a new active margin can be obtained simply by positioning the shell with its convex part upwards and applying downward pressure with both thumbs. This procedure breaks the lamellar

structure of the shell and creates numerous fragments with sharper and smaller edges that are therefore more manageable. The microscopic observation of two points of the *Anodonta* sp. Fragment before and after the experimentation allows us to observe fractures, polishing, and rounding areas like those observed in the archaeological remains (Fig. 7). It must be considered that polishing may also be created by post-depositional alterations which is not experimentally tested here. In this case, however, the polishing and rounding areas are in a specific spot, and not extended in “active” part of the archaeological shells. These characteristics corroborate the hypothesis of possible instrumental use of the malacological record.

The Anodontini include some of the most over-described species on the planet and have a Holarctic distribution from north-western America to Europe, parts of northern Africa and the Middle East (Riccardi et al., 2020). The fragments of these shells found in Riparo del Broion, generically determined as *Unio* sp. - *Anodonta* sp., certainly belong to one of the species still present today in Italy. Their distribution habitat is limited to large Adriatic rivers and streams, well-oxygenated lakes, and river basins and is delimited by the Italian Alps in the north, Apennines in the west, and Dinaric Alps in the east (Froufe et al., 2017).

These species live both along the banks and to a depth of 3 m in gravels, cobble, and sand. They are visible and partially outcropping and can be easily harvested by hand. The Neanderthals of Riparo del Broion could have collected them either a hundred meters downstream from the site, along the banks of a paleo-lake or watercourse that has now disappeared, or at few northwest of the site, at lake Fimon, a paleo-lake that is still present today.

On the other hand, the discovery of seven freshwater fishes allowed the determination of five *Exos lucius*, two canine teeth of Cyprinidae and one indeterminate cranial fragment. The presence of *Exos lucius* is already attested at Riparo del Broion, as it was recognized in the Uluzian levels 1f and 1 g. The size of the canines (Fig. 7) suggests large individuals, possibly over 2 kg. Nowadays, in southern Europe, specimens generally measure 15–20 cm in total length and weigh about 40–80 g in the first year, 35–45 cm and 350–800 g in the third, 50–60 cm and 1–2 kg in the fifth and, 65–75 cm and 2.5–4 kg in the eighth. Large

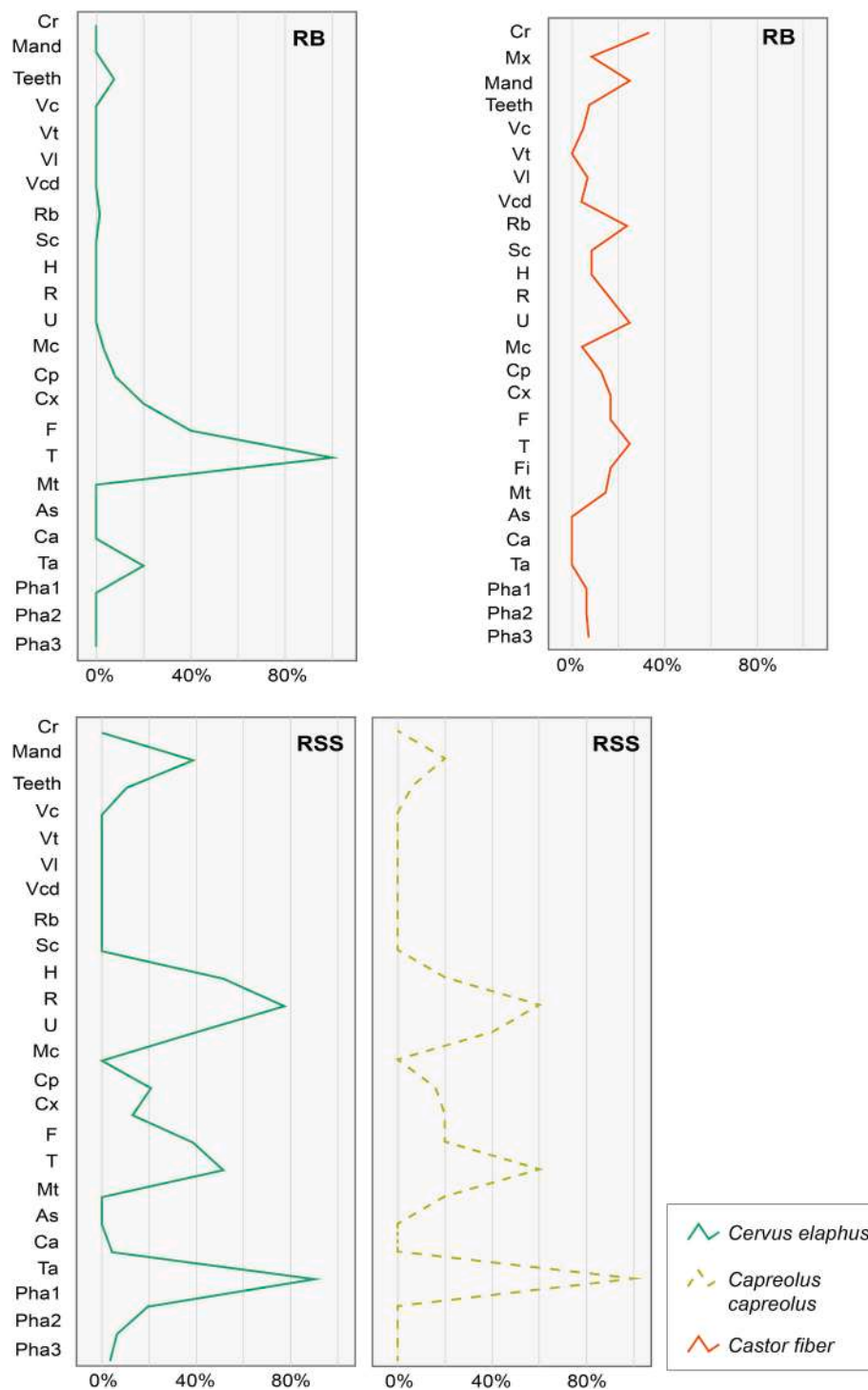


Fig. 3. Anatomical representation of the main species of each site: *Cervus elaphus* (%MAU) and *Castor fiber* (%ISu) from Riparo del Broion (stratigraphic unit US11), and *Cervus elaphus* (%MAU) and *Capreolus capreolus* (%MAU) from Roccia San Sebastiano cave (stratigraphic unit US3 sub-unit Cg) .

fish reach 1.75 m in total length and 48.0 kg (lifespan in the wild is about 26 years), (Bianco, 1995; Bianco and Delmastro, 2011).

4.1.6. Sr isotopes

Sr isotope ratios of $n = 3$ cervid enamel from Riparo del Broion range from 0.70524 to 0.70922 and are reported in Suppl. Fig. 3. Two out of three individuals at Riparo del Broion retain a non-local signal and only RB80 (0.70867) is fully compatible with the local baseline, determined through local rodents (Nava et al., 2020) and the bioavailable Sr isotope variability within a radius of ~10 km (see the Italian isoscape, Lugli

et al., 2022).

4.2. The Roccia San Sebastiano cave assemblage

4.2.1. Mammals taxonomic and anatomical data

We studied 3623 mammals remains as well as 7 birds from Roccia San Sebastiano cave (Table 1). Unlike the previous context (2.6%), it is important to underline that 35.8% were taxonomically and anatomically identified. The indeterminate remains (64.2%) were classified by weight and type of bone, but most of them are fragments less than 2 cm in length

Table 3Anatomical composition of *Castor fiber* from Riparo del Broion (stratigraphic unit US11).

	NISP	%NISP	MNE
Cranial	44	18.6	15
Cr	5	2.1	2
Mx	1	0.4	1
Mand	4	1.7	3
Teeth	34	14.4	9
Axial	126	53.4	45
Vc	2	0.8	2
VI	2	0.8	2
Vcd	5	2.1	5
Rb	115	48.7	34
St	1	0.4	1
Cl	1	0.4	1
Fore limbs	15	6.4	14
Sc	1	0.4	1
H	1	0.4	1
R	2	0.8	2
U	4	1.7	3
Cp	4	1.7	4
Mc	3	1.3	3
Hind limbs	21	8.9	16
Cx	5	2.1	2
F	2	0.8	2
T	3	1.3	3
Fi	3	1.3	2
Mt	8	3.4	7
Extremities	21	8.9	20
Mtp	2	0.8	1
Pha1	6	2.5	6
Pha2	6	2.5	6
Pha3	7	3	7
Indeterminate	9	3.8	
In	9	3.8	
Total	236		110

that could not even be identified on an anatomical level (74.7%).

