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A ZooMS-informed archaeozoological and taphonomic analysis comparing Neanderthal and *Homo sapiens* subsistence behaviours in Northwest Italy

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A ZooMS-informed archaeozoological and taphonomic analysis comparing Neanderthal and *Homo sapiens* subsistence behaviours in Northwest Italy

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Résumé

Ce projet contribue aux discussions en cours sur la transition du Paléolithique moyen au Paléolithique supérieur en Europe occidentale marquée par un tournant dans l'évolution de notre espèce, l'*Homo sapiens*. Alors que les Néandertaliens, nos plus proches cousins évolutionnaires disparaissent du registre fossile, les humains modernes qui ont migré hors d'Afrique, se dispersent rapidement à travers l'Eurasie. Les deux populations étaient exposées aux mêmes changements climatiques dramatiques caractéristiques de la transition, et pourtant, les Néandertaliens sont rapidement remplacés par les humains modernes. Par conséquent, ce phénomène suggère que les populations humaines modernes auraient pu être mieux adaptées face aux changements environnementaux.

Puisque le régime alimentaire est un bon moniteur de l'adaptation, cette recherche compare les stratégies de subsistance des deux espèces humaines ayant tour à tour occupé le site de Riparo Bombrini (Balzi Rossi, Ligurie, Italie). Une analyse archéozoologique et taphonomique a été effectuée sur les collections fauniques du Moustérien tardif et du Proto-Aurignacien afin d'obtenir la première comparaison détaillée du régime alimentaire et des comportements de chasse des Néandertaliens et des humains modernes sur l'un des seuls sites du nord-ouest de l'Italie entièrement documenté avec des méthodes archéologiques modernes. Étant donné que la nature très fragmentée des ossements animaux sur le site a été un obstacle aux analyses fauniques dans le passé, les méthodes d'analyse archéozoologique ont été complétées par le « collagen fingerprinting » (c.-à-d. zooarchéologie par spectrométrie de masse, ou ZooMS) afin d'assurer l'identification d'un maximum de spécimens pour atteindre une précision accrue de l'identification taxonomique. La préservation différentielle du collagène dans les restes squelettiques a également justifié le développement d'une méthode novatrice de dépistage du collagène utilisant la spectroscopie FTIR-ATR pour la présélection d'échantillons ZooMS.

Les résultats montrent que, tandis que Néandertal et *Homo sapiens* ont continuellement chassé les taxons ongulés disponibles à proximité de Riparo Bombrini, les niveaux de Moustérien tardif indiquent un rétrécissement du tableau de chasse associé à un mode de subsistance hyperlocal.

En revanche, les spectres fauniques se sont considérablement élargis dans le plus ancien Proto-Aurignacien, lorsque Riparo Bombrini était occupé comme camp de base logistique à long terme associé à un vaste territoire de subsistance. Les résultats fournissent également les premières données détaillées sur la subsistance des populations humaines durant la transition dans la région de l’arc liguro-provençal, établissant ainsi de nouvelles hypothèses à tester dans de futurs travaux concernant la nature changeante de leurs écologies.

Mots-clés : Transition Paléolithique moyen-supérieur, Proto-Aurignacien, Moustérien, Préhistoire méditerranéenne, Riparo Bombrini, Subsistance, Stratégies de chasse, Archéozoologie, Taphonomie, ZooMS.

Abstract

This project contributes to the ongoing debates over the Middle-Upper Paleolithic transition in Western Europe, which marks a turning point in the evolution of our species, *Homo sapiens*. While Neanderthals, our closest evolutionary relatives, went extinct at that time, modern humans who had migrated out of Africa dispersed very rapidly across Eurasia. While both populations were exposed to the same dramatic climatic shifts at the time, it is only the Neanderthals that quickly disappeared from the archeological record, suggesting that modern human populations may have been better adapted to react to environmental changes than Neanderthals.

Since diet is a good monitor of adaptation, this research compares the subsistence strategies of both human groups as they occupied, in quick succession, the site of Riparo Bombrini (Balzi Rossi, Liguria, Italy). An archeozoological and taphonomic analysis was conducted on Late Mousterian and Proto-Aurignacian faunal collections to produce the first direct comparison between Neanderthal and modern human diets and hunting strategies at one of the only sites in Northwest Italy entirely excavated using modern documentation methods. Because the highly fragmented nature of the animal bones at the site has hindered faunal analysis in the past, these approaches were complemented by collagen fingerprinting (i.e., Zooarcheology by Mass Spectrometry, or ZooMS) to identify as many specimens as possible as to species, thus yielding unprecedented accuracy in taxonomic identification. The challenging collagen preservation state also required developing a screening method using FTIR-ATR spectroscopy prior to ZooMS.

The results show that, while Neanderthals and modern humans continuously hunted prime-aged ungulate taxa available in a close range of Riparo Bombrini, the Late Mousterian levels indicate a narrower diet associated with a hyper-local subsistence range. In contrast, the faunal spectra broadened noticeably in the earliest Proto-Aurignacian, when Riparo Bombrini was occupied as a long-term logistical base camp within an extensive land-use strategy. The results also provide the first high-resolution view of human subsistence during the transition in the Liguro-Provençal arc region and set up test hypotheses about the changing nature of hominin behavioural ecology that can be further tested in future work.

Keywords: Middle-Upper Paleolithic transition, Proto-Aurignacian, Mousterian, Mediterranean prehistory, Riparo Bombrini, Subsistence, Hunting strategies, Archaeozoology, Taphonomy, ZooMS.

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List of Abbreviations

Ka: thousand years ago

Ma: million years ago

cal: calibrated

BP: before present

OIS: oxygen isotope stage

MIS: marine isotope stage

ZooMS: Zooarchaeology by mass spectrometry

FTIR: Fourier transformed infrared spectroscopy

ATR: attenuated total reflectance accessory

km: kilometre

cm : centimetre

m: metre

e.g.: *exempli gratia* (for example)

i.e.: *id est* (that is)

USA: United States of America

UK: United Kingdom

NSP: number of specimens

NISP: number of identified specimens

MNI: minimum number of individuals

MNE: minimum number of elements

MAU: minimum animal unit

BMD: bone mineral density

FUI: food utility index

CO/P: amide I to phosphate ratio

DNA: deoxyribonucleic acid

aDNA: ancient deoxyribonucleic acid

MALDI-TOF: matrix-assisted laser desorption/ionization – time-of-flight mass spectrometer

HCl: hydrochloric

HE4 : Heinrich event 4

À ma maman qui me soutient et me guide dans toutes mes aventures,

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Introduction

This research aims to tackle a crucial question in Paleolithic archaeology: How did the Neanderthals disappear from the Eurasian continent while our direct ancestors, *Homo sapiens* (or modern humans), thrived? This question has generated considerable public and scientific interest in addressing our species' origins and evolutionary success. In Paleolithic archaeology, the different evolutionary and cultural processes involved in the sudden disappearance of Neanderthals and other local hominin populations and the first dispersals of modern humans out of Africa is called the Middle-Upper Paleolithic transition (hereafter, the transition), which roughly corresponds to the timeframe bracketing 50 to 30 ka cal BP. Among other factors, the drastic and rapid climatic oscillations and the appearance of increased variability in the archaeological record contribute to complexifying discussions on the spatiotemporal timing of the transition and the nature of the interactions between modern humans and local populations in Europe and Asia before their extinction.

Because the hypothesis of cognitive and behavioural superiority of modern humans over Neanderthals no longer stands to explain the transition, many scholars today highlight the need to explore the different adaptive responses of Neanderthals and modern humans to local and regional environmental changes. Diet and subsistence are excellent proxies to discuss adaptive behaviours within a Human Behavioural Ecology framework through high-resolution archaeozoological and taphonomic studies. This research thus revolves around the following research question: Did modern humans have a selective advantage in subsistence strategies relative to Neanderthals that allowed them to better face the severe climatic changes that took place during the Middle-Upper Paleolithic transition?

This research question is addressed with the case study of Riparo Bombrini, a rockshelter site documenting the transition located in the Balzi Rossi cave complex (Ventimiglia, Liguria, Italy). The site's archaeological record has revealed interesting behavioural patterns regarding Proto-Aurignacian and Late Mousterian mobility and land-use management (Holt et al. 2019; Riel-Salvatore et al. 2013, 2021; Riel-Salvatore and Negrino 2018a, 2018b). However, previous faunal studies have shown that the heavy skeletal fragmentation hindered morphological identifications, thus obscuring meaningful subsistence interpretations (Holt et al. 2019).

Therefore, the taphonomically challenging faunal assemblages of Riparo Bombrini provide an excellent opportunity to apply and test the limits of the ZooMS (Zooarchaeology by Mass Spectrometry) technique with a mass sampling strategy to help taxonomic identifications of the fragmented skeletal remains. Applying this novel biomolecular technique raises a second methodologically oriented research question: How can ZooMS be adequately integrated into archaeozoological methodologies to help reconstruct past subsistence strategies?

This article-style dissertation is structured through five chapters addressing the research questions. The first two chapters aim to contextualize the research with a brief review of the phylogenetic and archaeological discussions related to the Middle-Upper Paleolithic transition (Chapter 1), followed by the presentation of Riparo Bombrini and its importance in the Liguro-Provençal arc (Chapter 2).

The following three chapters introduce three articles that address the different methodological challenges posed by the Riparo Bombrini faunal assemblages to answer our research question. Chapter 3 introduces the first paper published in 2019 in JAS:R (*Journal of Archaeological Science: Reports*), entitled “Portable FTIR for on-site screening of archaeological bone intended for ZooMS collagen fingerprinting analysis.” This paper aimed to resolve a central methodological problem we faced before being able to apply ZooMS at Riparo Bombrini: collagen preservation. We developed a novel on-site screening method for ZooMS FTIR spectroscopy while conducting our archaeozoological and taphonomic analysis. This paper also introduces methodological insights into possible ZooMS mass-sample strategies to maximize archaeozoological data, further explored and applied in Chapters 4 and 5.

Chapter 4 introduces the second paper published in a special issue of QI (*Quaternary International*) entitled “Archaeozoological, Taphonomic and ZooMS Insights into The Proto-Aurignacian Faunal Record from Riparo Bombrini.” This second paper aimed to test the application of the ZooMS and screening sampling methods to the archaeozoological and taphonomic analysis of the Proto-Aurignacian levels at Riparo Bombrini. This study yielded many behavioural insights into the prey selection, carcass transport, and carcass processing strategies adopted by modern humans at Riparo Bombrini. It also revealed the extent of the taphonomic factors affecting the faunal assemblages on the site, which warranted a more systematic approach to our subsequent faunal analysis.

Chapter 5 introduces the third and final paper to be submitted, entitled "Comparing Neanderthal and Modern Human Subsistence at Riparo Bombrini: an Archaeozoological and Multivariate Taphonomic Analysis with Integrated ZooMS." It presents the complete application of an archaeozoological analysis complemented by ZooMS on the three transitional levels (A1, A2, and MS) at Riparo Bombrini. This study also integrates a multivariate taphonomic analysis to address many taphonomic variables systematically and hierarchically and to highlight the leading causes of bone damage. This last paper addresses our main research question by reconstructing the subsistence patterns of Neanderthals and modern humans in the transitional levels at Riparo Bombrini and by contextualizing those observations at the regional level and in the context of current discussions on subsistence continuities and changes during the transition in Europe.

We conclude with a summary of those three papers' methodological, empirical, and conceptual contributions and a discussion about the research perspectives they open at Riparo Bombrini and in the Liguro-Provençal arc. Preliminary results on the faunal assemblages of the lower Mousterian levels at Riparo Bombrini are also presented in this discussion to demonstrate the importance of further research on the site.

Chapter 1 – The Middle-Upper Paleolithic transition in Eurasia

This chapter briefly reviews the conceptual and methodological debates surrounding the Middle-Upper Paleolithic transition. We first display the current state of knowledge of the biological emergence of the transition two main actors: anatomically modern *Homo sapiens* (or modern humans) and *Homo neanderthalensis* (or Neanderthals). This includes discussing how modern dating methods, genetic data, and new fossil discoveries have influenced these discussions. Secondly, we examine the current perspectives on transition in the archaeological record, how it is adjusted to the lack of hominin fossil evidence, and how it informs us on the timing of modern human dispersals and the nature of their interactions with other local hominins. Finally, we underscore the importance of the faunal record in order to discuss subsistence changes and continuities during the Middle-Upper Paleolithic transition. This topic will be further detailed and contextualized within the aims of this research in the second (Chapter 5) and third articles (Chapter 6).

1.1 Neanderthals and modern humans: a phylogenetic problem

All European transitional sequences show similar patterns of abrupt change in the archaeological record between the Middle Paleolithic and the Upper Paleolithic sequences. This change varies from region to region with the appearance of the so-called “transitional industries,” Early Upper Paleolithic industries, and Initial Upper Paleolithic industries. Despite the scarcity of human fossils for this key period, there is a general agreement that this variability can be interpreted as evidence of a population replacement (Hublin 2015). Therefore, the long-asked question of how this process of population change occurred is fundamentally a phylogenetic one.

1.1.1 Neanderthals as a distinct species

Recent genetic data suggests that *Homo sapiens* and *Homo neanderthalensis* shared their last common ancestor, presumably *Homo heidelbergensis*, sometime between 400 and 700 thousand years ago (ka) (Stringer 2016). Today, it is widely accepted that early *Homo* populations emerged in sub-Saharan Africa in the late Pliocene about ~2.5 million years ago (Ma) and subsequently dispersed within Africa and Eurasia by the end of the Early Pleistocene between ~1.8 and 1.4 Ma (Rolland 2010; Trinkaus 2006). By the end of the Middle Pleistocene (OIS 8), *Homo sapiens* and *Homo neanderthalensis* fossils possessed unique non-metric features and morphometric architecture that make them distinguishable from one another and other archaic hominins (Hublin 2009; Stringer 2016). According to the fossil record, while modern humans were populating Africa (OIS8-5a), Neanderthals occupied most of Western Eurasia. During the warmer episodes of OIS 5 between ~130-100 ka, Neanderthals' territory ranged from Western Europe to as far east as South Siberia. Their eco-geographical domain was limited to the North below 55°N, potentially because of the limited capacity of Neanderthals to live in peri-arctic landscapes (Hublin 2009; Serangeli and Bolus 2008). This interpretation is also supported by observing that large portions of European sites seem abandoned during the colder phases of OIS 6 and OIS 4 and later re-occupied (Hublin and Roebroeks 2009). To the South, Neanderthals have been documented in the Near East as far as present-day Israel, but to date, never in North Africa (Hublin 2009).

Before the 1980s, two main models dominated debates over modern human origins. The **multiregional evolution** hypothesis claimed the evolutionary continuity between local archaic Eurasian forms (including Neanderthals) and modern humans (Caspari and Wolpoff 2013; Frayer et al. 1993; Thorne and Wolpoff 1992; Wolpoff et al. 2000; Wolpoff and Caspari 1997). This hypothesis was mainly based on the significant morphological variability and the apparent regional continuity observed on hominin fossils in Asia as making greater sense than the idea of a population replacement in this part of the continent, considering that numerous fossils presented a mixture of modern and archaic traits (Rosenberg and Wu 2013; Smith and Ahern 2013). The multiregionalists were, however, vocally opposed by tenants of the **Out of Africa** model (e.g., Wilson and Cann, 1992; Tattersall, 1997; Klein, 2008). Based upon that theory, the recent evolutionary origin of modern humans would have migrated from Africa to the Near East around 50-40 ka before rapidly colonizing Europe, Asia, and Oceania. This hypothesis relies on the apparent extinction of Neanderthals in Europe, noticeable by the replacement of the Mousterian by the Aurignacian and by the absence of Neanderthal fossils after this timeframe. The tenants of the "Out of Africa" model also rejected the hypothesis of admixture between the last Neandertals and modern humans, a statement seemingly supported by the first mitochondrial DNA analyses (Krings et al. 1997; Smith and Ahern 2013; Wilson and Cann 1992).

Beginning in the 1980s, a number of major advances in genetic studies and absolute dating techniques (e.g., Electron spin resonance [ESR], thermoluminescence [TL], optically stimulated luminescence [OSL], uranium-series [U-series], etc.) were developed that significantly altered the practice and interpretations of paleoanthropology and archaeology. These provided a more precise chronological framework that went well beyond the limits of radiocarbon dating (Pearson 2013). As a result, the African origin of modern humans was widely supported by genetic data disclosing a higher degree of intra-population genetic variability among extant sub-Saharan African populations than in populations in other parts of the world (Stringer and Andrews 1988). Consequentially, the Out of Africa model became accepted by most scholars during the 1990s, including the archaeologists working on transitional sites in Europe.

1.1.2 Genomic data complexifies the linear phylogenies

There is currently a consensus on the broad phylogeny that led to the anatomical emergence of *Homo sapiens* between ~300-150 ka in Africa (Bergström et al. 2021; Hublin et al. 2017; Pearson 2013) and of *Homo neanderthalensis* at least ~350 ka ago in western Europe (Hajdinjak et al. 2018; Serangeli and Bolus 2008). Although the taxonomy varies between scholars, the phylogeny starts with *Homo erectus* present in Africa, Europe, and Asia, as far as the island of Java by 1.8-1.9 Ma. In Europe and Africa, between ~600-800 ka, a second broad evolutive stage is acknowledged by the occurrence of fossils with larger brains named *Homo heidelbergensis* (sometimes archaic *Homo sapiens* or *Homo bodoensis* in Africa – Roksandic et al. (2021)). This evolutive stage eventually led to the independent emergence of modern humans in Africa and Neanderthals in Eurasia (Pearson 2013; Stringer 2016).

In Europe, the large collection of hominin fossils from Sima de Los Huesos dated around 600 ka is so far the most convincing evidence of the early derived morphological characters of Neanderthals (Hublin 2009). Other fossils dated between ~400-600 ka, such as the mandible of Mauer in Germany (Bräuer and Schultz 1996) and the fossils of Tautavel in France (de Lumley 2015), show clear signs of morphological variability and are consequently also assigned to *Homo* *heidelbergensis*. Unfortunately, few fossils have been discovered dating between MIS 10 and 6, which gives the illusion of a morphological gap before the explosion of Neanderthal fossils dating from MIS5 found in western Eurasia (Hublin 2009). Adding to the complexity of the Eurasian evolutionary picture is the discovery of a new eastern Eurasian hominin population, the Denisovans, roughly contemporaneous to morphologically fully formed Neanderthals (Brown, Massilani, et al. 2021; Krause et al. 2010). To date, little is known of Denisovans morphology since only a few teeth, morphologically undiagnostic bone fragments and a distal manual phalanx have been recovered in a single cave site (Denisova) in the Altai mountains of Siberia. However, aDNA analyses demonstrated that the two sister groups were separated by more than 390 ka (Meyer et al. 2016; Prüfer et al. 2017; Slon et al. 2018; Brown et al. 2021).

In Africa, several fossils with more modern-like traits are categorized as late archaic *Homo sapiens* and dated circa 230-300 ka. This clade is essentially a fit-all category that includes all hominin fossils from this timeframe characterized by a mosaic of morphological features distinctive of extant *Homo sapiens* (or *Homo sapiens sensu stricto*) alongside more archaic traits. These fossils tend to be more abundantly found in eastern and southern Africa, often compelling scholars to suggest that one of these regions is the phylogenetic source for the origin of modern humans (Henn et al. 2018). The accumulating fossil, genomic, and archaeological data inclines to complexify the original picture of the Out of Africa model, leading to many issues when it comes to picturing human evolution with simple linear phylogenetic or taxonomic trees (Hublin et al. 2017; Stringer 2016). Consequently, alongside the traditional models that involve a single region for modern human origins, different new scenarios are discussed to better integrate the observed internal variability in Africa (Henn et al. 2018). These models often include some multiregional notions such as the possibility of more than one region of emergence, migrations within Africa that could have occurred before the expansions out of the continent, and possible interbreeding events between modern humans and other contemporaneous archaic populations (e.g., *Homo naledi*) (Henn et al. 2018; Scerri et al. 2018; Stringer 2016).

The possibility of genetic exchanges during the Middle Pleistocene in Africa is all the more plausible since it was demonstrated over a decade ago that at least some episodes of admixture occurred between modern humans and local Eurasian hominins outside of Africa (Green et al.

2010; Reich et al. 2010). The Denisovan genome sequenced from the phalanx discovered at Denisova cave showed that these hominins did not take part in the gene flow brought by Neanderthals into present-day Eurasians. However, it was demonstrated to have contributed to between 4-6 % of present-day Melanesians, which is interpreted as proof that Denisovan populations were widespread in eastern Asia, whereas Neanderthals lived essentially in western Eurasia (Reich et al. 2010). Moreover, recent genomic sequencing on another bone fragment recovered from the Denisova cave led to the discovery of a first-generation of Neanderthal-Denisovan offspring (Slon et al. 2018). From their observations on the young female hybrid from a Neanderthal mother and a Denisovan father, the authors of the discovery suggested that admixture between Neanderthal and Denisovan groups was common when they met, which probably occurred sometimes after 120 ka when some Neanderthal groups migrated east of West Eurasia (Slon et al. 2018; but cf. Brown et al. 2021).

In sum, the fossil record reveals distinct evolutionary histories of modern humans in Africa, Neanderthals in Western Eurasia, and most likely Denisovans in Eastern Eurasia. The genetic studies support the African origin of modern humans because most present-day humans' genes derive from Africa. However, unlike what the first proponents of the Out of Africa model suggested, all extant non-African populations hold a small percentage of Neanderthal genes. Therefore, it seems that the interactions between human populations at the time of the Middle-Upper Paleolithic transition in Western Eurasia were likely a more complex scenario than an abrupt and complete species replacement event.

1.2 Neanderthals and modern humans: an archaeological matter

In the 1990s, when the Out of Africa became the most accepted model for modern human origins, the discussions over the Middle-Upper Paleolithic transition in Europe mainly focused on the fate of Neanderthals. A significant number of debates among archaeologists thus revolved around three ideas, all endorsing the reconstruction of the replacement event: the rapid dispersal of modern humans out of Africa replacing local hominins, the little chances of admixture between modern humans and Neanderthals, and the fact that each cultural industry in the transitional record was directly associated with a hominin species (either Neanderthals or modern humans)

(Clark 2002). In the 1980s, archaeologists agreeing with the Out of Africa theory had consequently developed dispersal models based on those preconceptions. Two of those replacement models largely dominated the past four decades of research on the transition.

The first is the population dispersal model – the so-called "**Human Revolution**" model, claiming that the abrupt change in the European transitional material was proof of modern humans being cognitively and behaviorally superior to Neanderthals. In this model, modern humans gained a clear evolutionary advantage during the transition timeframe, which enabled them to colonize the Eurasian continent (e.g., Klein 1992; Mellars 1996; Mellars and Stringer 1989). The second model, known as the **indigenist model,** claimed that Neanderthals were cognitively and behaviorally equal to modern humans. This model was based on a reaction to the "human revolutionists" who pictured Neanderthals and other contemporaneous archaic species as less adaptable than modern humans. Without rejecting rapid dispersals of modern humans, the indigenists claimed that Neanderthals independently developed their own Upper Paleolithic before the arrival of modern humans in Europe (e.g., d'Errico et al. 1998; Zilhão 2000; Zilhão and d'Errico 1999, 2000).

Next to those replacement models, a third model, the **mosaic model,** emerged. Built on the insights of the increasing applications of behavioural ecology perspectives on the archaeological record, the mosaic model aligned itself with the multiregionalists' ideas of local behavioural continuity, allowing biological admixture between modern humans and other contemporaneous hominins. In that sense, it claimed that the transition was not a single abrupt event but a temporal and spatial mosaic of processes visible in the variability of the archaeological record (e.g., Clark, 1999, 2002, 2007; Straus, 2005, 2007). American archaeologists initiated this model as a critical response to both dispersal models, hence emphasizing the lack of conceptual framework and the "epistemological naivete" underlying most aspects of the debates on modern human origins (Clark 1999).

1.2.1 Mousterian = Neanderthals, Aurignacian = modern humans, and what is in between?

The chronological bracket (~30-50 ka cal. BP) of the Middle-Upper Paleolithic transition poses numerous methodological challenges, the foremost being that it sits on the practical limit for using radiocarbon dating (~55,000 years) (Higham 2011, 2008). This analytical challenge has long created debates about how to compare archaeological sequences corresponding to the transition. In this regard, the refinement of radiocarbon techniques, namely the development of AMS radiocarbon and calibration methods, helped create more reliable chronological frameworks of the transition. Large-scale chronological analyses such as the work of Higham et al. (2014) are now possible to better estimate the spatiotemporal overlap between Neanderthal and modern human occupations in Eurasia. However, the refinement of dating methods confronts a fundamental interpretive problem to understand the nature of the interactions between the two populations, i.e., the lack of hominin fossils. The near-absence of fossils associated with transitional sequences forced archaeologists and paleoanthropologists to largely rely on the tacit assumptions about the associated archaeological material to build the chronological framework of the disappearance of Neanderthals and the dispersals of modern humans in Eurasia.

The first issue is thus the authorship of the archaeological industries and the chronology of their appearance in the transitional record. The European fossil record, even if scarce, is fairly clear on the authorship of the Final Mousterian (Neanderthals) and the classic Aurignacian (modern humans) (Benazzi et al. 2015; Churchill and Smith 2000; Hublin 2015). The main source of debates resides in the various industries found chronologically and stratigraphically embedded between the Final Mousterian and the classic Aurignacian (or Aurignacian *sensu stricto*) on Western European sites.

These industries can be regrouped into three main categories: (1) transitional industries, (2) Initial Upper Paleolithic (IUP) industries, and (3) Early Upper Paleolithic industries. Phylogenetic relationships with all these industries have been assumed and debated despite the dearth of human fossils, the chronological overlap, and the inherent archaeological overlap between the three categories. As a result, transitional industries are often associated with the last

Neanderthals. At the same time, the two other categories are generally described as part of the Early Upper Paleolithic to reinforce their association with early modern human dispersals out of Africa.

(1) The transitional industries are relatively contemporaneous and were initially characterized by the fact that they all exhibit a mix of typo-chronological markers of the Middle and the Upper Paleolithic. They include the Châtelperronian (southwest and central France, Pyrenees region, and Spanish Basque country), the Uluzzian (southern and northeast Italy, and Greece), the Szeletian (Czech Republic and Hungary), and the Lincombian-Ranisian-Jerzmanowician (southern UK, Belgium, Germany, and Poland). For the human revolutionists, this mixing of Upper Paleolithic traits such as bladelet productions, bone tools, and symbolic behaviours was best explained by an acculturation phenomenon resulting from contacts between the local Neanderthals and the colonizing modern humans (Mellars 1989; Hublin 2015). Conversely, the indigenists claimed that Neanderthals independently developed the transitional industries before the arrival of modern humans (d'Errico et al. 1998). However, both dispersal models assume that Neanderthals made the transitional industries, and yet very few human fossils were found in direct association with these industries. Furthermore, the few fragmentary human fossil discoveries associated with transitional contexts were excavated for the most part more than 50 years ago and come from debated stratigraphic contexts (Hublin 2015).

A few examples are worth mentioning here. Perhaps the most iconic, and indeed the most studied and debated transitional industry, the Châtelperronian, had revealed a near-complete Neanderthal skeleton at the La-Roche-à-Pierrot site (Saint-Césaire) in France (Lévêque and Vandermeersch 1980). This significant discovery was interpreted as a Neanderthal burial in 1979; however, its stratigraphic association with the Châtelperronian was immediately debated. Nonetheless, two decades later, d'Errico and colleagues (1998) argued that Neanderthals made the Châtelperronian based on an until-then unpublished discovery of a Neandertal child mandible fossil excavated by Leroi-Gourhan in the 1950s at the Grotte du Renne site (Arcy-sur-Cure) in France (Leroi-Gourhan 1961; Leroi-Gourhan and Leroi-Gourhan 1964). The authors used this new fossil from another site to support the St-Césaire skeleton's integrity and further argued that Neanderthals produced the Châtelperronian in the 100 + sites containing Châtelperronian material. D'Errico and colleagues (1998) even argued that Neanderthals were the sole producers of all pre-Aurignacian industries in Western and Central Europe. Since this publication, the integrity of the Châtelperronian levels at both sites has been the subject of heated controversy (Bar-Yosef and Bordes 2010; Benazzi et al. 2011; Caron et al. 2011; Gravina et al. 2018; Higham et al. 2010; Welker et al. 2016; Zilhão et al. 2011). A recent study based on lithic refitting and spatial projection of diagnostic artifacts has revealed that the Neanderthal skeleton from La-Roche-à-Pierrot cannot be securely associated with the Châtelperronian layer (Gravina et al. 2018). At Arcy-sur-Cure, 28 Neanderthal small bone fragments were identified using collagen fingerprinting and DNA characterization, adding to the mandible fragment and the nine teeth described in the Châtelperronian layers (Welker et al. 2016). These bone fragments are believed to come from a single young individual and were directly dated and put into Bayesian models to confirm that they come from the Châtelperronian layer XI. However, Welker and colleagues (2016) specify that these models cannot infirm that the body ornaments and bone awls were intrusive from the overlying Aurignacian level.

The preconception attributing all transitional industries to Neanderthals remains a strong source of debate, particularly when discoveries or reanalyses bring nuancing evidence. The case of the two teeth that were discovered in the Uluzzian levels of Grotta del Cavallo in the 1960s is a good illustration of this situation. At the time of their discovery, the teeth were interpreted to be Neanderthal-like (Churchill and Smith 2000). Those teeth were incorporated into the indigenists argument claiming that Neanderthals were the sole producers of the transitional industries (d'Errico et al. 1998). However, the teeth were later morphologically reassigned to modern humans by Benazzi and colleagues (2011), which provoked heated debates (Banks et al. 2013b; Ronchitelli et al. 2014), and ironically led the indigenists to question the integrity of the assemblages from Grotta del Cavallo by claiming the teeth to be intrusive in the Uluzzian record (Moroni et al. 2018; Zilhão et al. 2015).

(2) The Initial Upper Paleolithic was first described in the 1980s on a transitional layer uncovered at Boker Tachtit in the Levant. It was later defined by Kuhn et al. (1999) to include several lithic collections from southwest Asia formerly regrouped as Emiran industries. All these collections showed a method of blade production combining Levallois features, generally associated with the

Middle Paleolithic, with Upper Paleolithic volumetric exploitation of the core’s volume (Kuhn and Zwyns 2014). The term IUP is today further broadened to include all industries featuring Levallois technology in blade production, including Central European industries such as the Bachokirian in Bulgaria and the Bohunician in Moravia (Hoffecker 2011), as well as many sites in northwest China and north Africa (Kuhn and Zwyns 2014). Despite the lack of human fossils in a secure IUP context, these industries were generally assumed to be the product of modern humans. The fact that all IUP industries are stratigraphically found underlying other Early upper Paleolithic industries has pushed some researchers to suggest that they reflect an early wave of modern human expansions into Eurasia. This first wave would then have been followed by a second wave associated with the Proto-Aurignacian industries in some eastern European sites (Hoffecker 2011).

Several hominin bone fragments were recently discovered in association with IUP artifacts on the site of Bacho Kiro in Bulgaria (Fewlass et al. 2020; Hublin et al. 2020). These fragments found through proteomic screening (or ZooMS screening) were directly dated to approximately 45 ky cal BP and identified as *Homo sapiens* through mitochondrial DNA. This recent discovery documents the earliest direct evidence of the presence of modern humans in western Eurasia. It also reinforces the hypothesis that IUP assemblages are associated with *Homo sapiens*, indicating that a few rapid waves of modern humans migrated from southwest Asia into Western Eurasia several millennia before the arrival of modern humans associated with Early Upper Paleolithic industries.

(3) In Western Europe, the Early Upper Paleolithic generally designates the industries corresponding to the early stages of the Aurignacian *sensu stricto*, i.e., the Proto-Aurignacian and the Early Aurignacian. It is, however, important to note that this concept has also referred to any early manifestations of *Homo sapiens*-made industries outside this region to highlight the diversity of the archaeological record during the transition (Kuhn et al. 2004). Some scholars thus also include the Uluzzian in the Early Upper Paleolithic, following the recent likely reassignment of this industry to modern humans (e.g., Benazzi et al. 2011; Romandini et al. 2020).

Depending on research teams and the study regions, the Proto-Aurignacian is also named archaic or initial Aurignacian in Cantabria and Mediterranean France, whereas Aurignacian Ia and

Aurignacian 0 are used to designate similar early Aurignacian industries in the Périgord (Bon 2002). The industries share common characteristics such as the dominance of bladelet technology (a characteristic that is especially pronounced in Liguria), long-distance raw material transfers, the presence of some osseous technology sometimes including antler points, and the presence of personal ornaments made on a range of animal and mineral raw materials (Anderson et al. 2015; Kuhn 2002; Riel-Salvatore and Negrino 2018a; Soulier 2013).

The Early Aurignacian is more closely linked to the attributes of the Aurignacian with distinct *chaînes opératoires* to produce bladelets and large blades, the presence of abundant bone tools and antler split-based points, and regionalized personal ornaments in their shape, size, and raw materials (Bon 2002; Soulier 2013). When Proto-Aurignacian and Early Aurignacian are documented on the same site, the first always underlies the second, reinforcing the interpretation of the Proto-Aurignacian as one of the first manifestations of the Upper Paleolithic in western Europe. The long history of research in this part of the continent has also shaped the idea that the Proto-Aurignacian industries reflect early rapid migrations of modern humans from eastern origins along the Ligurian corridor. Scholars advocating for the east-west “colonization” of the continent often evoke a cultural phyletic link between the European Proto-Aurignacian and the Levantine Ahmarian technocomplex (Kozlowski 2010; Mellars 2006). This, in turn, encouraged archaeologists to look for techno-morphological similarities with the Proto-Aurignacian in other bladelet assemblages from eastern Europe such as Kozarnika in Bulgaria, Siuren-I in Crimea, and Kostenski 1, 14, and 17, in South West Russia to fill the territorial gab between the Near East and western Europe (Demidenko and Otte 2000; Demidenko and Noiret 2012; Tsanova et al. 2012). However, recent dates indicate that the earliest manifestation of the Proto-Aurignacian is documented at the site of Isturitz at ~43-41 ka cal BP in southwestern France (Barshay-Szmidt et al. 2018). These dates would thus be more consistent with an indigenous origin of the technocomplex in Western Europe.

While the paleoanthropological record somewhat confidently associates the Early Aurignacian with modern humans, the authorship of the Proto-Aurignacian is less clear (Churchill and Smith 2000). Only two deciduous teeth, identified as *Homo sapiens*, were found in secure Proto-

Aurignacian contexts, one at Grotta di Fumane in north-east Italy and one at Riparo Bombrini (Benazzi et al. 2015).

1.2.2 The Human Revolution that was not

The authorship of the different industries associated with the transition was particularly crucial for developing the "Human Revolution" model. When Henry Breuil named and defined the Middle and the Upper Paleolithic at the beginning of the 20th century, transitional industries as defined today, including the Châtelperronian (called *Lower Perigordian* by Peyrony and *Lower Aurignacian* by Breuil), were classified as belonging to the Upper Paleolithic and were assumed to be produced by modern humans (Lucas et al. 2007). However, after the discovery of the Neandertal skeleton at St-Césaire, the authorship of the Châtelperronian was reassigned, and the title of the first genuine Upper Paleolithic industry was attributed to the "Aurignacian technocomplex" (Clark and Riel-Salvatore 2009).

The discipline then drifted into a quest for empirical evidence of modern humans' cognitive and behavioural superiority over Neanderthals. Two typological features observed in the later phases of the Aurignacian (Aurignacian I-V) were seen as especially important to differentiate the Upper from the Middle Paleolithic, i.e., the presence of systematic production of prismatic blades with a high degree of standardization and the rapid rate of technological change and typological diversification. These characteristics were interpreted as behavioural flexibility equal to the ones ethnographically observed in extant foragers (Clark and Riel-Salvatore 2009). In addition, an extensive list of behavioural characteristics, referred to as "modern behaviours" in the literature, was considered unique to modern humans by proponents of the "Human Revolution." This list included the exploitation of bone, ivory, and antler raw material, the systematic use of grinding and pounding stone tools destined to process plant food, the production of personal ornamentation (beads and pendants), decorated objects (portable art), and parietal art, the implementation of long-distance exchange networks, the use of efficient hunting tools such as the spear-thrower and the bow and arrow, the development of specialized hunting strategies, the storage of food, the organization of internal spaces in residential sites according to different specialized activities with the presence of structured hearths, and the practice of funerary rituals (e.g., White et al. 1982; Mellars 1998; Mellars 2004; Mellars 2005; Bar-Yosef 2002). The list of modern behavioural traits was developed as evidence for an abrupt cognitive change that co-occurred at the turn of the Upper Paleolithic with technological advances, extended social networks, a sense of identity, and the emergence of fully syntactical language (e.g., Klein 1992, 1995; Mellars 1991; Mithen 1996; Noble and Davidson 1993).

This approach peaked at the turn of the 21st Century when Africanists put a stop to what they referred to as "a profound Eurocentric bias and a failure to appreciate the depth and breadth of the African archaeological record (McBrearty and Brooks 2000, 453)." In their iconic paper, McBrearty and Brooks (2000) took all traits argued to be unique to modern humans in Europe and provided much older examples of these behaviours from the African record, thus providing evidence that anatomically modern humans were behaviorally modern long before they migrated out of Africa. McBrearty and Brooks (2000) were very conscious of the irony of using the same Eurocentric trait list they were criticizing to construct their argument, but they did so intending to underscore that those traits were used to prop up an indefensible paradigm. Because the African empirical evidence for "modern human behaviour" precedes the transition in Europe, McBrearty and Brooks (2000) suggested that the appearance of those traits could no longer be explained by a pattern of behavioural revolution but should instead be interpreted as a gradual evolutionary process.

Henshilwood and Marean (2003) also criticized the trait list approach by demonstrating that most of those modern behavioural traits had weak theoretical grounding and were exclusively empirically derived, a method that leads to circular reasoning. They suggested abandoning most traits of the list and redefining behavioural modernity as a "behaviour that is mediated by socially constructed patterns of symbolic thinking, actions, and communication that allow for material and information exchange and cultural continuity between and across generations and contemporaneous communities (Henshilwood and Marean 2003:635)". For Henshilwood and Marean (2003), the best way of detecting modern behaviours was thus to look for archaeological evidence of symbolic behaviours. Symbolic behaviours are, in fact, strongly associated with the capacity for abstract thinking and the evolution of fully syntactical language (d'Errico et al. 2003; Noble and Davidson 1993; Tattersall 2014).

Therefore, from the beginning of the 21st Century, discussions on the origins of modern human behaviour shifted to searching for archaeological evidence of symbolic behaviour. To discuss symbolic behaviours in the African record, McBrearty and Brooks (2000) defined them as the capacity to create arbitrary symbols, be they vocal or visual, and represent abstract concepts. When those symbols are reified in the cultural material, they can be detected in the archaeological record in the form of symbolic artifacts such as burials and other unique forms of treatment of the dead, personal ornamentation (beads, pendants, incised and notched objects), use of pigments, and figurative art (McBrearty and Brooks 2000; Henshilwood and Marean 2003). Such evidence is indeed found in increased quantity in the European Upper Paleolithic and the African Late Stone Age records. However, the Africanists showed that beads and personal ornaments, ochre nodules, engraved artifacts, and a few burials are also found on multiple Middle Stone Age sites. Finally, the earliest evidence of figurative art dated as early as 45 ka BP is not found in Europe but in the Indonesian record, therefore nuancing the “revolution” aspect of the Middle-Upper Paleolithic transition in Europe (Aubert et al. 2014, 2018; Brumm et al. 2021).

While the strongest opponents to the “Human Revolution” model rightly stressed the importance of looking into the archaeological material outside Europe, the proponents of the indigenist model started to look for modern behaviours in the European Mousterian record to prove that those traits also had much deeper roots in Neanderthal evolutionary history than previously believed (d’Errico 2003; d’Errico et al. 2003). This, in turn, initiated a hunt for archaeological evidence of modern behaviours in the Middle Paleolithic archaeological record. A large amount of literature on archaeological discoveries has accumulated over the past two decades, proving that Neanderthals were in many respects cognitively equal to *Homo sapiens*. For instance, Neanderthals had the capacity to hunt prime-aged and dangerous animals (e.g., Bar-Oz and Adler 2005; Gaudzinski and Roebroeks 2000; Rabinovich and Hovers 2004; Speth and Clark 2006; Speth and Tchernov 2001; Steele 2004), to broaden their diet to include low-ranked animal resources (Blasco et al. 2016; Blasco and Fernández Peris 2009, 2012; Cochard et al. 2012; Gómez-Olivencia et al. 2018; Hardy and Moncel 2011; Lloveras et al. 2018; Martínez Valle et al. 2016; Morin et al. 2019; Romero et al. 2017), to exploit coastal resources (Douka and Higham 2012; Villa et al. 2020; Zilhão et al. 2020), and to harvest wood and plants as a source of food, medicine and raw material to make digging tools and weapon spears (Aranguren et al. 2018; Barton et al. 1999; Hardy et al. 2020; Hardy and Moncel 2011; Hardy 2018; Henry et al. 2011; Lev et al. 2005; Power et al. 2018; Thieme 1997). They could also make blade-based technologies (Bar-Yosef and Kuhn 1999; Clark and Riel-Salvatore 2009), exploit lithic raw material on long distances (Féblot-Augustins 1993, 1997, 2009; Porraz and Negrino 2008; Rossoni-Notter et al. 2017; Slimak and Giraud 2007), craft complex technologies such as hafting adhesives like birch-bark tar (Grünberg 2002; Koller et al. 2001; Mazza et al. 2006; Pawlik and Thissen 2011), bone tools (Abrams et al. 2014; Ahern et al. 2004, 2004; Burke and d'Errico 2008; Castel et al. 2017; Costamagno et al. 2015; Daujeard et al. 2014; Gaudzinski 1999; Hardy et al. 2014; Jéquier et al. 2018, 2012; Mallye et al. 2012; Martisius et al. 2020; Münzel and Conard 2004; Romandini et al. 2015; Soressi et al. 2013), and string technologies (Hardy et al. 2020). They also have been shown to have organized their living space according to different areas of activities (Bourguignon et al. 2002; Henry et al. 2004; Riel-Salvatore et al. 2013; Speth 2006; Vallverdú et al. 2012; Vaquero and Pastó 2001), to have used symbolically mediated elements such as black and red pigments potentially to create corporeal designs on their skins (d'Errico et al. 2003; Peresani et al. 2013; Soressi and d'Errico 2007; Zilhão et al. 2010) and bird talons and feathers as personal ornamentation (Finlayson et al. 2012, 2019; Fiore et al. 2016; Laroulandie et al. 2016, 2020; Majkić et al. 2017; Morin and Laroulandie 2012; Peresani et al. 2011; Radovčić et al. 2015; Romandini et al. 2014). Finally, it is now recognized that they could bury their dead (Pomeroy et al. 2020; Rendu et al. 2014), engrave geometric patterns on bones (Leder et al. 2021), build complex structures deep in caves (Jaubert et al. 2016) and maybe even create parietal art (Hoffmann et al. 2018; Rodríguez-Vidal et al. 2014),

However, from the "mosaic" perspective on the fate of Neanderthals, the search for "modern human behaviour" in the Neanderthal record does not fully allow the discipline to dissociate itself from Eurocentric biases. For instance, Clark (1999, 2002, 2007) has argued that the lack of data alone could not explain why scholars are torn between radically different scenarios on modern human origins. He further argued that the lack of explicit conceptual framework in paleoarchaeology of European research tradition had pushed the discipline into methodological reductionism that resulted in the search for empirical evidence of modern behaviours in both Middle and Upper Paleolithic records without explicitly defining what "behavioural modernity" actually means (Clark 2007). In fact, according to proponents of the mosaic model, the profound Eurocentric bias that characterizes the trait list of modern behaviours partly resides in the basic analytical units (e.g., Mousterian, transitional industries, Aurignacian, etc.) on which it is based, categories that are in fact simple accidents of history mostly created by French prehistorians during the 19th Century to solve chronological problems before the widespread use of absolute dating methods (Clark 2007:20; Clark and Riel-Salvatore 2009).

Using similar arguments, some researchers suggested abandoning the concept of behavioural modernity altogether (Ames et al. 2013; Shea 2011) and instead refocusing our efforts away from the dichotomy between modern and non-modern archaeological records, too closely linked to the original Eurocentric bio-cultural comparison of behaviourally modern *Homo sapiens* and non-modern Neanderthals (and other archaic hominins). Instead, they recommended focusing on behavioural variability, documenting broader patterns, and analyzing their archaeological record fluctuations. These new lines of research, mostly focused on lithic technology and land-use strategies, greatly helped to deconstruct the perception of the Mousterian, and thus Neanderthal as a species, as an essentially homogenous unit with very little evolutionary change (e.g., Clark and Riel-Salvatore 2006; Delagnes and Meignen 2006; Kuhn 2013; Kuhn and Hovers 2006). The variability of Late Middle and Early Upper Paleolithic industries appear too great to be amalgamated into a simple scenario when considering different regions with distinct contextual settings, which necessarily influenced the way human populations adapted their behaviours as reflected, among other things, by variability in the lithic record.

Finally, the diversification of theoretical approaches to study the interactions between Neanderthals and modern humans has further highlighted how many hypotheses on the relationship between the two species sometimes remain influenced by deeply rooted Eurocentric, colonialist, and misogynistic concepts. For example, Sterling (2015) describes how black feminist theories are helpful to take a fresh look at the nature of the interactions between Neanderthals and modern humans. One of her case studies concerns the accumulating genetic data indicating that at least a few sexual encounters occurred between Neanderthals and modern humans. The nature of those interactions is central to the discussion surrounding modern human origins and their survival over Neanderthals. However, no direct evidence of Neanderthals and modern humans co-habitation has been found in the archaeological record, therefore hindering unbiased interpretation of the nature of those encounters. This lack of evidence comes as no surprise because such sporadic encounters are unlikely to be detectable within the archaeological resolution of the Middle-Upper Paleolithic transition. Sterling (2015) argues that while very few explicit interpretations of the nature of the sexual encounters between the two species can be found in the scientific literature, examples are more easily detectable in the media. She cites Stringer in a *New York Times* interview who refers to ethnographic models to describe the encounters as "aggressive acts between competing groups […]" (Sterling 2015:108). Sterling points out that even a short statement like this can strongly reinforce ideas of cultural evolution already present in the public sphere by implying that men are naturally violent and prone to abducting women. Yet, unidirectional aggressive encounters between colonizing modern humans and colonized Neanderthals could never explain why extant non-African *Homo sapiens* carry Neanderthal DNA because if hybrids were only raised within Neanderthal groups, they would be extinct altogether.

In sum, adopting conceptual frameworks that explicitly eschew Eurocentric notions of "colonization" and "acculturation" allow better discussions of Neanderthal and modern human interactions that portray Neanderthals as active agents in their evolutionary fate, thus avoiding the pitfalls of implying unidirectional and/or aggressive cultural transmission from modern humans to Neanderthals.

1.3 The importance of faunal remains to discuss subsistence behaviours during the transition

Until the 1980s, faunal remains found in stratigraphic association with prehistoric archaeological material were largely assumed to be the result of hominin hunting. Therefore, the list of all animal species was relegated to the appendix section of archaeological reports and presented as proof of hominin kill counts. With the emergence of processualism during the 1960s and 70s, important work from taphonomists in African contexts changed how animal remains were studied on prehistoric sites and challenged earlier simplistic interpretations about early hominin hunting strategies. For instance, Brain (1981) and Binford (1981) made strong cases based on skeletal element counts and marks on bone surfaces to prove that faunal assemblages on sites from South Africa and at Olduvai Gorge resulted from scavenging activities. Actualistic research through experimental archaeology and data from ethnographic and ethological studies became the norm to disentangle the human and non-human formation processes involved in accumulating faunal assemblages (Gifford-Gonzalez 1991). By tracing parallels with contemporary observations on the causal agents of various traces on bones, many scholars contributed to create an extensive reference collection of taphonomic alterations related to anthropic actions, carnivore actions, bone gnawing and trampling by different mammals, rodent gnawing, the effects of flowing water, weathering, etc. (see: Gifford-Gonzalez 1991 for literature review).

The work of Binford on European sites also contributed to shape early theories about Neanderthal subsistence behaviours (e.g., Binford 1981, 1985). His claim that Neanderthals were most likely scavengers of large mammals while occasionally hunting weak or smaller prey initiated a movement of reanalysis of many Mousterian faunal collections during the 1990s and helped to improve analytical methods to distinguish hunting from scavenging behaviours in Eurasian Middle Paleolithic and African Middle Stone Age contexts (Auguste 1995; Chase 1991; Conard 1997; Farizy and David 1992; Klein 1989; Klein and Cruz-Uribe 1996; Marean 1998; Marean and Kim 1998; Mellars 1996; Stiner 1994). The resulting consensus about Neanderthal hunting capacities did not diminish Binford's contribution to the discipline since his warning that animal skeletal remains can be accumulated by agents other than humans on archaeological sites is well-taken. Rather, the hunter/scavenger debates fueled by increasing amounts of taphonomic research based on an actualistic approach highlighted the problem of accounting for equifinality. The debate thus helped develop the array of standard archaeozoological methods employed today to study Paleolithic faunal assemblages that combine available data on the relative skeletal abundance, bone surface modification, and mortality profiles to discriminate the agent of skeletal accumulation and reconstruct human subsistence behaviours (Conard and Prindiville 2000).

The development and standardization of archaeozoological and taphonomic methods on Paleolithic faunal assemblages have allowed rigorous investigation into crucial evolutionary behaviours over the course of the transition, including shifts in prey selection, hunting strategies, carcass processing, raw material procurement, seasonality, mobility and land-use strategies, diet breadth, subsistence intensification, human-carnivore competition, and human-environment interactions. The trends of subsistence continuities and changes emerging from this research are described and discussed concerning Riparo Bombrini in Chapter 5 (Article 3).

Chapter 2 – Site presentation

This chapter introduces the site of Riparo Bombrini (Balzi Rossi), the focus of the research presented in this dissertation. We begin by discussing the transition on the regional scale of the Liguro-Provençal arc and then narrow in on the Balzi Rossi cave complex in its geographical, historical, geomorphological and chronological contexts before finally describing Riparo Bombrini itself. This exercise will further explain how this site, however methodologically challenging, is crucial for understanding hunter-gatherer subsistence behaviours during the Middle-Upper Paleolithic transition in Europe.

2.1 The Balzi Rossi in the transitional context of the Liguro-Provençal arc

The Balzi Rossi are embedded in a unique geophysical region that contributed to define past human subsistence, mobility, and socio-economic networks. The Pre-Alps constrict the cave complex and the region of Liguria as a whole to the North while the Mediterranean Sea borders the South, naturally shaping a narrow corridor that extends as far as 400 km from today's Rhône Valley in France to the Apennines in Italy. Consistent with bathymetry estimates indicating a mere possible extension of 1-2 km of the coast, one can infer that this corridor remained unremittingly narrow even during glacial times, thus considerably constraining human and animal circulation (Lumley 2016a; Tomasso and Porraz 2016). In fact, long-distance population moves would have been possible mostly on an East-West axis along the Mediterranean coast while North-South population moves would have been restricted to short distances between the shore and the mountains (Grimaldi et al. 2014; Porraz et al. 2010; Tomasso and Porraz 2016).

Furthermore, as part of a series of northern Mediterranean peninsulas (i.e., Iberia, Italy and Balkans), the Liguro-Provencal arc provided a refugium for animal populations (including hominins) during Pleistocene glaciations (Finlayson 2004; Finlayson et al. 2006; Valensi 2009; Van Andel et al. 2003). The broad biogeographical characteristics of those three peninsulas show that their topographic contexts and their overall Mediterranean climate led to the mitigation of seasonal climatic fluctuations during glacial periods. Dry summers and humid winters enabled temperate taxa to persist during glacial periods, sharing these regions with cold-adapted taxa (Valensi 2009). In the Liguro-Provençal arc, hominin populations had thereby sustained access to temperate prey species such as red deer and fallow deer, these animals remaining abundant in a region where Pre-Alps low altitude (~1400m) favoured forested environments during both glacial and temperate periods. The characteristic cliffs of the region also provided an ideal environment for caprids, and the limited but continuous presence of open areas enabled the recurrent presence of large bovids, horses and rhinoceros throughout the Pleistocene (Moussous 2014; Valensi 2009).

Recent studies on the region lithic technology and raw material sourcing have provided crucial information on population movements during the transition (Grimaldi et al. 2014; Porraz et al. 2010; Porraz and Negrino 2008; Rossoni-Notter et al. 2017; Rossoni-Notter and Simon 2016; Tomasso and Porraz 2016). These studies illustrate how, during this timeframe, the regional geophysical context and the availability of local raw material shaped the lithic procurement strategies adopted by human populations.

The geographic distribution of petrographic sources across the Liguro-Provençal arc has been extensively documented since the 1980s (Tomasso and Porraz 2016). As a result, more than 900 sources of lithic raw material are hereby recognized and can be roughly divided into four lithological areas: (1) Western Provence, where abundant sources of high quality flint are located in the Haute-Provence mountains (Monts de Vaucluse, Mont Ventoux, Lure mountain) and the Apt-Forcalquier basin; (2) Eastern Provence, where abundant sources of unequal quality (fine-grained) flints and rhyolite (Estérel) are located mostly in the French Pre-Alps; (3) Western Liguria, where a few sources of poor quality material (silicified limestone, limestone, quartzite, etc.) are located in the Italian Pre-Alps from Nice to San Remo, including the well-known known I Ciotti conglomerate, situated less than 5 km from the Balzi Rossi and mainly comprised of heterogeneous, poor-quality flint; and (4) Eastern Liguria, where abundant sources of high-quality raw materials are located, stretching into Emilia Romagna (the so-called jaspers of Monte Lama and Monte Pràrbera) and the Apennines in Northern Tuscany (*ibid*.).

The broad picture of raw material procurement patterns in the region reveals contrasting mobility strategies and socio-economic networks between the Mousterian and Proto-Aurignacian. Mousterian assemblages are characterized by opportunistic exploitations of raw materials available in the vicinity of each site (up to 30 km). In contrast, Proto-Aurignacian assemblages demonstrate a selection process intricately linked to the quality of the lithic material (Riel-Salvatore and Negrino 2009). Proto-Aurignacian sites located far from good quality flints are therefore characterized by a dominance of locally available raw material with a significant proportion of allochthonous lithotypes acquired 50-200 km off-site (e.g., Grotte de l'Observatoire, Riparo Mochi, and Riparo Bombrini), whereas sites located close to abundant high-quality flint sources tend to show a dominance of local raw material (e.g., Mandrin, La Laouza, l'Esquicho-Grapaou, Ronco del Gatto and Lemignano) (Porraz et al. 2010; Riel-Salvatore and Negrino 2009). This pattern in Proto-Aurignacian raw material procurement is yet reinforced by similar observations outside the Liguro-Provençal arc, namely at the Catalan site of L'Arbreda where 70% of the raw material is allochthonous (>100km) (Ortega Cobos et al. 2005).

Those patterns suggest a picture of eminently locally focused subsistence and mobility strategies for the Mousterian assemblages (Riel-Salvatore and Negrino 2009). Occasional allochthonous imports from up to 200 km, usually in the form of individual retouched implements, are documented on a few sites (e.g., Riparo Bombrini, Ex-Casinò, and Pié Lombard), thus suggesting larger raw material exploitation ranges than commonly observed in Mousterian contexts (Porraz and Negrino 2008). Porraz and Negrino (2008) interpreted this elongation of circulation distances as a result of the region's geophysical configuration that tends to constrain most population moves along an East-West axis through the Ligurian corridor. In contrast, the Proto-Aurignacian assemblages suggest a picture of much larger social networks in which human populations exploited available local raw materials, supplementing them by long-distance transfers (>130 km) in between the Pô and the Rhone valleys to acquire high-quality flints (Porraz et al. 2010).

Furthermore, while the initial hypothesis for the diffusion of the Proto-Aurignacian populations was one of continuous westward colonization spreading along the Liguro-Provençal corridor (e.g., Kozlowski and Otte 2000; Mellars 2004), this regional perspective on raw material circulation shows a strong link between southeastern French sites and northwestern Italian sites, with comparatively weaker links to the rest of the Italian peninsula. This is particularly visible on coastal sites like Grotte de l'Observatoire, Riparo Mochi, and Riparo Bombrini, in which Proto-Aurignacian assemblages contain large proportions of Provençal flints (Grimaldi et al. 2014; Porraz et al. 2010; Riel-Salvatore and Negrino 2018a). Therefore, these observations indicate that Proto-Aurignacian populations circulated back and forth along the corridor to acquire good-quality flints, suggesting that more nuanced hypotheses on modern human dispersals may be needed to fully account for the pattern.

How are these differences expressed in terms of subsistence behaviours? Unfortunately, high-resolution archaeozoological and taphonomic data on transitional sites are scarce in the Liguro-Provencal arc. Table 1 shows the available faunal data on Late Mousterian and Proto-Aurignacian assemblages in Liguria and Southeastern France in comparison with some Proto-Aurignacian sites in Southwestern France. This table demonstrates that the lack of data primarily originates in that most sites are well-known historically and were excavated using coarser methods than today's standards – often discarding smaller or unidentifiable fractions of fauna. In Liguria, the topographic context also introduces a considerable bias towards coastal sites, with very few cave sites discovered inland (e.g., Arma Veirana, Santa Lucia Superiore) and almost no open-air sites (i.e., Ex-Birreria, Ex-Casino, and Via San Francesco).

The paucity of available faunal data considerably hinders a synthetic understanding of the regional variability in subsistence behaviours during the Middle-Upper Paleolithic transition. However, this challenging situation also reveals the need for fine-grained archaeozoological and taphonomic studies on sites excavated with modern methods such as Riparo Bombrini. In Chapter 5, we will discuss our results within the context of the available regional faunal data and the comparative data from neighbouring regions of Southern France and the Italian Peninsula (Daujeard et al. 2012; Daujeard and Moncel 2010; Rendu et al. 2019; Romandini et al. 2020).

Table 1. – Available faunal data (marked with an X) on Late Mousterian and Proto-Aurignacian sites in the Liguro-Provençal arc

Archaeological sites	Faunal abundance	Archaeozoo. & tapho.	Modern excavations (>1950)	Source

Liguria (Balzi Rossi)				
Riparo Mochi (PA)	X		Yes	Alhaique (2000)
Riparo Mochi (M)	X		~1950	Arellano (2009)
Caviglione (M)	X		No	Moussous (2014)
Riparo Bombrini (PA)	X	X	Yes	Present study
Riparo Bombrini (M)	X	X	Yes	Present study
Liguria				
San Francesco (M)	X	X	No	Valensi and Psathi (2004)
Madonna dell'Arma (M)	X	X	No	*Ibid.*
Santa Lucia Superiore (M)	X	X	No	*Ibid.*
Caverna delle Fate (M)	X	X	No	Psathi (2003), Valensi and Psathi (2004)
Arma delle Manie (M)	X	X	No	*Ibid.*
Monaco				
Grotte de l'Observatoire (PA)			No	Romandini (2017), Brugal et al. (2017)
South-East France				
Lazaret (M)	X	X	No	Valensi and Psathi (2004)
Other comparative sites with PA sequences				
Fumane (PA)	X	X	Yes	Romandini et al (2020)
Les Abeilles (PA)	X	X	Yes	Soulier (2014)
Isturitz (PA)	X	X	~1950	Soulier (2013)
Saint-Césaire (PA)	X	X	Yes	Morin (2008)
Les Cottés (PA)	X	X	Yes	Rendu et al. (2019)

2.2 The Balzi Rossi cave complex

The Balzi Rossi cave complex is located on the Ligurian coast close to the French border at about 400 m east of the French borders and 8 km west of Ventimiglia (Italy). The complex comprises seven large south-facing karstic caves (Constantini, Fanciulli, Florestiano, Caviglione, Barma Grande, Baousso da Torre, and Grotte du Prince) opened on the sea and more or less 20 meters above its present-day sea level (Barale 2016). Nowadays, the steep cliffs of Jurassic limestone rise only 20 to 80 meters above the Mediterranean shore, but in the Upper Pleistocene Last Glacial Maximum a larger plain stretched in front of the caves, as sea levels were then 120 meters lower than today (Lumley 2016a). The Balzi Rossi was well-known by Paleolithic hunter-gatherers as attested by the imposing Middle and Late Pleistocene archaeological deposits found in all seven caves, often including the Middle-Upper Paleolithic transition (e.g., the 21m-long Mousterian sequence of Grotte du Prince; Elena Rossoni-Notter, Notter, and Simon 2017). Caves were not the sole focus of occupation during that time, as attested by the presence of three rockshelter sites (i.e., Lorenzi, Mochi, and Bombrini) and two open-air sites (i.e., Ex-Casino, Ex-Birreria) in the Balzi Rossi complex. These long archaeological sequences make the Balzi Rossi a crucial locality for our understanding of the Middle-Upper Paleolithic transition.

The recent lithological sourcing analyses on assemblages from the different Balzi Rossi sites demonstrate that the cave complex was a landmark passage point along the narrow circulation corridor between the Rhône valley and the Apennines during the Middle and Upper Paleolithic. This cave complex also became a symbolic landmark during the Gravettian and Epigravettian as evidenced by the twelve highly decorated burials, including double and triple burials, discovered in the different caves at the turn of the 20th Century, in addition to a variety of mobiliary and parietal art (Formicola and Holt 2015).

The Balzi Rossi likely stood out on the landscape during the Pleistocene, as they do today, because of the distinctive reddish staining of the cliffs as well as their physical position at the edge of one of the several bays that dot the Mediterranean coast in the region (Barale 2016). This made (and makes) the Balzi Rossi clearly visible from both edges of the bay: from the western part of today's city of Ventimiglia (~2km) eastward and from the Cap Martin up to 15 km westward. The reddish colour of the cliffs caused by iron oxi-hydroxides leaking on its walls is also what inspired their name, Balzi Rossi, which is the Italian translation from the local dialect "Baussi Russi" meaning "red rocks"(Formicola and Holt 2015). Other names attributed to the cliffs are present in the old and new literature, namely "Baousse Rousse" (Menton dialect), "Rochers Rouges" (French), "Grottes de Menton" (from 1860 in the literature), and the Grimaldi caves (from 1900, given after the name of a nearby village) (Barale 2016; Formicola and Holt 2015; Lumley 2016a; Moussous 2014; Rossoni-Notter et al. 2017). These different names are direct testimonies of the local importance of the cave complex as a cultural and geographical landmark, both in Italy and in France.

2.2.1 Brief history of the discovery and excavation of the Balzi Rossi

The first mentions of the Balzi Rossi in the literature come from a brief geological description written by the Swiss naturalist Horace-Bénédict de Saussure in his third tome of *Voyage dans les*

Alpes, in which he describes its distinctive rounded limestone caves shaped by the action of water (Saussure 1796). Excavations started about 50 years later with an initial exploration of the caves by the Prince of Monaco, Florestan I, in 1846 (Formicola and Holt 2015; Garrigue et al. 2016; Moussous 2014; Rossoni-Notter et al. 2017). Over the following 50 years, a number of wealthy scientists interested in the origin and evolution of humans conducted their own excavation projects as the caves were opened for anyone to excavate and were conveniently located close to many renowned seaside towns of the Italian Riviera and the Côte d'Azur. Among these excavators, it is worth mentioning Émile Rivière, a French doctor who visited the Balzi Rossi for the first time in 1869 while staying in Cannes for health problems. Émile Rivière conducted large-scale excavations in most of the caves from 1870 to 1875 (Garrigue et al. 2016). During his first explorations of the Balzi Rossi and its surroundings, he identified and named nine caves: cave 1 to 9 respectively, corresponding today to Fanciulli, Riparo Lorenzi, Florestiano, Caviglione, Barma Grande, Baousse di Torre, Grotte du Prince, an unnamed rockshelter, and Gerbaï cave (Lumley 2016a). His interest in the caves increased during the construction of the Genoa-Marseille railroad in 1871 when a large quantity of archaeological material and thick layers of ash were exposed in a twelve-meter-deep trench excavated on the talus in front of the Fanciulli, the Lorenzi and the Caviglione sites. In 1871 and 1872, Rivière obtained permission from the French Ministry for public instruction granting him exclusive access to all seven caves in which he initiated large scale excavations, starting with Grotta del Caviglione (4th cave after Rivière's denomination of the caves). His work was rewarded by a first major discovery – the Caviglione skeleton – in 1871, a burial covered with red ochre and decorated with abundant grave goods, initially named "l'Homme de Menton" by Rivière who interpreted the skeleton to be male. The skeleton was immediately transported in a block by train to the National Museum of Natural History in Paris. The burial was later renamed "la dame du Cavillon" after further analyses in the 1980s helped reassign the sex of the skeleton to as female (Formicola and Holt 2015). After this first discovery, Rivière unearthed no less than five other burials from 1872 to 1875 including three skeletons in the now destroyed Baousse di Torre as well as double burial of two young children in Fanciulli cave (Formicola and Holt 2015). Rivière's impressive discoveries would cause serious disputes for access to the caves in the years to come. In 1883 notably, Rivière firmly claimed his monopoly on the Barma Grande over Prince Albert I of Monaco who wanted to purchase it as he was later able to do with the Grotte du Prince in 1892 (Formicola and Holt 2015; Rossoni-Notter et al. 2017).

This quarrel was singularly unfortunate as it prevented excavations of scientific value in the Upper Paleolithic levels of Barma Grande similar to those later conducted in the Mousterian deposits of Grotte du Prince, Grotta del Caviglione, Riparo Lorenzi, and Grotta di Fanciulli between 1892 and 1905 by Léonce de Villeneuve under the tutelage of Albert I and in collaboration with eminent prehistorians and paleontologists like Marcellin Boule, René Verneau, and Émile Cartailhac (Cartailhac et al. 1906; Garrigue et al. 2016; Moussous 2014). Sadly, the decade between the dispute and Villeneuve's excavation campaigns left room for questionable practices as Francesco Abbo, a local entrepreneur, succeeded in purchasing Baousse di Torre and Barma Grande. Not only did he destroy the first by converting the site into a limestone quarry, but he also rapidly started to excavate the second in order to use the fill as fertilizer for his vineyard (Formicola and Holt 2015). In only a few weeks, more than eight meters of deposits were removed from the whole surface of the cave (28 m total length, 6.5m width at the entrance). Ironically enough, successive work at the site would eventually make him famous for the discovery of numerous burials, including a Gravettian triple burial of adolescents in 1892. These important finds attracted several amateurs and scientists to the site and, in 1898, inspired the English philanthropist Thomas Hanbury to finance the construction of a first small on-site museum (today's Old Museum of the Balzi Rossi Museum) in order to preserve the skeletons (Formicola and Holt 2015; Rossoni-Notter et al. 2017).

Starting in the 1930s, new excavation campaigns in the Balzi Rossi were organized by A.C. Blanc and L. Cardini of the *Istituto Italiano di Paleontologia Umana*, leading to the discovery of two new sites in 1938: Grotta Constantini and Riparo Mochi (Douka et al. 2012; Moussous 2014). The same year, Blanc and Cardini tested both Riparo Mochi and Riparo Bombrini. After assessing the levels rich in bladelets on both sites, they subsequently decided to enlarge the original trench at Riparo Mochi and organize three excavation campaigns (1941, 1942, 1949) that uncovered the site's famous Paleolithic deposits, spanning Mousterian, Proto-Aurignacian, Aurignacian, Gravettian, and Epigravettian levels over 10 meters of deposit.

During the second half of the 20th century, several projects were initiated by different research teams in the Balzi Rossi. The *Musée d'Anthropologie Préhistorique de Monaco* repeatedly excavated the lower levels of Grotte du Prince from 1965 on with a team led by L. Barral and later by S. Simone. Their campaigns succeeded in unearthing a human iliac bone dated to OIS 7 (Barral and Simone 1967; Bietti 1998; Moussous 2014). The *Istituto internazionale di studi liguri* engaged a few projects on different sites led by G. Vicino who discovered an engraved horse on the western wall of Grotta del Caviglione and a human incisor in the Proto-Aurignacian deposits of Riparo Bombrini. Finally, in 1995, the *Soprintendenza Archeologica della Liguria* supported a team led by A. Bietti to resume excavations at Riparo Mochi. Their first four campaigns aimed at reinvestigating the section uncovered by Blanc and Cardini and safeguarding its stratigraphy to expose it to visitors, while seven other successive field seasons focused essentially on the Mousterian layers (Douka et al. 2012).

Nowadays, ongoing excavation projects involve three sites: (1) Grotte du Prince under the scientific direction of the *Musée d'Anthropologie Préhistorique de Monaco* led by E. Rossoni-Notter, who also initiated a series of analyses on Villeneuve's excavation collections of the different caves curated in Monaco since the 19th Century (Moussous 2014; Rossoni-Notter et al. 2017; Rossoni-Notter and Simon 2016); (2) Riparo Mochi under the *Soprintendenza per i Beni Archeologici della Liguria* led by S. Grimaldi (Università di Trento); and (3) the Riparo Bombrini co-directed by F. Negrino (Università di Genova) and J. Riel-Salvatore (Université de Montréal) as part of an Italo-Canadian project.

