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## To den or not to den. Contributions to the taphonomic history of the Early Pleistocene site of Venta Micena 4 (Orce, Guadix-Baza Basin)

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## ABSTRACT

Venta Micena (Orce, Guadix-Baza Basin, Spain) is an Early Pleistocene locality renowned for the richness and quality of its palaeontological record. VM is spread over an area of 2.5 km<sup>2</sup>, where several exposed fossil outcrops are visible amidst its gorges and ravines. The best known of these sites, VM3, has been interpreted as a hyaena den. In addition, a new site, named VM4, has recently been the focus of fieldwork and taphonomic studies. The publication by Luzón et al. (2021) pointed out that VM4 presents a more complex history than VM3. First, two different sub-levels were identified: VM4-I and VM4-II. Secondly, the preliminary taphonomic analysis showed conspicuous differences with regard to VM3. Nevertheless, such interpretation has been challenged by Palmqvist et al. (2022) who proposed that VM3 and VM4 are both the result of a single depositional process, entailing the selective transport of skeletal parts by the giant extinct hyaena *Pachycrocuta brevirostris* back to its den. Using well-preserved faunal elements whose depositional context and provenance are reliable, in this paper we show that: 1) there are two clearly defined sub-levels in VM4 with some shared taphonomic characteristics as well as some notable differences; 2) VM3 and VM4 exhibit enough divergence to support differences in site formation

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Depositional events  
Open-air sites

processes; 3) The interpretation of both VM4-I and VM4-II is more consistent with their characterisation as open-air sites in which multiple agents and depositional processes contributed to its formation, rather than with hyaena dens. Nevertheless, excavations are still in progress at VM4 and therefore any results and interpretations ought to be considered as provisional.

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## 1. Introduction

Venta Micena (VM) (Orce, Guadix-Baza Basin) is an important Early Pleistocene palaeontological complex in southeastern Spain, well-known for its extensive and taxonomically diverse macrovertebrate fossil assemblage (e.g. Martínez-Navarro, 1991; Luzón et al., 2021; Palmqvist et al., 2022). The discovery of a cranial fragment (VM-0) initially attributed to the genus *Homo* (Gibert et al., 1983) put VM in the international spotlight. Beyond debates spurred in relation to this controversial specimen (e.g. Gibert et al., 1983; Gibert and Palmqvist, 1995; Borja et al., 1997; Moyà-Solà and Kölher, 1997; Palmqvist, 1997; Martínez-Navarro, 2002; Carandell Baruzzi, 2020), VM has become a flagship case-study in Pleistocene taphonomy as one of the main sites for studying the behaviour of *Pachycrocuta brevirostris*, alongside Fonelas (Arribas and Garrido, 2008; Garrido et al., 2010), Vallparadis (Madurell-Malapeira et al., 2011; 2017), Cueva Victoria (Madurell-Malapeira et al., 2015), Tsiotra Vryssi (Katsagoni et al., 2022) and others (Iannucci et al., 2021). This extinct giant hyaena has often been characterised as a scavenger that specialised in the exploitation of carcasses left by other carnivores, selectively transporting skeletal parts back to their dens (e.g. Arribas and Palmqvist, 1998, 1999; Palmqvist and Arribas, 2001; Espigares, 2010; Palmqvist et al., 2011, 2022; Pérez-Claros and Coca-Ortega, 2020). Nonetheless, other authors contest this interpretation of *Pachycrocuta* as a specialised scavenger, proposing instead that this species could have exhibited some hunting behaviour as part of a wider opportunistic strategy including the ability to kill their own prey and acquire carcasses from other carnivores (Vinuesa et al., 2016; Iannucci et al., 2021). This interpretation finds support in the works by Turner and Antón (1996) and Dennell et al. (2008), who suggested that the greater corpulence, size and body mass of *Pachycrocuta brevirostris*, alongside a gregarious social behaviour, may have favoured this species in their hunting capabilities, although the extent to which *Pachycrocuta* was a social carnivore and its relationship to their food procurement strategies is still subject of debate among palaeobiologists and palaeoneurologists (Holekamp et al., 2007a, 2007b, 2015; Arsznov et al., 2010; Sakai et al., 2011; Vinuesa et al., 2015, 2016).