From the total NISP of ungulates (99.85%) three families (Bovidae, Cervidae and Suidae) and six species of ungulates were identified in detail (Table 1 and Fig. 2) with a total of 218 remains (16.8% of the total ungulates NISP). Of these same, the best-represented taxa are *Cervus elaphus* (37.2% of the total ungulate remains) and *Capreolus* (16.5%), including 37.2% of bones classified as indeterminate cervids. The Bovidae family is comprised mainly by *Bos/Bison* (1.8%) and *Bos primigenius* (1.8%), but also by *Rupicapra rupicapra* (1.4%) and *Capra ibex* (0.9%). There are two bones of *Sus scrofa*. Carnivores are only represented by a phalanx of *Crocota crocota* and an upper incisive of *Canis lupus*.

The anatomical representation of the two main species (*Cervus elaphus* and *Capreolus*) is biased (Table 2; Fig. 3). Metatarsals, stylopodia, zeugopodia, and mandibles are the best-represented parts of *Cervus*, whereas metacarpals and phalanges have lower percentages. The result of the correlation between %MAU and the bone density calculated for *Cervus elaphus* is positive and significant ($r_s = 0.67$; $p = 0.00057$). In the case of *Capreolus*, metatarsals, radii, tibiae, and ulnae have the highest values; and other elements such as humeri, coxals, femurs and astragali are less represented. The axial skeleton and scapulae are completely absent in both species, as well as phalanges from *Capreolus*. The low MNE value does not allow us to calculate the correlation with bone density to assess transport strategies and attrition processes. However, diagenetic alterations would also be a cause.

Other ungulates are represented by few remains (Suppl. Table 1). In the case of caprines, two cranial elements of *Capra* and a molar, a humerus and a radius of *Rupicapra* were determined. Moreover, another fragment of humerus, several long bones from hind limbs and a second phalanx of Caprinae are also present. *Bos primigenius* is represented only by four bones (P/3, scapula, humerus, tibia) and *Bos/Bison* by other four (cranium, molar, tibia, third phalanx). One tooth and a femur diaphysis

of *Sus scrofa* were also determined.

We also classified 1063 remains as Ungulate by size categories, among which 51.8% are bones of small-medium-sized animals, whereas 13.7% and 10.9% are of medium-sized and small-sized species, that should correspond respectively to cervids and caprines. These remains are mainly fragments of indeterminate long bones, teeth and cranium fragments, and axial elements.

Regarding the MNI and the age-at-death, four individuals of *Cervus* (two juveniles, two adults, one senile) and three of *Capreolus* (one infantile, two adults) were calculated. The other species of ungulates are each represented by one adult individual, except for *Sus*, which also includes an infantile.

4.2.2. Mammals taphonomic data

The assemblage is almost completely fragmented, except for 15 complete bones (0.4%), which include: teeth, a residual phalanx and a carpal of cervids; several petrous bones, a sesamoid and a non-fused intervertebral disc of indeterminate ungulates; an incisor of *Canis lupus*. The fragmented bones were measured, and the most abundant length categories were 10–20 mm (determinate = 43.8%; indeterminate = 67.7%) and 20–30 mm (determinate = 28.1%; indeterminate = 14.6%). Only 4.2% and 0.2% (determinate and indeterminate, respectively) are larger than 50 mm, but are no more than 10 cm of length. The 0,2–10 mm category it is certainly underrepresented compared to the Riparo del Broion and corresponds to 9,3% of the total remains. The assemblage is affected by diagenetic processes. Concretion (44.8%) and manganese (42.7%) are the most abundant alterations, but in low degrees. Despite this, the surface of the bones was in a good condition to observe the modifications. A total of 809 modifications were registered, 99.5% are anthropogenic modifications and 0.5% carnivore marks (Table 4). Anthropogenic modifications include cut-marks, percussion marks and burnt bones (Suppl. Table 6). Cut-marks include slicing and scraping marks and are more abundant on long bones of small-medium-sized animals. In the case of *Cervus* (Fig. 5; Fig. 8), there are multiple slicing marks on the ramus caused by the disarticulation of the mandible; as well as multiple short slicing marks on a coxal that could have been produced during the removal of muscle insertions. Defleshing is also testified by multiple slicing marks on the diaphysis of long bones (humeri, radii, femurs, tibiae), and the removal of the periosteum from the metapodials. There are multiple strong, long slicing marks on the lateral part of a metatarsal that could have been produced during one of the initial stages of the skinning operations. For the *Capreolus* (Fig. 5; Fig. 8), there is evidence of defleshing on radii and femurs, and of the removal of the periosteum on radii, tibiae and metatarsals.

As far as percussion marks are concerned, flakes ($n = 155$) are the most abundant and were mainly observed on indeterminate long bones of diverse sized species, but also of *Cervus* (radii, metacarpals, metatarsals) and *Capreolus* (radii, metapodials). Notches are present on a mandible, a humerus and a radius of *Cervus*, on a metacarpal and a tibia of *Capreolus*, on two metatarsals of cervids, and on some long bones of indeterminate ungulates. Moreover, percussion stigmas were identified on a femur (*Sus*) and on an indeterminate long bone (medium-sized ungulate).

Thermal alterations affect 15.1% of the assemblage (Table 5), with higher values among the determinate bones (24.6%), mostly medium- and small-sized ungulates, compared to the indeterminate remains (9.8%). Charred elements (90.3%) are more abundant among all species and sizes, than calcinate ones (9.7%).

Carnivore modifications are almost absent (Table 4), five tooth marked elements are present: a simple score on a long bone of a large-medium-sized species; multiple scores on a long bone of a medium-sized animal; multiple pits on a long bone of a small-medium-sized creature; and multiple pits on a humerus distal epiphysis of a *Bos primigenius*. Moreover, there is a long bone fragment (10–20 mm in length) of a small-medium-sized species with moderate digestive corrosion.

Table 4

Anthropogenic modifications (PM = percussion marks; CM = cut-marks; RM = retoucher bones; BM = burnt bones) and non-anthropogenic modifications (Cto = tooth marks; Cdg = digestion) present in Late Mousterian bone assemblages from Riparo del Broion (stratigraphic unit US11) and Roccia San Sebastiano cave (stratigraphic unit US3 sub-unit Cg).

	RB					RSS						
	PM	CM	RM	BM	Cto	Cdg	PM	CM	RM	BM	Cto	Cdg
<i>Equus ferus</i>				1 (50)								
<i>Bos primigenius</i>											1 (33.3)	
<i>Bos/Bison</i>										1 (25)		
<i>Capra ibex</i>										1 (25)		
Caprinae				1 (20)		1 (20)	1 (14.3)	1 (14.3)		1 (15.3)		
<i>Megaloceros giganteus</i>		2 (18.2)		2 (18.2)								
<i>Alces-Megaloceros</i>	1 (100)											
<i>Cervus elaphus</i>	1 (5.3)	3 (15.8)	2 (10.5)	2 (10.5)			6 (7.4)	12 (14.8)	1 (1.5)	15 (18.5)		
<i>Capreolus capreolus</i>				2 (40)			3 (8.3)	6 (16.7)		6 (16.7)		
Cervidae	1 (2.7)	2 (5.4)	2 (5.4)	1 (2.7)			2 (2.5)	4 (5.1)		14 (17.7)		
<i>Sus scrofa</i>				4 (36.4)			1 (50.0)	2 (100)				
<i>Ursus arctos</i>		1 (33.3)		2 (66.7)								
<i>Ursus spelaeus</i>				1 (20)								
<i>Ursus sp.</i>				2 (66.7)								
<i>Canis lupus</i>				3 (42.9)								
<i>Alopex lagopus</i>				1 (100)								
<i>Felis silvestris</i>				1 (100)								
Carnivora indet.	1 (8.3)	1 (8.3)		3 (25)								
<i>Castor fiber</i>	1 (0.4)	14 (5.9)		34 (14.4)								
Ungulate very large	1 (100)											
Ungulate large	1 (2.4)	3 (7.3)		4 (9.8)			1 (6.3)	2 (25)		2 (12.5)		
Ungulate medium-large	6 (9)	2 (3)		10 (14.9)				1 (2.6)		7 (18.4)	1 (2.9)	
Ungulate medium	1 (2)			7 (14.3)			5 (3.4)	3 (2)		42 (28.6)		
Ungulate medium-small	3 (4.9)	2 (3.3)		13 (21.3)			44 (7.9)	46 (8.2)		141 (25.3)	1 (0.2)	2 (0.2)
Ungulate small		1 (10)		1 (10)				2 (1.7)		44 (37.6)		
Ungulate indet.				1 (6.7)						44 (22)		
Large size	10 (8.7)	5 (4.3)	3 (2.6)	10 (8.7)	2 (1.7)		1 (16.7)	1 (16.7)		1 (16.7)		
Medium-large size	5 (6.3)	2 (2.5)		13 (16.3)			4 (12.1)	1 (3.0)		7 (21.2)		
Medium size	1 (4)	1 (4)		5 (20)			6 (8.8)	2 (2.9)		24 (5.3)		
Small-medium size	1 (1.5)	1 (1.5)		60 (92.3)			81 (18.4)	4 (0.9)		116 (26.3)		
Small size		2 (1.6)		11 (8.5)						11 (28.2)		
Very small size				4 (44.4)								
Indeterminate	47 (0.2)	16 (0.1)	1 (0.004)	12,403 (54.5)	1 (0.004)		9 (0.5)	7 (0.4)	1 (0.1)	70 (4)		
Total	81	58	8	12,602	3	1	164	94	2	547	3	2