2.2.2 The neighbouring sites of Riparo Mochi and Grotta del Caviglione

The long history of research at the Balzi Rossi helped highlight its importance for Paleolithic research. However, it also had the perverse effect of affecting the scientific quality of the archaeological documentation as we know it today. Fortunately, two Middle-Upper Paleolithic sites were partly preserved, spared by the roughshod excavations and the construction of the railway that took place during the 19th Century: Riparo Mochi and Riparo Bombrini. The first two series of excavation campaigns at Riparo Mochi documented its stratigraphy with a more fine-grained approach than previously done elsewhere at the Balzi Rossi, which revealed for the first time the extent of the Middle and Upper Paleolithic occupations. The long stratigraphic sequence exposed at Riparo Mochi soon made it a reference point to discuss the early arrival of modern humans (associated with the Aurignacian) in Mediterranean Europe (Douka et al. 2012). A series of dates published in 2012 also provided a robust chronological framework for the transitional occupations of the rockshelter, revealing one of the earliest manifestations of the Proto-Aurignacian in Europe circa 42.7-41.6 ky cal BP (Douka et al. 2012; Holt et al. 2019).

After several excavation campaigns at Riparo Bombrini and the development of a dating program from 2002 to 2005, it became clear that the deposits from both rockshelters (Mochi and Bombrini) were chronologically contemporaneous. At Riparo Mochi, Proto-Aurignacian level (G) is thicker (~60 cm) but overall contemporaneous to Riparo Bombrini's Levels A1 and A2 (~30 cm), although the base of Level G yielded slightly earlier dates. In both rockshelters, the Proto-Aurignacian levels overlie a thick semi-sterile deposit characterized by very few lithic artifacts attributed typotechnologically to the Mousterian (Level H at Mochi, Level MS1-2 at Bombrini) underlain by denser Mousterian levels (top of Level I at Mochi, Levels M1-7 at Bombrini) (Holt et al. 2019). Although more dates would be essential to better assess the chronological relationship between the Mousterian levels of both sites, the archaeological correlation between the deposits suggests widespread occupations of the Balzi Rossi during the timeframe of the Middle-Upper Paleolithic transition. Unfortunately, the history of excavation at the Balzi Rossi limits our understanding of the spatial distribution of those occupations by modern humans and Neanderthals during OIS 3 as no other Proto-Aurignacian assemblages have so far been securely identified on any other previously excavated site of the complex. However, the location of both rockshelters strongly suggests that Grotta del Caviglione's entrance was similarly occupied during this timeframe. At Caviglione, the levels corresponding to the Proto-Aurignacian and Aurignacian were not singled out by Rivière, who excavated through the Gravettian levels down to the Mousterian level "Foyer inférieur" without individualizing a layer that could correspond to Early Upper Paleolithic occupations. However, a recent reanalysis of Rivière's collections pointed to a possible Aurignacian layer in the lowermost part of Rivière's lower level, as suggested by the presence of a split-based point (Lumley 2016b). No Proto-Aurignacian diagnostic tools were identified, which does not indicate the absence of such a level as diagnostic elements such as small bladelets could have easily been missed without fine-grained excavation methods.

In sum, Riparo Bombrini is, along with Riparo Mochi, the only site of the Balzi Rossi still preserving intact deposits corresponding to the Middle-Upper Paleolithic transition. Furthermore, Riparo Bombrini was entirely excavated with modern methods (post-1950) with the systematic georeferencing of piece-plotted artifacts and water-screening of all sediments. However, Riparo Bombrini cannot be studied as an independent residential camp, as demonstrated by its stratigraphic correlation with Mochi. Riparo Bombrini is located at the eastern most part of a long terrace opening in front of the different caves starting with Caviglione and Mochi, which probably extended westward towards Florestano, Lorenzi, Fanciulli, and Constantini. Reconstructions of the spatial organization of activities at Riparo Bombrini must therefore take into consideration that hunter-gatherers could have recurrently occupied the different parts of this long terrace with various spatial organizations according to their seasonal moves, among other factors (Riel-Salvatore et al. 2013).

2.3 Riparo Bombrini

2.3.1 Discovery of the site and excavation methods

Although E. Rivière acknowledged the existence of Riparo Bombrini after the construction of the railroad by the end of the 19th century, he never conducted excavations there. However, he noted the existence of a small cave entrance his post-war successors never found. However, this entrance is suspected to be located where a brick-walled water tank, currently used to store equipment and archaeological material, stands today (Vicino 1984). The portion of Riparo Bombrini that was not truncated by the railroad trench and the construction of the water tank was therefore preserved until Cardini dug small test pits in 1941 and 1942. He started with a first trench (3.5m long, 1.8m wide, 2.5m deep) along the northern wall of the water tank, where he only found mixed sediments also containing modern glass and ceramics (Vicino 1984). He then decided to open a 1.5m deep pit in the talus deposit located between the water tank and the railway tunnel, this time reporting the presence of hearths with layers rich in archaeological material in the bottom 50 cm (Riel-Salvatore et al. 2013; Riel-Salvatore and Negrino 2018a; Vicino 1984). Unfortunately, neither of these test pits were spatially positioned on the site by Cardini, and they could not be identified during recent excavation campaigns. This can in part be explained by the fact that the deposit above the *in situ* Proto-Aurignacian layers was likely much thicker in 1938 than 38 years later when Vicino started excavating them. The hearths described by Cardini could have been found above the Proto-Aurignacian layers or in a zone of the site nowadays made known to be disturbed.

In 1976, a 2x3m pit was excavated by Vicino close to the railway on the site western part, where a pillar was to be erected for the construction of a walkway above the site and the Marseille-Genoa railway. This walkway was, in fact, built to link the Balzi Rossi Museum to the other caves in anticipation of the 1976 *Union Internationale des Science Préhistoriques et Protohistoriques* (UISPP) meetings held in Nice (Riel-Salvatore et al. 2013). This infrastructure project involved tightly scheduled construction steps including building a platform above the brick-walled water tank to install the southern edge of the walkway, clearing dense vegetation from the zone above Bombrini, excavating the area where the pillar was to be erected, and installing the walkway. The work began in April of 1976 and had to be completed before the start of the meeting in mid-September of the same year.

Even though Vicino had to work within a short timeframe, he excavated the Proto-Aurignacian layers using the most fine-grained methods employed at the time, individually plotting every diagnostic artifact (and non-diagnostic bones >10cm) in three dimensions. He excavated in arbitrary 5cm-thick spits (Arabic numerals) within geomorphologically and culturally distinct levels (Roman numerals). Unfortunately, Vicino had to accelerate his work by the time he reached the Mousterian levels. He described having to systematically stop individualizing artifacts to rather collect the sole visible fragments, putting aside all the sediments spit by spit (Vicino 1984).

The 1976 excavations established the importance of the site by exposing a sequence spanning the Late Mousterian and the Proto-Aurignacian, which Vicino immediately linked to the deposit of Riparo Mochi located immediately on the other side of the railway (Vicino 1984). His work revealed that both Upper Paleolithic and Middle Paleolithic levels were rich in artifacts and faunal remains. Two notable discoveries in the Proto-Aurignacian helped put Riparo Bombrini on the map and inspired further work on the site 25 years later, namely the discovery of decorative elements such as an incised bird diaphysis and the discovery of a deciduous modern human incisor (Benazzi et al. 2015; Formicola 1989).

From 2002 to 2005, new excavations were carried out every summer at Riparo Bombrini with the collaboration of the Archaeological Superintendency of Liguria, the University of Pisa (Italy) and Duke University (North Carolina, USA), with the help of the *Museo di Archeologia Ligure* (Genova Pegli, Italy) and of the *Istituto Internazionale di Studi Liguri* (Bordighera, Italy). The team co-directed by F. Negrino, B. Holt, S. Churchill, and V. Formicola conducted four field seasons, intending to better understand the chronological and ecological contexts of the Middle-Upper Paleolithic transition in the region and clarify the stratigraphy exposed in 1976. They extended a trench along the railroad between Vicino's excavation pit and the rock shelter back wall. The 5 square meter trench (squares A1 to EE1) exposed some 1- to 1.5-meter-thick sediment deposits spanning the Proto-Aurignacian as well as a substantial sequence of Late Mousterian. The top Proto-Aurignacian layers were also explored over a surface of 7 m^2 immediately to the south of the trench (squares AA2-EE2, BB3, CC3) and two more square meters to the west of Vicino's excavation pit (squares D1, E1). The deposits were excavated using square meter units with arbitrary spits between 5 to 10 cm thick within distinct sedimentary units. Excavation methods also included the systematic three-dimensional plotting of all diagnostic artifacts (ochre, ornaments, bladelets, lithic greater than 2 cm, faunal remains greater than 5cm) and water-screening of all sediments through 2mm mesh sieves to recover smaller fractions of lithic, macrofauna, microfauna, charcoal, ochre, and shell (Riel-Salvatore et al. 2013).

From 2015 to 2019, five additional excavation campaigns were co-directed by F. Negrino (Università di studi di Genova) and J. Riel-Salvatore (Université de Montréal), with the administrative support from the *Soprintendenza Archeologia, Belle Arti e Paesaggio per la città metropolitana di Genova e le province di Imperia, La Spezia e Savona*, the *Polo Museale della Liguria*, and the *Museo Preistorico Nazionale dei Balzi Rossi*. These new excavations aimed at clarifying the transitional chronology, land-use patterns, subsistence strategies and the spatial distribution of the artifacts inside the rock shelter. The team employed essentially the same excavation methods previously used, implementing minor changes over time. Starting in 2017, the square-meter units were further fractioned into four quadrants (NE, SE, SW, NW), and faunal remains were piece-plotted from 2cm instead of 5 cm, allowing a more refined recording of the spatial distribution of the fragmented fauna. The smaller fraction of coprolites (<1cm) also started to be systematically recovered from the sieved fraction to document the impact of carnivore activities in the rockshelter. In 2018, the team also began to use a total station to allow georeferencing the site and piece-plotting artifacts as well as different archaeological structures.

2.3.2 Chronostratigraphic and paleoenvironmental context

The stratigraphy of the site was mainly reconstructed from the trenches excavated in 1976 and from 2002 to 2005 including all square units corresponding to row 1 (C1 to EE1). The labelling of the different levels was standardized during the 2002-2005 campaigns. After each excavation campaign, post-excavation analysis was systematically conducted by F. Negrino and his team to correlate each spit excavated to one of the identified cultural levels (i.e., A1, A2, MS1, MS2, M1-M7). The archaeological deposits can thus be divided into three macro-units which are further divided into sub-units (here referred to as levels) according to geoarchaeological distinctions:

Macro-Unit A (Proto-Aurignacian): Levels A1, A2, and A3

Macro-Unit MS (semi-sterile Mousterian): Levels MS1, MS2

Macro-Unit M (Late Mousterian): levels M1, M2, M3, M4, M5, M6, and M7

As mentioned in the last section, the 2002-2005 dating program helped clarify the site's chrono-stratigraphy and revealed continuous human occupations of the site spanning the interval 36-45 ky cal BP. The Macro-Units "M" and "MS" thus revealed a very recent Late Mousterian spanning 42-45 ky cal BP overlain by two Proto-Aurignacian "A" levels spanning 42-36 ky cal BP.

Starting at the base of the stratigraphy, Levels M1 to M7 form a 70 cm thick deposit of reddish sediments that get more clayey towards the base. The size of the clastic rocks decreases through Levels M3 to M6. The higher silt proportions in the top Mousterian levels, especially in M4, indicate dryer conditions and aeolian inputs. The silt is then progressively replaced by clay from M5 to M7, indicating progressive warming of temperatures. Palynological and microfaunal data agree with the picture of overall humid and temperate conditions throughout Macro-Unit M with a forested environment primarily comprised of sparse pine trees mixed with oak taxa and a variety of other trees and bushes typical of warm coastal landscapes (Holt et al. 2019).

The Mousterian Levels MS1 and MS2 are separated by an erosional surface from the overlying Levels A1 and A2. They sit on top of Level M1, forming a 30 to 40 cm-thick orange clayey deposit that incorporates large blocks of vault collapse, indicative of colder temperatures and accelerated freeze-thaw events during this period (Riel-Salvatore et al. 2013). The proportionally higher input of clay and Fe-oxides (present throughout Bombrini's sequence) also suggests a slightly higher accumulation of colluvium of *terra rossa* soils (Holt et al. 2019). Furthermore, the presence of an erosion channel along the rockshelter wall suggests episodes of intense but short-duration flow. Palynological and microfaunal data also indicate increasing aridity and cooling. These deposits are comparatively extremely poor in artifacts, but the nature of the lithic assemblage associates these levels with Mousterian occupations.

Level A3 is a 15 cm thick strip of sediment localized immediately against the rockshelter wall, probably having been mostly eroded away. Its content was initially interpreted as an early Proto-Aurignacian because of the occasional bladelets found in its otherwise almost sterile fill. However, the working hypothesis on this level has changed with the latest excavation campaigns and the documentation of slight remixing events along the rockshelter walls associated with water streaming and bioturbation. The bladelets recovered in A3 could be explained by this "rockshelter wall effect," helping these small pieces to percolate from the overlaying Proto-Aurignacian levels.

Finally, Levels A1 and A2 form a yellowish clayey loam deposit varying from 10 to 20 cm thick. Both levels contain rich Proto-Aurignacian assemblages with overlying "cuvette-type" hearths and trash pits. Palynological, anthracological, microfaunal and macrofaunal data all converge to indicate much colder temperatures than in the underlying levels. However, slight internal variations can be detected between the two levels, Level A1 being slightly more mesic than Level A2, the latter corresponding to Heinrich Event 4 (Holt et al. 2019; Riel-Salvatore and Negrino 2018b).

2.3.3 Site organization and mobility strategies

A first general model of shifts in site function, spatial organization and forager mobility strategies reflected in the lithic technological organization at Riparo Bombrini was designed by the analysis of the spatial distribution and density of artifacts in the different levels as well as the study of the nature of the lithic assemblages excavated between 2002 and 2005 (Negrino and Riel-Salvatore 2018; Riel-Salvatore 2007, 2010; Riel-Salvatore et al. 2013; Riel-Salvatore and Negrino 2018a).

Macro-Unit M shows overall patterns of local residential moves. Variability within the lithic assemblages reveals specific mobility changes by Neanderthals through their successive occupations of the site. The denser assemblages, comprising lower proportions of retouched pieces and distinct traces of repeatedly used hearths in Levels M2, M3, M4, and M5, suggest that the site was used as a base camp within a more logistical organization at that time. In contrast, the site might have been used as a base camp employed within residential land-use strategy in Levels M1, M6, and M7 as suggested by the lower density of artifacts with proportionally more retouched pieces (Riel-Salvatore et al. 2013).

The overlying Macro-Unit MS was initially interpreted as a highly ephemeral occupation of the site as suggested by its name, semi-sterile, thought to describe the low amount of archaeological material. However, the 2018-2019 field seasons, while supporting the previous interpretation of short-term occupations, have also revealed the presence of hearth features adjacent to the rockshelter wall. The current working hypothesis suggests that Riparo Bombrini was occupied as a task site or ephemeral residential based camp by the very last Neanderthals in the region, who would have adopted a “hyper-local” subsistence strategy (Riel-Salvatore et al. 2021).

Finally, the Macro-Unit A shows continuous occupations of the site as a residential base camp as suggested by the high density of artifacts and the internal organization of the site. The variability between the two levels in the bladelet production and lithic resource management has been interpreted as the manifestation of changing mobility strategies (*sensu* Binford) in response to this paleoclimatic instability. The colder Level A2 was associated with logistical mobility strategies, whereas the slightly warmer Level A1 was characterized with more residential strategies (Riel-Salvatore and Negrino 2018a).

Chapter 3 – FTIR screening and ZooMS mass-sampling integrated to archaeozoological methods

By definition, archaeozoology is an interdisciplinary discipline. Archaeozoologists analyze the animal remains within archaeological contexts to study the relationship between animals, humans, and their environments (Reitz and Wing, 2008; Steele, 2015; Albarella, 2017). Therefore, the discipline has the potential to address an array of anthropological questions regarding diet, hunting strategies, resource management and intensification, economic and social exchange networks, human demography, human mobility, gender roles, food sharing, social identity, rituals, environmental adaptation, climate reconstruction, site formation, etc. (Reitz and Wing, 2008; Steele, 2015). The development of new technologies has also begun to yield crucial new information on past subsistence behaviours. Among others, biomolecular analyses are increasingly integrated into faunal studies. Isotopes have been at the forefront of biomolecular studies in Paleolithic archaeozoology since they can shed new information on paleoenvironments, patterns of prey mobility, and past human dietary patterns. More recently, collagen fingerprinting (or ZooMS) was introduced as an excellent tool to identify animal species of morphologically unidentifiable skeletal remains (Buckley et al. 2009; Steele 2015).

In a special issue of the Journal of Archaeological Science (JAS) entitled "Scoping the Future of Archaeological Science: Papers in Honour of Richard Klein," Teresa E. Steele emphasized the enormous potential of the ZooMS in her overview of the current methodological questions and innovations in archaeozoology (Steele 2015). She also encouraged fellow archaeozoologists to:

> "[…] not be afraid of ZooMS taking over an important aspect of our discipline, the identification of bones to taxa; instead they should see the method as an opportunity to open up new research questions (Steele 2015:170)."

ZooMS can indeed permit the taxonomic identification of unidentifiable skeletal remains containing sufficiently preserved collagen. If applied with a mass sampling strategy (i.e., 100+ samples), it can improve the NISP's statistical significance. This leaves information about skeletal elements, age, sex, bone burning, and surface alterations to traditional archaeozoological methods. However, provided a well-defined and question-oriented mass-sampling, the full power of the ZooMS fully integrated into an archaeozoological analysis should also improve taxonomic identifications on data relevant to calculate the MNE, improve mortality profiles, and discriminate between carnivore and anthropic bone accumulation.

These methodological aspects will be addressed within the three papers introduced in this research. ZooMS sampling strategies will be discussed alongside the application of full archaeozoological and taphonomic analyses, starting with the identification of the morphologically preserved skeletal remains (taxa, skeletal parts, age, sex, and seasonality indices), followed by the application of quantification methods (NSP – Number of Specimen, NISP – Number of Identified Specimen, MNI (Minimum Number of Individuals, MNE – Minimum Number of Elements, and MAU – Minimum Animal Unit), and the identification of taphonomic processes of bone surface alteration (e.g., burning, cut marks, gnawing, etching, concretion) and fragmentation (fracture angles). All these methods are detailed and discussed within each article.

3.1 Data collection process

The collection studied in this thesis includes samples from all faunal assemblages recovered on the site from 1976 to the most recent excavations from 2015 to 2019. Prof. Fabio Negrino graciously granted full access to the collection curated in his laboratory at the *Università degli studi di Genova*. While there is no osteological reference collection in the laboratory, we benefited from the herbivore and carnivore skull collections curated by Giuliano Doria, director of the *Museo Civico di Storia Naturale di Genova*. Post-cranial skeletal remains were identified using osteological atlases (Barone 1975; Pales and Garcia 1981; Schmid 1972) and three open-source virtual collections: the 3D models provided by the Max-Planck-Gesellschaft Department of Human Evolution (https://www.eva.mpg.de/evolution/downloads.html), the 3D models of the Laetoli project (https://laetoli-production.fr), and the osteological photographic collection of the ArchéoZoothèque (https://www.archeozoo.org/archeozootheque). The logistics of the data collection involved travelling in two foreign countries: first analyzing the fauna, screening with the portable FTIR and sampling for ZooMS in Genoa, and then bringing bone samples to the

Manchester Institute of Biotechnology, where the ZooMS method was applied under the supervision of Dr. Michael Buckley.

The initial plan was to study all the faunal remains recovered at Riparo Bombrini from 1976 to 2018 (Levels A1, A2, MS, M1-M7) and divide the data collection into two phases over two years starting in Fall 2017: the first year would be devoted to studying the Proto-Aurignacian levels, and the following year to the Mousterian levels. However, the first test on ~100 samples from Layer A1 excavated in 2016 showed that the faunal collection was even more challenging than expected. The ZooMS generated negative results on all the samples, demonstrating that collagen did not preserve for proteomic analysis in this part of the site.

Therefore, we dedicated the two years following this first assessment (2016, 2017) to further refine our understanding of the differential preservation of the faunal collection and to the development of a method to screen bone samples for ZooMS (introduced in the next section). The revised plan for 2018 and 2019 aimed to sample faunal assemblages within the different site areas in a first larger-scale archaeozoological analysis on the Proto-Aurignacian levels in Fall 2018. This first data collection resulted in the second article (Chapter 4) and guided the subsequent data of the Proto-Aurignacian and the late Mousterian levels, which was completed in Fall 2019 for the third paper (Chapter 5).

3.2 Article 1 (published) – Portable FTIR for on-site screening of archaeological bone intended for ZooMS collagen fingerprinting analysis

Journal of archaeological science: reports (2019)

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3.3. Abstract

Faunal remains play an important role in helping reconstruct Palaeolithic hunter-gatherer subsistence and mobility strategies. However, differential bone preservation is an issue in southern European prehistoric sites, which often makes morphological identification impossible. Zooarchaeology by Mass Spectrometry (ZooMS) is a new, low-cost method that can improve NISP statistical significance in a replicable way by using diagnostic peptides of the dominant collagen protein as a fingerprint of animal (including hominin) species. It is also a powerful tool to assess collagen preservation for radiocarbon dating. This paper presents the proof of concept of a method for evaluating collagen preservation in a quick and minimally destructive way in the field prior to ZooMS analysis by using a portable Fourier Transform Infrared Spectrometer (FTIR) equipped with an attenuated total reflectance accessory (ATR). The method was tested on faunal assemblages from two north-western Italian sites: Riparo Bombrini and Arma Veirana. Both are important sites for understanding the Middle and Upper Palaeolithic of Liguria but are located in two distinct environmental contexts (coast vs. mountainous hinterland) that impacted collagen preservation. The relative abundance of collagen in powdered bone samples was evaluated by calculating the Amide I to phosphate ratio (CO/P) from spectra collected with two portable and three laboratory-based FTIR instruments. The bones were then analyzed by ZooMS and the results were compared to evaluate the effectiveness of using FTIR as a screening technique. Results indicate that FTIR instruments are excellent tools to predict collagen preservation in fragmented archaeological bones, but a screening method should be first calibrated on the analyzed faunal assemblage by conducting a test of the CO/P screening procedure with various measurement systems on a single FTIR instrument.

Keywords: Collagen fingerprinting, ZooMS, FTIR, Archaeozoology, Taphonomy, Palaeolithic

3.4 Introduction

Faunal remains represent one of the most abundant classes of artifacts recovered in many archaeological and palaeontological sites. The first step to any archaeozoological analysis is the taxonomic identification of skeletal remains that is crucial to calculate all measures of abundance (Number of Identified Specimens – NISP, Minimum Number of Individuals – MNI, Minimum Number of Elements – MNE, Minimum Anatomical Units – MAU, etc.) utilized to study past subsistence behaviours (Grayson 1984; Klein and Cruz-Uribe 1984; Lyman 2008; Marean et al. 2001). Good bone preservation is therefore critical for identifying skeletal elements to their original species through comparative anatomy. However, faunal remains are recovered as fragments due to a wide range of taphonomic processes that originate either in the breakage of fresh bones for their nutrient content by hominids and carnivores (Blumenschine 1988; Faith et al. 2007; Outram 2001) or in post-depositional destructive processes such as chemical weathering, trampling, deposit compaction, and bioturbation (Behrensmeyer 1978; Olsen and Shipman 1988). Whatever its cause, fragmentation reduces the likelihood of obtaining taxonomic information from bone morphology alone.

To address this issue, many alternative methods of taxonomic identification of archaeological bone have been developed. Although there are some non-molecular methods, such as histology (Martiniaková et al. 2007), the most promising are those that use ancient biomolecules for objective identification, particularly ancient DNA (aDNA; Burger et al., 2000) and protein-based methods (e.g., Brown, Douka, et al. 2021; Buckley et al. 2009; Buckley and Kansa 2011; Collins et al. 2010; Stewart et al. 2013; Welker et al. 2015). The latter has grown in popularity since they offer genus/species-level information in most cases; proteins can also survive millions of years beyond the limits of aDNA (in some cases; Rybczynski et al., 2013). This preservation potential is ideal for the timeframe of most archaeological assemblages, particularly those from Palaeolithic sites located in environments known for poor DNA preservation. Another advantage is that the collagen fingerprinting methodology can process large numbers of samples (i.e., in the thousands) at a relatively low cost compared to DNA-based methods (Buckley et al., 2016; 2017). When used for mass sampling, collagen fingerprinting can help find ancient hominin bones among fragmented faunal collections (Brown et al. 2016; Welker et al. 2016). Collagen fingerprinting further constitutes an appropriate screening method for radiocarbon dating collagen (Harvey et al. 2016).

3.4.1 ZooMS Collagen Fingerprinting

Collagen has long been thought to be a biomolecule with a highly conserved primary (i.e., amino acid sequence) structure due to its repeating patterns of the sequence Gly-Xaa-Yaa. This sequence is essential for maintaining the structural role of its triple-helix conformation (Ramshaw et al. 1998), where Xaa and Yaa are most commonly prolines and hydroxylated prolines. However, it has more recently been observed to contain enough differences to be useful for taxonomic separation (Buckley et al. 2009), with a greater number of amino acid substitutions in one of the three chains that make up its helix. These differences were initially employed to study domesticated taxa, including to separate the morphologically similar sheep and goat (*Ovis* from *Capra*; Buckley et al., 2010), but also proved very useful to study a wide range of wild fauna (Buckley et al. 2014; Buckley and Kansa 2011). ZooMS (Zooarchaeology by Mass Spectrometry) collagen fingerprinting is an ideal method because it is based on collagen, which, at more than 25% by dry weight is the most abundant protein in bone (e.g., Buckley et al., 2008), and present at more than 22% by dry weight of modern bone, and therefore has a relatively simple extraction procedure. Collagen can be extracted from a bone sample by adding an acid (e.g., hydrochloric acid or EDTA), or it can be further extracted from an acid-insoluble pellet through heating (i.e., gelatinization). The extracted "collagen" (albeit known to also contain a wide range of low abundance non-collagenous proteins; see Wadsworth & Buckley 2018) is then digested with an enzyme into protein fragments called peptides that are subsequently analyzed by soft-ionization mass spectrometry, usually Matrix Assisted Laser Desorption Ionization Time of Flight (MALDI-ToF) mass spectrometry.

Although ZooMS has been known to work on sample sizes as small as a few milligrams, and even in a non-destructive way (van Doorn et al. 2011; Martisius et al. 2020; McGrath et al. 2019), these approaches are typically applied only to better-preserved material. For more degraded samples, particularly those from sites with differential preservation of organics throughout - a common issue in Palaeolithic sites of southern Europe - these analyses would typically require more destructive sampling (e.g., typically ~25-100 mg). In order to minimize the extent of destructive analysis, especially when considering the potential rarity and/or importance of some specimens, notably those bearing anthropic modifications, a screening method that reduces this damage would be ideal.

3.4.2 FTIR analysis

Infrared spectroscopy measures the vibrational response of molecular bonds to infrared radiation, yielding spectra that are representative of the incident radiation absorption at particular wavelengths (Thompson et al. 2009). In archaeology, Fourier-transformed infrared spectroscopy (FTIR) has been utilized on bones for identifying diverse taphonomic processes, especially bone diagenesis since the technique provides information on both the organic and inorganic components of a sample (Chadefaux et al. 2009; Thompson et al. 2009). Some specific absorption peaks are of interest when considering archaeological bone samples, whether to study bone diagenesis (Dal Sasso et al. 2016; DeNiro and Weiner 1988; Weiner et al. 2007) or heat-induced transformations on bones (Ellingham et al. 2015; Lebon et al. 2008; Thompson et al. 2009, 2013; Thompson 2005). The crystallinity index (CI; reviewed by Thompson et al. 2011, 2013) is most commonly calculated to measure changes in bone microstructure related to heating or degradation over time (when the bone is fresh, the microstructure is less crystalline and less organized with smaller crystallites) (Berna et al. 2004), although some practitioners employ the similar measurement of splitting factor (SF; Weiner and Bar-Yosef 1990). The present study is mostly interested in the absorption peaks that could indicate the presence of collagen in a bone sample. We are therefore looking at the absorbance peaks within the region corresponding to the organic matrix (from 1700 to 1300 cm^{-1}), where two multicomponent peaks are best detectable, Amide I (~1650 cm^{-1}) and Amide II (1550 cm^{-1}) (Dal Sasso et al. 2016). An index generated from the ratio of the Amide I peak height to the height of the peak associated with phosphate (ν_3) has been shown to be a good indicator of potential collagen preservation in archaeological bones (Lebon et al. 2016; Trueman et al. 2004) and will be further investigated in this paper.

The most recent application of FTIR analysis on archaeological bones utilizes straight powders on an attenuated total reflection (ATR) accessory (Chadefaux et al. 2009; Dal Sasso et al. 2016; Le Meillour et al. 2018; Lebon et al. 2016; Marques et al. 2018; Snoek et al. 2014; Squires et al. 2011; Thompson et al. 2009, 2011, 2013; Trueman et al. 2004), instead of the more traditional transmission FTIR mode, in which powder samples are embedded in potassium bromide (KBr). The FTIR-ATR instrument differs from the FTIR-KBr in that it uses an internal infrared beam that is directed onto an optically dense crystal that is physically in contact with the sample. ATR spectra are distorted relative to spectra produced using KBr pellets. Differential depth of interaction between the beam and the sample results in overemphasis of peaks in the lower wavenumbers, and slight shifts in the shape and position of multicomponent peaks. The type of ATR crystal and its optics (e.g., single- versus multi-bounce) also determines the spectral range and the sensitivity of the instrument to different components in a sample. Furthermore, there are differences in sample preparation. Although FTIR-ATR analyses require more bone powder than KBr pellets, FTIR-ATR offers two considerable advantages: it permits quicker analyses (Dal Sasso et al. 2016; Thompson et al. 2009), and it requires fewer additional supplies in a field setting.

Many studies have utilized a portable FTIR in the field to identify primary and secondary minerals in archaeological sediment, detect organic components and evaluate bone diagenesis (e.g., Monnier 2018; Schiegl et al. 1996; Toffolo et al. 2015; Weiner et al. 1993, 2002). The main advantage of a portable instrument has been pointed out by Weiner and colleagues (1993) and Weiner (2010) is that it allows modifying sampling or excavation strategies during an ongoing project, thus saving time and sampling effort, as well as permitting adjustments to the research question, and resolving archaeological problems, according to the taphonomic context.

3.5 Aims

The aims of this study were to evaluate the feasibility of using a portable FTIR instrument equipped with a diamond ATR sampling accessory to screen bone samples on-site whilst conducting an archaeozoological and taphonomic analysis prior to carrying out ZooMS analyses. To do so, we evaluated samples from Riparo Bombrini and Arma Veirana, two Palaeolithic sites located in northwest Italy, measuring the ratio of the Amide I peak to the phosphate ν_3 peak (hereafter CO/P ratio, following terminology provided by Thompson et al. 2013) with two portable and three laboratory-based FTIR instruments and assessing collagen fingerprint quality with ZooMS.

3.6 Materials and Methods

Both Palaeolithic sites considered in this paper are located in the Ligurian region of northwest Italy but are approximately 80 km as-the-crow-flies apart (Fig. 1). They document distinct environmental and taphonomic contexts and different timeframes (Fig. 2, Table 1). Riparo Bombrini documents the transition from Middle to Upper Palaeolithic with Late Mousterian and Proto-Aurignacian layers (45-35 kya) (Riel-Salvatore et al. 2013) while Arma Veirana contains mainly older (>50 kya) Mousterian layers and some Final Epigravettian and Mesolithic deposits (Fig. 2). Archaeozoological analyses are currently conducted on both sites and should be the subject of publications in the near future. Only preliminary faunal results and taphonomic contextualization are discussed in this section.

Figure 1. – Map of Liguria showing archaeological sites sampled for this study (red dots), modern cities (black dots), and main rivers (blue lines). Modified from d-maps.com.

Riparo Bombrini is a collapsed rockshelter part of the Balzi Rossi prehistoric cave complex located within the confines of modern-day Ventimiglia on the Ligurian coast, adjacent to the French border. While first discovered in 1887, most of the excavations were held during the 21st century, making it the only site in the Balzi Rossi entirely excavated with modern methods (Riel-Salvatore et al. 2013; Riel-Salvatore and Negrino 2018a). The taphonomy of the site is quite challenging for faunal analysis; the faunal assemblages from the Proto-Aurignacian levels are almost entirely unidentifiable, and bones from the portion of the collection that is identifiable (<1%) can only be assigned to broad categories such as cervid, caprine or ungulate. The Mousterian layers (still under study) display a somewhat higher proportion of morphologically identifiable bones, although even in these deposits, faunal remains are still very poorly preserved, mostly due to the high degree of fragmentation (mainly dry fractures). Therefore, ZooMS collagen fingerprint identifications offer great promise in this context as an alternative approach to species identification.

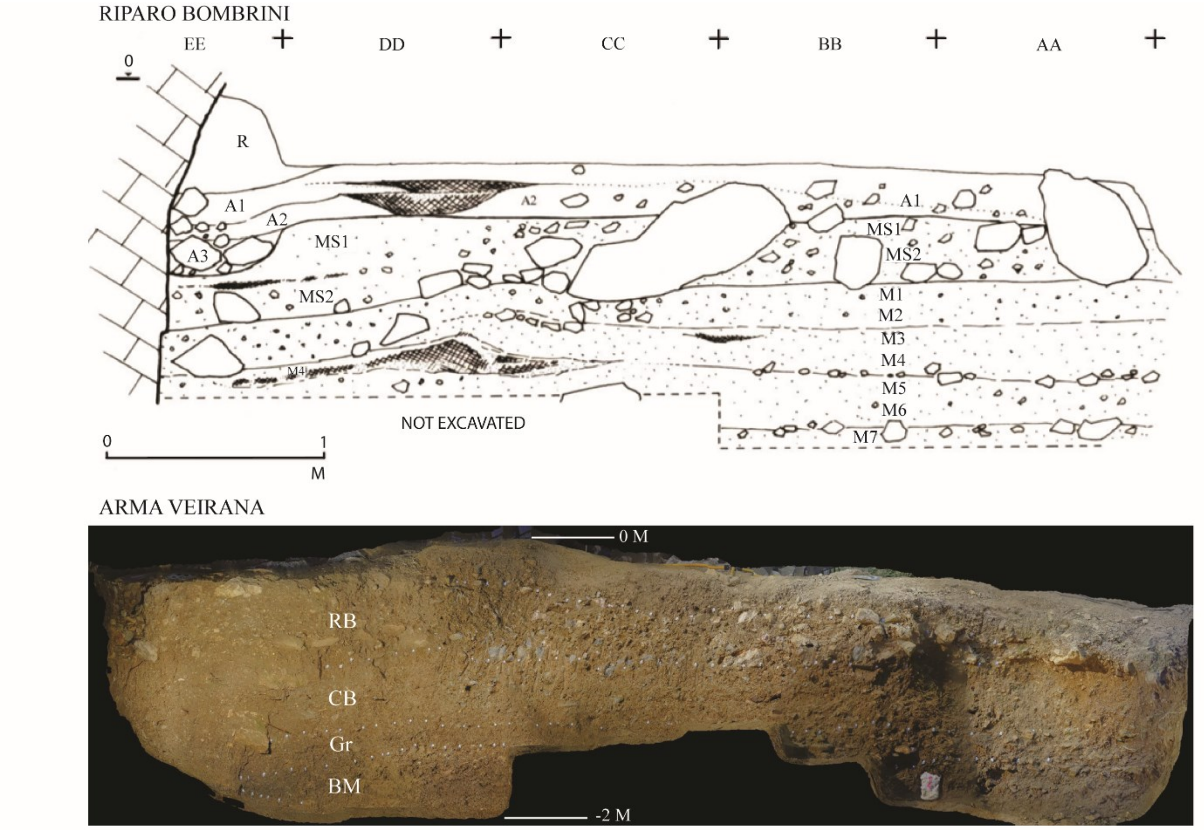

Figure 2. – Stratigraphy of Riparo Bombrini (top), stratigraphy of Arma Veirana (bottom).

Table 1. – The number of samples (N) per layer for each set of bone samples

Site	Layer	Associated industry	Set 1	Set 2	Set 3	Set 4
Riparo Bombrini	A1	Proto-Aurignacian	4	68	-	-
	A2	Proto-Aurignacian	4	69	96	32
	A3	Proto-Aurignacian	2	-	-	7
	A (A1 or A2)	Proto-Aurignacian	9	-	-	9
	MS1 & MS2	Mousterian	2	-	-	-
	M1	Mousterian	3	-	-	-
	M2	Mousterian	3	-	-	-
	M4	Mousterian	8	-	-	-
	M5	Mousterian	3	-	-	-
	M6	Mousterian	2	-	-	-
Arma Veirana	RB	Mousterian?	6	-	-	-

CB	Mousterian?	5	-	-	-
Gr	Mousterian	5	-	-	-
BM	Mousterian	17	-	-	-
		Total: 75	Total: 137	Total: 96	Total: 48

Arma Veirana in contrast, is a large, isolated cave located about 14 km inland from the Mediterranean coast, in a montane region at the border between Liguria and Piemonte, near the towns of Erli and Cerisola. This recently discovered site has been the subject of yearly excavations since 2015 and has yielded very rich faunal assemblages that are much better preserved than those from Riparo Bombrini. However, even with better preservation, the frequency of remains identifiable to a specific taxon is still less than 50% excluding sieving remains. For example, ongoing archaeozoological analyses show that the lowest stratigraphic level currently excavated which is called the "Black Mousterian" – in reference to the dark colour of the matrix and the nature of the archaeological material, is very rich in archaeological and faunal remains with a total number of excavated faunal remains of 552 (piece plotted remains only with no size threshold); within this level 9.6% of the fauna are completely unidentifiable, 63% of remains are identifiable as mammals with the remaining 37% of these identifiable to at least the family level. The above levels (Granular, Compact Brown, and Rocky Brown) are less densely inhabited by hominins and seem to be partly the result of other carnivore occupations, namely cave bear occupations.

All 356 bone samples were randomly selected in both sites' stratigraphy (Table 1) knowingly omitting to considerate the skeletal remains accumulator (carnivore versus human) or any other potential taphonomic processes that could have occurred on both sites. This was done in order to collect a taphonomically unbiased dataset and solely test the screening method in anticipation of future (and ongoing) archaeozoological analyses at Riparo Bombrini and Arma Veirana. Futhermore, most samples were selected in Riparo Bombrini's Proto-Aurignacian layers (bone sets 2, 3 and 4) with the aim of conducting a detailed archaeozoological and taphonomic study with integrated ZooMS sampling of levels A1 and A2. However, considering the very poor collagen preservation in those levels, it would be very risky and potentially not representative of other Palaeolithic sites in Europe to develop a screening method solely based on samples from those two levels at Riparo Bombrini. Therefore, samples from other levels at Riparo Bombrini, and especially from the better-preserved site of Arma Veirana, might come in handy to created and test the screening method for ZooMS.

3.6.1 FTIR-ATR

This study tests five different FTIR instruments (Table 2) for analysis of four sets of bone samples (see Fig. 2 for stratigraphic contexts) under varying conditions (see also Supplemental Information, Table S1) conducted over a period of three years. The first set of 75 samples were analyzed in the field laboratory in Italy using a portable FTIR instrument (Cary 630, Agilent Technologies) with a single bounce diamond crystal ATR accessory (PO1). The instrument was powered by a rechargeable battery pack and was controlled using the MicroLab software package on a laptop computer. Absorbance spectra were collected with a spectral range of 3000-400 cm^{-1}, a resolution of 4 cm^{-1}, and 64 co-added scans. Background measurements were taken every few samples (generally every 60 minutes). The bone samples received minimal preparation beyond drilling. Approximately 1 mg of the powder was pressed against the clean diamond crystal with an anvil and was discarded following measurement. Although the measurements took place inside a building, the setup was intended to simulate expedient analysis on-site. The bone samples ranged in quality, with some retaining moisture from the sediment matrix and others containing mineral contaminants. The quality of resulting spectra likewise varied, with some exhibiting noise in the region of the Amide I peak and others exhibiting additional mineral peaks.

Table 2. – Instrumentation

Instrument name (abbv.)	**Instrument type**	**Manufacturer**	**Spectral range employed**	**Primary measurement conditions**
Cary 630 (PO1)	Portable	Agilent	3000-400 cm^{-1}	Field laboratory, Erli, Italy
Spotlight 400 (LA1)	Laboratory bench	Perkin Elmer	4000-650 cm^{-1}	University laboratory, Manchester, United Kingdom
4500a (PO2)	Portable	Agilent	4000-650 cm^{-1}	Museum, Genoa, Italy

Spectrum 100 with Frontier benchtop (LA2)	Laboratory bench	Perkin Elmer	4000-450 cm^{-1}	University laboratory, Pavia, Italy
Cary 660 with GladiATR (LA3)	Laboratory bench	Agilent, Pike Technologies	4500-400 cm^{-1}	University laboratory, Tübingen, Germany

From the 75 original samples in the first set, 45 were randomly selected for further analyses and comparison using a laboratory benchtop FTIR instrument (LA1) located in Manchester. The analyses were carried out using a Perkin Elmer Spotlight 400 FTIR imaging system and equipped with a diamond ATR accessory within the attached Frontier benchtop unit of the same company. Spectra were collected in transmission format according to the automatic settings of the instrument with a spectral range of 4000-650 cm^{-1}, a resolution of 4 cm^{-1}, and 16 co-added scans. Again, approximately 1 mg of bone powder was pressed against a diamond crystal and background measurements were recollected every few samples.

The second set of bone samples (N=137) was first analyzed on yet another instrument (LA2), a laboratory benchtop Perkin Elmer Spectrum 100 in ATR mode, equipped with a diamond ATR accessory within the attached Frontier benchtop unit and ran with the Spectrum software package. Spectra were collected in transmission format according to the automatic settings of the instrument with a full spectral range of 4000-450 cm^{-1}, a resolution of 4 cm^{-1}, and 64 co-added scans. Background measurements were taken every few samples (also generally every 60 minutes).

A third set of bone samples (N=96) was analyzed with a second portable instrument (PO2) an Agilent 4500a, equipped with a single-bounce diamond ATR and internal battery. Relative to PO1, this instrument has a more limited default spectral range, and thus spectra were collected from 4000-650 cm^{-1}, at 4 cm^{-1} resolution, with 64 co-added scans.

Re-analyses were conducted on the first three sets with PO1 and PO2, and with a fifth instrument (LA3) a Cary 660 (Agilent) laboratory bench instrument equipped with a GladiATR Vision (Pike Technologies) single bounce diamond ATR accessory. The spectra from this instrument were collected over a spectral range of 4500-400 cm^{-1}, a resolution of 4 cm^{-1}, and with 32 co-added scans. From the first set, an additional 20 bones were analyzed using PO2 and LA3, from the second set, 13 bones were analyzed a second time using PO2, and from the third set, 42 bones were analyzed in duplicate using PO1 and LA3.

Finally, a fourth set of bone samples was first analyzed using instrument PO2 (N=48), and 47 of these samples were reanalyzed using both PO1 and LA3.

3.6.2 Spectral processing

The 356 spectra from the four sets of bones and all five instruments were exported in the Grams spectral format (.spc), compiled into multispectral documents, and processed using the Resolutions Pro (Agilent) software package. A total of 30 spectra were discarded prior to processing due to strong noise in the region of interest, peaks indicative of burning, or significant contamination from other minerals. The spectra from LA1 and LA2 were converted from transmittance to absorbance format. Peak height and area measurements were conducted within the Resolutions Pro software. Although available, ATR correction algorithms were not applied. The results were then exported to Microsoft Excel for calculation of the CO/P ratio.

Several different systems have been previously reported for the measurement of collagen in bone using FTIR-ATR. Lebon et al. (2016) employed an index based on the ratio of the area under the Amide I peak to the area under the phosphate ν_3 peak. Thompson et al. (2013) calculated the roughly equivalent CO/P index, which is the ratio of the peak height at 1650 cm-1 to the peak height at 1035 cm-1. Twelve different measurement systems were tested here in order to identify one or more measurement systems that could be best applied to spectra collected on different instruments and with varying amounts of noise and mineral contamination. The measurement parameters are listed in the Supplemental Information (Table S2) with examples illustrated here in Figure 3.

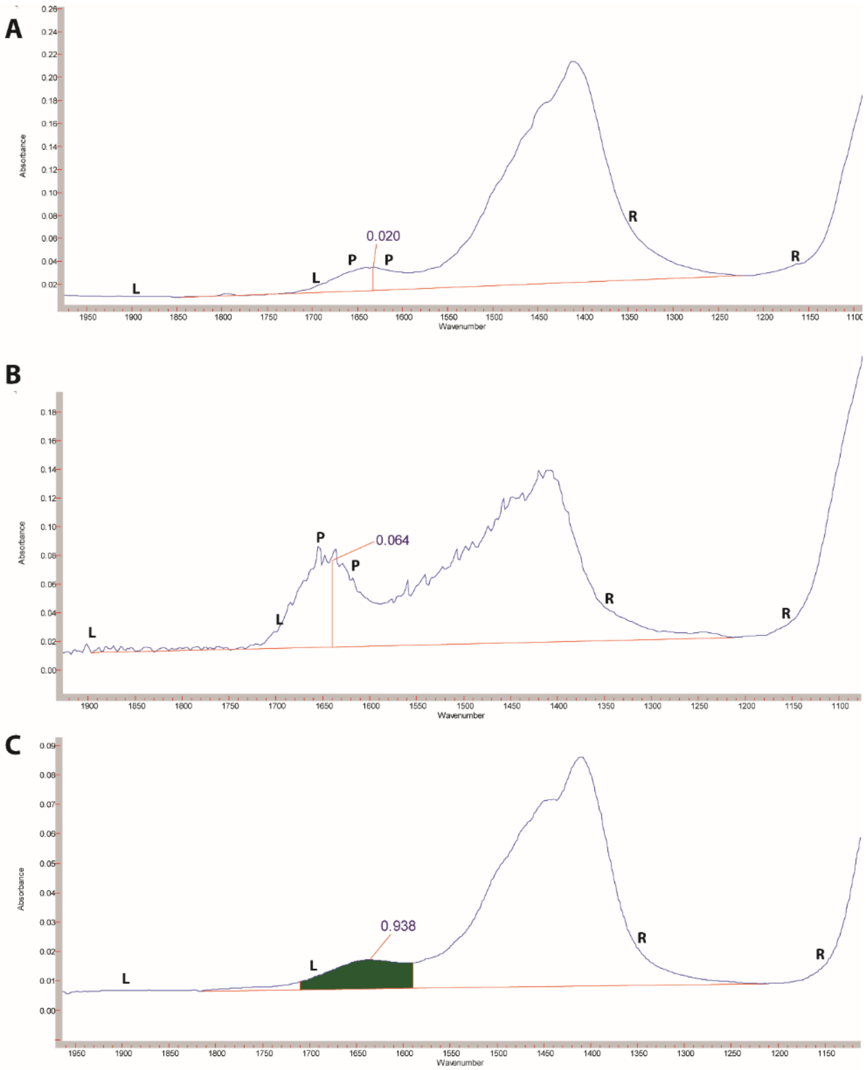

Figure 3. – Examples of three types of measurement systems. A) A peak height measurement. The baseline is drawn between the lowest value between two points on the left (L) and two points on the right (R). The height is the highest value between two points (P) and the baseline. B) An average height measurement on a spectrum with noise in the Amide I region. The height is an average value between two points (P). C) A peak area measurement. The area is bounded by the spectrum trace, the baseline, and two vertical lines defined at fixed points on the x-axis.

The measurement systems can be grouped into three types: (1) those based on absolute peak height, (2) those based on average peak height, and (3) those based on peak area. Baselines were drawn for each peak from either the lowest point between the two values to the left and right of the peak, or from absolute values. The phosphate ν_3 peak (P) was defined between 1025 and 990 cm^{-1}. The Amide I (CO) peak was defined between 1655 and 1625 cm^{-1}. Due to distortion from the ATR, these positions are equivalent to peaks measured in KBr spectra at 1035 and 1650 cm^{-1}, respectively. Following the application of the different systems, some spectra were discarded due to extremely sloping baselines that yielded negative measurements.

3.6.3 ZooMS collagen yield calculations and fingerprint analysis

A total of 260 bones from the first, second, and fourth set of samples were analyzed with ZooMS. Approximately 25 mg was demineralized with 1 mL 0.6 M HCl overnight. Following centrifugation at 12,400 x g for 1 min, the acid-soluble fraction was ultrafiltered into 50 mM ammonium bicarbonate (ABC) with two exchanges and recovered with 100 µL. This was digested with trypsin overnight and then spotted with alpha-cyano hydroxcinnamic acid matrix following Buckley et al. (2016, 2018). The acid-insoluble pellet of the first set of 75 samples was also heated for 3 hours at 75°C and likewise digested with trypsin overnight, and the digests prepared for MALDI following Buckley et al. (2009) but only collecting a 50% acetonitrile fraction. Animal species identifications were made using the collagen peptid markers listed in Table 3.

Table 3. – Collagen peptide markers (m/z) in this study (Buckley et al. 2009, 2017)

Taxa	**2t85(A)**	**2t43(B)**	**2t69(C)**	**2t69(D)**	**2t41/42(E)**	**1t55/56(F)**	**2t67(G)**	**2t76**
Ursus	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A
Bos/Bison	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A
Capra	1196.6	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A
Cervus	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A
Capreolus	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3059.4	N/A
Rangifer	1166.6	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A
Equus	1198.6	1427.7	1550.8	2145.1	N/A	2883.4	2999.4	N/A
Alopex	1226.6	1453.7	1566.8	2131.1	N/A	2853.4	2999.4	1548.8

*Avian markers *(m/z)* from Buckley et al. (2009): 1035.6, 1307.6, 1319.8, 1463.1, 1507.9, 1522.9, 2108.1, 2212.1, 2252.1, 2850.5, 3097.5, and 3113.5.

A collagen yield was calculated on the first set of 75 samples using sample weights, before and after collagen dissolution in HCl to calculate a simple mass fraction of relative collagen content. Raw bone powder was weighted using a scientific numeric scale before collagen dissolution and was dry frozen for second weighing.

3.6.4 Screening test

Testing a screening method required comparable data from ZooMS as a proxy for collagen quality so they could be further compared with CO/P ratios. To do so, we extrapolated three scores describing three levels of ZooMS identification success corresponding to different values of presence and quality of collagen in every sample: a score of 0 was assigned when no good collagen fingerprint was obtained, a score of 1 was assigned when some peptide markers were absent making it impossible to fully identify the taxa (e.g., unable to distinguish between reindeer and ibex, or assigned to a broad category such as ungulate), and a score of 2 was assigned to the best preservation state that permitted species-level identifications for the technique (Fig. 4). For the first set of samples, the soluble and insoluble pellets were combined to create the scores and the lower score of the two was kept (for details, see Table S4, S5, and S6 in Supplemental Information).

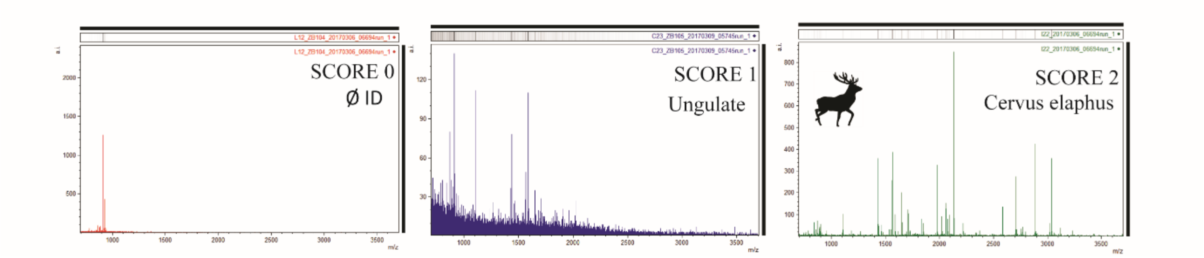

Figure 4. – MALDI-ToF mass spectra from tryptic digests of sample extracts corresponding to the three "identification" scores 0, 1 and 2, meaning a clear lack of collagen, a poor but obvious peptide signal, and a good quality collagen fingerprint respectively.

Box plots and statistical tests were run through Past3.14 software. One-way ANOVA tests were a best fit to compare the three scores to our potential collagen preservation indicators (i.e., CO/P ratios). However, the different sets of samples did not all satisfy all the conditions for a parametric test (i.e., minimum of 20 samples, curve normality, and equal variance). The non-parametric equivalent of ANOVA, Kruskal-Wallis, was therefore applied in those cases to test the significance of the difference between sample medians. The null hypothesis for each Kruskal-Wallis test was that there was no difference between ID scores 0, 1, and 2 when comparing the medians of their respective collagen yield or CO/P ratios.

A first test was done comparing the collagen yields obtained from the first set of samples. Then, a series of twelve tests for each measurement system was performed including all 260 spectra obtained from the different FTIR instruments. The same series of tests was further applied for each individual instrument: PO1, PO2, LA1, LA2, and LA3.

The ZooMS identification success rate before (i.e., initial Success Rate: SRi) and after (SR) screening with the FTIR was then calculated for the twelve measurement systems, again with all instruments combined, as well as for each individual instrument. To do so, the 75th percentile of ID score 0 was used as a theoretical screening threshold. To help further discussion, CO/P thresholds were also converted in weight percentage content (wt%) of collagen following this formula published by Lebon et al. (2016): collagen wt%=113.13 Amide I/PO_4+1.69. After eliminating all CO/P values under this threshold, the SR was calculated as follows: SR= (Score1+Score2)/(Score1+Score2+Score3)*100.

Finally, the SRi, the SR, the collagen wt% and the p-values from the Kruskal-Wallis tests helped select and evaluate which measurement system(s) was best fitted to each FTIR instrument to obtain the best screening method.

3.7 Results

3.7.1 ZooMS collagen fingerprint quality

ZooMS results for Set 1 showed very promising rates of successful identification for both sites, even at Riparo Bombrini where the bone preservation is extremely poor. 50% of the bones from Riparo Bombrini were assigned scores of 1 or 2, whereas 85% of the samples from Arma Veirana were assigned those scores (Fig. 5). However, Set 2, which like Sets 3 and 4, only comprises samples from Riparo Bombrini, yielded much less successful identifications with only 23% being assigned a score of 1 or 2. Finally, Set 4 showed the best collagen preservation at Riparo Bombrini with 68% of the bones assigned to scores 1 or 2. Set 3 was not analyzed with ZooMS and was therefore only included in the comparison between FTIR instruments. Overall identified taxa comprise red deer (*Cervus elaphus*), bear (*Ursus*), bovine (*Bos/Bison*), horse (*Equus*), wild goat (*Capra*), Roe deer (*Capreolus*), birds, cervids, and ungulates (Fig. 5).

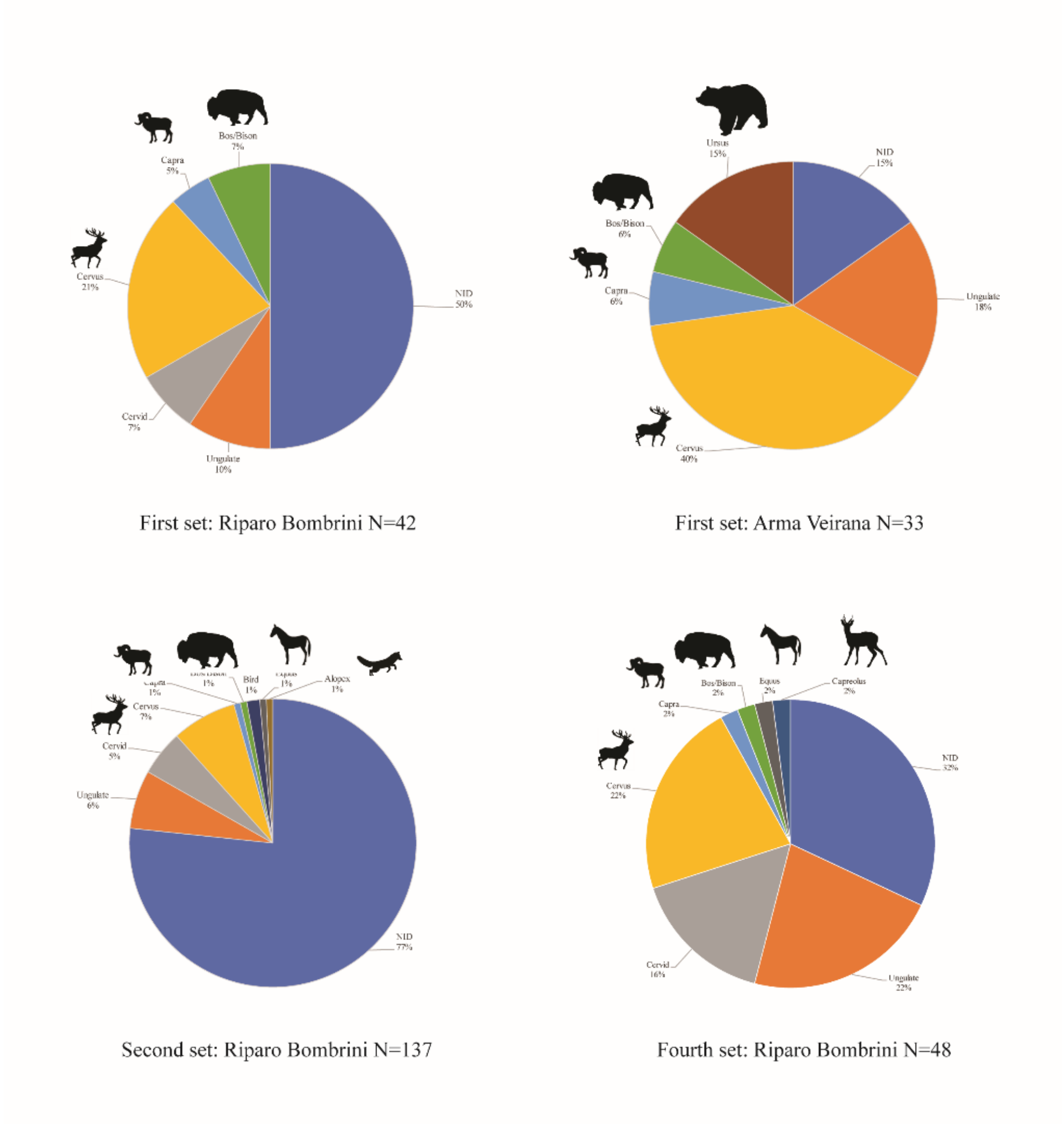

Figure 5. – Pie charts of faunal identifications with ZooMS of the first set of samples (Riparo Bombrini on the top left, Arma Veirana on the top right), the second set of samples (bottom left), and the fourth set of samples (bottom right). NID= Non-Identifiable (ID score 0) NB: the third set of samples was not analyzed with ZooMS.

3.7.2 ZooMS ID scores against yield and CO/P ratios

Both collagen yields and CO/P ratios should theoretically provide independent measures of collagen quantity in each sample, but the Kruskal-Wallis test on collagen yields revealed no significant difference between the ZooMS ID score medians (N=75, p=0.1614) (Fig. 6). However, we note that the yield results should be considered with caution because it is difficult to obtain reliable weight measurements from such small bone samples (20 mg or less). We would therefore recommend using samples of more than 50 mg when possible to calculate collagen yields.

On the other hand, all Kruskal-Wallis tests on CO/P ratios (except the ones produced with LA3: $p>0.05$, $N=65$) showed significant differences between the ID score medians, indicating that a sample's CO/P ratio appears to predict its collagen preservation. Table 4 shows the results from three measurement systems representing the three types of measurement systems: N absolute peak height, Q average peak height, and R peak area. The results obtained with all 12 measurement systems are summarized in the Supplemental Information (Table S7 and S8). Furthermore, the results from one of those systems (i.e., measurement N with PO2) is shown in a box plot (Fig. 7) to better illustrate the threshold selection process. In this figure, the red area shows that most of the samples that are poor in collagen (score 0) will be discarded with the selected threshold, and a few good samples (scores 1, and 2) will be discarded as well. From Table 4, one can observe that the SR vary considerably between instruments: from 76% to 94% SR for PO1, PO2, LA1, LA3, and ~45% SR for LA2.

Figure 8 presents in box plot form 35 samples analyzed in triplicate with instruments PO1, PO2, and LA3 to illustrate the variation between CO/P ratios according to the instruments used to collect the spectra which will also influence the selected threshold, here illustrated at the 75th quartile or score 0 for each instrument.

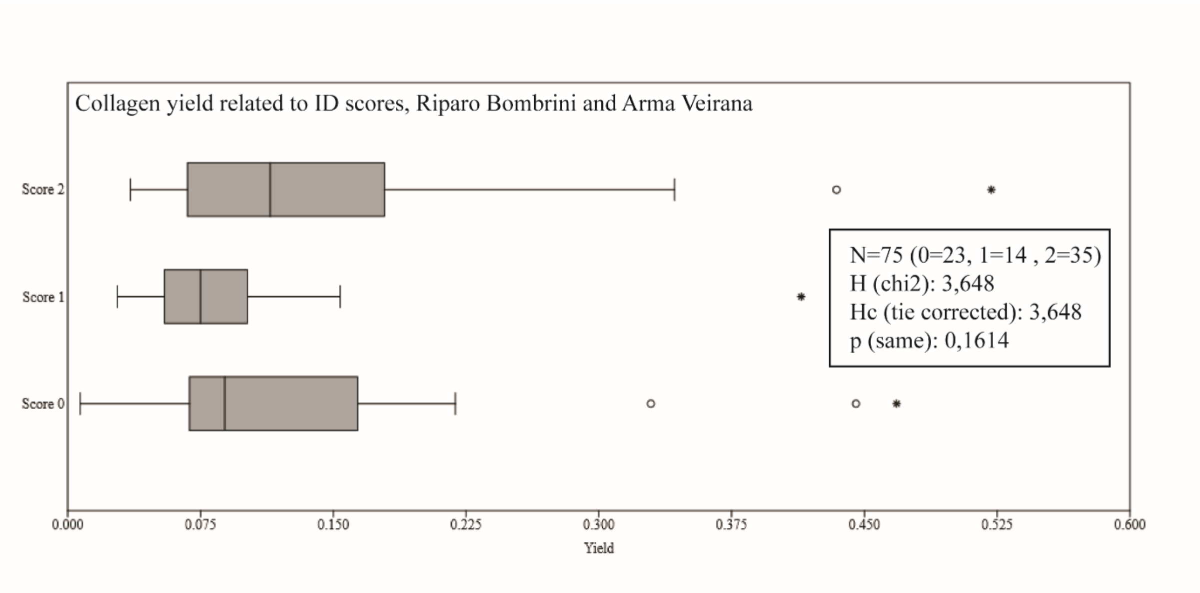

Figure 6. – Box plots representing collagen yield related to ID scores for the first set of samples, and Kruskal-Wallis test for equal medians.

Table 4. – Three measurement systems (N ,Q, and R) illustrating each measurement system types (height, averaged height, and area) tested on the fivel FTIR instruments (PO1, PO2, LA1, LA2, and LA3) including the number of samples (N), p values from the Kruskal Wallis tests (p), the selected threshold (Th), the threshold's associated collagen weight percentage content (Wt%), the initial ZooMS identification success rate (SRi), and the ZooMS identification success rate after applying the screening method (SR). The results of Measurement system N with PO2 is highlighted in red to indicate that it is further illustrated in Fig. 8 as an example.

Instrument	M.syst.	N	p	Th	Wt%	SRi	SR
PO1	N (height)	104	0.002042	0.05	7.83	63%	78%
	Q (a. height)	104	0.002577	0.05	7.56	63%	80%
	R (area)	104	0.008321	0.04	6.33	63%	76%
PO2	N (height)	86	0.000161	0.04	6.42	72%	88%
	Q (a. height)	87	0.000148	0.04	6.32	72%	89%
	R (area)	85	0.000106	0.03	5.32	72%	88%
LA1	N (height)	47	6.27E-05	0.03	5.10	68%	87%
	Q (a. height)	47	5.87E-05	0.03	5.10	68%	87%
	R (area)	47	0.000215	0.03	4.74	68%	90%
LA2	N (height)	131	2.85E-06	0.03	5.04	27%	49%

	Q (a. height)	130	4.64E-06	0.03	4.93	28%	53%
	R (area)	123	3.4E-05	0.02	4.19	29%	40%
LA3	N (height)	65	0.2082	0.05	7.35	75%	83%
	Q (a. height)	64	0.07743	0.05	6.87	75%	94%
	R (area)	63	0.06697	0.03	5.65	75%	79%

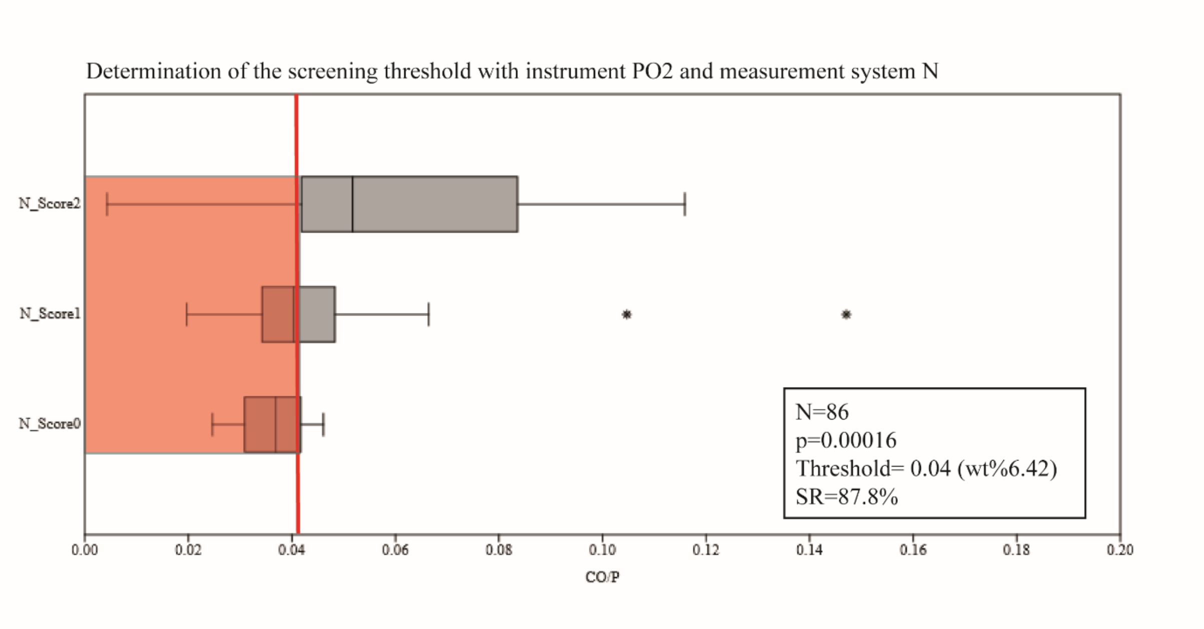

Figure 7. – Box plots illustrating an example of the determination of a screening threshold (red line) for selecting ZooMS samples with a portable FTIR (measurement system N with PO2). The red area represents discarded samples for ZooMS.

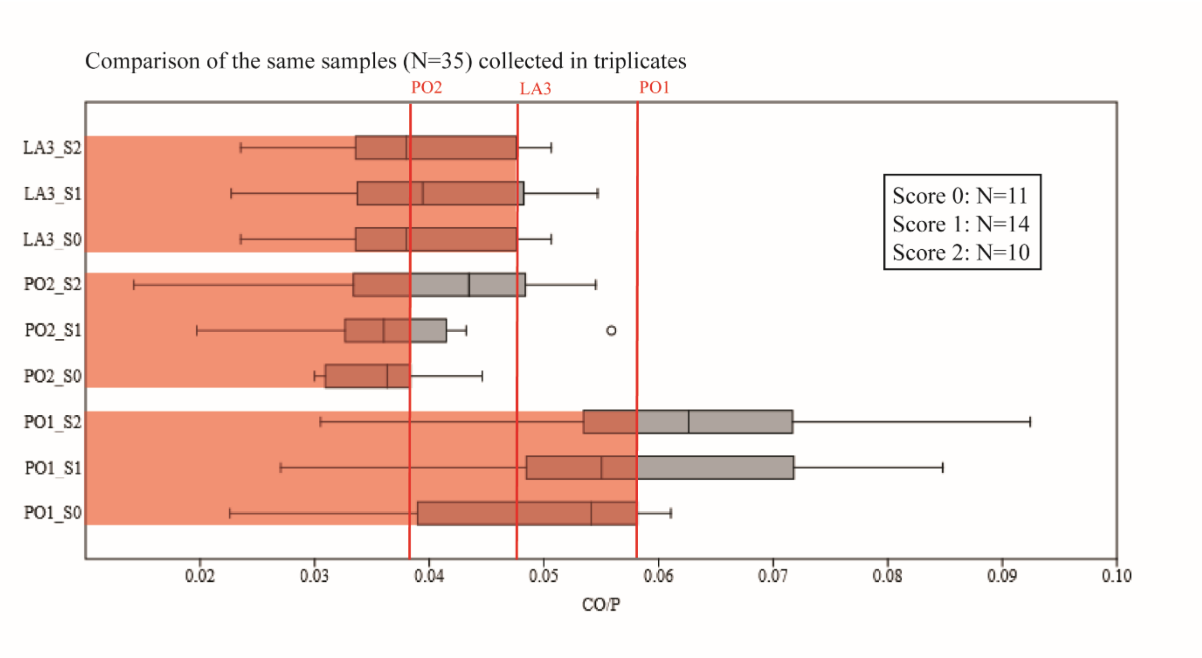

Figure 8. – Box plots illustrating the variation between CO/P values from samples collected in triplicates with three FTIR instruments (PO1, PO2, and LA3), their associated identification scores (S) 0, 1, 2, and the different thresholds that would be attributed for each instruments. The red areas represent discarded samples for ZooMS.