The history of research at Orce goes back to the 1970s. The discovery of VM took place in 1976 by three members of the *Instituto Provincial de Paleontología* (Sabadell, Barcelona, Spain): Josep Gibert, Jordi Agustí and Narcís Sánchez (Carandell Baruzzi, 2013). However, systematic fieldwork was not carried out at the site until 1982. Palaeontological interventions were conducted at several areas of VM (Cortes I–V and Sondeos I–V; VM4 = Sondeo IV), which provided many macrovertebrate fossils (Agustí et al., 1985; Espigares, 2010). The Early Pleistocene sites of Barranco León (BL) and Fuente Nueva 3 (FN3) were subsequently discovered in the wider landscape (e.g. Tixier et al., 1995; Turq et al., 1996), and they both have yielded unquestionable evidence of human presence and activities (e.g. Gibert et al., 1998, 1999; Barsky et al., 2010; Toro-Moyano et al., 2013; Ribot et al., 2015; Titton et al., 2018, 2020, 2021; Yravedra et al., 2021, 2022a).

Previous studies carried out on VM3 and synthesized in

Palmqvist et al. (2022) show several inconsistencies and inaccuracies that need to be mentioned. Among all the sectors discovered at VM, Corte III = VM3 (excavated between 1982 and 1995) stands out. Different authors have reported different values for the total excavated surface: Espigares (2010) noted that 326 m<sup>2</sup> were excavated, whereas Palmqvist et al. (2022) gave a reduced value of 220 m<sup>2</sup>. Similarly, the size of the fossil sample retrieved differs slightly depending on the author (Table 1). Regardless of the actual number of remains, the material retrieved from this fossil assemblage has formed the basis of dozens of scientific publications, turning VM into a classic site for understanding Quaternary Palaeontology in Europe and Early Pleistocene carnivore palaeoecology, particularly regarding the taphonomic characterisation of *P. brevirostris* (Arribas and Palmqvist, 1998, 1999; Palmqvist and Arribas, 2001; Espigares, 2010; Palmqvist et al., 2011, 2022).

From a taphonomic perspective, the large amount of bone remains recovered from this sector (VM3) has allowed researchers to conclude that this locality represents a hyaena den or *Pachycrocuta* camp, to where adult *Pachycrocuta* individuals selectively transported and intensively altered many skeletal remains of large herbivores. Most of these carcasses may have been hunted by other carnivores, particularly large sabre-toothed felids and canids, based on the mortality profiles and skeletal part profiles reported by Palmqvist et al. (1996), and Arribas and Palmqvist (1998, 1999). The role of VM3 as a hyaena den is further reinforced by the presence of numerous coprolites attributed to *P. brevirostris* (Palmqvist et al., 1996; Arribas and Palmqvist, 1998) as well as remains from juvenile and immature hyaena individuals (Palmqvist et al., 1996, 2011, 2022; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). Lastly, a recent paper has characterized the morphology of the tooth marks of a small sample from VM3, revealing that the main modifying agent is the large Pleistocene hyena *P. brevirostris* (Yravedra et al., 2022b).

### 1.1. Venta Micena 4 (VM4)

Even though Sondeo IV of Venta Micena was discovered by J. Gibert and it was known since the 1980s (Agustí et al., 1985), it is only recently that it has been recognised as an independent site, being renamed as VM4 (Granados et al., 2021; Luzón et al., 2021). VM4 is located 350 m away from VM3 (Fig. 1). To this date, 39 m<sup>2</sup> have been excavated over the course of seven field seasons: 2005, 2013–2015, and 2017–2019 (Luzón et al., 2021).

The stratigraphic sequence of VM is similar in all sectors. It has been defined on the basis of different sections and it consists of six units (A–F) (Anadón et al., 1986, 1987). Among these, Unit C, with a thickness between 2.3 and 3.4 m, has yielded the largest quantity and quality of mammal fossils. This unit is divided into three intervals C0–C1–C2 (Anadón et al., 1986, 1987) (Fig. 2). C0 is characterised by a whitish sandy lutitic limestone while units C1 and C2 consist of around 1.5 m of micritic limestone of palustrine and lacustrine origin (known as Venta Micena limestone or VM Stratum, which surges intermittently over 2.5 km<sup>2</sup>). The two richest bone assemblages (VM3 and VM4) are located along Unit 2-Interval C1 limestone, which presents a thickness between 80 and 120 cm

**Table 1**  
Number of identifiable and unidentifiable fossil remains from VM [VM3 according to Palmqvist et al. (2022)].