4.2.3. Bone industry and retouchers

We identified two remains with marks caused by the bones being used as retouchers. One is a long bone of an indeterminate animal. The other is a distal part of a tibia diaphysis of *Cervus* (Fig. 6), on which small linear and trihedral impressions, with mostly coinciding orientation, are placed on the dorsal-medial face of the bone. Moreover, on the same bone, multiple longitudinal scraping marks, as well as short, multiple and oblique scrapings related to the previous removal of the periosteum, were identified.

In addition, one remain was worked as bone industry (Fig. 9). It is an indeterminate long bone conserving part of the diaphysis and part of the epiphysis: 64.77 mm in length, 21.56 mm in width and 12.58 mm in thickness. The shape of the articulation looks like the proximal portion of a metapodial or a radius of a large- or medium-sized species, but the taxonomic identification was not possible. The bone presents an archaeological green fracture through the longitudinal edge of the diaphysis. The diaphysis was heavily re-shaped, modifying the whole surface of the tool, through fine scrapings (Figs. 9 and 1) and its use (Figs. 9, 2–4), sparing only a limited and slightly concave area of the original articulation surface. Furthermore, diagenetic alterations modified its surface, and only the distal portion clearly shows a polished surface shaping it as an awl (Figs. 9, 2–4). These features were already observed in other Final Middle Palaeolithic or even Early Upper Palaeolithic assemblages from France and Italy (e.g. Arrighi et al., 2020a; Caron et al., 2011; d'Errico et al., 2003; Martisius et al., 2022; Thun Hohenstein et al., 2018).

4.2.4. Avifaunal remains

The taxonomic analysis of the seven bird remains allowed the

identification of 2 taxa, despite the high fragmentation rate (Suppl. Table 4). A fragment of a humerus proximal epiphysis belongs to an unidentified medium-sized bird; a sternum fragment belongs to an unidentified medium-sized bird; a carpometacarpus distal epiphysis was referred to a Corvidae; two diaphysis fragments of long bones (likely one femur or tibiotarsus and a tarsometatarsus) belong to two small birds; a posterior phalanx has been referred to a medium-sized bird and, lastly, an ungual phalanx has been attributed to an Accipitridae.

From a taphonomic perspective, the most abundant natural alteration on bird bones is manganese dioxide staining. Digestion traces of carnivores or raptors or gnawing marks weren't detected. There is only one anthropogenic modification on the Accipitridae ungual phalanx, that is totally burned.

4.2.5. Sr isotopes

Sr isotope ratios of $n = 5$ cervids enamel from Roccia San Sebastiano cave range from 0.70852 to 0.70884 and are reported in Suppl. Fig. 2. All the individuals are fully compatible with the local baseline, determined through local modern plants and the bioavailable Sr isotope variability within a radius of ~10 km (see the Italian isoscape, Lugli et al., 2022).

5. Discussion

As a premise to the present discussion, one cannot but emphasize the huge discrepancy between the determined remains of Riparo del Broion (2.6%) and Roccia San Sebastiano (35.8%) despite the difference in the total number of remains (RB 23,945 vs RSS 3630), which is justified also by the extent of the investigated areas. This difference must certainly be

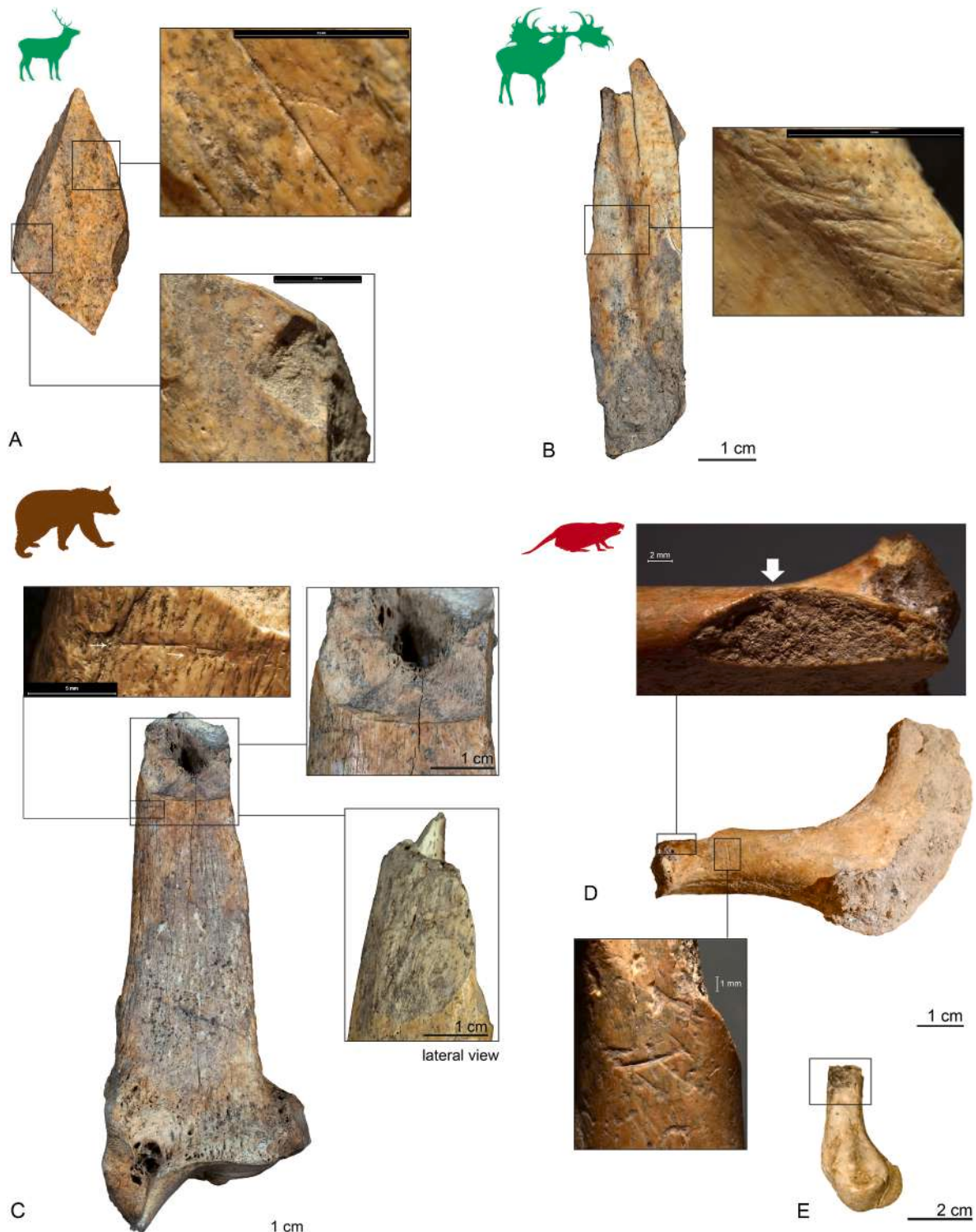


Fig. 4. Examples of anthropogenic modifications from Riparo del Broion (stratigraphic unit US11). A. percussion stigma and slice on a tibia of *Cervus elaphus*; B. slices on a tibia of *Megaloceros giganteus*; C. cut-mark and green bone fracture on a radius of *Ursus arctos*; D. percussion stigma and a slice on coxal of *Castor fiber*; E. burnt metapodial of *Castor fiber*.

sought between the different taphonomic characteristics of the two assemblages and/or in the human groups' mode of settlement.

Although concretion appears to be the main edaphic agent to have significantly altered the surfaces of the remains at both sites, it appears to be more prevalent at Roccia San Sebastiano (44.8%) than at Riparo del Broion (33.9%). Carnivores can be safely excluded among the agents of accumulation of the faunal assemblage for both sites, while

anthropogenic evidence related to bone fracturing show greater intensity at Roccia San Sebastiano (Table 4). No refits have been detected, probably also due to the high fragmentation degree of the remains for both sites.

