



Assessing Neanderthal occupation duration: Faunal evidence from sub-unit IIIb of Teixoneres Cave (Barcelona, Spain)

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ABSTRACT

Determining the duration of occupations at Middle Palaeolithic archaeological sites is essential to enhancing our understanding of Neanderthal behaviour and subsistence strategies. Identifying occupation length in these contexts presents significant complexity and is often ambiguous due to the palimpsest nature of the archaeological sites. This study examines faunal specimens from sub-Unit IIIb of Teixoneres Cave, focusing on both external and internal site areas, to estimate the duration of human occupations. Using zooarchaeological and taphonomic parameters, we evaluate the effectiveness of these methods for inferring occupation length. Our analysis shows that faunal remains—such as evidence of hunting, butchering, and carcass transport—are essential for reconstructing Neanderthal subsistence strategies and for understanding whether the site was used during one short-term occupation or across several distinct episodes over time. While certain results diverge from the features currently used in literature to define occupation duration, the spatial distribution of lithic artefacts, from sub-Unit IIIb at Teixoneres Cave support the hypothesis of short, repeated human occupations. This analysis focuses on applying and critically examining some of those theoretical assumptions, particularly those related to taphonomic and archaeozoological criteria. In this context, Teixoneres Cave serves as the dataset through which we test whether a real archaeological case supports the theoretical framework proposed in Lubrano et al. (2025). These findings contribute to ongoing discussions on the complexities of interpreting archaeological palimpsests and the methodological challenges involved in estimating the duration of Neanderthal occupations. Furthermore, the data place sub-Unit IIIb of Teixoneres within the broader framework of Middle Palaeolithic cave sites characterized by short-term human occupations in settings frequently utilized by large carnivores.

1. Introduction

Understanding the duration of occupations and the function of Middle Palaeolithic archaeological sites is one of the fundamental objectives in Palaeolithic archaeology, as it allows for a deeper knowledge of Neanderthal behaviour. The duration of human occupations is closely linked to the function of the site, although the available data are often unclear or incomplete (Bicho et al., 2006; Churchill, 2014; Dusseldorp, 2009; Schiffer, 1983; Vaquero, 2008). The function and duration of occupations are both influenced by the mobility patterns of hunter-

gatherer groups, who utilized a site for varying periods depending on the characteristics of the territory and seasonal factors (Kelly, 1992; Binford, 1980). Based on their function, sites can be categorized into residential sites, kill sites, butchering sites, and quarries for the collection of raw materials (Binford, 1980). The residential site was the place where activities were organized, from which expeditions for resource collection were launched, and to which resources were brought (Kelly, 1992). Other site types were more limited to specific activities such as prey on animals, butchering or collecting raw materials (Boismier et al., 2012; Farizy et al., 1994; Baena et al., 2008; Turq, 1988).

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In general, the function of a site can be inferred, though not always easily, from the remains uncovered. For example, butchering sites typically contain anatomical parts with less meat, which were not transported to the base camp. In contrast, residential sites contain remains associated with processing the more valuable parts and knapping activities (Binford, 1981; Bunn and Ezzo, 1993; Domínguez-Rodrigo and Pickering, 2003; Kelly, 1992; Isaac, 1983; Monahan, 1998; O'Connell et al., 1992).

Determining the duration of an occupation is more complex, as a residential site may have been inhabited for only a short period. Several factors make it difficult to estimate the duration of human occupations based on archaeological remains. Cave sites, for instance, often reflect both human activity and the presence of carnivores. Bears, hyenas, and other small carnivores used caves as shelters for hibernation or breeding (Torres et al., 2007), complicating the interpretation of the duration of human occupations. Moreover, slow sedimentation rates and post-depositional processes make it difficult to recover occupation floors, especially in caves and rock shelters (e.g., Goldberg and McPhail, 2006; Farrand, 2001). This challenge is compounded by the overlap of successive occupational events, referred to as the “palimpsest effect” (Bailey, 2007; Lucas, 2005; Vaquero, 2008; Mallol and Hernández, 2016; Bailey and Galanidou, 2009.). The term palimpsest is widely used in archaeology and other disciplines (Canals et al., 2003; Enloe, 2006) and refers to the layering of different activities, where the material traces are partially destroyed or altered. This process can erase earlier information, leaving only the most recent traces or resulting in the partial preservation and transformation of subsequent activities (Canals et al., 2003, Bailey and Galanidou, 2009). Additionally, the definition of short or long duration is difficult to pinpoint. However, ethnographic studies of modern hunter-gatherer populations can offer insight. In ethnoarchaeology, long-term campsites are occupied for several weeks or months, while short-term residential sites are used for only a few days or even hours (Carbonell, 2012).

One approach to addressing the interpretive complexity is the “dissection of palimpsests” (Mallol and Hernández, 2016; Vaquero 2008, 2012; Vermeersch, 2001), which employs a range of methods and techniques, including archeostratigraphy, micromorphology, zooarchaeology, taphonomy, and refitting of lithic and bone remains. These disciplines provide methodological tools for distinguishing between short and long-term occupations (Carbonell, 2002, 2012; Blasco et al., 2013b; Vaquero and Pastó 2001, Vaquero et al., 2007, 2019; Vaquero, 2012 Bargalló et al., 2020; Leierer et al., 2019; Cascalheira and Picin, 2020; Moclán et al., 2021, 2023; Mallol et al., 2013; Mellars, 1996; Marín et al., 2020; Moncel and Rivals, 2011). It is crucial to evaluate these data holistically, as relying on a single discipline does not provide a comprehensive interpretation. As we argue in Lubrano et al. (2025)—a state-of-the-art review outlining the main theoretical issues and unresolved questions surrounding these features—not all of the characteristics currently used in the literature to assess the duration of Neanderthal occupations are equally effective. Moreover, such features should always be considered collectively, concerning the broader set of variables that may influence the interpretation of occupation duration. Zooarchaeological and taphonomic analyses, such as examining taxonomic diversity, hunting spectrum, anthropogenic modifications, carcass transport, butchering practices, and carnivore activity, have been employed to estimate the duration of occupational events (Bargalló et al., 2020; Carbonell 2002, 2012; Vaquero and Pastó, 2001; Vaquero et al., 2007, 2019; Vaquero, 2012; Leierer et al., 2019; Cascalheira and Picin, 2020; Moclán et al., 2021, 2023; Mellars, 1996; Marín et al., 2020; Moncel and Rivals, 2011). Understanding how faunal resources were acquired and utilized—from hunting and processing prey to transporting and consuming carcasses at the site—helps clarify Neanderthal subsistence strategies and the characteristics of their occupations. Zooarchaeology and taphonomy are especially valuable in revealing whether the contexts or activities at a site were synchronous or diachronic.

This study focuses on the analysis of faunal remains from the outer and inner areas of sub-Unit IIIb of Teixoneres Cave, with the aim of evaluating the duration of occupations. The data presented here are contextualized within a broader framework that seeks to assess the applicability of zooarchaeological and taphonomic features in determining occupation length. Indeed, among the criteria currently considered for identifying occupation duration, several faunal characteristics are commonly used. These elements provide valuable insight into subsistence strategies (Díez and Rosell, 1998), behavioural patterns, and site-use dynamics. Specifically, taxonomic diversity, hunting spectrum, anthropogenic modifications, carcass transport, butchery practices, and carnivore modifications are considered highly significant factors (Bargalló et al., 2020; Carbonell, 2002, 2012; Vaquero and Pastó, 2001; Vaquero et al., 2007, 2019; Vaquero, 2012; Leierer et al., 2019; Cascalheira and Picin, 2020; Moclán et al., 2021, 2023; Mallol et al., 2013; Mellars, 1996; Marín et al., 2020; Moncel and Rivals, 2011). However, the analysis of faunal remains from sub-Unit IIIb reveals apparent inconsistencies when compared to these interpretive models. Taxonomic diversity, the hunting spectrum, carcass transport strategies, and carnivore modifications appear to challenge the validity of current faunal indicators used to infer the duration of human occupations. As argued in Lubrano et al., (2025), some of these zooarchaeological and taphonomic features commonly used for this purpose may need to be reconsidered, as their reliability can be significantly influenced by numerous contextual and taphonomic factors that must be carefully evaluated in each case. The analysis of the faunal assemblage from Unit IIIb of Teixoneres Cave takes advantage of some site unique features, making it particularly suitable for such studies. The horizontal excavation method over a wide area provides a comprehensive overview of the site, also allowing the observation of changes in the distribution of remains and the activities they represent through spatial analysis. Additionally, the multidisciplinary approach employed in the research project carried out at Teixoneres Cave is essential for an integrated, in-depth analysis of occupation duration. Finally, the availability of previous studies serves as a valuable starting point, offering an occupational context where human groups and carnivores alternated in their use of the cave.

2. Teixoneres Cave

Teixoneres Cave is located in Catalonia, near the town of Moià in the province of Barcelona (Spain), at an altitude of approximately 760 m above sea level (Fig. 1). Geomorphologically, the region belongs to the highlands situated between two major rivers: the Llobregat to the south and the Ter to the north. This discovery of this site has led to numerous archaeological investigations, with excavations conducted in the early 1950 s and 1970 s, during which several archaeological test pits were explored (Serrat and Albert, 1973; Rosell et al., 2010, 2017). In 2004, the Institut Català de Paleocologia Humana i Evolució Social (IPHES) resumed excavation work at the site.

Teixoneres Cave formed as part of the drainage system of the Torrent del Mal water stream, resulting from the development of a karst system within Paleogene limestone. The cave has a U-shaped structure and spans approximately 30 m in length. Teixoneres Cave is divided into three chambers: X, Y, and Z (Serrat and Albert, 1973). Chambers X and Z have entrances to the exterior, while Chamber Y connects the two. Chamber X, the largest of the galleries, measures about 30 m long and 5 to 6 m wide, situated in the western section and serving as the main entrance to the cave (Fig. 1).

Chamber X has a total surface area of approximately 93 m², which can be subdivided into an outer area (31 m²) and an inner area (62 m², including the unexcavated areas and archaeological test pits from the 1950 s and 1970 s). The chamber contains a 6-m-thick sediment package, for which different stratigraphic units have been described (Serrat and Albert, 1973; Serra-Rafols et al., 1957; Rosell et al., 2010, 2017). The latest geological studies (Zilio et al., 2021) along with extensive

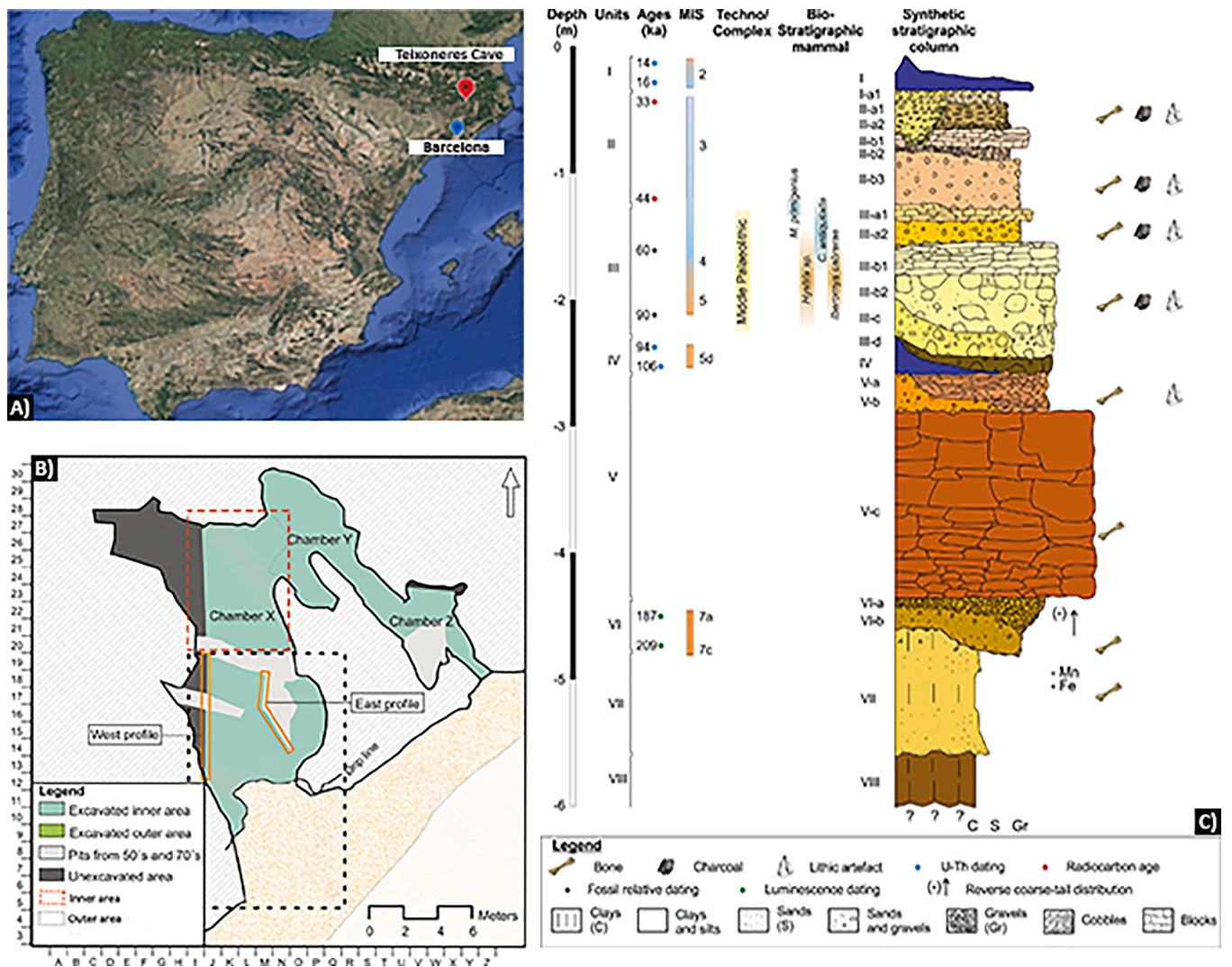


Fig. 1. A) Location of Teixoneres Cave; B) The ground plan and grid system of the excavation; C) Stratigraphic column of Chamber X in Teixoneres Cave. The images B) and C) were published in Zilio et al., 2021.

excavations considering stratigraphic, paleontological and archaeological data, have defined eight lithostratigraphic units: Unit I; Unit II; Unit III (IIIa, IIIb, IIIc, IIId); Unit IV; Unit V; Unit VI; Unit VII and Unit VIII (Zilio et al., 2021) (Fig. 1). Unit VI has been dated to 198 ± 11 thousand years ago (ka) using luminescence (pIR-IRSL) on optically-bleached potassium feldspar grains (Ochando et al., 2020). U-Th dating of two calcite flowstones, one at the top (Unit I), and another in the middle (Unit IV) of the sequence, places Unit IV at 100.3 ± 6.1 ka, corresponding to MIS 5c, while Unit I is likely within MIS 2, around 14 to 16 ka (Ochando et al., 2020; Tissoux et al., 2006).

The presence of *Hystrix* sp. and *Iberomys cabreræ* in Unit IIIb suggests a biochronological age of 90 to 60 ka BP (López-García et al., 2012). Radiocarbon dating of animal bones, some of which modified by humans, indicates human presence in Unit III from over 51,000 to 44,210 cal BP (Talamo et al., 2016). This aligns with MIS 3, a period marked by rapid climate fluctuations (Barron and Pollard, 2002; Van Andel, 2002). Palaeoecological data suggest that Unit III began during a cold and humid phase, becoming warmer and more temperate before transitioning to cold and arid conditions at its top (Álvarez-Lao et al., 2017; López-García et al., 2012; Rosell et al., 2017).

3. Material and methods

A total of 14,654 bone remains were analysed from stratigraphic sub-

Unit IIIb, of which 14,092 come from the outer area near the entrance of the cavity. Most of the analysed specimens were found in the outer area of Chamber X (square lines 5–19) and belong to sub-Unit IIIb (Zilio et al., 2021), while a smaller sample comes from the more interior squares (lines 20–30) stratigraphically identified as Unit III (Fig. 1B). The sedimentary structure of the inner area underwent different formative processes compared to the outer area, making it impossible to distinguish between sub-Units IIIa and IIIb in the inner part of the cave (Zilio et al., 2021). For the reasons mentioned above, the bone remains from the two areas were analysed separately. All remains were collected during the excavation seasons from 2003 to 2015. Regarding the remains of Leporidae, for the current work, only those elements registered with a specific location point and introduced in the database with an individual unique number were considered for the analysis and included in the NISP, excluding those recovered during the sorting process. More detailed data and in-depth information about this taxonomic group – including remains recovered during the sieving process – is available in the analysis conducted by Rufà et al. (2014), which thoroughly examines this species and the reasons for its accumulation. The same applies to the study of birds, whose detailed analysis is presented in Rufà et al. (2016). Further information about this taxonomic group is available in the analysis conducted by Rufà et al. (2014), which thoroughly examines this species and the reasons for its accumulation. The same applies to the study of birds, whose detailed analysis is presented in Rufà et al.

(2016).

Excavations at Teixonerres Cave are conducted using a 1 m² grid. The positions of all faunal remains longer than 2 cm (along their longest axis) are mapped, as well as smaller, identifiable remains that may be significant (impact flakes, tooth marks, etc.). The archaeozoological and taphonomic analysis of the entire sample was carried out. For each bone, the anatomical element was identified, although it was not always possible due to fragmentation. For this reason, body size was also considered to be able to classify those non-identified bones. Body size was determined following classic descriptions established by weight categories (e.g., Bunn, 1982): very large size (VLS) > 800 kg, large (LS) 200–800 kg, medium size (MS) 50–200 kg, small size (SS) 10–50 kg, and very small size (VSS) < 10 kg.

Taxonomic identifications were made by comparing remains with a reference anatomical collection at the Institut Català de Paleocologia Humana i Evolució Social (IPHES) and using comparative manuals (e.g., Barone, 1976; Hillson, 1992; Pales and Lambert, 1971; Schmid, 1972).

Age at death – categorised as immature, adult or senile – was determined through tooth eruption and wear, bone tissue characteristics, and the degree of bone fusion (Fernandez, 2009; Klein and Cruz-Urbe, 1984; Steele, 2002, 2003). Specifically, only the analysis of the teeth allowed for precise identification of age at death (Uzunidis et al., 2024), including more specific categories such as infant and juvenile. In contrast, epiphyseal fusion, bone texture alone only provided a broad categorisation as immature or mature individuals. Bone fracture analysis was conducted on remains larger than 2 cm, differentiating between fresh and dry fractures (Bunn, 1983; Villa and Mahieu, 1991). The study also recorded the presence of bone flakes (Brain, 1981; Capaldo and Blumenschine, 1994; Coil et al., 2020), adhering flakes (Vettese et al., 2020; Blasco et al., 2020), and signs of peeling (Arilla et al., 2014; Pickering et al., 2013; White, 1992), all indicative of fresh fractures.