3.8 Discussion

3.8.1 Taphonomy, Faunal spectrum, Riparo Bombrini and Arma Veirana

The faunal identifications presented above are in themselves very encouraging, since they show that ZooMS can be successful even in the most challenging taphonomic contexts. Although the samples were randomly selected throughout the stratigraphy, the identified faunal spectra from both Riparo Bombrini and Arma Veirana match well the expected diversity of the big game commonly found in Liguria throughout the Middle Palaeolithic and early Upper Palaeolithic (Negrino and Riel-Salvatore 2018; Riel-Salvatore and Negrino 2018a). As expected, red deer dominates both assemblages which is consistent with observations of their natural abundance in the region during this timeframe (Valensi and Psathi 2004). That said, collagen preservation seems very variable, especially at Riparo Bombrini. Even within this poorly preserved context, a breadth of animal species was identified from bone fragments smaller than 1cm, including a number of small animals (two birds and one arctic fox). This is encouraging for similar contexts in Palaeolithic archaeology in which the ZooMS technique appears, then, to hold considerable promise.

3.8.2 Comparing ZooMS fingerprint quality with Portable FTIR screening

The ability to predict ZooMS success with CO/P and not with the collagen yields calculated from the acid dissolution could either indicate that the yields are problematic or that the CO/P measurement is influenced by the state of collagen preservation in addition to its relative quantity (e.g., cross-linking). The latter cannot be assessed without performing further yield analyses to compare actual collagen content and CO/P ratios, an exercise which is beyond the scope of the present study.

However, the works on which this study builds (Lebon et al. 2016; Trueman et al. 2004) had already demonstrated the ability to predict collagen content based on CO/P ratios. Lebon and colleagues (2016) for instance, used two proxies known to predict collagen content in archaeological bones: the weight percentage content (wt%) of nitrogen (N), and the carbon to nitrogen ratio (C:N). Their method was successful for archaeological bones with relatively good preservation as they were able to predict collagen content with CO/P ratios when bones contained ~4 ±1.2 wt% of collagen. However, regarding the variability of collagen diagenesis, collagen content does not necessarily imply collagen quality, which is what is critical for stable and unstable isotopic analyses, and to some extent also DNA analyses (although see Wadsworth et al. 2017 demonstrating poor link between protein and DNA survival). Therefore, instead of using a proxy of absolute content, such as the wt%N, we used the ZooMS collagen fingerprint as a direct proxy for collagen quality, as it is already known to be a good screening method for radiocarbon dating (Harvey et al. 2016). Our results thus lend considerable support to Lebon et al.'s hypothesis that the CO/P ratio is not only correlated with collagen content, but also with its preservation (i.e., its quality) in archaeological bone samples. In further agreement with their conclusion, ZooMS identifications are generally successful above ~4wt% of collagen. However, it is not possible to compare CO/P ratios (and their associated wt% collagen calculations) in order to make interpretations about absolute collagen content, since there is considerable variability in the measurements conducted on the same samples across different FTIR instruments (Fig. 8). Furthermore, although quantitative analyses are possible using FTIR under specific measurement conditions (e.g., gasses in fixed pathlength cells), only semi-quantitative results are possible using ATR measurements on solids.

3.8.3 Adapting the screening method to the faunal collection and the FTIR instrument

A few observations can be made from Table 4. First, the success rates calculated after screening with FTIR are quite different between instruments, varying from a low 40% SR with LA2, to 90% SR with LA1. However, if we compare each SR to their respective SRi, all instruments help improving the ZooMS identification by 10% to 25%. The variable success rates are therefore probably best explained by the variability in collagen content from the different sets of samples (mostly < 4wt% in the fourth set of samples measured with LA1). Second, as shown in Figure 8, the different FTIR instruments will produce slightly different spectra which will influence the resulting CO/P ratio calculations. However, our calculated “success rate” should not in any way be interpreted as an indication of which instrument is better than another. The success rate is merely the reliability of using the 75th percentile as a cut-off to predict the outcome of ZooMS results. For some instruments, the LA3 for instance (Fig. 8), a different measurement system must be developed and perhaps a different cut-off might also be more appropriate.

Considering those observations, it appears that it is impossible to create a universal screening method for ZooMS with a fixed threshold. This implies that the first step of any ZooMS screening method should first be tested on a collection with the same instrument. The archaeozoologist who wants to screen samples for ZooMS would thus need to calibrate the method on site by first conducting a test of the CO/P screening procedure with various measurement systems. Based on our experience with the Riparo Bombrini material which was reported here, we recommend testing at least 200 bone fragments of unknown collagen quality in order to account for the now documented fact that surprises and preservation irregularities can occur even within a single faunal collection. Alternately, if ZooMS analyses were already performed on a collection in the past, it may be possible to calibrate an instrument using analyses on a smaller population of bone fragments with known variability in collagen quality (i.e., equal distribution of ID scores 0, 1 and 2). For example, one could choose 20 samples attributed to score 0, and the same amount attributed to scores 1, and 2, and then calibrate the screening method based on those reference samples.

Given the inter-instrument variability in measurement, another option would be to run the bone samples with a KBr instrument, since FTIR-KBr instruments generate less distortion to the spectra than ATR crystals, making it easier to compare the results obtained from different instruments. That said, the concept introduced in this paper aims to build an on-field screening method for ZooMS. Although portable FTIR-KBr instruments have been successfully used in field conditions in the past (Weiner et al. 1993), we consider that a portable FTIR-ATR instrument is more appropriate to screen for ZooMS, especially when mass sampling hundreds of bone fragments. This is because, contrarily to KBr, ATR can process samples more rapidly and because it does not require additional material to travel with (sometimes in the plane when archaeological projects are overseas) such as heat lamps, pellet press die holders, and measuring supplies. With FTIR-ATR, all one needs is the instrument (the size of a lunch box), a battery pack (if not integrated in the instrument), a laptop or mobile device to generate the spectra, grinding tools (a hand-sized scientific mortar and pestle), and a cleaning solution (hydrochloric acid, deionized water, or acetone) to clean the mortar and pestle between each sample. As a screening method, it would thus be easy to use anywhere, whether in a field laboratory with basic facilities or in a proper archaeozoology laboratory where bones can be sampled while taphonomic and archaeozoological analyses are being conducted.

3.8.4 Towards ZooMS sampling strategies in archaeozoology

In this paper, we have demonstrated that FTIR analyses can be utilized on site to identify better preserved bones and to help develop successful sampling strategies for ZooMS. With the increase in popularity of the ZooMS collagen fingerprinting approach to species identification within archaeology and palaeoanthropology, especially with mass sampling (Buckley et al. 2016), we urge the need to explicitly discuss appropriate sampling strategies. While most recent applications of the ZooMS in Palaeolithic archaeozoology have been mainly focused on justifying the usefulness of the method as a complementary tool to traditional archaeozoological and taphonomic analyses (Buckley et al. 2017), or on finding new hominin bone fragments (Brown et al. 2016; Welker et al. 2016), future studies should consider the relevance of analyzing an entire faunal collection with ZooMS. Although such a strategy would in theory give us a better representation of the faunal diversity at a site, sampling the entire collection would not resolve a certain number of problems common to archaeozoology as a whole. For instance, collagen fingerprinting cannot help in identifying anatomical parts essential to calculate the Minimum Number of Elements (MNE) and therefore does not seem particularly well-suited, at least at this stage, to help address questions related to behaviours like carcass transport or butchery practices. A prior archaeozoological analysis is essential to assess those questions. Consequently, a sampling strategy for ZooMS must be set according to the research question. In fact, by utilizing ZooMS to identify animal species, we do not aim to replace the traditional archaeozoological and taphonomic analyses, but rather to complement and rethink those crucial steps in faunal analyses.

We think it is essential to point out some examples of sampling strategies for ZooMS as an opening discussion towards integrating collagen fingerprinting into mainstream archaeozoological and taphonomic methods. Equifinality is one of the most discussed problems related to bone fragmentation in faunal analysis, as it causes difficulties in distinguishing the causal mechanism of two or more surface modifications (e.g., trampling vs cut marks), the identification of skeletal parts when too fragmented, and the differentiation between animals of similar sizes (Munro and Bar-Oz, 2004). The latter is of great interest in archaeozoology, particularly when calculating the MNE. Numerous methods already exist to tackle this problem such as using diagnostic landmarks on bone elements and refitting bone shafts (Marean et al. 2001; Morin et al. 2017a; Stiner 1994). ZooMS can help refine these methods, but only if it permits the adoption of a more appropriate sampling strategy, such as selecting anatomically identifiable bone fragments that are morphologically identifiable, but taxonomically indistinguishable because of their close body sizes.

Another prominent taphonomic problem in archaeozoology is differential skeletal survivorship depending on bone density, animal size, and age (small animals and young ones have more friable bones), which is often the cause of phenomena such as density mediated attrition and the underrepresentation of smaller species, and of fetal and juvenile individuals (Behrensmeyer 1978; Brain 1981; Lam et al. 2003; Lyman 2008; Marean 1998; Stiner 2002b). Differential skeletal survivorship can thus heavily distort the interpretation of human subsistence behaviours when considering seasonality indices, mortality profiles, and skeletal representation. Adopting a mass sampling strategy with ZooMS offer a great tool to help tackle this problem by allowing researchers to select a wide range of bone fragments with different cortical thicknesses to ensure a better representation of faunal diversity and mortality curves. Unfortunately, mass sampling with ZooMS does not guarantee that we are not sampling one animal multiple times which could distort the Minimum Number of Individuals (MNI), hence the importance of integrating ZooMS identifications within the entire range of tools used to reconstruct faunal exploitation strategies and of constantly reevaluating our tools to measure faunal abundance (NISP, MNI, MNE, MAU, etc.).

3.9 Conclusion

In sum, the data presented in this study provide further confirmation that CO/P ratios are reliable proxies for predicting collagen preservation. They therefore represent a promising avenue for the use of portable FTIR instrument as an in-field screening method for ZooMS collagen fingerprinting, provided that the method is first tested on a site-by-site basis with various CO/P measurement systems and a proposed minimum of ca. 200 bone samples to determine the taphonomic context of given faunal assemblages. Although the ZooMS technique is a particularly low-cost analytical method, there are clear examples where such a screening technique could be particularly interesting to researchers, whether due to specimen importance and/or the practicalities of sampling in different countries.

As mentioned above, an on-site screening tool such as the portable FTIR can also help assess stratigraphic integrity while the excavations are being conducted, identify archaeological features (e.g., combustion structures) and eventually tailor the sampling strategy as a result of data accumulation during ongoing fieldwork. Working with such an instrument while conducting archaeozoological and taphonomic analyses has now also been shown to be particularly useful, since FTIR can complement traditional taphonomic methods to assess diagenesis and the burning stages of bones. Weiner (2010) makes the case for the importance of a well-equipped field laboratory for on-site analysis, and our results strongly support this call to arms. In such a set-up optimized for archaeozoology, the bone samples can be first tested with FTIR, then drilled to obtain enough powder to divide into subsamples for ZooMS and other specialized analyses. This helps minimize the number of samples that export permits may be required for, and further reduces the chances of sample contamination during transport or storage.

3.10 Acknowledgements

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3.11 References

(References are grouped in the Bibliography)

3.12 Supplemental information

(See Appendix 1)

Chapter 4 – First analysis of the Proto-Aurignacian

This second paper aimed to test the application of the FTIR screening method and to apply the ZooMS to the archaeozoological and taphonomic analysis of the Proto-Aurignacian levels at Riparo Bombrini.

4.1 Article 2 (published) – Archaeozoological, Taphonomic and ZooMS Insights into The Proto-Aurignacian Faunal Record from Riparo Bombrini

Quaternary International Special issue (2020)

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4.2 Abstract

Human adaptation to climatic variations is being discussed at different scales and from diverse perspectives and specializations in Paleolithic archaeology. We suggest examining human mobility on the local scale through the faunal record to better understand human-environmental interactions during the early dispersal of anatomically modern humans along the Mediterranean coast. Riparo Bombrini is located in the renowned Balzi Rossi complex in Northwest Italy. The site offers an excellent opportunity to compare two distinct Proto-Aurignacian levels yielding well-documented and well-dated deposits. Previous studies of spatial, lithic, and raw material data from these two Proto-Aurignacian levels have revealed distinct mobility signatures as well as undeniable evidence for the resilience of the Proto-Aurignacian technocomplex during episodes of climatic instability including the HE4 event, circa 40ka cal BP. The highly fragmented nature of the animal bones at the site warrants the application of the ZooMS (Zooarchaeology by Mass Spectrometry) collagen fingerprinting technique. For this research we carried out taphonomic and archaeozoological analyses with integrated systematic ZooMS using a mass sampling strategy. The results suggest stability in hunting strategies over time in spite of the apparent shift in mobility strategies from Level A2 to Level A1 at Riparo Bombrini.

Keywords: Proto-Aurignacian, Early Upper Palaeolithic, hunting strategies, Paleolithic archaeozoology, taphonomy, ZooMS, Riparo Bombrini, Italy

4.3 Introduction

The Proto-Aurignacian technocomplex has long been thought to be one of the earliest cultural manifestations associated with the dispersal of anatomically modern humans along the Mediterranean coast. Numerous debates are still ongoing about the origin and the nature of the Proto-Aurignacian in Western Europe. Surprisingly, despite the relevance of subsistence to understand mobility strategies, complete and detailed archaeozoological analyses are very rare for Proto-Aurignacian or coeval assemblages (including other denominations such as Archaic Aurignacian, Aurignacian 0, Initial Aurignacian, etc.) (Pike-Tay et al. 1999; Soulier 2013, 2014). This implies that early anatomically modern humans' mobility and land-use strategies associated with Proto-Aurignacian assemblages in Western Europe have largely been discussed on the basis of the information available from lithic technology and raw material procurement alone. To the extent that they are presented, archeozoological data have mainly been used to provide some degree of environmental context or baseline information on subsistence strategies, with little attention paid to other behavioural dimensions they can shed light on (Brugal et al. 2017; Holt et al. 2019; Porraz et al. 2010; Riel-Salvatore and Negrino 2018a; Tomasso and Porraz 2016). However, it is now well established that faunal resources can hold a determinant place in hunter-gatherer's technological changes and mobility strategies (Burke 2006a, 2006b; Costamagno et al.

2006; Delagnes and Rendu 2011; Gaudzinski 2006; Gaudzinski and Roebroeks 2000; Niven et al. 2012; Rendu et al. 2012).

To support the traditionally accepted eastern origin of the Proto-Aurignacian, the technocomplex has been argued to have similarities to assemblages in Bulgaria (Kozarnika, Tsanova et al. 2012), Crimea (Siuren-I, Demidenko and Otte 2000; Demidenko and Noiret 2012) and SW Russia (Kostenki 17/II, Dinnis et al. 2019), as well as to the Levantine Ahmarian technocomplex (Mellars 2006). However, recent dates indicate that the earliest instance of the Proto-Aurignacian is documented at the site of Isturitz, in SW France (Barshay-Szmidt et al. 2018), supporting a potential indigenous origin for the technocomplex in western Europe (Anderson et al. 2015; cf. Kadowaki et al. 2015). This could also help explain early dates for this industry in other Western European sites and support a mosaic conceptualization of the Middle-Upper Paleolithic transition (Clark and Riel-Salvatore 2009; Maíllo-Fernández and de Quirós 2010; Straus 2005). It is important to highlight that, in all cases where the two industries have been documented at the same site, the Proto-Aurignacian underlies the Early Aurignacian. Furthermore, while some scholars argue for a general homogeneity of the Proto-Aurignacian, recent work on this technocomplex has shown to display a heretofore underappreciated degree of internal variability, at least some of which appears to be correlated to changes in overall mobility strategies (Falcucci et al. 2017, 2018; Riel-Salvatore and Negrino 2018a, 2018b). Thus, while debate continues as to whether it represents a southern European manifestation of a larger “Aurignacian” phenomenon that is represented in other parts of the continent by the Early Aurignacian, overall, it appears that the Proto-Aurignacian represents a distinct adaptation and technocomplex.

In order to contribute to ongoing discussions about the internal variability of the Proto-Aurignacian as a technocomplex, this paper presents an analysis of faunal remains from the two Proto-Aurignacian levels at the site of Riparo Bombrini (Liguria, NW Italy). We start by introducing the record from Riparo Bombrini as a case study, summarising the latest data published over the past few years and introducing its faunal collections as an important vector of information that has much to contribute to the ongoing discussions. One of the principal challenges that emerge is the highly fragmentary nature of the faunal remains from the site, which creates some particular difficulties in its analysis. A combination of archaeozoological, taphonomic, and Zooarchaeology by Mass Spectrometry (ZooMS) analyses prove to be a suitable and innovative methodological solution to this context, and its results are presented in the following section. The paper closes with a discussion that situates these new data in the context of the debate about the internal variability of the Proto-Aurignacian and highlights how the integration of faunal and other archaeological data is essential to shedding much-needed light on the cultural adaptations of Early Upper Paleolithic foragers in Europe beginning roughly 42,000 years ago.

4.3.1 Previous Work on the Proto-Aurignacian at Riparo Bombrini

Located in NW Italy in the storied Balzi Rossi site complex located immediately east of the border with France, Riparo Bombrini is a rockshelter of which a small part survives today (Fig. 1). The construction of the Genoa-Marseille railroad in the late 19th century used explosives to blast through part of the Balzi Rossi and truncated the talus deposit originally present in front of Grotta del Caviglione, the eastern edge of which is known today as Riparo Bombrini. A first testing in 1938 (Cardini 1938) was followed by a limited excavation in 1976 (Vicino 1984) and controlled excavations from 2002-05 (Holt et al. 2019). Since 2015, the site has been under excavation by two of the authors, with the stated aim of clarifying the timing and cultural dynamics of the Middle-Upper Paleolithic transition at one of the rare sites to have yielded diagnostic *Homo sapiens* remains in Proto-Aurignacian context (Negrino and Riel-Salvatore 2018; Riel-Salvatore and Negrino 2018a, 2018b).

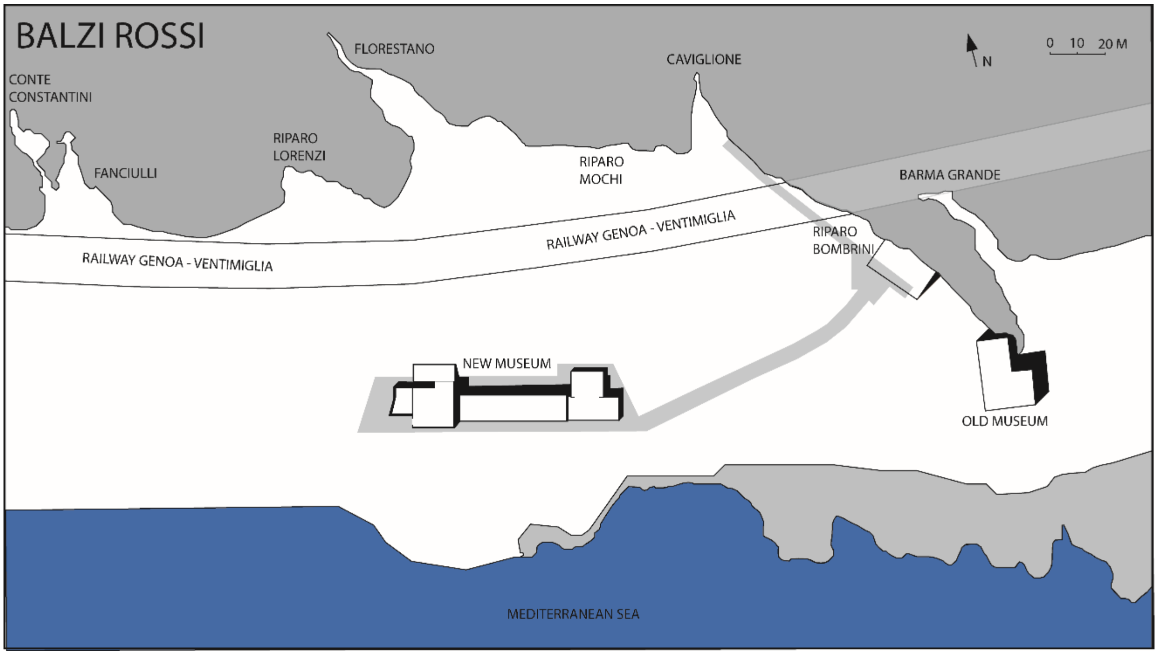


Figure 1. – Map of the Balzi Rossi cave complex (Ventimiglia, Italy) showing archaeological sites, including Riparo Bombrini, Riparo Mochi, and Grotta del Caviglione mentioned in the text.

These prior excavations have revealed that the site comprises very recent (42-45 ky cal BP) Late Mousterian deposits overlain by three Proto-Aurignacian levels spanning the interval 42ky-36ky cal BP (Fig. 2) (Benazzi et al. 2015; Higham et al. 2014; Holt et al. 2019). While an erosional disconformity separates the two technocomplexes, they do not appear to be separated by a significant time gap (Riel-Salvatore and Negrino 2018a). The site's chronology broadly corresponds to that documented at nearby Riparo Mochi, which represents the western edge of the Caviglione talus discussed above (Fig. 1) (Douka et al. 2012; Kuhn and Stiner 1998).

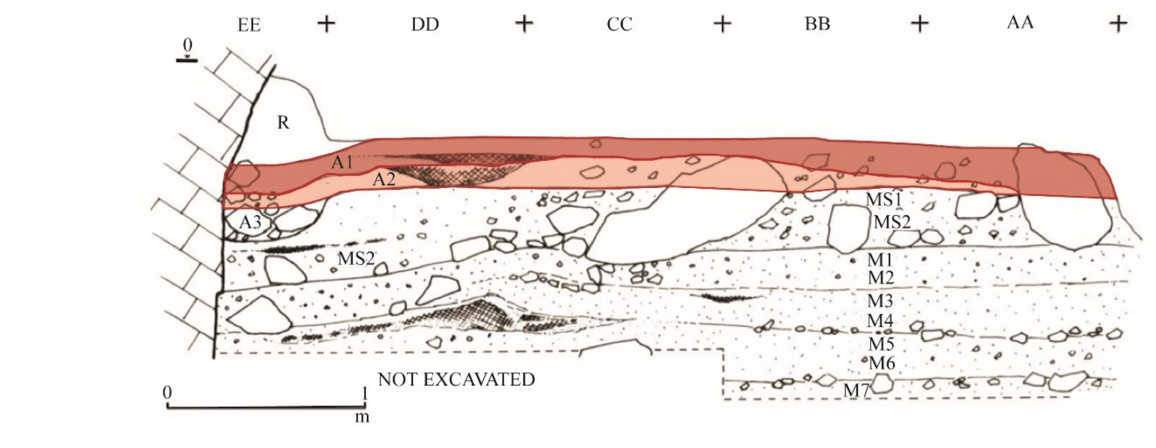


Figure 2. – Stratigraphy of Riparo Bombrini showing Proto-Aurignacian Levels A1 and A2.

One of the most striking elements to come out of prior work at Riparo Bombrini is that the Proto-Aurignacian levels, in spite of showing considerable lithic technotypological homogeneity (see Bertola et al. 2013), clearly document differences in mobility strategies and land-use patterns, with Level A1 showing a residential mobility strategy while Level A2 shows a logistical mobility strategy (Riel-Salvatore 2007, 2010). These differences are accompanied by differences in the production of bladelets and appear to correspond to adaptations to changing paleoenvironmental conditions (Riel-Salvatore and Negrino 2018a), which testify to the fact that Proto-Aurignacian technocomplex was a flexible one that permitted a great deal of resilience in forager behaviour across even dramatic paleoclimatic shifts including that corresponding with the eruption of the Phlegrean Fields ca. 39ky cal BP (Riel-Salvatore and Negrino 2018b).

Overall, micromorphology, pollen, faunal and microfaunal data published in Holt et al. (2019) associate Level A2 with a phase of climatic degradation that could correspond to just after Glacial Interstadial 9 (GI 9), dated around 40.2 ky cal BP (Rasmussen et al., 2014), and extend through the climatic instability associated with HE4 (~39.85±0.14ky to 38.2ky cal BP according to Giaccio *et al*. (2017)). In contrast, Level A1 is associated with slightly more temperate and mesic conditions (Arobba and Caramiello 2009; Holt et al. 2019; Riel-Salvatore and Negrino 2018a), lasting from around 38 to 36 ka cal BP (Holt et al. 2019; Riel-Salvatore and Negrino 2018b) which could correspond to Glacial interstadial 8 (GI8) according to the climato-stratigraphy detailed in Rasmussen et al. (2014).

Riparo Bombrini's Protoaurigacian Levels A1 and A2 are dense in remains of various kinds, especially lithics and faunal remains, and they also include features including *cuvette*-type hearths and pits. However, to date, only the Mousterian levels had benefited from a formal spatial analysis (Riel-Salvatore et al. 2013), which revealed that the site's Neanderthal occupants had distinct activity areas when they occupied it and that the positioning of these varied according to their overall mobility strategies. Given similarities in hearth placement in Levels A1 and A2 and in the Mousterian, the same may also have been true during the Proto-Aurignacian at the site. The presence of a potential third Proto-Aurignacian level is limited to a narrow band of deposits along the back wall of the shelter; these deposits likely represent a level that was largely eroded away and, due to its low artifact and faunal content and very limited spatial extent, it will be disregarded in the present analysis.

One of the outstanding questions about Proto-Aurignacian variability at Riparo Bombrini, and indeed much of the Proto-Aurignacian as a whole, is how faunal data fits into the equation (Anderson et al. 2015; Falcucci et al. 2017; Pike-Tay et al. 1999; Soulier 2013, 2014). By way of reference within the Balzi Rossi, at Riparo Mochi, the Proto-Aurignacian lithic assemblages have so far always been studied as a whole, thus masking potential variability within this industry at this site (e.g., Kuhn and Stiner 1998, but cf. Grimaldi et al. 2014;). Likewise, data on the large mammal assemblage have either been overlooked (Kuhn and Stiner 1998), or presented for level G as a whole, which is associated with the highest frequency of roe deer in the Mochi sequence, although red deer is also abundant (Alhaique et al. 2004; Berto et al. 2019). In a recent study of bone and antler technology at Mochi, Tejero and Grimaldi (2015:68) also make passing reference to the fact that "long bones were systematically fractured for bone marrow extraction and consumption" without providing detailed data in support of this observation. Recently published microfaunal data from Mochi indicate that its transitional levels are associated with "two cold and one slightly warm oscillations […] depicting a forest and bush reduction near the shelter"(Berto et al. 2019:21), but again all the material for Level G was studied as a whole, making finer-grained interpretations impossible. The same is also true of analyses of mollusk procurement (Stiner et al. 2000).

The situation is somewhat better at Bombrini, where faunal data (in this case species abundance) has been reported from the various levels at the site. Holt et al. (2019, Table 4) suggest that the species composition of the faunal assemblages from Riparo Bombrini indicates that the Proto-Aurignacian was accumulated under slightly colder conditions than the Late Mousterian, as shown by the higher frequency of bovids, mountain goats (*C. ibex*) and chamois (*R. rupicapra*) in those levels. As well, identified remains of rhinoceros and equids in Level A2 imply the presence of an open plain ecosystem between the base of the cliffs of the Balzi Rossi and the lower-lying Tyrrhenian Sea at that time. From a behavioural perspective, no taphonomic or skeletal element representation data have been published to date, but it is worth highlighting here the high degree of fragmentation of the Proto-Aurignacian faunal assemblages: only 1.82% (of 3842 bone fragments) and 0.87% (of 4245 fragments) of all animal bones could be identified in Levels A1 and A2, respectively (Holt et al. 2019:5), in spite of these assemblages being more than an order of magnitude larger than in the Late Mousterian (average number of bone fragments = 442, avg % identified = 2.26%). Seeing how most of the identifications reported in Holt et al. (2019) are generally based on teeth, it seems warranted to say that the Proto-Aurignacian faunal record at Riparo Bombrini is both more abundant and more fragmented than in the underlying levels, which hints at the fact that a distinct suite of taphonomic processes was at work in those levels compared to the Late Mousterian. The exact nature of these processes, their relevance to understanding variability in human behavioural strategies during the Proto-Aurignacian, whether they co-vary in any meaningful way with documented shifts in mobility strategies and lithic technology, remain a series of important open questions, however.

4.3.2 Evidence of Mobility Strategies in Fragmented Paleolithic Faunal Assemblages Enhanced by ZooMS Collagen Fingerprinting

In his forager/collector models, Binford (1980) documented a spectrum of behaviours in which he ultimately describes two opposite types of mobility patterns (i.e., residential vs logistical) that are still widely used in Paleolithic archaeology to discuss human dispersals and land-use patterns from a Human Behavioral Ecology perspective (Andrefsky 2009; Clark and Riel-Salvatore 2006; Delagnes and Rendu 2011; Kelly 1995; Lugli et al. 2019; Moncel et al. 2019; Riel-Salvatore and Negrino 2018a, 2018b; Schulting et al. 2008; Wißing et al. 2019). Binford originally developed his models within a Middle Range theoretical framework to distinguish opposite types of mobility through the identification of different types of site (residential mobility: base camp and localities; logistical mobility: base camp, field camp, station, and storage cache). However, a strict definition of the models is rarely applied today to avoid reductionist logic. In this paper, we are specifically interested in Binford's (1980) discussion of hunter-gatherer resource management. While hunter-gatherers with a residential mobility "map onto" the existing environment and adapt the way they acquire resources (e.g., food, raw material) to external constraints, hunter-gatherers with a logistical mobility adapt their subsistence strategies in specializing on a critical resource (e.g., lithic raw material, migratory preys) that would otherwise limit mobility. From an archaeological perspective, this distinction provides theoretical grounds to discuss the variability in resource management perceptible through the lithic record (raw material selection, lithic *chaîne opératoire*, reduction sequences, and tool maintenance) and the faunal record (prey selection, carcass transport, and carcass treatment). For instance, Delagnes and Rendu (2011) developed an approach that demonstrated a link between the transportability attributes of the different lithic technological systems (as potential mobility proxies) with the nature of the faunal assemblages stratigraphically associated with those systems. They were able to link faunal assemblages dominated by non-migratory species (e.g., red deer, roe deer) to lithic technological systems with a low potential for group mobility (higher duration of reduction sequences, single-purpose end-products with short use-life). Conversely, technological systems with high mobility potential (high versatility of blanks, long use-life, low investment in core preparation) were associated with faunal assemblages dominated by gregarious migratory species with predictable seasonal moves (e.g., reindeer).

In our study, we further explore the potential proxies for mobility strategies within the faunal record, specifically in terms of resource management. To do so, we selected three proxies for resource management that will be explored in the Proto-Aurignacian faunal record of Riparo Bombrini, namely prey selection, carcass transport, and carcass treatment. On a basecamp such as Riparo Bombrini, those three resource management proxies allow us to first discuss whether hunter-gatherers adopted a more generalist prey selection strategy, exploiting a range of available prey species in the environment surrounding the site, or if they specialized on a single gregarious migrating species, which would imply a higher degree of mobility and logistical planning (Brugal 1999; Costamagno et al. 2006; Gaudzinski 2006; Grayson and Delpech 2002; Pau Mellars 2004; Rendu et al. 2012). Second, carcass transport reconstruction helps us assess whether animals were hunted on a local scale and brought back whole to be processed at the site or if the animals were hunted far from the site and therefore first butchered at the kill site (Faith and Gordon 2007; Grayson 1989; Lupo 2001; Lyman 1985; Marean and Cleghorn 2003; O'Connell et al. 1988, 1990). And third, carcass treatment is generally discussed in terms of exploitation intensity measured either by the frequency of cut marks present on skeletal remains (see Domínguez-Rodrigo and Yravedra, 2009 for a good literature review) or the exploitation of bone marrow and bone grease (Costamagno 2013; Costamagno and Rigaud 2013; Morin 2007; Morin and Soulier 2017; Munro and Bar-Oz 2005; Outram 2001; Outram et al. 2005; Outram and Rowley-Conwy 1998; Stiner 2002a). The intensification of carcass processing is often seen as occurring hand-in-hand with increasing diet breadth as an adaptive response to external constraints such as environmental instability and demographic changes (Grayson and Delpech 1998; Morin et al. 2019; Stiner 2002a; Stiner and Munro 2002; Stiner et al. 2000). However, measuring the intensity of carcass exploitation using only one of these criteria can easily be misleading. The interpretation of cut mark frequencies for instance has been widely criticized because of the numerous taphonomic and cultural factors influencing those frequencies including fragmentation, butchery practices, carcass size, butchering tool types, and so on (Domínguez-Rodrigo and Yravedra 2009). Another example is provided by the fact that specific skeletal elements can be considered good raw material for the confection of tools while others are not. In the same way, the grease contained in cancellous bones can be exploited in different ways depending on whether it is used as a source of food or a source of fuel.

The intensity of carcass exploitation has recently been studied conjointly with lithic techno-economic patterns to discuss curation and mobility strategies (Costamagno 2013; Costamagno et al. 2006). We adopt a similar approach, borrowing the concept of curation from lithic analysis (see Andrefsky, 2009) in order to evaluate the degree of carcass curation defined as the process reflecting a carcass's actual exploitation at the base camp relative to its maximum physical utility, or potential for exploitation. The maximum physical potential exploitation implies extracting all possible resources on the carcass, including skin, tendons, meat, bone raw material, marrow and most importantly the grease contained in cancellous bones. Following this logic, a highly curated carcass does not imply that all those resources were intensively exploited, but it reflects the array of choices potentially made by hunter-gatherers to exploit some resources that will result in the exhaustion of all exploitable resources on a single carcass.

On a methodological perspective, prey selection and carcass transport can be assessed with traditional quantitative units used in archaeozoology, such as the Number of Identified Specimens (NISP) combined with the Minimum Number of Individuals (MNI) to evaluate the diversity of animal species exploited on the site, and measuring the Minimum Number of Elements (MNE) and skeletal representation to evaluate what carcass parts were brought back to the base camp for each exploited species (Grayson 1984; Lyman 2008; Marean et al. 2001; Morin et al. 2017a). Of course, those measurements must be combined with taphonomic analyses to ensure that the animal carcasses under consideration were indeed exploited by humans instead of other potential carnivores (e.g., wolves or hyenas). Carcass treatment, on the other hand, can be discussed by combining archaeozoological and taphonomic analyses and should include recording the nature of fragmentation from the indeterminate fraction of the faunal assemblage. If one can discriminate between the different post-depositional taphonomic effects that can fragment faunal remains such as carnivore action, animal and human trampling, deposit compaction, water action, and bioturbation, it is then possible to identify some anthropic fragmentation effects (if not masked by the extent of the post-depositional effects): tool manufacture (surface alterations), cooking, marrow and grease exploitation, and burning for fuel. As will be seen below, these last two behaviours were of special interest at Riparo Bombrini in the concept of carcass curation.

The sequence of activities leading to bone marrow and grease exploitation would start with the first known steps of animal exploitation: killing the animal, butchering it (cut marks, scraping marks for skinning, dismembering, filleting, etc.) and possibly processing some skeletal elements for craft purposes (manufacturing traces; grooving, polish, unfinished or broken bone tools). Marrow extraction alone implies the deliberate fracturing of long bone shafts to recover the cold marrow. This action typically produces numerous shaft fragments bearing dynamic impact fractures and bone flake removals (or splintering) around the area where the fresh bones were cracked open (Outram 2001; Munro and Bar-Oz 2005; Vehik 1977; Manne 2012). Finally, grease exploitation entails further carcass processing starting with the breakage of cancellous bones which is defined as grease processing by Morin and Soulier (2017), and potentially the boiling or heating of the crushed cancellous bones (grease rendering). In the case of grease rendering, a choice can be made between appendicular or axial bones at this point as they produce different types of grease (Binford 1978; Outram 2001; Vehik 1977; Wilson 1924). Archaeological evidence of grease rendering would therefore include comminuted cancellous bones to extract the grease and traces of cold marrow extraction on long bone diaphysis (percussion marks and bone flakes) since grease rendering is rarely observed without previous marrow extraction (Outram 2001). We could also expect to find concentrations of heat-cracked stones ethnographically used to heat water in a container made of wood or skin necessary to extract grease from crushed cancellous bones (Binford 1978; Manne 2012; Vehik 1977), although this criterion is questionable since it has been demonstrated that it is possible to boil water in perishable containers without the use of heated stones (Costamagno and Rigaud 2013; Speth 2015).

The identification of bone grease exploitation from archaeological faunal assemblages can be very tricky because of the numerous taphonomic processes (carnivore action, and post-deposition attrition) that can mimic the criteria normally used to identify anthropogenically induced bone fragmentation, such as the underrepresentation of long bone epiphyses in relation to shaft portions (Costamagno 2013; Morin and Soulier 2017). However, a suite of diagnostic criteria for grease exploitation was recently published by Morin and Soulier (2017) based on experimental archaeology, including morphological criteria such as the presence of crushing marks, tearing marks, and micro-inclusions from contact with hammerstones or anvils.

While grease rendering would mainly produce unburned fragmented bones, the use of bones for fuel results in burned bones associated with hearths. Experimental studies have demonstrated the utility of cancellous bone (particularly whole epiphyses) as complementary fuel to other combustibles such as wood (Costamagno et al. 2005; Marquer et al. 2010; Morin 2010; Théry-Parisot et al. 2004). The intentional burning of bone elements for fuel would result in a highly fragmented faunal assemblage with a high proportion of cancellous burned bones. The use of bones for fuel in Paleolithic contexts could derive from two potential incentives. The bones were either burned for specific activities such as lighting, heating, drying, or other (ritual, elimination of animal waste), or they were burned for opportunistic purposes when faced with a lack of other combustible (Marquer et al. 2010). However, bones do not have the same combustion properties as wood. While the latter is good for fire maintenance, indirect cooking, and transformation of raw material, bones do not produce embers and are therefore more adapted to producing durable flames for lighting, heating, cooking, and drying (Théry-Parisot et al. 2004).

When faced with a challenging taphonomic context such as the highly fragmented faunal record at Riparo Bombrini, all three proxies for resource management are very difficult to discuss. To partially remediate to this issue, we integrated the systematic ZooMS sampling to our archaeozoological and taphonomic analyses. ZooMS collagen fingerprinting takes advantage of the preservation properties of collagen which is the most abundant protein in bone, present at more than 22% by dry weight of modern bone (e.g., Buckley 2018). The method is based on the observation that the triple-helix structure of the collagen protein contains enough differences to be useful for taxonomic separation (Buckley et al. 2009). ZooMS collagen fingerprinting has therefore proved to be an excellent tool to identify a wide range of wild fauna (e.g., Brown, Douka, et al. 2021; Buckley et al. 2010, 2014; Buckley and Kansa 2011; Harvey et al. 2019; Richter et al. 2011; Welker et al. 2015) in order to improve NISP **s**tatistical significance. To a lesser degree, it also helps improving the skeletal representation when sampling identifiable skeletal parts of morphologically similar taxa (e.g., roe deer versus red deer) and of broad categories (e.g., Ungulate size 2) (see Pothier Bouchard et al., 2019 for discussion). To date, studies featuring the application of mass sampling (>100 bone samples) through ZooMS collagen fingerprinting of Paleolithic faunal assemblages have mainly focused on either identifying ancient hominin bone fragments (Brown et al. 2016; Devièse et al. 2017; Welker 2018), or proving the usefulness of the method as a complementary tool for taxonomic identifications and assessing bone collagen preservation (Buckley et al. 2017; Buckley and Kansa 2011; Welker et al. 2015, 2017). While there have been recent limited attempts at exploring the relationship between faunal composition and bone fragmentation (Sinet-Mathiot et al. 2019), there remains much conceptual and methodological work to be done in order to systematically integrate ZooMS into full archaeozoological and taphonomic studies of Paleolithic faunal assemblages. With this goal in mind, this study uses the Proto-Aurignacian faunal remains from the site of Riparo Bombrini to provide what is, to our knowledge, the first attempt at such an integration of these three lines of evidence in order to yield new information about human behavioural adaptations, the sum of which is greater than its individual parts.

4.4 Material and Methods

The faunal assemblage in study was sampled from two Proto-Aurignacian levels (A1 and A2) on three areas of the site. These areas (south, north, and outside) have been selected to be representative of three different features of the site (Fig. 3). The south area was entirely excavated from 2015 to 2017 and contained a pit feature in both Levels A1 and A2 (mainly concentrated on square FF3) which is interpreted as a discard feature. The north area was excavated between 2002-2005 and contains cuvette-type hearth features in both levels (concentrated on square DD1). The outside area was mostly excavated in 2002 and corresponds to two squares located outside the rockshelter where Levels A1 and A2 are more difficult to discriminate. This last area will therefore be attributed to a Level A1-A2 in this study.

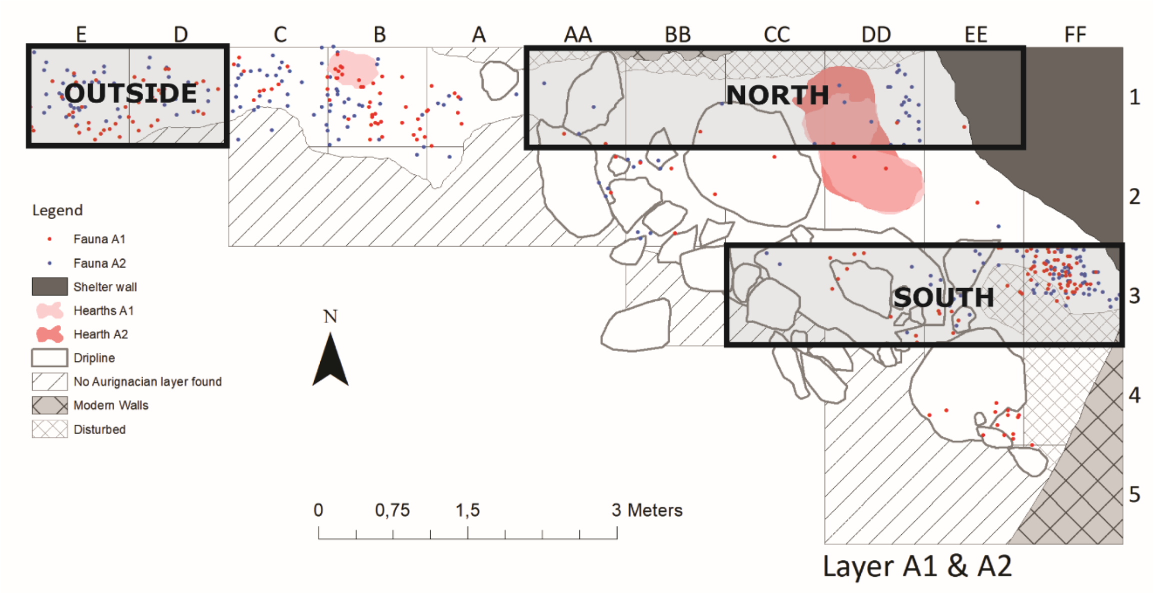


Figure 3. – Faunal distribution map combining plotted finds from Levels A1 and A2 at Riparo Bombrini, showing the three selected areas in this study: north, south, and outside.

4.4.1 Archaeozoology

A total of 32,351 bone fragments were analyzed. Taxonomic identifications were conducted using gross morphology and ZooMs. Skeletal remains that could not be identified to a species were assigned to a size category adapted from Brain (1981). The assemblages were quantified using standard archaeozoological methods (NISP, MNE, MNI; see Grayson 1984; Lyman 2008). When possible, age at death was determined using tooth wear stages on isolated teeth (Grant 1982; Hillson 2009) and epiphyseal fusion stages on long bones (Purdue 1983; Zeder et al. 2015). The relative abundance of taxa is usually quantified using a combination of NISP and MNI in archaeozoology to account for the effects of fragmentation on MNI. However, the extensive fragmentation of the Riparo Bombrini assemblages considerably hinders effort to quantify MNI, since the MNI values for all of the identified taxa only yield one individual (or two in the cases where a juvenile element was identified). We will therefore only consider the NISP to evaluate the abundance of each taxon in the present study. Furthermore, the abundance of skeletal remains is usually measured using MNE, but this index is equally affected by the state of fragmentation of the faunal assemblages. We therefore regrouped skeletal elements within skeletal portion categories (i.e., head, axial post-cranial, upper limb, lower limb, indeterminate limb, and foot; adapted from Stiner (2002b)) for each ungulate taxa to better allow interpreting carcass transportation strategies at Riparo Bombrini.

The limitations of NISP, MNI and MNE have been discussed elsewhere at length (Cannon 2013; Grayson 1984; Lyman 2008; Marean et al. 2001; Morin et al. 2017a; Reitz and Wing 2008) and apply to our study, as demonstrated by the paucity of identifiable skeletal elements, which we attribute to the high degree of fragmentation.

Unfortunately, MNE counts are used to calculate MAU (minimum anatomical unit) counts which are used in conjunction with indices of bone density to assess the impact of density mediated attrition on an assemblage, and in conjunction with indices of carcass utility, such as the FUI (food utility index, see Metcalfe and Jones 1988) to evaluate carcass transportation strategies.

The extent of post-depositional attrition is generally evaluated by calculating the correlation coefficient of % survivorship values and their corresponding bone mineral density (%survivorship/BMD) (Lyman 2008). The %survivorship values are calculated using MNE of a particular skeletal part in relation to the maximum MNE in the assemblage (Lyman 2008). Because denser skeletal tissues are more able to resist post-depositional breakage over time (Costamagno 2013; Lam and Pearson 2005; Lyman 1994; Morin and Soulier 2017; Stiner 2002b) density mediated attrition tends to result in the underrepresentation of long bone epiphyses, as well as the relative loss of smaller taxa and young animals (Lyman 1994). However, given the low MNI counts in our assemblages we were unable to test the impact of post-depositional attrition on skeletal representation using conventional methods.

Finally, another limitation related to quantification in archaeozoology is the interdependence of faunal remains, described as the probability of counting a skeletal element or an individual animal multiple times. This problem is usually tackled by comparing NISP for each taxon with their associated MNI in order to evaluate the degree of interdependence on the site and the likelihood of it influencing the NISP count. Using the MNI is not an option in this study, however, and we should therefore be aware that one animal can easily be counted more than once, which is especially true considering that we have analyzed a number of bone shaft fragments with ZooMS. However, chances are that the interdependence is not randomly distributed at Bombrini given that we have sampled three zones with well-defined archaeological features. This gives us the opportunity to better predict potential faunal aggregates associated with the discarding pit or the hearth features, for example.

4.4.2 Taphonomy

As discussed earlier, discriminating between the different taphonomic processes responsible for post-depositional attrition is crucial in order to be in a position to discuss human behaviour. For example, the underrepresentation of ungulate long bone epiphysis can be created by carnivore gnawing (Blumenschine 1988; Faith et al. 2007; Haynes 1983), anthropic grease exploitation (Costamagno 2013; Morin and Soulier 2017; Outram 2001; Outram et al. 2005; Vehik 1977), and the use of bone as fuel (Costamagno et al. 2005; Morin 2010; Théry-Parisot et al. 2004).

We attempted to evaluate the differential preservation of cervids skeletal elements (cervids are the most abundant taxa in the faunal collection), we combined all identified skeletal elements of the taxon categories corresponding to "*Cervus"* and "cervid", we first calculated the skeletal part profile by calculating %MAU using this equation: ([MAU*i*]100)/(maximum MAU in the assemblage) where *i* is a particular skeletal element part such as "distal femur" or proximal humerus" (Lyman 2008:238). We then calculated the correlation coefficient between the resulting %MAU and BMD derived from Lam et al. (1999), which is equivalent to the %suvivorship/BMD. Finally, we analyzed the resulting data with the nonparametric Spearman's correlation (r_s), to calculate the correlation coefficient, where H_0 = there is no link between bone mineral density and skeletal element survivorship (%MAU). The nonparametric equivalent of Pearson's correlation is also chosen here because of the very small sample size (N=9) and the fact that the data is not normally distributed.

However, the lack of MNE left us no choice but to find alternative ways to evaluate post-depositional bone attrition. We therefore had to turn on the indeterminate fraction of the faunal assemblage and to rely on the more generalized fact that denser skeletal tissue (mostly the cortical part of long bones) tends to better resist post-deposition attrition such as weather exposure, acidity of the surrounding sediments, water action, and carnivore action (Lyman 1994) by comparing the proportion of bone type categories (cortical, cancellous, axial cancellous, and appendicular cancellous).

To collect a maximum of taxonomic information from the heavily fragmented assemblages, we analyzed the non-identifiable (or indeterminate) bones in an efficient and rapid way, each bulk bag of fragmented bones collected in the sieve was first sorted between six size classes according to their maximum length (0-20 mm, 20-30 mm, 30-40 mm, 40-50 mm, 50-60 mm, 60-80 mm, 80-100 mm, >100 mm). Within each size class, any identifiable element was set aside, and the rest of the bones was subdivided into color classes to first separate burning levels (burned 1: slightly burned, burned 2: carbonized, burned 3: calcined; adapted from (Stiner et al. 1995) and (Marques et al. 2018)) from unburned bones, and bone types (cortical, cancellous, and when possible, cortical from bone shafts, axial cancellous, and appendicular cancellous). Each subdivision was finally quantified and weighed with a Tangent KP-103 scale (Max 120.0g, d=0.1g). When bone cortical surfaces were preserved (very rarely within size class 0-20 mm), long bone shafts were analyzed for fracture freshness (Outram 2001; Villa and Mahieu 1991) to calculate the mean Fracture Freshness Index (FFI; see Outram 2001) within each archaeological level and taphonomic alterations including concretion, root and microorganism etching, manganese coloration, trampling, anthropic percussion marks, cut marks, and bone manufacture (Behrensmeyer 1978; Fisher Jr 1995; Lyman 1994; Stiner et al. 1995). Plotted finds, identifiable bones (complete enough to be identified to the element), and teeth were also fully characterized with taphonomic alterations mentioned above. Surface modifications were analyzed using a Dino-Lite Edge Digital Microscope 20X-220X enhanced DOF used with DinoCapture 2.0 software.

4.4.3 ZooMS Sampling Integrated to the Faunal Analyses

Because collagen preservation is very compromised at Riparo Bombrini, we applied a screening method developed and tested elsewhere (Pothier Bouchard et al. 2019) using an Agilent 4500a, portable FTIR instrument equipped with a single-bounce diamond ATR and internal battery, while conducting the faunal analysis described above in Genoa. We systematically selected 20 to 30 bone samples to screen for ZooMS in each stratigraphic unit of every square meter analyzed. Plotted finds and morphologically identifiable bones (anatomical parts) were prioritized, and then a sample of smaller fractions (10-30 mm bone fragments) was randomly selected while trying to be representative of the diversity of bone types (cancellous, cortical, etc.) and animal size (diversity of cortical thicknesses based on size classes originally described by Brain 1981). We also attempted to sample fetal and juvenile bone fragments when collagen was preserved. This was done to improve the statistical significance of the skeletal representation (by sampling morphologically identifiable parts of unknown species), the diversity of the faunal spectra (by sampling a diversity of cortical thicknesses), and the seasonality evidence (by sampling fetal and juvenile bones). This sampling strategy helped improving the resulting data but is also the subject to some limitations since collagen preservation often varies according to the same taphonomic effects that contribute to bone fragmentation (Bar-Oz and Munro 2004; Dal Sasso et al. 2016; Le Meillour et al. 2018; Stiner et al. 1995; Trueman et al. 2004). In that sense, issues related to NISP and MNE measurements such as the interdependence of skeletal parts and the aggregation effect could be enhanced with ZooMS identification as discussed earlier (see Pothier Bouchard et al., 2019 for further discussion). Nevertheless, ZooMS identification greatly improved our data at Riparo Bombrini. When ZooMS identifications failed because of a lack of bone collagen, the data was collected to calculate a ZooMS success rate (successful ZooMS identification/failed ZooMS identification*100) which can in turn provide insights into faunal preservation in the different areas of the site.

Each selected bone was sampled for FTIR analysis. Approximately 1 mg of powder was produced using a mortar and pestle, and the powder was then pressed against the clean diamond crystal with an anvil and was discarded following measurement. Measurements were taken with the automatic settings of the instrument with a spectral range from 4000-650 cm^{-1}, at 4 cm^{-1} resolution, with 64 co-added scans. Each spectrum was exported in the Grams spectral format (.spc), and processed using Resolutions Pro (Agilent) to measure Amide I and Phosphate v3 peaks using measurement system N described in (Pothier Bouchard et al. 2019). The results were then exported to Microsoft Excel for calculation of the CO/P ratio. The screening threshold of 0.4 was selected; entailing a sample was rejected when its CO/P ratio was less than 0.4. When the calculated CO/P ratio scored 0.4 or more, it was considered suitable for ZooMS analysis.

Overall, a total of 612 bones were processed for acid-soluble ZooMS analysis following the method adapted from Buckley et al. (2009). The use of this acid-soluble fraction allows for potential future use of the insoluble pellet (obtained with the original bone pellet that is air-dried and stored after ZooMS analysis) for isotopic analyses, whether stable isotopes for dietary inferences (van der Sluis et al. 2014) or radiocarbon for dating (e.g., Harvey et al. 2016). For each bone sample, approximately 25-50 mg of bone powder was placed in a 1.5mL Eppendorf tube and demineralized with 1 mL of 0.6 M hydrochloric acid (HCl) overnight (18 h, 4°C). Following the centrifugation at 12,400 × g for 1 min to precipitate the pellet, 500 µL of the acid-soluble fractions were ultrafiltered with 10 kDa molecular weight cut-off membranes (MWCO), centrifuging again at 12,400 × g for 30 min. The remaining 500 µL of HCL solution was saved as a backup. Following demineralization, two independent volumes of 500 µL of 50 mM ammonium bicarbonate (ABC) were added to the ultrafilter to wash the filter, centrifuging at 12,400 × g for 30 min and discarding the through-flow after each spin. The collagen was then recovered with 200 µL 50 mM ABC. Half of the resulting ABC solution was saved as backup. The remaining 100 µL was put in a fresh Eppendorf tube and digested with trypsin overnight (18h, 37°C). 1µL of the sample was spotted the next day on a Bruker mass spectrometer (MS) target plate with 1µL of α-cyano-4-hydroxcinnamic acid matrix solution to allow co-crystalisation and air-dried following Buckley et al. (2016). MALDI-MS analyses were carried out on a Bruker Ultraflex II instrument, with a *m/z* window of 700-3,700 mass units and up to 2,000 laser acquisitions per spot. The obtained collagen fingerprints were analyzed with mMass software (v5.5.0) and animal species were identified using previously published collagen peptide markers from reference spectra following Buckley et al. (2009, 2017). (See Supplementary Table S1 for all peptide markers used in this analysis and Figure S1 for examples of collagen fingerprints of each identified species at Riparo Bombrini).

After identifying all resulting spectra, 33 acid-soluble samples were targeted to be further purified and fractioned using reverse phase chromatography with C18 solid phase extraction (SPE) pipette tips, following the manufacturer's protocol (Varian, UK). Each 100µL sample was first acidified with 10µL 0.1% trifluoroacetic acid (TFA) and eluted into two fractions of actenonitrile (ACN) concentrations: 10% ACN/0.1%TFA, and 50% ACN/0.1% TFA. Fractions were air-dried for 48 h and resuspended in 10µL 0.1%TFA. 1µL of each fraction was then spotted using the same procedure as the original acid-soluble samples. This method helped clarify some of our cervid identifications by improving the signal intensity of the A2T67(G) biomarker that is crucial to distinguish between *Cervus* (*m/z* value of 3033) and *Capreolus* (*m/z* value of 3059.4) (see Buckley et al. (2010) for further discussion on the isolation of collagen-peptid markers).

While certain deer genera can be discriminated with collagen fingerprinting, it should be noted that red deer (*Cervus elaphus*) and fallow deer (*Dama dama*.) are too closely related to be distinguished with ZooMS (Buckley and Kansa 2011). Since anecdotal fallow deer specimens were identified at Bombrini in the past (Holt et al. 2019), it is therefore not impossible that some of our *Cervus* identification also includes *Dama* specimens. Fortunately, those species are generally associated with similar environmental conditions and have similar behaviours, so the impossibility of discriminating between them should not be a major problem for our interpretations.

4.5Results

4.5.1 NISP and Skeletal Representation

The NISP results listed in Table 1 clearly show how the ZooMS provides a more complete picture of the Proto-Aurignacian faunal assemblages from Riparo Bombrini. Even with the combined ZooMS and morphological identification (Table 1, Fig. 4), however, the identification rate is still very low (1.2%). A large portion of the identified taxa corresponds to a broad “ungulate” category represented in yellow in Figure 4 (26% of total NISP). Nevertheless, as also shown in Figure 4 we were able to characterize and compare the taxonomic composition of Level A1 (Total NISP: N=47) and Level A2 (Total NISP: N=51). We observe that cervids (mainly represented by red deer - *Cervus elaphus*, but also roe deer - *Capreolus*) are the most abundant taxa in both levels. However, over 40% of the specimens in each level is represented by other ungulate taxa; bovines (*Bos/Bison*) and caprids (*Capra)* are slightly more abundant in Level A1, as opposed to Level A2 in which wild boar (*Sus*) and horse (*Equus*) are a little more abundant.

Table 1. – NISP results combining Levels A1 and A2 and separately showing taxa identified with morphology, with ZooMS, and with the combined data.

Taxa	**Morphology**	**ZooMS**	**Combined**
Cervus	0	88	88
Capreolus	0	2	2
Capra	2	27	29
Bos/Bison	2	44	46
Equus	6	7	13
Sus	6	1 (already morphologically identifiable)	6
*Bovid size 3**	5	0	5
Coelodonta/Diceros	0	1	1
Canis	0	1	1
Cervid	0	20	20
Cervid size 3	1	5	6
Cervid size 3/4	2	3	5
Cervid size 4	2	0	2
Ungulate	34	25	59
Ungulate size 2/3	29	0	25**
Ungulate size 3	9	2	11
Ungulate size 3/4	88	9	92**
Ungulate size 4	2	0	2
Carnivore size 3	4	0	4
Poor collagen	n/a	409	n/a
Indeterminate	32156 (99.4%)	n/a	31931 (98.7%)
Total	32348	644	32348

*Animal size categories are adapted from Brain (1981).

**Some of the bone fragments from this category were identified to a more precise (e.g., an "ungulate size 3/4" further identified with ZooMS to a "*Cervus*" category).

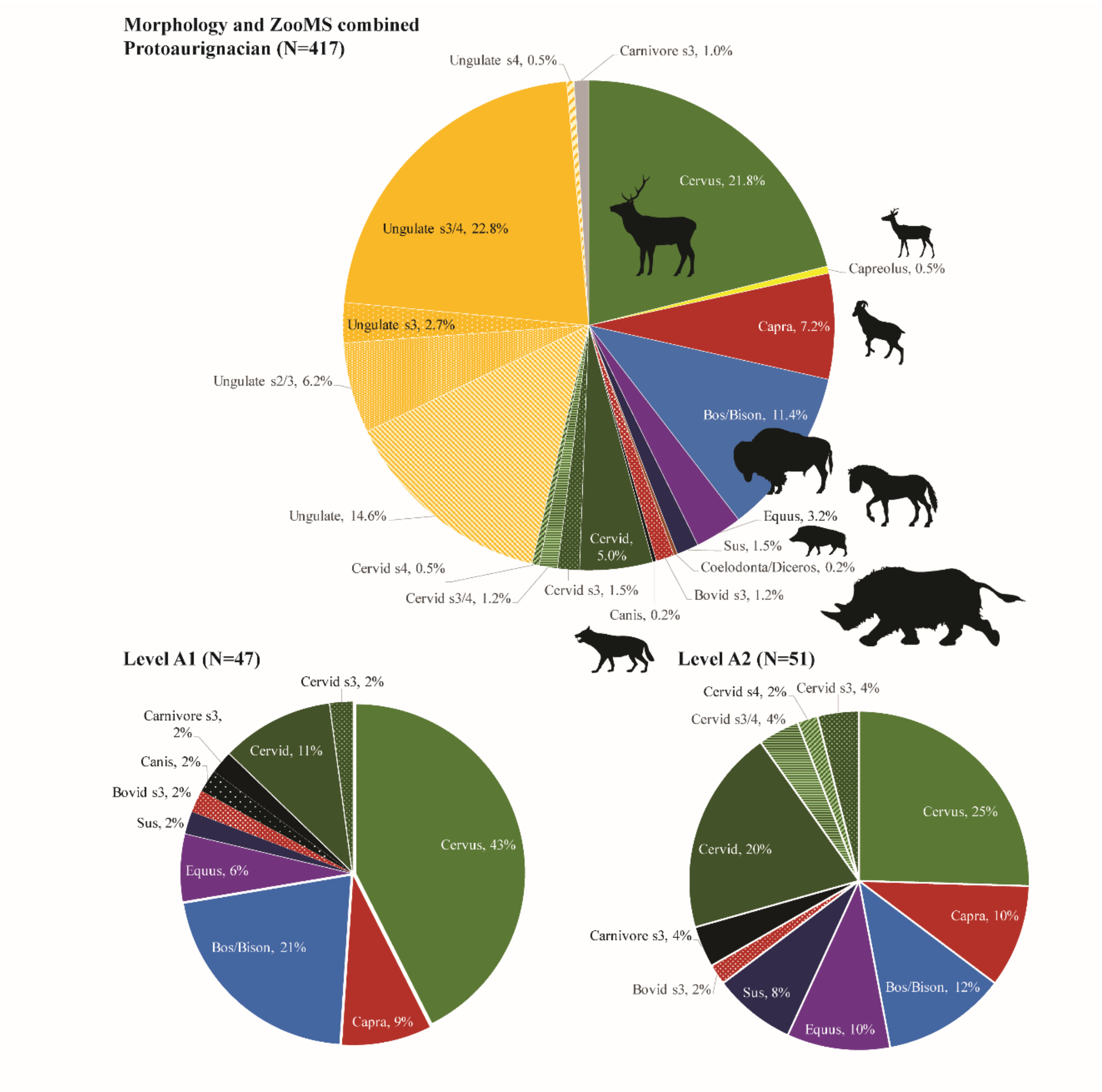


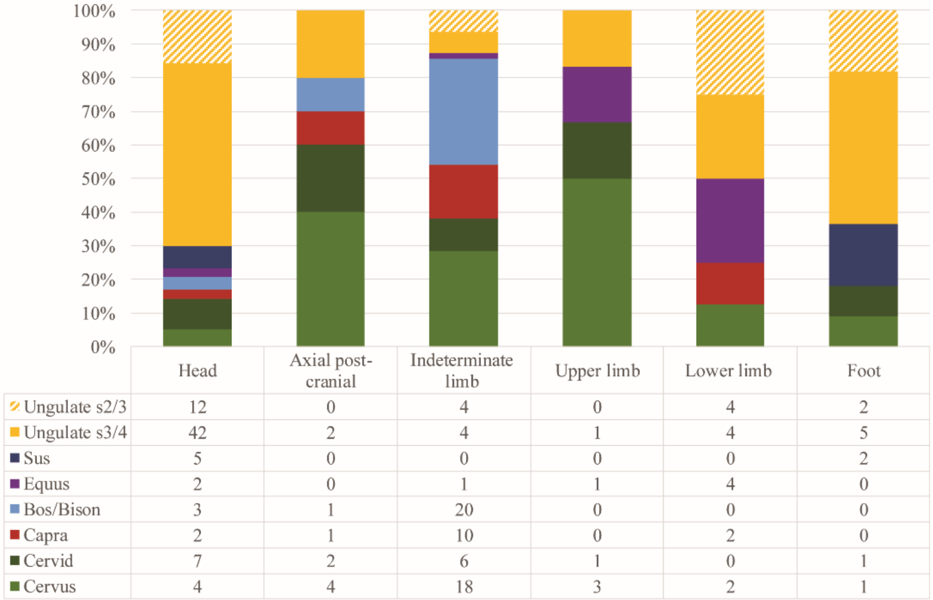
Figure 4. – Pie charts showing total NISP for Level A1 and A2 (upper), NISP of Level A1 (lower left), and A2 (lower right) both excluding the “Ungulate” categories. Animal silhouette images from http://phylopic.org/.

Figure 5 shows the skeletal representation of identified taxa from combined Levels A1 and A2 comparing morphological identification and the ZooMS results. The diagrams demonstrate how the ZooMS improved the skeletal representation data which was otherwise mostly restricted to the identification of anatomical elements within the “ungulate” category and the under-representation of most anatomical elements with the exception of teeth for most taxa. They also reveal that skeletal elements from all anatomical portions of ungulates, cervids and caprids (except the feet and upper limb for caprids) are found on the site. On the other hand, bovines are only represented by axial elements and a high number of bone shaft fragments (N=20), all identified with ZooMS. Equids are represented by a few teeth, some easily morphologically identifiable bone fragments from the lower limbs (tibia, carpal/tarsal), and a ZooMS identified femur. Suids are only represented by five teeth and two phalanges. The spatial and stratigraphic correspondence of the identified skeletal elements for these taxa are described in the supplemental information (Table S2).

Skeletal representation with morphology

	Head	Axial post-cranial	Indeterminate limb	Upper limb	Lower limb	Foot
▨ Ungulate s2/3	12	0	4	1	7	2
■ Ungulate s3/4	42	2	4	3	5	5
■ Sus	4	0	0	0	0	2
■ Equus	2	0	0	2	2	0
■ Bos/Bison	2	0	0	0	0	0
■ Capra	2	0	0	0	0	0
■ Cervus	0	0	0	0	0	0
■ Cervid	5	0	0	0	0	0

Skeletal representation with morphology and ZooMS



	Head	Axial post-cranial	Indeterminate limb	Upper limb	Lower limb	Foot
▨ Ungulate s2/3	12	0	4	0	4	2
■ Ungulate s3/4	42	2	4	1	4	5
■ Sus	5	0	0	0	0	2
■ Equus	2	0	1	1	4	0
■ Bos/Bison	3	1	20	0	0	0
■ Capra	2	1	10	0	2	0
■ Cervid	7	2	6	1	0	1
■ Cervus	4	4	18	3	2	1

Figure 5. – Skeletal representation of the identified taxa from combined Levels A1 and A2 at Riparo Bombrini.

Figure 6 shows the relationship between %MAU of cervids (*Cervus* + “cervid”) and bone mineral density. Most of the skeletal parts are represented by a single skeletal element, which resulted in a statistically insignificant correlation between %MAU and BMD (r_s = -0.24, p = 0.56)

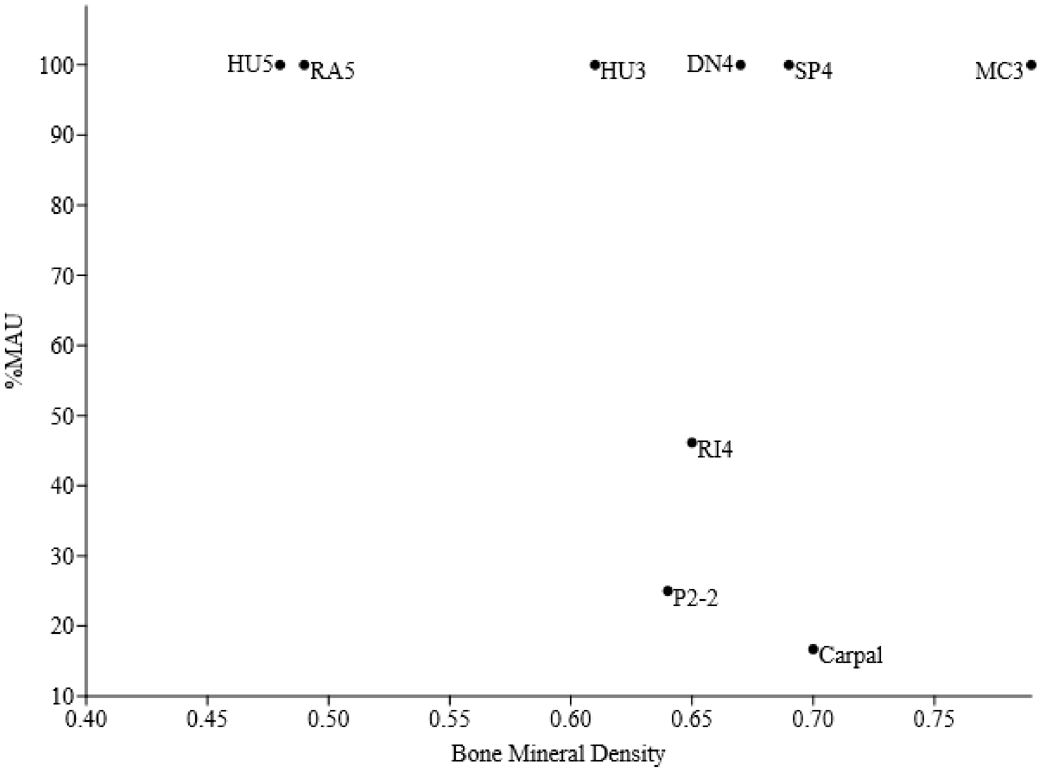


Figure 6. – Relationship between %MAU of cervids and bone mineral density. All density scan sites are detailed Lam et al. (1999): *HU* humerus, *RA* radius, *DN* mandible, *SP* scapula, *MC* metacarpal, *RI* rib, *P2* second phalanx.

4.5.2 Sex, Age, and Seasonality

There are currently no reliable data that could strongly indicate a preferred season of occupation in the Riparo Bombrini Proto-Aurignacian faunal assemblages. Except for the bovines, most of the documented hunted taxa are not particularly migratory animals and could have been available around the site year-round. A few cervid antler fragments could indicate either the acquisition of male animals or the gathering of fallen antlers. Lastly, the very few age diagnostic skeletal elements listed in Table 2 show the presence of at least three juvenile taxa on the site and some fetal skeletal remains, unfortunately too fragmented to be identified to element or taxon. Interestingly enough, all bone fragments corresponding to juvenile taxa and fetal bones come from either Level A1-A2 or Level A2. This could suggest seasonal occupations, namely spring occupations, in Level A2.