A different use and/or intensity of frequentation by the Neanderthal groups of these two sites seem, however, to be able to account for the unexpected discrepancy in the NISP percentage. In fact, the use of fire

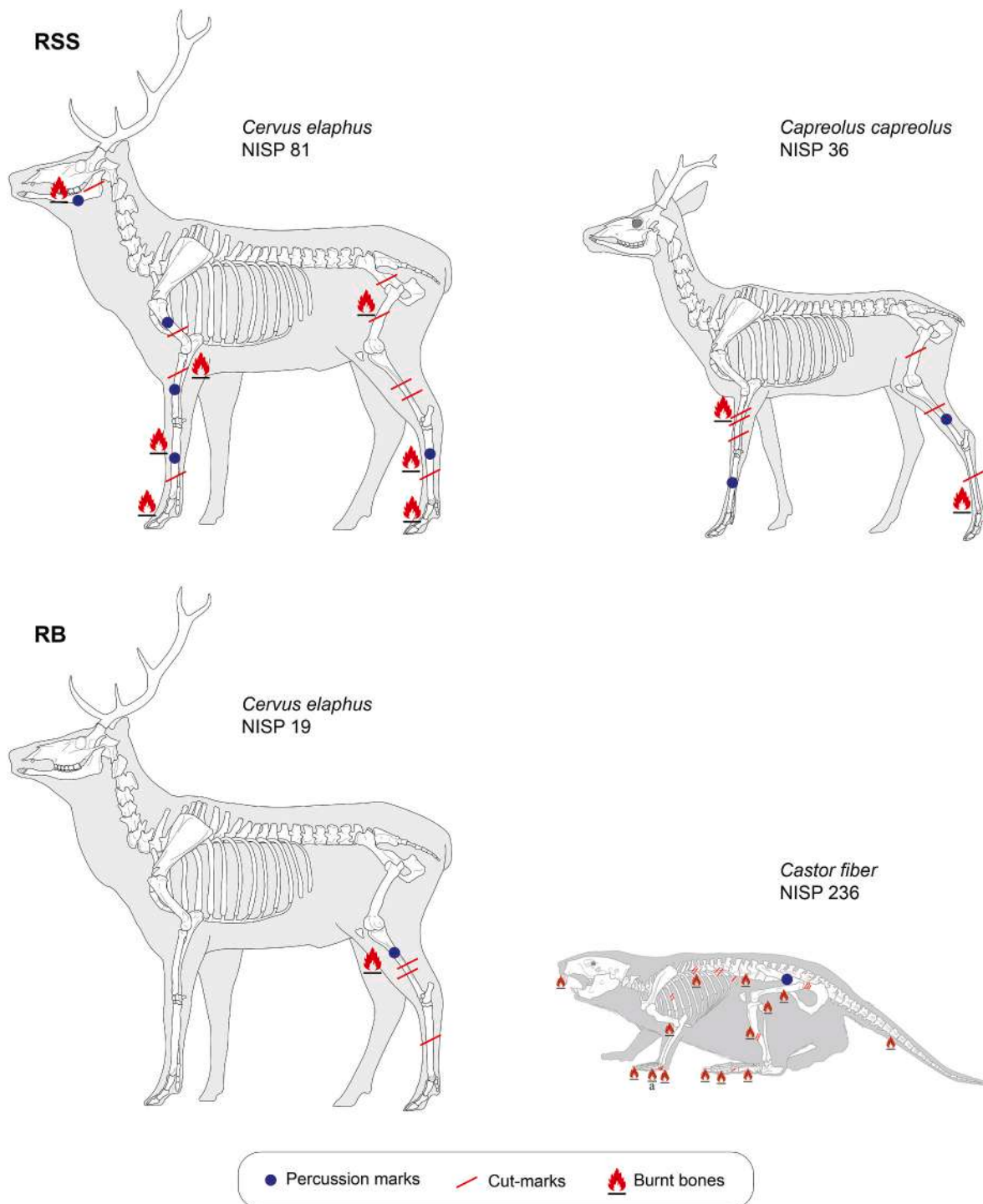


Fig. 5. Localization of anthropogenic modifications on the main species of each site: *Cervus elaphus* and *Castor fiber* from Riparo del Broion (stratigraphic unit US11), and *Cervus elaphus* and *Capreolus capreolus* from Roccia San Sebastiano cave US3 sub-unit Cg).

highlights how this activity significantly intervened in altering the osteological assemblage in the north-eastern Italian site, affecting 52.9% of the remains versus 15.1% at Roccia San Sebastiano (Table 5). Temperature intensity also reflects this disproportion with at least 18.36% of remains being calcined at Riparo del Broion versus 9.6% at Roccia San Sebastiano.

5.1. Subsistence activities at Riparo del Broion

The faunal assemblage of Riparo del Boion consists of a wide breadth

of taxa, including ungulates, carnivores, rodents, birds, fish, and shellfish. Regarding the ungulate spectrum, cervids are the most abundant group. Red deer also stands out in geographically close contexts such as Fumane Cave (Fiore et al., 2004; Romandini, 2012; Romandini et al., 2014a, 2020a) and San Bernardino Cave (Romandini et al., 2020a; Terlato et al., 2021).

The anatomical representation of red deer is skewed towards the hind limb, but because of the low quantity of remains, a correlation between %MAU and bone density cannot be calculated, which makes it difficult to explain the absence of axial skeleton, forelimbs and extremity

Table 5

Characteristics of the burnt remains by taxa and degree from Riparo del Broion (stratigraphic unit US11) and Roccia San Sebastiano cave (stratigraphic unit US3 sub-unit Cg).

	RB				RSS			
	Charred degree	Calcinate degree	NISP burnt	%NISP burnt	Charred degree	Calcinate degree	NISP burnt	%NISP burnt
Determinate	90	6	96	15.3	289	29	318	24.6
<i>Equus ferus</i>	1		1	50				
<i>Bos/Bison</i>					1		1	25
<i>Capra ibex</i>					1		1	50
Caprinae	1		1	20	1		1	14.3
<i>Megaloceros giganteus</i>	2		2	18.2				
<i>Alces alces</i>	1		1	50				
<i>Cervus elaphus</i>	2		2	10.5	15		15	18.5
<i>Capreolus capreolus</i>	2		2	40	5	1	6	16.7
Cervidae	1		1	2.7	14		14	17.7
<i>Sus scrofa</i>	4		4	36.4				
Ungulate large	4		4	9.8	2		2	12.5
Ungulate medium-large	10		10	14.9	6	1	7	18.4
Ungulate medium	6	1	7	14.3	39	3	42	28.6
Ungulate medium-small	13		13	21.3	130	11	141	25.3
Ungulate small	1		1	10	39	5	44	37.6
Ungulate indet.	1		1	6.7	36	8	44	
<i>Ursus arctos</i>	2		2	66.7				
<i>Ursus spelaeus</i>	1		1	20				
<i>Ursus sp.</i>	1		1	11.1				
<i>Canis lupus</i>	2	1	3	42.9				
<i>Alopex lagopus</i>	1		1	100				
<i>Felis silvestris</i>	1		1	100				
Carnivora indet.	2	1	3	25				
<i>Castor fiber</i>	31	3	34	14.4				
Indeterminate	10,198	2308	12,506	53.9	205	24	229	9.8
Large size	10		10	8.7	1		1	16.7
Medium-large size	13		13	16.3	7		7	21.2
Medium size	5		5	20	23	1	24	35.3
Small-medium size	39	21	60	92.3	103	13	116	26.3
Small size	7	4	11	8.5	11		11	28.2
Very small	3	1	4	44.4				
Indeterminate	10,121	2282	12,403	54.5	60	10	70	4
Total	10,288	2314	12,602	52.9	494	53	547	15.1

of limbs. However, the presence of almost only cranial and hind limb bones, maybe is due to a selective transport, as in San Bernardino and Fumane Cave (Fiore et al., 2004; Romandini et al., 2014a, 2020a; Terlato et al., 2021). Freshly fractured bones, percussion marks, and cut-marks indicate meat and marrow exploitation, in the case of red deer and other ungulates too. Moreover, at Riparo del Broion the category of bone fragments < 10 mm accounts for as much as 64.6% of the total (whereas at Roccia San Sebastiano only 9.3%) and a high number of remains with thermal alterations (52.9%) is registered too. These evidence, together with the presence of ten hearths could suggest that some anatomical elements were used as fuel in this context. These data are coherent with the Late Mousterian levels at Grotta di Fumane (Romandini et al., 2020a).