The analysis of bone surface modifications (BSM) involved the use of Olympus SZ1144TR binocular microscope (magnification from 15x to 40x). All modifications occurring during the biostratigraphic phase (after death but prior to burial) and the fossil-diagenetic phase (after burial) were identified (Fernández-López and Fernández-Jalvo, 2002). Specifically, all traces of anthropogenic origin such as cut marks (incisions, scraping, sawed and chop marks) (Binford, 1981; Potts and Shipman, 1981; Shipman and Rose, 1983; Shipman et al., 1984a; Fernández-Jalvo and Andrews, 2016), percussion marks (flake, parasite flake – a term used to refer to bone flakes produced by percussion that, instead of detaching completely, remain partially attached to the bone, cortical and medullary flake, cortical scare, impact flake, percussion notch, retoucher) (Binford, 1981; Blumenschine, 1995; Blumenschine and Selvaggio, 1988; Bonnicksen, 1979; Pickering and Egeland, 2006; Bromage and Boyde, 1984; Domínguez-Rodrigo et al., 2009; Shipman, 1981; Fernández-Jalvo and Andrews, 2016), those produced by carnivores (crenulated edges, scores, pits, pitting, punctures, digestion, peeling, crushing, cylinder diaphysis, furrowing, scooping marks) (Blumenschine, 1995; Bunn, 1981; Selvaggio, 1994; Shipman, 1981; Brain, 1981; Blasco et al., 2020; Domínguez-Rodrigo and Piqueras, 2003), and those of other natural origin (manganese, weathering, trampling, root etching, concretion, abrasion, rounding, polishing) and manganese (Andrews and Cook, 1985; Behrensmeyer et al., 1986; Blasco et al., 2008; Courtenay et al., 2020; Domínguez-Rodrigo et al., 2009; Domínguez-Rodrigo and Barba, 2006; Domínguez-Rodrigo et al., 2009; Backwell et al., 2012; Fejfar and Kaiser, 2005; Jans et al., 2004; Pesquero et al., 2010; Coard, 1999; Courty et al., 1989; Behrensmeyer, 1978, 1990; Cáceres, 2002; Pickering et al., 2013; Quintana, 2007; Shipman 1981; Shipman and Rose, 1983; Lyman, 1994; Fernández-Jalvo and Andrews, 2016) have been analysed and reported in this study.

Additionally, thermo-alteration was recorded by documenting the degree of burning observed on the bone surfaces. Different colouration degrees were established to categorise them (Shipman et al., 1984b; Stiner et al., 1995; Costamagno et al., 2006, 2009; Cáceres, 2002; Blasco et al., 2013a): 0) unburnt; 1) small brown or black areas; 2) brown

colouration on bones; 3) black (charred); 4) grey (calcined); 5) white (calcined). Double coloration on the same surface suggests differential exposure to heat. This type of alteration has been interpreted by several authors (e.g., Gifford-Gonzalez, 1989; Rosell et al., 2012; Gabucio et al., 2014; Blasco et al., 2014, 2016) as indicative of possible roasting of meat over embers prior to defleshing. The positioning of the prey—or already skinned portions of it—on the fire for roasting may result in uneven thermal alteration of the bones, depending on the amount of flesh covering the surface at the time of exposure. Defleshed areas of bone tend to be more directly exposed to heat and consequently show more advanced degrees of burning. As for calcined remains, according to Mentzer (2009), a bone becomes fully calcined only when directly exposed to flames. This can occur in various contexts: for example, when bones are thrown into the hearth for cleaning purposes (Shipman, 1981) when they are used as fuel (Théry-Parisot, 2002; Costamagno et al., 2009; Morin, 2010), or when hearts are built on top of unburied or semi-buried bones (Walters, 1988; Bennett, 1999; Gallo et al., 2025). It is important to note that these scenarios are not mutually exclusive; it is likely that multiple processes overlapped, leading to complex bone modifications and even the destruction of archaeological traces related to primary hominin activities (Stiner et al., 1995). In analysing burnt remains, we must also consider unintentional actions, which might be also reflected in the faunal record by the presence of double colorations, with similar or varying degrees of burning between the cortical and medullary surfaces. Some specimens also show non-homogeneous grade 2 coloration, consistent with Bennett's (1999) descriptions of bones burned post-burial. Lastly, we must also include what has been referred to in the literature as a “burning sandwich pattern” (Cerdá et al., 2005; Blasco et al., 2016). This pattern, characterized by the presence of intracortical tissue with a different coloration than that observed on the outer side, is also detected in our assemblage. This differentiated colour distribution is the result of uneven burning, in which heat and oxygen acted more effectively on the outer portions of the bone compared to the inner ones, which remained partially isolated. In cross-section, the bone displays a central intracortical area with a different coloration—generally lighter and indicative of a lower degree of burning—enclosed between two outer cortical surfaces showing more intense combustion. This appearance visually resembles a sandwich, hence the term “burning sandwich pattern” used to describe this specific phenomenon.

Following the archaeozoological and taphonomic analysis, the complete sample was quantified. The quantification first involved the measure of abundance for each taxon and body size through the number of identified specimens (NISP) (Lyman, 1994), the minimum number of elements (MNE) (Pickering, 2002; Saladié et al., 2011; Yravedra and Domínguez-Rodrigo, 2009), the minimum number of individuals (MNI) (Lyman, 1994). For this study, MNE and MNI values were calculated exclusively for specimens identified at the species level, with the exception of *Oryctolagus cuniculus* and birds, for which we refer to the detailed taphonomic and quantitative analyses by Rufà et al. (2014, 2016). No MNE or MNI values were assigned to specimens identified only at the genus level. NISP was determined by counting the total number of specimens attributable to specific parts of the skeleton, such as cranial fragments, isolated teeth, or limb bone shafts. This differs from NR, which includes the total number of remains, regardless of whether they are identified (Grayson, 1984). The term NISPs is used when the calculation is based on body size. The percentages of the different surface modifications were also counted to assess whether access to carcasses of different sizes was primary or secondary. The percentage of Relative Abundance (RA%) (Behrensmeyer, 1978 Lyman, 1994, Binford, 1981, 1984) was calculated for the outer and inner area. Considering the characteristics of the site and the peculiar nature of the two distinct areas, we believe that the use of different quantification methods is justified and appropriate. The use of %MAU for the inner area reflects the distinct formation processes and occupational patterns associated with each space. The outer area of Teixonerres Cave is characterized by a

greater presence of anthropogenic activity, including butchering and tool use, which justifies the use of Relative Abundance (RA%) to assess the overall distribution and frequency of anatomical elements within a more diverse and intensive human occupational context. In contrast, the inner area is predominantly associated with carnivore activity and shows a lower quantity and diversity of faunal remains. In this context, Minimum Anatomical Units (%MAU) offers a more reliable means of assessing skeletal representation, as it focuses on the relative frequency of individual skeletal parts without requiring a Minimum Number of Individuals (MNI)—a parameter that is less meaningful in low-density or highly fragmented assemblages. Moreover, %MAU is particularly appropriate for identifying which anatomical parts were preferentially selected or consumed by carnivores, which is central to understanding the formation processes in the inner cave. In sum, the choice to apply different quantification methods is not arbitrary but is adapted to the taphonomic characteristics and accumulation agents in each area, to ensure methodological appropriateness and interpretive accuracy. To further support the analysis of differences between the two areas, the ratio between anthropogenic modifications (AnthM) and carnivore damage (CarnM) was also calculated to comparatively assess the intensity of human and carnivore activity in different parts of the cave.

4. Results

4.1. Sub-Unit IIIb – outer area

A total of 14,092 bone remains were found in the area near the entrance of the cavity, belonging to stratigraphic sub-Unit IIIb (Table 1). Of these, 1,897 specimens (14 %) were identified at the specific level, representing 18 species (Table 1). The most represented animals are ungulates, particularly *Cervus elaphus* (43.8 %), *Capreolus capreolus* (8.1 %), and equids including *Equus ferus* (4 %), *Equus hydruntinus* (0.9 %). Bovids account for 3.8 % of the identified remains, with *Bos primigenius* (2.2 %) being distinguishable among them. Carnivores are also notably present, mainly represented by *Ursus spelaeus* (1.9 %). Medium and small carnivores include *Crocota crocuta* (0.4 %), *Canis lupus* (0.1 %), *Vulpes vulpes* (0.2 %), *Lynx* sp. (0.8 %), and *Martes foina* (0.1 %).

A total of 12,195 remains (86.5 %) were attributed to categories based on weight sizes: very large size (0.1 %), large size (6.5 %), medium size (30.2 %), small size (43.3 %), and very small size (1.5 %), while 18.4 % could not be identified by body size (Table 1). Among the identified bones, 650 are epiphyses, while the rest are diaphyses of anatomically and non-anatomically identifiable bones. Of the total epiphyses, 13 show traces of burning and 231 exhibit carnivore modifications.

The MNI (Minimum Number of Individuals) is 104 and was

Table 1

NISP and NME of Teixoneres Cave sub-Unit IIIb outer area. Aves and Leporidae data are based on previous publications (Rufà et al., 2014, 2016). Neo = neonatal; I = infantile; J = juvenile; Imm = immature; A = adult; S = senile.

TAXA/size body class	Outer area								Inner area								
	NISP	NME	NMI	I	J	Imm	A	S	NISP	NME	NMI	Neo	I	J	Imm	A	S
<i>Ursus spelaeus</i>	36	34	6		1		4	1	18	16	3				1	1	1
<i>Crocota crocuta</i>	7	5	1				1		6	6	1					1	
<i>Canis lupus</i>	1	1	1				1		1	1	1					1	
<i>Vulpes vulpes</i>	3	3	1				1		/	/							
<i>Lynx</i> sp.	15	14	4		1	1	2		4	4	1					1	
<i>Martes foina</i>	1	1	1				1		/	/							
Unidentified Canidae	4	/							/	/							
Unidentified Felidae	/	/							1	/							
<i>Equus ferus</i>	75	75	8		1	1	4	2	8	8	2					1	1
<i>Equus hydruntinus</i>	17	17	2		1		1		4	4	1					1	
<i>Equus</i> sp.	83	/							10	/							
Rhinocerotidae	5	5	1			1			4	1	1			1			
<i>Bos primigenius</i>	31	30	4		1	1	1	1	16	16	3				1	2	
Bovidae large size	41	/							10	/							
<i>Capra pyrenaica</i>	9	9	4		1	1	2		/	/							
<i>Rupicapra pyrenaica</i>	5	5	2			1	1		/	/							
<i>Cervus elaphus</i>	832	586	48	2	4	9	32	1	105	79	14	1	2	1	3	7	
<i>Capreolus capreolus</i>	153	122	18	2	1	5	10		12	12	2		1			1	
Unidentified Cervidae	104	/							1	/							
<i>Sus scrofa</i>	3	3	2			1	1		/	/							
Unidentified Ungulata	1	/							/	/							
<i>Oryctolagus cuniculus</i>	28	/							/	/							
Unidentified Leporidae	384	/							6	/							
Corvidae	10	/							/	/							
<i>Gyps fulvus</i>	/	/							1	/							
<i>Bufo bufo</i>	/	/							1	/							
Passeriformes	1	/							/	/							
Phasianidae	2	/							/	/							
Strigidae	1	/							/	/							
Unidentified Birds	/	/							4	/							
Large size	788	/							58	/							
Very large size	1	/							/	/							
Medium size	3690	/							178	/							
Small size	5280	/							60	/							
Very small size	181	/							4	/							
Indet size	2255	/							40	/							
Total NISP indet	12,195	/							340	/							
Unidentified bones	11,969	/							1	/							
Unidentified teeth	226	/							339	/							
Total NISP	14,092	/							562	/							

determined based on the most common skeletal element (mainly dental remains). Most of the individuals are adults (59.6 %), although young individuals (35.6 %, including infantile, juvenile, and immature specimens) are also present, along with a small percentage of senile individuals (4.8 %). Among the indeterminate specimens, immature

individuals account for 43 %, adults 54 %, and senile individuals 3 %. (Table 1).

Anatomically, within the taxonomically identified sample, the most frequently found remains are from the appendicular skeleton (50.8 %). Specifically, among the appendicular elements, 27.2 % are from the

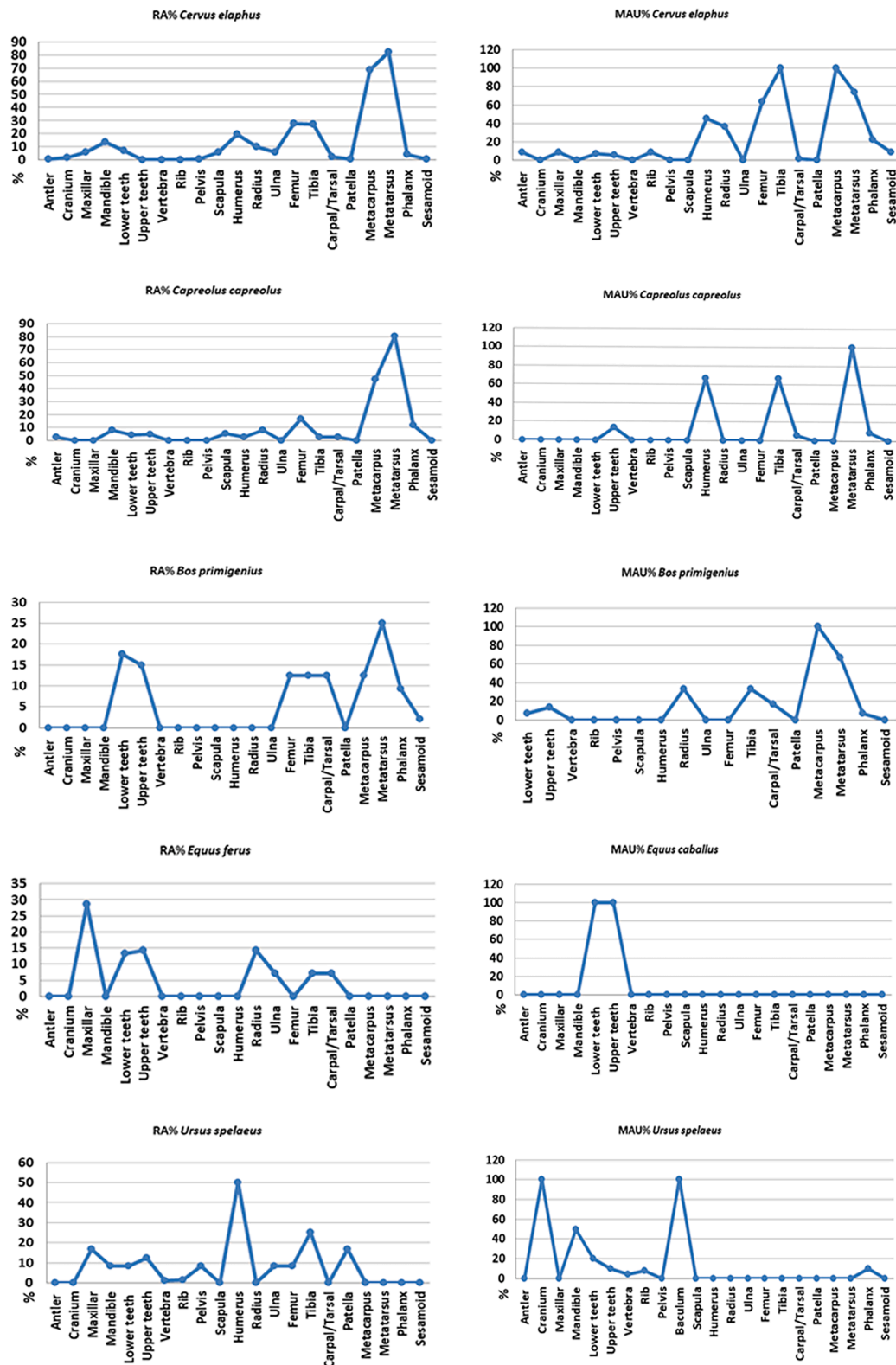


Fig. 2. For the most represented taxa in Teixoneres Cave: 1) Relative Abundance Percentage (RA%) in the outer area and 2) Minimum Animal Units (MAU%) in the inner area. Taxa displayed are as follows: A) *Cervus elaphus*, B) *Capreolus capreolus*, C) *Bos primigenius*, D) *Equus ferus*, and E) *Ursus spelaeus*.

stylopods, 28.8 % from the zeugopod, and 36.4 % from the autopod. The axial skeleton, accounting for 49.2 % of the remains, is primarily represented by cranial elements, particularly teeth, which make up 36.7 % of the findings.

In contrast, ribs and vertebrae are represented by 16.5 % and 7.4 %, respectively. Few articular bones and several phalanges are recorded within the sample (Supplementary Table 1).

The anatomical representation of the assemblage is uneven, with a clear overrepresentation of specific limb bones—particularly metapodials, tibiae, and femora—compared to other skeletal elements such as scapulae, pelvis, or articular bones. Specifically, regarding the most represented species, *Cervus elaphus* shows a scarcity of cranial and pelvic girdle remains, as well as scapular elements, while the appendicular skeleton is particularly abundant, represented primarily by tibiae (NISP 62), femurs (NISP 52), and metapodials (NISP 251). Limb bones are also the most represented for both *Capreolus capreolus* (61) and *Bos primigenius* (5), with a substantial number of isolated teeth found in the latter species (NISP 19 and 19 respectively). Among the Equidae, numerous isolated teeth are present (NISP 141), while appendicular skeletal elements are less common; however, the tibia is relatively well-represented (NISP 5). In the case of *Ursus spelaeus*, in addition to limb bones, particularly the humerus (NISP 6), isolated teeth (NISP 14) and vertebral remains, some of them complete, (NISP 3) as well as ribs (NISP 1) were recovered. For other families, teeth are often the most common or exclusive remains. For the family Rhinocerotidae, only teeth were found (NISP 5), and for hyenas, teeth represent the most common remains (NISP 5).

For the most represented animals, Relative Abundance Percentage (RA%) (Fig. 2) was calculated. Overall, isolated teeth are the most frequently found elements, followed by the appendicular skeleton. Metapodials are numerous, while articular bones are present but in smaller quantities. Vertebrae, pelvis, cranial elements, and ribs are relatively scarce. Regarding the fragmentation of the sample, very few anatomical elements are intact, with 87.1 % measuring less than 5 cm in length (Fig. 3). Considering the angle, delineation, and surface of the fractures (Villa and Mahieu 1991), we believe that the breakage observed in the outer area was predominantly produced on fresh bones. Mixed and transverse fractures more frequently exhibit irregular surfaces. In the proportion between smooth and jagged surfaces, the majority of remains for which fracture type could be analysed display smooth fractures (NR 14,137). Lastly, the most represented fracture types are curved and smooth oblique fractures, as well as longitudinal and smooth oblique fractures. (Fig. 4). Considering the angle, delineation, and surface of the fractures (Villa and Mahieu 1991), we believe that the breakage observed in the outer area was predominantly produced on fresh bones.