Table 2. – Age determinations

Taxa	**Square**	**Level**	**Fetal**	**Juvenile**	**Adult**	**Old**	**Element**	**Tooth wear stage***	**Height (mm)**
NID	E1	A1_A2	2				Indeterminate		
	DD1	A2	1				Indeterminate		
	EE1	A2	2				Indeterminate		
	EE3	A2	1				Indeterminate		
	FF3	A1_A2	1				Indeterminate		
Sus	FF3	A2		1			phalanx fusing		
	E1	A1_A2		1			molar or premolar	stage 1	
	DD1	A1_A2				1	premolar	stage 5	
Cervid	E1	A1_A2		1			phalanx unfused		
	D1	A1_A2		1			decidual premolar 4	stage 3	
	DD1	A2			1		upper molar	stage 4	9
Capra	EE1	A2		1			decidual premolar 4	stage 2	
Bos_Bison	DD1	A2			1		upper molar	stage 3	
	EE1	A1			1		lower molar	stage 3	23.7

*Gross stage estimation: stage 0 = unworn, stage 1= slightly worn, stage 2= worn, stage 3 = very worn, stage 4 = extremely worn.

4.5.3 Fragmentation and Taphonomy

Figure 7 shows the distribution of all faunal remains within six fragment size classes. The fact that the first size category (0-20 mm) is the largest attests to the fact that the overall degree of fragmentation of the Proto-Aurignacian faunal remains is extremely severe. The logged data (LOG 10) in Figure 7 shows that the faunal remains are slightly more fragmented in the south area, and especially in Level A2: remains are more abundant in the 0-20 mm size category and proportionally less abundant than the rest of the collection in the larger size categories. On the other hand, the outside area of the site contains a higher proportion of larger bones (>30 mm) than the rest of the collection.

	0-20	20-30	30-40	40-50	50-60	60-80	80-100	100<	Part and whole
▨ South A1	8073	83	44	10	6	0	0	0	9
▨ South A2	7148	42	12	3	1	1	0	0	10
■ North A1	3511	146	52	21	6	4	0	0	15
■ North A2	7921	240	53	28	13	6	1	2	20
■ Outsite	3642	289	97	34	10	9	3	1	18

Figure 7. – Number of bone fragments for each size categories excluding teeth (upper), and normalized proportion of the same set of bone fragments in each size categories using LOG 10 (lower).

Table 3 summarises all taphonomic data recorded on long bone shaft fragments that helped further characterize the preservation state of the faunal remains and all anthropic traces found on bone surfaces. The mean FFI scores show a clear dominance of dry fractures throughout the collection. While some slight preservation variability can be observed between the site areas (the scores are slightly higher inside the rockshelter, than outside) when comparing mean FFI scores, it is not significant enough to assess the nature (anthropic or post-depositional) of this variability. The %ZooMS success, however, demonstrates a clear preservation bias. Indeed, 78% of the bone samples recovered outside the shelter yielded enough well-preserved collagen to allow ZooMS animal identification. In contrast, ZooMS success was never greater than 30% inside the rockshelter. This indicates that some taphonomic effects played a greater role in collagen and bone diagenesis inside the rockshelter.

Table 3. – Summary of taphonomic data within each Proto-Aurignacian levels (A1 and A2) and site areas (south, north, and outside).

	South A1	**South A2**	**North A1**	**North A2**	**Outside A1-A2**
Mean FFI score	5.94	5.74	5.43	4.84	4.47
ZooMS success rate	18.7% (N=134)	29.2% (N=89)	26.7% (N=90)	9.4% (N=128)	77.8% (N=171)
Anthropic percussion (N)	0	0	2	0	7
Cut marks (N)	0	2	0	0	1
Ochred bones (N)	0	0	1	92	0
Flakes (N)	0	1	1	13	2
Bone manufacture (N)	0	0	0	1	1
Bone tools (N)	2 awl fragments*	1 needle tip, 1 awl*	0	0	0
Decorative elements (N)	0	0	1 incised bird diaphysis*	0	0
Proportion of total burned bones (%)	43.6% (N=8225)	29.4% (N=7221)	50.4% (N=3756)	55.1% (N=8283)	38.8% (N=4106)
Proportion of cancellous burned bones (%)	1.7% (N=8225)	4.3% (N=7221)	6.0% (N=3756)	13.5% (N=8283)	9.5% (N=4106)
Proportion of cancellous bones (burned and unburned combined) (%)	4.1% (N=8225)	8.9% (N=7221)	9.7% (N=3756)	19.3% (N=8283)	17.8% (N=4106)

*Previously published (Holt et al., 2019)

The main post-depositional alterations observable on long bone shaft surfaces, namely concretion, root etching, and manganese coloration, are presented in Figure 8. Carnivore gnawing is episodic on the faunal assemblage and only one wolf specimen was found in Level A1 (Fig. 4). Root and microorganism etching as well as a light manganese coloration are present throughout the collection but are especially pronounced on the faunal remains recovered outside the rockshelter. Concretion heavily affected the whole collection but particularly in the north area and outside the rockshelter.

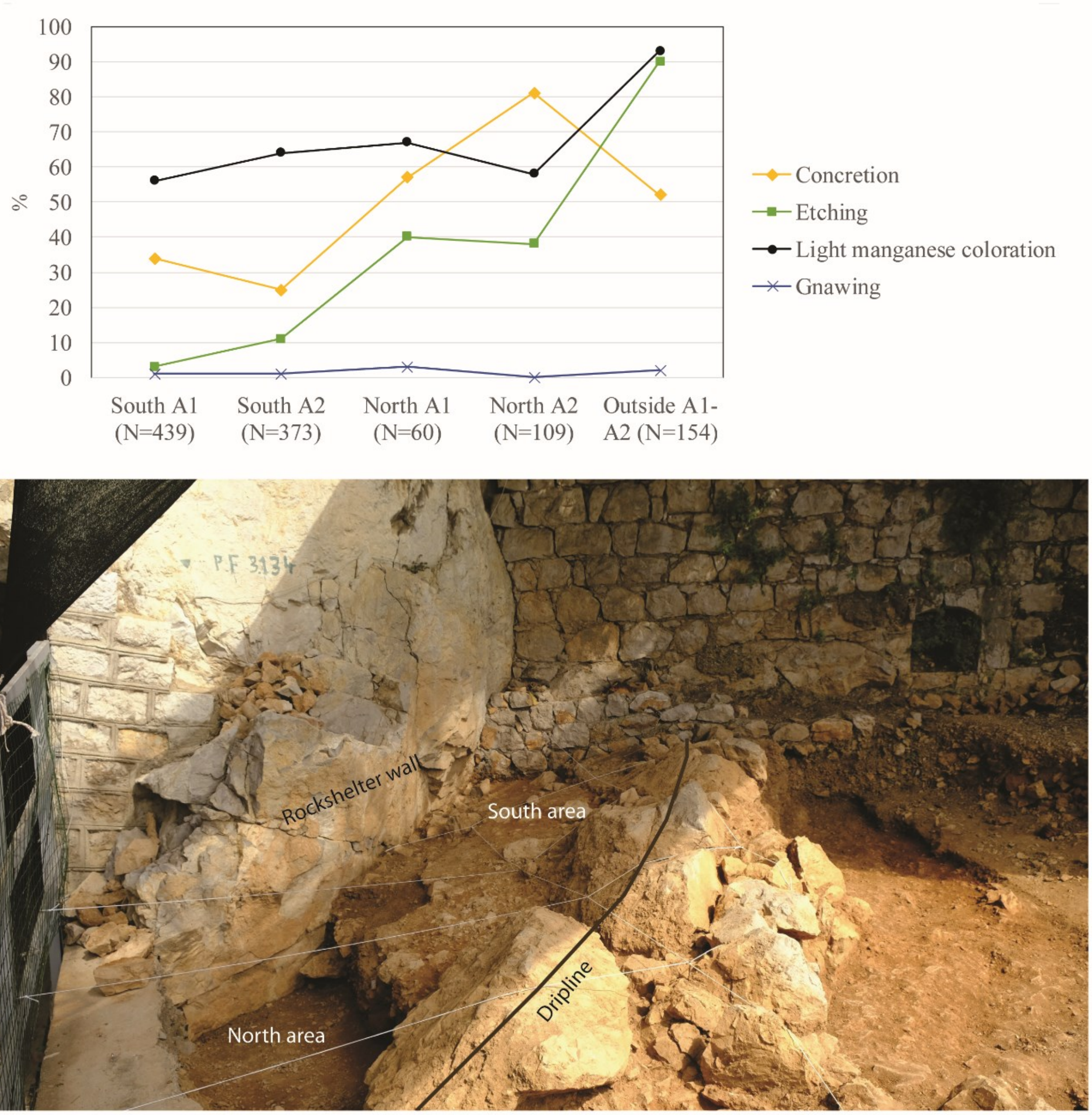


Figure 8. – Proportion of taphonomic effects (concretion, etching, manganese, and carnivore gnawing) on long bone shafts within each Proto-Aurignacian levels (A1 and A2) and site areas (south, north, and outside) (above), site contextualization showing north and south areas delimited by the original rockshelter wall and the dripline.

Figure 9 and 10 show examples of anthropic actions recovered in the Proto-Aurignacian faunal collection at Riparo Bombrini and listed in Table 2: a bone needle tip located in the south area (Fig. 9), a bone flake (or splinter) located outside the rockshelter (Fig. 9), a grooved bone located in the north area, and burned bones covered with dots of ochre concentrated near the hearth feature (Fig. 10).

Figure 9. – Example of anthropic marks: (1) grooving, (2) needle tip, (3) bone flake, magnification 20X, scale = 3 mm.

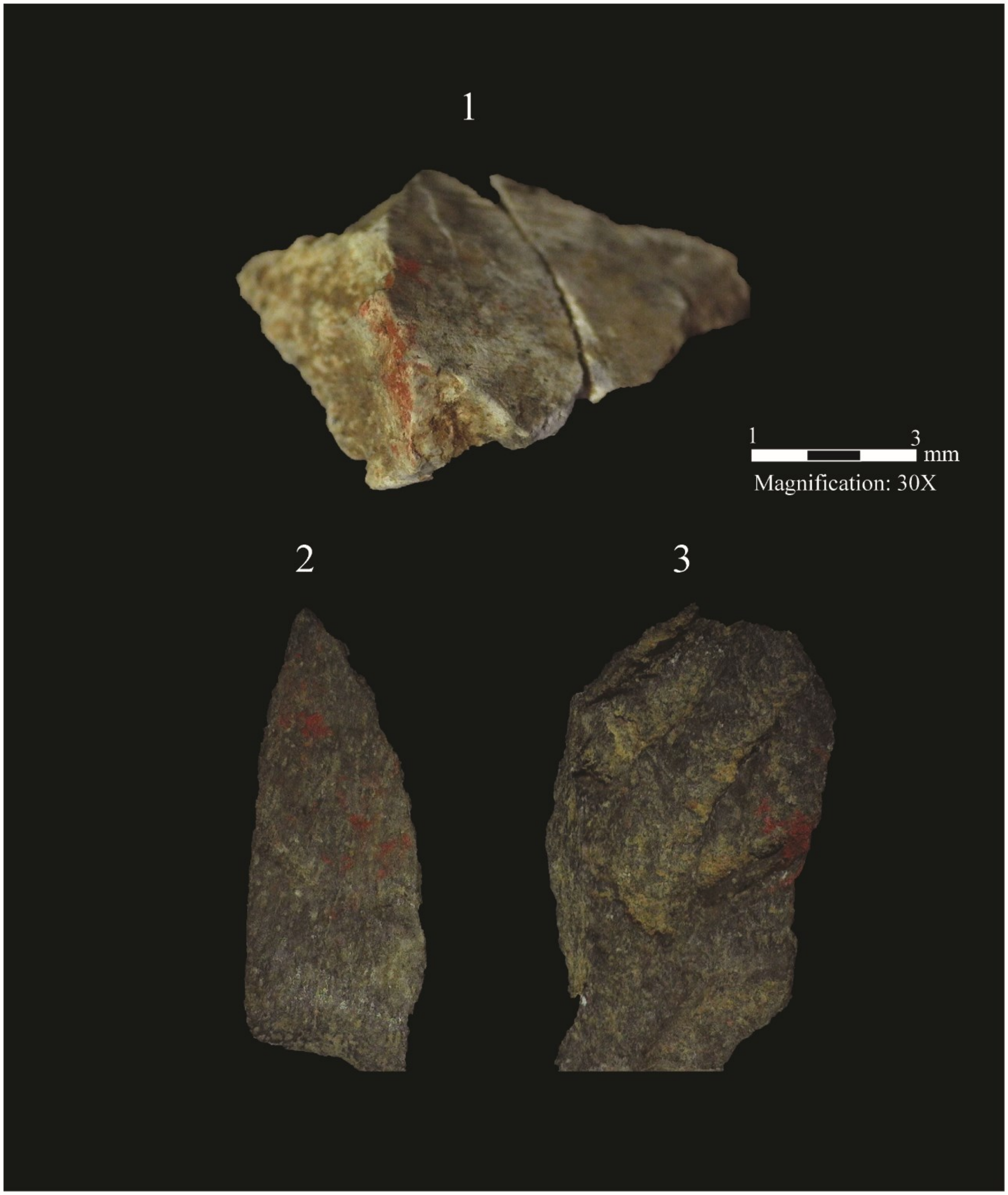


Figure 10. – Example of calcined (1) and carbonized (2, 3) bone fragments covered with dots of red ochre, magnification 30X, scale=3mm.

Figure 11 shows the proportions of six bone types (appendicular cancellous, axial cancellous, indeterminate cancellous, appendicular cortical or bone shaft, and indeterminate) in eight size classes (0-20 mm, 10-20 mm, 20-30 mm, 30-40 mm, 40-60mm, 60-80mm, 80-100mm, and 100<mm) within each level and site area. First, there is some spatial patterning in these data. Compared to the south and the outside areas, a larger proportion of cancellous bones (mostly indeterminate, but also axial and appendicular) are distributed in the north area, which is where hearths were found in both levels. In contrast, the south area, interpreted as having been used mainly as a trash pit in both levels, is dominated by indeterminate and bone shaft fragments, while a mixture of bone types can be found outside the rockshelter, including a slightly higher proportion of better preserved and bigger flat bones, mostly rib fragments. Second, comparing Levels A1 and A2 inside the rockshelter, we can observe a higher proportion of cancellous bones in Level A2 both in the north and south areas.

Figure 11. – Proportion of six bone types in relation with six size classes within each level (A1 and A2) and site areas (south, north, and outside), excluding the part and whole anatomical elements.

Figure 12 shows the proportion of burned and unburned bone fragments distributed by bone type (appendicular cancellous, axial cancellous, indeterminate cancellous, appendicular cortical or bone shaft, and indeterminate) within each level and in each site area. Comparing the site areas, one striking observation is that outside the rockshelter, few bone shaft fragments or flat bones are burned. In contrast, over 70% of appendicular and indeterminate cancellous bones are burned. Less than 10% of axial cancellous bones are burned, however, thus displaying a different pattern from the other two types of cancellous bones. The indeterminate category, which is the most abundant, generally tends to follow the same pattern of fragmentation as the cortical bone as it mostly contains very small (>10mm) fragments with no intact surfaces. The same trends are observed in the south area inside the rockshelter, although with slightly higher proportions of burned bones across all bone type categories, except for appendicular cancellous bones. Finally, the hearth area (north) shows a distinct pattern since it displays a much higher proportion of burned, cancellous bones. This pattern is especially pronounced for Level A2 and it is coupled with a high concentration of calcined bones across all bone type categories. Calcined bones are generally associated with direct exposure of a bone surface with high temperatures such as those produced by flames. Also, the distinct pattern observed on axial cancellous bones outside the rockshelter is not apparent inside the rockshelter (Fig. 12).

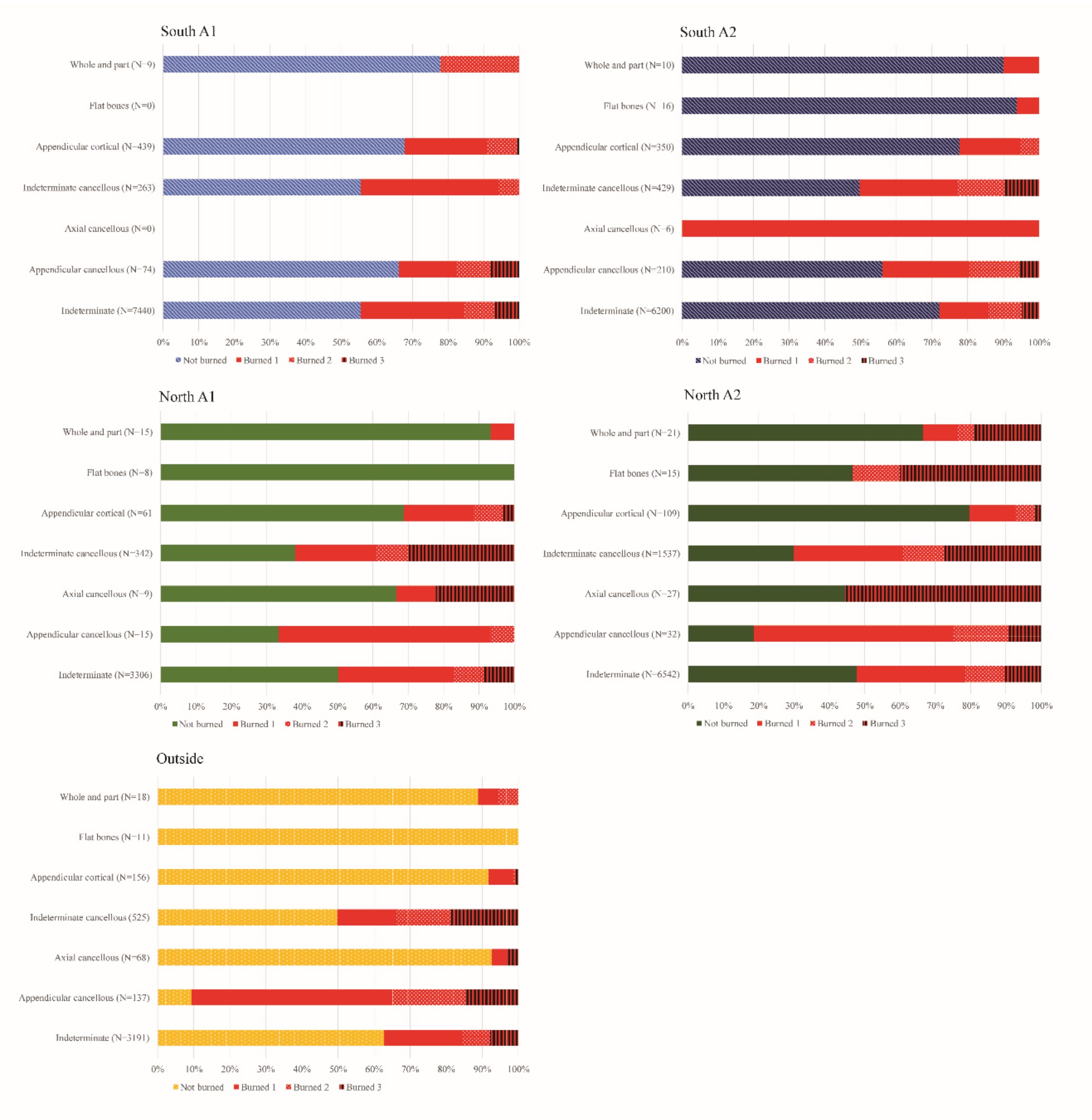


Figure 12. – Proportions of burned (burned 1, burned 2, burned 3) and unburned bones in relation with seven bone type categories within each level (A1 and A2) and site areas (south, north, outside).

Finally, Figure 13 shows a summary of all anthropic subsistence-related data recovered on the site (NISP, skeletal representation, anthropic marks, etc.) spatially contextualized in two faunal distribution maps corresponding to Level A1 and Level A2.

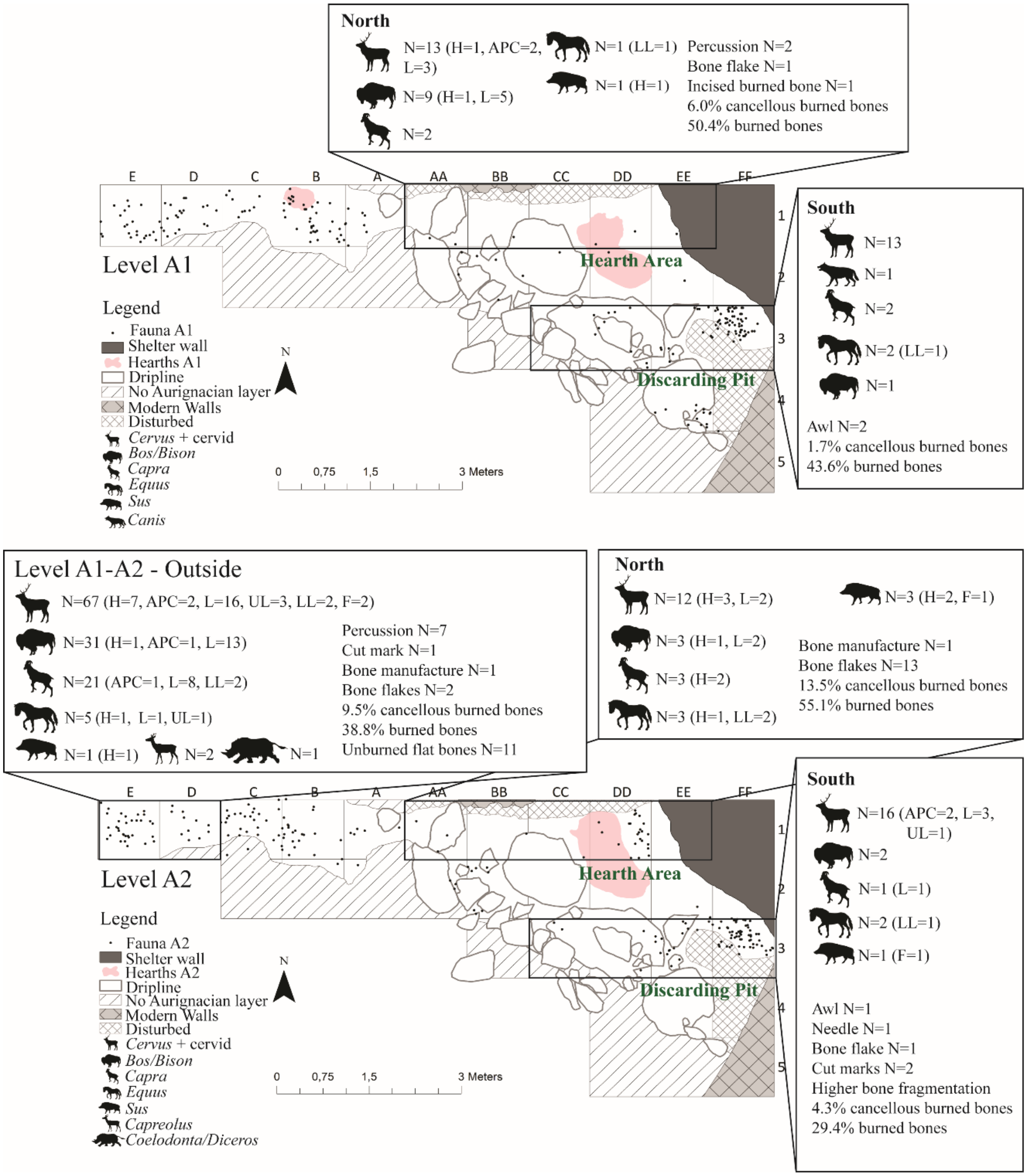


Figure 13. – Distribution maps (Level A1: top, Level A2: bottom) of all plotted faunal remains with summarised archaeozoological data, including NISP and skeletal representation (H head, APC axial post cranial, L limb, UP upper limb, LL lower limb, F foot), and anthropic taphonomic data within each site area (south, north, and outside). Animal silhouette images from http://phylopic.org/.

4.6 Discussion

4.6.1 Faunal Diversity and Hunting Strategies

Before including the ZooMS identification results, the total NISP included only 16 fragments identified to species and a few bones identified to broader categories (cervid, bovid, carnivore, and ungulate). Unfortunately, 409 of the 644 ZooMS samples were too poor in collagen to provide taxonomic identification (Table 2). This issue will be addressed in the future by tightening our screening threshold in the sampling process with a portable FTIR. Nevertheless, the 235 positive ZooMS samples considerably improved our understanding of the diversity of fauna hunted during the Proto-Aurignacian (Fig. 4). As expected, cervids, mainly red deer but also some ZooMS identified roe deer (N=2), dominate the faunal assemblage in both levels. However, bovines, mountain goats, horses, and wild boars also seem to have been regularly hunted, since they account for more than 40% of the NISP (Fig. 4) in both levels. Even if our sample size remains very low, the diversity of the faunal assemblage, which is comparable in Level A1 and Level A2, points to more generalist rather than specialized hunting strategies.

As concerns paleoenvironmental reconstructions, the macrofauna does not disagree with previous reconstructions based on pollen and microfauna (Holt et al., 2019). Cervids in both levels are compatible with forested environments. Equids in both levels as well and one specimen of rhinoceros in Level A1-A2 suggest the presence of an open plain close to the site. However, the proportions of the different species do not specifically point towards warmer conditions in Level A1. On the contrary, while proportions of caprids are similar in both levels, the higher proportion of bovines and a lower proportion of wild boar would indicate colder conditions and more open habitats. However, environmental reconstructions based on the presence and absence of macrofauna can sometimes be misleading as paleoenvironments are different from today and often contain a mosaic of ecotypes and extinct taxa that are difficult to compare with extant environments (e.g., hyenas living in the same ecotype as mammoths, reindeers, horses). Likewise, it is important to appreciate that the faunal assemblages from both levels, while distinct, nonetheless represent palimpsests accumulated over several millennia during a period of remarkable climatic volatility, so that the presence of a few cold-adapted species is not enough to reflect distinct environmental conditions. Furthermore, the specific species of bovine at Riparo Bombrini is unknown and could lead to different environmental reconstructions as it is well documented that some extant species of bison live in small groups with local mobility in forested environments while others live in arid conditions and migrate in large herds on open steppes (Julien et al. 2012). It should also be noted that most of the bovines identified on the site come from the exterior of the rockshelter in which Levels A1 and A2 are undifferentiated (Fig. 13). Also, the bovines used to compare Levels A1 and A2 are very few and were almost all clustered within the eastern section of the hearths (Fig. 13). This cluster could therefore be subject to archaeological aggregate biases.

While our sample is small and too aggregated to resolve the question of environmental patterns, we have already pointed out that the picture that emerges is one of overall continuity in animal procurement strategies across Levels A1 and A2, which is especially interesting from a behavioural perspective. The abundance of red deer in the region comes with no surprise and hunter-gatherers would have been able to take advantage of their abundance around the site year-round. However, the fact that bovines, wild goats, wild boars, and horses were also part of the targeted species hints towards a generalist strategy, which suggests Proto-Aurignacian foragers exploited the whole spectrum of animals available locally.

One way to verify if Proto-Aurignacian hunter-gatherers were indeed hunting on a local scale is to reconstruct carcass transport through the information available from skeletal representation. Unfortunately, because the skeletal representation data are very scarce (Fig. 5), very few interpretations can be securely drawn from them. Nevertheless, Figure 5 suggests that some cervid carcasses, represented by the presence of all body portions in both Proto-Aurignacian levels, were brought to the site whole, implying that they were available close to the site. The diversity of skeletal parts for the other animal species is very poorly documented, but anecdotally, axial and appendicular elements are present for most taxa, again suggesting the transport of at least a few whole carcasses, since axial skeletal parts are often left at the kill site if the animals are hunted far from the base camp. Similarly, both ungulate categories (size 2/3 and size 3/4) include skeletal remains from most body portions. Another element supporting the idea that complete carcasses were brought to Riparo Bombrini comes from the indeterminate fraction of the assemblage. In fact, the constant presence of axial cancellous and flat bones (especially outside the rockshelter) agrees with the hypothesis of a number of carcasses being brought back whole at Riparo Bombrini. In sum, despite the scarcity of the information provided by the relative abundance measurements and skeletal representation, the overall hunting strategy appears to have been a local generalist one throughout the Proto-Aurignacian.

4.6.2 Fragmentation, Bone as Food and More

Results from the taphonomic analysis indicate that most of the heavy bone fragmentation observed in the Proto-Aurignacian levels of Riparo Bombrini was caused by post-depositional forces, as suggested by the very high mean FFI scores in both levels which show a dominance of dry fractures (Table 2). Soil compaction, likely largely the result of blasting operations during the construction of the railway in the 19th century, coupled with concretion at least partially explains the heavy fragmentation and collagen degradation at the site (Fig. 8). Heavy concretion affects the entire collection inside the rockshelter, particularly in the north area, closer to the back wall of the rockshelter where the blasting events would have been most intense (Fig. 8). The concretion could also be related to taphonomic processes causing chemical bone dissolution (Karkanas et al. 2000; Stiner et al. 2001; Trueman et al. 2004; Weiner et al. 1995, 2007), but we would have to characterize sediment mineralogy in order to assess this (Stiner et al. 2001). This was unfortunately not possible at the moment.

However, some macroscopic observations agree with the fact that anthropic actions also contributed to bone fragmentation, and perhaps to some degree, also to bone diagenesis at the site. First, even though concretion particularly affected bone fragments from the north area, it is also present outside the rockshelter (in higher proportions than in the south area), coupled with heavy etching action, whereas the collagen is better preserved and the FFI mean score is lower in this area (Fig. 8, Table 2). This implies that different taphonomic processes occurred inside and outside the rockshelter. Second, while bone dissolution cannot be ruled out for the loss of smaller fragments in some areas at this point and should be assessed in the future since phosphate and carbonate diagenesis in bones is a known phenomenon in Mediterranean sites (Stiner et al. 2001), the diversity of skeletal tissue documented at the site (Fig. 12) indicates that more fragile bone (e.g., cancellous bones) is well represented inside the rockshelter and is in fact slightly less abundant outside the rockshelter, where bone collagen is better preserved. If dissolution events such as water flows had occurred inside the rockshelter during the Proto-Aurignacian, the more fragile bones would have been the first to be destroyed. Given these different patterns, it therefore seems warranted to propose that the heavy fragmentation of bone remains in both Proto-Aurignacian levels at Bombrini is at least partially due to human activities. This is further supported by the fact that underlying Mousterian levels contain better preserved faunal remains (at least at the macroscopic level). Additional factors support a high intensity of human occupation at the site throughout the Proto-Aurignacian, namely the low incidence of carnivore modification documented in both levels (Table 2, Fig. 8), the high density of archaeological remains, and the preponderance of burned bones (Table 2, Fig. 12).

It is unsurprisingly very difficult to characterize carcass treatment on the site since, apart from burned bones, evidence of anthropic actions is very scarce (Table 2) and is partially masked by the high degree of dry fractures and bone surface erosion. Nevertheless, a few cut marks, grooving marks, bone flakes, and bone tools were recovered from all parts of the site (Table 2, Fig. 9). A small concentration of burned and unburned bones covered with dots of red ochre was also uncovered in square DD1 in Level A2 (Fig. 10). Since the ochre covers both fresh and dry bone fractures, this dotting is likely simply the result of proximity of the bone fragments to numerous ochre fragments present in the sediment in Level A2. Most of the fragments bearing percussion marks come from outside the rockshelter, but a few are also found in the north area from Level A1 (Table 2, Fig. 13). The bone flakes are spread across the three areas of the site and in both levels, but a marked concentration is located in the north area from Level A2 (Table 2, Fig. 13). Cut marks and bone tool manufacture marks (grooving) are very scarce and found in all parts of the site. Finally, in both levels, all bone tools (awl and needle fragments) were recovered in the southern part of the site (Table 2, Fig. 13).

As stated above, two kinds of human behaviours are known from the archaeological and the ethnographic records to produce heavily fragmented faunal assemblage: (1) bone marrow and grease extraction, and (2) the use of bones as fuel. Bone marrow extraction is a well-known behaviour among prehistoric and extant high-latitude hunter-gatherer groups, among whom it is an almost universal behaviour (Vehik, 1977; Binford, 1978; Outram, 2001). Considering the bone flakes and percussion marks on long bone shafts documented in both Proto-Aurignacian levels, it is reasonable to hypothesize that marrow extraction took place in Bombrini (Table 2). Furthermore, from a spatial perspective, two small bone flake concentrations can be seen. The first is located outside the rockshelter and is associated with a concentration of bones bearing percussion marks and a diversity of skeletal body parts including 11 unburned flat bone fragments (Fig. 13). These combined observations agree with the first stages of butchery and bone cracking away from the site's main living area. The second bone flake concentration is found in Level A2 and is located in the north area, close to the hearth. This second concentration is not associated with percussion marks on long bone shafts, either because they were not preserved or because those flakes are related to a different activity such as bone tool manufacture (Fig. 13). Diagnostic evidence of grease rendering is not detectable on the faunal remains at Riparo Bombrini. If at some point, there were concentrations of heavily crushed appendicular and cancellous bones bearing fresh fracture outlines on the site, they are now completely masked by post-depositional processes. In addition, no fire-cracked rocks have so far been recovered in the Proto-Aurignacian levels.

In contrast, diagnostic evidence of the use of bone as fuel is found in the high proportion of burned cancellous bones around the hearths (north area) compared to the other site areas. This is especially noticeable in Level A2, where cancellous burned bones represent 13.5% of the north area's assemblage compared to 6.0% in Level A1. However, in both levels, over 50% of bone fragments in the north area are burned (Fig. 12). Furthermore, in Level A2, a large proportion of the burned bones are in fact calcined (burned 3), especially within bone type categories corresponding to whole and fragmented epiphyses, flat bones, indeterminate cancellous, and axial cancellous bones. These patterns suggest that hunter-gatherers selected the spongy parts of the carcasses from both appendicular and axial body parts filled with grease, to fuel the hearth to produce durable flames. This may have been done to perform specific illumination, heating, drying, rituals, and/or discard activities (Costamagno et al. 2005; Marquer et al. 2010; Morin 2010; Théry-Parisot et al. 2004). Alternatively, the use of cancellous bone for fuel could have been related to the opportunistic use of spongy bones when faced with a lack of wood in the environment (potentially related to length of occupation).

4.6.3 Mobility and Resource Management at Riparo Bombrini

The data about subsistence patterns presented in this study also permit a refined understanding of what was so far known about mobility and resource management at Riparo Bombrini. Table 4 summarises the trends drawn from the available lithic, environmental and now faunal data and to compare them across Levels A1 and A2 to reach new insights about variability in Proto-Aurignacian behaviour.

Table 4. – Comparison of the organisational strategies employed in levels A1 and A2 at Riparo Bombrini as described in Riel-Salvatore and Negrino (2018a, 2018b) and added information from the faunal and spatial data.

Previously observed behaviours in the Proto-Aurignacian levels at Riparo Bombrini	
Continuous dominance of bladelets	
Same *Chaîne opératoire* to produce bladelets: flexible technocomplex	
Level A1: Residential mobility	Level A2: Logistical mobility
Warmer climate*	**Colder climate***
Shorter occupations of the base camp	**Resilience through HE4**
↑ Curated lithic organization	Longer occupations of the base camp
↑ Retooling	↑ Cores and unbroken bladelets
Stouter, but shorter bladelets	Longer, narrower bladelets
Focus on local raw material	↑ exotic raw material
Additional observations made from the faunal and spatial data	
Continuous faunal diversity: generalist hunting strategies close to the site	
Continuous occupation of the base camp with distinct areas of domestic activities	
Less defined faunal aggregations	↑ aggregation of faunal remains
Less systematic use of bones as fuel	↑ bone flakes and faunal concentration next to the hearth
	↑ proportion of burned cancellous bones
	Seasonal occupations

*Combined data from microfauna, pollen, and macrofauna in Holt et al. (2019), and Riel-Salvatore and Negrino (2018a).

Previous studies had already highlighted continuity in some behavioural dimensions between the two levels, namely the dominance of bladelets produced within the same *chaîne opératoire* indicative of a flexible technocomplex (Riel-Salvatore and Negrino 2018b, 2018a). The consistent production of very polyvalent hunting armatures throughout the Proto-Aurignacian is congruent with our conclusion that the faunal record indicates an overall generalist hunting strategy implemented close to the site. Along with the bladelet-based lithic technology that characterizes the Bombrini Proto-Aurignacian, the hunting activities appear to have been flexible, allowing hunter-gatherers a great deal of resilience in the face of considerable environmental instability, including dramatic paleoclimatic shifts such as Heinrich Event 4 and the eruption of the Phlegrean Fields ca. 39ky cal BP. Thus, both hunting strategies and lithic technological organization combine to reinforce the interpretation of Bombrini having served as a base camp characterized by distinct, spatially discrete activity areas. Outside the rockshelter, the uniformly distributed faunal remains, the presence of percussion marks, cut marks, bone flakes, bone tool manufacture marks (grooving), and a diversity of skeletal body parts with mixed burned and unburned remains, are characteristic of different behaviours related to butchering activities, bone marrow extraction, and a general discard area (Fig. 13). In contrast, the north area is characterized by the presence of one cuvette-type hearth in each level, around which a more restricted set of activities was documented, including bone tool manufacture (grooving marks), the use of red ochre, and the use of bones as fuel, as suggested by the high concentrations of cancellous burned bones (Fig. 12). Finally, the south area contains a higher proportion of heavily fragmented burned and unburned faunal remains in addition to broken bone tools (awls and needles) concentrated in a depression interpretable as a refuse pit identified mostly in square FF3 (Fig. 13).

In addition to this behavioural continuity in faunal exploitation, however, some notable differences also exist between the two levels, and these agree with the previous conclusions drawn from the lithic record. Indeed, variability in lithic technological organization has previously been interpreted to show that Level A1, which is associated with overall warmer climates, was characterized with a more residential mobility strategy while Level A2 shows a logistical mobility strategy associated with colder climates and longer occupations of the base camp (Riel-Salvatore 2007, 2010). Several lines of evidence from Level A2 indicate that Proto-Aurignacian groups occupied the site for prolonged periods of time. First, faunal remains are more spatially concentrated inside the rockshelter, and more fragmented inside the discarding pit, which may indicate a greater degree of site maintenance. Second, the higher density of faunal remains in the north areas (A1: N=3756; A2: N=8283) in addition to a concentration of ochre and bone also indicate specific repetitive hearth-related activities over longer periods of time.

At first glance, patterns of carcass curation less clearly distinguish Levels A1 and A2, since both assemblages indicate the use of bones as fuel. Nevertheless, we propose that fuel management changed overtime, since in Level A2, all grease-rich skeletal parts of carcasses appear to have been systematically used as fuel, likely to extend flame durability. In Level A1, in contrast, the pattern appears to shift to a more sporadic use of cancellous bones as fuel. This scenario is strengthened by (1) the higher proportion of cancellous burned bones documented in Level A2 as a whole; (2) the higher proportion of calcined bones around the hearth in Level A2; and (3) by the fact that it also yielded an overall much larger number of cancellous bones, including indeterminate, appendicular, and axial cancellous burned and unburned bones (A1: N=412; A2: N=1596).

Furthermore, the prolonged occupations in Level A2 are potentially associated with seasonal occupations of the site during spring and summer as demonstrated by the presence of fetal remains and a few juvenile ungulate taxa (Table 2). Seasonal occupations of the site are also congruent with a logistical mobility strategy.

4.7 Conclusion

In sum, this study has yielded important new methodological, empirical and behavioural insights into the Proto-Aurignacian occupations of Riparo Bombrini. These, in turn, have important implications for our understanding of some of the earliest *Homo sapiens* adaptations in Western Europe. Methodologically, the notion of *carcass curation*, as reconstructed by the crossing of archaeozoological, taphonomic, spatial and proteomic data, has been shown to have considerable analytical promise, in addition to providing a coherent framework to integrate interlocking sets of information gleaned from heavily fragmented faunal assemblages that can be seen as having only limited analytical potential from a traditional archaeozoological perspective. This approach further shows that a considerable amount of information can be extracted from challenging faunal assemblages, with distinct strands of data combining to form more solid inferential cables that can serve as working hypotheses that can be integrated with other lines of evidence (e.g., lithics) and structure ongoing analyses at the site. Furthermore, the present paper is the first application of the ZooMS screening method first proposed elsewhere (i.e., Pothier Bouchard et al. 2019) to obtain usable data about prehistoric forager behaviours at Riparo Bombrini that complements and considerably enhances our understanding of prey selection by Proto-Aurignacian hunters.

This ties into the empirical contribution of this analysis, since our results provide the first detailed analysis of Proto-Aurignacian large mammal exploitation at the Balzi Rossi and indeed in the Liguro-Provençal arc more broadly. Historically, large fauna has been largely excluded from consideration in synthetic analyses of the Riparo Mochi sequence (e.g., Kuhn and Stiner 1998), outside of oblique mentions to its heavily fragmented state (Tejero and Grimaldi 2015:68; Moussous, pers. comm.), which contrast to the relatively better-preserved nature of the Gravettian faunal assemblages at the same site (Tagliacozzo et al. 2012). This has led to a great deal of attention being paid to its mollusk assemblage (e.g., Stiner 1999) to the exclusion of the rest of the faunal assemblage. Likewise, outside of a partial species list (Brugal et al. 2017; Onoratini and Simon 2004), little is known about Proto-Aurignacian faunal exploitation patterns at nearby Grotte de l'Observatoire in Monaco, and a recent publication on the 2002-2005 excavations at Riparo Bombrini is limited to species identification (Holt et al. 2019). Thus, our systematic application of the ZooMS proved to be an excellent means of tackling heavily fragmented faunal assemblages. Mass sampling with ZooMS fingerprinting does not solve all issues related to bone fragmentation in Paleolithic archaeozoology, however. As we have detailed elsewhere (Pothier Bouchard et al. 2019), much work remains to be done to develop an adequate conceptual framework to fully integrate ZooMS into archaeozoological research. Such a framework will need to eschew randomly sampling of hundreds of bones within the smaller indeterminate fraction of faunal assemblages in favour of tailoring sampling strategies to specific hypothesis-testing approaches that seek to answer questions related to past subsistence behaviors.

The present study is a first step in this direction, and our results show the promise of such efforts, since it has already yielded important new data about Proto-Aurignacian settlement dynamics at Riparo Bombrini, namely that animal carcasses, and especially those of red and roe deer, were in all likelihood brought whole to the site. Similarly, the evidence we present for systematic, large-scale marrow extraction is the first such evidence for these behaviours in *Homo sapiens* in the region and indicates a sustained effort at maximizing the nutritional utility of hunted prey. Additionally, the use of bones as fuel documented at Riparo Bombrini also broadens our understanding of carcass curation behaviours by human foragers, likely also suggesting a polyvalent use of fuel sources to sustain different kinds of flame and heat in different contexts. Finally, the combined impacts of purposeful fragmentation for marrow extraction and of the use of bone as fuel inside the rockshelter help explain the heavily fragmented and initially challenging nature of the faunal assemblages at Riparo Bombrini. It also highlights that modern taphonomic effects such as the impact of soil compaction resulting from railroad construction and demolition on the state of the faunal collection do not fully explain the state of the collections. This leads to the further implication that Proto-Aurignacian anthropic manipulations likely bear a substantial portion of the blame for the poor state of collagen preservation of the faunal remains recovered from inside the shelter. This is compounded by our demonstration that the Riparo Bombrini faunal assemblages yield extremely limited traces of carnivore modifications.

On the behavioural front, the results presented here also both support and nuance previous interpretations about the internal variability of the Proto-Aurignacian at Riparo Bombrini. First, it reinforces the idea that the technocomplex was an adaptable strategy that allowed a great deal of flexibility to respond to shifts in local conditions to favour the long-term resilience of the human occupation of the region. Specifically, the generalist strategy we evidenced in both Proto-Aurignacian levels at Bombrini indicates a broad rather than narrowly focused subsistence strategy. This agrees well with the mollusk data from Riparo Mochi that suggest that foragers were broadening their diets from the very beginning of the Upper Paleolithic (Kuhn and Stiner 1998; Stiner 1999), another element that argues against a specialized subsistence base in the Ligurian Proto-Aurignacian. On both levels, it seems clear that the site was used as a base camp around which other activities on the landscape were organized.

That said, the faunal data from Level A2 also indicate that, during the accumulation of this level, the site was used for longer periods of time, as shown by the more organized spatial separation of activity areas and by the greater abundance of faunal remains that accumulated over the same site surface in that level compared to Level A1. To this, we can add the apparent systematic use of cancellous bone to feed fires in Level A2, which contrasts with its more sporadic use for this purpose in Level A1. This again may reflect longer occupation in Level A2, which, along with seasonal occupations of the site, agrees with previous interpretation of that level's lithic assemblage showing a more logistical land-use strategy, when the site would have been used as a base camp for prolonged periods of time during a generally colder phase (Riel-Salvatore & Negrino 2018a, 2018b). In sum, the faunal data appear to dovetail nicely with what could be gleaned from the lithic record to underscore that the Proto-Aurignacian comprised a fair amount of internal variability, which is likely linked to its longevity as a human adaptive system in the region.

Finally, the faunal data presented in this analysis provide additional support for the adaptive polyvalence of the Proto-Aurignacian, showing it was able to weather very different climatic regimes. This therefore reinforces the previous conclusions of some of the authors that there is not, at least in the Ligurian region, a solid basis to argue that the Proto-Aurignacian was narrowly adapted to limited ecological conditions. This provides another explanation for the apparent longevity of the technocomplex as the quintessential early *Homo sapiens* adaptation in the region, in contrast to what other scholars have argued for other regions (Banks et al. 2013a). While this does not resolve outstanding questions about the potential links, or lack thereof, between the Proto-Aurignacian and Early Aurignacian, the fact that an independent line of evidence, in this case, animal bone assemblages, again supports the internal dynamism of the Proto-Aurignacian at the Balzi Rossi certainly highlights that such a reductive view of early modern human settlement dynamics is unwarranted at a continental scale. Further, the method employed here to approach the notion of carcass curation through the combination of archaeozoology, taphonomy and ZooMS and to link it to broader questions about land-use and settlement organization, shows that it holds much promise to extract meaningful behavioural data from even the most fragmented of assemblages. This opens a pathway to the study of comparable assemblages, such as those from nearby Riparo Mochi, for instance, in order to contribute to the necessary integration of technological and subsistence data to reach an appropriately complete view of the Proto-Aurignacian as an anthropological phenomenon (Soulier 2013, 2014).

4.8 Acknowledgment

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4.9 References

(References are grouped in the Bibliography)

4.10 Supplemental information

(See Appendix 2)

Chapter 5 – Complete analysis of the transitional levels and regional opening

This paper fully integrates the ZooMS to the archaeozoological analysis of the transitional levels (i.e., A1, A2, and MS) at Riparo Bombrini. The challenging preservation state of the faunal remains also called for the application of an intra-site multivariate approach to the taphonomic analysis. The results of this faunal analysis are contextualized and discussed within the regional settings of the Liguro-Provençal arc and our current knowledge of Neanderthals and modern human subsistence behaviours during the transition.

5.1 Article 3 – Comparing Neanderthal and Modern Human Subsistence at Riparo Bombrini: an archaeozoological and multivariate taphonomic analysis with integrated ZooMS

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5.2 Abstract

The details of the subsistence shifts over the course of the Middle-Upper Paleolithic transition in the Liguro-Provencal arc remain elusive, in spite of the unique archaeological deposits documenting that shift in the region. Part of the challenge in getting a clear picture has been taphonomic and methodological. For instance, in the Balzi Rossi site complex, faunal assemblages dating to the interval 43-36 ky cal BP are notoriously fragmented, which impedes straightforward taxonomic identification and the application of most conventional archaeozoological methods. Likewise, collagen preservation is often poor, making identification through proteomics challenging. This study analyzes three assemblages from one of the Balzi Rossi sites, Riparo Bombrini, using an integrated methodological approach that combines archaeozoological methods, multivariate taphonomic analysis and FTIR-aided mass ZooMS sampling. The results indicate that the Proto-Aurignacian faunal assemblages from Levels A1 and A2 were accumulated almost exclusively by *Homo sapiens* foragers, whereas the final Mousterian documented in Level MS was accumulated as a result of brief, alternating site visits by Neanderthals and medium-sized carnivores. While human faunal exploitation strategies in all three levels focused on locally available prime-aged cervids, often brought back whole and processed extensively at the site, Neanderthal range preys in Level MS was relatively narrow. In contrast, a wider range of taxa was exploited by modern humans in the Proto-Aurignacian, when Riparo Bombrini was occupied as a long-term logistical base camp. In the Proto-Aurignacian levels, bone also appears to have regularly been used as fuel, indicating likely prolonged fall/winter occupation, particularly for Level A2. These results provide the first high-resolution view of human subsistence during the transition in the region and set up test hypotheses about the changing nature of hominin behavioural ecology that can be further tested in future work.

Keywords: Middle-Upper Paleolithic transition, Proto-Aurignacian, Mousterian, Mediterranean prehistory, Liguria, Balzi Rossi, Riparo Bombrini, Subsistence, hunting strategies, Archaeozoology, Taphonomy, Multivariate approach, ZooMS.

5.3 Introduction

Recent regional overviews of the subsistence patterns in the faunal record of western France and the Italian Peninsula highlight differences in adaptive behaviour between Neanderthals and modern humans during the Middle-Upper Paleolithic transition (Rendu et al. 2019; Romandini et al. 2020). The observed changes in human-environmental relationships regarding hunting technology, human-carnivore interactions, carcass processing, and the range of exploited animal prey and raw materials could have played an important evolutionary role for modern human adaptations when they first arrived in western Europe and, potentially, in the demise of Neanderthals. However, the absence of high-resolution archaeozoological data in the Liguro-Provençal arc has hindered our understanding of the patterns of subsistence continuities and change in this region which connects the Italian Peninsula with other West European regions during the transition.

This paper explores the subsistence adaptations during the Middle to Upper Palaeolithic transition in the Liguro-Provençal arc by presenting the first detailed diachronic archaeozoological and taphonomic analysis with integrated ZooMS of the transitional sequence at Riparo Bombrini (i.e., Levels A1, A2, and MS). Our main goal is to reconstruct and compare the hunting strategies and patterns of animal exploitation of the three assemblages, which document the final Neanderthal occupations of the site (MS) and the first occupations of the site by modern humans (A1, A2). Furthermore, the heavy level of fragmentation of the faunal remains provides an excellent opportunity to apply and test the limits of the multivariate taphonomic approach in challenging context and to evaluate how to effectively implement a mass ZooMS technique to complement this approach (Behrensmeyer 1991; Bar-Oz and Munro 2004; Bar-Oz and Dayan 2003).

We start by contextualizing the Middle-Upper Paleolithic transition and the debates surrounding Neanderthal and modern human subsistence behaviours in Western Europe and discussing how the multivariate taphonomic approach can help resolve key methodological difficulties related to subsistence reconstructions. We then offer an overview of the biogeographical, topographic, and paleoenvironmental settings of the Liguro-Provençal arc and synthesize previous research on subsistence and land-use strategies in this region which is critical to understand the Middle-Upper Paleolithic transition. This includes a summary of prior and ongoing work at Riparo Bombrini (Balzi Rossi) to further highlight the site's importance and the need for an exhaustive archaeozoological and multivariate taphonomic analysis with integrated ZooMS.

5.3.1 Subsistence behaviours during the transition

The study of faunal assemblages associated with transitional contexts has contributed significantly to understand behavioural continuities and discontinuities during the Middle-Upper

Paleolithic transition in Europe and southwestern Asia. Other than the crucial information on relative chronology and paleoenvironmental context that can be obtained from paleontological studies, archaeozoological and taphonomic studies provide unique insights into the diet and subsistence behaviours of prehistoric hunter-gatherers through the identification of most steps of the sequence of animal exploitation, from the hunting tactics and carcass transport strategies to the differential processing and eventual discard of animal remains. At a regional scale, these data are helpful for discussing adaptative mobility and land-use patterns through studies of seasonality, site function, and lithic raw material procurement.

Over the past two decades, archaeozoological studies of Mousterian assemblages have provided increasing information on the range and regional variability of hunting and, more broadly, subsistence strategies of Neanderthals. For instance, most Middle Paleolithic assemblages document the selection of prime-aged adults (e.g., Bar-Oz and Adler 2005; Gaudzinski 2000; Gaudzinski and Roebroeks 2000; Hoffecker and Cleghorn 2000; Rabinovich and Hovers 2004; Speth and Clark 2006; Speth and Tchernov 2001; Steele 2004). Faunal assemblages dominated by single species of gregarious and non-gregarious ungulates also indicate that Neanderthal groups employed flexible hunting strategies that ranged from drive tactics to recurrent selective hunting events and communal hunting of migrating species (Burke 2000a; Costamagno et al. 2015; Gaudzinski 2006; Niven 2006; Rendu et al. 2012). This shows they took full advantage of the local environments they occupied and implies they considered the topography of the landscape and the behaviour of their prey (Burke 2000a; White et al. 2016). Monospecific assemblages also suggest Neanderthals could exploit their landscapes logistically (Binford 1980, *sensu* 1981), as demonstrated by evidence of task-specific hunting and carcass processing camps (Costamagno et al. 2006, 2015) and the potential storage of meat surpluses (Rendu et al. 2012). Many Middle Paleolithic faunal assemblages also document the exploitation of marine resources on nearshore sites and slow- and fast-moving small animal species, mainly in the Mediterranean basin and central Europe (Bertacchi et al. 2021; Blasco and Fernández Peris 2012; Cortés-Sánchez et al. 2011; Finlayson et al. 2012; Fiore et al. 2016; Hardy et al. 2013; Hardy and Moncel 2011; Morin et al. 2019; Stiner 2001; Zilhão et al. 2020). Overall, these different lines of data establish that

Neanderthals exploited a broad range of seasonally available resources specific to their local environments.

If Neanderthals were once thought to be inefficient hunters, unable to practice prey selection (e.g., Binford 1981, 1984, 1985; Stiner 1991a, 1994), they are now recognized as skillful hunters (Chase 1986;1991; Klein 1989; Farizy and David 1992; Stiner 1994; Auguste 1995; Klein and Cruz-Uribe 1996; Mellars 1996; Conard 1997; Thieme 1997; Marean 1998; Marean and Kim 1998; Voormolen 2008). The position of Neanderthals at the top of the food chain is also supported by isotopic studies, which reveal a meat-dominated diet, focused on large and very large mammals comparable to other top predators (Bocherens 2009, 2011, 2011; Bocherens et al. 2005; Richards et al. 2000, 2001; Richards and Trinkaus 2009; Wißing et al. 2019). Recent methodological developments in isotopic studies (e.g., the analysis of individual amino acids rather than bulk collagen composition) also allow the disentangling of aquatic from terrestrial food resources (Drucker et al. 2017; Naito et al. 2016). The results indicate that Neanderthals occupied a higher trophic ecological niche, distinct from hyenas and that plant-based foods accounted for>20% of their protein intake (Naito et al. 2016). In sum, isotopic data now complement the results of many other recent studies of dental calculus, tooth microwear, and fecal biomarkers showing that non-animal foods represented a considerable component of Neanderthal diets throughout western Eurasia (Fiorenza et al. 2015; Henry et al. 2011; Power et al. 2018; Rampelli et al. 2021; Sistiaga et al. 2014; Yates et al. 2021). Recent studies of early modern human fossils point to similar trends of omnivory, with higher nitrogen values in some cases (Richards and Trinkaus 2009) reinterpreted as the result of the consumption of mammoth meat, in agreement with the archaeozoological record (Drucker et al. 2017).

A growing, interdisciplinary understanding of Neanderthal subsistence has now invalidated their putative behavioural and cognitive inferiority relative to modern humans, at least from the standpoint of subsistence. The reconstruction of subsistence strategies in transitional contexts provides insightful information on behavioural continuities and discontinuities across the Middle-Upper Paleolithic transition and the potential adaptive implications of these changes. Inter-assemblage continuities in the patterns of taxonomic composition and skeletal representation are highlighted in numerous western Eurasian sites with long transitional sequences (MIS5-MIS3)

(Adler et al. 2006; Bar-Oz and Adler 2005; Discamps et al. 2011; Grayson and Delpech 2002, 2008; Luret et al. 2020; Münzel and Conard 2004; Rendu et al. 2019; Yravedra 2013; Yravedra et al. 2016). When significant changes in taxonomic composition are observed in the transitional record, as exemplified for instance by the dominance of reindeer in numerous Early Upper Paleolithic assemblages in southwestern France, they are best attributable to climatically driven adaptations (Grayson and Delpech 2002, 2008; Morin 2008, 2012) as opposed to Mellars' (2004; 1989, 1996, 1998) hypothesis of a fundamental behavioural shift towards highly specialized hunting capacities.

Patterns of continuity in hunting strategies across the transition have pushed some scholars to argue that faunal assemblages are not best suited to discuss behavioural differences between Neanderthals and modern humans (e.g., Bar-Oz and Adler 2005). Others, in contrast, point to significant changes observable in the transitional and Early Upper Paleolithic records that directly reflect differences in hunting techniques and resource management, namely the appearance of long-range projectile weapons and the increasing implementation of animal products as raw material to manufacture tools and ornaments (Bertacchi et al. 2021; Niven 2006; Rendu et al. 2019; Soulier 2014). Gaudzinski-Windheuser and Kindler (2012) recommend that subsistence strategies be interpreted against a clear environmental background and considered in the context of broader subsistence and social systems, allowing archaeozoologists to contribute meaningfully to behavioural discussions. Indeed, holistic approaches are a promising research avenue to address evolutionary issues from an archeozoological perspective. Several such studies have successfully addressed changes in diet breadth and subsistence intensification in response to demographic fluctuations (Morin 2008; Morin et al. 2019; Stiner 2001, 2002a) and changes in social organization and human-environment interactions associated with technological innovation and human-carnivore competition (Rendu et al. 2019; Soulier 2013, 2014).

Regional patterns of land-use and resource management are best addressed by combining faunal and lithic records within a clear environmental context (Burke 2000; Patou-Mathis 2000; Stiner 1992). The results of the faunal analysis presented here will be discussed below in the light of published archaeological data documenting the lithic assemblages, as well as spatial context and paleoenvironmental data (Holt et al. 2019; Riel-Salvatore et al. 2013, 2021; Riel-Salvatore and Negrino 2018a, 2018b).

5.3.2 Regional perspective on the Liguro-Provençal arc

The Liguro-Provençal arc is a unique geophysical corridor constrained by the pre-alps to the North and the Mediterranean Sea to the South, linking peninsular Italy to the western European mainland. It extends approximately 400 km from today's Rhône Valley in southeastern France to today's Po valley in northeastern Italy (Fig. 1). Its peculiar topography would have considerably constrained human and animal circulation, directing movement on an East-West axis along the Provençal and Ligurian littorals and limiting North-South moves to short distances between the shore and the mountains (Grimaldi et al. 2014; Negrino and Riel-Salvatore 2018; Porraz et al. 2010; Tomasso and Porraz 2016). Along with other Mediterranean peninsular environments, this region also provided a refuge zone for mammals during the Pleistocene, as recorded by the continuous presence of temperate taxa sharing the environment with cold-adapted taxa during glacial periods (Carvalho and Bicho 2021; Finlayson 2004; Finlayson et al. 2006; Riel-Salvatore et al. 2021; Valensi 2009; Van Andel et al. 2003).

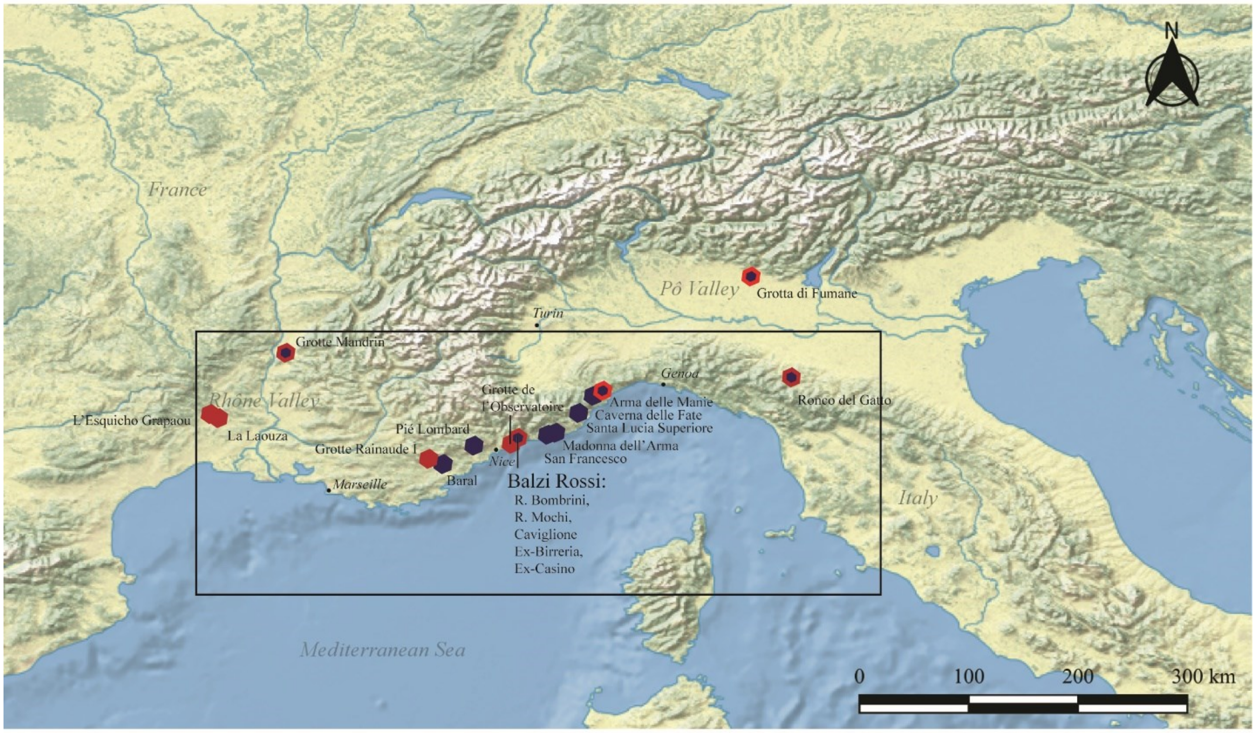

Figure 1. – Map of the Liguro-Provençal arc showing some of the key sites discussed in the text (Proto-Aurignacian sites in red, Mousterian sites in blue) Basemap produced in QGIS with Natural Earth data

This region is of particular interest to document subsistence changes and continuities between Neanderthals and modern humans in biogeographical refugium settings. The increased number of sites dating to MIS5-3 unveils the desirable and rich environment of Liguria and Provence during the Middle Paleolithic (Daujeard and Moncel 2010; Negrino and Tozzi 2008; Porraz and Negrino 2008; Valensi and Psathi 2004). The broad picture reveals contrasting raw material procurement strategies and socio-economic networks between the late Mousterian and the Proto-Aurignacian. Recent studies of raw material sourcing provide crucial information about how the geophysical context and the availability of lithic raw material shaped the resource management strategies adopted by human populations in the Liguro-Provençal arc (Grimaldi et al. 2014; Porraz et al. 2010; Porraz and Negrino 2008; Rossoni-Notter et al. 2017; Rossoni-Notter and Simon 2016; Tomasso and Porraz 2016).

Mousterian assemblages are primarily characterized by the opportunistic exploitation of local raw materials nodules (i.e., up to 30 km) regardless of the quality of the raw material. In contrast, the Proto-Aurignacian assemblages show a selection process intricately linked with the quality of the lithotype, even within generally poor-quality local raw material (Riel-Salvatore and Negrino 2009). As a result, Proto-Aurignacian sites along the shore, located far from good quality flint outcrops, are characterized by a predominance of local raw materials with a considerable proportion of allochthonous lithotypes found between 50 and 200 km away (e.g., Grotte de l'Observatoire, Riparo Mochi, and Riparo Bombrini). In contrast, sites close to abundant high-quality flint sources tend to be dominated by local raw materials (e.g., Mandrin, La Laouza, l'Esquicho-Grapaou, Ronco del Gatto and Lemignano) (Porraz et al. 2010; Riel-Salvatore and Negrino 2009).

Considering those distinct patterns, interpretations of land-use strategies depict Neanderthals having locally-focused subsistence and mobility strategies (Riel-Salvatore and Negrino 2009). Nevertheless, occasional allochthonous elements (i.e., from outcrops up to 200 km distant) in the form of end products on a few sites along the shore (e.g., Riparo Bombrini, Ex-Casinò, and Pié Lombard) suggest more extensive raw material exploitation ranges than commonly observed in Mousterian contexts. Porraz and Negrino (2008) indicated that the particular east-west geophysical configuration of the Ligurian corridor contributed to the elongation of circulation distances, potentially motivating punctual inter-groups exchanges of end-products.

In contrast, the Proto-Aurignacian assemblages depict modern humans having much more extensive social networks in which modern human populations made use of the available local raw material while making long-distance moves (i.e., >130 km) in between the Po and the Rhone valleys to exploit high-quality flints (Porraz et al. 2010). Moreover, the coastal Ligurian and Monegasque sites (i.e., Grotte de l'Observatoire, Riparo Mochi, and Riparo Bombrini) show a higher abundance of Provençal lithotypes than eastern Ligurian and central Italian ones (Grimaldi et al. 2014; Porraz et al. 2010). This pattern suggests that modern humans circulated back and forth along the corridor, acquiring good quality flint along their travels. This strong link between Ligurian and southeastern French sites also supports the growing evidence of the west European indigenous origin of the Proto-Aurignacian technocomplex (Anderson et al. 2015; Kadowaki et al.

2015), contrasting with the initial hypothesis of westward colonization through the Liguro-Provençal corridor (e.g., Kozlowski and Otte 2000; Paul Mellars 2004).

In addition, two sites – Riparo Bombrini and Riparo Mochi – located in the Balzi Rossi cave complex of Liguria document very recent Mousterian levels directly underlying Proto-Aurignacian deposits dated to ca. 42 ky cal BP. A recent analysis of the so-called "Semi-Sterile Mousterian" (corresponding to Level MS) at Riparo Bombrini proposes that it represents Neanderthal adaptations under refugium conditions during the cold interval between the GI-11 and GI-10 while modern humans were already present in neighbouring regions (Riel-Salvatore et al. 2021). This interpretation is supported by the contemporaneity of the Uluzzian expanding across the Italian peninsula to the east while the Proto-Aurignacian was already present to the west (Barshay-Szmidt et al. 2018, 2020). From these recent Mousterian levels, it would thus appear that the last Neanderthals of Liguria contracted demographically and geographically, adopting flexible lithic technological organization and increased residential mobility, and exploiting increasingly local resources (Riel-Salvatore et al. 2021).

5.3.2.1 The faunal record

Insights from archaeozoological studies on subsistence changes and continuities also suffer from a dearth of sites excavated with modern methods. The only two Proto-Aurignacian faunal assemblages documented in Liguria (i.e., Riparo Mochi and Riparo Bombrini) are strongly affected by an array of taphonomic forces that considerably hinder taxonomic identifications (Alhaique 2000; Holt et al. 2019; Pothier Bouchard et al. 2020). At Riparo Mochi, the work of Stiner and colleagues on the assemblage excavated at the beginning of the 20th century focused on the contribution of mollusk and bird remains, documenting the broadening of animal exploitation during the Upper Paleolithic in Mediterranean regions (Stiner 1999; Stiner et al. 1999, 2000). Insights on the mammalian fauna come from preliminary analyses of a more recently excavated (i.e., 1995-1996) sample that highlighted the dominance of cervid over caprine remains and the negligible presence of carnivore activities in the scarce Proto-Aurignacian faunal assemblage (Alhaique 2000). At Riparo Bombrini, our previous archaeozoological and taphonomic analysis with integrated ZooMS of the Proto-Aurignacian levels revealed that modern humans continuously exploited various taxa that could be found near the site, primarily red deer, followed by mountain goats, bovines, horses, and wild boars. We also identified changing patterns of the site organization and the management of grease-rich bones as fuel associated with changing land-use and mobility strategies, warranting further investigation of these levels (Pothier Bouchard et al. 2020).

Outside the Balzi Rossi, only one site, Grotte de l'Observatoire in Monaco, offers additional insights on a Proto-Aurignacian assemblage in the Liguro-Provençal arc. However, recent analyses highlight the methodological complexity associated with recovery biases of these collections excavated several decades ago (Brugal et al. 2017; Romandini 2017). The faunal remains stratigraphically associated with Proto-Aurignacian hearths at Grotte de l'Observatoire include a high abundance of whole carcasses of mountain goats with no apparent anthropic butchery marks. In addition, the abundant coprolites and the various carnivore taxa identified in this context suggest alternating occupations between humans, bears, and other carnivore predators (*ibid*).

Exhaustive archaeozoological and taphonomic studies on Proto-Aurignacian assemblages are rare even outside our region of interest. Romandini and colleagues (2020) recently identified a few behavioural trends in a survey of transitional sites in northeastern and peninsular Italy. For instance, they highlighted a general increase of calcined bones in Proto-Aurignacian and Uluzzian contexts compared with late Mousterian assemblages in northeast Italy, suggesting changes in fire management that might be associated with intensified use of hearths for cooking or fuel management. Changes in butchery and marrow extraction during the early Upper Paleolithic might also be reflected by the higher relative abundance of cut marks in northeastern Italy and the higher amount of ungulate limb extremities and broken phalanges in southern Italy. Finally, they observed evidence of taxonomic broadening visible through the increased exploitation of bear and small and medium carnivores for skin and fur in Proto-Aurignacian and Uluzzian contexts. However, they suggest that further taphonomic studies are needed to corroborate these observations.