The burning and calcined modifications observed also on avian bones, could suggest that at least part of the birds was introduced into the cave by Neanderthals, although accidental combustion cannot be excluded. The burning traces on the posterior phalanxes possibly indicate the discard of these non-edible parts of the bird carcass and their consequent direct contact with embers (Laroulandie, 2001). These data, along with the presence of the tarsometatarsus of cf. *Gallinago media* with one cut-mark, supports the probable use of birds as food source by Neanderthals living in Riparo del Broion. In northeast Italy at Grotta di Fumane (USS A4; A5+A6; A6 and A9) and Grotta del Rio Secco (Layer 7) in stratigraphic levels chronologically close to the US 11 of Riparo del Broion, the exploitation of birds for food and non-food purposes is an established practice (Fiore et al., 2004, 2016; Peresani et al., 2011a; Romandini, 2012; Romandini et al., 2014b, 2016).

Carnivore remains are scarce if compared with other sites such as Rio Secco or Fumane Cave (Romandini et al., 2018a, 2020a), but species variability is, however, remarkable. Their presence as an accumulation

agent cannot be established because there are only three bones with carnivore modifications. Therefore, they could act as opportunistic agent, consuming the leftovers from the Neanderthals. Interestingly is the butchering mark registered on a remain of brown bear, also recognized in other contexts of the same geographical area (Romandini et al., 2018b).

Regarding the presence of beaver, the abundant number of remains and the anthropogenic modifications in Riparo del Broion confirms that the hunting and exploitation of this rodent was an opportunistic and yet consistent strategy across Berici Hills (Terlato et al., 2021; Romandini et al., 2018b) and at the same time a unicum for the Late Mousterian period. Beaver bones are recorded also in other contexts of southern Italy such as Valle Radice and Carnello sites in Latium region, Liri-Garigliano basin (MIS 5 and 4) and from Grotta Reali (MIS 3), upper Volturno basin in Molise region, but in total there are only a dozen remains without anthropogenic marks (Salari et al., 2020).

Concerning Riparo del Broion, a comparable and similar site but dated to ~130,000 years ago (Rink et al., 1995) in the Mediterranean region is Krapina Cave (Croatia), which yielded cut-marked beaver bones (Miracle, 2007). Beaver remains (NISP 353, MNI 19) mostly come from Krapina layer 1 (*Castor fiber* zone) and consist of – as in the case of Riparo del Broion – teeth, cranial bones, upper hind limb bones, a pelvis, and lower hind limb bones. Also in this case, cut-marks on mandibles, tibia and ulna suggest skinning and/or removal of limb extremities; cut-marks on the ilia were probably produced by disarticulation or defleshing.

Apart from this context, the documentation regarding the exploitation of beavers (*Castor fiber*) during the Palaeolithic in Europe is generally scarce. This may be attributed to the limited presence of beaver remains at archaeological sites and/or a lack of research focused

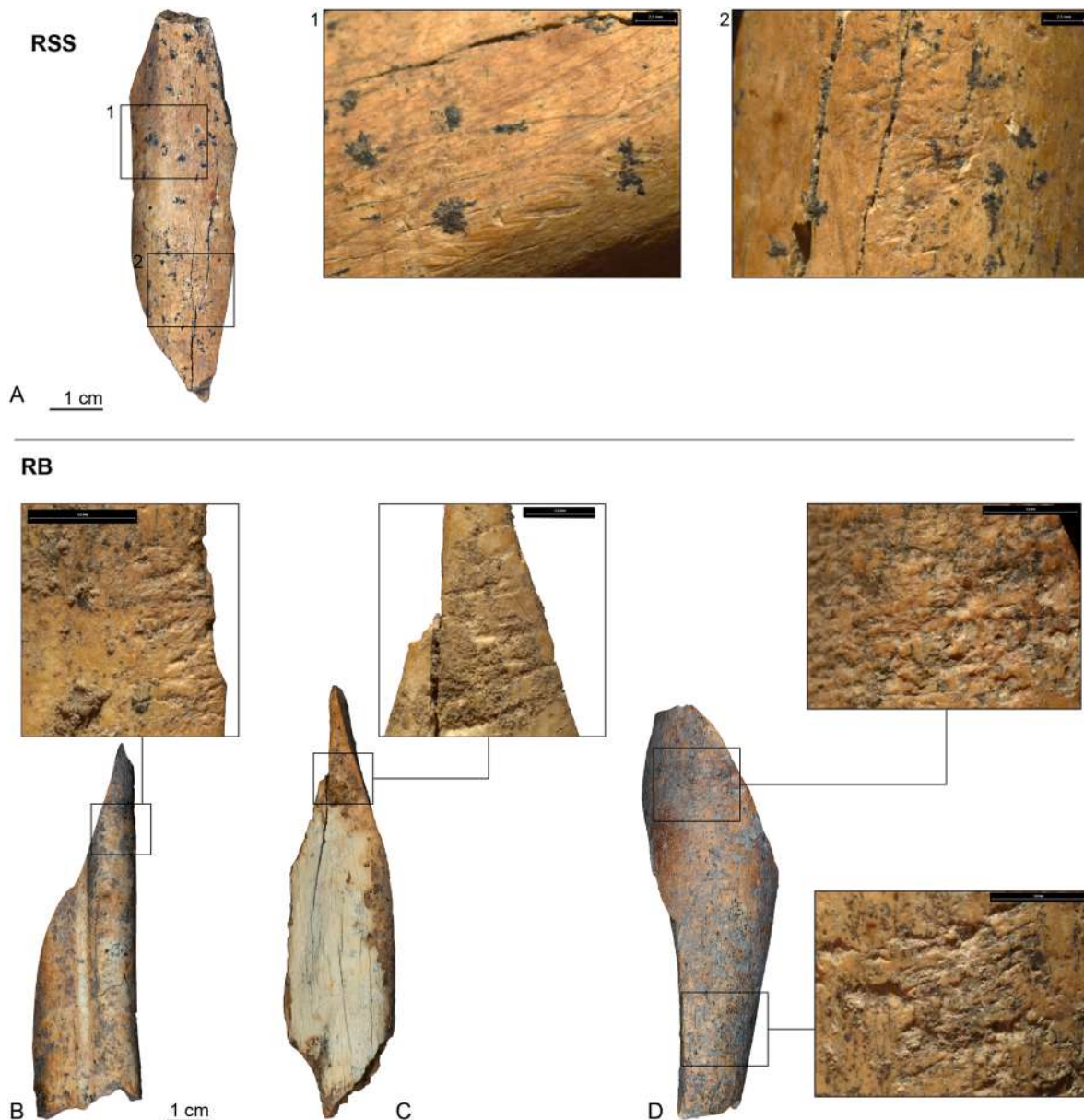


Fig. 6. Retoucher bones from stratigraphic unit US3 sub-unit Cg of Roccia San Sebastiano cave (A) and from stratigraphic unit US11 of Riparo del Broion (B, C, D).

on this species. Although beavers are often included in mammal assemblages, taphonomic analyses specifically targeting them have been rarely conducted. Cut marks have been found on beaver remains in Germany. Beaver exploitation has been identified at Taubach, as reported by Dusseldorp in 2012 (Dusseldorp, 2012), and at Lehringen, where cut marks were observed on a pelvis fragment, as noted by Gaudzinski (2004). In Spain, at Bolomor cave, level XI, two burnt beaver bones were discovered, as documented by Blasco et al. (2013). In France, beaver exploitation has been described at Pech-de l'Azé-IV (level 8) with cut-marks on a single bone, as reported by Dibble et al. (2009); at Pech-de-l'Azé I (level 7), with cut-marks on two remains, as documented by Rendu (2010); and at the Grand Abri aux Puces, where cut-marks were found on mandibles, cranial elements, pelvis, and metapodials, along with burnt bones, as described by Slimak et al. (2010).