Hominids and carnivores were the primary biological agents that affected the assemblage in sub-Unit IIIb. Anthropogenic modifications (AnthM) account for 9.6 % of the sample, while carnivore damage (CarnM) (such as scores, pits, punctures, crenulated edges, etc.) represent 11.6 % (Fig. 5). Specifically, *Cervus elaphus* is the species with the highest number of anthropogenic modifications, followed by large-sized Bovidae and *Capreolus capreolus* (Supplementary Table 3). For all species with anthropogenic modifications, there is also a presence of remains with carnivore modifications.

In some cases, both anthropogenic and carnivore damage are found on the same bone surface, as observed in *Ursus spelaeus*, *Cervus elaphus*, *Capreolus capreolus*, and *Bos primigenius*. In contrast, equids display only a single remain with anthropogenic modifications, while carnivore modifications are more prevalent.

On the other hand, *Rupicapra pyrenaica*, *Capra pyrenaica*, and small carnivores such as *Lynx lynx* and *Vulpes vulpes* show only carnivore modifications. In contrast, equids present only one remain bearing anthropogenic modifications, whereas carnivore induced alterations are more frequent (NR 14). Similarly, *Rupicapra pyrenaica*, *Capra pyrenaica*, *Lynx lynx*, and *Vulpes vulpes* exhibit exclusively carnivore modifications. Overall, the proportion of modifications produced by humans and carnivores is fairly similar, although the number of remains with carnivore marks slightly exceeds those showing anthropogenic alterations. Among the latter, cut marks are the most frequent (4.2 %), but percussion notches, impact flakes, cortical scars, flakes, retouchers, and cortical flakes are also present (Figs. 6, 7). Among the anthropogenic modifications, cut marks are the most prevalent (4.2 %), although percussion notches, impact flakes, cortical scars, flakes, retouchers, and cortical flakes have also been found (Figs. 6, 7; Supplementary Tables 3, 5). Breakage is especially observed on indeterminate long bones, followed by femora and tibia. Most of the percussion marks are located on the diaphyses, affecting all surfaces. All butchering activities were identified, as various types of marks were observed. Incisions are predominant on limb bones (Supplementary Table 3). Surface damage from bone breakage was also analysed. Evidence of percussion notches, impact flakes, cortical and medullary flakes, as well as flakes and retouchers, was documented (Figs. 6, 7; Supplementary Table 3).

All types of carnivore marks were identified and often appear simultaneously on the surface of the bones (Fig. 8; Supplementary Table 4). Some bone fragments present an overlapping of anthropogenic and carnivore marks, accounting for 0.8 % of the sample (Fig. 9; Supplementary Table 5). In some cases, it was possible to observe that human activity occurred first, as carnivore damage was found on top of the human modifications (Fig. 9).

In the outer area, 2,469 burnt remains were recovered, representing 17.5 % of the total faunal remains (Fig. 5), with 0.3 % measuring > 5 cm.

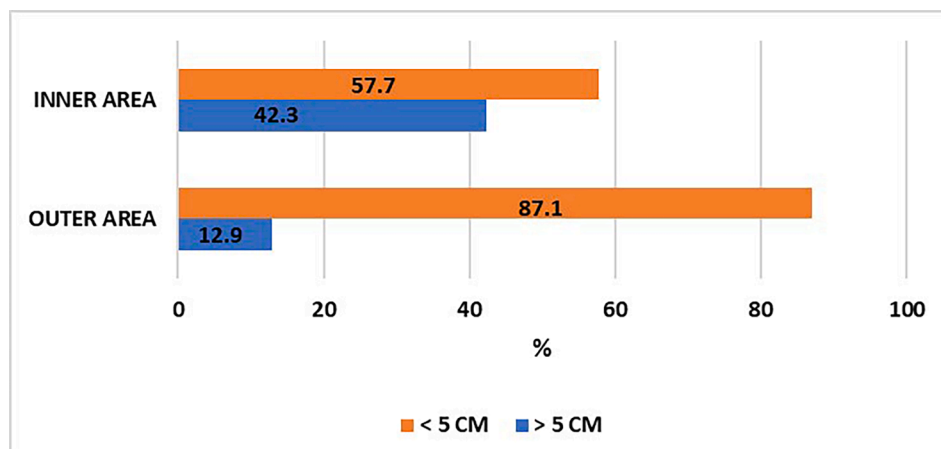


Fig. 3. Bones dimensions from outer and inner area of Teixoneres Cave.

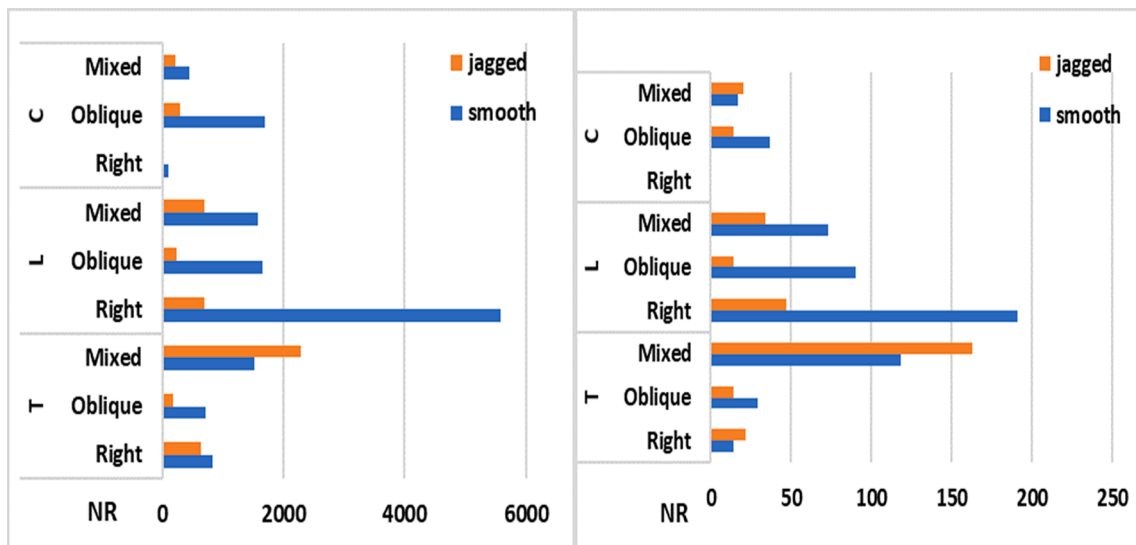


Fig. 4. Bone breakage based on delineation, angle and surface from outer and inner area of Teixoneres Cave. T = transverse, C = curved, L = longitudinal; referring to the delineation of fracture outlines.

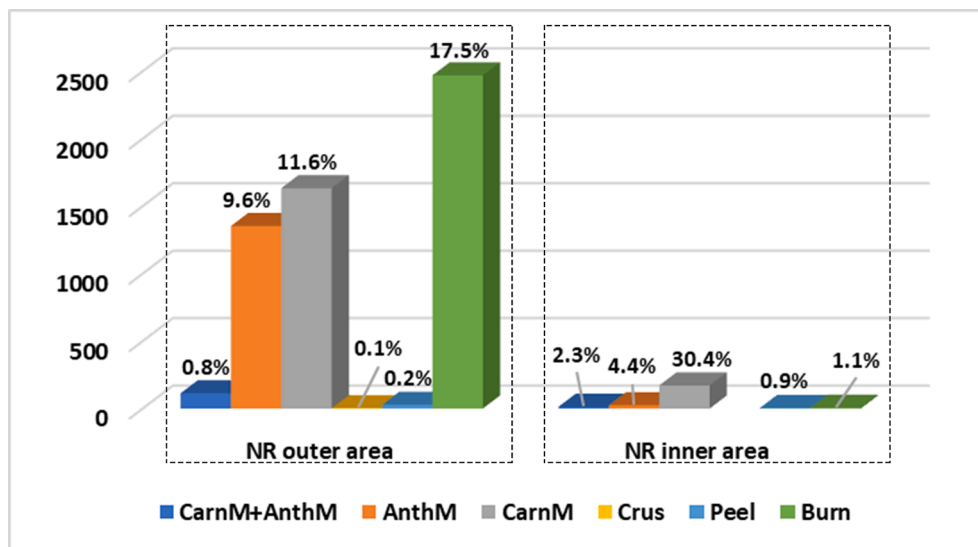


Fig. 5. Anthropogenic modifications (AnthM) on bones include cut marks, percussion notches, impact notches, impact flakes, cortical scars, cortical flakes, flakes, retouchers. Carnivore modifications (CarnM) include pits, pitting, scores, punctures, crenulated edges, digestion, furrowing, scooping marks, cylinder diaphysis). Crushing, peeling, and burning remains are displayed separately. These data refer to the inner and outer areas of Teixoneres Cave.

Some of those present also show cut marks, impact flakes, cortical scars, cortical flakes, retouchers, flakes, percussion pits, and percussion notches (NR 139).

It was found that the most commonly recovered burnt bones exhibit grade 3 or double coloration, primarily represented by the combination of grades 2 and 3 on the same surface (Fig. 10). Additionally, 548 NR show different coloration between the medullary and cortical surfaces, and 31 NR exhibit the so-called “burning sandwich pattern”. Most of the bones with burnt surfaces belong to taxonomically unidentified faunal remains (98.7 %) (Table 2).

Lastly, regarding natural traces, there is a significant presence of manganese staining (29.7 %), fissures (18.2 %), and root etching (7.3 %). Trampling marks were observed on 5.7 % of the analysed sample, while abraded bones showing signs of polishing and rounding represent 1.7 % and 1.2 %, respectively.

4.2. Unit III – Inner area

A total of 562 bone remains were found in the inner area of Chamber X (from square 20 to rear wall), and stratigraphically attributed to Unit III (Table 1). A total of 222 specimens (39.5 %) from the entire sample were identified at the taxonomic level, representing 12 species (Table 1). The most represented large mammals are *Cervus elaphus* (47.3 %), *Bos primigenius* (7.2 %), and *Capreolus capreolus* (5.4 %). Within the faunal context of this area, the percentage of *Ursus spelaeus* is significant, accounting for 8.1 %. A total of 340 remains (60.5 %) were attributed to categories established by weight sizes: large size (17 %), medium size (52.4 %), small size (17.6 %), and very small size (1.2 %). No remains were classified as very large size, while 11.8 % could not be identified by body size. Among the identified bones, 70 are epiphyses, while the rest are diaphyses of anatomically and non-anatomically identifiable bones. Of the total epiphyses, none show traces of burning and 30 exhibit carnivore modifications.



Fig. 6. Example of anthropogenic modifications (AnthM) from sub-Unit IIIb outer area: 1) chop mark on a large-sized femur; 2) scraping marks on the metacarpus of *Cervus elaphus*; 3) Parasite flake on the cortical surface (detail a) and percussion notches on the medullary surface (detail b) of a *Cervus elaphus* tibia; 4) Incisions on small-sized long bone; 5) Incisions on a burnt (degree 2 + 3) small-sized long bone; 6) Impact flake of a small-sized long bone; 7) Percussion notch (detail a) and incisions (detail b) on the metacarpus of *Capreolus capreolus*; 8) Parasite flake of a medium-sized long bone; 9) Incisions on the mandible of *Capreolus capreolus*.

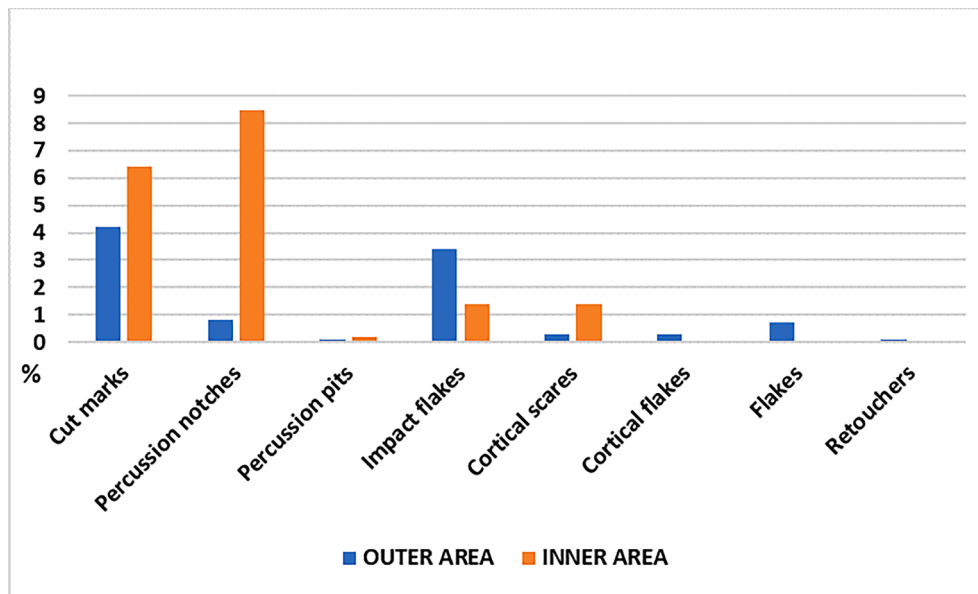


Fig. 7. All anthropogenic modifications at inner and outer areas of Teixoneres Cave.

The MNI is 28 based on the most common skeletal element, primarily dental remains, considering species and ages at death. Among the taxonomically identified remains, adults (57.1 %) are the most represented, followed by young individuals (39.3 %, a percentage that includes different age categories), and senile individuals, represented by a single remain, account for 3.6 % (Table 1). Among the indeterminate specimens, immatures constitute 28.5 %, adults make up 71.5 %, while no senile individuals were identified. Anatomically, the most frequently found remains are from the appendicular skeleton (63.5 %). Specifically, among the elements of the stylopods, 24.3 % were recorded, 32.3 % from the zeugopod, and 38.9 % from the autopod (Supplementary Table 2).

The axial skeleton, accounting for 36.5 % of the remains, is primarily represented by teeth (40 %). In some cases (e.g., Canidae), only dental remains were found. Conversely, in the total sample recovered, ribs and vertebrae represent 10.9 % and 4.8 %, respectively (Supplementary Table 2).

For the most commonly represented species, Relative Abundance (RA%) and Minimum Animal Units (%MAU) were calculated (Fig. 2). The RA% data reveal a predominance of teeth—especially due to their greater preservation potential—along with metapodials and some long bones, such as the humerus (see Supplementary Information section 1. for more details). The %MAU data suggest a predominance of cranial elements, mostly teeth, and larger bones rich in nutritious tissues, such as the femur, tibia and metapodial. The frequency with which these bones were transported to the back of the cave indicates that the carnivores considered them particularly valuable due to their high energy content. Regarding breakage patterns, according to Villa and Mahieu, (1991), the sample predominantly exhibits smooth fractures, characterised by a combination of right-angle breaks and longitudinal delimitation. Mixed and transverse fractures show the most cases of irregular surfaces. In the proportion of smooth versus jagged surfaces, the majority of remains for which fracture type could be analysed display smooth fractures (NR 596). Lastly, the most represented fracture types are smooth longitudinal and mixed transverse irregular fractures (Fig. 4). In the case of fractures from the inner area, the breakage appears to have occurred predominantly on dry bones, and the percentage of bones smaller than 5 cm is slightly higher (57.5 %) than that of bones measuring more than 5 cm (42.3 %) (Fig. 3). A comparison between the outer and inner areas of Teixoneres Cave reveals that the inner area exhibits greater assemblage entirety than the outer area.

Anthropogenic modifications (AnthM) in the inner area account for 4.4 % of the sample (Fig. 5), while carnivore damages (CarnM) account for 30.4 % (Fig. 5). All butchering activities were recorded, as various types of cut marks were found on different anatomical elements (Supplementary Table 6). Among the anthropogenic modifications, percussion notches are the most prevalent (48 %), followed by cut marks (36 %), impact flakes (8 %), and cortical flakes (8 %) (Figs. 7, 11). The most frequently impacted bones are the femoral diaphysis and metapodials, with percussion marks observed on all surfaces. Among the cut marks, incisions are the most represented (Supplementary Table 6). When comparing the two areas (Fig. 7), the inner area displays a lesser percentage of anthropogenic modifications relative to the number of remains recovered. Nonetheless, this is largely a result of the smaller sample size in the inner area, whereas the outer area holds the highest absolute number of anthropogenic modifications (Fig. 7).

Carnivore modifications were documented on 30.4 % of the remains (Fig. 5). All types of carnivore marks were identified and are often present simultaneously on the surface of the bones (Fig. 12; Table 7 Supplementary information). Bone fragments with overlapping anthropogenic and carnivore marks account for 2.3 % of the remains (Fig. 13; Supplementary Table 8). One example is a bone fragment that could not be identified beyond the family level, consisting of the left pelvis of a juvenile individual (Fig. 14).