The general patterns highlighted in Italy seem to agree with the few well-documented Proto-Aurignacian assemblages in Western and Southwestern France (i.e., Les Cottés, Le Piage, Isturitz, Les Abeilles, El Castillo, Gatzarria) (Morin 2008, 2012; Rendu et al. 2019; Soulier 2013). These studies point out the exploitation of carnivores such as fox, wolf, bear, and hyena for skin and fur starting in the Châtelperronian and increasing in frequency through the Proto-Aurignacian and Early Aurignacian. They also point out similar patterns of bone exploitation for fuel, beginning at the end of the Middle Paleolithic and increasing in the Proto-Aurignacian and Early Aurignacian. In addition, Soulier (2013, 2014) identified distinctive subsistence patterns on two Proto-Aurignacian base camps: Les Abeilles and Isturitz. Her work highlights that modern human groups recurrently occupied base camps seasonally. They intercepted large groups of ungulates during the fall rutting season to take advantage of the highest quality of meat, marrow, and furs. Soulier also observes that winter occupations seem linked to prolonged occupations of the base camps during which multiple families could have aggregated to do different activities. For instance, she suggested that the exploitation of bone fuel could be related to meat smoking to stockpile for future consumption during harsher seasons or extended stays. The cave sites were rarely occupied during late spring and summer, which she suggested could indicate that hunter-gatherers exploited littoral or richer environments during these seasons. Soulier (2013) also highlights more solitary hunting expeditions targeting large ungulates such as bovines and horses starting in the Proto-Aurignacian, continuing in the Early Aurignacian. Most importantly, she points out the abandonment of the practice of collaborative ambush hunting using the topography often documented in Mousterian contexts (e.g., White, Pettitt, and Schreve 2016). She attributes this shift in hunting strategies to fundamental changes in human-environment interactions, potentially related to the development of projectile technology. Those subsistence reconstructions constitute crucial comparative data on Proto-Aurignacian subsistence strategies for our study.

Although no deposits analogous to the Semi-Sterile Mousterian was documented in the Liguro-Provençal arc so far, the rich Mousterian record on sites dating between MIS 5-3 (i.e., Madonna dell'Arma, Caverna delle Fate, Arma delle Manie, Santa Lucia Superiore and Via San Francesco) provided much information on Neanderthals' subsistence strategies and paleoenvironmental data before the transition (Psathi 2003; Valensi 2009; Valensi et al. 2004). However, most of these sites were excavated before the second half of the 20th century, limiting discussions of regional trends on large temporal scales. Valensi and Psathi's (2004) synthesis highlights the constant dominance of red deer in all assemblages, revealing the persistence of rich forested environments in this biogeographical refugium. The continuous strong presence of ibex in mountainous environments suggests the exploitation of readily available game as a function of local topography. In addition, hunting strategies seem to have targeted prime-aged individuals in the vicinity of the sites, as shown by the presence of all skeletal portions of medium and large ungulates. Valensi and Psathi (2004) point out one exception, Le Manie, where limbs and cranium dominate the skeletal representation of the deer, suggesting differential carcass transport. Le Manie was also identified as a residential base camp with recurrent and increasingly prolonged seasonal occupations throughout MIS5-3 (Psathi 2003).

Finally, a few exhaustive inter-site archaeozoological studies carried out in the Rhone Valley and the Massif Central bring interesting comparative insights on Neanderthal subsistence, site function, and land-use management in neighbouring regions to the west (Daujeard et al. 2012; Daujeard and Moncel 2010; Raynal et al. 2013). Those studies show that Neanderthals primarily exploited locally sourced taxa available in the different environments (i.e., cervids in forested habitats, caprines in rocky settings, and bovines and equids in open landscapes), agreeing with the patterns observed on Ligurian sites. In addition, they demonstrate that Neanderthal land-use strategies were embedded in deep knowledge of the topography of the territory and seasonal resource variability. Throughout MIS 7-3, Neanderthals adopted various subsistence strategies in these regions, making residential moves between different types of sites (i.e., residential camps, hunting camps, and stopping-places). The patterns of lithic circulation and seasonality of occupations of some contemporaneous sites led Daujeard and Moncel (2010) to suggest that Neanderthals organized their territory logistically (*sensu* Binford), modifying their occupation modes according to seasons, topographies, and biotopes. Furthermore, they show that sites located in the plains of the Rhone Valley were more diverse than mid-mountain sites. The latter mainly were occupied as regular short-term camps during favourable seasons (Daujeard et al. 2012).

5.3.3 Neanderthal and modern human occupations at Riparo Bombrini

Riparo Bombrini is a rockshelter located in the Balzi Rossi site complex in northwest Italy. The site corresponds to the easternmost edge of a long talus slope opening in front of the cave complex (Fig. 2). Due to its small size, Riparo Bombrini is one of the few sites to have been overlooked by the coarse excavations of the 19th century when the Balzi Rossi became famous for their multiple Upper Paleolithic burial discoveries (see Formicola and Holt 2015). Émile Rivière first acknowledged the site in 1871 during the construction of the Genoa-Marseille railway, which truncated the talus in front of Grotta del Caviglione, exposing rich archaeological deposits and simultaneously destroying the northern part of Riparo Bombrini.

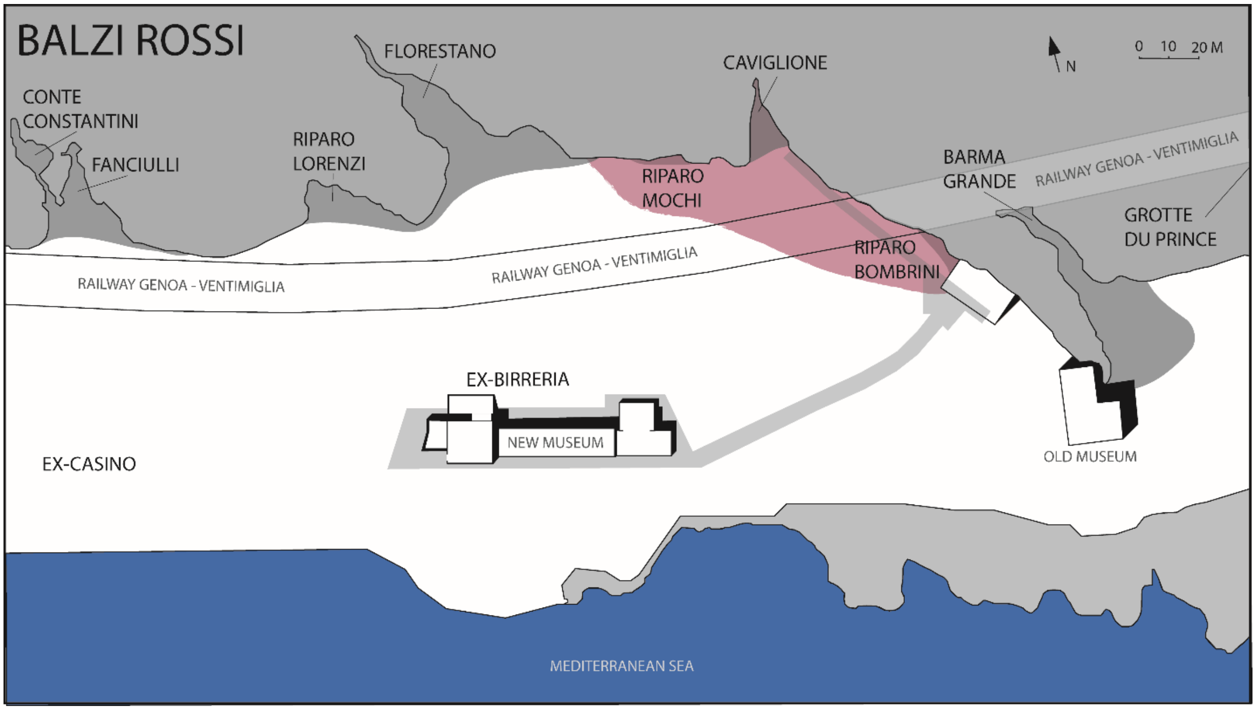

Figure 2. – Cartographic sketch of the Balzi Rossi showing the talus connecting Riparo Mochi, Grotta del Caviglione, and Riparo Bombrini (in red).

The long stratigraphic sequence documented at Riparo Mochi is today considered a reference point to discuss the early arrival of modern humans in Mediterranean Europe (Douka et al. 2012; Kuhn and Stiner 1998). A dating program during the 2002-2005 excavations at Riparo Bombrini also helped assess the general stratigraphic correspondence between Riparo Mochi and Riparo Bombrini (Holt et al. 2019), indicating that these rockshelters were part of a large talus slope opening in front of Grotta del Caviglione that was recurrently occupied during the Late Pleistocene.

Along with Riparo Mochi, Riparo Bombrini is thus the only site in the Balzi Rossi to have preserved *in situ* Late Mousterian and Proto-Aurignacian deposits and to have been excavated with modern methods. The site was excavated in three phases with fine-grained methods systematically documenting the spatial coordinates of artifacts and water sieving. A first limited excavation in 1976 of six square metres outside the shelter itself yielded rich Late Mousterian and Proto-Aurignacian deposits and a deciduous *Homo sapiens* incisor in Level A2 (Benazzi et al. 2015; Formicola 1989; Vicino 1984). Subsequently, more extensive controlled excavations from 2002-05 were organized on both sides of the 1976 excavation pit to investigate the nature and the chronology of the transitional deposit across the entire site (Higham et al. 2014; Holt et al. 2019; Riel-Salvatore et al. 2013). Finally, two of the authors conducted excavations on a more extensive area inside the dripline from 2015-2019 to clarify the formation history of the site and the nature and temporality of the Middle-Upper Paleolithic transition at Riparo Bombrini (Negrino and Riel-Salvatore 2018; Riel-Salvatore and Negrino 2018a, 2018b).

The robust chronological framework for the transitional occupations of Riparo Bombrini reveals very recent Mousterian levels (i.e., M7-MS) dated 42-45 ky cal BP. The top Mousterian Levels MS1 and MS2, while not directly dated yet, have been correlated to a period covering the cold interval between the GI-11 and GI-10 (~43-42 ky cal BP) with the overlying Proto-Aurignacian levels (A1 and A2) dated between 42-36ky cal BP, acting as *terminus ante quem* (Benazzi et al. 2015; Holt et al. 2019) (Fig. 3).

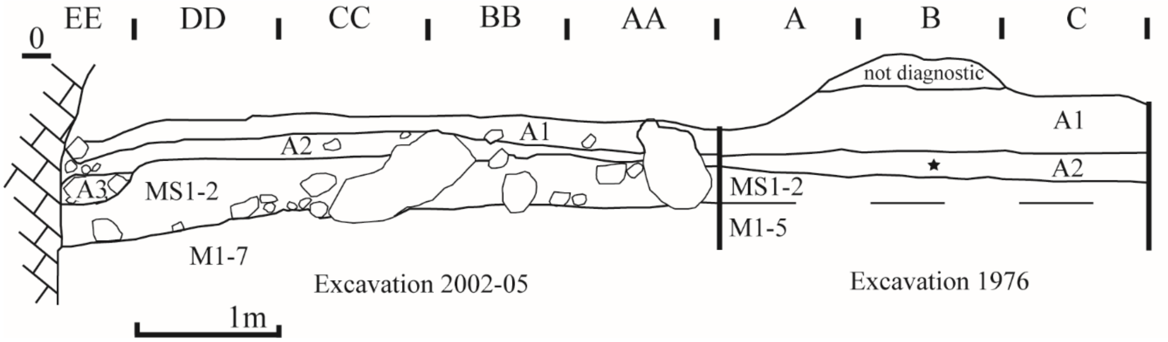

Figure 3. – Stratigraphic sequence of Riparo Bombrini based on the 2002-2005 and 1976 excavations. The star shows the position of the human incisor in Level A2. (modified from Benazzi et al. 2015).

Paleoenvironmental data, including sedimentology, palynology and microfauna, indicate overall temperate conditions and forested environments in Mousterian Levels M7-M1 (Arobba and Caramiello 2009; Holt et al. 2019). The overlying Levels MS1-MS2 document a climatic shift towards increasingly cold and arid conditions. These levels (hereafter merged in one "Level MS" as they are undifferentiated outside the dripline) correspond to a 30 to 40 cm thick orangeish clayey loam that incorporates large limestone blocks resulting from the partial collapse of the rockshelter roof as a result of increasing freeze-thaw action. Level MS is also characterized by some episodes of water action, as shown by an erosion channel against the rockshelter wall. This level, also called the "Semi-Sterile Mousterian," corresponds to the last traces of Neanderthal occupations on the site and show much lower densities of artifacts than the underlying Mousterian deposits. It is probable it corresponds to Level H at Riparo Mochi (Alhaique et al. 2000; Bietti and Negrino 2007; Kuhn and Stiner 1992).

The climatic deterioration continues in the Proto-Aurignacian levels, which began accumulating under much colder and arider conditions. Levels A1 and A2 form a yellowish clayey loam deposit varying from 10 to 30 cm thick each. Both levels contain rich assemblages with overlying "cuvette-type" hearths and discarding features. Slightly different environmental conditions are recorded between Level A2 and Level A1. The latter corresponds to somewhat more temperate and mesic conditions than the first, which is chronologically associated with the cold phase of the Heinrich Event 4. These paleoenvironmental data are also visible in the macrofaunal record with more abundant warm-adapted taxa (i.e., Suidae and Cervidae) in the Mousterian Levels M7-M1 and increasing abundance of cold-adapted taxa (i.e., Bovinae, Equidae, and Caprinae) in Levels MS, A2, and A1 (Holt et al. 2019; Pothier Bouchard et al. 2020). The continuous presence of red deer in all levels also agrees with the refugium biogeographical settings of Liguria during the Upper Pleistocene characterized by mixed open and forested environments during colder phases (Riel-Salvatore et al. 2021). Furthermore, anthracological data indicate that human groups primarily collected wood from shrubby species available close to the site in both Mousterian and Proto-Aurignacian levels (Holt et al. 2019).

Previous research on the transitional levels at Riparo Bombrini (i.e., MS, A2, A1) highlighted contrasting occupations of the site. Level MS was described as “semi-sterile” in the past to emphasize the paucity of artifacts in this thick deposit which also mirrors the phenomenon documented in Level H of the neighbouring Riparo Mochi (Bietti and Negrino 2007). Nevertheless, new data from the 2015-2019 excavations at Riparo Bombrini has considerably increased the artifactual and faunal corpus, allowing updating behavioural and biogeographical interpretations of this level (Riel-Salvatore et al. 2021). The most striking new evidence includes the discovery of an ovoidal combustion area directly underlying the Proto-Aurignacian hearths close to the rockshelter back wall. The combustion area is also associated with most artifacts recorded in Level MS and the highest density of red ochre recovered throughout the Mousterian levels. The renewed analyses warrant testing the hypothesis that Level MS corresponds to Neanderthals' adaption to an ecologically stable micro-refugium manifested by increased mobility in a restrained territory. This “hyperlocal” adaptation is also marked by opportunistic lithic exploitation of locally sourced raw material (<5km) and the exclusive use of very flexible knapping methods (i.e., Discoid technology).

The Proto-Aurignacian Levels A1 and A2 are both rich in artifacts and faunal remains. The combination of different factors, including the density of archaeological remains, the overlying cuvette-type hearths and possible trash pits, and the curated bladelet-based technology, was interpreted to indicate the continuous occupation of the site by modern humans in both levels. Furthermore, variability between the two levels in the bladelet production and lithic resource management was interpreted as the manifestation of changing mobility strategies (*sensu* Binford) in response to paleoclimatic instability. The colder Level A2 was thus associated with logistical mobility strategies, whereas the slightly warmer Level A1 was characterized with more residential strategies (Riel-Salvatore and Negrino 2018a). Our previous archaeozoological analysis showed stability in hunting strategies despite the mobility shift, attesting to the flexibility of modern humans' hunting technology (Pothier Bouchard et al. 2020). Although general patterns of site organization and fuel management identified in the faunal record were associated with these changing land-use and mobility strategies, our previous analysis did not include assemblages from outside the dripline which could have obscured crucial evidence about practices such as waste management and spatially segregated butchering activities.

5.4 Material and Methods

5.4.1 Faunal assemblage

The three phases of excavation on the site (1976, 2002-2005, and 2015-2019) used slightly different recovery standards, which affected the taphonomic resolution of the different faunal assemblages. The 1976 salvage excavation was carried out with various degrees of resolution within the stratigraphy due to the limited time frame to finalize the work (Vicino 1984). Vicino thus recorded the Proto-Aurignacian layers (A1 and A2) using the most fine-grained methods available at the time, i.e., by excavating one square-meter unit in 5cm thick arbitrary spits and individually plotting in three dimensions all artifacts, diagnostic bones, and non-diagnostic bones larger than ten centimetres. The sediments were also water-sieved on-site, providing fine-grained faunal assemblages. However, Vicino accelerated the excavation of the Mousterian levels, including Levels MS1 and MS2, to reach the expected depth of the salvage excavation pit. His spits varied from 5 to 10 cm, and he reported having collected only the visible fragments while putting aside all the sediments spits by spits for future analysis, therefore, not systematically recording smaller, non-diagnostic artifacts and skeletal remains. These sediments are currently being water-sieved at the University of Genoa (Italy) under the supervision of F. Negrino and should bring better light to the taphonomic factors acting on the Mousterian faunal assemblages outside the rockshelter in the future. As for now, the Mousterian faunal assemblages from 1976 are characterized by larger diagnostic elements and a few bone fragments of varying sizes recovered during Vicino's fieldwork.

The team excavating the 2002-2005 deposits used similar methods to Vicino's original fine-grained fieldwork. The square-meter units were excavated with arbitrary spits of 5 cm thick in which diagnostic artifacts were systematically piece-plotted three-dimensionally along with faunal remains larger than 5cm. All sediments were also water-screened using 2cm mesh sieves and small fractions of bones, ochre, lithic, shells, and others retained for analysis (Riel-Salvatore et al. 2013). The 2015-2019 deposits started with the same excavation methods as previous excavations. From 2016, we operated small changes to maximize the taphonomic resolution of the faunal remains by subdividing the square-meter units into 50cm subunits, piece-plotting bone fragments larger than 2cm, and collecting the smaller fraction (>1cm) of coprolites from the sieve. The team also acquired a total station in 2018 that allowed georeferencing the site and the different structures on the site and digitalized the spatial distribution of all piece-plotted finds from 1976 and forth within the ArcGIS software.

The faunal remains recovered during the 1976 salvage excavation were never formally analyzed and published. However, this collection accounts for a large part of the faunal remains recovered on the site, especially regarding the Proto-Aurignacian levels. This four-square-meter area is located outside the rockshelter, delimited by the dripline, and comprises thicker deposits than those excavated inside the rockshelter (Fig. 4). Consequently, these faunal assemblages are of great interest to tackle the levels corresponding to the transition at Riparo Bombrini, despite the varying degree of recovery resolution. Furthermore, the 1976 collections are the only ones that document both Proto-Aurignacian layers and the Semi-Sterile Mousterian outside the rockshelter (see Pothier Bouchard et al. 2020 for discussion).

On the other hand, A. Arellano (Musée de Préhistoire Régionale de Menton, France) examined the faunal remains recovered during the 2002-2005 archaeological campaigns. Her work provided the first portrait of the vertebrate taxonomic composition on the site (Holt et al. 2019; Riel-Salvatore and Negrino 2018a b). This first formal archaeozoological analysis focussed on the faunal remains recovered from a five square meter trench (squares A1 to EE1) and helped to discuss the paleoenvironmental implications of the macrofauna in the two Proto-Aurignacian and nine Mousterian levels along with other paleoenvironmental data (Holt et al. 2019; Riel-Salvatore and Negrino 2018b; Riel-Salvatore et al. 2013). However, the high level of skeletal fragmentation on the site (more than 93% of the fauna was described as measuring less than 2cm) severely hindered morphological taxonomic identification. Holt et al. (2019) suggested a hypothesis of intensive meat and marrow exploitation by modern humans and Neanderthals to explain the pattern of fragmentation.

In 2015, therefore, we initiated an exhaustive archaeozoological and taphonomic analysis of the faunal remains from Riparo Bombrini, including systematic ZooMS sampling as part of the new five-year excavation project on the site. We included the faunal remains from previous excavations in this analysis, in addition to new samples recovered from ongoing excavations. Our main objectives were to examine site formation processes and provide a detailed picture of the variability of the hunting and subsistence strategies employed by human groups occupying Riparo Bombrini during the Middle-Upper Paleolithic transition. Our first archaeozoological study focused on a sample of the Proto-Aurignacian assemblages recovered from 2002-2005 and 2015 and 2016. This study revealed the importance of integrating ZooMS as a tool for countering poor taxonomic identification due to fragmentation. It also highlighted the differential state of preservation of the faunal remains on the site, which needs to be factored into the interpretation of the assemblages (Pothier Bouchard et al. 2019, 2020).

5.4.2 Sampling strategy for the archaeozoological analysis

The observations about the state of preservation of the faunal remains at Riparo Bombrini drawn from previous studies were crucial to designing our sampling strategy for Levels A1, A2, and MS. Since our goals are to clarify human subsistence behaviour across the transition at the site and to permit subsequent inter-site comparisons despite the poor preservation of the skeletal remains at Riparo Bombrini, our sampling strategy sought to meet three objectives: (1) the maximization of morphological and taxonomic identifications, (2) a high taphonomic resolution, and (3) an adequate representation of the different parts of the site.

Our initial archaeozoological and ZooMS analyses of the Proto-Aurignacian assemblages revealed that the skeletal remains recovered outside the rockshelter (squares A, B, C, D, and E) are better preserved (for both morphological and proteomic identification) than those from most areas inside the dripline (Pothier Bouchard et al. 2020). Therefore, we selected a first two-square-meter area of the site, corresponding to square-units C1 and C2, outside the dripline, for systematic ZooMS sampling in stratigraphic Levels A1, A2, and MS (Fig. 4). We later extended this sample to include an area inside the rockshelter, covering units AA1, BB1, CC1, and DD1, mostly excavated 2002-2005, and units DD2 and EE3, excavated 2016-2019.

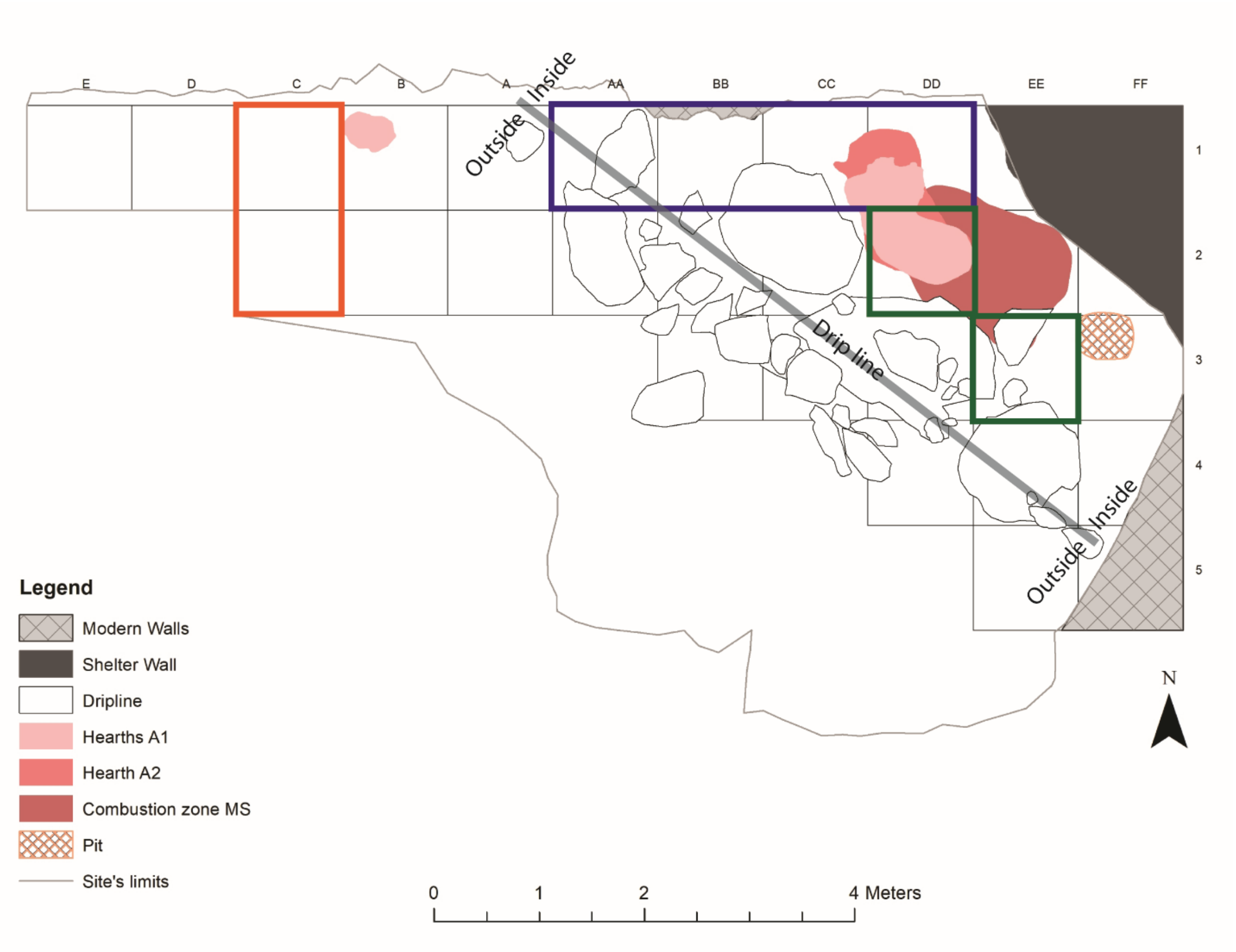

Figure 4. – Map of Riparo Bombrini showing overlapped features documented in Levels A1, A2, and MS, and the square-meter units selected for our analysis.

In total, this corresponds to over 50% of the undisturbed excavated areas on the site. It also includes the bulk of the faunal remains and artifacts concentrated in C1-C2 outside the rockshelter, and DD1-DD2, where hearth features are present within all three stratigraphic levels. In addition, units DD2 and EE3 are especially crucial to discuss taphonomic features related to carnivore activities on the site because they were excavated during the most recent campaigns with the systematic recovery of coprolites, including small-fraction samples. Finally, although we did not include all square-meter units in this archaeozoological and multivariate taphonomic analysis, we will discuss our results within the context of the spatial distribution of the entire faunal record in relation to the archaeological features (i.e., hearths, discarding pits).

5.4.3 Archaeozoological methods

We analyzed a total sample of 19,804 bone fragments (or Number of Specimens – NSP) drawn from Levels A1 (NSP=4488), A2 (NSP=10,423), and MS (NSP=4893).

5.4.3.1 Taxonomic analysis

We conducted taxonomic identifications using gross morphology and systematic ZooMs sampling (the sampling strategy of which is detailed in the taphonomic methods section below). We identified teeth by consulting the reference collection of herbivore and carnivore skulls curated by the *Museo Civico di Storia Naturale di Genova*. We identified skeletal remains using osteological atlases (Barone 1975; Pales and Garcia 1981; Schmid 1972) and three open-source virtual collections: the 3D models provided by the Max-Planck-Gesellschaft Department of Human Evolution (https://www.eva.mpg.de/evolution/downloads.html), the 3D models of the Laetoli project (https://laetoli-production.fr), and the photographic osteological collection of the ArchéoZoothèque (https://www.archeozoo.org/archeozootheque). When skeletal remains of ungulates could not be identified to a species, we assigned them minimally to size categories adapted from Brain (1981) and Bunn (1986): **smaller ungulates** size 1 – <50kg (e.g., *Rupicapra rupicapra*, *Capreolus capreolus*) and size 2 – 50-100kg (e.g., *Capra ibex*, *Sus scrofa*, *Dama dama*); **larger ungulates** size 3 – 100-300kg (e.g., *Rangifer tarandus*, *Cervus elaphus*) and size 4 – 300-1000kg (e.g., *Bos/Bison*, *Equus sp.*); **megafauna** size 5 – >1000kg (e.g., *Mammuthus sp.*, *Coelodonta sp.*). Intermediate categories such as Cervidae size 2/3 or artiodactyl size 3/4 were often more appropriate at Riparo Bombrini, considering the high level of bone fragmentation. Carnivores are classified within three size classes: size 1 – small carnivores (e.g., *Vulpes vulpes*), size 2 – medium carnivores (e.g., *Canis lupus*, *Crocuta crocuta*), and size 3 – large carnivores (e.g., *Ursus sp.*).

5.4.3.2 Age and sex

We recorded information related to age, sex, and seasonality when possible. Since the mineral composition of teeth results in better preservation compared with bones, teeth were the primary source of ageing information at Riparo Bombrini.

We carried out age determinations using extant references of wear patterns and eruption stages of Cervinae and Capreolinae (Brown and Chapman 1991; Carter 2006; d'Errico and Vanhaeren 2002), Caprinae (Payne 1973, 1987), Bovinae (Grant 1982), Suidae (Grant 1982; Magnell 2006), Equidae (Bignon 2006; Fernandez and Legendre 2003; Levine 1982), Ursidae (Stiner 1998), and Canidae (Gipson et al. 2000). We also measured the crown heights of morphologically intact teeth of Cervidae and Equidae and applied the quadratic crown height method (QCHM) using Klein et al.'s formula (Klein et al. 1981; Klein and Cruz-Uribe 1984).

In rare cases in which bone extremities survived, we determined the age of skeletal remains using epiphyseal fusion (unfused, fusion line, fused) and epiphyseal stages for Cervinae (Carden and Hayden 2006; Reitz and Wing 2008), Bovinae (Koch 1932 in Julien 2011), and Caprinae (Zeder 2006).

Although precise age determinations using the methods described above are always best, particularly for discussions about seasonal hunting strategies, the reconstruction of long-term prey selection and resource management does not require such fine-grained data (Stiner 1994). Where poor preservation of the occlusal surfaces of ungulate teeth precluded the use of species-specific wear patterns and crown height measurements we applied a system of three age categories (i.e., juveniles, prime adults, and old adults). We adapted Discamp and Costamagno (2015)'s age systems for our age categories of the main hunted ungulate taxa as follows: Caprinae (J: 0-1.5 yrs, A: 1.5-8 yrs, O: >8 yrs), Cervinae (J:0-2 yrs, A: 2-12 yrs, O: >12 yrs), Bovinae (J:0-3 yrs, A: 3-12 yrs, O: >12 yrs), and Equidae (J:0-2 yrs, A: 2-15 yrs, O: >15 yrs).

We identified sex using the presence/absence of canines for Equidae and Cervidae (primarily present in male individuals and absent or vestigial in females) and of antlers for Cervidae (male) excluding Rangifer. The presence of unshed antlers and juvenile prey contributed to discussions about the seasonality of occupations on the site. Microwear analysis could not be used on these collections as most teeth either had damaged occlusal surfaces or were cemented in concretion.

5.4.3.3 Quantification methods

We applied standard archaeozoological quantification methods, including measures of taxonomic abundance (Number of Identified Specimens – NISP, and Minimum Number of Individuals – MNI), measures of skeletal part frequencies (Minimum Number of Elements – MNE, and Minimum Animal Units – MAU) and measures of food utility (Food Utility Index – FUI) (Grayson 1984; Lyman 2008; Metcalfe and Jones 1988). We created pie charts, line graphs, and ternary plots of these results with Microsoft Excel software, and produced scatterplots and ran statistical tests using Past 3.14 software.

We summarised taxonomic abundance for the three assemblages in a table with the NISP and MNI tallies for each taxon. We then illustrated the relative abundance of prey taxa and carnivores with pie charts synthesizing the NISP tallies at the family and sub-family levels (e.g., Cervinae, Capreolinae, Caprinae, Bovinae, Suidae, and Equidae). These groupings were used to facilitate inter-assemblage visual comparisons because the combination of morphology and ZooMS provide different levels of taxonomic identification resulting in numerous subdivisions of the taxonomic categories (morphology = species or size categories associated with family and sub-family; ZooMS = genus or family in the absence of some biomarkers when collagen preservation is poor).

Our NISP and MNI tallies are affected by the usual problems related to measuring taxonomic abundance, such as intertaxonomic variability, differential preservation, the interdependence of skeletal remains, and differential recovery (see Grayson 1984; Morin et al. 2017a for discussion and literature reviews). The high degree of fragmentation at Riparo Bombrini hinders the MNI count to the point of reducing most MNI tallies to either one or two individuals per taxon. For this reason, NISP is preferred over MNI and other MNI-derived measures (e.g., biomass measures, meat weight) when discussing taxonomic abundance on the site. Nonetheless, we calculated the fragmentation index (NISP divided by the MNI) of a few more abundant taxa following Klein and Cruz-Uribe (1984:25) to address the issue of fragmentation of the skeletal remains in our multivariate taphonomic analysis.

Where possible, we calculated MNE according to three criteria: (1) the overlap of skeletal elements and diagnostic anatomical landmarks as proposed in Morin et al. (2017a); (2) the age and sex of the skeletal remains, and; (3) the size of the specimens. We did not draw or scan all the identifiable elements in this analysis because the degree of skeletal fragmentation meant that the small number of elements available for study could be laid out on a table and directly tested for overlaps. Like MNI, MNE is strongly influenced by sample size, fragmentation, and aggregation (Lyman 2008; Marean et al. 2001; Morin et al. 2017a, 2017b). Thus, the high level of fragmentation precluded us from calculating most MNE-derived quantitative values. For instance, we could not apply the NISP:MNE ratio (ratio of anatomically incomplete specimens to the MNE associated with these specimens) of specific long bones to measure the intensity of fragmentation since MNE tallies rarely exceeded values of one or two per skeletal element, even within the most abundant taxonomic categories.

However, we calculated the MNE-derived MAU (and %MAU) for two sufficiently abundant taxonomic categories: cervids size 2/3 and the combined artiodactyl and ungulates size 3/4. MAU counts and %MAU are calculated following (Binford 1984).

Owing to the degree of fragmentation, we mainly use skeletal-part frequencies on the nominal scale, using NISP counts of the skeletal elements (NISPe), a simple count of all skeletal elements (right, left and indeterminate sides) for each taxon. We group the NISPe tallies of all skeletal elements by skeletal region following Stiner (2002b). We add two indeterminate categories (indeterminate limb and indeterminate) because many taxonomic identifications result from ZooMS identifications on morphologically unidentifiable skeletal elements.

We summarise the NISPe values in a table at the family and sub-family levels and two broader size categories (ungulate size 1/2 and ungulate size 3/4). We then illustrate the normalized NISPe values (NISPe value of a skeletal portion divided by the highest NISPe and multiplied by 100) of the most abundant taxa (according to NISP counts) with line graphs. Although this method of calculating and illustrating skeletal part frequencies involves a higher risk of interpretive bias, it is the only method that allows us to discuss carcass treatment and carcass transport for all of the taxa present at Riparo Bombrini.

The relative abundance of skeletal elements in an archaeological assemblage can result from density-mediated attrition or human transport decisions predicated on economic utility (Faith and Gordon 2007). We tested density-mediated attrition in skeletal abundance using bivariate plots and Spearman's rank-order correlation coefficient. The %MAU is the mathematical equivalent of the %survivorship (Lyman 1994:255). We plotted the available %MAU data of two taxonomic categories (cervid size 2/3 and the combined artiodactyl and ungulate size 3/4) against bone mineral density (BMD) values for deer obtained from Lyman (1994). We calculated Spearman's rank correlation coefficient (r_s), testing the link between bone mineral density and skeletal element survivorship. The nonparametric equivalent of Pearson's correlation is chosen because of the small sample sizes, and because the data is not normally distributed.

We tested the correlation between skeletal abundance and economic utility using the same method. The FUI is a general index that includes three components of economic utility: meat, marrow and bone grease. To our knowledge, no utility indices have been developed explicitly for large European cervids, therefore, we used the standardized FUI (sFUI) values obtained for caribou (Metcalfe and Jones 1988).

Since our samples for both taxonomic categories (ungulate ½ and ungulate ¾) are very low (MNE ≤ 5), we explored Faith and Gordon's (2007) approach and calculated Shannon's Evenness index on high-survival elements. This quantitative method is based on the observation that high-survival elements (i.e., long bones, mandible, and cranium) and low-survival elements (i.e., cancellous portions, vertebrae, ribs, pelves, scapulae, phalanges, and small compact bones) are differentially affected by taphonomic processes. Although the Shannon Evenness index should allow us to distinguish subtle variation in the skeletal representation, our sample size is too small to allow us to discriminate between transport strategies but it should help to qualify our discussions about sample size effect, bone attrition, and transport strategies (Faith and Gordon 2007).

Finally, we calculated four measures of taxonomic structure and composition based on the NISP of ungulate taxa at the genus level (see Lyman 2008; Grayson 1984): (1) the taxonomic Richness S or NTAXA calculated as the number of taxonomic categories (on the family and sub-family level) present in the assemblages, (2) the taxonomic heterogeneity H calculated with the Shannon index ($H = - \Sigma P_i(\ln P_i)$), where P_i is the proportion P of the taxon i in the assemblage, and (3) two different indexes of taxonomic evenness: the evenness index e derived from H and the log of NTAXA using the formula $e = H/\ln S$ and the reciprocal of Simpson's index $1/D$ with the formula $1/ \Sigma P^2_i$. We also tested the correlation between taxonomic richness (NTAXA) and sample size (ΣNISP) by calculating the Pearson linear correlation of the different faunal assemblages (see Grayson and Delpech 1998).

5.4.3.4 Taphonomic analysis: Multivariate taphonomic approach

Faunal analysts need to consider the unique taphonomic history that contributed to the skeletal accumulation of each assemblage before interpreting them in terms of human behaviour. One of the methodological approaches that can be used for such research is the multivariate taphonomic approach. The multivariate approach was designed to ensure the use of standardized taphonomic variables, allowing faunal analysts to compare different faunal assemblages while controlling for their unique depositional histories. The power of this approach was demonstrated on a series of Epipaleolithic assemblages in the Levant (Bar-Oz and Dayan 2003; Bar-Oz and Munro 2004). The process involves choosing multiple independent taphonomic variables, which are used within hierarchically organized lines of investigation and expressed in tables and line graphics to easily assess how they vary within and across faunal assemblages (see Behrensmeyer 1991).

At the scale of the individual site with multiple faunal assemblages (e.g., a Middle-Upper Paleolithic transitional sequence), the multivariate taphonomic approach is most beneficial for resolving issues of equifinality by highlighting the leading causes of bone attrition. Bar-Oz and Munro (2004) suggest tackling this problem through elimination, starting with a first line of investigation that addresses density-mediated attrition. Then, depending on the results, additional lines of investigation are incorporated to explore how these previously identified agents of bone alteration (e.g., geological processes, bioturbation, carnivore ravaging, human action) are differentially involved in the process of bone destruction. This *intra-site* multivariate taphonomic approach can be applied to any faunal collection.

We follow Bar-Oz and Dayan (2003) in dividing the taphonomic variables into general subsets of analysis such as (1) mode of preservation (e.g., fragmentation level, bone survivorship), (2) damage caused by natural agents (e.g., carnivore action, rodent gnawing, abrasion, etching, weathering), and (3) damage caused by humans (e.g., cut marks, percussion marks, burning). The variables can then be used in an *inter-site* multivariate taphonomic analysis that is a simple and powerful analytical tool to identify macro-scale subsistence changes. The critical aspect of the multivariate taphonomic approach is that it defines the representativeness of the faunal assemblage and offers the possibility of inter-assemblage comparisons (Behrensmeyer 1991).

We used taphonomic indices to reconstruct depositional and post-depositional processes affecting the state of preservation of the archaeozoological assemblages. We analyzed plotted finds, complete and partial elements, and bone shaft fragments with intact cortical surfaces. We recorded bone surface alterations, including post-depositional alterations (abrasion, polish, concretion, root and microorganism etching, rodent gnawing, manganese coloration, and weathering) according to three stages of intensity (stage 1: <50% covered, stage 2: >50% covered, and stage 3: entirely covered). We recorded the presence/absence of trampling, carnivore alterations (puncture, gnawing, and digestion), and anthropic alterations (percussion mark, percussion flake or splinter, cut mark, and bone manufacturing such as grooving and drilling marks) (Behrensmeyer 1991; Blumenschine 1988, 1995; Blumenschine et al. 1996; Domínguez-Rodrigo et al. 2009; Domínguez-Rodrigo and Yravedra 2009; Fisher Jr 1995; Lyman 1994; Stiner et al. 1995). We also recorded burning levels according to a simplified set of colour classes (unburned, carbonized, and calcined) adapted from Stiner et al. (1995) and Marques et al. (2018): (Table 1).

Table 1. – Description of the bone burning categories selected in this study

	Colour description	Colour categories (Stiner 1995)	Stage of combustion (Marques et al. 2018)
Unburned	No visible burning coloration	0	Intact or dehydration (0 to 250°C)
Carbonized	All black or traces of black	1, 2, and 3	Decomposition of the organic component (400 to 600°C)
Calcined	Transition from black to white/blue/greyish or completely white/grey	4, 5, and 6	Inversion and fusion (600 to 1000°C)

Fracture freshness angles were recorded for long bone shafts (Villa and Mahieu 1991), and we calculated the mean Fracture Freshness Index (FFI) according to Outram (2001). All surface modifications were identified using a Dino-Lite Edge Digital Microscope 20X-220X with enhanced DOF, operated with DinoCapture 2.0 software.

In most archaeozoological analyses, the small fraction is the first to be set aside because it rarely includes morphologically identifiable remains and, therefore, very few behavioural inferences are possible. However, at Riparo Bombrini, this fraction makes up the bulk of the fauna (from 95 to 99% of the NSP). It was thus essential to collect a maximum of taphonomic information from the whole assemblage rapidly and efficiently. We conducted the taphonomic study of the fine fraction using the same protocols applied in a previous analysis (see Pothier Bouchard et al. 2020). We first sorted each bulk bag of the fine fraction of bones collected in the sieve into six size classes according to their maximum length (0-20 mm, 20-30 mm, 30-40 mm, 40-50 mm, 50-60 mm, 60-80 mm, 80-100 mm, >100 mm). Within each size class, we set aside all identifiable elements for further analysis with the plotted finds. We subdivided the indeterminate fraction by burning levels (unburned, carbonized, and calcined). We further subdivided these categories into bone type categories (appendicular cancellous, axial cancellous, indeterminate cancellous, appendicular cortical, flat bones, teeth, cranial, and indeterminate). Finally, we quantified each subdivision and weighed it with a Tangent KP-103 scale (Max 120.0g, d=0.1g).

5.4.4 Intra-site multivariate taphonomic analysis

We carried out a detailed intra-site multivariate taphonomic analysis of the three faunal assemblages. As a first step, maps of the spatial distribution of the piece-plotted faunal remains were produced, showing the archaeological features associated with each faunal assemblage. The analysis then begins with a general description of taphonomic variables affecting the bulk of the assemblages, following previous multivariate taphonomic studies (e.g., Behrensmeyer 1991; Bar-Oz and Adler 2005; Bar-Oz and Munro 2004; Lyman 1994). We grouped the variables into four categories: (1) general assemblage data, (2) bone preservation, (3) long bone damage associated with natural taphonomic processes, and (4) long bone damage associated with anthropic processes. The values for these variables are summarised in the results tables and then further illustrated with line graphs to facilitate inter-assemblage comparisons.

The first category of variable provides contextual information. The second describes the extent of bone damage in the different assemblages, and the third and fourth categories of variables describe the surface alterations observed on long bone shaft fragments. All these variables are expressed as percentages of the NSP of long bones (NSP.lb).

Next, we conduct an intra-site multivariate analysis hierarchically, discriminating between the agents of bone accumulation and bone attrition using three lines of investigation: (1) bone completeness and fragmentation, (2) agents of bone accumulation, and (3) on-site carcass treatment. The values for these variables are presented similarly, summarised in the results tables and illustrated with line graphs.

5.4.4.1 First line of investigation: bone completeness and fragmentation

We based our first line of investigation on a specific set of taphonomic variables suggested by Bar-Oz and Munro (2004, 211 Table 4) to investigate bone completeness and fragmentation, adding a few variables more adapted to the heavy fragmentation rates encountered at Riparo Bombrini. We grouped these taphonomic variables into three categories: (1) density-mediated attrition, (2) post-depositional *in situ* attrition, and (3) pre-depositional fragmentation. We then use these variables to compare smaller ungulates (small game) and larger ungulates (large game), to better highlight how some taphonomic variables differentially affected them.

The first category of variables investigates how density-mediated factors influence each assemblage's bone fragmentation patterns. The lack of data precluded us from calculating two of Bar-Oz and Munro (2004)’s variables to evaluate the extent of density-mediated attrition of long bones (i.e., NISP: MNE ratios of specific long bones, and ratios of proximal to distal humeri and tibiae). Instead, we used three additional variables more suited to the Bombrini assemblages: (1) the percentage of bone fragments larger than four centimetres of small and large games to compare the intensity of fragmentation between those taxonomic categories, (2) a ratio of appendicular cancellous bone to appendicular cortical bone according to NSP to assess overall survivorship of less dense cancellous bones, and (2) a ratio of small compact bones (tarsals, carpals, sesamoids, and phalanx) to long bones and axial elements (excluding loose teeth) according to the NISP of small game and large game.

The second category of variables addresses the problem of post-depositional attrition.

The third category of variables compares the mean FFI of the two taxonomic sub-groups – small and large game – to evaluate the differential proportion of fractures made on dry versus green bones for these specific faunal categories.

5.4.4.2 Second line of investigation: agents of bone accumulation

This second step of our multivariate taphonomic analysis further investigates the nature of pre-depositional alterations that affected the faunal assemblages. It aims explicitly to distinguish if the skeletal remains were mainly accumulated on the site by human groups or by other large carnivores such as wolves or hyenas. We grouped this second set of taphonomic variables into two categories: (1) carnivore action and (2) human action.

The first category of variables compares six variables to estimate the relative abundance of carnivore bone accumulators on the site: (1) the percentage of carnivores, (2) the abundance and density (3) of coprolites, (4) the percentage of long bone shafts with more than half of their circumference, (5) the percentage of gnawed bones, and (6) the percentage of head elements.

The second category of variables evaluates the role of humans in the accumulation of the faunal assemblages: (1) the percentage of percussion, (2) the percentage of burned bones, and (3) the skeletal portion representation (dominated by a specific skeletal portion or not).

The two sets of variables compare the two taxonomic sub-groups – small and large game – to evaluate potential distinct accumulation patterns between these categories.

Finally, we describe other relevant qualitative criteria for identifying potential agents of faunal accumulation in the assemblages such as: the presence of anthropic marks on carnivore bones, the presence of overlapping carnivore alteration and anthropic marks, and the presence of carnivore decidual teeth (Brugal et al. 1997; Cruz-Uribe 1991a; Klein and Cruz-Uribe 1984; Lyman 1994; Pickering 2002; Stiner 1994; Villa et al. 2010).

5.4.4.3 Third line of investigation: on-site carcass processing

This third and last step of our intra-site multivariate taphonomic analysis investigates patterns of anthropic carcass processing. We grouped the taphonomic variables into three different categories: (1) marrow extraction, (2) grease rendering, and (3) bone as fuel.

In the first category of variables, (1) the mean FFI of long bone shaft fragments, (2) the percentage of bone flakes, and (3) the percentage of percussion marks are investigated at the family and sub-family levels to get a more detailed picture of differential carcass treatment between taxa.

The second category compares (1) the percentage of unburned cancellous bones and (2) the percentage of unburned epiphyseal cancellous bones, both according to NSP and NISP, for small and large game. We selected these variables based on the ethnoarchaeological and experimental observations that grease processing and grease rendering involve crushing and boiling the cancellous parts of post-cranial bones (Costamagno 2013; Morin and Soulier 2017; Outram 2001; Vehik 1977).

We grouped thirteen taphonomic variables in the third category, calculating these variables according to NSP because most burned bone falls in the smaller indeterminate fraction of the faunal assemblages.

Experimental archaeology has demonstrated that cancellous bone from whole epiphyses can complement other combustible materials such as wood (Costamagno et al. 2005; Morin 2010; Théry-Parisot et al. 2004). Therefore, the intentional burning of bones for fuel should be reflected in the archaeological record by higher proportions of heavily heated cancellous bones. We investigated this by comparing the percentage of unburned and burned cancellous bones, cancellous calcined bones, and burned long bone shaft fragments.

5.4.4.4 ZooMs sampling strategy

Finally, to help improve the statistical significance of our sample, specifically with respect to taxonomic identifications, we based our ZooMS sampling strategy on four criteria selected to maximize information gain. (1) We prioritized bones morphologically identified to a skeletal element associated with a broad taxonomic category (e.g., ungulate size 3/4, artiodactyl size 1/2) over non-identifiable bones, helping to clarify the skeletal representation data. (2) Using the same logic, we prioritized taxonomically unidentifiable bones of known age (i.e., fetal or juvenile bone structure) and bones identified to a skeletal element to maximize age and seasonal data acquisition. (3) We preferentially selected bones with specific surface alterations such as anthropic action (e.g., percussion marks, cut marks, splinters) and carnivore action (e.g., gnawing, tooth punctures, gastric digestion) to assess taphonomic attrition biases better. (4) Finally, we carried out a random selection of bones of variable size and cortical thickness on the indeterminate fraction of the collection in an attempt to improve the NISP tally and help assess faunal diversity and post-depositional attrition; it bears emphasizing that the attribution of animal size categories according to cortical thickness classes was shown to be highly variable in other ZooMS analyses (Sinet-Mathiot et al. 2019).

5.4.5 FTIR screening and ZooMS protocol

Because collagen preservation is compromised at Riparo Bombrini, we applied a screening method using a portable FTIR developed and tested elsewhere (Pothier Bouchard et al. 2019) while conducting the faunal analysis at the University of Genoa (Italy). We systematically selected 20 to 30 bone samples to screen for ZooMS in each stratigraphic unit of every square meter analyzed using the sampling strategy described in the taphonomic methods above. We processed each selected bone using an Agilent 4500a portable FTIR instrument equipped with a single-bounce diamond ATR and internal battery following the method detailed in Pothier Bouchard et al. (2020). The screening threshold of 0.6 was selected; entailing a sample was rejected when its CO/P ratio was less than 0.6. When the calculated CO/P ratio scored 0.6 or more, it was considered suitable for ZooMS analysis.

We followed the ZooMS protocols previously applied at Riparo Bombrini (Pothier Bouchard et al. 2019, see 2020). The bones samples (N=439) were first processed with low through-put acid-soluble ZooMS analysis following the method adapted from Buckley et al. (2009). We carried out MALDI-MS on a Bruker Ultraflex II instrument, with a *m/z* window of 700-3,700 mass units and up to 2,000 laser acquisitions per spot. We analyzed the obtained collagen fingerprints with mMass software (v5.5.0), and we identified animal species using previously published collagen peptide markers from reference spectra following Buckley et al. (2009, 2017) (See Supplementary Table S1 for all peptide markers used in this analysis). The resulting spectra exhibiting lower collagen preservation (i.e., missing peptid markers) were selected for further analysis (Table 2). We first applied the same ZooMS protocol on the acid-insoluble residue of 48 samples identified to a wide taxonomic category (e.g., ungulate) following Buckey et al. (2009). Next, we purified and fractioned 105 samples using reverse phase chromatography (RPC) with C18 solid phase extraction (SPE) pipette tips, following the manufacturer's protocol (Varian, UK). This method helped clarify some of our cervid identifications by improving the signal intensity of the A2T67(G) biomarker, essential to distinguish between *Cervus* (*m/z* value of 3033) and *Capreolus* (*m/z* value of 3059.4), and between *Rupicapra* (*m/z* value of 3033) and *Capra* (*m/z* value of 3093.4) (see Buckley et al. 2010 for further discussion on the isolation of collagen-peptide markers). However, it is worth noting that red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) are too closely related to be distinguished with ZooMS (Buckley and Kansa 2011). It is thus possible that some of our *Cervus* ZooMS identification also includes anecdotal *Dama* specimens (see Pothier Bouchard et al. 2020).

Table 2. – Number of bone samples selected for ZooMS in Levels A1, A2, and MS

	Acid-soluble	**Acid-insoluble**	**RPC**
Level A1	188	16	56
Level A2	224	14	37
Level MS	27	18	12

5.5 Results

5.5.1 Summary of the archaeozoological data

5.5.1.1 Relative abundance of taxa

All three assemblages show overall rich faunal spectra dominated by large Cervinae, most likely corresponding to red deer with some fallow deer (Table 3). Cervinae account for more than 50% of the identified taxa at the family and sub-family levels in the Proto-Aurignacian Level A1 (Fig. 5), whereas it is proportionally less abundant in Level A2 (34%) and Level MS (46%). Capreolinae, mostly corresponding to roe deer, are also slightly more abundant in Level A1 (5%) than in the two underlying levels (A2=2%, MS=0) (Fig. 5). Caprinae are also constantly present, with more variable proportions between the assemblages as they are more abundant in the Proto-Aurignacian than in the Mousterian. In Level A1, they are the second most abundant taxon (24%), whereas they account for 20% in Level A2 and 11% in Level MS. Bovinae, corresponding to either *Bison* or *Bos*, are only present in the Proto-Aurignacian levels. They are the second most abundant taxon in Level A2 (25%), whereas they account for 12% in Level A1. Suidae and Equidae are ubiquitous in lower abundance, although the first is proportionally most abundant in Level MS (9%) and the second in Level A2 (10%). Finally, carnivores are present in low abundance in the Proto-Aurignacian, whereas they account for 19% of the total NISP in Level MS (Fig. 5). Most of the remains are unidentifiable medium-sized (2/3) carnivores, likely corresponding to Canidae or Hyenidae. The presence of a few Ursidae teeth in Levels A2 and MS is also worth mentioning (Table 3).

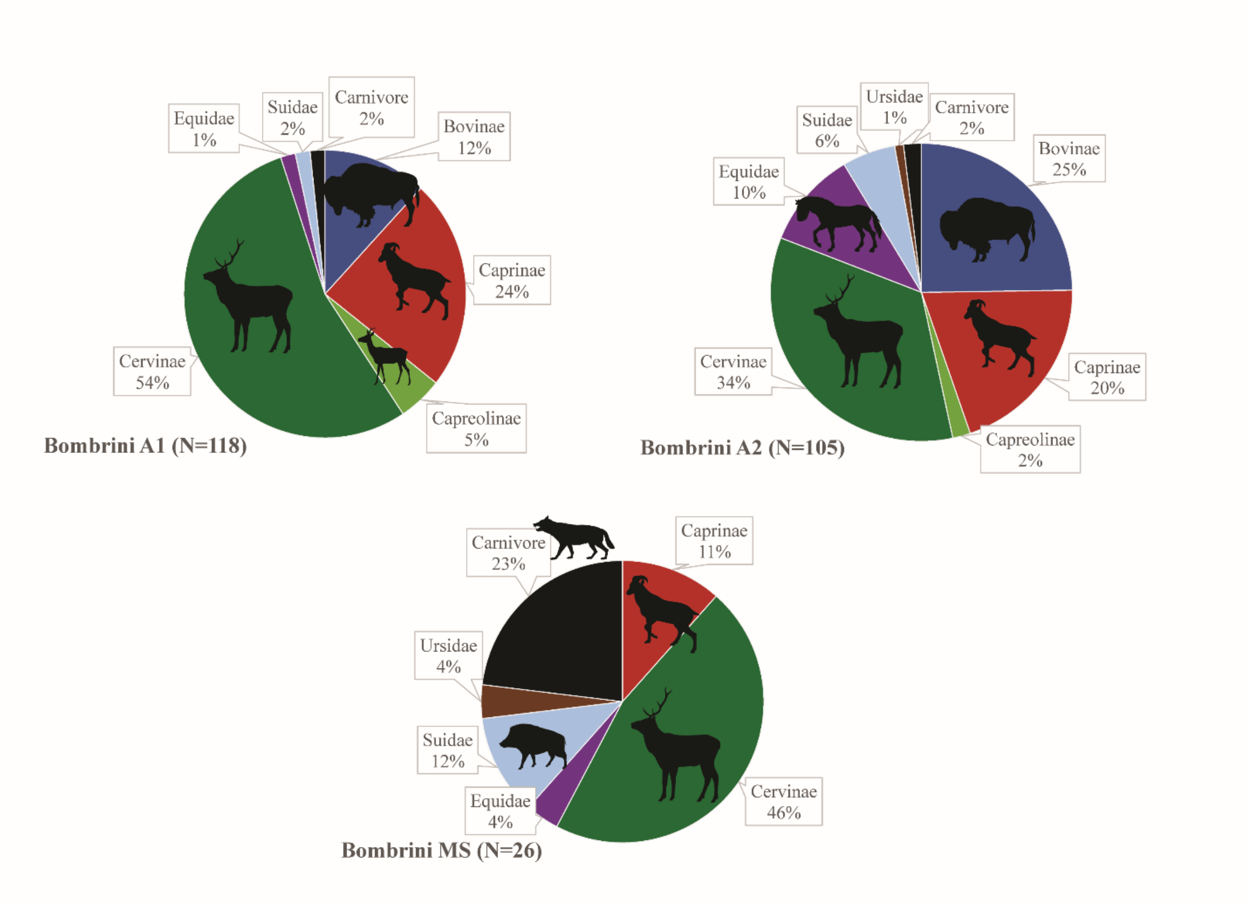

Figure 5. – Relative abundance (%NISP) of the main taxa (family and sub-family) in Levels A1, A2, and MS.

Table 3. – Relative abundance of taxa at Riparo Bombrini

	Bombrini A1			**Bombrini A2**			**Bombrini MS**		
	NISP	**%NSP**	**MNI**	**NISP**	**%NSP**	**MNI**	**NISP**	**%NSP**	**MNI**
Taxa									
herbivores									
Bos/Bison	14	0,31%	1	25	0,24%	1	n/a	n/a	n/a
Capra ibex	23	0,51%	1	21	0,20%	1	3	0,06%	1
Capreolus sp.	6	0,13%	1	2	0,02%	1	n/a	n/a	n/a
Cervus elaphus	3	0,07%	1	n/a	n/a	n/a	1	0,02%	1
Cervus sp.	60	1,34%	1	36	0,35%	1	11	0,22%	1
Dama dama	1	0,02%	1	n/a	n/a	n/a	n/a	n/a	n/a
Diceros/Coelodonta	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Equus sp.	2	0,04%	1	11	0,11%	2	1	0,02%	1
Sus scrofa	2	0,04%	1	6	0,06%	1	3	0,06%	1
Bovid s.2/3	1	0,02%	1	n/a	n/a	n/a	2	0,04%	1
Caprine s.2/3	5	0,11%	1	n/a	n/a	n/a	n/a	n/a	n/a

Cervid s.2/3	n/a	n/a	n/a	n/a	n/a	n/a	1	0,02%	1
Cervid s.3/4	5	0,11%	1	3	0,03%	1	4	0,08%	1
Cervid s. indeter.	2	0,04%	1	8	0,08%	1	3	0,06%	1
Artiodactyle s.2/3	n/a	n/a	n/a	3	0,03%	1	6	0,12%	2
Artiodactyle s.3/4	14	0,31%	1	35	0,34%	3	12	0,25%	1
Artiodactyle s.inteter.	n/a	n/a	n/a	3	0,03%	1	7	0,14%	1
Ungulate s.2/3	4	0,09%	1	1	0,01%	1	n/a	n/a	n/a
Ungulate s.3/4	14	0,31%	1	40	0,38%	1	12	0,25%	1
Ungulate s.indeter.	17	0,38%	1	15	0,14%	1	1	0,02%	1
Carnivores									
Ursus sp.	n/a	n/a	n/a	1	0,01%	1	1	0,02%	1
Carnivore s. 2/3	n/a	n/a	n/a	n/a	n/a	n/a	1	0,02%	1
Carnivore s.3/4	2	0,04%	1	2	0,02%	1	5	0,10%	1
Total NISP	175	3,90%	16	212	2,03%	22	74	1,51%	19
Indeterminate	4313	96,10%		10211	97,97%		4819	98,49%	
Total NSP	4488	100,00%	16	10423	100,00%	22	4893	100,00%	19

The taxonomic composition of the three faunal assemblages from Bombrini shows that Level A1 is richer than Level A2, and that Level MS has the lowest number of identified taxa (Table 4). The relationship between the ΣNISP and the NTAXA within the sub-assemblages (divided between site areas) shows a statistically significant correlation (r=0.94, p=0.0048) between sample size and taxonomic richness. This indicates that variation in sample size affects taxonomic composition between the different areas of the site and between the smaller assemblage of the Level MS and the larger assemblages of Levels A1 and A2. Level A1 (ΣNISP = 111) is richer but less evenly distributed than A2 (ΣNISP=101) which explains our results (Table 4).

Table 4. – Taxonomic composition of ungulates at Riparo Bombrini. Richness (NTAXA), heterogeneity with Shannon index (H), evenness with evenness index (e) and reciprocal of Simpson’s index (1/D).

Faunal assemblages	**ΣNISP**	**NTAXA**	***H***	***e***	***1/D***
Level A1	111	7	1.254	0.644	2.600
Level A2	101	6	1.527	0.595	4.043
Level MS	19	4	1.028	0.742	2.215
Level A1 - inside	21	5	0.882	0.548	2.921
Level A1 - outside	90	7	1.157	0.595	2.360
Level A2 - inside	26	6	1.277	0.713	4.630
Level A2 - outside	75	6	1.068	0.596	3.718
Level MS - inside	5	3	0.688	0.627	2.778
Level MS - outside	14	4	0.655	0.472	1.849

5.5.1.2 Skeletal frequencies

The skeletal representation for all three assemblages (NISPe) is summarised in Table 5. The results show that skeletal representations are head-dominated (mostly comprised of teeth). However, we observe some tendencies in terms of taxonomic abundance at the family and sub-family levels (Fig. 6, 7, and 8). The ungulates size 3/4 are also relevant to discuss transport strategies of larger ungulates as their skeletal remains are more abundant (Table 5).

Table 5. – Skeletal representation (NISPe) of Bombrini A1, Bombrini A2, Bombrini MS. H=head, A/h=antler/horn, N=neck, A=axial skeleton, Uf=upper forelimb, Uh=upper hindlimb, Lf=lower forelimb, Lh=lower hindlimb, Il=indeterminate limb, T=toes, I=indeterminate

NISPe values	**H**	**A/h**	**N**	**A**	**Uf**	**Uh**	**Lf**	**Lh**	**Il**	**T**	**I**
Taxa Level A1											
Cervidae 1/2 (N=6)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	4	n/a	2
Cervinae (N=69)	8	n/a	n/a	5	1	n/a	2	2	23	1	27
Caprinae (N=29)	3	n/a	n/a	4	n/a	n/a	n/a	n/a	13	1	8
Bovinae (N=14)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	10	n/a	4
Equidae (N=2)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2
Suidae (N=2)	1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	1
Ungulate 1/2 (N=4)	n/a	n/a	n/a	n/a	n/a	n/a	1	2	1	n/a	n/a
Ungulate 3/4 (N=28)	9	n/a	n/a	n/a	1	1	n/a	2	9	4	2
Carnivore (N=2)	1	n/a	n/a	1	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Taxa Level A2											
Cervidae 1/2 (N=2)	n/a	n/a	n/a	n/a	n/a	1	n/a	n/a	n/a	n/a	1
Cervinae (N=39)	5	1	n/a	1	n/a	n/a	n/a	n/a	16	n/a	16
Caprinae (N=21)	3	n/a	n/a	n/a	1	n/a	n/a	n/a	10	n/a	7
Bovinae (N=25)	2	n/a	n/a	n/a	n/a	n/a	1	1	8	1	12
Equidae (N=11)	4	n/a	n/a	n/a	n/a	n/a	1	2	1	n/a	3
Suidae (N=6)	2	n/a	n/a	1	1	n/a	n/a	n/a	n/a	1	1
Ungulate 1/2 (N=4)	3	n/a	n/a	n/a	n/a	n/a	1	n/a	n/a	n/a	n/a
Ungulate 3/4 (N=75)	45	n/a	2	3	1	2	1	n/a	9	6	6
Carnivore (N=2)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	2	n/a	n/a
Ursidae (N=1)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	1	n/a	n/a
Taxa Level MS											
Cervidae 1/2 (N=1)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	1	n/a
Cervinae (N=15)	2	n/a	n/a	7	n/a	3	1	n/a	n/a	n/a	2
Caprinae (N=5)	5	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Bovinae (N=0)	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Equidae (N=1)	1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Suidae (N=2)	2	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Ungulate 1/2 (N=6)	4	n/a	n/a	n/a	n/a	n/a	n/a	1	n/a	1	n/a
Ungulate 3/4 (N=26)	15	n/a	n/a	6	n/a	n/a	n/a	n/a	n/a	2	3
Carnivore (N=6)	6	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Ursidae (N=1)	1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a

Level A1 shows two different patterns of skeletal frequency. First, the two less abundant taxa illustrated in Figure 6, Cervidae size 1/2 and Bovinae, are represented by indeterminate limbs and indeterminate skeletal elements. The latter category mainly comprises small cortical bone fragments (<2 cm) identified with ZooMS. Second, Caprinae follows a similar pattern with a predominance of indeterminate limbs and skeletal elements but include some elements of the axial skeleton and the head. Cervinae shows a dominance of limbs, toes, and head elements. The few medium carnivore elements come from the head and the axial skeleton (Fig. 6, Table 5).

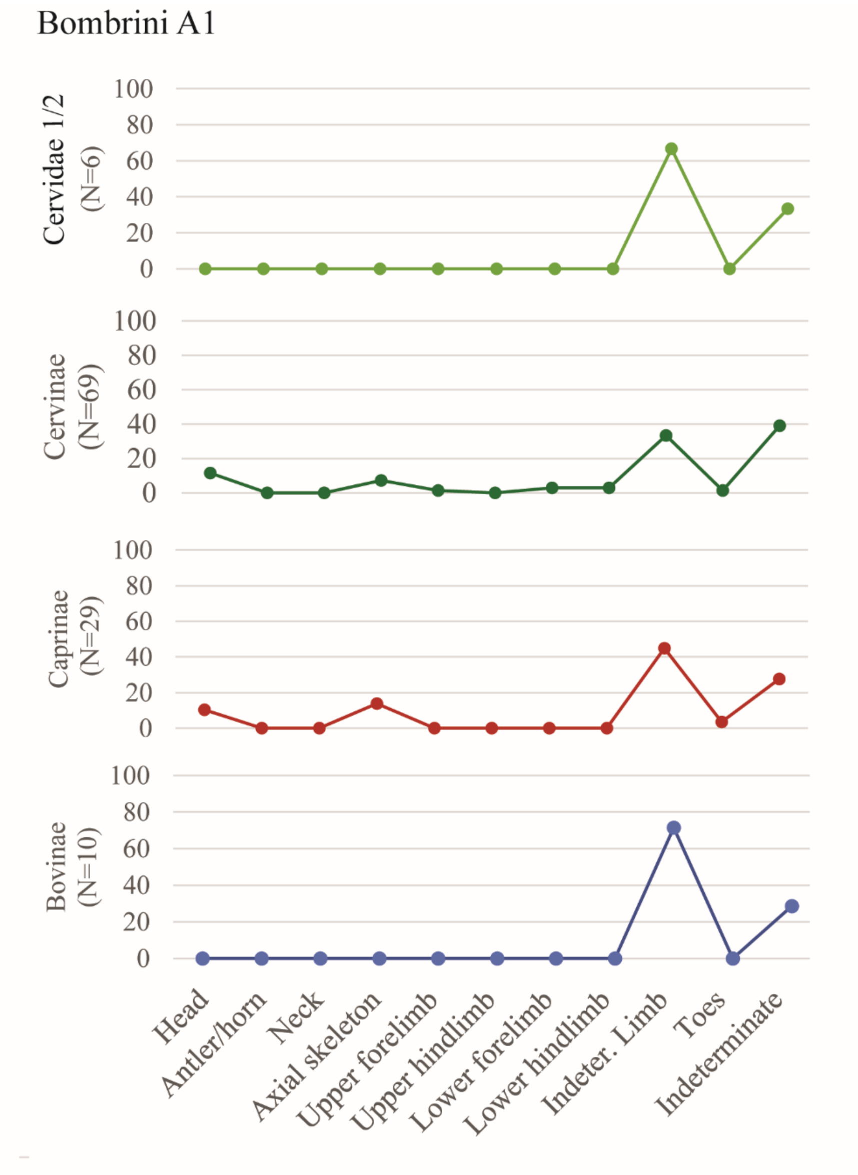

Figure 6. – Skeletal frequencies (%NISPe) of the most abundant taxa according to NISP in Level A1

Level A2 shows that Cervinae and Caprinae follow similar patterns with skeletal elements from the head, indeterminate limbs, and indeterminate skeletal elements dominating, coupled with a weak representation of the rest of the skeleton. In contrast, Bovinae are dominated by skeletal elements from the lower limbs with a few head elements, and Equidae are split between the two categories (Fig. 7).