Currently the presence of fish remains at Riparo del Broion confirms the availability of water fresh ponds. The determination of *Exos lucius* allows us to outline some characteristics. This species has its optimal habitat in moderately flowing lowland waters, with sandy bottoms, rich in submerged vegetation. It is a territorial species, the adults move to

deeper, cooler waters during the warmer months. In larger lakes, the summer distribution is within 300 m of the shore, in 4 m deep waters, while on windy days, they move offshore into shallow waters. Considering these characteristics, a catch by humans or ursids might be more likely at the beginning (Guillaud et al., 2021), during or at the end of the winter season, when *E. lucius* is well active but closer to the banks in shallow or medium-low waters (Bianco, 1995; Bianco and Delmastro, 2011). In recent years, archaeological research has provided solid evidence of the consumption of freshwater fish by Neanderthals. In some cases, fish bones from Middle Palaeolithic were found in inland caves near rivers, often alongside stone tools and animal remains. To establish this evidence as human fishing activity it is crucial to eliminate other fish predators, particularly cave-dwelling carnivores and raptors, as potential alternative accumulators. In an exhaustive review of freshwater fish remains from Middle Palaeolithic sites in Western Europe dated from MIS 11 to MIS 3, Guillaud et al. (2021) have critically assessed elements in favour and against Neanderthals as agents of fish assemblages. Their results suggest that for several sites, such as Vaufray, Baume-Vallee, Barasses II, Baume Moula- Guercy, Walou, and Cueva

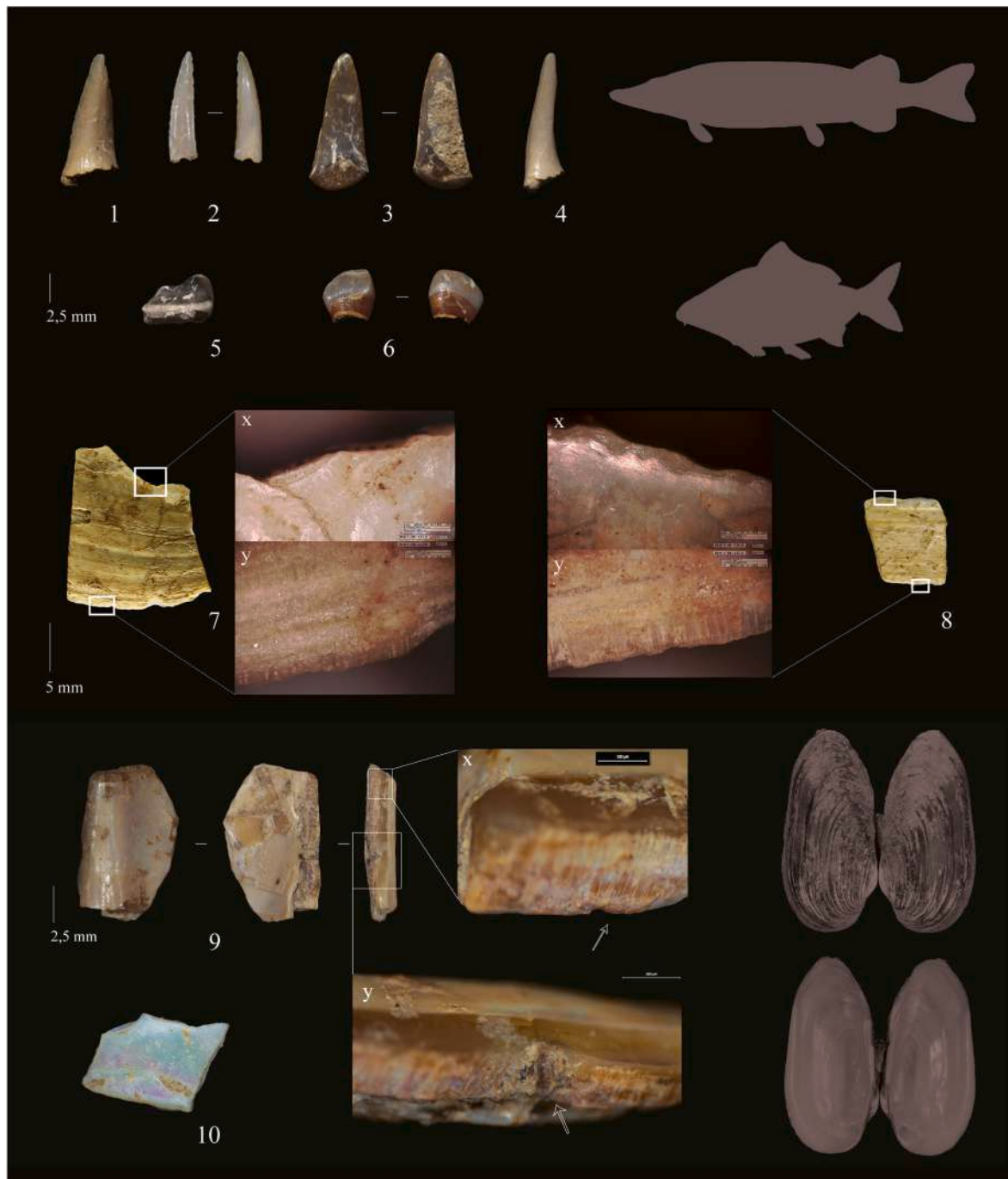


Fig. 7. Fish and shells remains from Riparo del Broion (stratigraphic unit US11). 1–4) *Exos lucius* canine's teeth; 5–6) Cyprinidae teeth (the number 5 is burnt); 7–9) Unionide, *Anodonta* sp. Fragments with inner edge details of evident and punctual polish traces (x) and the outer natural edges of the shell (y). In 8 y are noted gnawing marks typical of small rodents. 10) mother-of-pearl fragment. Bottom right current specimen of Unionide (*Anodonta* sp.).

Millan, Neanderthals possibly captured and consumed relatively large fish (over 1 kg).

Several freshwater fish remains were found at Abri du Maras (France), dated to ~ 90 ka ago. These remains were associated with stone tools on the surface of which preserved flakes of what may be fish scales (Hardy and Moncel, 2011; Hardy et al., 2013). Overall, however, the studies suggest opportunistic and intermittent fishing activities.

The use of marine shells, often associated with colouring substances, and the use of natural pigments that can be associated with seafood sustainment is well documented (Cortés-Sánchez et al., 2011; Peresani et al., 2013; Romagnoli et al., 2016; Romagnoli, 2018; Stiner, 1993; Zilhão et al., 2010) but evidence of use and/or consumption of

freshwater species is scarce. Neanderthal groups living at Riparo del Broion, among 44.5 and 50.0 ka cal BP, have certainly found the *Unio* shells in the valley overlooked by the shelter (135 m a.s.l.). References to the occasional use of Unionidae by Neanderthals are very sporadic. It has been possible to identify some of these specimens in Krapina but the taphonomic analysis (they are intact or semi-intact) suggests their secondary repositioning with respect to anthropic frequentation (Miracle, 2007).

The experimental approach carried out in this work, however, was extremely useful for a first interpretation of the traces recognized on the archaeological remains came from Riparo del Broion and will certainly be extended. Following experimentation, the use of 'fresh' valves is



Fig. 8. Examples of anthropogenic modifications from Roccia San Sebastiano cave (stratigraphic unit US3 sub-unit Cg). *Capreolus capreolus*: A. percussion notch with flake on a femur; B. scrapers on a metatarsal; C. percussion notch and scrapers on a tibia. *Cervus elaphus*: D. slices on a metatarsal; E. slices on a mandible; F. scrapers on a metacarpal; G. percussion notch on a radius.

preferred, given their excellent capacity for scraping actions aimed, for example, at processing plant materials or cleaning meat from the bone. In addition, food exploitation cannot be excluded given the large size of the shellfish (Suppl Fig. 2 and 2-3). The stratigraphic units associated with the Upper Palaeolithic (US 1 and its sub-units) lack fragmented nacreous material. This absence highlights the exclusivity of *Unio* exploitation in Mousterian levels, a unique case in Italy up to now.

These considerations related to the evidence recognized at Riparo del Broion, along with other studies, support the importance of freshwater resources in the Neanderthal diet and broaden our understanding of their eating habits and adaptability to different ecosystems.