Comparing the outer and the inner area of Teixoneres Cave, the ratio between anthropogenic modifications and carnivore damage ($R = \text{AnthM}/\text{CarnM}$) yields a value of 0.8, which, as previously mentioned, is a value to consider. To further understand the meaning of this result, the percentage difference of the value was calculated. The results indicate that bones bearing signs of carnivore activity are more numerous than those showing evidence of human activity. Furthermore, the result shows that carnivore traces are 20 % more common than anthropogenic ones. In fact, carnivore modifications in the outer area account for 11.6 %, while anthropogenic modifications represent 9.6 %. Although the ratio between these two types of traces is relatively balanced, it suggests that, despite a slightly higher presence of carnivores in the outer area of Teixoneres, human occupations are detected – as demonstrated by the percentage of anthropogenic modifications. This finding becomes even clearer when examining the results from the inner area of the cave, where calculating the ratio between the two values and the subsequent percentage difference reveals a markedly higher presence of carnivores compared to humans. In fact, 90 % of the traces found

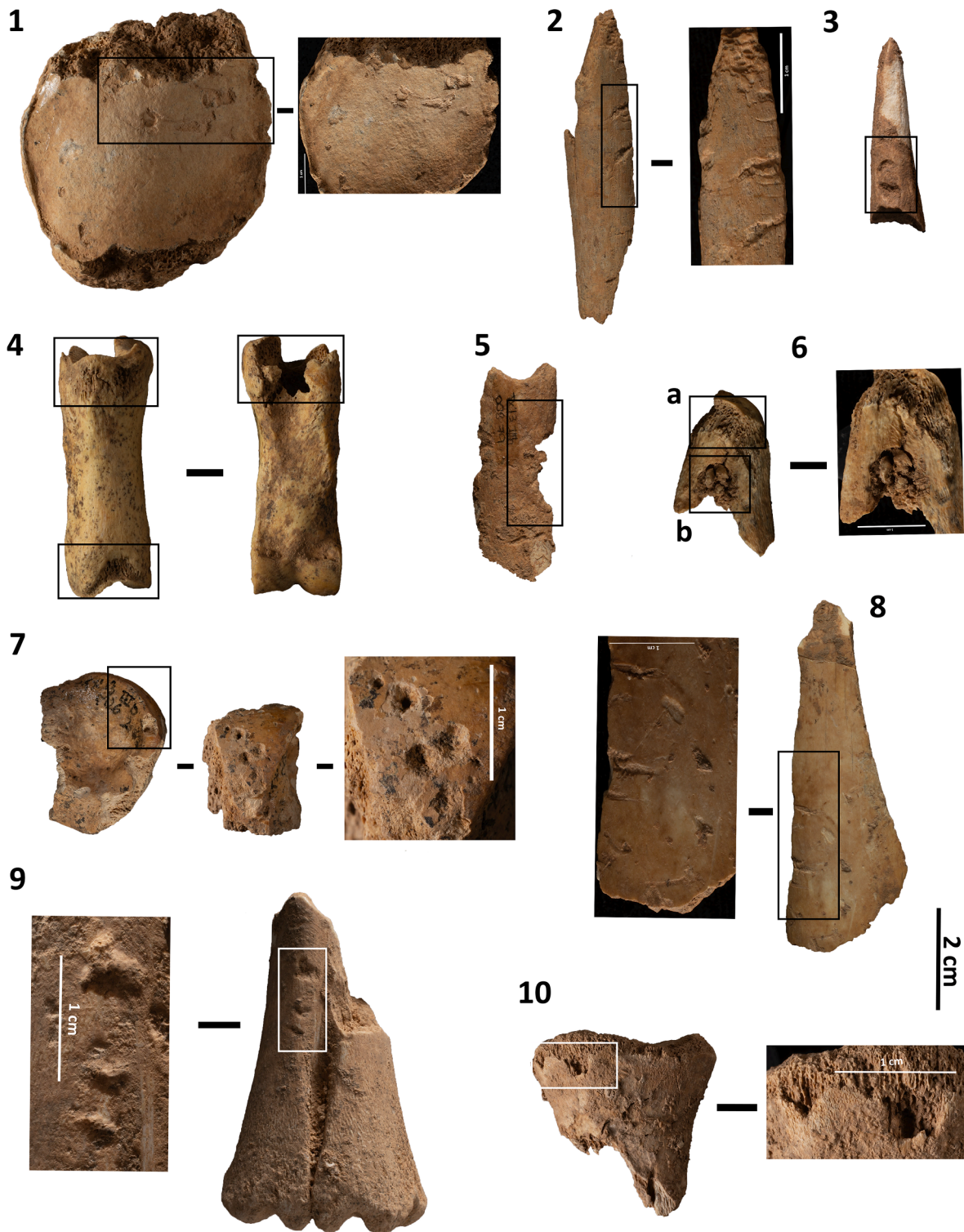


Fig. 8. Example of carnivore modifications (CarnM) from sub-Unit IIIb: 1) Pits and crenulated edges on an *Ursus spelaeus* patella; 2) Scores on a medium-sized femur; 3) Pits on a Cervidae antler; 4) Digestion (degree 1) on a *Cervus elaphus* first phalanx; 5) Crenulated edge on a small-sized femur; 6) Digestion (degree) and puncture on a *Cervus elaphus* calcaneus; 7) Pits on a *Capreolus capreolus* metacarpus; 8) Scores on a medium-sized femur; 9) Pits on a *Cervus elaphus* metatarsus; 10) Pits on small-sized radius.

in this area can be attributed to carnivores. In the inner area only six burnt remains were recovered (1.1 %). Of these, three specimens measure > 5 cm, only one burnt specimen, a deer tibia, was identified taxonomically. None of the burnt remains showed anthropogenic

modifications. Regarding the taphonomic nature of these remains, we can confidently exclude percolations from the upper level, as a layer of stones separates it from the level under analysis, and the chronology is confirmed by radiocarbon dating (Talamo et al., 2016). The hypothesis



Fig. 9. Example of coexistence of anthropogenic and carnivore modifications from sub-Unit IIIb: 1) Crenulated edge and scores (detail a) and incisions on a *Capreolus capreolus* femur; 2) Pits (detail a) and incisions (detail b) of a large-sized Bovidae femur; 3) Incisions (detail a) and crenulated edge and scores (detailed b) on a medium-sized tibia; 4) Overlapping of pits and incisions on a large-sized long bone. In this case, it was possible to identify evidence of primary human access, as the incisions were made first.

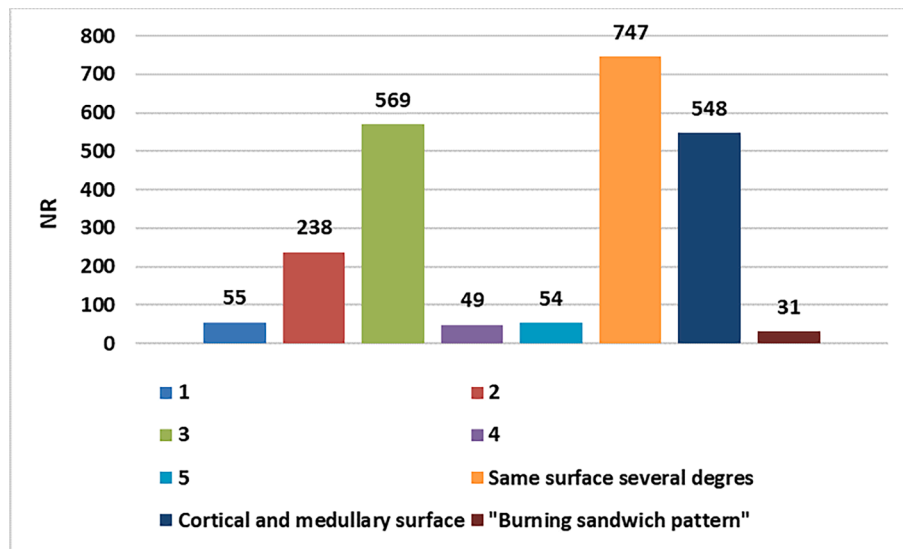


Fig. 10. Distribution of burnt bones in the outer area of Teixoneres Cave sub-Unit IIIb categorized by combustion degree (Stiner et al., 1995), intervals, and multiple degrees observed on the same or different bone surfaces. This rate includes all less frequent intervals within the assemblage.

Table 2

Identified and unidentified burnt remains of Teixoneres Cave outer area.

Outer area	NR	%
Unidentified burnt remains	2, 436	98.7
Identified burnt remains	33	1.3

that these remains may be associated with a hearth structure can also be dismissed, as no hearth features have been identified. We also considered the possibility that the fragments might belong to the same bone. In this case, by evaluating the anatomical element, the specific portion, and the age (when identifiable), we estimate that the burnt fragments correspond to a minimum of four distinct bones. The most plausible explanation appears to involve carnivore activity; it is likely that the burnt bones originated in the outer area and were subsequently transported to the inner area by carnivores.

Finally, regarding post-depositional modifications, fissures represent 30.2 %, manganese staining 57.6 %. Lower values are observed for the rounded sample (5.7 %), polished (2.8 %), with trampling marks (6.4 %) and root marks (2.4 %). If we correlate the percentage of trampling with the fracture condition—indicating that most bones were broken when dry, it is plausible to interpret this pattern as being related to trampling activity.

5. Discussion

In the discussion that follows, we will address a set of zooarchaeological and taphonomic features that are commonly employed in the literature to infer the duration of human occupations (e.g., Bargalló et al., 2020; Carbonell, 2002, 2012; Vaquero and Pastó, 2001; Vaquero et al., 2007, 2019; Vaquero, 2012; Leierer et al., 2019; Cascalheira and Picin, 2020; Moclán et al., 2021, 2023; Mallol et al., 2013; Mellars, 1996; Marín et al., 2020; Moncel and Rivals, 2011). These include aspects such as taxonomic diversity, hunting spectrum, anthropogenic and carnivore modifications, and carcass transport patterns. Each of these features will be examined individually in relation to the faunal assemblage from Teixoneres Cave sub-Unit IIIb, with special attention to the differences between the outer and inner areas and their distinct formation processes, which significantly influence the archaeological signal.

5.1. Taxonomic diversity

Taxonomic diversity emerges as a particularly significant factor and it refers to the variety of species present in a faunal assemblage, regardless of whether they were hunted or used by humans. In the relevant discussion regarding the duration of the occupations, high taxonomic diversity is considered a diagnostic factor for long-term occupations, whereas low taxonomic diversity is commonly seen as an indicator of short-term occupations. However, short-term occupations can exhibit high variability when there are many occupations overlapped, as they are characterized by their immediacy, leading to this variability (Blasco et al., 2013b).

Specifically, Teixoneres Cave sub-Unit IIIb contains 17 identified taxa, which appears inconsistent with the criteria typically used to assess occupation duration, but this apparent contradiction can be explained by several factors. First, both long-term and repeated short-term occupations can produce a similar taxonomic record due to the palimpsest effect, which is favoured by the low sedimentation rate. In sub-Unit IIIb, the accumulation of herbivores occurred throughout the year, particularly during the summer (Sánchez-Hernández et al., 2014, 2016, 2020; Uzunidis and Rivals, 2023; Uzunidis et al., 2024). Another aspect, and perhaps the most influential, is the ecological.

context in which the site was located at the time of occupation (Burke, 2000). Ochando et al. (2020, p.16) highlighted for the sub-Unit IIIb environment of Teixoneres Cave a high concentration of oak pollen, which “reveals a landscape that offered a broad and constant spectrum of possibilities for past human populations occupying the cave during its sedimentary infilling history (198–35 ka)”. The diversity of animal remains in Teixoneres Cave sub-Unit IIIb showing evidence of anthropogenic processing, suggests varied subsistence strategies.

Additional paleoenvironmental data come from microfauna studies, further supporting the hypothesis of favourable environmental conditions (López et al., 2012; Fernández-García et al., 2022). The small mammal assemblage from sub-Unit IIIb in Teixoneres Cave indicates a predominance of woodland habitats, and *Apodemus sylvaticus*, a species representative of forested environments, is present in greater abundance (López et al., 2012). In contrast, the macrofauna study in sub-Unit IIIa reveals a higher percentage of remains from *Coelodonta antiquitatis* and *Mammuthus primigenius* (Álvarez-Lao et al., 2017). This data clearly indicates colder environments during sub-Unit IIIa. The higher density of remains in sub-Unit IIIb compared to the overlying level also supports the idea of better climatic conditions during the formation of



Fig. 11. Example of anthropogenic modification from Unit III inner area: 1) Incisions on an *Equus* sp. metatarsus (details a and b); 2) Incision on the Humerus of *Ursus spelaeus*.

stratigraphic sub- Unit IIIb. This suggests that the cave was used by Neanderthals more frequently or intensively than the upper sub-Unit IIIa. The lack of a clear definition of “low” or “high” taxonomic diversity complicates this analysis. When considering taxonomic diversity, aspects such as the influence of carnivore activity are not always taken into account (Blasco et al., 2013b). The presence of carnivores could also affect the taxonomic variability found at a site, as carnivores may have included new taxa in the assemblage, some of which were not human-predated. The evidence of carnivore activity at Teixoneres Cave sub-Unit IIIb is 11.6 %, indicating that carnivores played a not negligible role in the accumulation of faunal remains at the site. As indicated by the results, all taxa identified in the taxonomic register exhibit signs of damage caused by carnivores, but not all the taxonomic groups present signs of anthropogenic activity, relativizing the taxonomic diversity observed at Teixoneres. In the case of *Cervus elaphus*, the most abundant species in the assemblage, numerous remains show both anthropic traces and carnivore-inflicted damage. Accordingly, it is considered that both human groups and carnivores contributed to the accumulation of these remains, with neither group predominating. Less represented species, such as the lynx and the fox, show only signs of carnivore damage (CarnM) (Supplementary Table 3). A different interpretation applies to the inner area, where a reduction in anthropic traces is observed, limited to only one species, *Cervus elaphus*, which is also the most prevalent in this part of the cave. In this area, however, carnivore marks are predominant, found on the majority of the species recovered

from the faunal assemblage of the inner area.

The level of mobility exhibited by human groups could also influence species presence. For example, it seems that in short-term occupations, the most abundant taxa typically reflect the taxonomic availability in the immediate surroundings, without following a selection criterion (David and Kramer, 2001). At the same time, greater mobility and the presence of a hunting spectrum in more distant and ecologically diverse areas could facilitate the presence of different animals in the residential site. When discussing the concept of high taxonomic diversity among the species found in Teixoneres Cave sub-Unit IIIb, we must be cautious: this apparent variety may not fully reflect the true biodiversity of the environment. Archaeological sites and their faunal assemblages cannot be regarded as perfect snapshots of past moments (Shipman, 1981; Fernández-Jalvo et al., 2011). Instead, they are shaped by a complex interplay of accumulation agents, post-depositional processes, and conservation dynamics, both before and after excavation—including recovery, analysis, and curation (Fernández-Jalvo et al., 2011; Shipman, 1981). One critical aspect to consider when assessing taxonomic diversity is the differential preservation of species, which significantly affects our palaeoecological reconstructions. Factors such as bone density and osteological structure determine the likelihood of preservation, often resulting in underrepresentation of more fragile skeletal elements (Clark and Kietzke, 1967; Andrews, 2006; Battista and Schultz, 2024). Moreover, biotic and abiotic accumulation and preservation factors, along with thanatic variables (Battista and Schultz, 2024), can alter the



Fig. 12. Example of Carnivore modifications from Unit III inner area: 1) Crenulated edge (detail a) and scores (detail b) on an *Ursus spelaeus* humerus; 2) Pitting on a fragment of an *Ursus spelaeus* baculum; 3) Scores on a Phalanx II of *Lynx* sp.; 4) Pits on the metatarsus of *Bos primigenius*; 5) Scores (detail a) and crenulated edge, and pitting on a large-sized Bovidae radius; 6) Pit on a fragment of Ursidae cranium.



Fig. 13. Example of the coexistence of anthropogenic and carnivore modifications from Unit III inner area: 1) Scores and pits (detail a) on the cortical surface and an impact notch on the medullary surface (detail b) of a *Cervus elaphus* femur; 2) Scores (detail a) on the cortical surface and an impact notch on the medullary surface (detail b) of a *Cervus elaphus* femur.



Fig. 14. Coexistence of anthropogenic and carnivore modifications on a Rhinocerotidae pelvis. Detail a: Pit; Detail b: Incisions; Detail c: Chop mark; Detail d: Longitudinal incision; Detail e: Crenulated edge and scores; Detail f: Crenulated edges and rodent gnawing.

observed taxonomic composition of an assemblage. This may either inflate or reduce the apparent species diversity (Andrews, 2006). Post-fossilization disturbances, including reworking processes—such as the mixing of fossils from different stratigraphic layers or time periods due to percolation or sediment shifts—are well documented and contribute to palimpsestic assemblages (Fernández-López, 1991; Fernández-López and Fernández-Jalvo, 2002; Andrews, 2006). Two main aspects should be considered when reconstructing taxonomic diversity: (1) most

assemblages integrate remains from multiple habitats, which may not correspond to modern analogues (Andrews, 2006); (2) taxonomic diversity may reflect predator–prey dynamics, selective transport, or varied preservation conditions influenced by environmental factors (Brain, 1981; Shipman, 1981; Lyman, 1994). In predator-driven assemblages, diversity is shaped by the behaviour and diet of the accumulator, including hunting strategies and prey selection. Environmental conditions such as soil acidity, weathering, temperature fluctuations,

humidity, and microbial or fungal activity can further distort the palaeoecological signal. Additionally, as outlined by Clark and Kietzke (1967), a wide range of taphonomic filters—including biotic, thanatic, perthotaxic (post-mortem disturbance), taphic (burial), anataxic (post-burial disturbance), sullegic (collection), and trephic (curation) processes—can affect faunal representation. In cases of hydraulic transport, biases may also arise from the differential representation of disarticulated elements, depending on size and robustness. Sampling biases—related to excavation strategies, sample size, and documentation practices—also play a central role, especially when considering small-body versus large-body remains (Faith and Lyman, 2019). To address these issues, it is essential to adopt taphonomic-aware analytical frameworks, acknowledging how environmental conditions, excavation and sampling strategies, and analytical biases affect fossil assemblages. As emphasized by Behrensmeier et al., (2000), all these variables contribute to distorting the actual image of biodiversity, meaning that the data we collect must always be interpreted through a lens that critically evaluates preservation and sampling biases. The observed diversity is, in fact, influenced by human and carnivore activities, which selected, hunted, and transported specific species to this area. We are not seeing a complete and unbiased representation of the original fauna, but rather a selection shaped by the behaviours of predators and hunters. In this sense, the concept of a hunting spectrum may help us understand that what we find is not necessarily the entire range of species present in the environment, but a collection conditioned by the preferences and practices of those exploiting these resources. In any case, paleoenvironmental data suggest a predominantly woodland context, from which the most represented species, *Cervus elaphus*, originates, confirming the importance of a forested environment rich in resources for both human and animal communities.

5.2. Hunting spectrum and carcass transport

Different from taxonomic diversity is the hunting spectrum. The hunting spectrum, or the range of animals hunted by human groups, represents another key variable used in examining the duration of Neanderthal occupations, as it reflects the relationship between humans and animals. As suggested by the feature currently applied to identify the duration of occupations (Bargalló et al., 2020; Carbonell, 2012; Leierer et al., 2019; Cascalheira and Picin, 2020; Moclán et al., 2021, 2023; Marín et al., 2020; Moncel and Rivals 2011), short-term occupations are characterised by a “varied” hunting spectrum, whereas long-term occupations exhibit a specialised hunting spectrum.

At Teixoneres Cave sub-Unit IIIb, the main species that show more anthropogenic marks related to carcass processing (Supplementary Table 3) are three taxa (*Cervus elaphus*, *Capreolus capreolus* and *Bos cf. primigenius*). This contradicts the prevailing paradigm concerning the hunting spectrum used to define the duration of occupations. Moreover, it is important to highlight the lack of a clear definition of both “specialised” and “varied” hunting spectrum (Costamagno et al., 2006; Chase, 1987; Binford, 1968; Burke, 2000; David and Enloe, 1993; Mellars, 1973; White, 1982). No study provides a specific range of taxa to define these categories. Blasco et al., (2013b) suggest that up to three species can be considered “dominant taxa,” while any species beyond this number are labelled as “non-dominant species.” Furthermore, the same analysis defines a faunal record as exhibiting high taxonomic diversity when it includes more than fifteen species. Therefore, there is no consensus in the literature on a clear numerical range to distinguish “low” from “high” taxonomic variability. Moreover, short but repeated occupations at different times of the year and across various seasons can result in similar faunal records as those of a prolonged occupation in terms of the hunting spectrum.

Additionally, due to the palimpsest effect, we might interpret this data as the result of a single occupational event. Finally, we need to include in this parameter the high fragmentation of the remains caused by anthropic activity, trampling, and all the taphonomic processes that

influence our ability to identify remains with butchery marks. In fact, at sub-Unit IIIb of Teixoneres Cave, especially in the outer area, the high fragmentation has led to the presence of numerous unidentified remains with anthropogenic traces.