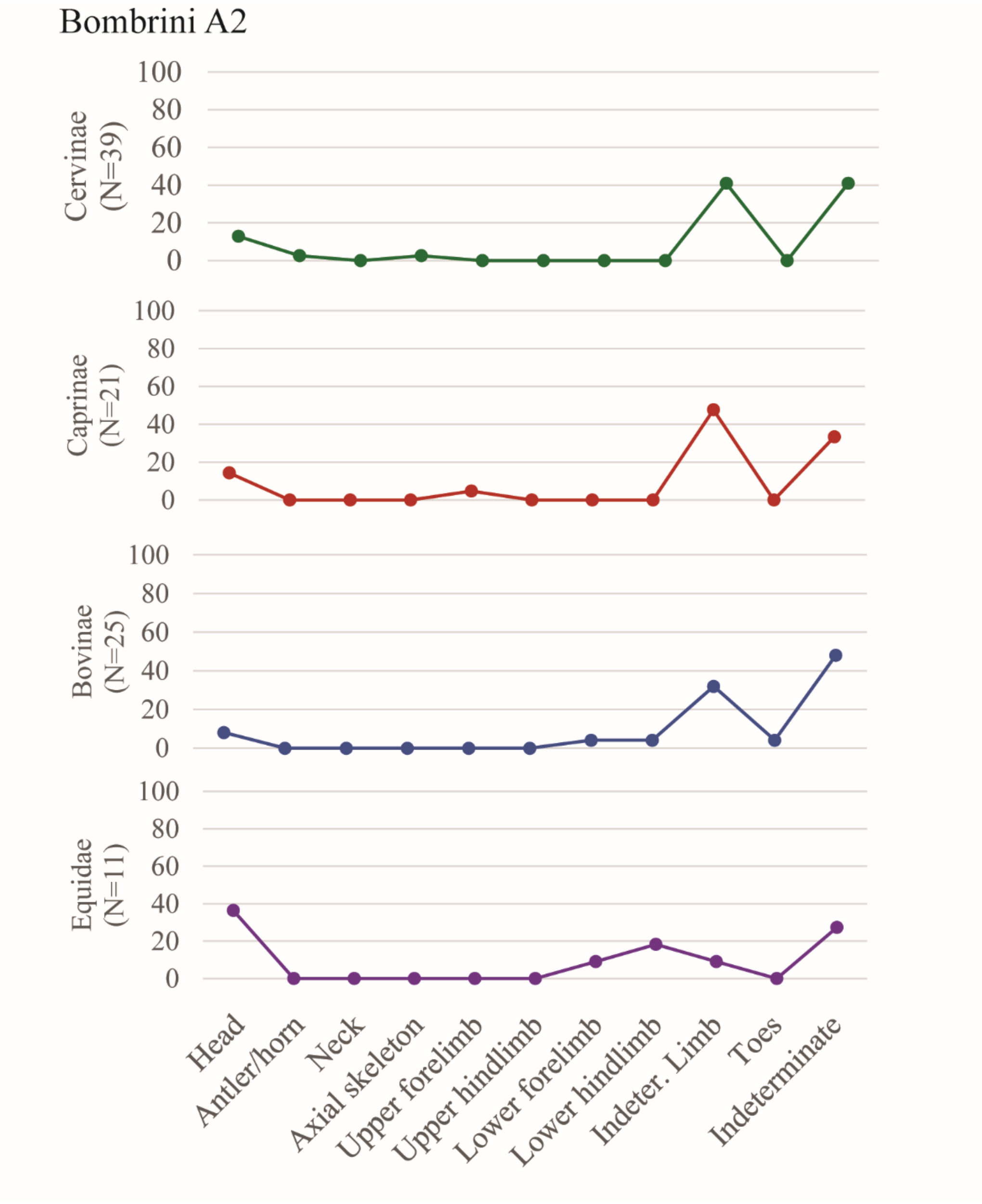

Figure 7. – Skeletal frequencies (%NISPe) of the most abundant taxa according to NISP in Level A2

Level MS is distinctive because head elements are present for almost all taxa, including medium carnivores and Ursidae (Fig. 8). The main exception is Cervinae, as it shows a predominance of skeletal elements from the axial skeleton – mostly ribs – and a few upper limbs and head elements. Cervidae size 1/2, although less abundant than other taxonomic categories, show a few elements of the lower limb and toes in addition to being head-dominated (Table 5).

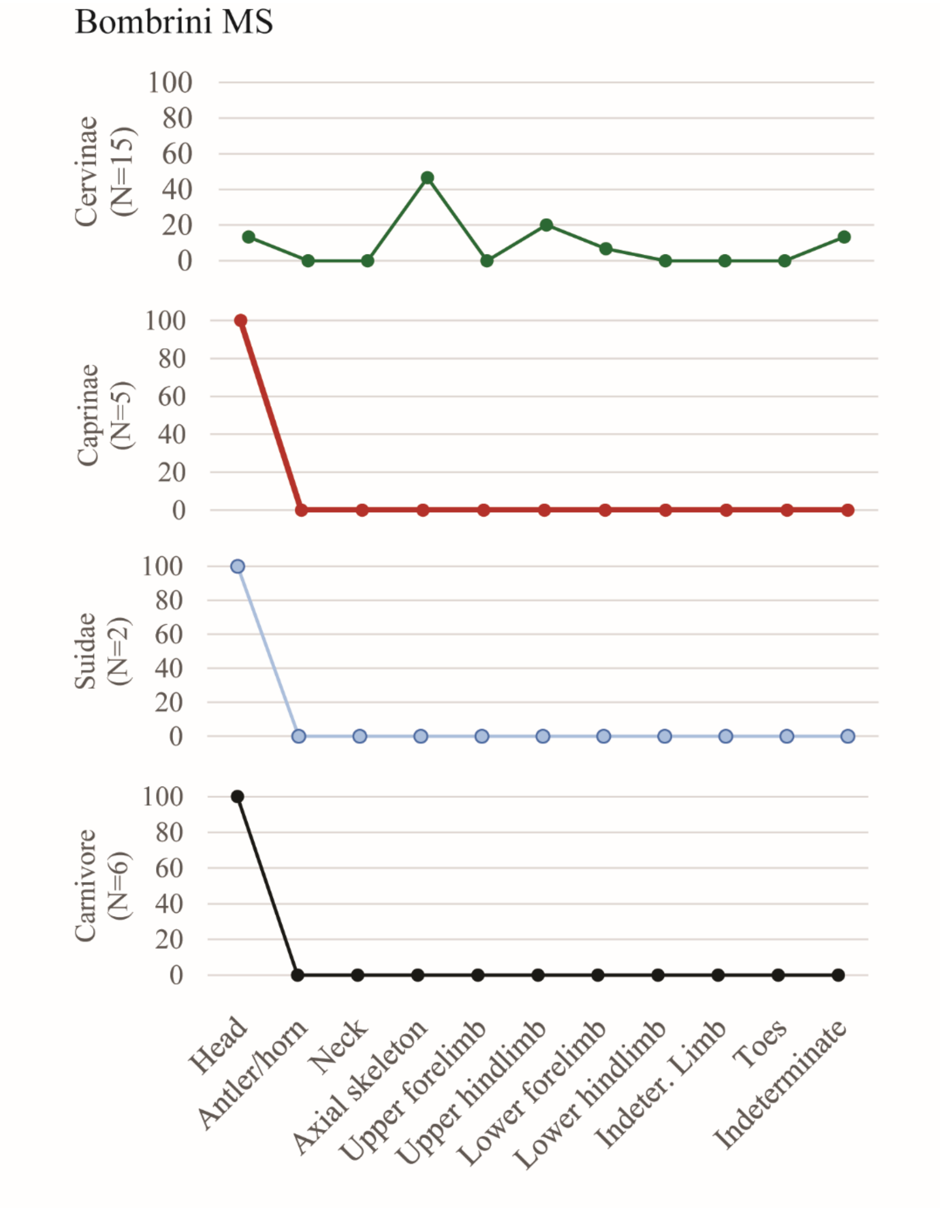

Figure 8. – Skeletal frequencies (%NISPe) of the most abundant taxa according to NISP in Level MS

5.5.1.3 Age, sex, and seasonality indices

The age determinations in Table 6 show the dominance of prime-age adult ungulates in the three assemblages. In Level A1, we identified four specimens (MNI = 2) of prime-aged Cervinae, one prime-aged ibex and one older wild boar. In Level A2, larger ungulates show more varied mortality profiles with four Cervinae teeth (MNI = 1; teeth too fragmented to distinguish between red deer and fallow deer) and one Bovinae tooth identified to prime-age adults, whereas two out of the three Equidae correspond to a juvenile and the third corresponds to an older animal. Post-cranial elements also indicate the presence of one prime-aged Bovinae, one juvenile and one prime-aged larger artiodactyls, and an indeterminate fetal animal. In Level MS, all ungulate teeth correspond to prime-age adults: one red deer, two ibex (MNI = 1), and one horse, except one tooth corresponding to an older ibex. The post-cranial elements correspond to adult Cervinae specimens (MNI =1) and one juvenile specimen of smaller artiodactyls. This level also includes carnivore teeth corresponding to juvenile animals.

Two skeletal elements allowed us to identify the presence of male ungulates at Riparo Bombrini (Table 6). The first is a Cervinae antler fragment recovered in Level A2, and the second is the canine of a prime-aged (~2-4 years) Cervinae recovered in Level MS. Although the antler was too altered to be aged, the fact that this fragment survived the heavy taphonomic alterations on the site suggests that it was fully mineralized before its deposition. This element could thus indicate the hunting of a male deer near the end of its antler cycle during late summer, fall, or early winter or collecting the shed antler during spring or summer. In addition, the presence of a fetal bone in Level A2 also points to the hunting of a gestating female animal in winter or spring.

Table 6. – Data on age, sex, and seasonality in Levels A1, A2, and MS

	Area	Element	Age estimate	J	A	O	Sex	Season
Taxa Level A1								
Cervus elaphus	outside	maxillary with M2	2-3.5 years	n/a	1	n/a	n/a	n/a
Cervus elaphus	outside	indeter. molar maxillary	< 3 years	n/a	n/a	n/a	n/a	n/a
Cervus elaphus	outside	P2 maxillary	2-3 years	n/a	1	n/a	n/a	n/a
Dama dama	outside	indeter. molar maxillary	< 4 years	n/a	n/a	n/a	n/a	n/a
Capra ibex	outside	P3 maxillary	1-3 years	n/a	1	n/a	n/a	n/a
Sus scrofa	inside	indeter. premolar	>3 years	n/a	n/a	1	n/a	n/a

Bovidae size 1/2	inside	indeter. molar mandibular	n/a	n/a	1	n/a	n/a	n/a
Taxa Level A2								
Teeth								
Cervus sp.	outside	P4 mandibular	5-6.5 years	n/a	1	n/a	n/a	n/a
Cervidae size 2/3	inside	indeter. molar	n/a	n/a	1	n/a	n/a	n/a
Cervidae size 2/3	inside	P1 mandibular	2-3 years	n/a	1	n/a	n/a	n/a
Capra ibex	inside	indeter. molar	<4 years	n/a	n/a	n/a	n/a	n/a
Bos/Bison	inside	indeter. molar	n/a	n/a	1	n/a	n/a	n/a
Equus sp.	outside	molar/premolar maxillary	<2 years	1	n/a	n/a	n/a	n/a
Equus sp.	outside	premolar mandibular	>10 years	n/a	n/a	1	n/a	n/a
Equus sp.	outside	M3 maxillary	1-2 years	1	n/a	n/a	n/a	n/a
Artiodactyla size 3/4	inside	indeter. molar	< 2 years	1	n/a	n/a	n/a	n/a
Bones								
Cervidae size 2/3	inside	antler	n/a	n/a	n/a	n/a	male	winter/ spring
Bos/Bison	outside	radius prox. epiphysis	>3.5-4 years	n/a	1	n/a	n/a	n/a
Artiodactyla size 3/4	outside	indeter. rib	n/a	1	n/a	n/a	n/a	n/a
Artiodactyla size 3/4	outside	stylohyoid	n/a	n/a	1	n/a	n/a	n/a
Indeterminate	inside	long bone	fetal	n/a	n/a	n/a	n/a	winter/ spring
Taxa Level MS								
Teeth								
Cervus elaphus	outside	canine	2-4 years	n/a	1	n/a	male	n/a
Capra ibex	outside	M3 maxillary	3-4 years	n/a	1	n/a	n/a	n/a
Capra ibex	inside	M2 mandibular	1.5-2 years	n/a	1	n/a	n/a	n/a
Capra ibex	inside	P2 maxillary	8-10 years	n/a	n/a	1	n/a	n/a
Equus sp.	outside	I1 maxillary	3-9 years	n/a	1	n/a	n/a	n/a
Ursus sp.	inside	M1 maxillary	n/a	1	n/a	n/a	n/a	n/a
Carnivore size 3	inside	M1 mandibular	< 1 year	1	n/a	n/a	n/a	n/a
Carnivore size 3	inside	indeter. canine	< 1 year	1	n/a	n/a	n/a	n/a
Bones								
Cervus sp.	outside	Femur dist. epiphysis	2-4 years	n/a	1	n/a	n/a	n/a
Cervus sp.	outside	Rib 3-6 prox. epiphysis	n/a	n/a	1	n/a	n/a	n/a
Cervidae size 2/3	outside	Rib 3-6 prox. epiphysis	n/a	n/a	1	n/a	n/a	n/a
Cervidae size 2/3	outside	Rib 7-10	n/a	n/a	1	n/a	n/a	n/a
Cervus sp.	outside	Ulna prox. epiphysis	>2-7 years	n/a	1	n/a	n/a	n/a
Artiodactyla size 1/2	inside	tibia prox. epiphysis	<2 years	1	n/a	n/a	n/a	n/a

5.5.1.4 Differential bone survivorship (density and transport decisions)

Few taxa provided sufficient data to allow us to test the correlation between relative skeletal abundance (%MAU), bone mineral density (BMD), and an index of food utility (sFUI) except for ungulates size 3/4 in Levels A1, A2, and MS, and cervids size 2/3 in Levels A1 and MS. The correlation coefficients (r_s) (Tables 7 and 8) indicate a stronger correlation between skeletal frequencies and bone mineral density than indices of food utility for both taxonomic categories. However, only two levels show statistically significant correlations between skeletal representation and BMD: Level MS (cervid size 2/3: r_s = 0.87, p=0.057) and Level A2 (ungulate size 3/4: r_s = 0.94, p=0.0024). These results are no doubt affected by the small sample size (see MNE values in Tables 7 and 8); the assemblages are classified in Lyman's (1994:264) "class 4" of the possible combinations of the coefficient correlations of %MAU with sFUI and BMD which describes the faunal assemblages as either ravaged or fluvially sorted.

Table 7. – Correlations between %MAU and sFUI, %MAU and BMD of Cervid size 2/3, and their possible interpretation according to Lyman (1994:264, Fig. 7.13)

Cervid size 2/3	**Level A1 (MNE =8)**	**Level A2 (MNE = 2)**	**Level MS (MNE = 10)**
%MAU:sFUI	r_s=-0.32 (p=0.53)	n/a	r_s =0.19 (p=0.69)
%MAU:BMD	r_s =0.60 (p=0.27)	n/a	r_s =0.87 (p=0.057)
Interpretation	Insignif.	n/a	Lag or ravaged

Table 8. – Correlations between %MAU and sFUI, %MAU and BMD of Ungulate size 3/4, and their possible interpretation according to Lyman (1994:264, Fig. 7.13)

Ungulate size 3/4	**Level A1 (MNE = 10)**	**Level A2 (MNE=13)**	**Level MS (MNE = 6)**
%MAU:sFUI	r_s =0.51 (p=0.23)	r_s =-0.21 (p=0.59)	r_s =-0.33 (p=0.83)
%MAU:BMD	r_s =0.52 (p=0.22)	r_s =0.94 (p=0.0024)	r_s =0 (p=1)
Interpretation	Insignif.	Lag or ravaged	Insignif.

The small sample sizes and the positive correlation between bone survivorship and bone mineral density suggest that the faunal assemblages are heavily damaged and unsuitable for the analysis of skeletal transport decisions. Unfortunately, Shannon's Evenness Index could not be applied due to the limitations mentioned above.

5.5.2 Multivariate Intra-site Taphonomic Analysis

5.5.2.1 General taphonomic observations

General taphonomic observations on the faunal assemblages of Levels A1, A2, and MS are summarised in Table 9.

Table 9. – General taphonomic observations

	Level A1		**Level A2**		**Level MS**	
	inside	outside	inside	outside	inside	outside
General assemblage data						
NSP	3656	832	9001	1422	4852	41
NISP	59	114	95	116	50	24
NSP.lb	130	95	148	103	59	1
Quarry data						
Size of studied area (m2)	6	2	6	2	6	2
Deposit volume (m3)	0.6	0.33	0.99	0.25	1.81	0.19
N total piece-plotted artifacts (with fauna)	223	67	362	192	346	36
%piece-plotted fauna (total artifacts)	9	16	13	15	42	69
Density of piece-plotted artifacts (N/m3)*	372	203	366	784	191	189
Density of piece-plotted fauna (N/m3)*	32	33	46	118	81	132
Density of bone fragments (NSP/m3)*	6093	2521	9092	5804	2681	2016
Spatial arrangement of bones – in plan view	n/a	n/a	n/a	n/a	Random	n/a
Spatial arrangement of bones – in profile	n/a	n/a	n/a	n/a	Horizontal	n/a
Spatial distribution of fauna – patchiness	Patchy	Slightly patchy	Highly patchy	Even	Slightly patchy	Slightly patchy
Bone state of preservation						
%identifiable before ZooMS (NSP)	1.0	4.4	0.8	3.8	0.9	56
%bone fragments <2 cm (NSP)	93	76	96	84	96	37
Long bone damage of natural processes (NSP.lb)						
%Abrasion stage 2 <	18	31	36	36	61	n/a
%Abrasion and polish	7	8	5	n/a	27	n/a
%Concretion stage 2 <	20	23	34	25	66	n/a
%manganese coloration stage 2 <	18	35	15	55	20	n/a
%Trampling	1	2	2	1	n/a	n/a
%Etching stage 2 <	2	5	7	6	n/a	n/a
%Carnivore gnawing	2	n/a	1	4	10	n/a

%Weathering stage 2 <	2	13	5	9	n/a	n/a
%Modern fractures	15	20	23	33	69	100
% Fresh fracture angles	13	54	28	48	31	100
Mean FFI score	5.48	4.12	4.97	4.02	4.92	n/a
Long bone damage of anthropic processes (NSP.lb)						
%Burned (carbonized + calcined)	32	21	22	25	7	n/a
% anthropic percussion	3.1	6.3	n/a	4.9	n/a	n/a
% cut marks	n/a	n/a	n/a	1.9	n/a	n/a
N percussion flakes	3	15	13	3	n/a	n/a
N bone manufacture	2	n/a	2	n/a	n/a	n/a

*The measures of density correspond to the theoretical concentration of remains per cubic meters.

The general assemblage data shows that the largest faunal assemblage according to the NSP is located in Level A2 (NSP=10423), followed by Levels MS (NSP=4893) and A1 (NSP=4518). In each stratigraphic level, the faunal assemblages outside the rockshelter are smaller than the assemblages inside the rockshelter. The densities of all skeletal remains (NSP), illustrated in Figure 9, indicates a higher density of skeletal remains in Level A2 (NSP/m^3 = 14,896), followed by Level A1 (NSP/m^3 = 8,614), and finally Level MS (NSP/m^3 = 4,697). In addition, the faunal assemblages outside the rockshelter are less dense in all stratigraphic levels. However, in Level A1 the volumetric density outside the dripline is comparable to Level MS.

The data also shows that while the concentration of piece-plotted remains (artifacts and fauna) in Proto-Aurignacian levels is denser in artifacts than the Mousterian level, the latter shows similar artifact densities inside and outside the rockshelter. In contrast, artifact densities in A1 are higher inside the rockshelter, whereas Level A2 shows a much higher density of artifacts outside the dripline. On the other hand, the relative abundance of piece-plotted fauna further demonstrates that faunal remains account for a much higher proportion of the total archeological record in Level MS (>40%) than in both Proto-Aurignacian levels (<20%) except for the deposit located outside the dripline in Level A2.

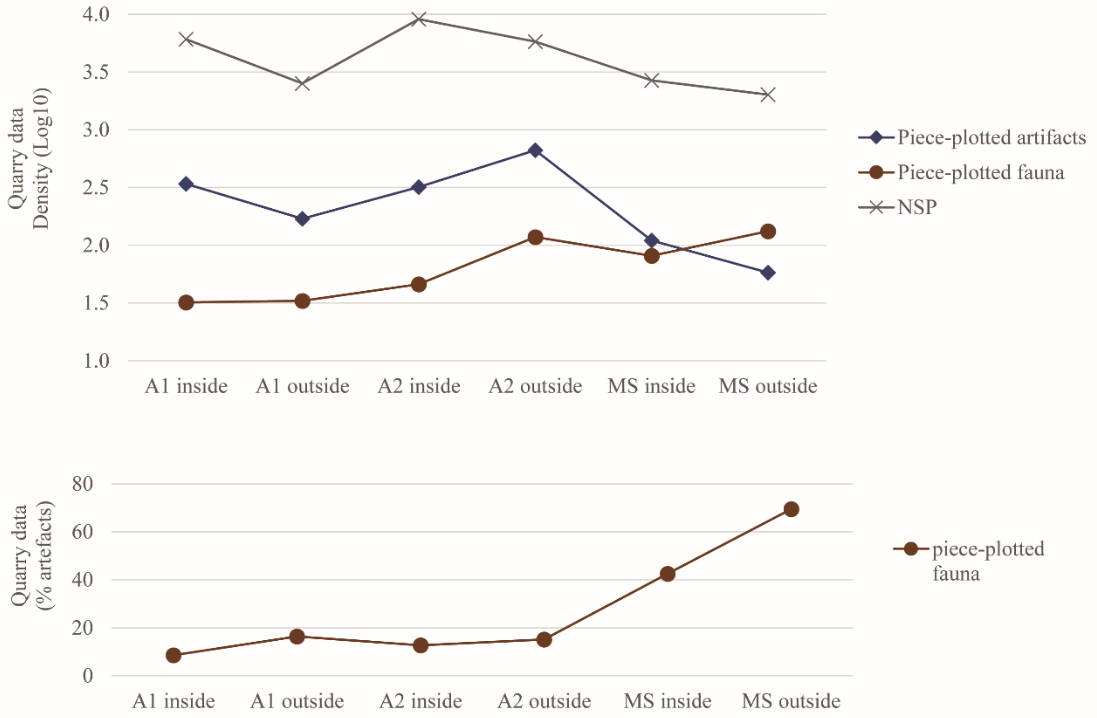

Figure 9. – Quarry data: line graphics illustrating the density artifacts and fauna recovered on the site(top), the relative abundance of piece-plotted fauna (bottom).

The spatial distribution of the piece-plotted fauna (Figures 10, 11, and 12) shows different patterns. In Level A1, a cluster of bones surrounds the small combustion feature in square-unit B1. Inside the rockshelter, the distribution of the skeletal remains is more homogeneous except in square-unit FF3, where a high concentration of bones fills a discarding pit. In Level A2, bone concentrations are associated with two features (i.e., hearth and trash pit) and are uniformly distributed outside the dripline. In addition, there are small clusters of bones in both Proto-Aurignacian levels in between the large blocks shaping the drip line. In Level MS, a concentration of bones has formed in the combustion area. A few collapse events of the rockshelter roof during the deposition of Level MS explain why some of the skeletal remains were recovered under the largest blocks.

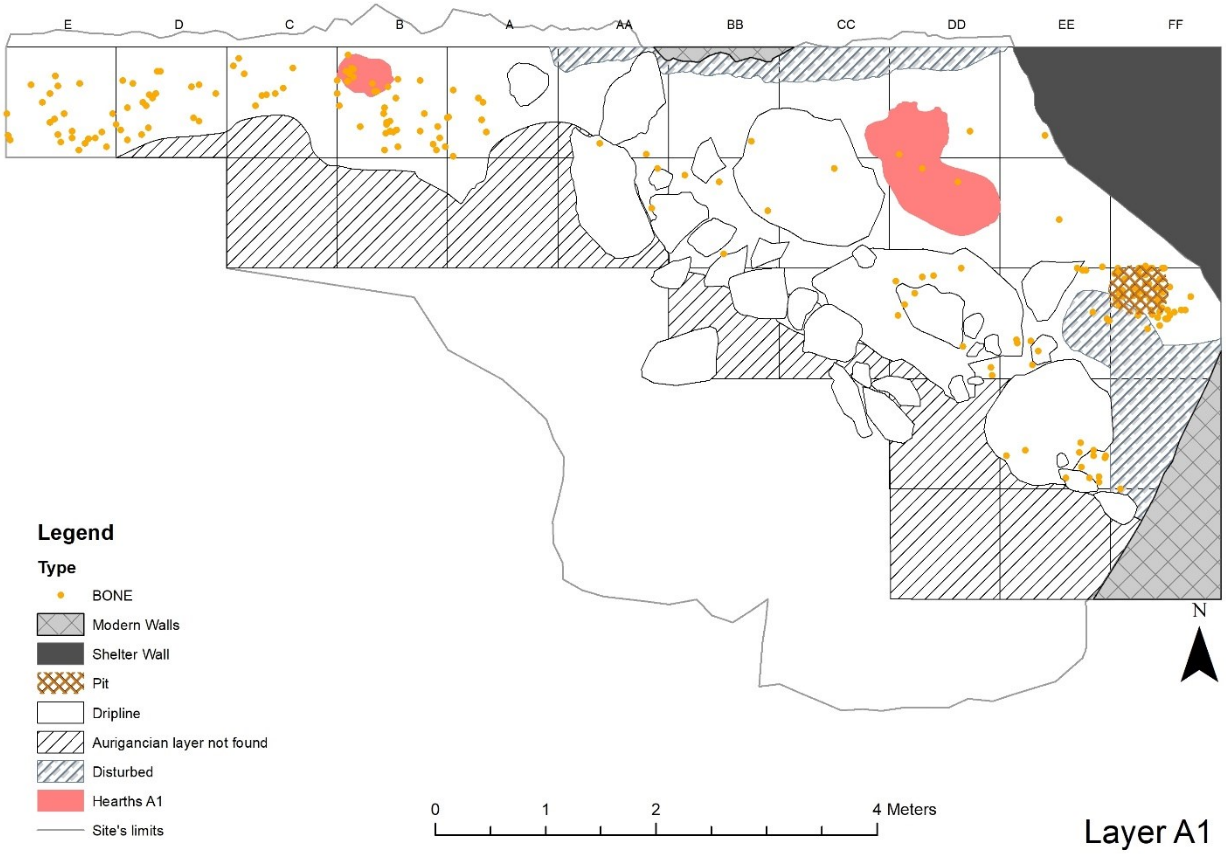

Figure 10. – Spatial distribution of the piece-plotted bones in Level A1

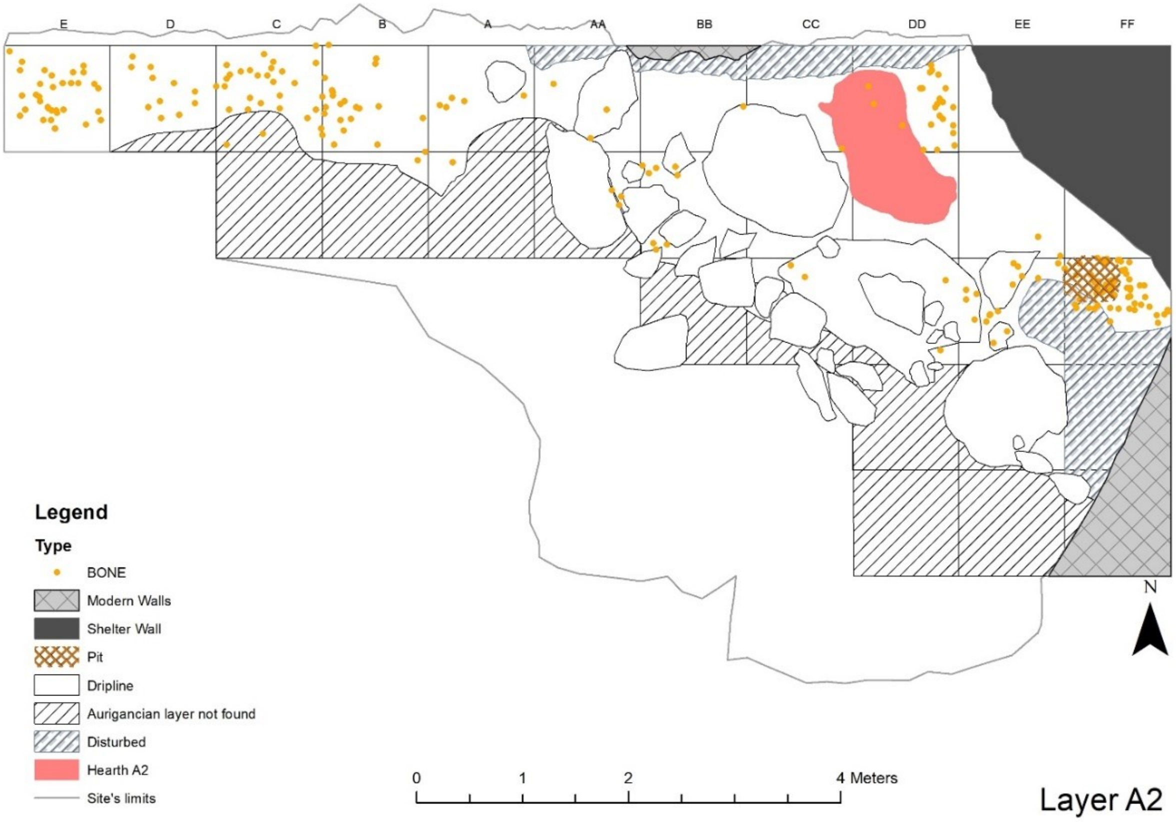

Figure 11. – Spatial distribution of the piece-plotted bones in Level A2

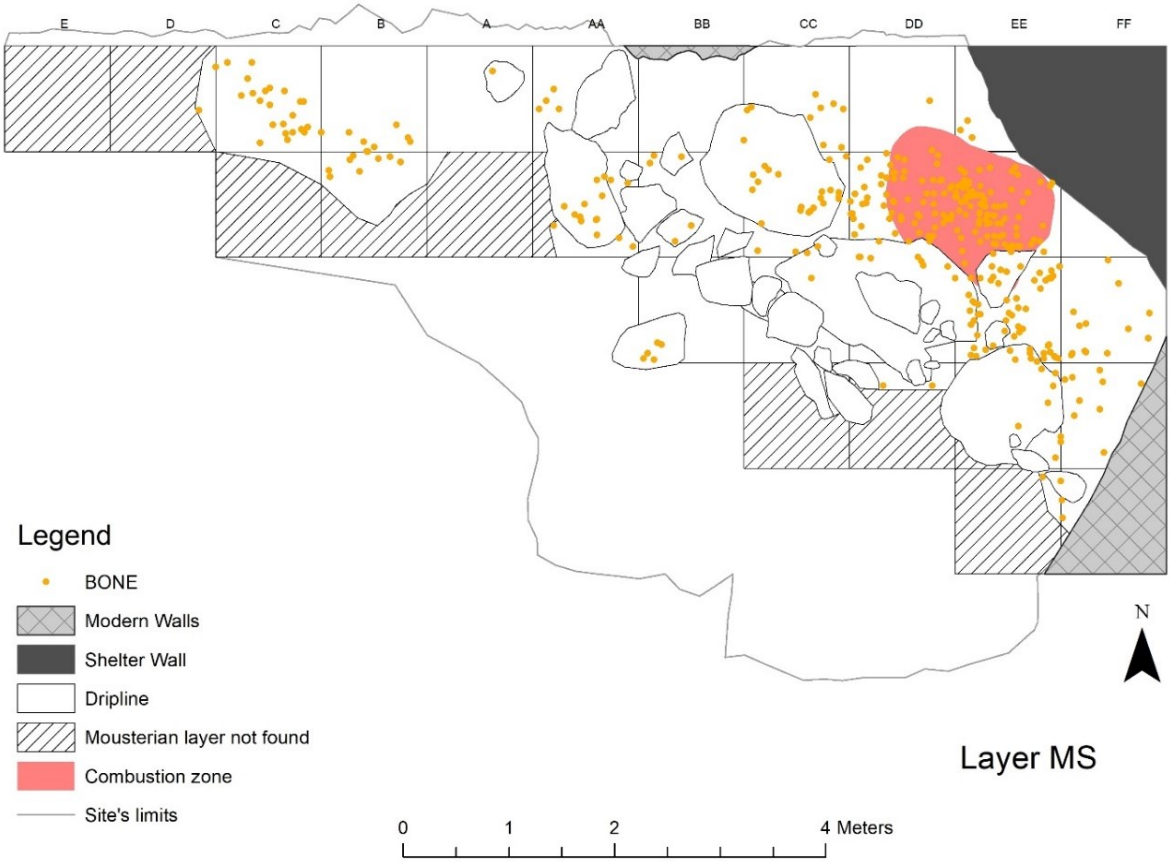

Figure 12. – Spatial distribution of the piece-plotted bones in Level MS

The bone state of preservation data indicates a low rate (<5%) of identifiable skeletal remains in all Proto-Aurignacian faunal assemblages and Level MS inside the rockshelter, whereas 56% of the Level MS outside the rockshelter is identifiable (Table 9). This pattern is related to the size of the skeletal remains (and thus, the degree of fragmentation). The nature of the remains in Level MS, characterized by a comparatively small collection (NSP=41), larger bones, including a few near-complete skeletal elements in anatomical connexion, facilitated taxonomic identification.

The long bone surface alteration data shows that the most salient alterations are abrasion and concretion, which cover over 60% of the long bone shaft fragments in Level MS and affect between 25 and 35% of the long bone shaft fragments in Level A2 and between 15 and 25% in Level A1 (Table 9, Fig. 13). The overall high levels of modern fractures follow a similar pattern to the concretions, as the excavation of heavily concreted skeletal remains often necessitates hammers and chisels on the field. The mean FFI scores are relatively high (>4/6), indicating a large proportion of breakage on dry bones in all assemblages. The degree of dry breakage is higher inside the rockshelter, especially within Level A1. The percentages of fresh fracture angles follow similar patterns to the mean FFI scores, which never account for more than 31% of the long bones inside the rockshelter. Level A1 is also characterized by a lower abundance of long bone fragments with fresh fracture angles (13%). However, the data available outside the rockshelter shows a much higher abundance of fresh fracture angles in this area in both Proto-Aurignacian levels accounting for approximately 50% of the long bones.

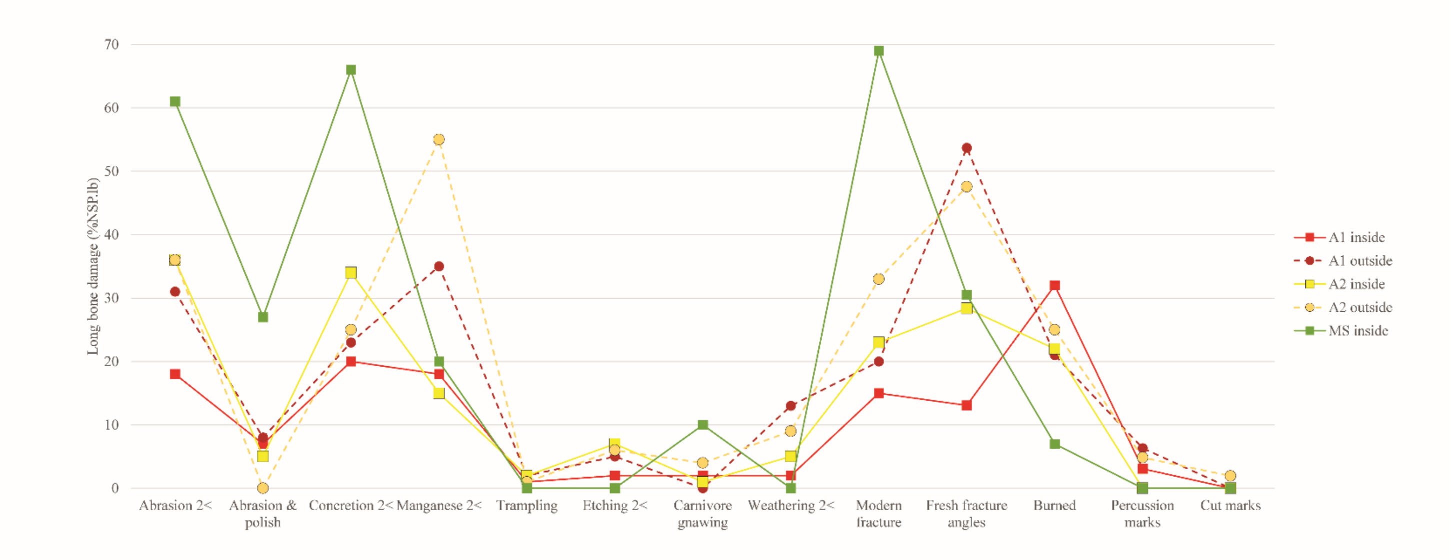

Figure 13. – Line graphic illustrating long bone surface damage in Levels A1 (top), A2 (middle), and MS (bottom).

The intensity of manganese staining is similar in the three assemblages but tends to vary spatially within each assemblage. In Levels A1 and A2, manganese coloration is higher outside (A1=35%, A2=55%) the rockshelter. Taphonomic observations on long bone shafts are not available for Level MS outside the rockshelter as a single long bone shaft was recovered in this area, but manganese coloration in Level MS inside the drip line is similar to the overlying Proto-Aurignacian levels (affecting between 15 and 20% of the bones). Other taphonomic processes, including abrasion and polish, trampling, root and microorganism etching, carnivore gnawing, and weathering, generally affect less than 10% of the Proto-Aurignacian long bone shaft assemblages (Table 9). However, slight variations include higher levels of bone weathering outside the rockshelter, especially in Level A1. Taphonomic processes also vary inside the rockshelter in Level MS. Abrasion and polish, along with carnivore alterations, are relatively more abundant in this assemblage affecting respectively 27 and 10% of the long bone shafts. In addition, there are no traces of trampling, etching, or weathering in this assemblage.

All three assemblages of long bone shaft fragments showed very few anthropic surface alterations (Fig. 13, Table 9). Cut marks are absent from Levels A1 and MS altogether and are only present on two bone shaft fragments in Level A2 – outside. Percussion marks are somewhat more abundant, being present on 3% of the long bone shafts in Level A1 – inside, 6% in Level A1 – outside, and 5% in Level A2 – outside.

The most salient anthropic alteration observed on long bone shafts at Riparo Bombrini is burning (Fig. 13, Table 9). The level of long bone shaft burning is high in both Proto-Aurignacian levels (up to 32% in Level A1 – outside). In contrast, only 7% of the MS assemblage shows traces of burning inside the rockshelter. Finally, a few bone splinters resulting from direct percussion were identified in both Proto-Aurignacian layers with a concentration inside the rockshelter in Level A2, associated with the hearth area (N=13). In addition, we identified four bone fragments with modifications related to tool manufacture inside the rockshelter in Levels A1 (N=2) and A2 (N=2).

5.5.2.2 First line of investigation: bone completeness and fragmentation

The results of our first line of investigation are summarised in Table 10. Many of the taphonomic variables related to bone completeness and fragmentation did not produce significant results due to the low NISP and NISP.lb data for small and large game, especially inside the rockshelter. However, some interesting observations shed light on density-mediated attrition, post-depositional attrition, and pre-depositional fragmentation within the assemblages.

Table 10. – Taphonomic observations on bone completeness and fragmentation

	Level A1		**Level A2**		**Level MS**	
	Inside	Outside	Inside	Outside	Inside	Outside
General data						
NISP small game	9	32	10	23	10	4
NISP large game	31	82	65	85	21	20
NISP.lb small game	4	16	n/a	12	n/a	n/a
NISP.lb large game	10	38	9	28	n/a	1
Density-mediated attrition						
Frag. index (NISP/MNI) Cervid size 2/3	68.5		39		15	
Frag. index (NISP/MNI) Artio&Ung size 3/4	28		51.7		25	
Small game: large game ratio (NISP)	0.29	0.39	0.15	0.27	0.52	0.2
%bone fragments >4cm (NISP) small game	n/a	3	10	22	n/a	75
%bone fragments >4cm (NISP) large game	6	29	9	32	5	80
Compact bones:long bones and axial elements (NISPe) small game	n/a	0.05 (N=22)	1 (N=2)	0.07 (N=15)	1 (N=2)	0.5 (N=3)
Compact bones:long bones and axial elements (NISPe) large game	0.25 (N=15)	0.1 (N=53)	0.08 (N=14)	0.4 (N=48)	1 (N=4)	n/a
Appendicular cancellous bone:appendicular cortical bone (NSP)	0.5 (N=192)	0.03 (N=98)	0.6 (N=236)	0.2 (N=119)	0.05 (N=62)	1 (N=2)
Post-depositional *in situ* attrition						
%completeness of tarsals and carpals small game	n/a	n/a	n/a	n/a	n/a	n/a
%completeness of tarsals and carpals large game	n/a	50 (N=2)	n/a	62.5 (N=4)	n/a	n/a
%completeness of phalanx1 and phalanx2 small game	n/a	100 (N=1)	100 (N=1)	n/a	n/a	100 (N=1)
%completeness of phalanx1 and phalanx2 large game	25 (N=3)	25 (N=1)	25 (N=1)	25 (N=4)	25 (N=2)	n/a
Cranial:tooth elements (NSP)	0.07 (N=88)	0.5 (N=24)	0.02 (N=188)	n/a	0.03 (N=104)	0.4 (N=7)
Cranial:tooth elements (MNE) small game	n/a	1 (N=2)	n/a	n/a	n/a	1 (N=4)
Cranial:tooth elements (MNE) large game	n/a	0.8 (N=11)	n/a	n/a	n/a	n/a
Pre-depositional fragmentation						
Mean FFI (NISP.lb) small game	5.8	4.3	n/a	3.08	n/a	n/a
Mean FFI (NISP.lb) large game	5	3.4	6	2.6	n/a	2

That bone attrition being influenced by bone density was first suggested by the results of the Spearman's correlation (r_s) between bone survivorship and bone mineral density in Levels A2 and MS (Tables 7 and 8). The bone fragmentation index for large ungulates does not add any relevant information due to low MNI counts. In the Proto-Aurignacian, the ratio of small to large game is lower inside the rockshelter, which indicates a lower abundance of more friable, small game skeletal remains in this area of the site. In contrast, the ratio is higher inside the rockshelter in Level MS.

The results of bone completeness according to the NSP data, are illustrated in Figure 14. Note that the much smaller sample of Level MS outside the rockshelter (NSP=41) introduces a strong bias to our taphonomic results.

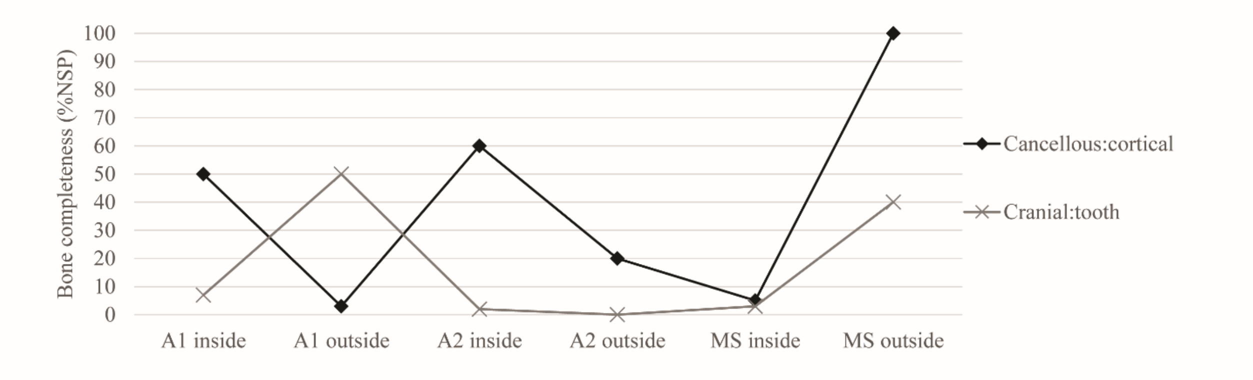

Figure 14. – Line graphic of bone completeness according to NSP in Bombrini A1, Bombrini A2, and Bombrini MS

Additional taphonomic variables comparing bone completeness for small and large game are illustrated in Figure 15. The relative abundance of bones larger than four centimetres and the ratio of compact to appendicular and axial skeletal remains indicate enhanced density-mediated attrition inside the rockshelter throughout the assemblages.

In Level A2, the ratio of compact to appendicular and axial elements of large game is lower inside the rockshelter, which agrees with the density-mediated attrition observed with the abundance of large (>4cm) skeletal remains. In contrast, the ratios are lower outside the rockshelter in Levels A1 and MS. The small game ratios suffer from a lack of data that may skew the results except for Levels A1 and A2 outside the rockshelter (NISP = 22 and 15, respectively).

The following three variables illustrated in Figure 15 are concerned explicitly with post-depositional *in situ* attrition, namely the tarsal/carpal index, the phalanx index, and the cranial to tooth ratio. The low number of carpals and tarsals identified throughout the assemblages (N=6) considerably hinder the usefulness of the tarsal/carpal completeness index.

The phalanx completeness index shows somewhat more promising results in all areas of the site, with more data available for large ungulates. In all assemblages in which phalanges are identified, large game phalanges tend to be fragmented and rarely more than 25% complete, whereas the few small game phalanges are always whole. In Levels A1 and A2, most of the phalanges are characterized by dry fractures and are heavily covered by concretion, which seems to have preserved their morphological integrity. In Level MS all of the preserved phalanges are heavily covered with concretion except for one large cervid recovered outside the rockshelter, altered by carnivore gnawing. One large ungulate phalanx epiphysis was embedded in concretion inside the rockshelter and showed fresh fracture angles.

The cranial to tooth ratio could only be illustrated in Levels A1 and MS outside the rockshelter but the sample size is low.

Finally, the mean FFI index, which potentially indicates pre-depositional attrition, shows overall higher values inside the rockshelter for both small and large game, when data is available. Large games are characterized by higher levels of fresh fractures than small games throughout the assemblages.

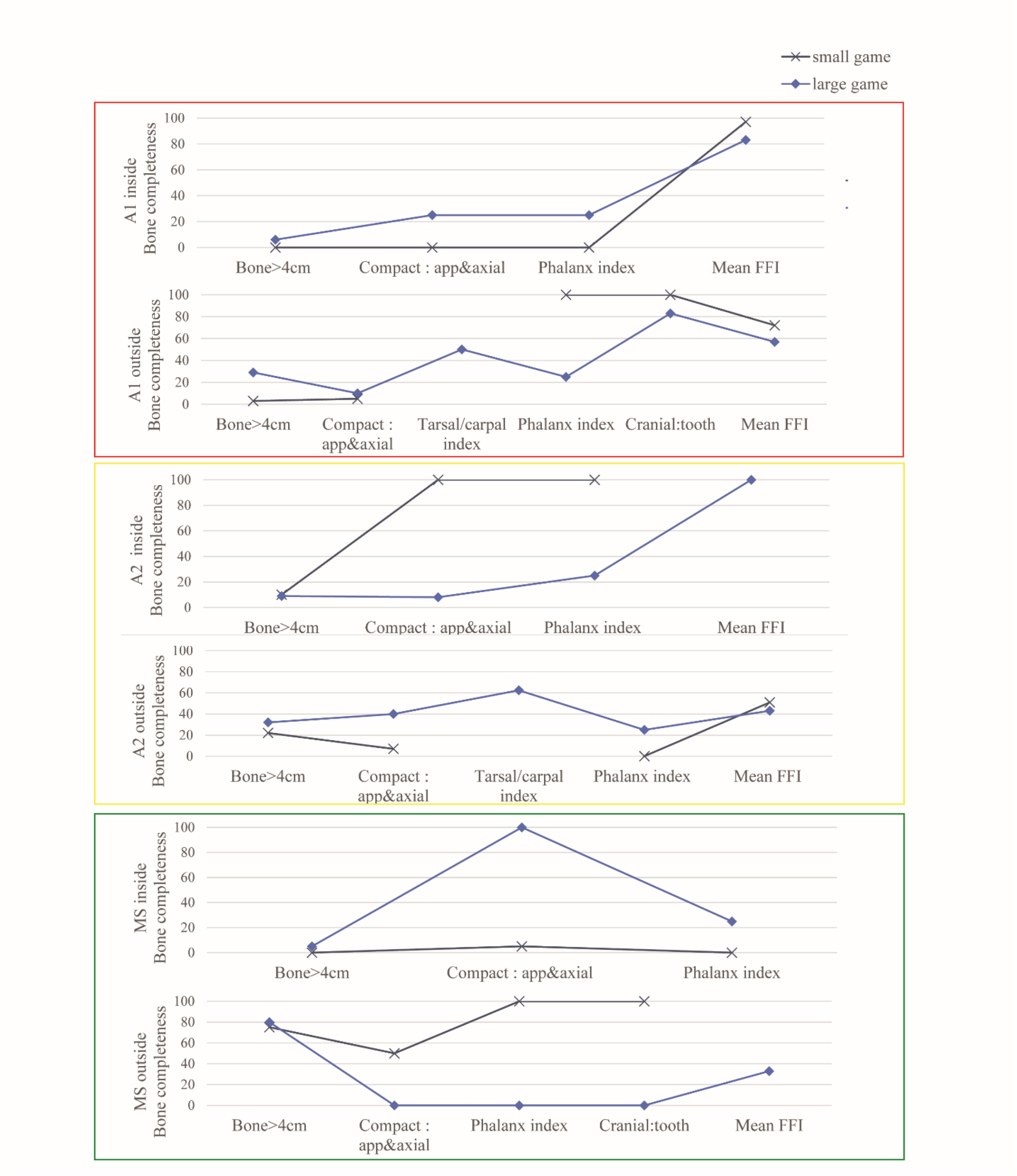

Figure 15. – Line graphics of bone completeness comparing small and large games in Bombrini A1 (top), Bombrini A2 (middle), and Bombrini MS (bottom)

5.5.2.3 Second line of investigation: agents of bone accumulation

The results of our second line of investigation are summarised in Table 11. Although all three assemblages are extensively fragmented, data from NSP, coprolite density, and NISP from large and small species have revealed some patterns related to whether humans or carnivores accumulated the faunal remains on the site.

Table 11. – Taphonomic observations on bone accumulation

	Level A1		**Level A2**		**Level MS**	
	Inside	Outside	Inside	Outside	Inside	Outside
General Data*						
Carnivore action						
% NISP small and large carnivores	3.3	n/a	1	1.7	14	n/a
N Coprolites	427	n/a	1141	n/a	4586	n/a
Density of coprolites g/m3 of sediment	106	n/a	88	n/a	154	n/a
% long bone shafts >1/2 circumference (NSP.lb)	4.6	9.5	11.4	4.9	23.7	100
% long bone shafts >1/2 circumference (NISP.lb) small game	n/a	12.5	n/a	16.7	n/a	n/a
% long bone shafts >1/2 circumference (NISP.lb) large game	n/a	18.4	22.0	7.1	n/a	100
% gnawed (NSP)	0.08	n/a	0.04	0.8	2	7.3
% gnawed (NISP) small game	n/a	n/a	n/a	13	20	50
% gnawed (NISP) large game	3.2	n/a	n/a	7.1	9.5	5
% head (NISP) small game	22.2	6.3	30.0	4.3	80.0	100.0
% head (NISP) large game	9.7	13.4	10.8	9.4	28.6	15.0
% head (NSP)	2.4	2.9	2.1	2.7	2.1	17.1
Human action						
% percussion marks (NISP) small game	n/a	n/a	n/a	4.3	n/a	n/a
% percussion marks (NISP) large game	9.7	3.7	n/a	4.7	n/a	n/a
% burned bones (NISP) small game	44.4	0	20	0	n/a	n/a
% burned bones (NISP) large game	3.2	4.9	21.5	15.3	n/a	n/a
Skeletal portions representation (NISPe) small game	limb		limb		head	
Skeletal portions representation (NISPe) large game	limb		head and limb		axial	

*Relevant general data is provided in the preceding multivariate tables

The carnivore action data shows a higher abundance of indices related to carnivore activities in the Mousterian deposit than in the Proto-Aurignacian deposits (Fig. 16, Table 11). Almost 45% of the total weight of coprolites recovered on the site comes from Level MS, versus 25% and 30% in Levels A2 and A1, respectively. In addition, the %NISP of small and large carnivores approaches 15% in Level MS, whereas it never surpasses 5% in the Proto-Aurignacian levels. It is also worth noting that all carnivore skeletal remains are located inside the rockshelter in Level MS and Level A1. The two elements in Level A2 are split between both sides of the dripline.

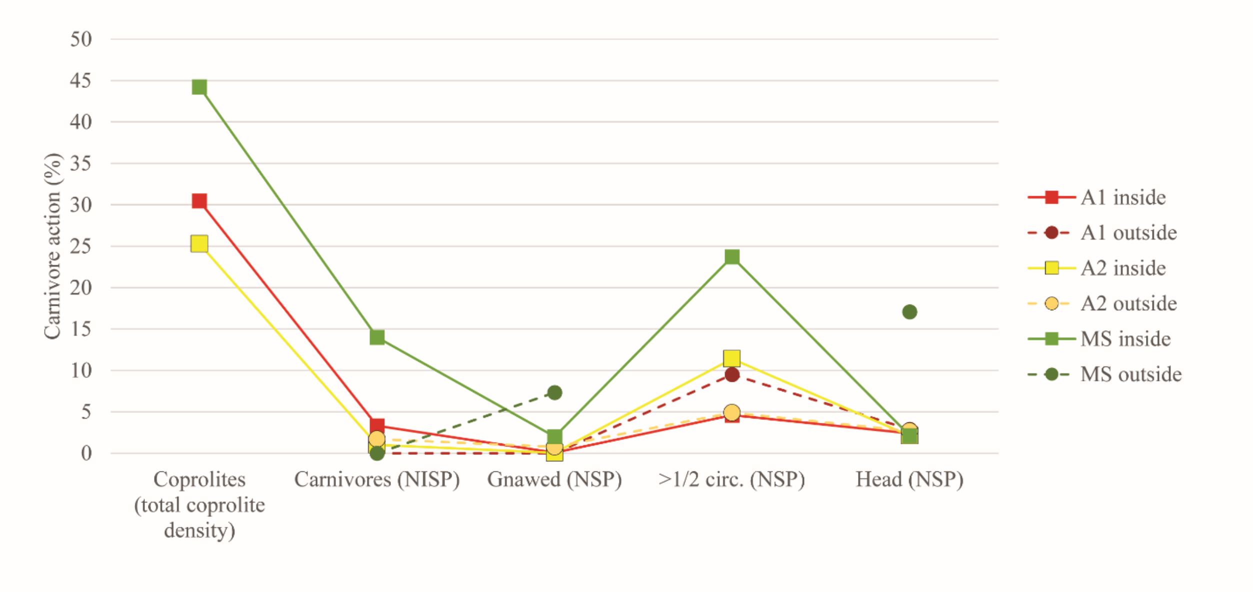

Figure 16. – Carnivore and human action comparing small and large games in levels A1 (top), A2 (middle), and MS (bottom). Note that the scale changes on the y axis in the bottom graphic.

Overall, carnivore alterations on bone surfaces (gnawing, digestion, and punctures) are scarce at the site. However, they remain proportionally more frequent in Level MS, both inside and outside the rockshelter. The higher abundance of bone shaft fragments with a near-complete circumference (> ½) inside and the proportionally higher abundance of head elements outside in this level could also be associated with carnivore activities.

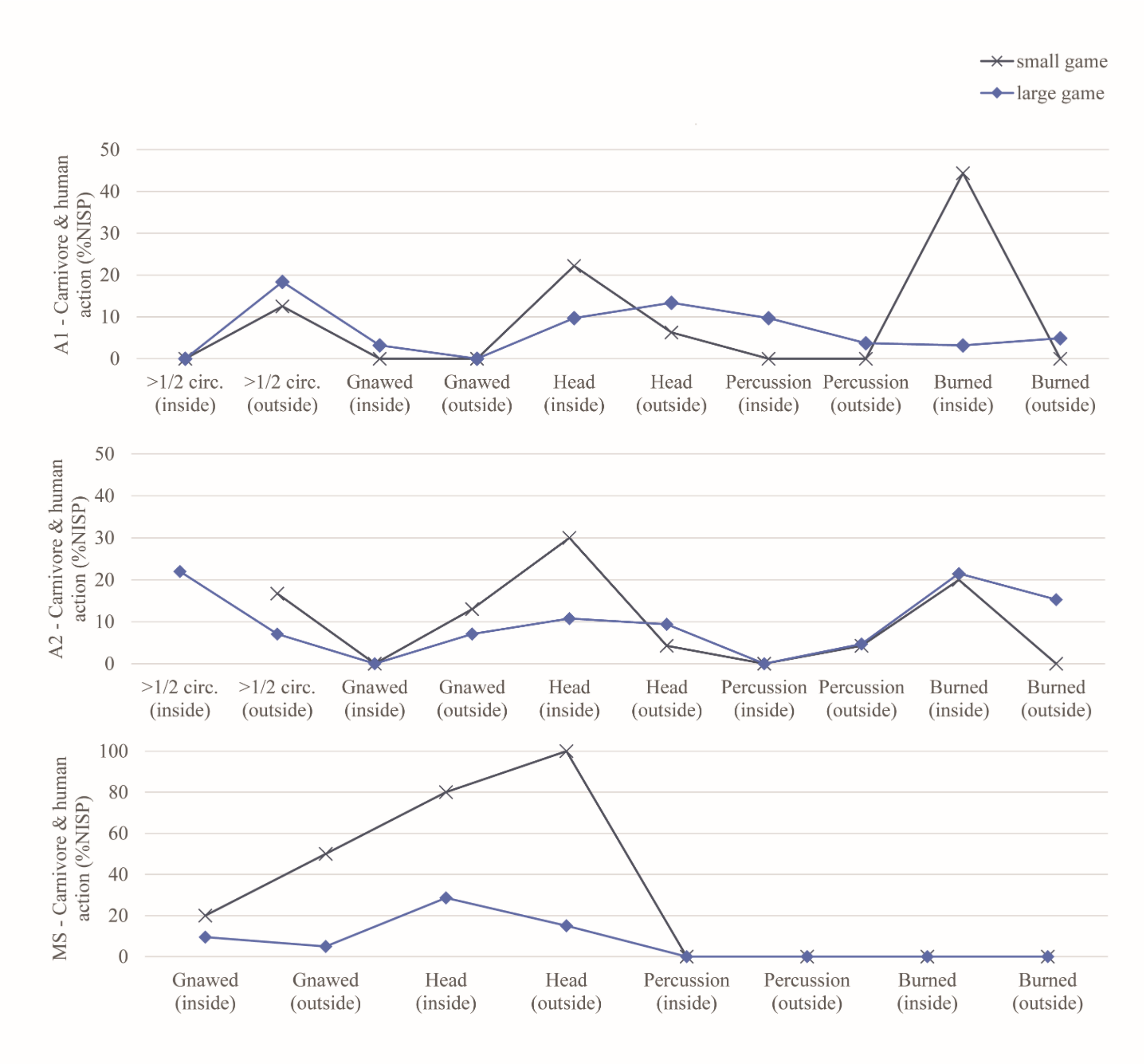

Figure 17. – Carnivore and human action comparing small and large games in Levels A1 (top), A2 (middle), and MS (bottom). Note that the scale changes on the y axis in the bottom graphic.

The data comparing small and large games shows different patterns between the three levels (Fig. 17). The carnivore surface alterations in Level MS affected a higher proportion of small species NISP(20% inside and 50% outside), including three digested adult caprine teeth. Incidentally, these teeth account for 100% of the caprine NISP in this level. The large species account for less than 10% of their NISP, including three cervid elements and one old equid incisor.

In Level A1, only one skeletal remain showed gnawing damage. In Level A2, carnivore alterations are more abundant outside the rockshelter. They account for 10% of the small game and 7% of the large game respective NISPs. It should also be noted that all identified faunal remains affected by carnivore alterations in the Proto-Aurignacian assemblages are post-cranial skeletal elements. In contrast, they include a mix of cranial and post-cranial remains in the Mousterian deposits.

Unfortunately, data on long bone shaft circumference could not be compared between small and large species in Level MS due to the lack of identifiable long bones. The data available for the Proto-Aurignacian levels shows that long bone shafts with near-complete circumferences of both taxonomic categories do not bear carnivore alterations. Most bone fragments instead show fresh fracture angles, especially outside the rockshelter. Small species are slightly more abundant outside the rockshelter for this taphonomic variable in Level A2, whereas the opposite pattern is visible in Level A1.

Elements of the head of large and small ungulates are present throughout the assemblages. In the three assemblages, small taxa are more frequent inside the rockshelter. This pattern is also observed outside the rockshelter in Level MS, whereas head elements are similarly frequent for small and large species in the Proto-Aurignacian assemblages for this area.

The taphonomic variables associated with human activities, namely percussion marks and burned bones, are absent from the Mousterian. In Level A1, percussion marks were only identified on large animal remains, and they are more frequent inside than outside the rockshelter. Burned large animal bones are scarce in this level, whereas almost half of the small species NISP inside the rockshelter are burned.

In Level A2, remains bearing percussion marks are absent inside the rockshelter, and they appear to be similarly frequent on small and large animal remains outside the rockshelter. The burned bones are similarly frequent across animal categories inside the rockshelter, whereas no burned small animal remains were identified outside the rockshelter.

Finally, although the Spearman's correlations between %MAU and FUI calculated earlier are not statistically significant, the qualitative skeletal representation using NISPe shows diverging patterns of skeletal portions between small and large game. In Level A1, limb elements dominate both taxonomic categories. In Level A2, limb elements dominate small game, whereas large animal remains are split between head and limb elements. In Level MS, small animals are head-dominated, whereas axial elements dominate among larger taxa.

5.5.2.4 Third line of investigation: on-site carcass processing

The results of our third line of investigation are summarised in Table 12.

Table 12. – Taphonomic observations on carcass processing

	Level A1		Level A2		Level MS	
	Inside	Outside	Inside	Outside	Inside	outside
General data						
NISP Cervinae	10	59	12	27	3	13
NISP.lb Caprinae	n/a	12	n/a	11	n/a	n/a
NISP.lb Capreolinae	n/a	4	n/a	n/a	n/a	n/a
NISP.lb Cervinae	3	24	2	14	n/a	1
NISP.lb Bovinae	5	5	n/a	7	n/a	n/a
NISP.lb Equidae	n/a	n/a	2	n/a	n/a	n/a
Marrow extraction						
Mean FFI (NISP.lb) Caprinae	n/a	3.08	n/a	3.4	n/a	n/a
Mean FFI (NISP.lb) Capreolinae	n/a	5.25	n/a	n/a	n/a	n/a
Mean FFI (NISP.lb) Cervinae	5.3	3.08	6	2.4	n/a	2
Mean FFI (NISP.lb) Bovinae	4.4	3.4	n/a	3.1	n/a	n/a
Mean FFI (NISP.lb) Equidae	n/a	n/a	6	n/a	n/a	n/a
%bone flakes (NISP) Cervinae	n/a	15.3	n/a	n/a	n/a	n/a
%bone flakes (NISP) Capreolinae	n/a	16.7	n/a	n/a	n/a	n/a
%bone flakes (NISP) Caprinae	n/a	4	n/a	n/a	n/a	n/a
%bone flakes (NISP) Suidae	n/a	100	n/a	n/a	n/a	n/a
%bone flakes (NISP) Bovinae	n/a	n/a	n/a	4.8	n/a	n/a
%percussion (NISP) Cervinae	n/a	3.4	n/a	n/a	n/a	n/a
%percussion (NISP) Caprinae	n/a	n/a	n/a	5.9	n/a	n/a
%percussion (NISP) Bovinae	25	n/a	n/a	9.5	n/a	n/a
Grease rendering						
%cancellous unburned bones (NSP)	3.5	5.6	5.3	2.2	1.9	4.9
%epiphysial cancellous unburned bones (NSP)	0.8	0.1	0.5	0.6	0.1	2.4
%cancellous bones (NISP) small game	n/a	3.1	n/a	n/a	n/a	n/a
%epiphysial cancellous bone (NISP) small game	n/a	n/a	n/a	n/a	n/a	n/a
%cancellous bones (NISP) large game	3.2	4.9	1.5	8.2	n/a	5
%epiphysial cancellous bone (NISP) large game	n/a	1.2	n/a	4.7	n/a	n/a
Bone fuel (NSP)						
%burned bones	55.0	40.7	51.2	55.9	24.8	24.4
%calcined bones	10.3	6.0	12.1	6.7	1.7	7.3
%cranial unburned bones	2.0	2.6	1.7	1.9	2.1	14.6
%cranial burned bones	0.4	0.2	0.4	0.8	0.1	2.4
%axial post-cranial unburned bones	0.3	2.0	0.4	1.5	0.2	36.6

%axial post-cranial burned bones	0.3	0.1	0.2	0.1	n/a	n/a
%appendicular unburned bones	2.6	9.4	1.4	6.3	1.4	9.8
%appendicular burned bones	1.3	1.9	0.5	2.3	0.1	2.4
%cancellous bones	7.4	4.7	17.1	4.9	2.2	4.9
%cancellous burned bones	3.9	1.4	11.7	2.7	0.4	2.4
%cancellous calcined bones	1.6	0.7	4.5	0.8	n/a	n/a
%burned long bone diaphysis fragments	1.1	2.4	0.4	1.8	0.1	n/a

The taphonomic variables indicative of bone marrow extraction are scarce, as shown by the small samples in Table 12. The mean FFI shows only slight variability between taxa in Level A1. Outside the rockshelter, long bones of Caprinae, Cervinae, and Bovinae show relatively low scores (i.e., mean FFI ~ 3), whereas the scores for Cernivae and Bovinae are slightly more elevated inside the rockshelter, indicating dryer fractures in this area. This difference is particularly marked in Cervinae for which its mean FFI equals 3.1 outside the rockshelter and 5.4 inside.

In Level A2, the data available outside the rockshelter indicates slightly lower mean FFI scores than the overlying level for large ungulates (i.e., Cervinae and Bovinae), whereas the Caprinae score is somewhat higher. The scarce data inside the rockshelter indicates that Cervinae and Equidae are characterized by dry fractures only (mean FFI=6).

All the data available for bone splinters and percussion marks come from the Proto-Aurignacian levels (Table 12). The taxonomic identification of bone splinters with ZooMS reveals five different taxa, i.e., Caprinae, Capreolinae, Suidae, Cervinae, and Bovinae. The number of bone splinters for each identified taxon does not appear to be related to their relative abundance in the assemblages. For instance, the splinters identified to Cervinae in Level A1 account for 15% of its NISP (NISP = 59), whereas they account for 16% of the much less abundant Capreolinae taxon (NISP = 6). Also, the single Suidae bone fragment identified in Level A1 is in fact a bone splinter.

The identified skeletal remains bearing percussion marks reveal a less varied taxonomic portrait as they correspond to Cervinae and Bovinae in Level A1, and Caprinae and Bovinae in Level A2. In addition, the percussion marks on Bovinae are slightly more frequent in Level A1 than Level A2.

The taphonomic variables indicative of grease rendering show a low abundance of unburned cancellous bones throughout the assemblages (Table 12). Unburned cancellous and appendicular cancellous bones account for less than 6% of the total NSP throughout the site, however.

Finally, the taphonomic variables indicating the use of bone as fuel reveal more precise patterns of variability in the faunal assemblages (Table 12, Fig. 18). The total amount of burned and calcined bones corroborates the general patterns observed on long bone shaft surfaces, showing much higher numbers of burned bones in the Proto-Aurignacian assemblages than in the Mousterian assemblage. Furthermore, the highest frequency of burned bones is recorded in Level A1 – inside, and in Level A2 – outside. In contrast, the highest relative abundances of calcined bones are found in Levels A1 and A2 inside the rockshelter.

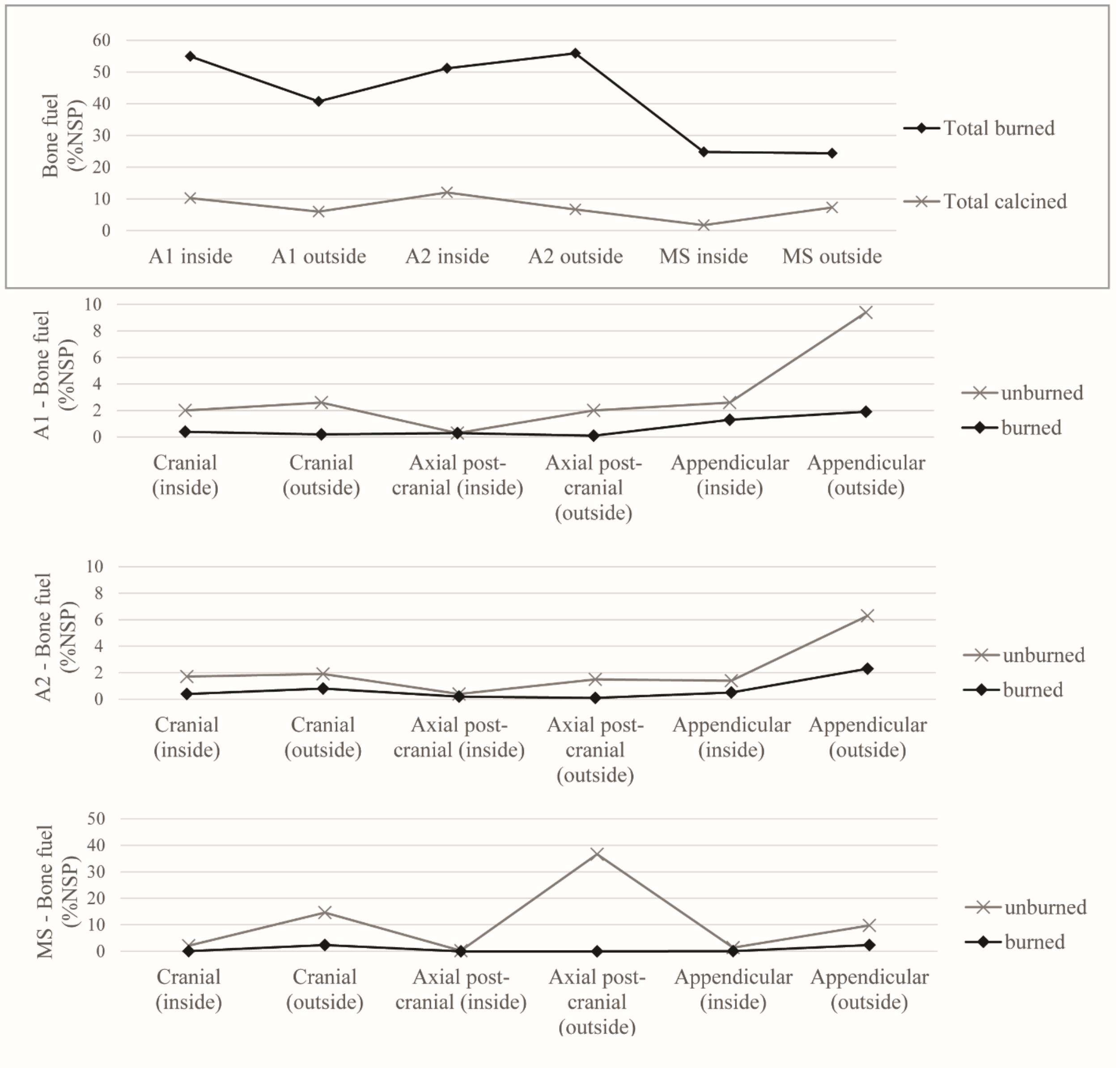

Figure 18. – Line graphic of bone fuel according to NSP comparing relative abundance of burned and unburned between skeletal portions in Levels A1, A2, and MS. Note that scales change between graphics on the y axis.