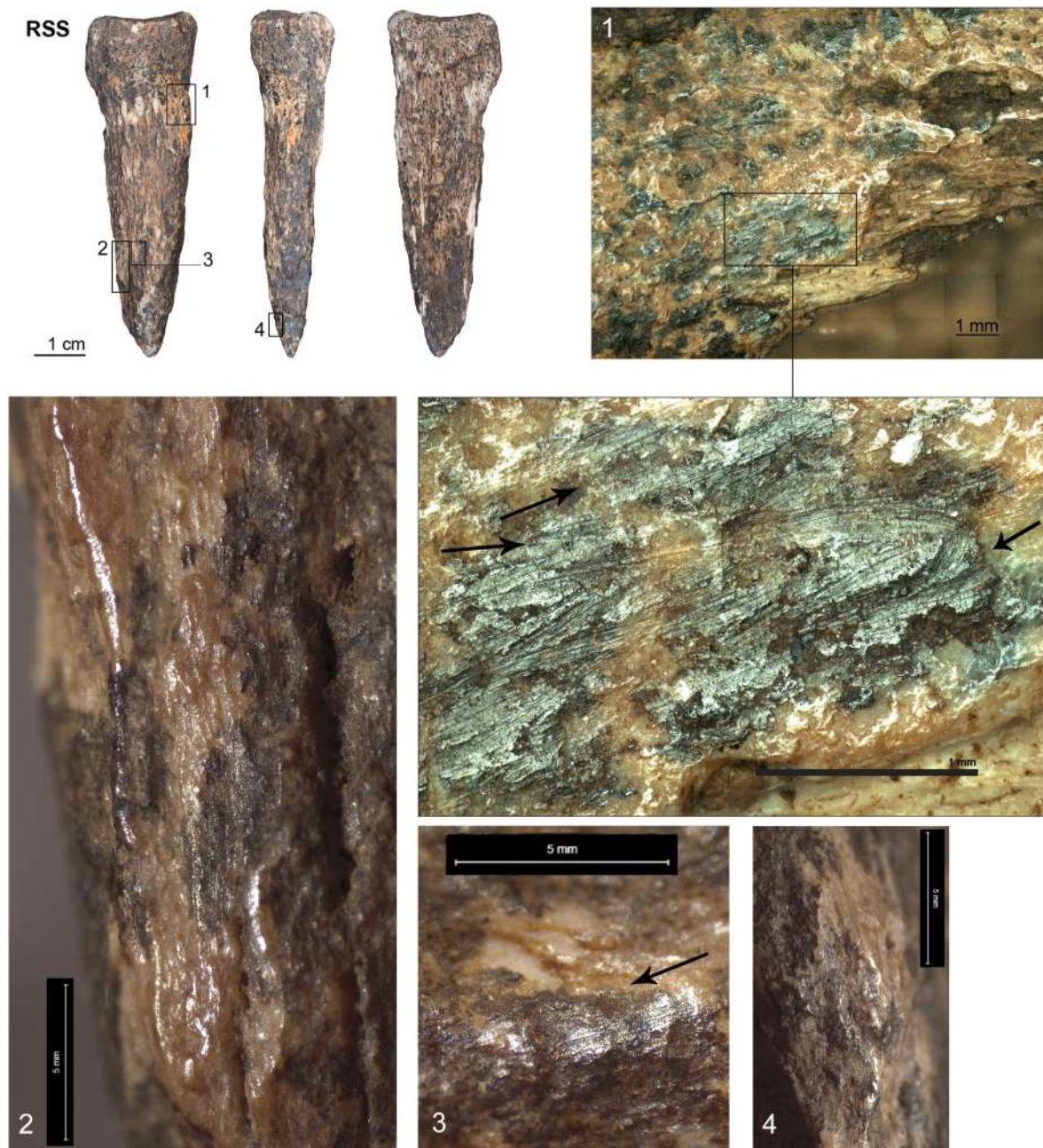


Fig. 9. Bone industry from Roccia San Sebastiano cave (stratigraphic unit US3 sub-unit Cg). 1–2) scraping marks (1) and traces of use on polish; 3–4) evident and punctual polished traces from use, photographed in reflective light at the stereomicroscope.

5.2. Subsistence activities at Roccia San Sebastiano

In central-south-western Italy, only a few sites present with dated Late Mousterian levels. Among them, only Grotta di Castelcivita (46–42 ky BP; Gambassini, 1997; Romandini et al., 2020a) provided zooarchaeological and taphonomic data. In this framework, the site of Roccia San Sebastiano provides new insights in this area.

Its taxonomic spectrum is mainly composed of cervids, among which red deer is the most abundant taxon followed by roe deer. The anatomical composition of red deer is not complete. Based on the correlation between %MAU and the density, we can assume that the absence of some elements is due to attrition and Neanderthals could transport complete individuals to the site. Furthermore, we have recorded most of the anthropogenic marks (e.g., cut-marks, percussion marks, and green bone fractures) on red deer, roe deer and on

indeterminate cervids that might suggest a selective ungulate hunting strategy.

The presence of other ungulate species such as caprines, bovines or wild boar is scarce. This composition is in line with the taxa seen in Castelcivita (geographically close to RSS), where cervids are the principal group (Masini and Abbazzi, 1997). Although fallow deer is the best-represented species in the oldest pits, red deer increases in the following ones.

In general, in southern Italy, Late Mousterian deposits exhibit evidence of generally temperate conditions. In this phase, cervids are the most common ungulates in the Tyrrhenian region (where is located Roccia San Sebastiano) while *Bos primigenius* is the most represented species in Ionian contexts. At Grotta di Castelcivita and Roccia San Sebastiano (south Italy) this phase is characterised by the same palaeoenvironmental trend documented at Fumane (Fiore et al., 2004; Masini

and Abbazzi, 1997; Romandini et al., 2020a) and Riparo del Broion (north Italy).

Like other assemblages from the Late Middle Palaeolithic (see compilation in Romandini et al., 2020a), bones from Roccia San Sebastiano cave are very fragmented. Even small bones such as phalanges are fragmented. Green bone fractures are abundant among long bones and metapodials, but also on mandibles and phalanges. These fractures together with the presence of percussion marks indicate the systematic access to the long bone marrow of all species. Ungulates were processed at the site, as suggested by evidence of disarticulation, defleshing, and the removal of the periosteum before fracturing them. Burnt bones are not particularly abundant (15.1%) and are almost charred. Therefore, the use of bones as fuel is excluded for Roccia San Sebastiano but it may be suggested for Riparo del Broion (Costamagno et al., 2005; Th  ry-Parisot et al., 2004). Fire could be used during the processing or consumption of prey. Human groups that occupied the cave, exploited the prey for meat and marrow, as usual in other sites (Romandini et al., 2020a). But the anthropogenic modifications are higher (36.1% over the determinate remains) than in Castelcivita (7.5%). Moreover, in Roccia San Sebastiano cave, there are two carnivore bones, and only five remains (0.4% over the determinate remains) show carnivore marks, a low percentage in comparison with the 4.5% of Castelcivita. This does not allow us to infer the carnivore agent and its activity but shows up that Neanderthals are the main responsible of the faunal accumulations.

Considering the exploitation of ungulates in the Ionian contexts, some Late Mousterian assemblages (Grotta del Cavallo and Riparo l'Oscurusciuto) exhibit a lack or a scarcity of long-bone epiphyses and the end parts of limbs (Boscatto and Crezzini, 2006, 2012; Romandini et al., 2020a). This evidence cannot be attributed to carnivores, differential bone density and other post-depositional processes. Some studies suggest a relationship between bone frequency and their content in marrow and fat, which was probably crucial in the choice to select specific anatomical parts and to carry them back to camps/sites (Boscatto and Crezzini, 2006, 2012). At Riparo l'Oscurusciuto spongy bones were not systematically used as fuel in hearths (Spagnolo et al., 2016), suggesting their possible use as food (Costamagno and Rigaud, 2014).

Regarding the avian bones, recognized in Roccia San Sebastiano, the absence of taphonomic modifications related to carnivores and nocturnal or diurnal raptors suggests that their presence in the cave could be due to natural death. As an exception, the burned claw of an Accipitridae possibly represents the result of an interaction between Neanderthals and raptors.

5.3. Late Neanderthal adaptation to different environments

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 Roccia San Sebastiano cave in south Italy and Riparo del Broion in north Italy.

These two separate areas from Italy offer different possibilities of resource exploitation for the latest Neanderthal groups. The paleo-environmental conditions and the orography near the sites determine the more available animal prey at each site. In both areas, cervids are the most abundant ungulate prey, accessible in forests and meadows with temperate climate. Caprines and large bovids are less abundant, but their identification is related to both alpine biotopes with particularly rocky landscape, favourable to the former, and with open environments and dense forests with wetlands more suitable for the latter. The presence of wild boars portrays forested environments with a high density of low vegetation. The elk at Riparo del Broion marks the presence of low flow bodies of water. On the other hand, the presence of equids at Riparo del Broion, which is extremely rare regarding the coeval sites in northern Italy, documents the presence of open areas near the site, where hyenas and lions could also be found. The high variability of taxa among carnivores at this site is well suited to all the described types of

environments.