When considering the hunting spectrum as an indicator of occupation duration, several essential factors must be accounted for to clearly determine occupation length. Foremost is environmental availability, as the ecological context of the site—together with variability, and predictability of resources—significantly influences the observed taxonomic profile (e.g., Blasco et al., 2013b; Burke, 2000; Vaquero, 2012). The second factor involves the decisions made by humans to capture prey. Hunting decisions were influenced by contingent circumstances and economic strategies that considered the energy expenditure in relation to the quality of resources (e.g., Blasco and Fernández Peris, 2012; Blasco et al., 2013b; Bettinger, 2009; Vaquero 2012). The third factor pertains to the type and duration of occupations (Blasco et al., 2013b). Regarding functionality, the main types of Neanderthal sites identified include residential sites, hunting camps, kill/butchery sites, and lithic extraction areas (quarry sites). Since the function of a site reflects the type of activities conducted by the groups occupying it, this factor can influence results related to the hunting spectrum and, to a greater extent, carcass transport.

Although a site may serve a specific function (e.g., a residential camp), its faunal assemblage may differ from other sites within the same category. This variation can arise from the seasonal nature of the occupation, where specific species were targeted at particular times of the year. Additionally, contingent decisions, which remain difficult to identify, may have further influenced the selection of species. Therefore, the taxonomic spectrum within a site category may exhibit diversity, shaped not only by the primary function of the site but also by seasonal, environmental, and unpredictable factors affecting subsistence strategies. Comparative analyses (Lubrano et al., 2025) reveal no significant differences between sites identified as residential and hunting camps. For instance, at hunting camps as Navalmaillo F and D (e.g., Moclán et al., 2021), the low taxonomic diversity observed is similar to residential sites as Abric Romani levels O and J, Teixoneres Cave unit III (e.g., Bargalló et al., 2020; Rosell et al., 2012, 2017). On the contrary, that comparison indicates that differences are not primarily related to the number of species hunted. A completely different scenario emerges at quarry sites, where groups, depending on their mobility patterns, gathered raw materials. These sites lack faunal remains as they were specifically used for raw material procurement and initial lithic processing (e.g., Sciuto et al., 2021; Terradas and Ortega, 2017). Additionally, the duration of occupations plays a crucial role in shaping the hunting spectrum. Prolonged human presence, associated with greater territorial control, promotes a high variability in potentially hunted species. When using the hunting spectrum as a distinguishing feature for occupation duration, a general assumption posits that short-term occupations are characterized by a varied hunting spectrum, whereas long-term occupations display a specialized hunting spectrum (e.g., Daujeard and Moncel, 2010; Marín et al., 2020). In the taxonomic records of faunal assemblages associated with late Middle Palaeolithic short-term occupations, a consistent observation emerges: one or more species systematically dominate in number over others. For example, sub-Unit IIIb of Teixoneres Cave has previously been identified through a multidisciplinary analysis as a residential camp resulting from short but repeated occupations (Zilio et al., 2021; Rosell et al., 2017; Picin et al., 2020a, 2020b). Despite the short duration of these occupations, according to the general assumption (short-term occupations correspond to a varied hunting spectrum), the hunting spectrum analysis of this sub-Unit seems to contradict this definition used to identify occupation duration. In fact, in Teixoneres Cave sub-unit IIIb, three taxa (*Cervus elaphus*, *Capreolus capreolus* and *Bos cf. primigenius*) are primarily hunted. This could suggest that specific environmental and climatic conditions must have favoured the greater availability of these species. Recent studies on micro-wear indicate that the Neanderthal groups who

occupied Teixoneres about 50,000 years ago primarily did so during the summer (Uzunidis and Rivals, 2023; Uzunidis et al., 2024). The repeated occupations, particularly during this time of year, must have ensured a consistent availability of these species near the cave. We exclude the idea of a specialized hunting strategy with the intention of specifically targeting deer, although a clear and unambiguous definition of specialized hunting has yet to be established. Similarly, we cannot exclude the possibility that the Neanderthal in Teixoneres were aware of the abundant availability of deer in the area, which may have influenced their return to the site. For instance, Lubrano et al. (2025) noted a rare case of a varied hunting spectrum at Level VII of Amalda I Cave (Sánchez-Romero et al., 2020; Yravedra, 2010). For long-term occupations, the majority of case studies demonstrate the presence of three or four taxa, not a single species as Burke's (2000) definition might suggest. Exclusively, coeval site comparisons, such as those by Lubrano et al. (2025), show a predominance of red deer in levels like M at Abric Romaní and Saint Marcel, even though Saint Marcel has also been defined as a site of selective red deer hunting (Richard et al., 2021; Daujeard et al., 2012, 2014; Daujeard and Moncel, 2010; Moncel et al., 2010, 2015; Lateur et al., 2023). Similarly, sites such as Mauran, La Rouquette, Les Pradelles, and La Quina represent hunting camps associated with short-term occupations where specialized hunting was evident (Rendu et al., 2011; Rendu and Armand, 2009; Soulier, 2008; Costamagno et al., 2006). In such cases, specialized hunting for specific taxa contradicts the hunting spectrum indicator assumption (short-term occupations = varied hunting spectrum). This demonstrates not only that specialized hunting can affect the hunting spectrum recorded, but also that numerous factors associated with the "contingent circumstance" or "economic strategies" for specialized hunting are critical to consider (e.g., Lubrano et al., 2025; Blasco et al., 2013b). Furthermore, the concept of "specialized" warrants closer examination, as the lack of a unified definition for specialization is widely recognized (e.g., Costamagno et al., 2006; Chase, 1987; Binford, 1968; David and Enloe, 1993; Mellars, 1973; White, 1982). This ambiguity extends not only to what defines specialization but also to the term "varied," for which no consensus exists. Short-term but repeated occupations at different times of the year could misleadingly group hunted taxa from various occupations and seasons as belonging to a single occupational period. Similarly, long-term occupations spanning multiple seasons could favour the availability of a greater range of species to hunt. Additionally, high levels of fragmentation or inadequate preservation of bone surfaces may hinder taxonomic and taphonomic identification. Consequently, the full range of species present in assemblages and those hunted may remain unidentified. Considering all these elements, Lubrano et al. (2025) advocate for cautious use of the hunting spectrum as an indicator of occupation duration.

Conversely, the site's function significantly influences carcass transport, another indicator proposed for evaluating occupation duration. In evaluating carcass transport strategies, it is also crucial to consider the role of bone preservation and differential survivability. The representation of skeletal elements in faunal assemblages does not always reflect actual transport decisions, as it is conditioned by taphonomic filters. Bones differ in macrostructure and density, leading to unequal resistance to post-depositional processes such as trampling, weathering, and carnivore activity. This concept of attrition—first outlined by Stiner (2002) and further developed by Pickering et al. (2003)—highlights that not all skeletal parts have the same chance of preservation. As a result, our reconstructions of transport behaviour may be biased toward the better-preserved, denser elements, like limb shafts, while underrepresenting more fragile anatomical parts. Considering Stiner's model and its implications, the low frequency of epiphyseal fragments observed in both the outer and inner areas of Teixoneres Cave sub-Unit IIIb may reflect this same concept of attrition. Epiphyses, being less dense and richer in fat content, are more prone to early destruction—particularly by carnivores. This interpretation is further supported by the presence of epiphyseal fragments bearing carnivore modifications

within the assemblage. An additional factor to consider when discussing carcass transport and skeletal part representation is the function of an archaeological site. In fact, at hunting or butchery sites, less valuable remains are more likely to be left in situ or transported selectively, favouring the most useful portions. In contrast, at residential sites, the richest portions of carcasses are transported (e.g., Marín et al., 2017; Saladié et al., 2011; Schoville and Otárola-Castillo, 2014; White, 1955; Binford, 1978, 1981) to enable communal consumption of prey at the location where the entire group resided. This behaviour is influenced by site occupation duration and the necessity of resource preservation (e.g., Blasco et al., 2019). Researchers as Daujeard et al., 2019; Daujeard and Moncel, 2010; Moncel and Daujeard, 2012; Moncel, 2010; Moncel et al., 2004, 2019; Marín et al., 2020 emphasize the importance of carcass transport in determining occupation length. Specifically, long-term occupations are associated with the transport of either the entire carcass or the most nutritionally valuable skeletal elements, which also implies direct access to the carcass (Rodríguez-Hidalgo et al., 2015; Stiner et al., 2009), as well as cooperative hunting (Marean and Assefa, 1999; Monahan, 1998; Saladié et al., 2011; Stiner, 2013). In contrast, short-term occupations are characterized by a different transport strategy. In the case of Teixoneres Cave, the best parts of the carcass are present in both examined areas. By calculating the Relative Abundance Percentage (RA %) for the most common species, it emerges that all anatomical portions were transported, although certain elements are more frequently represented. The sample is dominated by long bones, such as metatarsi, metacarpals, femora, and tibiae, which are the bones showing the most anthropogenic marks, suggesting a preference for limbs. This observation appears to contradict the features previously applied in studies to identify occupations, as Teixoneres Cave—described as a site of repeated short-term occupations—records primarily the transport of the most nutritious parts of carcasses. We must consider the presence of carnivores in the cave, which may have influenced this outcome by introducing certain anatomical portions, to which human groups might also have gained secondary access. Notably, a percentage of bones bear traces from both accumulating agents, often making it impossible to determine which had access first. Interpretation becomes clearer, however, when bones show exclusively anthropogenic modifications or carnivore damage. Skeletal elements such as vertebrae and ribs are poorly represented, likely due to their fragility. These data reflect the behaviour of the Neanderthal groups that occupied Teixoneres cave, who tended to select and transport primarily portions with higher nutritional value or those that were easier to carry, while leaving behind those that were less practical or heavier. Conservation factors, post-depositional processes, and anthropogenic fractures resulting from marrow extraction probably played a significant role in the preservation and identification of the bones. These observations suggest that post-depositional processes may also have contributed to the fragmentation of the assemblage. This is closely related to the concept of bone fragmentation intensity, a key zooarchaeological indicator linked to in-situ attrition, butchery practices, taphonomic history, and taxonomic composition (Stiner, 2002; Outram, 2001; Lyman, 2008; Yeshurun et al., 2007). A high number of small fragments often reflects repeated breakage, typically related to marrow extraction, but the presence of trampling marks (5.7 %) highlights the contribution of natural processes as well. Since fragmentation indices do not consider the skeletal origin of fragments or distinguish between intentional and unintentional damage, random fracture patterns may suggest non-anthropogenic causes. This aligns with the concept of equifinality, where different taphonomic agents—such as human activity, carnivore gnawing, trampling, or environmental factors—can produce similar patterns (Pickering et al., 2003; Lyman, 2008), resulting in "random dynamic fragmentation" shaped by multiple overlapping processes.

Additionally, we must not overlook the presence of carnivores in the cave, which may have transported some remains outside (Arilla et al., 2020; Binford et al., 1988; Blumenschine, 1993; Camarós et al., 2013; Rosell and Blasco, 2009), increasing some of the biases observed. In

conclusion, unlike short-term occupation sites, Teixoneres Cave sub-Unit IIIb shows no evidence of distinct transport strategies based on prey size.

5.3. Anthropogenic modifications

The literature typically used to describe the duration of Neanderthal occupations states that the percentage of anthropogenic modifications (AnthM) represents an additional element used to identify the duration of occupations (Bargalló et al., 2020; Carbonell, 2002, 2012; Vaquero and Pastó, 2001; Vaquero et al., 2007, 2019; Vaquero, 2012; Leierer et al., 2019; Cascalheira and Picin, 2020; Moclán et al., 2021, 2023; Mallol et al., 2013 Mellars, 1996; Marín et al., 2020; Moncel and Rivals, 2011). Based on current interpretative frameworks, short-term occupations exhibit a medium-to-high rate of human modification, while long-term occupations show higher rates. The first limitation of the method lies in defining what constitutes a 'medium' and 'high' rate, as there is no specific value or range to identify them. Presumably, this issue could be addressed by exclusively highlighting a higher percentage of anthropic traces to support the notion of increased human activity. For this study, the features were compared with the results from Teixoneres Cave. First of all, at Teixoneres Cave, it is necessary to distinguish between the two areas under examination. In fact, the outer area presents a higher percentage of remains with anthropogenic traces, while the inner area shows fewer remains with such traces.

While this difference could be explained by the greater number of remains in the area near the entrance, a more comprehensive understanding arises when comparing anthropogenic traces with those left by carnivores (see the section on carnivore modifications). Furthermore, the higher quantity of traces left on the bone surface due to human presence is also supported by spatial distribution (Zilio et al., 2021).

Among the large mammals, deer is the species with the highest number of anthropogenic modifications in both areas, followed by bovines and roe deer. This situation may be related to the concept of the hunting spectrum, which includes the species that were hunted and the reasons why some were preferred over others (see the section on the hunting spectrum).

We can further support this hypothesis with the high percentage of bone fragmentation. In fact, there are numerous taxonomically unidentified bones, often also anatomically unidentified, that exhibit anthropogenic traces. Anatomically, in the outer area, the bones most frequently showing signs of anthropogenic intervention, in order of prevalence, are the metacarpus, humerus, metatarsus, tibia, and femur. In the inner area, the most affected bones are the femur, radius/ulna, metacarpus, and metatarsus. The bones exhibiting the highest concentration of anthropogenic traces are those richest in nutritional value (e.g., Binford, 1981; Outram, 2001; Lyman, 1994; Marean and Cleghorn, 2003; Marín et al., 2017). These carcasses were typically processed at the kill site before being transported, butchered, and distributed among the group at the residential site (e.g., Binford, 1980; Carbonell, 2012). Occasionally, metapodials were consumed at the kill sites, as observed at Qesem Cave (Blasco et al., 2019). In the case of sub-Unit IIIb of Teixoneres Cave, no specific traces related to storage and delayed consumption of bone marrow emerge, as indicated by Blasco et al. (2019). On the contrary, it is likely that the high number of metapodials is due to the morphological characteristics of these bones, which, even when fragmented, can still be identified. This is particularly evident considering that many long bones, while remaining indeterminate, show anthropogenic traces mostly in the outer area (6.7%). Nevertheless, remains that are less rich in meat, but interesting for acquiring other elements such as hide, are also found, as well as for the production of tools made from hard animal materials (e.g., mandibles or antlers) (e.g., Binford, 1981; O'Connor, 2000; Marinelli et al., 2024).

All anthropogenic traces were identified as evidence of various activities related to carcass processing performed on different anatomical elements, likely in areas of the site where resources were shared among

the group.

5.4. Carnivore modifications

At Teixoneres Cave, sub-Unit IIIb, traces of carnivore activity correspond to 11.6% in the outer area, and 30.4% in the inner area. A comparison of the data reveals that the outer area exhibits a lower percentage of carnivore modifications than the inner area, which, in turn, also shows a reduced incidence of anthropogenic modifications. The ratio between carnivore damage and human-related modifications in the two areas of Chamber X aligns perfectly with the behaviour of the carnivores identified. The inner area provided an ideal space for large carnivores to establish their den (hyenas), and likely occasional refuges for species such as lynxes and foxes (Rosell et al., 2010, 2017). As observed by Rufà et al. (2014, 2016), small carnivores and raptors played an important role in the accumulation of lagomorphs and birds in Teixoneres Cave. In fact, the Leporidae assemblage was created through a mix of contributions, with small carnivores and raptors playing a significant role. Foxes (*Vulpes vulpes*) and eagle owls (*Bubo bubo*) appear to have been the primary agents responsible for modifying the leporid remains, as indicated by mechanical alterations and evidence of digestive processes. Nevertheless, the potential involvement of other carnivores, such as lynxes, cannot be entirely ruled out as contributors to the formation of the assemblage. Although no measurements of carnivore-induced modifications (e.g., tooth mark dimensions; see Landt 2007) were conducted in this study, and despite the well-known challenges in distinguishing accumulation agents in macrofaunal contexts—as opposed to those involving small prey—the new faunal analysis provides evidence supporting the active role of bears, hyenas (as also indicated by the presence of coprolites), and foxes in the accumulation and modification of the assemblage, particularly within the inner area of the cave (Rufà et al., 2014; Rosell et al., 2010, 2017).

Human groups tend to use the area closest to the entrance when occupying a natural shelter (Bordes, 1968; Medina-Alcaide et al., 2021; Clottes and David, 1998; Cichocki and Kodric-Brown, 2014; Flannery, 2002). The result of the ratio between anthropogenic modifications (AnthM) and carnivore damage (CarnM) allows us to assert that. At Teixoneres Cave Unit III, carnivores played a predominant role in the accumulation and consumption of bones, likely also through scavenging activities following human occupation, particularly in the inner area. Furthermore, an additional aspect related to carnivore modifications is highlighted by the %MAU analysis. The analysis of %MAU shows that the bones most frequently bearing traces of carnivores belong to the limbs. This is unsurprising, as these anatomical elements are among the richest in meat mass. It can be hypothesized that these bones were scavenged from the area near the entrance when human groups left the cave, or that carnivores transported them there to feed undisturbed. The hypothesis of scavenging on remains left by humans assumes that these remains were still sufficiently fresh when the human groups abandoned the cave, allowing medium- and large-sized carnivores to occupy the more internal part of Teixoneres Cave. This would support the hypothesis of brief human occupations alternating with the presence of carnivores.