In both Proto-Aurignacian assemblages, appendicular skeletal remains are more abundant than the two other skeletal categories outside the rockshelter. In this category, burned bones are also proportionally more abundant in Level A2 than Level A1 outside the rockshelter. In contrast, the Level MS assemblage is almost devoid of burned bones in all skeletal categories.

The degree of burning between bone type categories is illustrated in Figure 19. A pattern appears within the appendicular skeletal portion in Level A2 inside the rockshelter. The relative abundance of burned and calcined cancellous bones is much higher than that of burned bone shaft fragments. This pattern is also visible in the same area of the site in Level A1 but much more weakly expressed than in Level A2. Outside the rockshelter, burned bone shaft fragments are more or as frequent as burned cancellous bones. In Level MS, all the bone type categories are less abundant than in the Proto-Aurignacian deposits.

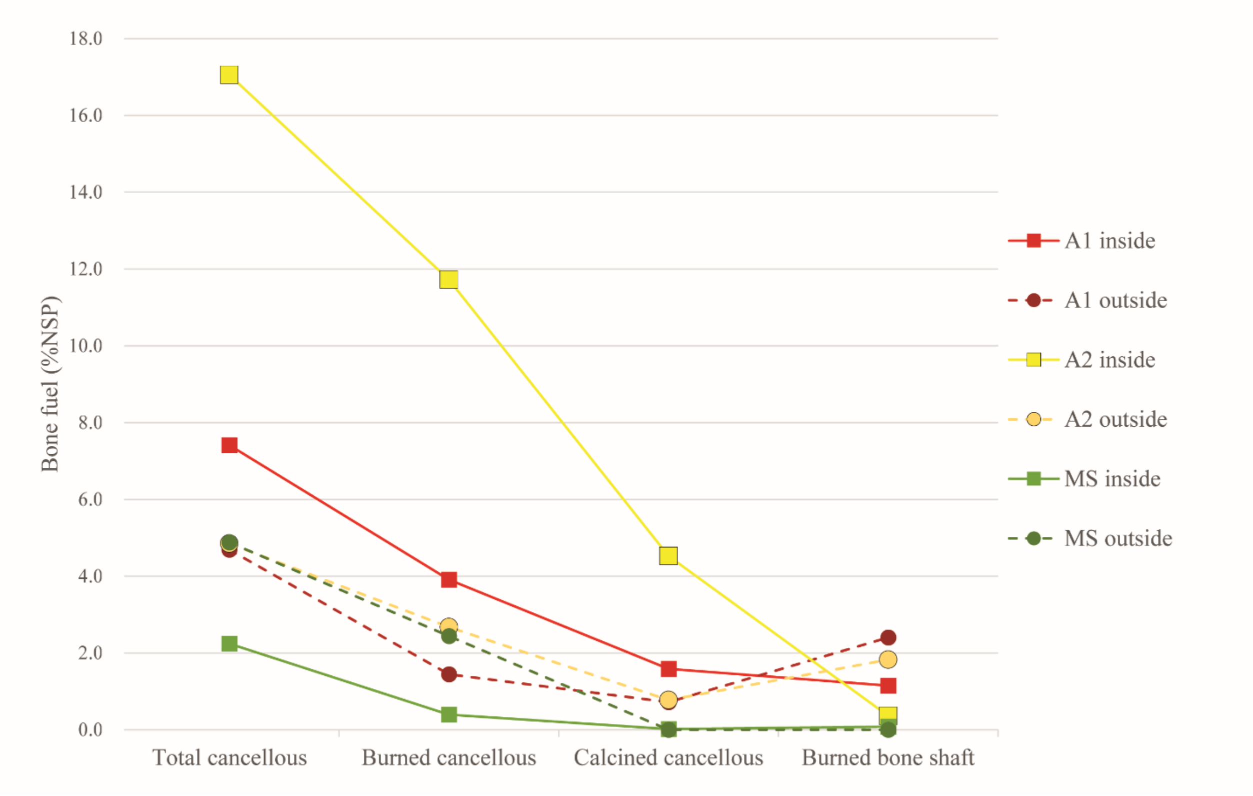

Figure 19. – Line graphic of bone fuel according to NSP in Levels A1, A2, and MS

5.6 Discussion

5.6.1 Leading causes of preservation bias and attrition

Our first line of taphonomic investigation points to high levels of bone fragmentation in all three assemblages, with more pronounced attrition rates inside the rockshelter across all assemblages *versus* better morphological and molecular preservation outside the dripline, e.g., in Level MS.

This is reflected in the ratio of NISP/MNI before ZooMS, per taxon and per skeletal element and the low abundance of large (>4cm) skeletal remains for both small and large ungulates.

The positive correlation between bone mineral density and skeletal survivorship demonstrates that this bone attrition is density-mediated in Levels A2 and MS.

The leading causes of bone attrition are natural, post-depositional *in situ* factors such as bone-crushing by sediment compaction and repeated freeze-thaw cycles (Lyman 1994; Marean 1991) and the action of carnivores and humans. The high mean FFI scores, globally, suggest that a lot of breakage occurred early in the depositional history of the assemblages which tends to support the hypothesis that carnivore and/or human action, rather than weathering, is responsible for at least some of the bone attrition.

Abiotic processes could have played a small role in the attrition of the Proto-Aurignacian faunal remains outside the rockshelter, as shown by the relatively high abundance of heavy weathering in this area. However, the abundance of burned bones and the presence of a few percussion marks in both Proto-Aurignacian levels suggest that human action contributed to the fragmentation of the skeletal remains in these levels, explaining their high mean FFI scores. The completeness index of compact bones and phalanges also supports this hypothesis, since humans will have processed larger ungulate phalanges preferentially. In addition, the few unburned large ungulate tarsals and carpals from the Proto-Aurignacian levels are almost all morphologically intact.

Although the lower ratios of small to large game inside the rockshelter in both Proto-Aurignacian levels could partly be due to density-mediated attrition, documented in this area, the spatial variation in these ratios inside and outside the shelter may also be related to patterns of human activity. The higher ratio of small to large game in Level A1 outside the rockshelter (i.e., 0.39) could indicate differential carcass treatment rather than differential rates of density-mediated attrition inside and outside the shelter, as it is also accompanied by a higher abundance of large (>4cm) skeletal remains of larger ungulates and a high cranial to tooth ratio according to NSP. Both taphonomic variables indicate lower fragmentation rates outside the shelter than in other areas of the site. In contrast, the higher ratios of appendicular cancellous to appendicular cortical bone in Levels A1 and A2 inside the rockshelter could be the result of specific human activities involving epiphysial bones, such as preparation for bone grease extraction or fuel (Costamagno 2013; Costamagno et al. 2005).

One of our goals is to compare subsistence activities across the Middle-Upper Paleolithic transition, to which end we now compare the Proto-Aurignacian levels with Level MS. Relative to the Proto-Aurignacian as a whole, Level MS shows a greater abundance of piece-plotted fauna relative to total artifacts, relatively low artifact density per volume, a higher frequency of carnivore bone damage and the sporadic presence of near-complete skeletal elements in anatomical connection. In addition, the MS faunal assemblage shows pronounced differential preservation across different areas of the site, being much less fragmented outside the rockshelter. The high skeletal fragmentation, the low cranial to tooth ratios, and the near absence of small compact bones inside the rockshelter indicate a high degree of post-depositional *in situ* attrition in Level MS and the impact of density-mediated attrition. These taphonomic signals co-occur with the highest abundance of modern fractures, associated with the use of hammers and chisels on concreted sediments during the excavations. In contrast, the area outside the rockshelter, where concretions do not occur, has the best morphological and molecular preservation of all three occupations.

The high ratio of small to large game observed inside the rockshelter (i.e., 0.52), where the remains are more fragmented than outside, is thus best explained by diverging taxonomic compositions between the two parts of the site than by density mediated attrition causing differential loss of smaller ungulate skeletal remains. This distinctive taxonomic composition warrants further investigation into the role of carnivores in the accumulation and consumption of the ungulate remains in Level MS and their potential contribution to pre-and post-depositional skeletal attrition.

In sum, our first line of investigation shows that all three faunal assemblages at Riparo Bombrini were considerably affected by *in situ* post-depositional attritional factors. However, the density-mediated attrition documented in the Proto-Aurignacian is also the result of pre-depositional anthropic factors, perhaps marrow and grease extraction and/or the use of bone as fuel. Pre- and post-depositional attritional factors had less impact on the Mousterian assemblage, where excavation methods suited to heavy concretions explain the pattern of bone fragmentation. However, there is also an abundance of carnivore damage (especially in Level MS), and the presence of some anthropic marks that warrant investigating the agents of bone accumulation and anthropic carcass processing activities on all three levels.

5.6.2 Agents of bone accumulation

Although post-depositional attrition factors destroyed (e.g., abrasion) or masked (e.g., concretion) most of the bone surface in our assemblages, making it difficult to identify alterations that help discriminate between agents of bone accumulation, our second line of investigation points to a primary anthropic accumulation in the Proto-Aurignacian and to a mixed accumulation by humans and carnivores in the Late Mousterian.

The hypothesis of human accumulation in the Proto-Aurignacian levels is supported by the high volumetric density of artifacts, the higher frequency of burned bones in the faunal assemblages, the presence of percussion marks and percussion splinters (despite the poor bone preservation), and the low frequency of gnawing, abrasion, and polish on bone surfaces. Of the few carnivore skeletal remains, one medium-sized accessory metapodial is partially carbonized and was recovered inside the hearth structure in Level A1, which hints at the potential exploitation of carnivores by Proto-Aurignacian foragers.

Furthermore, none of the ungulate skeletal remains bearing green fractures, percussion marks, or cut marks show carnivore alteration. The rare gnawed skeletal remains in those levels may thus be the result of carnivore scavenging butchery secondary products. Unfortunately, no overlapping carnivore and anthropic alterations have been identified that could validate this hypothesis. However, gnawing damage is commonly recorded on human-generated fauna, as bone refuse areas attract scavengers once hunter-gatherers move their residential site (Stiner 1994).

In Level MS, however, the higher frequency of abrasion, polish and carnivore gnaw marks inside the rockshelter suggests that carnivores also occupied the site and possibly contributed to bone accumulation and bone fragmentation. Whether carnivores used Riparo Bombrini as a den in

Level MS is more difficult to establish. The most convincing argument for carnivore accumulation is the high frequency of carnivore remains (>20%NISP), which suggests denning activities associated with a high rate of carnivore alterations on the faunal assemblages and the presence of long bone whole cylinders (Blumenschine 1988; Brugal et al. 1997; Cruz-Uribe 1991b; Klein and Cruz-Uribe 1984; Pickering 2002; Stiner 1991b, 1994). Although most carnivore gnaw marks were destroyed by *in situ* post-depositional factors, other diagnostic remains such as small, digested splinters and coprolites are more resistant due to their compact nature and were systematically recovered through water sieving between 2018 and 2019 at Riparo Bombrini. Their high frequency in a faunal assemblage may thus well reflect sustained carnivore occupations.

Most of the diagnostic remains of carnivore activities recovered in Level MS are coprolites and small digested bones, which corroborates the high level of post-depositional bone attrition. Although Level MS contains the largest number of coprolites and digested bones of any level at Bombrini, their relative abundance is not exceedingly high, especially compared with known hyena dens. The volumetric density (g/m3) of coprolites is, in fact, just slightly higher than in Level A1. Further, small digested bones recovered in this level account for less than 2% of the NSP inside the rockshelter.

Other evidence lends support to the denning scenario. For instance, the few carnivore teeth recovered in Level MS (one bear and two medium-sized carnivores) belong to juvenile animals, which is sufficient to argue for punctuated denning episodes inside the rockshelter according to Pickering's criteria (2002). Level MS is also head-dominated inside the rockshelter and axial-dominated outside, contrasting with the limb-dominated assemblages in the Proto-Aurignacian deposits. The nature of the ungulate prey accumulated by these predators is difficult to assess. All caprine remains recovered in this level are digested, indicating that carnivores consumed them. Mountain goats were probably available around the Balzi Rossi and could have been easily dragged whole to the site.

Furthermore, most gnawed and digested remains identified in Level MS correspond to small compact elements with low nutritional value, such as teeth and phalanges, despite the fact that the assemblage is dominated by limb elements. Although this could be an artifact of the poor overall degree of preservation, it can also suggest that the prey carcasses were intensively ravaged (Haynes 1982; Marean 1991; Pickering 2001) or again, that predators were scavenging human kills.

The few cervid skeletal remains bearing carnivore alterations (%gnawed=12.5) in Level MS were recovered inside the rockshelter and mixed with other gnawed, carnivore skeletal remains and artifacts (i.e., lithics and ochre) within the hearth area. Two faunal remains with carnivore alterations (i.e., one horse tooth and one deer phalanx) were recovered at the top of the deposit. In contrast, the *in situ* cervid ribs and other cervid skeletal remains are located three to ten centimetres lower in the sequence, in association with lithic implements. These cervid skeletal elements are also devoid of carnivore alterations, and some of them show fresh fracture angles. The absence of gnawing on these skeletal remains suggests they were buried before scavengers could reach them. In sum, the data from Level MS suggest that it is a palimpsest and that both carnivores and humans contributed to the bone accumulation through alternating short-term occupations of the site.

5.6.3 Hunting strategies at Riparo Bombrini

The general picture of human hunting activities at Riparo Bombrini suggests the exploitation of large cervids and other medium and large taxa in the environment surrounding the rockshelter. However, the relative abundance of different ungulate taxa varies notably across the three assemblages. In Level MS, the small faunal sample and the taphonomic context indicate a few hunting episodes by humans primarily focused on red deer.

In the Proto-Aurignacian levels, the larger faunal assemblages show distinct patterns of faunal richness and diversity. In Level A1, the taxonomic composition is essentially identical to the underlying Level A2. Level A1 is less evenly distributed, however, as shown by the higher relative abundance of red deer, particularly outside the rockshelter. This difference in taxonomic evenness between the two Proto-Aurignacian levels can be explained in one of two ways: differential carcass treatment involving bone fragmentation or more focussed prey selection strategies in Level A1.

The heavy fragmentation of the Proto-Aurignacian assemblages complicates discussions about taxonomic diversity and possible behavioural changes in diet breadth, however. The relative abundance of each taxon in the Proto-Aurignacian levels mostly agrees with previous studies of the site (Pothier Bouchard et al. 2020; Holt et al. 2019). Our previous study indicated a higher abundance of bovine taxa inside the rockshelter in Level A1, however, whereas the pattern observed in Holt et al. (2019) is more in line with our current results. The diverging taxonomic evenness and this variability in bovine abundance highlight the interpretive issues occurring at Riparo Bombrini, most likely due to small samples.

While hunters seem to have selected prime-age red deer, the age determination of the other ungulate prey differs across the three levels. However, a small sample size precludes drawing mortality profiles for these taxa. However, the few teeth and aged post-cranial elements in Level A2 suggest that hunters selected prime-age bovines, whereas they hunted horses more opportunistically (Table 6). The data on Caprinae also suggests the hunting of prime adults in the three levels.

Transport decisions are also difficult to discuss because of the high level of fragmentation, as shown by the strong bias towards teeth and indeterminate skeletal elements identified to a taxon with ZooMS (Table 5) and evidence of density-mediated attrition (above). Nevertheless, the presence of elements of the whole skeleton of Cervinae, including the head and axial elements, indicate that the hunters brought some carcasses whole on the site in all three levels.

In Level A1, smaller prey such as Caprinae were probably hunted close to the site and brought back whole as indicated by the presence of head and axial elements. In contrast, larger prey, namely Bovinae and Equidae, might have been dressed in the field given the absence of head and axial elements.

Level A2 shows similar transport decision patterns. However, Bovinae and Equidae teeth and head elements of ungulates size 3/4 hint at the transport of either a few whole carcasses or the heads of larger animals back to the site. This suggests that animals were hunted very close to the site, likely on the low-lying coastal plain that existed in front of the Balzi Rossi during MIS 3. In

Level MS, hunters sporadically exploited red deer close to the rockshelter and brought back whole carcasses.

Data from ethology and ethnological models help flesh out the potential hunting strategies adopted at Riparo Bombrini. Red deer are not a particularly migratory species and would have been available year-long around the Balzi Rossi. However, the composition of herds changes seasonally; females form stable social groups with their young while males are solitary most of the year except during summer when they sometimes seek high-quality forage in small groups to prepare for the fall rut (Steele 2002). Small groups of hunters would have been sufficient to take advantage of deer’s flight patterns. The dominance of prime adults in the three levels at Riparo Bombrini suggests that red deer were readily available year-round and provided a reliable food source near the site.

During summer, deer herds often move to higher altitudes to flee harmful insects or due to food availability and decreasing snow cover (Steele 2002). At Riparo Bombrini, seasonality evidence is scarce. However, the proximity of the Pre-Alps would allow the hunting of deer herds in higher altitudes within walking distance from the site. In Level A2, the incomplete deer antlers do not offer clues as to the season of occupation of the site. The procurement of shed antlers for their technical properties is recorded on many early Upper Palaeolithic sites in Europe, including Proto-Aurignacian deposits in France (Soulier 2013; Tejero 2014). However, the use of antler as a raw material has so far not been documented in the Proto-Aurignacian levels at Riparo Bombrini and its neighbouring site Riparo Mochi (Tejero and Grimaldi 2015). The hunting of prime-aged stags during late summer, fall, or early winter, when they would have had antlers, thus seems more likely in Level A2. The few indeterminate fetal bones recovered in this level suggest winter or early spring seasonal occupations, however, assuming these bones correspond to ungulate taxa.

Bovines (i.e., bison and aurochs) are gregarious animals that are rarely hunted opportunistically by single hunters. These large ungulates usually organize in cow or mixed herds and bull herds. Older males tend to be solitary or will form a small herd. Large aggregations (>100 individuals) form during seasonal migrations, but for the rest of the year bovines generally form herds of ten to twenty animals which are more or less sedentary depending on the habitat (forested vs grassland) and available resources (Julien 2011; White et al. 2016). Male herds are typically smaller than mixed and female herds, but they are more dangerous to hunt as bulls can become very aggressive at the sight of danger. The adult animals recovered in the Proto-Aurignacian levels at Riparo Bombrini indicate that bovines were probably hunted using collaborative strategies. The dominance of appendicular skeletal remains for this taxon further suggests that the limbs were selected after primary butchery was accomplished on the kill site or at a secondary hunting camp. Cow or mixed herds would have been a good target for hunters using driving tactics, but MNI counts do not suggest this strategy.

Except for Asiatic and African asses, most extant feral equids are non-territorial, gregarious animals grouped in small harems ranging from three to ten animals. The harems typically comprise a male with multiple females and their offspring. The home range of equid bands varies according to available seasonal resources, from a few square kilometres in the summer to up to 30 square kilometres in winter. The social structure of equids also includes smaller herds of two to three bachelor males and solitary males (Burke 2006b; White et al. 2016). At Riparo Bombrini, the presence of equids is mostly limited to Level A2 and suggests the opportunistic exploitation of single animals. The two juvenile teeth identified in this level correspond to one or two individuals between one and two years old, which approximately corresponds to the age at which juveniles leave their birth herd to join a bachelor group (males) or another harem (females) (White et al. 2016). The presence of head elements indicates that whole equid carcasses or heads were transported on the site. Proto-Aurignacian hunters could have taken advantage of the random flight response to danger typical of bachelor herds and often reported in harems when equids are taken by surprise. The fleeing of horses in random directions could have facilitated the targeting of isolated animals.

Caprines (which includes goats, ibex and chamois) are social ungulates living in sexual segregation most of the year. Males and females with their offspring live in separate groups of varying size and regroup during the rutting season in autumn (Acevedo and Cassinello 2009). The herds are transhumant and tend to move to higher altitudes during the summer, when the reduced snow cover offers richer feeding grounds. Caprines might have been readily available at close range from the Balzi Rossi during colder seasons, therefore. The coordinated fleeing patterns of ibex herds and the smaller home ranges of mixed herds during the rutting season would also have facilitated ambush strategies to hunt these ungulates. Adult caprines are the second most abundant taxon in the Proto-Aurignacian levels suggesting that hunters regularly targeted herds possibly close to the site.

Finally, the social organization of wild boars is also characterized by sexual segregation. However, males live alone most of the year, whereas females and their offspring form small matriarchal herds of less than ten animals (Dardaillon 1988; Maselli et al. 2014). The males' solitary behaviour could have facilitated the hunting of single prey.

Red deer, chamois and ibex are sympatric in alpine regions (Schweiger et al. 2015) although Red deer preferentially occupy lower altitude, wooded areas. Suitable habitat for these species would have been locally available in Balzi Rossi. Wild boar are more likely to establish home ranges in humid and wooded areas and their presence at Riparo Bombrini likely reflects the presence of woodland or gallery forest somewhere on the coastal plain.

5.6.4 Differential carcass treatments and site function through time

In our previous study of the Proto-Aurignacian levels, we identified contrasting patterns of carcass treatment and waste management inside the rockshelter (Pothier Bouchard et al. 2020). In both levels, most butchery activities were concentrated around the hearth areas, whereas broken bone tools (i.e., awl tips and fragments) were discarded in a pit located against the back wall of the rockshelter along with broken bladelets and other lithic debris and a high concentration of small burned and unburned bones. While the general internal organization of the site was maintained in the Proto-Aurignacian levels, as shown by the overlying features (i.e., hearth and trash pit), we also identified a few notable differences between the two levels. For instance, the faunal remains in Level A2 were more abundant and aggregated around the archaeological features. In addition, we identified a higher abundance of burned cancellous bones in Level A2, indicating a more systematic use of ungulate carcasses as a source of fuel. We suggested that these differences resulted from prolonged occupations of the site, coupled with a more logistical strategy of resource management in Level A2. Unfortunately, we could not document changes in carcass treatment outside the rockshelter. As a working hypothesis, we suggested that the site's exterior was used as a refuse disposal or the area where primary butchery activities took place, as shown by the presence of unburned axial elements and bone splinters.

The results of our current third line of investigation on carcass treatment agree with the patterns previously outlined on the Proto-Aurignacian levels and bring more precise distinctions about the spatial organization of the activities between the two Proto-Aurignacian levels and between the Proto-Aurignacian and the Late Mousterian levels.

5.6.4.1 Carcass butchering and marrow extraction

The higher abundance of unburned axial post-cranial (i.e., ribs and vertebrae) and appendicular elements outside the dripline suggest that primary steps of carcass butchery (e.g., disarticulation of the axial skeleton) occurred in this area in Levels A1 and A2. Bone cracking for marrow extraction – and possibly tool manufacture, is attested in both Proto-Aurignacian levels despite high post-depositional *in situ* attrition. The abundance of fresh fracture angles and percussion marks supports these secondary butchering activities taking place outside the rockshelter in the Proto-Aurignacian levels (Fig. 20).

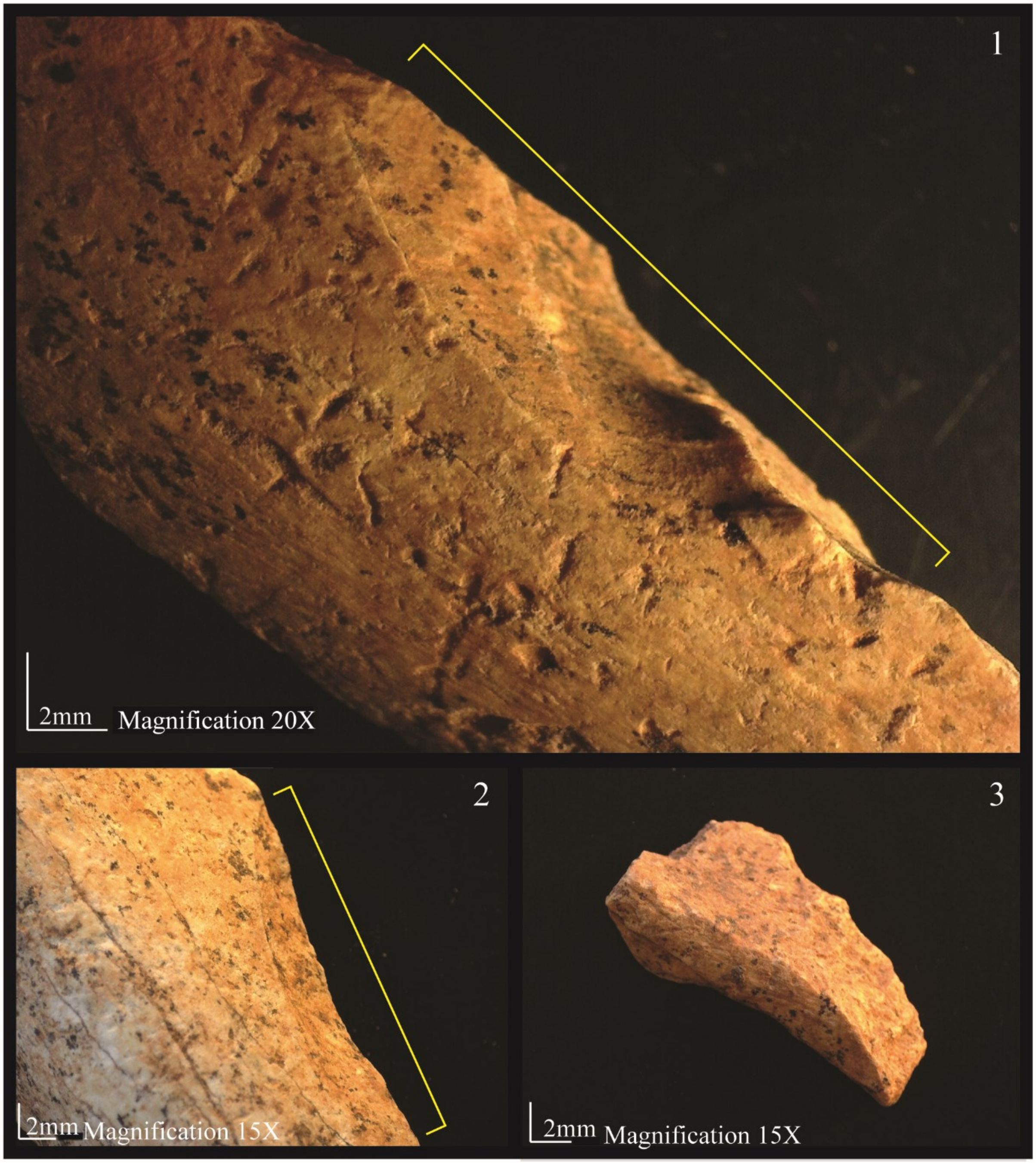

Figure 20. – Examples of anthropic marks in the Proto-Aurignacian levels: (1) and (2) percussion marks, (3) bone splinter.

In addition, bone marrow cracking might have been more recurrent outside the rockshelter in Level A1 than in the underlying level, as there is a much higher concentration of bone splinters, resulting from direct percussion of long bones, associated with the secondary combustion feature. These splinters are primarily attributed to Cervinae (N=9), but also Capreolinae (N=1), Caprinae (N=1), and Suidae (N=1). This concentration of splinters comes together with the highest relative abundance of fresh fracture angles and percussion marks on long bones on the site. Percussion marks were only identified on Cervinae, and fresh fracture angles were primarily identified on Cervinae long bones (39% of the long bones with fresh fracture angles), followed by Caprinae (14%) and Bovinae (6%). The small combustion feature recorded in the area outside the drip line in Level A1 could thus correspond to short occupations of the site, independent from the occupations occurring closer to the rockshelter wall. Alternatively, the combustion feature could correspond to specific activities involving primary and secondary carcass processing of Cervinae carcasses. However, the presence of other taxa bearing anthropic marks and the relatively high density of artifacts associated with the combustion feature appear better to support the first scenario. The relatively low volumetric density of bone fragments (NSP), comparable to Level MS, also supports shorter occupations.

Inside the rockshelter, the scarce data suggests that mostly secondary butchery activities occurred around the hearths in both Proto-Aurignacian levels. However, a higher concentration of percussion flakes can be seen in Level A2. Although none of the bone splinters could be identified with ZooMS because of the poor collagen preservation in this part of the site, these remains suggest that long bone cracking took place more recurrently inside than outside the rockshelter in Level A2. This pattern contrasts with the near absence of splinters in Level A1 around the larger hearth. However, overall, minimal bone working activities took place in this area of the site in both levels.

Carcass butchering and marrow extraction are more difficult to document in Level MS because of the heavy concretion covering much of the faunal remains. The absence of bone flakes, percussion marks, and cut marks, even on the better-preserved remains outside the rockshelter, suggests minimal processing of the carcasses. However, the relative abundance of fresh fracture angles is proportionally comparable to Level A2 inside the rockshelter. It thus appears that

Neanderthals processed some carcasses to extract their marrow content in this site area. The presence of a deer's first phalanx with fresh fracture angles also supports marrow extraction on Cervinae.

Outside the rockshelter, the well-preserved deer ribs found in partial anatomical alignment do not bear any disarticulation cut marks. However, the absence of such marks on ribs does not rule out the possibility that humans exploited these remains. Experimental work on deer carcasses demonstrated that the disarticulation of deer rib cages could be efficiently done using direct percussion only, leaving most of the ribs intact, except the first and last ribs sometimes bearing fractures on their proximal ends (Vigne 2006). Two of the deer ribs in Level MS show similar fractures indicating disarticulation activities. A 3-6th rib (piece-numbered 486) shows fresh fracture angles between the epiphysis and the body of the rib, and a 7-10th rib (piece-numbered 501) shows the type of right-angled fracture on the proximal epiphysis documented by Vigne (2006) on rear ribs (Fig. 28). Furthermore, the two red deer femur fragments (one mid-shaft fragment and one distal epiphysis) located in this area bear helical fractures, typical of long bone-cracking for marrow extraction (Outram 2001; Villa and Mahieu 1991).

Figure 21. – Cervid ribs with stigmata of disarticulation with direct percussion in Level MS: (up)C1.IV/1.486, (bottom)C1.IV/1.501. Vicino’s fieldnotes indicating their *in situ* recovery.

5.6.4.2 Grease rendering

It seems unlikely that modern humans and Neanderthals extracted grease with grease rendering techniques at Riparo Bombrini. However, grease rendering can be difficult to identify in faunal assemblages heavily affected by post-depositional factors such as those from Riparo Bombrini because both taphonomic factors show a comparable signature, i.e., heavy fragmentation and the underrepresentation of long bone epiphyses (Costamagno 2013). In the Mousterian level, the presence of complete ungulate skeletal element inside and outside the rockshelter, including grease-rich long bone epiphyses, is proof enough of the absence of this behaviour. In the Proto-Aurignacian, pre-and post-depositional factors affected the cortical and the cancellous parts of long bones, hindering discussions about skeletal representation. However, the heavier fragmentation level, even outside the rockshelter, hints at the presence of anthropic pre-depositional factors affecting grease-rich skeletal elements. Three factors, however, suggest that grease rendering was not a determinant factor of bone attrition in these levels. First, the collagen preservation in unburned cancellous and cortical bones outside the rockshelter indicates that they were not boiled to extract their grease content. Second, although not essential to prove grease extraction, the absence of large quantities of heated rocks also agrees with our scenario. Finally, the presence of carnivore scavenging on the faunal assemblages discarded by humans, especially outside the rockshelter in Level A2, also supports the absence of systematic grease rendering. Actualistic experiments further demonstrate that the skeletal elements most attractive to scavengers in faunal assemblages discarded by humans are the ones rich in grease (i.e., vertebrae, ribs, pelvis, and long bone epiphyses) (Marean et al. 1992; Marean and Spencer 1991). A faunal assemblage heavily processed to extract grease would thus become largely uninteresting for carnivore scavengers.

5.6.4.3 Bone fuel

Finally, it appears that the main pre-depositional biotic factor affecting the Proto-Aurignacian faunal assemblages is the use of grease-rich bones for fuel. Our third line of research supports the pattern of bone fuel (i.e., abundant burned bones and over-representation of carbonized and calcined cancellous bones) previously identified in the Proto-Aurignacian levels. This pattern is also much more evident in Level A2 (Fig. 19), supporting our hypothesis that modern humans exploited ungulate carcasses more intensively there than in Level A1. In addition, the pattern of using bone as fuel is absent outside the rockshelter in both Proto-Aurignacian levels. In Level A1, the absence of this pattern around the small combustion area supports the hypothesis of shorter occupations in this area where fuel management would have been more expedient. In contrast, grease-rich elements for fuel during a prolonged period involve curating fuel resources, that is the systematic exploitation of cancellous skeletal elements, which also entails the segregation of butchery activities and more organized waste management strategies.

In sum, the differential patterns of carcass treatment and the spatial distribution of the faunal remains agree with, and thus lend additional support to, previous hypotheses on the evolution of the functions and occupation lengths of hominin occupations of Riparo Bombrini. Table 13 summarises the faunal record's interpretive information with additional data from the lithic record that helps create an informed portrait of the types of occupations in Levels A1, A2, and MS.

Table 13. – Summary of faunal and lithic data regarding site function at Riparo Bombrini

	Level A1	**Level A2**	**Level MS**
Taphonomy			
Anthropic Pre-depositional attrition	High	Highest	Medium
Carnivore Pre-depositional attrition	Lowest	Low	Medium
In situ Post-depositional attrition	High	High	Highest
Faunal data			
Agents of bone accumulation	Recurrent human	Recurrent human	Alternating human/carnivore
Seasonality of animal procurement	Mostly aseasonal	Seasonal (maybe winter/spring)	n/a
Animal procurement strategy	Mostly selective	Selective with opportunistic hunts	Mostly selective
Carcass transport strategy	Mostly whole carcasses	Whole carcasses with best pieces of Bovinae	Mostly whole carcasses
Butchery activities	Primary and secondary inside and outside	Primary outside, secondary inside and outside	Primary and secondary (no specific spatial data)
Waste management	Less organized	Curated (organized)	Expedient
Bone fuel management	Curated	Systematized	None
Lithic data			
Technological system	Bladelet-based	Bladelet-based	Discoid flaking
Density of artifacts	High	Highest (outside)	Lowest
Abundance of retouched tools (including bladelets)	High	Highest	Lowest
Chaîne opératoire completeness	Complete	Complete	Partial
Site function hypothesis	**Short-term base camp**	**Long-term base camp**	**Ephemeral camp**

In both Proto-Aurignacian levels, modern humans used Riparo Bombrini as a residential base camp. This site function is highlighted by the high artifact density, the high abundance of retouched tools, the spatially organized activities, and the presence of the complete sequences of carcass butchery and lithic chaîne opératoire. Furthermore, the different criteria summarized in Table 13 suggest changes in how the base camp was occupied, from extended and more intensive occupations in Level A2 to shorter and less spatially organized occupations in Level A1.

In Level A2, modern humans selectively hunted adult ungulates and occasionally hunted weaker ungulates of other species close to the site. Although seasonality indices are scarce, it seems that hunter-gatherers recurrently occupied Riparo Bombrini during winter and spring. They systematically used grease-rich elements to fuel the fire inside the rockshelter during their extended stays, entailing careful waste management, including trash pits inside the rockshelter. The area outside the rockshelter was used as a discard area, including a "bone dump," as supported by the uniformly distributed skeletal accumulation of mostly primary butchering and the higher density of artifacts. The more extensive piling of skeletal remains in this area also attracted predators after hunter-gatherers left the site during their regular moves.

In Level A1, modern humans continued selectively hunting adult ungulates, although no evidence points to seasonal occupations or the opportunistic exploitation of large ungulates. The focus on adults could result from the site's shorter occupations, which would not have required extra opportunistic hunting in a close range of the site. Hunter-gatherers also kept exploiting bones for fuel inside the rockshelter. However, they did so less systematically, entailing less organized waste management as shown by the more uniformly distributed discarded faunal remains around the hearth and the pit features. In addition, modern humans occupied the site for shorter periods, especially outside the rockshelter, where there are much lower densities of faunal remains and artifacts, and where primary and secondary butchering took place with no systematic use of bone fuel.

In Level MS, the archaeozoological and taphonomic data agree with the recent hypothesis of scant, ephemeral occupations of the site by Neanderthals. These very short occupations are highlighted by the low density of artifacts, the low abundance of retouched tools, and the truncated lithic chaîne opératoire. Neanderthals selectively hunted adult ungulates during their short stays and occupied the site with no clear seasonal preference. Outside the dripline, alternating occupations with carnivores might have been sufficiently spaced apart to allow the faunal remains discarded by humans to be buried by natural sedimentation before attracting scavengers. In this area, the scarce amount of burned bones and artifacts and the presence of *in situ* deer ribs showing evidence of disarticulation suggest the presence of a single or very few episodes of Neanderthal occupations. Inside the rockshelter, the slightly denser and patchier distribution of artifacts and faunal remains suggest that this part of the site was more actively occupied during the short stays, also alternating with a few carnivore denning occupations. The specific function of the site is not as clear as the length of the occupations. The presence of red ochre in association with the large combustion area could be the result of specific tasks such as pelt and hide preparation, but there is no evidence of such activities in the faunal assemblage or the lithic record (e.g., no abundance of scrapers). The lack of distinct activity areas, the random distribution of the faunal remains, and the diffuse nature of the hearth instead suggest that Neanderthals occupied Riparo Bombrini repeatedly as a halt or short-term camp.

5.6.5 Subsistence, land-use, and mobility strategies at Riparo Bombrini

Our results agree and broaden previous mobility and land-use strategy hypotheses at Riparo Bombrini during the transition timeframe. Table 14 summarises the state of knowledge regarding behavioural changes in the organizational strategies observed in Levels MS, A2, and A1.

Table 14. – Summary of the subsistence and mobility at Riparo Bombrini from present and previous research (Holt et al. 2019; Pothier Bouchard et al. 2020; Riel-Salvatore et al. 2013; Riel-Salvatore and Negrino 2018a, 2018b).

	Level A1	**Level A2**	**Level MS**
Paleoenvironment*	More temperate and mesic	Cold and arid, HE4	Coldest and most arid
Resource procurement strategies			
Large ungulate exploitation	Close range, except Bovinae (marrow- and meat-rich elements)	Close range, except Bovinae (marrow- and meat-rich elements)	Close range
Small ungulate exploitation	Close range	Close range	n/a
Techno-economic strategy**	Curated	Less curated	Expedient

Chaîne opératoire completeness on local resources (<5km)**	Complete	Complete, More bladelets and finished tools (effective availability)	Complete, mostly flakes and chunks
Chaîne opératoire completeness on circum-local resources (10-20km)**	Partial, bladelets only	Partial, bladelets only	Partial, sporadic flakes
Chaîne opératoire completeness on exotic resources (30-350km)**	Complete Higher frequency of debris of curated tools	Complete Higher frequency of retouched tools (material “stockpiling”)	Partial, sporadic flakes and chunks
Hypotheses on subsistence and mobility			
Degree of mobility	High	Low	Very high
Mobility strategy	Residential	Logistical	Residential
Subsistence range	Extensive Strong link with SE France	Extensive Strong link with SE France	Hyper-local Weak link with SE France
Diet breadth	Broad	Broadest	Possibly narrower

5.6.5.1 The Semi-Sterile Mousterian

Previous research on Level MS advanced the hypothesis that this deposit reflects the adaptation of some of the last Neanderthals in Italy in the context of the Ligurian biogeographical refugium (Riel-Salvatore et al. 2021). In this context, Neanderthals took advantage of the proximity of the “I Ciotti” conglomerates to adopt a hyper-local subsistence range, as shown by the near-absence of circum-local and exotic materials in this level. The predominance of a discoid reduction strategy taking over the Levallois documented in underlying Mousterian levels also suggests an increased degree of mobility. The versatility and portability of this technological system agree with the expedient techno-economic strategy established in the lithic record, which would have been advantageous in a highly mobile residential organization (see Delagnes and Rendu 2011). The faunal record also agrees with this scenario where Neanderthals seem to have mostly exploited adult red deer, a high utility prey probably available in the immediate vicinity of Riparo Bombrini. This focus on red deer contrasts with the underlying Mousterian levels at Riparo Bombrini and with all the faunal assemblages of the Liguro-Provençal arc, which document rich and diverse faunal assemblages throughout the Late Pleistocene, including small, medium, and large mammals and molluscs (Valensi and Psathi 2004).

5.6.5.2 Proto-Aurignacian levels

The Proto-Aurignacian levels mark a significant shift towards extended social and subsistence ranges in addition to the continuous production of a flexible bladelet-based technocomplex (Riel-Salvatore and Negrino 2018b). At Riparo Bombrini, it appears that the subsistence range of modern humans was primarily driven by the desire to obtain prime quality flint, mostly in western and eastern Provence and to a lesser extent in eastern Liguria and northern Tuscany. Along the Ligurian corridor, modern humans exploited locally available raw material of inferior quality with a "readily available" strategy while occupying the residential base camps, and they carried higher-quality flints throughout their seasonal moves.

The faunal record of Riparo Bombrini mostly follows the "readily available" strategy, although the hunting spectrum is broader than the one observed in Level MS. Most ungulate prey species – small and large – were probably hunted near the Balzi Rossi, and at least some were brought back whole to be processed on-site. The flexible Proto-Aurignacian technocomplex thus facilitated a generalist hunting strategy that was used to exploit the available fauna surrounding Riparo Bombrini.

The logistic mobility proposed for Level A2 is reflected in the faunal record through the seasonality indices, suggesting recurrent occupations of the site, probably during different seasons~~.~~The longer occupations of the logistic base camp (or seasonal reoccupations) are visible through the spatial organization of the activities on the site, which required systematic waste management resulting in a large discard area outside the living space (i.e., outside the dripline) and the cleaning of debris surrounding the hearth inside the rockshelter. Prolonged stays also involved fuel management during harsher seasons that parallel the patterns observed on Proto-Aurignacian sites of western France (Soulier, 2013). Based on ethnographic models, Soulier (2013) attributed the exploitation of weaker prey such as older ungulates or stags to increased episodes of solitary hunting, which the polyvalent throwing spears would have facilitated. She also suggested that fuel management could be associated with meat smoking to produce surpluses during harsher times. In a logistically organized mobility with prolonged occupations, solitary hunters or small hunting parties and meat stock-piling would have been advantageous in times of resource rarefaction.

In contrast, the shorter occupations and the curated lithic organization in Level A1 correspond to more residential mobility. Modern humans mainly exploited locally sourced lithic material to produce bladelets and tools, as shown by the higher frequency of “I Ciotti” retouched tools and cores. The higher abundance of exotic debris indicates that modern humans carried the curated tools or blanks away from the site in the context of their short residential stays. The lack of a strong seasonal signal in the faunal remains could suggest that modern human groups inhabited Riparo Bombrini briefly and during different seasons, as they also seem to have done in Level A2. The shorter residential stays are also highlighted by the absence of a “bone dump” outside the rockshelter, where a small combustion area with fewer faunal remains and artifacts correspond to brief independent activities with no specific pattern indicating the use of bone as fuel, which could be due to either seasonal or interannual climate conditions since Level A1 documents warmer and more mesic paleoenvironmental conditions than Level A2 (Holt et al. 2019).

5.6.6 Subsistence continuities and changes during the transition in the Liguro-Provençal Arc

This research has refined our understanding of patterns of subsistence change and continuity during the Middle-Upper Paleolithic transition in the Liguro-Provençal arc. The available data on the faunal composition and skeletal representation during this interval suggests that Neanderthals and modern humans continuously exploited locally available medium and large ungulates, primarily selecting prime adults and transporting whole carcasses or the meatier parts of larger ungulates back to their residential sites (Pothier Bouchard et al. 2020; Valensi and Psathi 2004). The Late Mousterian and Proto-Aurignacian faunal assemblages thus reflect the biogeographic dynamics of a refugium area where warm-adapted taxa cohabited with increasingly higher proportions of cold-adapted taxa, a trend that reached its apex during HE4 in the Proto-Aurignacian record of Riparo Bombrini.

Similar patterns were recently reported for the rest of the Italian Peninsula, where the onset of the HE4 is generally contemporaneous with Uluzzian sites. The few well-documented stratified sites in northeastern Italy (e.g., Grotta di Fumane) and southern Italy (e.g., Grotta del Cavallo and Grotta di Castelcivita) also show increasing amounts of cold-adapted taxa in Uluzzian and Proto-

Aurignacian levels (Romandini et al. 2020; Tagliacozzo et al. 2013). These patterns agree with previous observations on the transitional record of other European and West Asian regions, suggesting that changes in ungulate taxonomic composition primarily reflect higher-order environmental changes. For instance, recent research in southwestern France has shown a progressive narrowing of the diet associated with climatic cooling and the HE4, pushing modern humans to focus largely on reindeer at many Early Aurignacian sites (Rendu et al. 2019). While this reliance on one ungulate species might have created demographic pulses in continental regions (Morin 2008), the Liguro-Provençal arc, and the Italian peninsula more generally, likely benefitted from more stable conditions. At the Balzi Rossi, these conditions could have fostered the patterns of short occupations documented for Neanderthals associated with very late "Semi-Sterile" Mousterian (shortly before ~42k cal BP). However, the drastic cooling does not coincide with a technological turnover suggested by some researchers (Riel-Salvatore & Negrino 2018a; cf. Banks et al., 2013). Instead, the Proto-Aurignacian of the Balzi Rossi lasts through HE4 in Level A2 followed by slightly more mesic conditions up until ~36ka cal BP, while the Early Aurignacian is already well established in western regions (Riel-Salvatore and Negrino 2018b). The chronology of the Balzi Rossi combined with the subsistence and taphonomic data presented here thus provide the first detailed insights into the patterns of subsistence adaptations of Proto-Aurignacian groups to the HE4 for the region.

The taxonomic composition of transitional Liguro-Provençal sites shows little change in the frequency of small game exploitation. Evidence of small, fast game exploitation is nearly absent from the region's Late Mousterian and the Early Upper Paleolithic faunal assemblages, except for three incised tubular bird bones in the Proto-Aurignacian at Riparo Bombrini (Holt et al. 2019). Other than these remains, bird and small mammal remains are scarce at Riparo Bombrini despite the modern recovery methods employed on the site, which agrees with Stiner's observations at neighbouring Riparo Mochi (Stiner 1999; Stiner et al. 1999; Stiner and Munro 2002). The scarcity of small taxa in the transitional record of the Balzi Rossi may indicate that modern humans did not need to expand their diet breadth thanks to the continuous availability of sufficient numbers of medium and large ungulates in the region. Alternatively, this apparent lack of subsistence intensification may be a result of the substantial degree of post-depositional alteration documented in this study. In this context, ZooMS mass sampling did not provide additional information on small taxa, though this may again be because poor preservation did not allow the recovery of collagen from smaller bone fragments.

In the Liguro-Provençal arc, Valensi and Psathi (2004) documented regular short-term late summer and early winter occupations (i.e., Grotte du Lazaret, Caverna delle Fate, Arma delle Manie), which agrees with our tentative observations at Riparo Bombrini, suggesting that Neanderthal groups exploited large herds of cervids during the rutting season. In the neighbouring regions of the Rhone Valley and Massif Central, Daujeard and colleagues (2012) also identified a close link between Neanderthals' mobility, site occupations, and the seasonal abundance of the hunted species. For instance, they document regular fall occupations of the Sainte-Anne I hunting camp located in the Massif Central, where mortality profiles indicate the killing of horses and cervids of all age categories (i.e., juvenile, adult, and old), perhaps as the result of ambush kills during seasonal aggregations.

In the Liguro-Provençal arc, the poor preservation of most faunal assemblages resulted in little evidence of animal exploitation for functional or symbolic purposes, and this is certainly the case for Riparo Bombrini. Valensi and Psathi (2004) documented several Ursidae bones bearing skinning marks and at least one Late Mousterian bone retoucher. At the Balzi Rossi, no retouchers have been recovered in either the Mousterian or the Aurignacian levels. The documented bone industry mainly includes the bone awls found in the Proto-Aurignacian of Riparo Bombrini and the Early Aurignacian of Riparo Mochi (Holt et al. 2019; Pothier Bouchard et al. 2020; Tejero and Grimaldi 2015).

Proto-Aurignacian symbolic objects include abundant gastropod shell beads from both sites with a few personal ornaments made of incised bird diaphyses, worked steatite and grooved fossil belemnite worn as pendants, however (Holt et al. 2019). To date, these assemblages have not yielded proof of *in situ* antler, ivory, or tooth working, whereas the Early Aurignacian of Riparo Mochi documented several split-based points with one ivory bead and a few tooth beads along with the continuous production of gastropod beads (Stiner 1999; Tejero and Grimaldi 2015). It thus appears that the range of animal raw materials was slightly narrower in the Proto-

Aurignacian occupations of the Balzi Rossi, agreeing with the overall narrower range of symbolic and functional objects made from animal raw material in the Proto-Aurignacian of western France.

5.7 Conclusion

In conclusion, our study has yielded detailed insights into the patterns of subsistence adaptations of the very last Neandertals associated with Level MS and the first modern humans of the Proto-Aurignacian on the taphonomically challenging site of Riparo Bombrini. This, in turn, allows us to discuss subsistence behaviours during the transition for the first time in the Liguro-Provençal arc. Some of the obvious problems when dealing with heavily fragmented faunal assemblages such as the ones analyzed here were overcome by applying a multivariate taphonomic approach to our archaeozoological analysis, which includes integrated mass ZooMS sampling.

Our results reveal that the unique topographic and environmental settings of the Liguro-Provençal arc profoundly influenced past subsistence, mobility and resource management strategies of Neanderthals and modern humans. For example, the abundant prey availability of the region would have allowed the adoption of flexible hunting strategies in response to external stresses, which could partly explain the lasting Neanderthal occupations documented in the Balzi Rossi and the subsistence adaptations of the Proto-Aurignacian groups to the HE4.

The flexible hunting capacities of both human species are shown by the continuous taxonomic diversity documented in the transitional faunal assemblages of the Liguro-Provençal arc, which reflects the local biogeographic dynamics. However, evidence from the combined mortality profiles, carcass treatment, and the technological record of Riparo Bombrini also indicate changing adaptations to external stresses in the Balzi Rossi across this transition. The last Neanderthals to have occupied the site seem to have focused on locally available red deer during their brief occupations, possibly in response to changing ecological conditions and the arrival of new groups in the neighbouring regions (i.e., Proto-Aurignacian in France, Uluzzian in Italy). In contrast, the Proto-Aurignacian levels reveal patterns of shifting mobility strategies within a larger territory against a backdrop of climate instability.

Among the scenarios explaining Neanderthals demise, cognitive or behavioural inferiority no longer stands. Scenarios integrating behavioural ecology instead highlight the role of subsistence versatility, demographic change and increased social connectedness to explain the adaptive success of modern humans in Europe, which could ultimately have resulted in the competitive exclusion of Neanderthal groups (e.g., Kuhn and Stiner 2006; O'Connell 2006; Shea and Sisk 2010; Stiner and Kuhn 2006). The larger land-use territories, the implementation of long-range weapons, and the changing status of carnivores and the use of several animal raw materials all indicate changing human-environmental interactions during the Proto-Aurignacian that would have increased demographic robustness and human resilience towards environmental instability (Kuhn and Stiner 2007a, 2007b).

Testing those scenarios in the Liguro-Provençal arc warrants future research on subsistence strategies of transitional sites. At Riparo Bombrini, ongoing excavation projects on the underlying Mousterian levels (M1-M7) will allow us to obtain high-resolution data covering the entire site. The available faunal data on these levels is so far restricted to taxonomic lists based on morphological identification of the 2002-2005 excavation campaigns (Holt et al. 2019) and our preliminary results of the faunal abundance and skeletal frequencies identified with ZooMS and morphology of the small collection excavated in 1976 (see Chapter 6).

On the regional scale, future research would benefit from inter-site multivariate approaches to allow behavioural comparisons between faunal assemblages with known taphonomic histories and within fine-grained chrono-stratigraphic and paleoenvironmental settings. Unfortunately, this approach is hindered by the lack of Proto-Aurignacian and Late Mousterian sites excavated with modern methods in the region. However, our research team is planning new projects on sites with long stratigraphic sequences such as Arma degli Zerbi and Caverna delle Arene Candide located in the Finalese to identify Proto-Aurignacian levels and possibly "Semi-Sterile Mousterian" levels. The application of archaeozoological and taphonomic analyses with integrated ZooMS mass sampling on these faunal assemblages would bring the needed resolution to directly compare contemporaneous faunal assemblages and bring new insights into the subsistence adaptations of the very last Neanderthals and the first modern humans outside the Balzi Rossi in the Liguro-Provençal arc.

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5.9 References

(References are grouped in the Bibliography)

5.10 Supplemental information

(see Appendix 3)

Chapter 6 – Conclusion

In conclusion, the results presented in the three articles prepared as part of this research project offer many new empirical data and interpretive insights to help answer our original research question: Did modern humans have an adaptive advantage in subsistence capacities over Neanderthals that allowed them to better face the severe climatic changes during the Middle-Upper Paleolithic transition?

This question is specifically addressed in Chapters 4 and 5 by applying a high-resolution archaeozoological and taphonomic analysis with integrated ZooMS at Riparo Bombrini. The combined evidence of the taxonomic composition, skeletal frequencies, mortality profiles, and the technological record supports the hypothesis that Neanderthals and modern humans were well-adapted not only to exploit the available range of animal species in their immediate environment but also to adopt and tailor their subsistence and land-use strategies along the residential – logistical continuum (*sensu* Binford) (Pothier Bouchard et al. 2020; Riel-Salvatore et al. 2013; Riel-Salvatore and Negrino 2018a, 2018b).

Furthermore, the results of the faunal analysis on the Proto-Aurignacian levels both support and nuance previous interpretations about its internal variability. First, continuities in the large faunal spectra in Levels A1 and A2 attest to the polyvalence of the technocomplex that allowed modern human groups to maintain a generalist and mostly local hunting strategy. In addition, the abundance of both warm-adapted and cold-adapted species in the Ligurian biogeographical refugium probably helped maintain this prey selection strategy throughout the climatic instability surrounding the HE4.

However, the faunal data from Level A2 also indicate that contrasting subsistence and mobility strategies could be linked to changing environmental conditions. The combined evidence of a seasonal signal, more organized spatial segregation of activities with a large discard area outside the living area and more curated use of bones for fuel, reflects either prolonged occupations or recurrent seasonal reoccupations in Level A2. This pattern agrees with the previous interpretation of that level's lithic assemblage showing a more logistical land-use strategy when the site would have been used as a base camp for prolonged periods during a generally colder phase (Riel-Salvatore & Negrino 2018a, 2018b). The prolonged stays during harsh seasons might have also involved episodes of solo hunting of solitary prey, facilitated at that point in time by the development of polyvalent long-range weapons. Parallelling Soulier's (2013) observations in Western France, fuel management during these less mobile stays could be associated with food stockpiling activities, such as meat smoking.

In Chapter 5, the results on the final Mousterian Level MS (or "semi-sterile Mousterian") suggest that the last Neanderthals in the region occupied the site while focusing on locally available red deer during brief visits. The selective hunting of such profitable prey – probably available close to the site – agrees with the previously advanced hypothesis that Level MS reflects hyper-local adaptations, possibly in response to changing ecological conditions and the arrival of new groups in the neighbouring regions (i.e., the Proto-Aurignacian in France, the Uluzzian in Italy). In this context, the Balzi Rossi could reveal late-lasting pockets of Neanderthal groups with reduced demography (Riel-Salvatore et al. 2021). The faunal composition in Level MS also contrasts with the underlying Mousterian levels at Riparo Bombrini, which document rich and diverse faunal assemblages (Holt et al. 2019).

In turn, the faunal data collected on the transitional levels of Riparo Bombrini carry important implications regarding scenarios about species replacement and about the adaptations of some of the earliest *Homo sapiens* in Western Europe. Some pieces of evidence associated with Riparo Bombrini's Proto-Aurignacian thus support the hypothesis that changing human-environmental interactions would have increased demographic robustness and human resilience to environmental instability (Kuhn and Stiner 2007a, 2007b). Indisputable further evidence of gastropod shell beads and personal ornaments production made of incised bird diaphyses, worked steatite, and grooved fossil belemnite (Holt et al. 2019) supports the observed diversification of animal raw materials used in the symbolic and functional spheres in the European early Upper Paleolithic (e.g., Romandini et al. 2020; Soulier 2014; Stiner 1999). The low impact of carnivore ravaging on the Proto-Aurignacian faunal assemblages, along with the presence of a single burned medium-sized carnivore element, align with the hypothesis of a shift of carnivores' status from competitors to prey during the transition (Rendu et al. 2019).

Furthermore, evidence of larger land-use territories combined with a lithic record indicating the implementation of long-range weapons clearly highlight the role of subsistence versatility, demographic change and increased social connectedness in the scenarios explaining the adaptive success of modern humans in Europe, ultimately possibly resulting in the competitive exclusion of Neanderthal groups (e.g., Kuhn and Stiner 2006; O'Connell 2006; Shea and Sisk 2010; Stiner and Kuhn 2006).

6.1 Integrating ZooMS to archaeozoological and taphonomic analysis

On the methodological front, the three articles provide insights into the secondary research question: How can ZooMS be adequately integrated into archaeozoological methodologies to tackle past subsistence strategies? Chapter 3 presents a promising avenue for the use of a portable FTIR instrument as an in-field screening method for ZooMS collagen fingerprinting, which has been further developed since the publication of our article (Pal Chowdhury et al. 2021). The FTIR screening method was also successfully applied at Riparo Bombrini in both Chapters 4 and 5. Its application on the poorly preserved faunal remains of the site also confirms the importance of testing 100+ samples variously distributed on the site to best adjust the screening threshold for ZooMS mass sampling.

The development of the FTIR screening method provides an excellent means of exploring adequate conceptual frameworks to integrate ZooMS mass sampling into archaeozoological research. As a complementary analytical tool to archaeozoological analysis, the ZooMS mass sampling has so far been applied to increase the statistical significance of the NISP tally. With this particular goal, the ZooMS is thus primarily applied to the indeterminate fraction of the faunal assemblages since it can generate crucial information on the taxonomic identification of unidentifiable bone fragments. The method has proven beneficial in improving overall taxonomic identifications (e.g., Buckley and Kansa 2011; Welker et al. 2015; Buckley, Harvey, and Chamberlain 2017) and highlighting differences in taxonomic composition caused by specific attritional factors (e.g., percussion-based fragmentation) (Sinet-Mathiot et al. 2019).

While much work on that front remains to be done, Chapters 4 and 5 have already demonstrated that, by tailoring sampling strategies to specific hypothesis-based approaches, ZooMS taxonomic identifications can improve many dimensions of our interpretations about past subsistence behaviours (i.e., taxonomic composition, faunal abundance, skeletal representation, mortality profiles, and seasonality).

In this regard, our study on the Proto-Aurignacian faunal assemblages of Riparo Bombrini in Chapter 4 shows that the ZooMS has successfully improved skeletal representation data (in our case: the NISPe) in addition to the faunal abundance data (NISP) (Pothier Bouchard et al. 2020). This first test helped strengthen our sampling strategy applied in Chapter 5, which we oriented towards four goals: (1) improving taxonomic composition and faunal abundance by randomly selecting unidentifiable bones of variable sizes, (2) improving skeletal frequency by prioritizing bone fragments identified to a skeletal element within broad taxonomic categories, (3) improving mortality profiles and data on seasonality by targeting fetal and juvenile bone fragments, and (4) distinguishing specific agents of skeletal alteration and accumulation by selecting bones with anthropic and carnivore surface alterations. As shown in Table 1, our sampling strategy in Chapter 5 helped improve all the targeted aspects, except the mortality profiles.

Table 1. – Comparison between the specimen counts identified with morphology alone and ZooMS (family, genus, or species).

		Level A1	**Level A2**	**Level MS**
Faunal abundance (NISP)	Morphology	12	22	20
	ZooMS	119	96	19
Skeletal frequency (NISPe)	Morphology	12	21	20
	ZooMS	75	52	15
Fetal and juvenile elements (N)	Morphology	0	2	2
	ZooMS	0	0	0
Elements with anthropic or carnivore alterations (N)	Morphology	0	0	5
	ZooMS	17	15	4

Applying the ZooMS on unidentifiable bone fragments considerably increased the NISP counts of most taxonomic categories, allowing us to discuss each assemblage's faunal abundance and taxonomic composition. However, the ZooMS does not resolve the interpretive biases associated with the NISP. Therefore much conceptual and methodological work remains to be done to fully integrate the method into archaeozoological studies in Paleolithic contexts. Our sampling strategy on the taphonomically challenging faunal assemblages of Riparo Bombrini shows that the ZooMS success is primarily influenced by differential preservation. Because collagen preservation is dependent on bone density, random ZooMS sampling creates a bias against more fragile bones, namely juvenile and fetal bones, cancellous bones (as opposed to cortical bones), and small taxa. Our taxonomic identifications in Chapter 5 show this phenomenon with the amount of ZooMS identified cortical bones (long bones and indeterminates), accounting for 76 % of the total identified ZooMS samples, in contrast with no positive result on juvenile and fetal bones.

In addition, since collagen preserves well in the dense cortical bones of large taxa, ZooMS sampling of those abundant types of bone fragments can be influenced by differential bone breakage. These biases are mostly a concern regarding the interdependence of skeletal remains – i.e., one animal can be counted several times, which may exaggerate sample sizes across taxa. The random ZooMS sampling does not exaggerate all taxonomic categories equally and could create an error propagation phenomenon regarding NISP tallies. Nevertheless, the NISP remains the best quantification unit to discuss faunal abundance and taxonomic composition (Grayson 1984; Morin et al. 2017b). This is especially true for faunal assemblages with intensified fragmentation levels that have reduced MNI tallies to one or two individuals per taxonomic category and have decreased NISP tallies as the bone fragments become unidentifiable (Lyman 2008:253). In this context, the ZooMS can highlight those bone fragments belonging to taxonomic categories that might have been absent or underestimated using morphological identifications only. At Riparo Bombrini, the ZooMS has undoubtedly helped improve discussions about faunal abundance and about taxonomic composition within each assemblage.

Furthermore, in Chapter 5, applying the ZooMS on identifiable skeletal elements allowed us to consider bone survivorship on an ordinal scale for two taxonomic categories (i.e., cervid size 2/3 and ungulate size 3/4). However, the overall poor morphological preservation on the site only allowed discussing carcass transport on the nominal scale even with the help of the ZooMS. Using NISP tallies of skeletal elements (NISPe) possibly brought the same interpretive limits as those affecting taxa's NISP. The NISPe precludes from applying advanced statistical analyses that would necessitate specimen-dependent variables (e.g., MNE, MAU) (Grayson 1984). However, the NISPe can be informative on the qualitative level when contextualized within the spatial distribution of the skeletal remains. In the case of Riparo Bombrini, the ZooMS highlighted the presence of long bone shaft fragments of Bovinae and Equidae in the Proto-Aurignacian levels, two taxa that were otherwise poorly represented with morphological identifications (Holt et al. 2019). The aggregation of the bone fragments in specific areas of the site suggests that the same animals were probably counted many times for these taxa. However, these aggregations, resulting in the overrepresentation of hind limb bone fragments, also revealed possible carcass transport strategies focused on meat and grease-rich skeletal parts and some specific behaviours focused on bone breakage.

In short, while the ZooMS can exaggerate some of the interpretive biases related to NISP tallies, its influence on the taxonomic and skeletal composition of an assemblage can also reveal anthropic behaviours that would be impossible to identify based on morphology alone. However, the full power of the ZooMS as a complementary tool is only fully demonstrated when it is integrated within the archaeozoological and taphonomic analyses. This is because differential preservation remains the main challenge to interpreting heavily fragmented faunal assemblages. In the specific case of Riparo Bombrini, differences in bone preservation vary according to bone density and within the different areas of the site. Our window into taxonomic identifications (with morphology and ZooMS) is thus severely biased towards the exterior of the rockshelter. In addition, the loss of collagen in bones affected by anthropic behaviours due to exposure to heat (i.e., through cooking, grease rendering, and use of bone as fuel) also hinders ZooMS identification by creating taxonomic identification biases towards unheated skeletal elements.

As concerns the many methodological challenges encountered in our project, the multivariate taphonomic approach applied in Chapter 5 helped tackle those by organizing the variables and structuring our investigation of the different faunal assemblages. This approach has introduced a simple way to organize taphonomic data hierarchically, following three lines of investigations to tackle primary sources of taphonomic alterations at Riparo Bombrini (i.e., post-depositional attrition, agent of accumulation, and anthropic carcass treatment). This systematic process applied to each assemblage helped resolve some issues of equifinality at the site. For instance, although the high fragmentation level of the Proto-Aurignacian faunal assemblages results from heavy post-depositional attrition, it can also be partly explained by intensive carcass processing by human foragers.

Previous applications on better preserved Epipaleolithic contexts highlighted the importance of comparing independent taphonomic variables among well-represented archaeozoological sub-groups to ensure reaching a high degree of taphonomic resolution (Bar-Oz and Munro 2004). The scarce data within each taxonomic and age category made this aspect particularly challenging at Riparo Bombrini. The best solution was to create broad taxonomic categories (i.e., medium and large game) to observe how given taphonomic variables varied between more fragile and more robust skeletal remains, an essential comparison to assess the influence of density-mediated attrition. In addition, we adapted many taphonomic variables to the poor morphological preservation by using NSP tallies of bone types (e.g., cancellous and cortical bones) and surface alterations (e.g., burning, concretion, manganese). Therefore, our application of the multivariate taphonomic approach proved to be useful even on these challenging faunal assemblages.

6.2 Research perspectives and preliminary results on levels M1-M5 (1976)

To summarize, our research has demonstrated the utility of applying an exhaustive archaeozoological and taphonomic analysis with an integrated ZooMS sampling strategy to tackle a faunal collection previously considered too fragmented to generate much in the way of meaningful behavioural information. However, the methodological challenges encountered in our investigation of the Riparo Bombrini faunal collections highlighted the need for further research on the site and other transitional sites in the Liguro-Provençal arc.

Due to limited samples of morphologically identifiable skeletal remains at Riparo Bombrini, the diverse taphonomic forces that affected these faunal remains (i.e., heavy skeletal fragmentation, differential pre- and post-depositional preservation) also considerably hindered the behavioural reconstructions regarding carcass transport, mortality profiles, and seasonality. Although the two first aspects shall remain challenges at Riparo Bombrini, the question of seasonality in occupation of the site could be reinforced by additional specialized analyses such as cementochronology (e.g., Rendu 2010) and stable isotopes (e.g., Julien et al. 2012) on the few morphologically preserved ungulate teeth.

Furthermore, ongoing excavation projects on the underlying Mousterian levels at Riparo Bombrini (i.e., M1-7) will allow our team to obtain additional high-resolution data covering the Mousterian sequence on the entire site surface. Preliminary results on faunal abundance with integrated ZooMS applied on the small 1976 assemblages indeed show that interesting patterns emerge, which warrants the study of newly excavated faunal remains.

For instance, the faunal abundance of the three levels considered here (Table 2, Fig. 1; Levels M1-2, M3-4, and M5) enriches the available taxonomic lists based on the morphological identification of the 2002-2005 excavation campaigns (Holt et al. 2019:146, Table 4). Despite our small sample, the ZooMS on fragmented long bones allowed us to increase the faunal richness of some assemblages with the presence of Capreolinae in Level M1-2, Rhinocerotidae in Level M3-4, and Hyaenidae, Bovinae, and Caprinae in Level M5. These preliminary results also strengthen some of the faunal abundance patterns identified in Holt et al. (2019), such as the continuous presence of Cervinae and the increased amount of Suidae in Level M3-4. The taxonomic diversity of Level M3-4, which contrasts with the dominance of Cervinae in Level M1-2, may reflect changes in subsistence patterns and paleoenvironment context, agreeing with the rich archaeological record with recurrently used hearths and more logistical occupations documented in this level (Riel-Salvatore et al. 2013).

Table 2. – Relative faunal abundance (%NISP) of Bombrini M1-2, Bombrini M3-4, and Bombrini M5.