Cervids Sr isotopes likely indicate different animals' home-ranges or humans' hunting strategies at the two sites. Specifically, while all the Roccia San Sebastiano individuals show local isotope signature (possibly within a radius of 10-km), two out of three individuals at Riparo del Broion retain a non-local signal. RB80 is of interest, displaying an $^{87}\text{Sr}/^{86}\text{Sr}$ ratio compatible with the volcanic geology of the Euganean Hills, ~30 km-far from Broion (see Lugli et al., 2022). This, in turn, may suggest that either: a) Neanderthals hunting strategies were different at the two sites, with individuals from northern Italy moving further away to hunt compared to southern Italy hominins; or b) the home-range sizes of the cervids at the two sites was different, maybe due to the diverse ecological constraints or to the type of herd (Georgii, 1980; Georgii and Schr  der, 1983). It is worth noting that northern and southern Italy present deeply different geolithologies, with the latter mostly composed by sedimentary carbonate formations with a relatively homogeneous Sr isotope ratio. Such evidence suggests that eventual movements of Roccia San Sebastiano cervids might have been masked by areas with overlapping $^{87}\text{Sr}/^{86}\text{Sr}$ ratios.

Nevertheless, the most striking issue is the documentation of aquatic resources in Riparo del Broion. The presence of numerous beaver bones, fish remains, even of medium to large dimensions, freshwater shells and bird species such as *Cygnus cygnus* and *Gallinago media* (the first fossils occurrence in north-Eastern Italy for both species) are related to the existence of water biotopes. Today, a few kilometers northwest of the site, at Fimon, there are traces of an ancient lake. Therefore, near the shelter, Palaeolithic human groups had access to areas of water or low-density lake environments (Peresani et al., 2019; Romandini et al., 2020a). On the contrary, Roccia San Sebastiano cave is placed at 40 m a.s.l. And, at the time of Neanderthal occupation, the seacoast was 10–13 km (current at 5 km) away, but there is no evidence of exploitation of sea resources. While at European level the presence of freshwater fish in Mousterian contexts is documented (see compilation in Blasco et al., 2022; Guillaud et al., 2021), in Italy, this type of activity seems to be concentrated on the sites located in the Berici Hills. These different subsistence patterns could be maybe due to different behaviour in relation to the seasonality and the duration of the occupations.

The taxonomic composition of Riparo del Broion is similar to those found at other sites in north-eastern Italy, although the proportion between each group shows some notable differences (Romandini et al., 2020a; Terlato et al., 2021). Therefore, the faunal assemblages of Mousterian sites from north-eastern Italy, in general, could be grouped in two classes (Fig. 10): 1. Sites with a predominance of ungulates; 2. Sites with a predominance of carnivores. Fumane Cave and San Bernardino Cave are placed in the first groups while Rio Secco represents the second class. The case of Riparo del Broion seems to represent a new third class (3) of sites with a predominance of rodents. In comparison, Roccia San Sebastiano cave could be also included in the first group of sites, as well as other south sites like Castelcivita.

Beaver and marmot are relevant in Upper Palaeolithic sites from Italy (e.g. Monin et al., 2006; Nannini et al., 2022; Romandini et al., 2012b) due to their number of remains and their resource exploitation by human groups. As we have already seen for these and the small game in other European areas (Cochard et al., 2012; Hockett and Bicho, 2000; Morin et al., 2020; Real, 2020; Tom  , 2005; Tom   and Chaix, 2003). However, their presence in Italian Mousterian assemblages is scarce (Bernard-Guelle, 2002; Romandini et al., 2018b, 2020a; Salari et al., 2020; Thun Hohenstein and Peretto, 2005). On the contrary, beaver has an important role in the Riparo del Broion subsistence activities, where Neanderthal groups exploited this specie for fur and meat. There is no evidence of the consumption by other predators.

Regarding the hunting and processing pattern, there are some common characteristics between Neanderthal groups from both areas, and some differences too. At Riparo del Broion, human groups seem to transport red deer partially to the site, as the anatomical composition and the isotope analysis indicate. On the contrary, at Roccia San

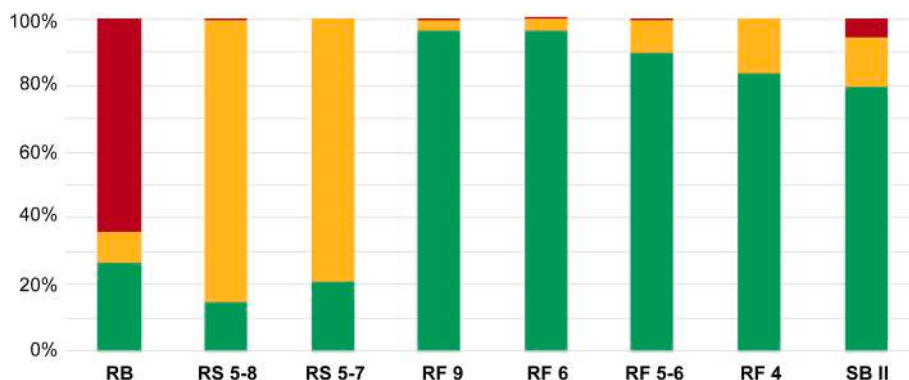


Fig. 10. Taxonomic spectrum (ungulates, carnivores and rodents) of Late Mousterian stratigraphic units from North-eastern Italy sites: Riparo del Broion (RB), Rio Secco Cave (RS), Fumane Cave (RF) and San Bernardino cave (SB).

Sebastiano cave, hunting deer was probably easier near the site, in the surrounding plain, and, therefore, they could transport the whole carcasses to the cave, though we have lack in some skeleton parts. On the other hand, the diet for all of Neanderthals from both areas includes mainly meat and marrow from ungulate prey. In the case of Riparo del Broion, the presence of carnivore remains could be due to natural origin, but also to human activities. There is only one bear bone with cut-marks, but several burnt bones of carnivores and low percentages of tooth-marks and absence of coprolites that could prove the use of the site as a den. Although the human exploitation of carnivores is well-known and more frequent during the Upper Palaeolithic from all Europe, evidences from Middle Palaeolithic sites are increasing (e.g. [Blasco et al., 2010](#); [Caparrós et al., 2012](#); [Charles, 1997](#); [Gabucio et al., 2014](#); [Real et al., 2017](#); [Romandini et al., 2018a, b](#); [Sanchis et al., 2019](#); [Smith et al., 2021](#); [Wojtala et al., 2020](#)).

Finally, both in the north and in the south, Neanderthals took advantage of their ungulate prey not only for food but also as non-food products. They used the diaphysis of long bones of medium and large animals as retouchers and points. This is a well-known practice seen in Italy and other areas of Europe (e.g. [Arrighi et al., 2020b](#); [Caron et al., 2011](#); [d'Errico et al., 2003](#); [Romandini et al., 2015](#); [Thun Hohenstein et al., 2018](#)). The discovery of a long bone (probably a metapodial) with traces linked to the realization of a rudimentary awl at Roccia San Sebastiano and probable evidence of work tools use (not yet precisely identified at the current state of experimentation) of fresh-water shells valve fragments at Riparo del Broion, seem to highlight some peculiar behavioral aspects or at least rare for these hominins.

6. Conclusion

This first zooarchaeological comparison of the Mousterian levels of Roccia San Sebastiano cave and Riparo del Broion allowed to point out environmental conditions, strategies and modes of subsistence of two Neanderthal groups, including children ([Oxilia et al., 2022](#); [Romandini et al., 2020b](#)), who lived at the geographical extremes of the Italian peninsula towards the end of the Middle Palaeolithic.

This first archeozoological study carried out on two newly uncovered Late Mousterian contexts indicates that geographical regional setting played an important role in defining the exploitation of different resources: from almost specialized small game (Broion) to selective ungulates (San Sebastiano) hunting strategies. At Riparo del Broion, Neanderthals have probably practiced fishing and shellfish gathering from freshwater lake environment, as an additional source of food to be alternated with the exploitation of semi-aquatic resources like beavers and terrestrial ones like cervids.

On the contrary, human groups at Roccia San Sebastiano cave almost exclusively practiced red deer hunting. Nevertheless, the complete absence of shellfish and fish remains, even though the sea was visible a

few kilometers to the west of the cave, is remarkable. Although the excavated area is small, this absence could be due to a selective behaviour or to a different occupation pattern. These findings might be particularly relevant for interpreting regional patterns of change in subsistence/adaptive strategies, considering that large game is generally considered a higher-rank resource than small game.

Author contributions

I declare that all authors have made substantial contributions for this submission.

In detail: M.R. conceived the ideas, coordinated the research and wrote the paper with substantial support from S.S., C.R., F.L., L.T., L.C., F.B., E.B., G.M., D.D., C.C., M.P., S.B. F.L., L.T., L.C., F.B. carried out the cervids isotopes, shells and relative experimentation, bird remains and pollen-vegetation data analysis. M.R., S.S. and C.R. carried out analysis of osteological materials and related statistical elaborations. M.R., C.R., S.S. F.L., L.T., L.C., E.B. and C.C. provided crucial ideas towards the overall interpretation of the data. C.C., M.P. and S.B. reviewed the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2023.108233>.

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