5.5. Burning

For Teixoneres Cave sub-Unit IIIb, we observed a higher percentage of bones with burning grades 2 and 3 and a lower percentage with grades 4 and 5. In some cases, also within the outer area, bones have been found exhibiting double burning coloration, each distributed across the medullary and cortical surfaces, which supports the interpretation that fire was primarily used for roasting rather than for disposal purposes. Another aspect worth highlighting is the high fragmentation of the burnt bones (99.7% measure < 5 cm), which is attributable to the fire activity itself, trampling, and often the weight of the sediment (e.g., Schiffer, 1983; Stiner et al., 1995). Spatial analysis

reveals significant differences in the distribution of burnt bones between the outer and inner areas of the cave. The outer area contains a significantly higher concentration of burnt remains, a pattern associated with hearths near the entrance of Chamber X. The outer area contains a significantly higher concentration of burnt remains, a pattern associated with hearths near the entrance of Chamber X. Although no published data are currently available regarding the presence of hearths in sub-Unit IIIb of the outer area, the presence of hearths in the overlying sub-Unit IIIa highlights the importance of this area for human occupations. In fact, in sub-Unit IIIa, near the entrance, three hearths were identified, two overlapping and a third located 50 cm away (Rosell et al., 2017). These flat, ephemeral structures, recognized by layers of red sediment covered with darker sediments containing charcoal and burnt bones (Rosell et al., 2010, 2017), suggest repeated, short-lived occupations in this zone. Moreover, burnt remains show a clear spatial gradient around these hearths, with higher concentrations of lithic tools, faunal fragments, and burnt bones near the structures, decreasing with distance. The distribution of charcoal follows a similar pattern, with areas exhibiting high degrees of bone burning (grade 5) concentrated in the outer entrance of the cave (Zilio et al., 2021). The analysis of sub-Unit IIIb further supports these observations. In the innermost part of Teixoneres Cave, the six identified burnt remains are as follows: one diaphyseal fragment of a tibia belonging to an adult deer; one diaphyseal fragment attributable to an immature medium-sized animal; two fragments assigned to a long bone of medium size; and finally, two fragments associated with an unidentified bone of indeterminate size. Considering the possibility that some of these fragments may come from the same skeletal element, we can conclude that the burnt remains correspond to at least four distinct bones. Concentrated burnt bone deposits in the outer cave area suggest short but recurrent occupations within specific zones. The inner area, by contrast, shows only sporadic burnt remains, indicating limited anthropogenic activity in this space (Zilio et al., 2021). This pattern suggests that human groups repeatedly reoccupied previously used spaces, reigniting hearths in established locations. Finally, the spatial integrity of burnt faunal remains demonstrates that carnivore activity during human absences did not significantly disturb the original archaeological arrangement. These findings corroborate the zooarchaeological data, emphasizing the deliberate organization of activities and site-use patterns during human occupations at Teixoneres Cave. In sub-Unit IIIa, directly above IIIb, near the entrance, three hearths were identified, two overlapping and a third located 50 cm away (Rosell et al., 2017). These flat, ephemeral structures, recognized by layers of red sediment covered with darker sediments containing charcoal and burnt bones (Rosell et al., 2010, 2017), suggest repeated, short-lived occupations in this zone. Moreover, burnt remains show a clear spatial gradient around these hearths, with higher concentrations of lithic tools, faunal fragments, and burnt bones near the structures, decreasing with distance. The distribution of charcoal follows a similar pattern, with areas exhibiting high degrees of bone burning (grade 5) concentrated in the outer entrance of the cave (Zilio et al., 2021). The analysis of sub-Unit IIIb further supports these observations. Concentrated burnt bone deposits in the outer cave area suggest short but recurrent occupations within specific zones. The inner area, by contrast, shows only sporadic burnt remains, indicating limited anthropogenic activity in this space (Zilio et al., 2021). This pattern suggests that human groups repeatedly reoccupied previously used spaces, reigniting hearths in established locations. Finally, the spatial integrity of burnt faunal remains demonstrates that carnivore activity during human absences did not significantly disturb the original archaeological arrangement. These findings corroborate the zooarchaeological data, emphasizing the deliberate organization of activities and site-use patterns during human occupations at Teixoneres Cave.

5.6. Evidence supporting short-term human occupations at Teixoneres Cave sub-Unit IIIb

The interpretation regarding the duration of human occupations, as inferred from our zooarchaeological and taphonomic data, is supported and reinforced by a broader set of multidisciplinary evidence. Our results point to short-term occupations by human groups who primarily exploited the most available species within a context of broad taxonomic diversity. Anthropogenic activity appears to have alternated with evidence of carnivore presence, suggesting that the cave was used intermittently by both humans and carnivores. Previous multidisciplinary studies provide evidence supporting the short and repeated occupations of human groups during the formation of sub-Unit IIIb at Teixoneres Cave. Key insights come from the study of lithics.

The important use of local raw material, mainly quartz, combined with the high fragmentation of the operative chains of the transported artefacts supports the hypothesis of high mobility of Middle Palaeolithic human groups in this territory that recurrently visited the site (Picin et al., 2020a, 2020b; Muñoz del Pozo et al., 2021; Rosell et al., 2017; Bustos-Pérez et al., 2017).

Another important element comes from the study of spatial distribution. Unit III has been interpreted as a palimpsest formed through alternating occupations by human groups and carnivores. Spatial analysis shows that faunal remains, lithic artefacts, hearths, and charcoal fragments are significantly concentrated near the cave entrance, suggesting that hominins likely carried out various activities in this area. Meanwhile, carnivores seemed to prefer the more sheltered inner sections of the cave (Zilio et al., 2021).

Previous analyses show that the human groups occupying the cave during the formation of sub-Unit IIIb hunted prey throughout the year, particularly during the summer season (Sánchez-Hernández et al., 2014, 2016, 2020; Uzunidis et al., 2024). These studies indicate that at Teixoneres Cave sub-Unit IIIb, mainly open areas are exploited in summer with a predation mostly focused on large gregarious ungulates.

Regarding the outer area, the overlap of bones with anthropogenic and carnivore traces supports the hypothesis of alternating occupations, suggesting the absence of prolonged Neanderthal presence in the cave. Moreover, the consumption of human refuse by carnivores can lead to the fragmentation and even the disappearance of several bones and other anthropogenic traces, such as hearths and lithic tools (Camarós et al., 2013; Marean and Bertino, 1994; Blasco and Rosell, 2009; Binford, 1978, 1980, 1981; Blumenschine, 1988). The presence of carnivores in the cave is linked to their use as dens by bears, hyenas, and other smaller carnivores or raptors (Arilla et al., 2019a, 2019b, 2020).

The final aspect to consider is the sedimentation rate. In Unit III of Teixoneres Cave, sub-Unit IIIb for example is dated to 45,000 cal BP at the top and over 52,000 years BP at the base, which means a sediment layer of 35–65 cm accumulated over thousands of years. During this formation period, the sediment incorporated a series of human occupation events alternating with carnivore activity. This low sedimentation rate contributed to overlap several occupational events, creating a palimpsest. It is highly likely that during subsequent occupations, human groups reused what was left by previous occupants (Lemorini et al., 2015; Preysler et al., 2015; Bailey and Galanidou, 2009; Vaquero et al., 2015), which in turn influenced the use and structuring of the space (e.g., Bailey and Galanidou, 2009). Distinguishing these occupational episodes remains a significant challenge (Rosell et al., 2017; Zilio et al., 2021), and further studies are needed to refine our understanding of the nature of these repeated occupations and the role of Teixoneres Cave in the subsistence and mobility strategies of Middle Palaeolithic human groups. The convergence of evidence from multiple disciplines corroborates and strengthens the zooarchaeological and taphonomic data presented in this study. These findings are particularly significant, as they offer a clear understanding of the subsistence strategies employed by Neanderthal groups at Teixoneres Cave. Moreover, they provide a valuable basis for comparison with other contemporaneous

archaeological contexts. This multidisciplinary alignment supports the interpretation of sub-Unit IIIb as a space associated with short-term, repeated human occupations, interspersed with carnivore activity.

6. Conclusion

The study of the faunal remains from sub-Unit IIIb of Teixoneres Cave provides valuable insights into the debate surrounding Neanderthal occupation duration. Zooarchaeological and taphonomic analyses confirm previous multidisciplinary studies, suggesting short, repeated human occupations alternating with carnivore presence. Evidence from the faunal assemblage shows that humans predominantly occupied the areas near the entrance, while carnivores favoured the more interior zones. This study's importance lies not only in providing new data on Teixoneres Cave but also in offering critical reflections on the application of zooarchaeology and taphonomy to define Neanderthal occupation duration. For this reason, it is essential to continue exploring the topic, as it will provide further insights into Neanderthal behaviour and contribute to a deeper understanding of their occupation patterns. This ongoing investigation will help refine the methods used to assess occupation duration and offer a more accurate picture of Neanderthal subsistence and spatial use.

Declarations

Ethics approval

Not applicable.

Consent to participate

All authors have provided their approval for manuscript submission.

Consent for publication

All authors consent to the submission of the manuscript to Archaeological and Anthropological Sciences.

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Declaration of competing interest

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

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Appendix A. Supplementary material

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References

- Álvarez-Lao, D.J., Rivals, F., Sánchez-Hernández, C., Blasco, R., Rosell, J., 2017. Ungulates from Teixoneres Cave (Moia, Barcelona, Spain): presence of cold-adapted elements in NE Iberia during the MIS 3. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 466, 287–302.
- Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 241 (3–4), 572–589.
- Andrews, P., Cook, J., 1985. Natural modifications to bones in a temperate setting. *Man, New Ser.* 20 (4), 675–691.
- Arilla, M., Rosell, J., Blasco, R., Domínguez-Rodrigo, M., Pickering, T.R., 2014. The “bear” essentials: actualistic research on *Ursus arctos arctos* in the Spanish Pyrenees and its implications for paleontology and archaeology. *PLoS One* 9, e102457.
- Arilla, M., Rufà, A., Rosell, J., Blasco, R., 2019a. Small carnivores' cave-dwelling: neo-taphonomic study of a badger (*Meles meles*) sett and its archaeological implications. *Hist. Biol.* 32 (7), 951–965.
- Arilla, M., Rosell, J., Blasco, R., 2019b. Contributing to characterize wild predator behavior: consumption pattern, spatial distribution and bone damage on ungulate carcasses consumed by red fox (*Vulpes vulpes*). *Archaeol. Anthropol. Sci.* 11, 2271–2291.
- Arilla, M., Rosell, J., Blasco, R., 2020. A neo-taphonomic approach to human campsites modified by carnivores. *Sci. Rep.* 10, 6659.
- Backwell, L.R., Parkinson, A.H., Roberts, E.M., d'Errico, F., Huchet, J.B., 2012. Criteria for identifying bone modification by termites in the fossil record. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 337–338, 72–87.
- Baena, J., Polo, J., Báez, S., Cuartero, F., Roca, M., Lázaro, A., Nebot, A., Pérez-González, A., Pérez, T., Rus, I., Rubio, D., Martín Puig, D., Manzano, C., González, I., Márquez, R., 2008. Tecnología musteriense en la región madrileña: un discurso enfrentado entre valles y páramos de la Meseta sur. *Treballs Arqueol.* 14, 249–278.
- Bailey, G., 2007. Time perspectives, palimpsests and the archaeology of time. *J. Anthropol. Archaeol.* 26, 198–223.
- Bailey, G., Galanidou, N., 2009. Caves, palimpsests and dwelling spaces: examples from the Upper Palaeolithic of south-east Europe. *World Archaeol.* 41 (2), 215–241.
- Bargalló, A., Gabucio, M.J., Gómez de Soler, B., Chacón, M.G., Vaquero, M., 2020. Rebuilding the daily scenario of Neanderthal settlement. *J. Archaeol. Sci. Rep.* 29, 102–139.
- Barone, R., 1976. Anatomie comparée des mammifères domestiques: Ostéologie. Vigot Frères, Paris.
- Barron, E., Pollard, D., 2002. High-resolution climate simulations of oxygen isotope stage 3 in Europe 1. *Quat. Res.* 58 (3), 296–309.
- Battista, F., Schultz, C.L., 2024. Sampling and collector biases as taphonomic filters: an overview. *An. Acad. Bras. Ciênc.* 96 (4), e20231242.
- Behrensmeier, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4 (2), 150–162.
- Behrensmeier, A.K., Kathleen, D.G., Yanagi, G.T., 1986. Trampling as a cause of bone surface damage and pseudo cut marks. *Nat.* 319, 768–771.
- Behrensmeier, A.K., Kidwell, S.M., Gastaldo, R.A., 2000. Taphonomy and Paleobiology. *Paleobiology* 26 (S4), 103–147.
- Behrensmeier, A.K., 1990. Transport/hydrodynamics of bones. In: Briggs, D.E.G., Crowther, P.R. (Eds.), *Paleobiology: a synthesis*. Blackwell Scientific Publications, Oxford, pp. 232–235.
- Bennett, J.L., 1999. Thermal alteration of buried bone. *J. Archaeol. Sci.* 26 (1), 1–8.
- Bettinger, R.L., 2009. Hunter-Gatherer foraging: five simple models. Eliot Werner Publications, Clinton Corners, New York.
- Bicho, N., Haws, J., Hockett, B., 2006. Two sides of the same coin – rocks, bones and site function of Picareiro Cave, central Portugal. *J. Anthropol. Archaeol.* 25, 485–499.
- Binford, L.R., 1968. Early Upper Pleistocene adaptations in the Levant. *Am. Anthropol.* 70, 707–717.
- Binford, L.R., 1978. Dimensional analysis of behavior and site structure: learning from an Eskimo hunting stand. *Am. Anthropol.* 43 (3), 330–361.
- Binford, L.R., 1980. Willow smoke and dogs' tails: hunter-gatherer settlement systems and archaeological site formation. *Am. Antiq.* 45, 4–20.
- Binford, R., Mills, M.G.L., Stone, N.M., 1988. Hyena Scavenging behavior and its implications for the interpretation of faunal assemblages from FLK 22 (the Zinj floor) at Olduvai Gorge. *J. Anthropol. Archaeol.* 7 (2), 99–135.
- Binford, L.R., 1981. *Bones: Ancient men and modern myths*. Academic Press, Orlando.
- Binford, L.R., 1984. Faunal remains from Klasies River Mouth, studies in archaeology. Academic Press, Orlando.
- Blasco, R., Fernández Peris, J., 2012. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). *Quat. Int.* 252, 16–31.
- Blasco, R., Rosell, J., Fernández Peris, J., Cáceres, I., Vergés, J.M., 2008. A new element of trampling: an experimental application on the Level XII faunal record of Bolomor Cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 1605–1618.
- Blasco, R., Rosell, J., 2009. Who was the first? an experimental application of carnivore and hominid overlapping marks at the Pleistocene archaeological sites. *C. r. Palevol.* 8 (6), 579–592.
- Blasco, R., Rosell, J., Domínguez-Rodrigo, M., Lozano, S., Pastó, I., Riba, D., Vaquero, M., Fernández Peris, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013a.