	Bombrini M1-2			**Bombrini M3-4**			**Bombrini M5**		
	NISP	**%NSP**	**MNI**	**NISP**	**%NSP**	**MNI**	**NISP**	**%NSP**	**MNI**
Taxa									
herbivores									
Bos/Bison	1	0.5%	1	4	0.6%	1	2	1.0%	1
Capra ibex	2	1.0%	1	4	0.6%	1	2	1.0%	1
Capreolus sp.	1	0.5%	1	0	0.0%	0	0	0.0%	0
Cervus elaphus	2	1.0%	1	0	0.0%	0	0	0.0%	0
Cervus sp.	14	6.8%	1	37	5.7%	1	19	9.5%	1
Dama dama	0	0.0%	0	0	0.0%	0	0	0.0%	0
Diceros/Coelodonta	0	0.0%	0	1	0.2%	1	1	0.5%	1
Equus sp.	0	0.0%	0	2	0.3%	1	2	1.0%	1
Sus scrofa	2	1.0%	1	26	4.0%	1	9	4.5%	1
Bovid s.2/3	1	0.5%	1	0	0.0%	0	0	0.0%	0
Caprine s.2/3	0	0.0%	0	0	0.0%	0	0	0.0%	0
Cervid s.2/3	0	0.0%	0	0	0.0%	0	1	0.5%	1
Cervid s.3/4	2	1.0%	1	0	0.0%	0	2	1.0%	1
Cervid s. indeter.	0	0.0%	0	2	0.3%	1	2	1.0%	1
Artiodactyl s.2/3	0	0.0%	0	0	0.0%	0	0	0.0%	0
Artiodactyl s.3/4	1	0.5%	1	3	0.5%	1	1	0.5%	1
Artiodactyl s.inteter.	0	0.0%	0	1	0.2%	1	0	0.0%	0
Ungulate s.2/3	0	0.0%	0	0	0.0%	0	0	0.0%	0
Ungulate s.3/4	0	0.0%	0	3	0.5%	1	1	0.5%	1
Ungulate s.indeter.	0	0.0%	0	0	0.0%	0	0	0.0%	0
Carnivores									
Canis lupus	0	0.0%	0	0	0.0%	0	0	0.0%	0
Hyena sp.	0	0.0%	0	1	0.2%	1	0	0.0%	0
Ursus spelaeus	0	0.0%	0	0	0.0%	0	0	0.0%	0
Ursus sp.	0	0.0%	0	2	0.3%	1	1	0.5%	1
Vulpes vulpes	0	0.0%	0	0	0.0%	0	0	0.0%	0
Carnivore s. 2/3	0	0.0%	0	0	0.0%	0	0	0.0%	0
Carnivore s.3/4	0	0.0%	0	3	0.5%	1	0	0.0%	0
Carnivore s.indeter.	0	0.0%	0	0	0.0%	0	0	0.0%	0
Total NISP	26	12.7%	9	89	13.6%	13	43	21.4%	12
Indeterminate	179	87.3%		564	86.4%		158	78.6%	
Total NSP	205	100.0%	9	653	100.0%	13	201	100.0%	12

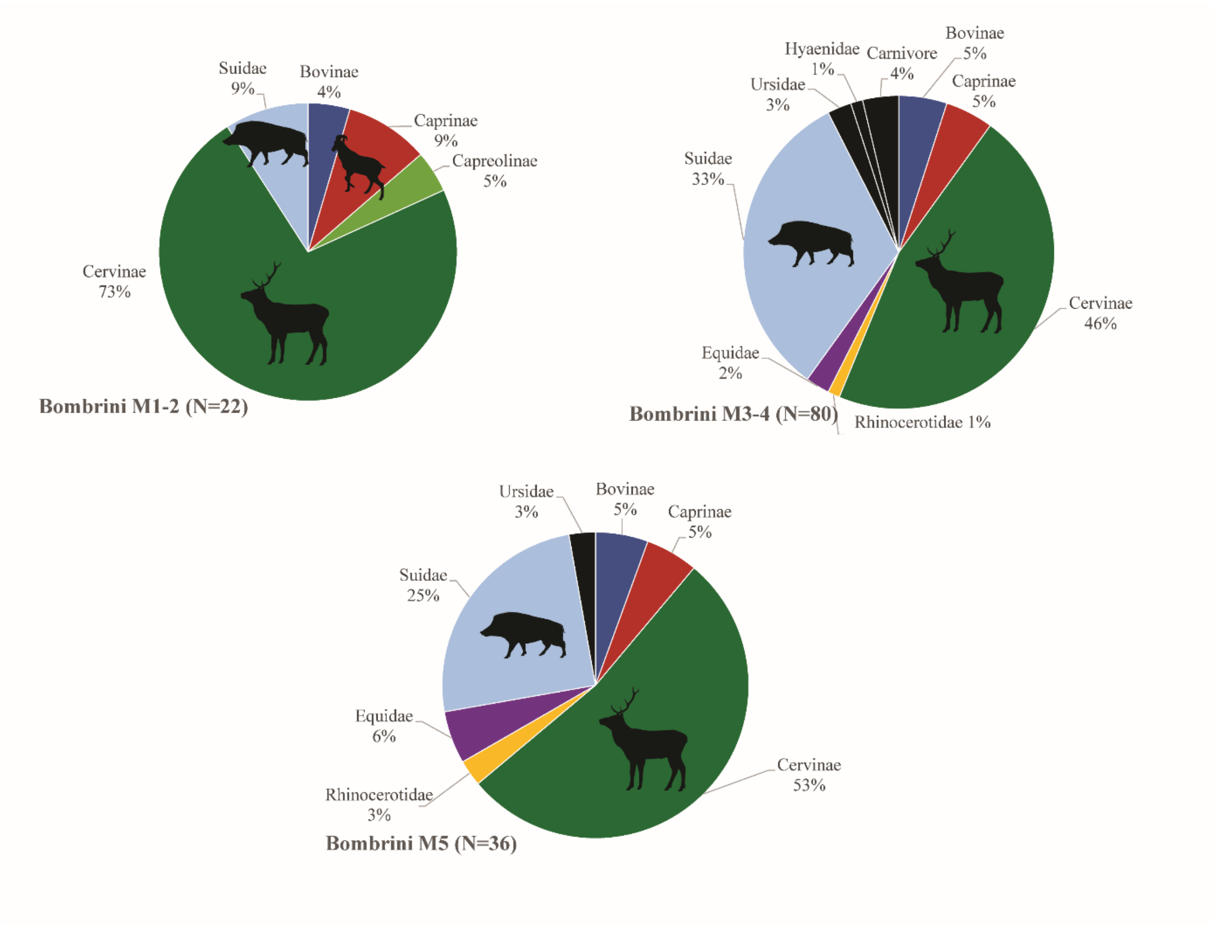

Figure 1. – Relative faunal abundance (%NISP) of Bombrini M1-2, Bombrini M3-4, and Bombrini M5

Further high-resolution archaeozoological and taphonomic analysis with integrated ZooMS focused on those levels will thus allow us to obtain a better picture of the successive shifts in mobility and subsistence strategies associated with the Late Mousterian at Riparo Bombrini. The results can, in turn, be contextualized with previous subsistence reconstructions obtained at the regional scale of the Liguro-Provençal arc. Final Mousterian sites dated to OIS 5-3 such as Arma delle Manie and Caverna delle Fate near the present-day town of Finale Ligure, and Madonna dell'Arma and San Francesco near the town of San Remo show different types of occupations by Neanderthals and carnivores. Archaeozoological and taphonomic studies on the faunal remains reveal a dominance of carnivore occupations – especially cave bears at Caverna delle Fate, whereas Neanderthals and carnivores alternately occupied Madonna dell'Arma (Valensi and Psathi 2004). In contrast, traces of carnivore activity were scarce at Arma delle Manie and Via San Francesco, suggesting that Neanderthals were the primary agents of bone accumulation at those sites. All the faunal assemblages are dominated by cervids, followed by various medium and large ungulate species, agreeing with Riparo Bombrini's faunal data, and likely mostly reflecting the natural diversity of biotopes in the region. On the sites primarily occupied by Neanderthals (i.e., Arma delle Manie and Via San Francesco), medium and large ungulates assemblages impart prime-dominated mortality profiles and the transport of meatier anatomical parts. Despite those observations, Valensi and Psathi (2004) argued that the faunal data was insufficient to reconstruct detailed hunting strategies. The lack of high-resolution archaeozoological data on those sites is primarily due to the historical context of their excavations prior to the 1970s, when archaeologists often discarded the smaller unidentifiable skeletal fragments.

While our research at Riparo Bombrini provides a first picture of subsistence behaviours during the transition in the Liguro-Provençal arc, much work remains to be done to fill in the archaeozoological data gaps at the regional scale. Since Proto-Aurignacian sites are so far exclusively documented in the region at the Balzi Rossi (i.e., Riparo Bombrini and Riparo Mochi) and at Grotte de l'Observatoire in Monaco, such work could start with new excavation projects on sites with long archaeological stratigraphies. In the Balzi Rossi, Riparo Lorenzi is a rockshelter located between Grotta dei Fanciulli and Grotta di Florestano, to the west of Riparo Mochi and Riparo Bombrini. Given that its deposits appear to be largely intact on most of the site's surface, modern excavations undertaken at this rockshelter could shed new light on the western part of the Balzi Rossi. Additionally, its deposits are known from largely anecdotal testing conducted at the turn of the 20th century to span the transition with a long Upper Paleolithic sequence (Rossoni-Notter et al. 2017), making this site a promising locale to further explore the transition at the Balzi Rossi.

Outside the Balzi Rossi, a few sites located in the Finalese province would also greatly benefit from new search projects to uncover and analyze transitional levels. Among these, Caverna delle Arene Candide, Arma degli Zerbi, Arma dell'Aquila, Arma delle Manie, Arma dello Stefanin, and Arma Veirana show great potential due to their long archaeological sequences. On the coast, the

Caverna delle Arene Candide is a large cave site opening on the Mediterranean sea, located near the present-day town of Finale Ligure. The site is well-known for its Neolithic and late Upper Paleolithic deposits, including a Final Epigravettian "necropolis" and rich Gravettian burials (Gravel-Miguel et al. 2017). A test pit also yielded levels contemporaneous with the Aurignacian level F at Riparo Mochi. Although diagnostic artifacts have not yet been recovered in this test pit, the cave shows excellent potential for future excavation projects to uncover Proto-Aurignacian and possibly final Mousterian deposits (Riel-Salvatore et al. 2018).

Further inland, Arma degli Zerbi is a cave site opening on the Aquila valley, located some 4 km away from Finale Ligure. Its deposits were in part destroyed by clandestine excavations, exposing at the same time a long sequence with rich stratigraphic levels, some of which containing Dufour bladelets – diagnostic of the Proto-Aurignacian (Negrino et al. 2018). In the same valley, Arma dell'Aquila is a cave site excavated between 1938-40 (Biagi and Starnini 2021). While Neolithic levels there are well-documented, a few Upper Paleolithic artifacts were uncovered from three hearths in the lowermost deposits, suggesting the site was occupied during the Late Epigravettian and perhaps even the Early Upper Paleolithic. Both sites would thus benefit from modern excavations to clarify their stratigraphic sequences.

Further east, the Arma delle Manie cave is located a few kilometres away from the coast (Cauche 2007). The site has revealed thick deposits containing Neolithic levels at the top and Mousterian levels dated between OIS 5 -3 at the bottom. Research has mostly focused on the final Mousterian collections exposed between 1979 and 1980 (Cauche 2007; Cauche et al. 2002; Psathi 2003; Valensi and Psathi 2004). However, several areas of the site remain unexcavated and could benefit from new excavations to refine its chronological framework and to uncover early Upper Paleolithic levels overlying the final Mousterian.

Finally, Arma dello Stefanin is an inland cave site opening on the Pennavaira valley about 22 km from the present-day Ligurian shore (Girod 1987). Excavations carried out in the 1950s and the 1980s revealed Epigravettian and Neolithic occupations (Anfossi 1972; Barker et al. 1990; Biagi et al. 1987; Girod 1987), leaving open the possibility of uncovering older Upper Paleolithic and possibly transitional levels in the underlying deposits. Ongoing projects led by C. Gravel-Miguel,

F. Negrino and J. Riel-Salvatore at Arma dello Stefanin should soon clarify the length and nature of the sequence. In the neighbouring Neva valley, the Arma Veirana cave, excavated between 2015-2019, has revealed rich Mousterian and late Epigravettian levels (Hodgkins et al. 2021; Pothier Bouchard et al. 2019). A richly decorated Mesolithic infant burial was recently discovered in deposits located in the middle area of the cave (Hodgkins et al. 2021). While there is an erosional gap between the Mousterian and the late Upper Paleolithic levels in this area, the back of the cave contains a much thicker unexcavated deposit that could preserve the transitional sequence.

Furthermore, documenting the Proto-Aurignacian on these sites would increase the chances of identifying stratigraphic levels similar to the “semi-sterile Mousterian” observed in Level MS at Riparo Bombrini and its coeval Level H at Riparo Mochi. As shown in our research, these levels are crucial to our comprehension of the transition in the region. At Riparo Bombrini, the Proto-Aurignacian levels are used as a *terminus ante quem* to date these deposits that document late Neanderthal occupations lasting until ca. 42ka cal BP (Riel-Salvatore et al. 2021). The nature of the archaeological material also reveals contrasting patterns of subsistence strategies and site function when compared to the available data from underlying Mousterian levels on the site and other well-documented final Mousterian sites in the region and in the neighbouring Rhone Valley.

For instance, the patterns in Level MS do not include bone fuel management, heavy lithic and artifact accumulations, and year-round occupations that would describe long-term residential camps, according to Daujeard and Moncel (2010). However, some evidence of short-term regular hunting camps is visible in Level MS, namely alternating occupations with other carnivore predators – suggestive of short stays by Neanderthals and the presence of burnt bones and mostly local lithic raw material. Nonetheless, the low density of artifacts would best agree with brief stopping places described by Daujeard and Moncel (2010). Furthermore, many pieces of evidence suggest base-camp occupations by Neanderthals: the selective hunting of profitable prey (i.e., adult deer), the presence of primary and secondary butchering steps, and the presence of a conspicuous combustion feature.

Level MS could thus correspond to a different type of site function, resembling a residential base camp characterized by very brief stays and a high degree of residential mobility. This scenario would agree with the hypothesis that Neanderthals could have adopted a hyperlocal subsistence and land-use strategy in response to fluctuating ecological conditions and the arrival of new groups in neighbouring regions (i.e., the Proto-Aurignacian in France and the Uluzzian in Italy) (Riel-Salvatore et al. 2021). Therefore, testing this hypothesis warrants uncovering contemporaneous assemblages outside the Balzi Rossi to expand our knowledge about the behaviours observed in the "semi-sterile Mousterian" of Riparo Bombrini.

The results of our research thus open a pathway to renewed archaeozoological studies of contemporaneous assemblages at Riparo Bombrini excavated with modern techniques (e.g., Levels G-H at Riparo Mochi) and new excavation projects in the Balzi Rossi (e.g., Riparo Lorenzi) and in the Finalese area in order to contribute to the necessary integration of technological and subsistence data and reach an appropriately complete view of the transition in the Liguro-Provençal arc.

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Appendices

Appendix 1 – Supplemental information of article 1 (Pothier Bouchard et al. 2019)

Table 1. – List of all the samples analysed in this study with indication (X) of which instruments were used to produce spectra, and whether ZooMS has been completed.

Bone ID	PO1	PO2	LA1	LA2	LA3	ZooMS
B100	X		X			X
B101	X		X			X
B102	X		X			X
B103	X					X
B104	X		X			X
B105	X		X			X
B106	X		X			X
B107	X		X			X
B108	X		X			X
B109	X					X
B110	X					X
B111	X					X
B112	X			X		X
B113	X	X			X	X
B114	X	X			X	X
B115	X	X			X	X
B116	X	X			X	X
B117	X	X			X	X
B118	X	X			X	X
B119	X	X			X	X
B120		X				X
B121	X	X			X	X
B122	X	X			X	X
B123	X	X			X	X
B124	X	X			X	X
B125						X
B126	X	X			X	X
B127	X	X			X	X
B128	X	X			X	X
B129	X	X			X	X
B130	X	X			X	X
B131	X	X			X	X
B132	X	X			X	X

B133	X	X			X	X
B134	X	X			X	X
B135	X	X			X	X
B136	X	X			X	X
B137	X	X			X	X
B138	X	X			X	X
B139	X	X		X	X	X
B140	X	X			X	X
B141	X	X			X	X
B142	X	X			X	X
B143	X	X			X	X
B144	X	X			X	X
B145	X	X			X	X
B146	X	X			X	X
B147	X	X			X	X
B148	X	X			X	X
B149	X	X			X	X
B150						X
B151	X	X			X	X
B152	X	X			X	X
B153	X	X			X	X
B154	X	X			X	X
B155	X	X			X	X
B156	X	X			X	X
B157	X	X			X	X
B158	X	X			X	X
B159	X	X			X	X
B160	X	X			X	X
B161	X	X			X	X
B162	X	X			X	X
B164				X		X
B165				X		X
B166				X		X
B167				X		
B168				X		
B169				X		
B170				X		
B171				X		
B172				X		
B173				X		X
B174				X		X
B175				X		
B176				X		X
B177				X		X
B178				X		X
B179				X		X
B181				X		X
B182				X		X

B183		X	X
B184		X	X
B185		X	X
B186		X	X
B187		X	X
B191		X	X
B192		X	X
B194		X	X
B195	X	X	X
B198		X	X
B199	X	X	X
B200		X	X
B201		X	X
B204		X	X
B205		X	X
B207		X	X
B208		X	X
B209	X	X	
B211		X	X
B212		X	X
B215		X	X
B216		X	X
B217		X	X
B218		X	X
B220		X	
B223		X	X
B224		X	X
B225		X	X
B228		X	X
B229		X	X
B230		X	X
B231		X	X
B232		X	X
B233		X	X
B234		X	X
B235		X	X
B236		X	X
B237		X	X
B238	X	X	X
B239		X	X
B240		X	X
B241	X	X	X
B242		X	X
B243		X	X
B244		X	X
B245		X	X
B246		X	X
B247		X	X

B248		X	X
B249		X	X
B250		X	X
B251		X	X
B252		X	X
B253		X	X
B254		X	X
B255		X	X
B256		X	X
B257		X	X
B258		X	X
B259		X	X
B260		X	X
B261		X	X
B264		X	X
B281		X	X
B282		X	X
B283		X	X
B284		X	X
B285		X	X
B286		X	X
B286A		X	X
B287		X	X
B288		X	X
B289		X	X
B290		X	X
B296		X	X
B299		X	X
B304		X	X
B306		X	X
B307		X	X
B308		X	X
B309		X	X
B310		X	X
B312		X	
B313		X	X
B314		X	X
B315		X	X
B316		X	
B317		X	X
B318	X	X	X
B319		X	X
B320		X	
B321		X	X
B322		X	X
B330		X	
B334		X	X
B335		X	X

B336				X		X
B337				X		X
B338				X		
B340				X		X
B341				X		X
B342				X		X
B343				X		X
B344				X		X
B345				X		X
B346				X		X
B347		X		X		X
B348				X		X
B349				X		X
B350		X		X		X
B351		X		X		X
B352				X		X
B353		X		X		X
B354				X		X
B356				X		X
B357				X		
B358				X		X
B359				X		X
B360				X		X
B361				X		X
B362				X		
B363				X		X
B364				X		X
B365				X		X
B366				X		X
B367				X		X
B368		X		X		X
B369		X		X		X
B370				X		X
B371				X		X
B385				X		X
B386				X		
B390		X		X		X
B393				X		X
B394	X	X			X	
B396		X				
B411	X	X			X	
B414	X	X			X	
B415	X	X			X	
B416	X	X			X	
B417		X				
B418		X				
B419		X				
B420		X				

B421	X
B422	X
B423	X
B424	X
B425	X
B426	X
B427	X
B428	X
B429	X
B430	X
B432	X
B433	X
B435	X
B436	X
B437	X
B438	X
B439	X
B440	X
B441	X
B442	X
B443	X
B444	X
B445	X
B446	X
B447	X
B448	X
B449	X
B450	X
B451	X
B452	X
B453	X
B454	X
B455	X
B456	X
B457	X
B458	X
B459	X
B460	X
B461	X
B462	X
B463	X
B464	X
B465	X
B466	X
B467	X
B468	X
B469	X
B470	X

B473		X				
B474	X	X			X	
B475	X	X			X	
B476	X	X			X	
B477	X	X			X	
B478	X	X			X	
B479	X	X			X	
B480	X	X			X	
B481	X	X			X	
B482	X	X			X	
B483	X	X			X	
B484	X	X			X	
B486	X	X			X	
B487	X	X			X	
B488	X	X			X	
B489	X	X			X	
B490	X	X			X	
B491	X	X			X	
B492	X	X			X	
B493	X	X			X	
B494	X	X			X	
B498	X	X			X	
B499	X	X			X	
B500	X	X			X	
B501	X	X			X	
B502	X	X			X	
B503	X	X			X	
B504	X	X			X	
B505	X	X			X	
B506	X	X			X	
B507	X	X			X	
B508	X	X			X	
B511	X	X			X	
B512	X	X			X	
B513	X	X			X	
B514	X	X			X	
B515	X	X			X	
B516	X	X			X	
B71	X		X			X
B72	X		X			X
B73	X		X			X
B74	X		X			X
B77	X		X			X
B78	X		X			X
B79	X		X			X
B80	X		X			X
B81	X		X			X
B82	X		X			X

B83	X		X			X
B84	X		X			X
B85	X					X
B86	X		X			X
B87	X		X			X
B88	X		X			X
B89	X		X			X
B90	X					X
B91	X		X			X
B92	X					X
B93	X		X			X
B94	X		X			X
B95	X					X
B96	X		X			X
B97	X		X			X
B98	X					X
B99	X		X			X
V21	X	X	X		X	X
V22	X		X			X
V23	X					X
V24	X					X
V25	X		X			X
V26	X	X			X	X
V27	X	X				X
V28	X	X				X
V29	X					X
V30	X				X	X
V31	X	X	X		X	X
V32	X	X	X			X
V33	X				X	X
V34	X	X	X		X	X
V36	X		X		X	X
V37	X					X
V38	X	X	X		X	X
V39	X	X	X		X	X
V40	X		X			X
V41	X	X			X	X
V42	X		X			X
V43	X	X			X	X
V44	X					X
V45	X					X
V46	X	X			X	X
V47	X					X
V48	X	X			X	X
V49	X	X			X	X
V50	X					X
V51	X	X			X	X
V52	X	X	X		X	X

V53	X		X
VN8_2		X	X

Table 2. – Measurement systems tested. All units are cm^{-1}

Meas. Syst.	**Type**	**P peak**	**P left baseline (min.)**	**P right baseline (min.)**	**CO peak**	**CO left baseline (min.)**	**CO right baseline (min.)**	**Index range***
A**	Height	1025-990	1350-1142	850-660	1655-1625	1900-1700	1350-1180	0-0.83
B**	Height	1025-990	1350-1140	850-660	1655-1625	1900-1700	1350-1180	0-0.83
C	Height	1025-990	1200-1150	850-660	1655-1625	1900-1700	1350-1180	0-0.83
D	Height	1025-990	1350-1140	850-800	1655-1625	1900-1700	1350-1180	0-0.83
E	Height	1025-990	1200-1150	850-800	1655-1625	1900-1700	1350-1180	0-0.83
F	A.height	1025-990	1200-1150	850-800	1655-1625	1900-1700	1350-1180	0-0.63
G	A.height	1025-990	1350-1140	850-660	1655-1625	1900-1700	1350-1180	0-0.62
H	A.height	1025-990	1200-1150	850-660	1655-1625	1900-1700	1350-1180	0-0.62
I	A.height	1025-990	1350-1140	850-800	1655-1625	1900-1700	1350-1180	0-0.62
J	Area	1140-890	1200-1150	850-800	1710-1590	1900-1700	1350-1180	0-0.35
K	Area	1140-890	1350-1140	850-660	1710-1590	1900-1700	1350-1180	0-0.35
L	Area	1140-890	1200-1150	850-660	1710-1590	1900-1700	1350-1180	0-0.35
M	Area	1140-890	1350-1140	850-800	1710-1590	1900-1700	1350-1180	0-0.35
N	Height	1025-990	1150	850-660	1655-1625	1900-1700	1350-1180	0-0.84
O	Height	1025-990	1150	850-800	1655-1625	1900-1700	1350-1180	0-0.85
P	A.height	1025-990	1150	850-800	1655-1625	1900-1700	1350-1180	0-0.63
Q	A.height	1025-990	1150	850-660	1655-1625	1900-1700	1350-1180	0-0.63
R	Area	1140-890	1150	850-800	1710-1590	1900-1700	1350-1180	0-0.36
S	Area	1140-890	1150	850-660	1710-1590	1900-1700	1350-1180	0-0.36

*The Index range is the maximum and minimum values of the ratio of the CO/P measurements. The upper value was generated from measurements on a sample of a modern bone (scapula from a juvenile wild pig).

**There are only slight differences between measurement systems A and B. We include system A in this study because it was used in a preliminary study.

Table 3. – First set of samples: Peptide markers of the soluble pellets, ZooMS identifications, and associated scores (AV: Arma Veirana, RB: Riparo Bombrini, NID: not identifiable)

Site	**ZooMS Sample**	**Peptide Markers: soluble pellet**								**ZooMS ID**	**Score**	**Yield**
		2t85(A)	2t43(B)	2t69(C)	2t69(D)	2t41/42(E)	1t55/56(F)	2t67(G)	2t76			
AV	V21	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.119103774
AV	V22	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.067204301
AV	V23	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.107655502
AV	V24	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.045058884
AV	V25	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.114327062
AV	V26	A	1427.7	A	2131.1	N/A	A	A	N/A	Ungulate	1	0.039503386
AV	V27	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	0.091182365
AV	V28	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3059.4	N/A	*Capreolus*	2	0.054532056
AV	V29	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	0.085122699
AV	V30	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.070809249
AV	V31	A	1427.7	A	2131.1	N/A	2883.4	3093.4	N/A	Ungulate	1	0.075077399
AV	V32	1196.2	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2	0.434239857
AV	V33	A	A	A	A	A	A	A	A	NID	0	0.101030928
AV	V34	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.322479649
AV	V35	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	0.289320388
AV	V36	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	0.132743363
AV	V37	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.176661264
AV	V38	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	0.091864539
AV	V39	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.183043478
AV	V40	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.073555166
AV	V41	A	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	1	0.087134105

AV	V42	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	0.050626566
AV	V43	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.073265405
AV	V44	A	A	A	A	A	A	A	A	NID	0	0.070712136
AV	V45	A	A	A	A	A	A	A	A	NID	0	0.068725869
AV	V46	1196.2	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2	0.065201465
AV	V47	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.141315519
AV	V48	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	0.179518564
AV	V49	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	0.168993387
AV	V50	A	A	A	A	A	A	A	A	NID	0	0.218968531
AV	V51	A	A	A	A	A	A	A	A	NID	0	-0.00127088
AV	V52	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	1.08466899
AV	V53	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.137704918
RB	B71	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.177687477
RB	B72	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	0.178832117
RB	B73	A	A	A	A	A	A	A	A	NID	0	0.110831234
RB	B74	A	A	A	A	A	A	A	A	NID	0	0.329346093
RB	B75	A	A	A	A	A	A	A	A	NID	0	0.445230608
RB	B76	A	A	A	A	A	A	A	A	NID	0	0.173803526
RB	B77	A	1427.7	1580.8	2131.1	N/A	2853.4	A	N/A	*Cervus/Capreolus*	1	0.153846154
RB	B78	A	A	A	A	A	A	A	A	NID	0	0.118367347
RB	B79	A	A	A	A	A	A	A	A	NID	0	0.123349679
RB	B80	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.239533288
RB	B81	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.342735043
RB	B82	A	A	A	A	A	A	A	A	NID	0	0.088685015
RB	B83	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.116654164
RB	B84	A	A	A	A	A	A	A	A	NID	0	0.103393425
RB	B85	A	A	A	A	A	A	A	A	NID	0	0.468233799
RB	B86	A	A	A	A	A	A	A	A	NID	0	0.070904645
RB	B87	A	A	A	A	A	A	A	A	NID	0	0.079731744
RB	B88	A	A	A	A	A	A	A	A	NID	0	0.084022638

RB	B89	A	A	A	A	A	A	A	A	NID	0	0.08882015
RB	B90	A	A	A	A	A	A	A	A	NID	0	0.006997901
RB	B91	A	A	A	A	A	A	A	A	NID	0	0.163766633
RB	B92	A	A	A	A	A	A	A	A	NID	0	0.053571429
RB	B93	A	A	A	A	A	A	A	A	NID	0	0.085284281
RB	B94	A	A	A	A	A	A	A	A	NID	0	0.028120375
RB	B95	A	A	A	A	A	A	A	A	NID	0	0.025198939
RB	B96	A	A	A	A	A	A	A	A	NID	0	0.026954178
RB	B97	A	A	A	A	A	A	A	A	NID	0	0.062143967
RB	B98	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	0.067551267
RB	B99	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	0.109880372
RB	B100	1196.2	1427.7	1550.9	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.053053053
RB	B101	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	0.067644276
RB	B102	A	1427.7	A	2131.1	A	A	A	N/A	Ungulate	1	0.074779378
RB	B103	A	A	A	A	A	A	A	A	NID	0	0.057888763
RB	B104	A	A	A	A	A	A	A	A	NID	0	0.059007599
RB	B105	A	1427.7	A	2131.1	A	A	A	N/A	Ungulate	1	0.414276402
RB	B106	A	1427.7	1550.8	2131.1	N/A	A	A	N/A	*Cervus/Capreolus*	1	0.078637511
RB	B107	A	A	A	A	A	A	A	A	NID	0	0.077248677
RB	B108	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.521696252
RB	B109	A	A	A	A	A	A	A	A	NID	0	0.054617676
RB	B110	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.035353535
RB	B111	1196.23	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2	0.043594903
RB	B112	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	0.172222222

Table 4. – First set of samples: Peptide markers of the acid-insoluble pellets, ZooMS identifications, associated scores, and final ZooMS ID and scores (combined with the soluble pellets). (AV: Arma Veirana, RB: Riparo Bombrini, NID: not identifiable).

Site	**Sample**	**Peptide Markers: acid-insoluble pellet**								**ZooMS ID**	**Score**	**Final ZooMS ID**	**Final Score**
		2t85(A)	2t43(B)	2t69(C)	2t69(D)	2t41/42(E)	1t55/56(F)	2t67(G)	2t76				
AV	V21	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V22	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V23	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V24	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V25	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V26	A	A	A	A	A	A	A	A	NID	0	Ungulate	1
AV	V27	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	*Ungulate*	1
AV	V28	A	1427.7	1580.8	2131.1	N/A	2883.4	3059.4	N/A	*Capreolus*	1	*Capreolus*	1
AV	V29	1196.2	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2	*Ungulate*	1
AV	V30	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V31	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	*Ungulate*	1
AV	V32	1196.2	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2	*Capra*	2
AV	V33	A	A	A	A	A	A	A	N/A	NID	0	*NID*	0
AV	V34	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2

AV	V35	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	*Bos/Bison*	2
AV	V36	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	*Ungulate*	1
AV	V37	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervus/Capreolus*	1	*Cervus*	2
AV	V38	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	*Ursus*	2
AV	V39	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V40	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V41	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	*Ursus*	2
AV	V42	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	*Ursus*	2
AV	V43	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V44	A	A	A	A	A	A	A	A	NID	0	*NID*	0
AV	V45	A	A	A	A	A	A	A	A	NID	0	*NID*	0
AV	V46	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	*Capra*	2
AV	V47	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
AV	V48	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	*Ursus*	2
AV	V49	1233.7	1453.7	1566.8	2163.1	N/A	2853.4	2957.4	N/A	*Ursus*	2	*Ursus*	2
AV	V50	A	A	A	A	A	A	A	A	NID	0	*NID*	0
AV	V51	A	A	A	A	A	A	A	A	NID	0	*NID*	0
AV	V52	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	*Bos/Bison*	2
AV	V53	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B71	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B72	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	*Bos/Bison*	2
RB	B73	A	A	A	A	A	A	A	A	NID	0	*NID*	0

RB	B74	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B75	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B76	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B77	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervus/Capreolus*	1	*Cervid*	1
RB	B78	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B79	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B80	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B81	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B82	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B83	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B84	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B85	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B86	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B87	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B88	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B89	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B90	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B91	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B92	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B93	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B94	A	1427.7	A	A	N/A	A	A	N/A	Ungulate	1	*Ungulate*	1
RB	B95	A	A	A	A	A	A	A	A	NID	0	*NID*	0

RB	B96	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B97	A	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervus/Capreolus*	1	*Ungulate*	1
RB	B98	1196.2	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2	*Capra*	2
RB	B99	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	*Bos/Bison*	2
RB	B100	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B101	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2	*Bos/Bison*	2
RB	B102	A	A	A	A	A	A	A	A	NID	0	NID	1
RB	B103	A	A	A	A	A	A	A	A	NID	0	*NID*	0
RB	B104	A	1427.7	1550.8	2131.1	N/A	A	A	N/A	*Cervus/Capreolus*	1	*Cervid*	1
RB	B105	A	1427.7	A	2131.1	N/A	A	A	N/A	Ungulate	1	Ungulate	1
RB	B106	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B107	A	1427.7	A	2131.1	N/A	A	A	N/A	Ungulate	1	*Ungulate*	1
RB	B108	A	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2
RB	B109	A	1427.7	1550.8	2131.1	N/A	2853.4	A	N/A	*Cervus/Capreolus*	1	*Cervid*	1
RB	B110	A	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervus/Capreolus*	1	*Cervus*	2
RB	B111	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra/Rangifer*	1	*Capra*	2
RB	B112	1196.2	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2	*Cervus*	2

Table 5. – Second set of samples: Peptide markers of the soluble pellets, ZooMS identifications, and associated scores. (RB: Riparo Bombrini, NID: not identifiable).

Site	**Sample**	**Peptide Markers: soluble pellet**								**ZooMS ID**	**Score**
		2t85(A)	2t43(B)	2t69(C)	2t69(D)	2t41/42(E)	1t55/56(F)	2t67(G)	2t76		
RB	B173	A	A	A	A	A	A	A	A	*NID*	0
RB	B174	A	A	A	A	A	A	A	A	*NID*	0
RB	B175	A	A	A	A	A	A	A	A	*NID*	0
RB	B176	A	A	A	A	A	A	A	A	*NID*	0
RB	B177	A	1427.7	1580.8	2131.1	N/A	A	A	N/A	*Ungulate*	1
RB	B178	A	A	A	A	A	A	A	A	*NID*	0
RB	B179	A	A	A	A	A	A	A	A	*NID*	0
RB	B181	A	A	A	A	A	A	A	A	*NID*	0
RB	B182	A	A	A	A	A	A	A	A	*NID*	0
RB	B183	A	A	A	A	A	A	A	A	*NID*	0
RB	B184	A	A	A	A	A	A	A	A	*NID*	0
RB	B187	A	A	A	A	A	A	A	A	*NID*	0
RB	B191	A	1427.7	1580.8	2131.1	A	A	A	N/A	*Ungulate*	1
RB	B192	A	A	A	A	A	A	A	A	*NID*	0
RB	B194	A	A	A	A	A	A	A	A	*NID*	0
RB	B195	A	A	A	A	A	A	A	A	*NID*	0
RB	B198	A	A	A	A	A	A	A	A	*NID*	0
RB	B199	A	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B200	A	A	A	A	A	A	A	A	*NID*	0
RB	B201	A	A	A	A	A	A	A	A	*NID*	0
RB	B204	A	A	A	A	A	A	A	A	*NID*	0
RB	B205	A	A	A	A	A	A	A	A	*NID*	0
RB	B207	A	A	A	A	A	A	A	A	*NID*	0

RB	B208	A	A	A	A	A	A	A	A	*NID*	0
RB	B269	A	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B211	A	A	A	A	A	A	A	A	*NID*	0
RB	B212	A	A	A	A	A	A	A	A	*NID*	0
RB	B215	A	A	A	A	A	A	A	A	*NID*	0
RB	B216	A	A	A	A	A	A	A	A	*NID*	0
RB	B217	A	A	A	A	A	A	A	A	*NID*	0
RB	B218	A	A	A	A	A	A	A	A	*NID*	0
RB	B223	A	A	A	A	A	A	A	A	*NID*	0
RB	B225	A	A	A	A	A	A	A	A	*NID*	0
RB	B229	A	A	A	A	A	A	A	A	*NID*	0
RB	B230	A	A	A	A	A	A	A	A	*NID*	0
RB	B231	A	A	A	A	A	A	A	A	*NID*	0
RB	B232	A	A	A	A	A	A	A	A	*NID*	0
RB	B233	A	A	A	A	A	A	A	A	*NID*	0
RB	B234	A	A	A	A	A	A	A	A	*NID*	0
RB	B235	A	A	A	A	A	A	A	A	*NID*	0
RB	B164	A	A	A	A	A	A	A	A	*NID*	0
RB	B165	A	A	A	A	A	A	A	A	*NID*	0
RB	B166	A	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervid*	1
RB	B185	A	A	A	A	A	A	A	A	*NID*	0
RB	B186	A	A	A	A	A	A	A	A	*NID*	0
RB	B224	A	A	A	A	A	A	A	A	*NID*	0
RB	B228	A	A	A	A	A	A	A	A	*NID*	0
RB	B236	A	A	A	A	A	A	A	A	*NID*	0
RB	B239	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervid*	1
RB	B243	A	A	A	A	A	A	A	A	*NID*	0
RB	B244	A	A	A	A	A	A	A	A	*NID*	0
RB	B247	A	A	A	A	A	A	A	A	*NID*	0
RB	B249									*Bird*	2

RB	B255	A	A	A	A	A	A	A	A	*NID*	0
RB	B256	A	A	A	A	A	A	A	A	*NID*	0
RB	B258	A	A	A	A	A	A	A	A	*NID*	0
RB	B260	A	A	A	A	A	A	A	A	*NID*	0
RB	B284	A	A	A	A	A	A	A	A	*NID*	0
RB	B287	A	A	A	A	A	A	A	A	*NID*	0
RB	B289	A	1427.7	1580.8	2131.1	A	A	A	N/A	*Ungulate*	1
RB	B290	A	A	A	A	A	A	A	A	*NID*	0
RB	B304	A	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervid*	1
RB	B312	A	A	A	A	A	A	A	A	*NID*	0
RB	B313	A	A	A	A	A	A	A	A	*NID*	0
RB	B315	1208.6	1427.7	1580.8	2131.1	N/A	2853.4	3033.4	N/A	*Bos/Bison*	2
RB	B317	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B319	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B322	A	A	A	A	A	A	A	A	*NID*	0
RB	B334	A	A	A	A	A	A	A	A	*NID*	0
RB	B330	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B340	A	A	A	A	A	A	A	A	*NID*	0
RB	B342	A	1427.7	1550.8	A	N/A	A	A	N/A	*Ungulate*	1
RB	B352	A	A	A	A	A	A	A	A	*NID*	0
RB	B358	A	A	A	A	A	A	A	A	*NID*	0
RB	B360	A	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervid*	1
RB	B363	A	A	A	A	A	A	A	A	*NID*	0
RB	B364	A	A	A	A	A	A	A	A	*NID*	0
RB	B365	A	A	A	A	A	A	A	A	*NID*	0
RB	B237	A	A	A	A	A	A	A	A	*NID*	0
RB	B238	A	A	A	A	A	A	A	A	*NID*	0
RB	B240B	A	1427.7	1550.8	A	N/A	A	A	N/A	*Ungulate*	1
RB	B241	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2

RB	B242	A	A	A	A	A	A	A	A	*NID*	0
RB	B245	1198.6	1427.7	1550.8	2145.1	N/A	2883.4	2999.4	N/A	*Equus*	2
RB	B246	A	A	A	A	A	A	A	A	NID	0
RB	B248	A	A	A	A	A	A	A	A	NID	0
RB	B250	A	A	A	A	A	A	A	A	NID	0
RB	B251	A	A	A	A	A	A	A	A	NID	0
RB	B252	A	A	A	A	A	A	A	A	NID	0
RB	B253	A	A	A	A	A	A	A	A	NID	0
RB	B254	A	A	A	A	A	A	A	A	NID	0
RB	B257	A	A	A	A	A	A	A	A	NID	0
RB	B259	A	A	A	A	A	A	A	A	NID	0
RB	B261	A	A	A	A	A	A	A	A	NID	0
RB	B264	A	A	A	A	A	A	A	A	NID	0
RB	B281	A	A	A	A	A	A	A	A	NID	0
RB	B282	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	1
RB	B283	A	A	A	A	A	A	A	A	NID	0
RB	B285	A	A	A	A	A	A	A	A	NID	0
RB	B286A	A	1427.7	1580.8	2131.1	N/A	2883.4	A	N/A	Ungulate	1
RB	B288	A	A	A	A	A	A	A	A	NID	0
RB	B296	A	A	A	A	A	A	A	A	NID	0
RB	B299	A	A	A	A	A	A	A	A	NID	0
RB	B306	A	A	A	A	A	A	A	A	NID	0
RB	B307	A	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	Ungulate	1
RB	B309	A	A	A	A	A	A	A	A	NID	0
RB	B310	A	A	A	A	A	A	A	A	NID	0
RB	B314	A	A	A	A	A	A	A	A	NID	0
RB	B320	A	A	A	A	A	A	A	A	NID	0
RB	B321	A	A	A	A	A	A	A	A	NID	0
RB	B336	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervid*	2
RB	B337									*Bird*	2

RB	B341	A	A	A	A	A	A	A	A	NID	0
RB	B343	A	A	A	A	A	A	A	A	NID	0
RB	B344	A	A	A	A	A	A	A	A	NID	0
RB	B345	A	A	A	A	A	A	A	A	NID	0
RB	B346	A	A	A	A	A	A	A	A	NID	0
RB	B347	A	A	A	A	A	A	A	A	NID	0
RB	B348	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B349	A	A	A	A	A	A	A	A	NID	0
RB	B350	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B351	1196.6	1427.7	1580.8	2131.1	N/A	2883.4	3093.4	N/A	*Capra*	2
RB	B353	1226.6	1453.7	1566.8	2131.1	N/A	2853.4	2999.4	A	*Alopex*	2
RB	B354	A	1427.7	1550.8	A	A	A	A	N/A	Ungulate	1
RB	B356	A	1427.7	1550.8	A	A	A	A	N/A	Ungulate	1
RB	B367										2
RB	B359	A	A	A	A	A	A	A	A	NID	0
RB	B362	A	A	A	A	A	A	A	A	NID	0
RB	B366	A	A	A	A	A	A	A	A	NID	0
RB	B369	A	1427.7	1550.8	2131.1	N/A	2883.4	A	N/A	*Cervid*	1
RB	B368	1196.6	1427.7	1550.8	2131.1	N/A	2883.4	3033.4	N/A	*Cervus*	2
RB	B364	A	A	A	A	A	A	A	A	NID	0
RB	B370	A	A	A	A	A	A	A	A	NID	0
RB	B371	A	A	A	A	A	A	A	A	NID	0
RB	B386	A	A	A	A	A	A	A	A	NID	0
RB	B390	A	A	A	A	A	A	A	A	NID	0
RB	B393	A	A	A	A	A	A	A	A	NID	0

Table 6. – Fourth set of samples: Peptide markers of the soluble pellets, ZooMS identifications, and associated scores. (RB: Riparo Bombrini, NID: not identifiable).

Site	**Sample ID**	**Peptide Markers**							**ZooMS ID**	**ID score**
		2t85(A)	2t43(B)	2t69(C)	2t69(D)	2t41/42(E)	1t55/56(F)	2t67(G)		
RB	B113	A	A	A	A	N/A	A	A	NID	0
RB	B114	A	A	A	A	N/A	A	A	NID	0
RB	B115	A	A	A	A	N/A	A	A	NID	0
RB	B116	A	1427,7	A	2131,1	N/A	A	A	*Ungulate*	1
RB	B117	A	1427,7	1550,8	2131,1	N/A	2883,4	A	*Cervus*	2
RB	B118	A	1427,7	1550,8	2131,1	N/A	A	A	*Cervus*	2
RB	B119	A	A	A	A	N/A	A	A	NID	0
RB	B120	1196.2	1427.7	1580.8	2131.1	N/A	2883,4	3093.4	*Capra*	2
RB	B121	A	1427,7	A	2131,1	N/A	A	A	*Ungulate*	1
RB	B122	1196,2	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B123	A	A	A	A	N/A	A	A	NID	0
RB	B124	A	A	A	A	N/A	A	A	NID	0
RB	B125	1196,2	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B126	A	A	A	A	N/A	A	A	NID	0
RB	B127	1198,6	1427,7	1550,8	2145,1	N/A	2883,4	2999,4	*Equus*	2
RB	B128	A	1427,7	1550,8	2131,1	N/A	A	A	Cervid	2

RB	B129	A	A	A	A	N/A	A	A	NID	0
RB	B130	A	A	A	A	N/A	A	A	NID	0
RB	B131	A	A	A	A	N/A	A	A	NID	0
RB	B132	1196,2	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B133	A	A	A	A	N/A	A	A	NID	0
RB	B134	A	1427,7	1580,8	2131,1	N/A	2883,4	A	*Ungulate*	1
RB	B135	A	A	A	A	N/A	A	A	NID	0
RB	B136	1196,6	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B137	1196,6	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B138	A	1427,7	1550,8	2131,1	N/A	2883,4	A	Cervid	1
RB	B139	1196,6	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B140	A	1427,7	1550,8	2131,1	N/A	2883,4	A	Cervid	1
RB	B141	A	A	A	A	N/A	A	A	NID	0
RB	B142	A	1427,7	1580,8	2131,1	N/A	A	A	*Ungulate*	1
RB	B143	A	1427,7	1550,8	2131,1	N/A	A	A	*Ungulate*	1
RB	B144	A	1427,7	1580,8	2131,1	N/A	2883,4	3093,4	*Ungulate*	1
RB	B145	A	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B146	A	1427,7	1580,8	2131,1	N/A	A	A	*Ungulate*	1
RB	B147	1208,6	1427,7	1580,8	2131,1	N/A	2883,4	3033,4	*Bos/Bison*	2
RB	B148	A	1427,7	1580,8	2131,1	N/A	A	A	*Ungulate*	1
RB	B149	A	1427,7	1580,8	2131,1	N/A	A	A	*Ungulate*	1
RB	B150	1196,6	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2

RB	B151	A	1427,7	1550,8	2131,1	N/A	A	A	Cervid	1
RB	B152	A	1427,7	1580,8	2131,1	N/A	2883,4	A	*Ungulate*	1
RB	B153	A	1427,7	1550,8	2131,1	N/A	A	A	Cervid	1
RB	B154	A	1427,7	1550,8	2131,1	N/A	2883,4	3059,4	*Capreolus*	2
RB	B155	A	A	A	A	N/A	A	A	NID	0
RB	B156	1196,6	1427,7	1550,8	2131,1	N/A	2883,4	3033,4	*Cervus*	2
RB	B157	1196,6	1427,7	A	2131,1	N/A	A	A	*Ungulate*	1
RB	B158	A	1427,7	1550,8	2131,1	N/A	A	A	Cervid	1
RB	B159	A	A	A	A	N/A	A	A	NID	0
RB	B160	A	1427,7	1550,8	2131,1	N/A	2883,4	A	Cervid	1
RB	B161	A	1427,7	1550,8	2131,1	N/A	2883,4	A	Cervid	1
RB	B162	A	A	A	A	N/A	A	A	NID	0

Table 7. – Twelve measurement systems tested on FTIR instruments PO1, PO2, and LA1 including the number of samples (N), p values from the Kruskal Wallis tests (p), the selected threshold (Th), the threshold's associated collagen weight percentage content (Wt%), the initial ZooMS identification success rate (SRi), and the ZooMS identification success rate after applying the screening method (SR). The three measurement systems illustrated in the text (N, Q, and R) are highlighted in green, and the results of measurement system N with PO2 is outlined in red to indicate that it is further illustrated with box plots in Fig. 8 as an example.

		PO1						**PO2**						**LA1**					
Meas. Syst.	type	N	p	Th	Wt%	SRi	SR	N	p	Th	Wt%	SRi	SR	N	p	Th	Wt%	SRi	SR
A	height	104	0.0017	0.05	7.81	63%	78%	86	0.00026	0.04	6.43	72%	88%	47	5.8E-05	0.03	5.2	68%	85.7%
B	height	104	0.0017	0.05	7.81	63%	78%	86	0.00026	0.04	6.43	72%	88%	47	5.8E-05	0.03	5.2	68%	85.7%
C	height	104	0.0017	0.05	7.81	63%	78%	86	0.00027	0.04	6.41	72%	88%	47	6.3E-05	0.03	5.2	68%	85.7%
D	height	104	0.0022	0.05	7.90	63%	78%	86	0.00032	0.04	6.54	72%	88%	47	5.6E-05	0.03	5.2	68%	85.7%
E	height	104	0.0019	0.05	7.90	63%	78%	86	0.00035	0.04	6.52	72%	88%	47	5.6E-05	0.03	5.2	68%	85.7%
F	a.height	104	0.003	0.05	7.60	63%	80%	86	0.00015	0.04	6.35	72%	85%	47	3.9E-05	0.03	5.2	68%	85.7%
G	a.height	104	0.0026	0.05	7.56	63%	80%	86	0.00012	0.04	6.18	72%	89%	47	4.0E-05	0.03	5.2	68%	85.7%
H	a.height	104	0.0026	0.05	7.56	63%	80%	86	0.00013	0.04	6.18	72%	89%	47	4.4E-05	0.03	5.2	68%	85.7%
I	a.height	104	0.0032	0.05	7.60	63%	78%	86	0.00013	0.04	6.36	72%	85%	47	3.9E-05	0.03	5.2	68%	85.7%
J	area	104	0.0092	0.04	6.23	63%	78%	85	0.00009	0.03	5.30	72%	88%	47	1.9E-04	0.03	4.7	68%	89.7%
K	area	104	0.0086	0.04	6.18	63%	80%	85	0.00010	0.03	5.17	72%	91%	47	2.0E-04	0.03	4.7	68%	86.7%
L	area	104	0.0084	0.04	6.18	63%	82%	85	0.00009	0.03	5.15	72%	91%	47	2.0E-04	0.03	4.6	68%	86.7%
M	area	104	0.0098	0.04	6.25	63%	78%	85	0.00009	0.03	5.32	72%	88%	47	1.8E-04	0.03	4.7	68%	89.7%
N	height	104	0.002	0.05	7.83	63%	78%	86	0.00016	0.04	6.42	72%	88%	47	6.3E-05	0.03	5.1	68%	86.7%
O	height	104	0.002	0.06	7.98	63%	86%	86	0.00021	0.04	6.51	72%	88%	47	6.3E-05	0.03	5.1	68%	86.7%
P	a.height	104	0.0034	0.05	7.59	63%	80%	86	0.00020	0.04	6.41	72%	88%	47	5.2E-05	0.03	5.1	68%	86.7%
Q	a.height	104	0.0026	0.05	7.56	63%	80%	87	0.00015	0.04	6.32	72%	89%	47	5.9E-05	0.03	5.1	68%	86.7%
R	area	104	0.0083	0.04	6.33	63%	76%	85	0.00011	0.03	5.32	72%	88%	47	2.2E-04	0.03	4.7	68%	89.7%
S	area	104	0.0083	0.04	6.33	63%	76%	85	0.00011	0.03	5.32	72%	88%	47	2.2E-04	0.03	4.7	68%	89.7%

Table 8. – Twelve measurement systems tested on FTIR instruments LA2, and LA3, including the number of samples (N), p values from the Kruskal Wallis tests (p), the selected threshold (Th), the threshold's associated collagen weight percentage content (Wt%), the initial ZooMS identification success rate (SRi), and the ZooMS identification success rate after applying the screening method (SR). The three measurement systems illustrated in the text (N, Q, and R) are highlighted in green, and the results of measurement system N with PO2 is outlined in red to indicate that it is further illustrated with box plots in Fig. 8 as an example

		LA2						**LA3**					
Meas. Syst.	type	N	p	Th	Wt%	SRi	SR	N	p	Th	Wt%	SRi	SR
A	height	125	4.1E-05	0.03	5.20	29%	43.5%	65	2.1E-01	0.05	7.34	75%	82.6%
B	height	125	4.1E-05	0.03	5.20	29%	43.5%	65	2.1E-01	0.05	7.34	0.75	82.6%
C	height	138	1.3E-06	0.03	5.12	26%	45.1%	65	2.1E-01	0.05	7.30	0.75	82.6%
D	height	125	3.9E-05	0.03	5.23	29%	43.5%	65	2.3E-01	0.05	7.45	0.75	82.6%
E	height	125	4.4E-05	0.03	5.19	29%	43.5%	65	2.2E-01	0.05	7.41	0.75	82.6%
F	a.height	137	2.6E-06	0.03	5.15	26%	45.8%	64	7.9E-02	0.05	6.97	0.75	94.4%
G	a.height	124	3.9E-05	0.03	5.18	29%	45.5%	64	8.0E-02	0.05	6.87	0.75	94.4%
H	a.height	124	4.4E-05	0.03	5.15	29%	46.5%	64	7.9E-02	0.05	6.86	0.75	94.1%
I	a.height	137	2.7E-06	0.03	5.13	26%	45.8%	65	5.3E-02	0.05	6.93	0.74	94.4%
J	area	123	2.8E-05	0.02	4.18	29%	40.7%	64	3.8E-02	0.03	5.57	0.73	79.5%
K	area	123	2.2E-05	0.02	4.12	29%	40.7%	64	3.1E-02	0.03	5.47	0.73	85.3%
L	area	123	2.5E-05	0.02	4.12	29%	43.6%	64	3.1E-02	0.03	5.45	0.73	84.8%
M	area	138	4.8E-07	0.02	4.24	26%	39.7%	64	3.9E-02	0.03	5.61	0.73	79.5%
N	height	131	2.9E-06	0.03	5.04	27%	48.8%	65	2.1E-01	0.05	7.35	0.75	82.6%
O	height	131	3.0E-06	0.03	5.09	27%	48.8%	65	2.3E-01	0.05	7.44	0.75	79.2%
P	a.height	130	5.8E-06	0.03	4.97	28%	50.0%	64	8.2E-02	0.05	6.98	0.75	89.5%
Q	a.height	130	4.6E-06	0.03	4.93	28%	52.6%	64	7.7E-02	0.05	6.87	0.75	94.4%
R	area	123	3.4E-05	0.02	4.19	29%	40.0%	63	6.7E-02	0.03	5.65	0.75	79.5%
S	area	123	3.4E-05	0.02	4.19	29%	40.0%	63	6.7E-02	0.03	5.65	0.75	79.5%

Appendix 2 – Supplemental information of article 2 (Pothier Bouchard et al. 2020)

Table 1. – Peptid markers used to identify the different animal taxa in this study from Buckley et al. (2009, 2010, 2017; 2011), and Brown et al. (2016).

Taxa	2t85(A)	2t43(B)	2t45(C)	2t69(D)	1t66/67	2t41/42(E)	1t55/56(F)	2t67(G)	2t76
Herbivores									
Bos/Bison	1208.6	1427.7	1580.8	2131.1	N/A	N/A	2853.4	3033.4	
Capra	1196.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3093.4	
Cervus/Dama	1196.6	1427.7	1550.8	2131.1	N/A	N/A	2883.4	3033.4	
Capreolus	1196.6	1427.7	1550.8	2131.1	N/A	N/A	2883.4	3059.4	
Coelodonta/Diceros	1198.6	1453.7	1550.8	2145.1	N/A	N/A	2869.4	2999.4	
Equus	1198.6	1427.7	1550.8	2145.1	N/A	N/A	2883.4	2999.4	
Mammuthus	N/A	1453.7	1579.8	2115.1	N/A	N/A	2853.4	3015.4	
Ovibos	1208.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3033.4	
Rangifer	1166.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3093.4	
Rupicapra/Ovis	1196.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3033.4	
Sus	1196.6	1453.7	1550.8	2131.1	N/A	N/A	2883.3	3033.4	
Carnivores									
Alopex	1226.6	1453.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1548.8
Canis	1226.6	1453.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1576.8
Crocuta	1207.6	1453.7	1566.8	2147.1	2246.1	2808.3	2853.4	2999.4	
Gulo/Mustela/Martes	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2999.4	
Homo	1235.6	1477.8	1580.8	2115.1	N/A	2832.4	2885.4	2957.4+ 2959.4	
Lutra	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2973.4	
Lynx	1207.6	1453.7	1566.8	2163.1	N/A	N/A	2853.4	2999.4	
Meles	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2957.4	
Panthera	1207.6	1453.7	1566.8	2147.1	2216.1	2820.3	2853.4	2999.4	
Ursus	1233.7	1453.7	1566.8	2163.1	N/A	N/A	2853.4	2957.4	
Vulpes	1226.6	1437.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1548.8
Lagomorphs									
Oryctolagus	1235.6	1453.7	1566.8	2129.1	N/A	2836.3	2883.4	2957.4	
Lepus	1235.6	1453.7	1566.8	2129.1	N/A	2808.3	2883.4	2957.4	
Rodents									
Castor	1193.6	1427.7	1576.8	2129.1	N/A	N/A	2883.4	2999.4	

Table 2. – Skeletal representation

Taxa	**Square**	**Level**	**Skeletal portion**					
			Head	Axial post-cranial	Indeterminate Limbs	Upper limbs	Lower limbs	Feet
Cervus	E1	A1_A2	1 tooth, 2 cranium frag.	2 ribs	9	2 humeri, 1 scapula	1 radius-ulna, 1 metacarpal	1 tarsal or carpal
	D1	A1_A2	1 cranium frag.		4			
	AA1	A1			1			
	DD1	A1		1 rib	2			
	DD1	A2			2			
	FF3	A2		1 rib				
Total *Cervus*			4	4	18	3	2	1
Capra	E1	A1_A2		1 rib	6		1 metacarpal	
	D1	A1_A2			2		1 radius-ulna	
	DD1	A1			1			
	DD1	A2	1 tooth					
	EE1	A2	1 tooth					
	FF3	A2			1			
Total *Capra*			2	1	10		2	
Bos_Bison	E1	A1_A2	1 cranium frag.	1 rib	9			
	D1	A1_A2			4			
	DD1	A1			5			
	DD1	A2	1 tooth		1			
	EE1	A2			1			
	EE1	A1	1 tooth					
Total *Bos_Bison*			3	1	20			
Equus	FF3	A1					1 hamatum	
	FF3	A2					1 lunate	
	E1	A1_A2	1 tooth		1	1 femur		
	DD1	A2	1 tooth			2 tibiae		
Total *Equus*			2		1	3	2	

Sus	E1	A1_A2	1 tooth					
	CC1	A2	2 teeth					1 phalanx
	DD1	A1	1 tooth					
	FF3	A2						1 phalanx
Total *Sus*			5					2
Cervid	E1	A1_A2	1 antler		3			1 phalanx
	D1	A1_A2	1 cranium frag., 1 tooth					
	CC1	A1	1 tooth					
	DD1	A2	1 antler, 2 teeth					
	DD1	A1		1 rib				
	EE3	A2		1 rib	1	1 femur		
	FF3	A2			2			
Total Cervid			7	2	6	1		1

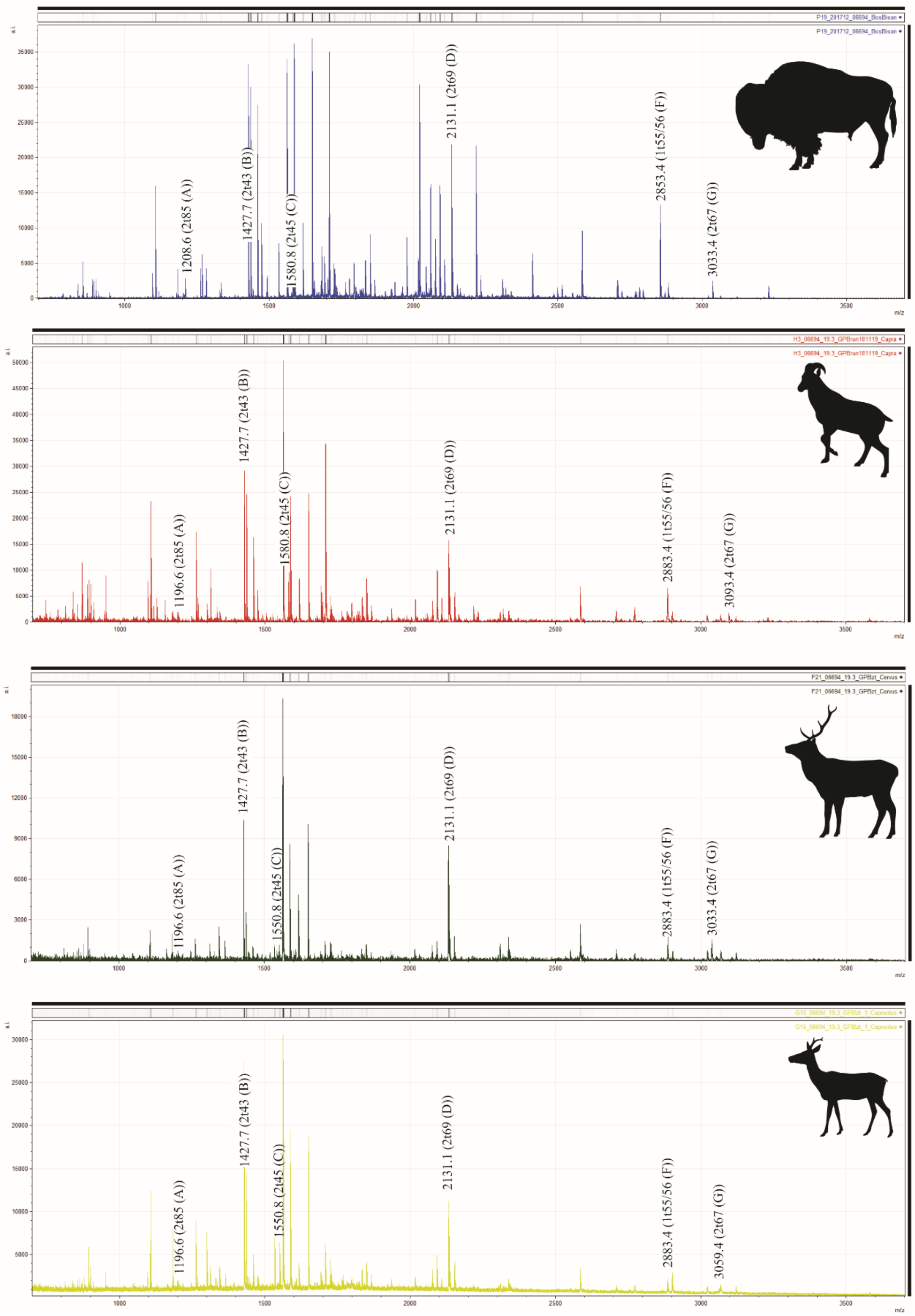

Figure 1. – Examples ZooMS spectra from Bombrini corresponding starting from above to: *Bos/Bison*, *Capra*, *Cervus*, and *Capreolus*. Animal silhouette images from http://phylopic.org/.

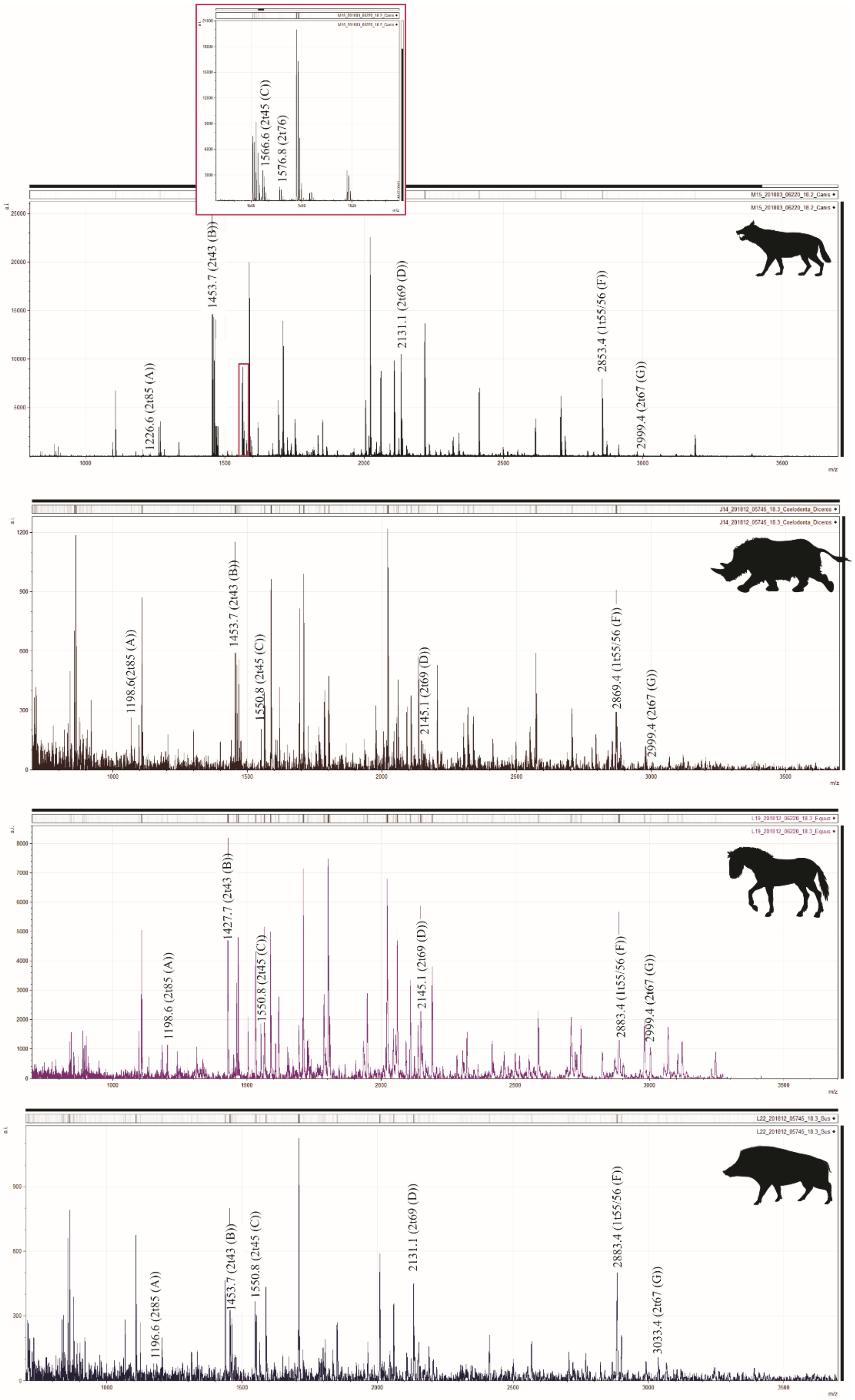

Figure 2. – Examples ZooMS spectra from Bombrini corresponding starting from above to: *Canis*, *Coelodonta/Diceros*, *Equus*, and *Sus*. Animal silhouette images from http://phylopic.org/.

Appendix 3 – Supplemental information of the article 3

Table 1. – Peptid markers used in ZooMS identifications. Buckley et al. (2009, 2010, 2011, 2017), and Brown et al. (2016)

Taxa	2t85(A)	2t43(B)	2t45(C)	2t69(D)	1t66/67	2t41/42(E)	1t55/56(F)	2t67(G)	2t76
Herbivores									
Bos/Bison	1208.6	1427.7	1580.8	2131.1	N/A	N/A	2853.4	3033.4	
Capra	1196.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3093.4	
Cervus/Dama	1196.6	1427.7	1550.8	2131.1	N/A	N/A	2883.4	3033.4	
Capreolus	1196.6	1427.7	1550.8	2131.1	N/A	N/A	2883.4	3059.4	
Coelodonta/Diceros	1198.6	1453.7	1550.8	2145.1	N/A	N/A	2869.4	2999.4	
Equus	1198.6	1427.7	1550.8	2145.1	N/A	N/A	2883.4	2999.4	
Mammuthus	N/A	1453.7	1579.8	2115.1	N/A	N/A	2853.4	3015.4	
Ovibos	1208.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3033.4	
Rangifer	1166.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3093.4	
Rupicapra/Ovis	1196.6	1427.7	1580.8	2131.1	N/A	N/A	2883.4	3033.4	
Sus	1196.6	1453.7	1550.8	2131.1	N/A	N/A	2883.3	3033.4	
Carnivores									
Alopex	1226.6	1453.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1548.8
Canis	1226.6	1453.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1576.8
Crocuta	1207.6	1453.7	1566.8	2147.1	2246.1	2808.3	2853.4	2999.4	
Gulo/Mustela/Martes	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2999.4	
Homo	1235.6	1477.8	1580.8	2115.1	N/A	2832.4	2885.4	2957.4+ 2959.4	
Lutra	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2973.4	
Lynx	1207.6	1453.7	1566.8	2163.1	N/A	N/A	2853.4	2999.4	
Meles	1235.6	1453.7	1566.8	2147.1	N/A	N/A	2853.4	2957.4	
Panthera	1207.6	1453.7	1566.8	2147.1	2216.1	2820.3	2853.4	2999.4	
Ursus	1233.7	1453.7	1566.8	2163.1	N/A	N/A	2853.4	2957.4	
Vulpes	1226.6	1437.7	1566.8	2131.1	N/A	N/A	2853.4	2999.4	1548.8
Lagomorphs									
Oryctolagus	1235.6	1453.7	1566.8	2129.1	N/A	2836.3	2883.4	2957.4	
Lepus	1235.6	1453.7	1566.8	2129.1	N/A	2808.3	2883.4	2957.4	
Rodents									
Castor	1193.6	1427.7	1576.8	2129.1	N/A	N/A	2883.4	2999.4	