- Learning by heart: cultural patterns in the faunal processing sequence during the Middle Pleistocene. *PLoS One* 8, e55863.
- Blasco, R., Rosell, J., Fernandez Peris, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013b. Environmental availability, behavioural diversity and diet: a zooarchaeological approach from the TD10-1 sublevel of Gran Dolina (Sierra de Atapuerca, Burgos, Spain) and Bolomor Cave (Valencia, Spain). *Quat. Sci. Rev.* 70 (15), 124–144.
- Blasco, R., Rosell, J., Gopher, A., Barkai, R., 2014. Subsistence economy and social life: a zooarchaeological view from the 300 kya central hearth at Qesem Cave. *Israel. J. Anthropol. Archaeol.* 35, 248–268.
- Blasco, R., Rosell, J., Sañudo, P., Avi Gopher, A., Barkai, R., 2016. What happens around a fire: Faunal processing sequences and spatial distribution at Qesem Cave (300 ka), Israel. *Quat. Int.* 398, 190–209.
- Blasco, R., Rosell, J., Arilla, M., Margalida, A., Villalba, D., Gopher, A., Barkai, R., 2019. Bone marrow storage and delayed consumption at Middle Pleistocene Qesem Cave, Israel (420 to 200 ka). *Sci. Adv.* 5 (10), eaav9822.
- Blasco, R., Arilla, M., Domínguez-Rodrigo, M., Andrés, M., Ramírez-Pedraza, I., Rufá, A., Rivals, F., Rosell, J., 2020. Who peeled the bones? an actualistic and taphonomic study of axial elements from the Toll Cave Level 4, Barcelona, Spain. *Quat. Sci. Rev.* 250, 106661.
- Blumenschine, R.J., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15 (5), 483–502.
- Blumenschine, R.J., 1995. Percussion marks, tooth marks, and experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. *J. Hum. Evol.* 29, 21–51.
- Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nat* 333, 763–765.
- Blumenschine, R.J., 1993. A carnivore's view of archaeological bone assemblages. In: Hudson, J. (Ed.), *From Bones to Behaviour. The Center for Archaeological Investigations, Southern Illinois University, Carbondale, IL*.
- Boismier, W.A., Gamble, C., Coward, F., 2012. Neanderthals among mammoths: excavations at Lynford Quarry. *English Heritage Monographs, Norfolk UK*.
- Bonnichsen, R., 1979. Pleistocene bone technology in the Beringian refugium. *National Museum of Man, Ottawa*.
- Bordes, F., 1968. *The Old Stone Age*. McGraw-Hill, New York.
- Brain, C.K., 1981. *The hunters or the hunted? An introduction to African cave taphonomy*. University of Chicago Press, Chicago.
- Bromage, T.G., Boyde, A., 1984. Microscopic criteria for the determination of directionality of cutmarks on bone. *Am. J. Phys. Anthropol.* 65, 359–366.
- Bunn, H.T., 1981. Archaeological evidence for meat-eating by Plio-Pleistocene hominids from Koobi Fora and Olduvai Gorge. *Nat* 291, 574–577.
- Bunn, H.T., Ezzo, J.A., 1993. Hunting and scavenging by Plio-Pleistocene hominids: nutritional constraints, archaeological patterns, and behavioural implications. *J. Archaeol. Sci.* 20, 365–398.
- Bunn, H.T., 1982. *Meat eating and human evolution: studies on the diet and subsistence patterns of Plio-Pleistocene hominids in East Africa*. University of California, California.
- Bunn, H.T., 1983. Comparative analysis of modern bone assemblages from a hunter-gatherer camp in the Kalahari Desert, Botswana, and from a spotted hyena den near Nairobi. Kenya. In: Clutton-Brock, J., Grigson, C. (Eds.), *Animals and Archaeology: Hunters and Their Prey*. International Series, Oxford, pp. 143–148.
- Burke, A., 2000. The view from Starosele: faunal exploitation at a middle Palaeolithic site in western Crimea. *Int. J. Osteoarchaeol.* 10, 325–335.
- Bustos-Pérez, G., Chacón, M.G., Rivals, F., Blasco, R., Rosell, J., 2017. Quantitative and qualitative analysis for the study of Middle Palaeolithic retouched artifacts: Unit III of Teixoneres cave (Barcelona, Spain). *J. Archaeol. Sci. Rep.* 12, 658–672.
- Cáceres, I., 2002. *Tafonomía de yacimientos antrópicos en Karst. Complejo Galería (Sierra de Atapuerca, Burgos), Vanguard Cave (Gibraltar) y Abric Romaní (Capellades, Barcelona)*. PhD Dissertation, Universitat Rovira i Virgili.
- Camarós, E., Cueto, M., Teira, L.C., Tapia, J., Cubas, M., Blasco, R., Rosell, J., Rivals, F., 2013. Large carnivores as taphonomic agents of space modification: an experimental approach with archaeological implications. *J. Archaeol. Sci.* 40 (2), 1361–1368.
- Canals, A., Vallverdú, J., Carbonell, E., 2003. New archaeo-stratigraphic data for the TD6 level in relation to *Homo antecessor* (Lower Pleistocene) at the site of Atapuerca, North-Central Spain. *Geoarchaeol.* 18 (5), 481–504.
- Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing in bovid long bones. *Am. Antiq.* 59, 724–748.
- Carbonell, E., 2002. *Abric Romaní Nivell I. Models d'ocupació de curta durada de fa 46.000 anys a la Cinglera del Capelló (Capellades, Anoia, Barcelona)*. Grup de Recerca d'Autoecologia Humana del Quaternari, Universitat Rovira i Virgili, Tarragona.
- Carbonell, E., 2012. High resolution archaeology and Neanderthal behavior: time and space in Level J of Abric Romaní (Capellades, Spain). Springer, New York.
- Cascalheira, J., Picin, A., 2020. *Short-term occupations in paleolithic archaeology: definition and interpretation*. Springer Cham (Interdisciplinary Contributions to Archaeology).
- Cerdá, M.P., García-Prósper, E., Serra, A.S., 2005. Estudio bioarqueológico de las cremaciones del funerario romano del "solar de la morería" de Sagunto. *ARSE: Boletín anual del Centro Arqueológico Saguntino* 39, 229–268.
- Chase, P.G., 1987. Spécialisation de la chasse et transition vers le Paléolithique supérieur. *L'anthropologie* 91, 175–188.
- Churchill, S.E., 2014. *Thin on the Ground: Neanderthal Biology, Archeology, and Ecology*. Wiley-Blackwell, Hoboken, N.J.
- Clark, J., Kietzke, K.K., 1967. Paleocology of the lower Nodular Zone, Brule Formation, in the Big Badlands of South Dakota. In: Clark, J., Beerbower, J.R., Kietzke, K.K. (Eds.), *Oligocene Sedimentation, Stratigraphy, Paleocology and Paleoclimatology in the Big Badlands of South Dakota*. Fieldiana Geology Memoirs 5, 111–155.
- Clottes, J., Lewis-Williams, D., 1998. *The Shamans of Prehistory: Trance and Magic in the Painted Caves*. Harry N. Abrams, New York.
- Coard, R., 1999. One bone, two bones, wet bones, dry bones: transport potentials under experimental conditions. *J. Archaeol. Sci.* 26, 1369–1375.
- Coil, R., Yezzi-Woodley, K., Tappen, M., 2020. Comparisons of impact flakes derived from hyena and hammerstone long bone breakage. *J. Archaeol. Sci.* 120, 105167.
- Costamagno, S., Théry-Parisot, I., Castel, J.C., Brugal, J.P., 2009. Combustible ou non? Analyse multifactorielle et modèles explicatifs sur des ossements brûlés paléolithiques. In: Théry-Parisot I., Costamagno, S., Henry, A. (Eds.), *Proceedings of the XVth World Congress UISPP (Lisbon, 4–9 September 2006)*. BAR Int. Ser. 1914. Archaeopress, Oxford, 69–84.
- Costamagno, S., Meignen, L., Beauval, C., Vandermeersch, B., Maureille, B., 2006. Les Pradelles (Marillac-le-Franc, France): a Mousterian reindeer hunting camp? *J. Anthropol. Archaeol.* 25, 466–484.
- Courtenay, L.A., Huguet, R., Yravedra, J., 2020. Scratches and grazes: a detailed microscopic analysis of trampling phenomena. *J. Microsc.* 277, 107–117.
- Courty, M.A., Goldberg, P., MacPhail, R., 1989. *Soils and micromorphology in archaeology*, manuals in Archaeology. Cambridge Univ. Press, Cambridge.
- Daujeard, C., Fernandes, P., Guadelli, J.L., Moncel, M.H., Santagata, C., Raynal, J.P., 2012. Neanderthal subsistence strategies in Southeastern France between the plains of the Rhône Valley and the mid-mountains of the Massif Central (MIS 7 to MIS 3). *Quat. Int.* 252, 32–47.
- Daujeard, C., Moncel, M.H., 2010. On Neanderthal subsistence strategies and land use: a regional focus on the Rhone Valley area in southeastern France. *J. Anthropol. Archaeol.* 29, 368–391.
- Daujeard, C., Moncel, M.H., Fiore, I., Tagliacozzo, A., Bindon, P., Raynal, J.P., 2014. Middle Palaeolithic bone retouchers in Southeastern France: variability and functionality. *Quat. Int.* 326–327, 492–518.
- Daujeard, C., Vettese, D., Britton, K., Béarez, P., Boubles, N., Crégut-Bonnouze, E., Desclaux, E., Lateur, N., Pike-Tay, A., Rivals, F., Allué, E., Chacón, M.G., Puaud, S., Richard, M., Courty, M.-A., Gallotti, R., Hardy, B., Bahain, J.J., Falguères, C., Pons-Branchu, E., Valladas, H., Moncel, M.H., 2019. Neanderthal selective hunting of reindeer? the case study of Abri du Maras (south-eastern France). *Archaeol. Anthropol. Sci.* 11, 985–1011.
- David, F., Enloe, J.G., 1993. L'exploitation des animaux sauvages de la fin du Paléolithique moyen au Magdalénien. In: Desse, J., Audouin-Rouzeau, F. (Eds.), *Exploitation des animaux sauvages à travers le temps, 13èmes Rencontres Internationales d'Archéologie et d'Histoire d'Antibes*, Éditions APDCA, Juan-les-Pins, pp. 29–47.
- Díez, J.C., Rosell, J., 1998. Estrategias de subsistencia de los homínidos de la Sierra de Atapuerca. In: Aguirre, E. (Ed.), *Atapuerca y la Evolución Humana*. Fundación Ramón Areces, Madrid, 361–390.
- Domínguez-Rodrigo, M., Barba, R., 2006. New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: the carnivore-hominid carnivore hypothesis falsified. *J. Hum. Evol.* 50, 170–194.
- Domínguez-Rodrigo, M., Pickering, T.R., 2003. Early hominid hunting and scavenging: a zooarchaeological review. *Evol. Anthropol.* 12, 275–282.
- Domínguez-Rodrigo, M., de Juana, S., Galán, A.B., Rodríguez, M., 2009. A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 36, 2643–2654.
- Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *J. Archaeol. Sci.* 30, 1385–1391.
- Dusseldorp, G.L., 2009. *A View to a Kill: Investigating Middle Palaeolithic subsistence using an optimal foraging perspective*. Sidestone Press, Leiden.
- Enloe, J.G., 2006. Geological processes and site structure: assessing integrity at a late Paleolithic open-air site in northern France. *Geoarchaeol.* 216 (6), 523–540.
- Faith, J.T., Lyman, R.L., 2019. *Paleozoology and paleoenvironments: fundamentals, assumptions, techniques*. Cambridge University Press.
- Farizo, C., David, F., Jaubert, J., Leclerc, J., 1994. Fonctionnement du site: Hommes et bisons. In: *Hommes et bisons du Paléolithique Moyen à Mauran (Haute-Garonne)*. Gall. Préhist. Suppl. 30, 239–245.
- Farrand, W.R., 2001. Sediments and stratigraphy in rockshelters and caves: a personal perspective on lessons learned. *J. Archaeol. Sci.* 28 (11), 1383–1400.
- Fejfar, O., Kaiser, T.M., 2005. Insect bone-modification and paleoecology of Oligocene mammal-bearing sites in the Doupov Mountains, Northwestern Bohemia. *Palaeontol. Electron.* 8 (1), 1–11.
- Fernandez, P., 2009. De l'estimation de l'âge individuel dentaire au modèle descriptif des structures d'âge des cohortes fossiles: L'exemple des Equidae et du time specific model en contextes paléobiologiques pléistocènes. *Bull. Soc. Préhist. Fr.* 106, 5–14.
- Fernández-García, M., López-García, J.M., Royer, A., Lécuyer, C., Rivals, F., Rufá, A., Blasco, R., Rosell, J., 2022. New insights in Neanderthal palaeoecology using stable oxygen isotopes preserved in small mammals as palaeoclimatic tracers in Teixoneres Cave (Moia, northeastern Iberia). *Archaeol. Anthropol. Sci.* 14, 106.
- Fernández-Jalvo, Y., Andrews, P., 2016. *Atlas of taphonomic identifications. Vertebrate paleobiology and paleoanthropology Series*. Springer, Dordrecht.
- Fernández-Jalvo, Y., Scott, L., Andrews, P., 2011. Taphonomy in palaeoecological interpretations. *Quat. Sci. Rev.* 30 (11–12), 1296–1302.
- Fernández-López, S., 1991. Taphonomic concepts for a theoretical biochronology. *Rev. Esp. Paleontol.* 6 (1), 37–49.
- Fernández-López, S.R., Fernández-Jalvo, Y., 2002. The limit between biostratigraphy and fossilization. In: De Renzi, M., Pardo-Alonso, M.V., Belinón, M., Peñalver, E.,

- Montoya, P., Márquez-Aliaga, A. (Eds.), Current topics on taphonomy and fossilization. Ajuntament de València, València, pp. 27–37.
- Flannery, K.V., 2002. The cultural evolution of civilizations. Harvard University Press, Cambridge.
- Gabucio, M.J., Cáceres, I., Rosell, J., Saladié, P., Vallverdú, J., 2014. From small bone fragments to Neanderthal activity areas: the case of Level O of the Abric Romaní (Capellades, Barcelona, Spain). *Quat. Int.* 330, 36–51.
- Gallo, G., Aldeias, V., Stahlschmidt, M., 2025. Revisiting the thermal alteration of buried bone. *J. Archaeol. Sci. Rep.* 63, 105080.
- Gifford-Gonzalez, D., 1989. Ethnographic analogues for interpreting modified bones: some cases from East Africa. In: Bonnichsen, R., Sorg, M. (Eds.), Bone modification, 179–246.
- Goldberg, P., McPhail, R.I., 2006. Practical and Theoretical Geoarchaeology. Blackwell Science, Malden, MA.
- Grayson, D.K., 1984. Quantitative Zooarchaeology: Topics in the Analysis of Archaeological Faunas. Academic Press, Orlando.
- Hillson, S., 1992. Mammal bones and teeth: an introductory guide to methods of identification. Institute of Archaeology. University College London, London.
- Isaac, G.L., 1983. Bones in contention: competing explanations for the juxtaposition of Early Pleistocene artifacts and faunal remains. *Anim. Archaeol.* 1, 3–19.
- Jans, M.M.E., Nielsen-Marsh, C.M., Smith, C.I., Collins, M.J., Kars, H., 2004. Characterisation of microbial attack on archaeological bone. *J. Archaeol. Sci.* 31, 87–95.
- Kelly, R.L., 1992. Mobility/sedentism: Concepts, archaeological measures, and effects. *Annu. Rev. Anthropol.* 21, 43–66.
- Klein, R.G., Cruz-Uribe, K., 1984. The Analysis of Animal Bones from Archaeological Sites. Prehistoric Archeology and Ecology series. The University of Chicago Press, Chicago.
- Landt, M.J., 2007. Tooth marks and human consumption: ethnoarchaeological mastication research among foragers of the Central African Republic. *J. Archaeol. Sci.* 34 (10), 1629–1640.
- Lateur, N., Moncel, M.H., Mocochain, L., Fernandes, P., 2023. Fréquentations des réseaux karstiques profonds par Néanderthal. Nouveaux exemples à la grotte de Saint-Marcel (Ardèche, France). *C. R. Palevol.* 22 (15), 265–277.
- Leierer, L., Jambriña-Enríquez, M., Herrera-Herrera, A.V., Connolly, R., Hernández, C. M., Galván, B., Mallol, C., 2019. Insights into the timing, intensity and natural setting of Neanderthal occupation from the geoarchaeological study of combustion structures: a micromorphological and biomarker investigation of El Salt, unit Xb, Alcoy, Spain. *Plos One* 14 (4), e0214955.
- Lemorini, C., Venditti, F., Assaf, E., Parush, Y., Barkai, R., Gopher, A., 2015. The function of recycled lithic items at late lower Paleolithic Qesem Cave, Israel: an overview of the use-wear data. *Quat. Int.* 361, 103–112.
- López-García, J.M., Blain, H.A., Burjachs, F., Ballesteros, A., Allué, E., Cuevas-Ruiz, G.E., Rivals, F., Blasco, R., Morales, J.I., Rodríguez-Hidalgo, A., Carbonell, E., Serrat, D., Rosell, J., 2012. A multidisciplinary approach to reconstructing the chronology and environment of southwestern European Neanderthals: The contribution of Teixoneres cave (Moia, Barcelona, Spain). *Quat. Sci. Rev.* 43, 33–44.
- Lubrano, V., Rufá, A., Blasco, R., Rivals, F., Rosell, J., 2025. Solving the puzzle of Neanderthal occupations: A reassessment of temporal indicators of occupation duration. *Archaeol. Anthropol. Sci.* in press.
- Lucas, G., 2005. The archaeology of time. Routledge, London.
- Lyman, R.L., 1994. Vertebrate taphonomy. Cambridge University Press, Cambridge.
- Lyman, R.L., 2008. Quantitative paleozoology. Cambridge University Press.
- Mallol, C., Hernández, C., 2016. Advances in palimpsest dissection. *Quat. Int.* 417, 1–2.
- Mallol, C., Hernández, C.M., Cabanes, D., Sistiaga, A., Machado, J., Rodríguez, Á., Galván, B., 2013. The black layer of Middle Palaeolithic combustion structures: Interpretation and archaeostratigraphic implications. *J. Archaeol. Sci.* 40 (5), 2515–2537.
- Marean, C.W., Assefa, Z., 1999. Zooarchaeological evidence for the faunal exploitation behavior of Neanderthals and early modern humans. *Evol. Anthropol.* 8, 22–37.
- Marean, C.W., Bertino, L., 1994. Intrasite spatial analysis of bone: Subtracting the effect of secondary carnivore consumers. *Am. Ant.* 59 (4), 748–768.
- Marean, C.W., Cleghorn, N.E., 2003. Large mammal skeletal element transport: applying foraging theory in a complex taphonomic system. *J. Tapho.* 1 (1), 15–42.
- Marín, J., Saladié, P., Rodríguez-Hidalgo, A., Carbonell, E., 2017. Neanderthal hunting strategies inferred from mortality profiles within the Abric Romaní sequence. *PLoS One* 12 (11), e0186970.
- Marín, J., Daujeard, C., Saladié, P., Rodríguez-Hidalgo, A., Vettese, D., Rivals, F., Boulbes, N., Crégut-Bonnoure, E., Lateur, N., Gallotti, R., Arbez, L., Puaud, S., Moncel, M.H., 2020. Neanderthal faunal exploitation and settlement dynamics at the Abri du Maras, level 5 (south-eastern France). *Quat. Sci. Rev.* 243, 106472.
- Marinelli, F., Moncel, M.H., Lemorini, C., 2024. The use of bones as tools in late lower Paleolithic of Central Italy. *Sci. Rep.* 14, 11666.
- Medina-Alcaide, M.A., Garate, D., Intxaurre, I., Sanchidrián, J.L., Rivero, O., Ferrier, C., Libano, I., 2021. The conquest of the dark spaces: an experimental approach to lighting systems in Paleolithic caves. *PLoS One* 16 (6).
- Mellars, P.A., 1973. The character of the Middle–Upper Palaeolithic transition in Southwest France. In: Renfrew, C. (Ed.), The Explanation of Cultural Change, London, pp. 255–276.
- Mellars, P., 1973. The character of the middle–upper Palaeolithic transition in southwest France. In: Renfrew, C. (Ed.), The Explanation of Culture Change: Models in Prehistory. Duckworth, London, pp. 255–276.
- Mellars, P.A., 1996. The Neanderthal legacy. Princeton University Press, Princeton.
- Mentzer, S.M., 2009. Bone as a fuel source: the effects of initial fragment size distribution. In: Fuel management during the Palaeolithic and Mesolithic period. New tools, new interpretations. Proceedings of the XVth World Congress (Lisbon, 4–9 September 2006). Archaeopress, Oxford, BAR Int. Ser. 1914, 49–60.
- Moclán, A., Huguet, R., Márquez, B., Laplana, C., Galindo-Pellicena, M.A., García, N., Hugues-Alexandre, B., Álvarez-Laó, D.J., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2021. A Neanderthal hunting camp in the central system of the Iberian Peninsula: a zooarchaeological and taphonomic analysis of the Navalmaillo Rock Shelter (Pinilla del Valle, Spain). *Quat. Sci. Rev.* 269, 107–142.
- Moclán, A., Huguet, R., Márquez, B., Álvarez-Fernández, A., Laplana, C., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2023. Identifying activity areas in Neanderthal hunting camps (the Navalmaillo rock shelter, Spain) via spatial analysis. *Archaeol. Anthropol. Sci.* 15, 44.
- Monahan, C.M., 1998. The Hadza carcass transport debate revisited and its archaeological implications. *J. Archaeol. Sci.* 25, 405–424.
- Moncel, M.H., 2010. L'Abri des Pêcheurs (Ardèche, sud-est France). Des occupations néandertaliennes dans une «grotte en forme de fissure». *Annales D'université "valahia" Târgoviște. Section D'archéologie et D'histoire* 12 (2), 7–21.
- Moncel, M.H., Daujeard, C., Crégut-Bonnoure, E., Fernandez, P., Faure, M., Guérin, C., 2004. L'occupation de la grotte de Saint-Marcel (Ardèche, France) au Paléolithique moyen: Stratégie d'exploitation de l'environnement et type d'occupation de la grotte. L'exemple des couches i, j et j'. *Bull. Soc. Prehist. Fr.* 101 (2), 257–304.
- Moncel, M.H., Rivals, F., 2011. On the question of short-term Neanderthal site occupations: Payre, France (MIS 8–7), and Taubach/Weimar, Germany (MIS 5). *J. Anthropol. Res.* 67 (1), 47–75.
- Moncel, M.H., Allué, E., Bailon, S., Barshay-Szmidt, C., Béarez, P., Crégut-Bonnoure, E., Daujeard, C., Desclaux, E., Debard, E., Lartigot-Campin, A.S., Puaud, S., Roger, T., 2015. Evaluating the integrity of palaeoenvironmental and archaeological records in MIS 5 to 3 karst sequences from southeastern France. *Quat. Int.* 378, 22–39.
- Moncel, M., Daujeard, C., 2012. The variability of the Middle Palaeolithic on the right bank of the Middle Rhône Valley (southeast France): Technical traditions or functional choices? *Quat. Int.* 247, 103–124.
- Moncel, M. H., Daujeard, C., Crégut-Bonnoure, E., Boulbes, N., Puaud, S., Debard, E., Bailon, S., Desclaux, E., Escude, E., Roger, T., Dubar, M., 2010. Nouvelles données sur les occupations humaines du début du Pléistocène supérieur de la moyenne vallée du Rhône (France). Les sites de l'Abri des Pêcheurs, de la Baume Flandin, de l'Abri du Maras et de la Grotte du Figuier (Ardèche). *Quaternaire. Revue de l'Association française pour l'étude du Quaternaire*, 21(4), 385–411.
- Moncel, M.H., Fernandes, P., Willmes, M., James, H., Grün, R., 2019. Rocks, teeth, and tools: new insights into early Neanderthal mobility strategies in South-Eastern France from lithic reconstructions and strontium isotope analysis. *PLoS One* 14, e0214925.
- Morin, E., 2010. Taphonomic implications of the use of bone as fuel. *Palethnologie. Archéologie et sciences humaines* 2. <http://journals.openedition.org/palethnologie/9086>.
- Muñoz del Pozo, A., Gómez de Soler, B., BustosPérez, G., Chacón, M.G., Picin, A., Blasco, R., Rivals, F., Rufá, A., Rosell, J., 2021. Analysis and classification of Middle Palaeolithic lithic raw materials from Teixoneres Cave: Project overview and initial results. *Acta IMEKO*, 12(3), 1–7.
- O'Connell, J.F., Hawkes, K., Blurton-Jones, N.G., 1992. Patterns in the distribution, site structure and assemblage composition of Hadza kill-butcher sites. *J. Archaeol. Sci.* 19, 319–345.
- O'Connor, T., 2000. The archaeology of animal bones. University Press, Texas.
- Ochando, J., Carrión, J.S., Blasco, R., Rivals, F., Rufá, A., Demuro, M., Arnold, L.J., Amorós, G., Munuera, M., Fernández, S., Rosell, J., 2020. Neanderthals in a highly diverse, Mediterranean-Eurasian forest ecotone: the Pleistocene pollen records of Teixoneres Cave, northeastern Spain. *Quat. Sci. Rev.* 241, 106429.
- Outram, A.K., 2001. A new approach to identifying bone marrow and grease exploitation: why the "indeterminate" fragments should not be ignored. *J. Archaeol. Sci.* 28 (4), 401–410.
- Pales, L., Lambert, C., 1971. Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire. University of Michigan Library Digital Collections.
- Pesquero, M.D., Ascaso, C., Alcalá, L., Fernández-Jalvo, Y., 2010. A new taphonomic bioerosion in a Miocene lakeshore environment. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295 (1–2), 192–198.
- Picin, A., Chacón, M.G., Gómez de Soler, B., Blasco, R., Rivals, F., Rosell, J., 2020a. Neanderthal mobile toolkit in short-term occupations at Teixoneres Cave (Moia, Spain). *J. Archaeol. Sci. Rep.* 29, 102165.
- Picin, A., Blasco, R., Arilla, M., Rivals, F., Chacón, M.G., Gómez de Soler, B., Talamo, S., Rosell, J., 2020b. Short-term Neanderthal occupations and carnivores in the North-east of Iberian Peninsula. In: Cascabeira, J., Picin, A. (Eds.), Short-Term Occupations in Paleolithic Archaeology: Definition and Interpretation. Interdisciplinary Contributions to Archaeology. Springer Cham, pp. 183–216.
- Pickering, T.R., 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *Int. J. Osteoarchaeol.* 12 (2), 127–141.
- Pickering, T.R., Egeland, C.P., 2006. Experimental patterns of hammerstone percussion damage on bones: implications for inferences of carcass processing by humans. *J. Hum. Evol.* 50, 443–470.
- Pickering, T.R., Marean, C.W., Dominguez-Rodrigo, M., 2003. Importance of limb bone shaft fragments in zooarchaeology: a response to "on in situ attrition and vertebrate body part profiles". *J. Archaeol. Sci.* 30, 1469–1482.
- Pickering, T.R., Dominguez-Rodrigo, M., Heaton, J.L., Yravedra, J., Barba, R., Bunn, H. T., Musiba, C., Baquedano, E., Diez-Martín, F., Mabulla, A., Brain, C.K., 2013. Taphonomy of ungulate ribs and the consumption of meat and bone by 1.2-million-year-old hominins at Olduvai Gorge, Tanzania. *J. Archaeol. Sci.* 40, 1295–1309.
- Potts, R., Shipman, P., 1981. Cutmarks made by stone tools on bones from Olduvai Gorge, Tanzania. *Nature* 291, 577–580.

- Preysler, J.B., Nieto-Márquez, I.O., Navas, C.T., Cueto, S.B., 2015. Recycling in abundance: Re-use and recycling processes in the lower and Middle Paleolithic contexts of the central Iberian Peninsula. *Quat. Int.* 361, 142–154.
- Quintana, C.A., 2007. Marcas de dientes de roedores en huesos de sitios arqueológicos de las sierras de Tandilia, Argentina. *Archaeofauna* 16, 185–196.
- Rendu, W., Armand, D., 2009. Saisonnalité de prédation du Bison du gisement moustérien de La Quina (Gardes-le-Pontaroux, Charente), niveau 6c. Apport à la compréhension des comportements de subsistance. *Bull. Soc. Prehist. Fr.* 106, 679–690.
- Rendu, W., Bourguignon, L., Costamagno, S., Meignen, L., Soulier, M.-C., Armand, D., Beauval, C., David, F., Griggo, C., Jaubert, J., Maureille, B., Park, S.-J., 2011. Mousterian hunting camps: Interdisciplinary approach and methodological considerations. In: Bon, F., Costamagno, S., Valdeyron, N. (Eds.), *Hunting camps in Prehistory: Current archaeological approaches*. P@lethnology 3, 151–166.
- Richard, M., Pons-Branchu, E., Genuite, K., Jaillet, S., Joannes-Boyau, R., Wang, N., Genty, D., Cheng, H., Price, G.J., Pierre, M., Dapoigny, A., Falguères, C., Tombret, O., Voinchet, P., Bahain, J.J., Moncel, M.H., 2021. Timing of Neanderthal occupations in the southeastern margins of the Massif Central (France): a multimethod approach. *Quat. Sci. Rev.* 273, 107241.
- Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., Carbonell, E., 2015. Hominin subsistence and site function of TD10.1 bone bed level at Gran Dolina site (Atapuerca) during the late Acheulean. *J. Quat. Sci.* 30, 679–701.
- Rosell, J., Blasco, R., Rivals, F., Chacón, G., Menéndez, L., Morales, J.I., Rodríguez-Hidalgo, A., Cebriá, A., Carbonell, E., Serrat, D., 2010. A stop along the way: the role of Neanderthal groups at Level III of Teixoneres Cave (Moia, Barcelona, Spain). *Quaternaire* 21 (2), 139–154.
- Rosell, J., Baquedano, E., Blasco, R., Camarós, E., 2012. New insights on hominid-carnivore interactions during the Pleistocene. *J. Taphon.* 10 (3–4), 125–128.
- Rosell, J., Blasco, R., 2009. Home sharing: Carnivores in anthropogenic assemblages of the Middle Pleistocene. *J. Taphon.* 7 (4), 305–324.
- Rosell, J., Blasco, R., Rivals, F., Chacón, G.M., Arilla, M., Camarós, E., Rufá, A., Sánchez-Hernández, C., Picin, A., Andrés, M., Blain, H.A., López-García, J.M., Iriarte, E., Cebriá, A., 2017. A resilient landscape at Teixoneres Cave (MIS 3; Moia, Barcelona, Spain): the Neanderthals as disrupting agents. *Quat. Int.* 435, 195–210.
- Rufá, A., Blasco, R., Rivals, F., Rosell, J., 2014. Leporids as a potential resource for predators (hominins, mammalian carnivores, raptors): an example of mixed contribution from level III of Teixoneres Cave (MIS 3, Barcelona, Spain). *C.R. Palevol* 13, 665–680.
- Rufá, A., Blasco, R., Rivals, F., Rosell, J., 2016. Who eats whom? Taphonomic analysis of the avian record from the Middle Paleolithic site of Teixoneres Cave (Moia, Barcelona, Spain). *Quat. Int.* 421, 103–115.
- Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Cáceres, I., Vallverdú, J., Rosell, J., Bermúdez de Castro, J.M., Carbonell, E., 2011. Carcass transport decisions in Homo antecessor subsistence strategies. *J. Hum. Evol.* 61, 425–446.
- Sánchez-Hernández, C., Rivals, F., Blasco, R., Rosell, J., 2014. Short, but repeated Neanderthal visits to Teixoneres Cave (MIS 3, Barcelona, Spain): a combined analysis of tooth microwear patterns and seasonality. *J. Archaeol. Sci.* 49, 317–325.
- Sánchez-Hernández, C., Rivals, F., Blasco, R., Rosell, J., 2016. Tale of two timescales: Combining tooth wear methods with different temporal resolutions to detect seasonality of Palaeolithic hominin occupational patterns. *J. Archaeol. Sci. Rep.* 6, 790–797.
- Sánchez-Hernández, C., Gourichon, L., Blasco, R., Carbonell, E., Chacón, G., Galván, B., Hernández-Gómez, C.M., Rosell, J., Saladié, P., Soler, J., Soler, N., Vallverdú, J., Rivals, F., 2020. High-resolution Neanderthal settlements in Mediterranean Iberian Peninsula: a matter of altitude? *Quat. Sci. Rev.* 247, 106523.
- Sánchez-Romero, L., Benito-Calvo, A., Marín-Arroyo, A.B., Agudo-Pérez, L., Karampaglidis, T., Rios-Garizar, J., 2020. New insights for understanding spatial patterning and formation processes of the Neanderthal occupation in the Amalda I cave (Gipuzkoa, Spain). *Sci. Rep.* 10, 8733. Schiffer, M.B., 1983. Toward the identification of formation processes. *Am. Antiq.* 48, 675–703.
- Schiffer, M.B., 1983. Toward the identification of formation processes. *Am. Antiq.* 48, 675–703.
- Schmid, E., 1972. *Atlas of Animal Bones for Prehistorians, Archaeologists and Quaternary Geologists*. Elsevier Publishing Company, Amsterdam.
- Schoville, B.J., Otárola-Castillo, E., 2014. A model of hunter-gatherer skeletal element transport: the effect of prey body size, carriers, and distance. *J. Hum. Evol.* 73, 1–14.
- Sciuto, C., Lamesa, A., Whitaker, K., Yamaç, A., 2021. *Carved in Stone: The Archaeology of Rock-Cut Sites and Stone Quarries*. BAR Publishing, Oxford.
- Selvaggio, M.M., 1994. Carnivore tooth marks and stone tool butchery marks on scavenged bones: archaeological implications. *J. Hum. Evol.* 27, 215–228.
- Serra-Rafols, J.D.C., Villalta, J.F., Thomas, J., Fuste, M., 1957. *Livret guide des excursions B2-B3: Alentours de Barcelona et Moia*. In: *V Congrès International del INQUA, Madrid*, pp. 5–25.
- Serrat, D., Albert, J.F., 1973. Estudio sedimentológico de los materiales de relleno de la Cova de les Teixoneres. *Speleon* 20, 63–70.
- Shipman, P., Rose, J., 1983. Early hominid hunting, butchering, and carcass processing behaviors: approaches to the fossil record. *J. Anthropol. Archaeol.* 2, 57–98.
- Shipman, P., Fisher, D.C., Rose, J., 1984a. Mastodon butchery: Microscope evidence of carcass processing and bone tool use. *Paleobiol* 10 (3), 358–365.
- Shipman, P., Foster, G., Schoeninger, M., 1984b. Burnt bones and teeth: an experimental study of color, morphology, crystal structure and shrinkage. *J. Archaeol. Sci.* 11 (4), 307–325.
- Shipman, P., 1981. *Life History of A Fossil: An Introduction to Taphonomy and Paleocology*. Harvard University Press, Cambridge.
- Soulier, M.C., 2008. *Étude des dents de renne du gisement des Pradelles (Charente, France): revue critique des méthodes d'estimation d'âge dentaire, saisonnalité et profils de mortalité*. Mémoire de Master, Université Toulouse II - Le Mirail, Toulouse.
- Steele, T.E., 2003. Using mortality profiles to infer behavior in the fossil record. *J. Mammal.* 84, 418–430.
- Steele, T.E., 2002. Red deer: Their ecology and how they were hunted by Late Pleistocene hominids in Western Europe. PhD Dissertation, Stanford University, Stanford.
- Stiner, M.C., 2002. On in situ attrition and vertebrate body part profiles. *J. Archaeol. Sci.* 29 (9), 979–991.
- Stiner, M.C., 2013. An unshakable Middle Paleolithic? trends versus conservatism in the predatory niche and their social ramifications. *Curr. Anthropol.* 54, 288–304.
- Stiner, M.C., Kuhn, S.L., Weiner, S., Bar-Yosef, O., 1995. Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* 22 (2), 223–237.
- Stiner, M.C., Barkai, R., Gopher, A., 2009. Cooperative hunting and meat sharing 400–200 kya at Qesem Cave. *Israel. Proc. Natl. Acad. Sci.* 106, 13207–13212.
- Talamo, S., Blasco, R., Rivals, F., Picin, A., Chacón, M.G., Iriarte, E., López-García, J.M., Blain, H.A., Arilla, M., Rufá, A., Sánchez-Hernández, C., Andrés, M., Camarós, E., Ballesteros, A., Cebriá, A., Rosell, J., Hublin, J.J., 2016. The radiocarbon approach to Neanderthals in a carnivore den site: a well-defined chronology for Teixoneres Cave (Moia, Barcelona, Spain). *Radiocarb.* 58 (2), 247–265.
- Terradas, X., Ortega, D., 2017. Flint quarrying in north-eastern Iberia: Quarry sites and the initial transformation of raw material. *Antiquity* 91, 1–6.
- Théry-Parisot, I., 2002. Fuel management (bone and wood) during the lower Aurignacian in the Pataud rock shelter (lower Palaeolithic, Les Eyzies de Tayac, Dordogne, France). *Contribution of experimentation. J. Archaeol. Sci.* 29 (12), 1415–1421.
- Tissoux, H., Falguères, C., Bahain, J.J., Rosell, J., Cebriá, A., Carbonell, E., Serrat, D., 2006. Datation par les séries de l'Uranium des occupations moustériennes de la Grotte des Teixoneres (Moia, Province de Barcelone, Espagne). *Quaternaire* 17, 27–33.
- Torres, T., Ortiz, J.E., Cobo, R., De la Hoz, P., García-Redondo, A., Grün, R., 2007. Hominid exploitation of the environment and cave bear populations, the case of *Ursus spelaeus* Rosenmüller-Heinroth in Amutxate cave (Aralar, Navarra-Spain). *J. Hum. Evol.* 52, 1–15.
- Turq, A., 1988. *Le Paléolithique inférieur et moyen en Haut-Agenais: état des recherches*. Rev. Agenais 115, 83–112.
- Uzunidis, A., Blasco, R., Brugal, J.-P., Fourcade, T., Ochando, J., Rosell, J., Rousset, A., Rufá, A., Sánchez Goñi, M.F., Texier, P.J., Rivals, F., 2024. Neanderthal hunting grounds: the case of Teixoneres Cave (Spain) and Pié Lombard rockshelter (France). *J. Archaeol. Sci.* 168, 106007.
- Uzunidis, A., Rivals, F., 2023. Where and when? Combining dental wear and death seasons to improve paleoenvironmental reconstruction through ungulate diets. *J. Archaeol. Sci. Rep.* 52.
- Van Andel, T.H., 2002. The climate and landscape of the Middle Part of the Weichselian Glaciation in Europe: the stage 3 Project. *Quat. Res.* 57, 2–8.
- Vaquero, M., 2008. The history of stones: Behavioural inferences and temporal resolution of an archaeological assemblage from the Middle Palaeolithic. *J. Archaeol. Sci.* 35 (12), 3178–3185.
- Vaquero, M., Bargalló, A., Chacón, M.G., Romagnoli, F., Sañudo, P., 2015. Lithic recycling in a Middle Paleolithic expedition context: evidence from the Abric Romaní (Capellades, Spain). *Quat. Int.* 361, 212–228.
- Vaquero, M., Chacón, M.G., Rando, J.M., 2007. The interpretative potential of lithic refits in a Middle Paleolithic site: the Abric Romaní (Capellades, Spain). In: Schürmann, U.A., De Bie, M. (Eds.), *Fitting Rocks. Lithic refitting examined*, BAR Int. Ser. S1596, Archaeopress, Oxford, pp. 75–89.
- Vaquero, M., Pastó, I., 2001. The definition of spatial units in Middle Palaeolithic sites: the hearth-related assemblages. *J. Archaeol. Sci.* 2, 1209–1220.
- Vaquero, M., Romagnoli, F., Bargalló, A., Chacón, M.G., Gómez de Soler, B., Picin, A., Carbonell, E., 2019. Lithic refitting and intrasite artifact transport: a view from the Middle Palaeolithic. *Archaeol. Anthropol. Sci.* 11 (9), 4491–4513.
- Vaquero, M., 2012. Introduction: Neanderthal behavior and temporal resolution of archaeological assemblages. In: Carbonell E (Ed.), *High resolution archaeology and Neanderthal behavior: Time and space in Level J of Abric Romaní (Capellades, Spain)*. Springer, New York, pp. 1–16.
- Vermeersch, P.M., 2001. Middle Paleolithic settlement patterns in West European open-air sites: Possibilities and problems. In: Conard, N.J. (Ed.), *Settlement dynamics of the Middle Paleolithic and Middle Stone Age*, Tübingen: Kerns Verlag, pp. 395–417.
- Vettese, D., Blasco, R., Cáceres, I., Gaudzinski-Windheuser, S., Moncel, M.H., Hohenstein, U.T., Daujeard, C., 2020. Towards an understanding of hominin marrow extraction strategies: a proposal for a percussion mark terminology. *Archaeol. Anthropol. Sci.* 12 (48).
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48.
- Walters J., 1988. Fire and bones: patterns of discard. In: Meehan, B., Jones, R. (Eds), *Archaeology with ethnography: an Australian perspective*. Canberra, Australian National University: 215–221.
- White, R., 1982. Rethinking the Middle/Upper Paleolithic transition. *Curr. Anthropol.* 23, 169–192.
- White, T.E., 1955. Observations on the butchering techniques of some aboriginal peoples: Nos. 7, 8, and 9. No. 7: The dog bone from the buffalo pasture site; No. 8: The dog bone from the rock village site; No. 9: The bison and elk bone from the nightwalker's butte in the bull pasture site. *Am. Antiq.* 21, 170–178.
- White, T.D., 1992. *Prehistoric cannibalism at Mancos 5MTUMR-2346*. Princeton Univ. Press, Princeton.

- Yeshurun, R., Marom, N., Bar-Oz, G., 2007. Differential fragmentation of different ungulate body-size: a comparison of gazelle and fallow deer bone fragmentation in Levantine prehistoric assemblages. *J. Taphon.* 5 (3), 137–148.
- Yravedra, J., 2010. A Taphonomic Perspective on the Origins of the Faunal remains from Amalda Cave (Spain). *J. Taphon.* 8 (4), 301–334.
- Yravedra, J., Domínguez-Rodrigo, M., 2009. The shaft-based methodological approach to the quantification of long limb bones and its relevance to understanding hominid subsistence in the Pleistocene: application to four Palaeolithic sites. *J. Quat. Sci.* 24, 85–96.
- Zilio, L., Hammond, H., Karampaglidis, T., Sánchez-Romero, L., Blasco, R., Rivals, F., Rufà, A., Picin, A., Chacón, M.G., Demuro, M., Arnold, L.J., Rosell, J., 2021. Examining Neanderthal and carnivore occupations of Teixoneres Cave (Moià, Barcelona, Spain) using archaeostratigraphic and intra-site spatial analysis. *Sci. Rep.* 11, 4339.