Number of identifiable specimens	Number of unidentifiable specimens	Reference
6454 from Table 2 (6453 from text): 5822 anatomically and taxonomically identified + 632 anatomically identified	>10,000	Arribas and Palmqvist (1998)
6884: 5960 anatomically and taxonomically identified + 924 anatomically identified	>10,000	Espigares (2010)
8150: 6331 anatomically and taxonomically identified + 1819 anatomically identified	“Several thousands” [of shaft bones]	Palmqvist et al. (2022)

(Fig. 1). Granados and collaborators have shown slight stratigraphical and geochemical differences between the upper intervals at Unit 2 (C1 and C2), as well as between the two palaeosurfaces VM4-I and VM4-II (Granados et al., 2021). This notion is reinforced by the definition of two stratigraphic and sedimentological boundaries corresponding to two different depositional episodes in VM4 Unit 2-C1 (Luzón et al., 2021).

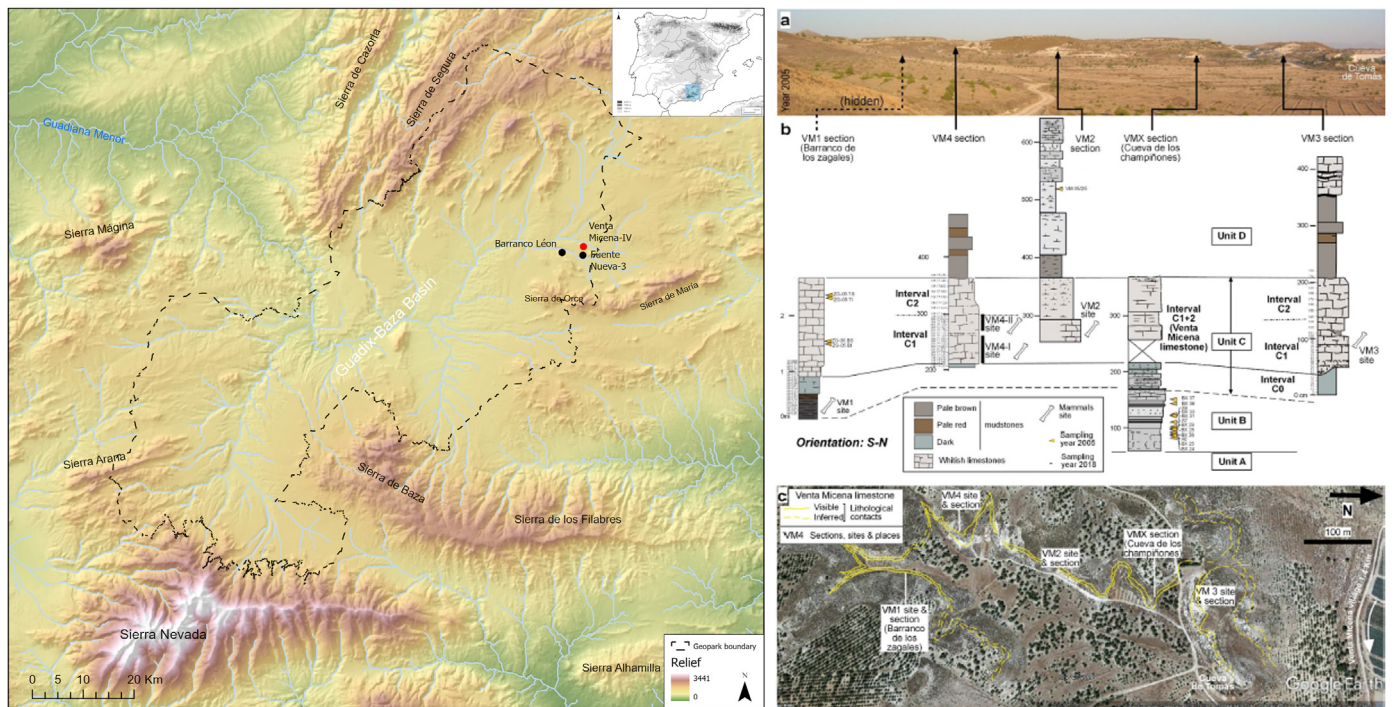
VM4 would have been located near the edge of a lacustrine environment centered around the relatively large and saline endorheic Baza lake (Oms et al., 2011; Granados et al., 2021). Unit C would correspond to a regressive phase of the lake, which fostered surgenies of subterranean freshwater springs, thus favouring the development of an attractive ecosystem for the faunal species found at VM4 and other nearby sites (Luzón et al., 2021; Granados et al., 2021). The Venta Micena Unit C faunal assemblage comprises a series of typical Late Villafranchian macro- and micromammal species (see Luzón et al., 2021; Palmqvist et al., 2022 for different taxonomic proposals).

From a chronological point of view, Unit C of VM has been dated using the combined uranium series–electron spin resonance method, and the mean age is  $1.37 \pm 0.25$  Ma (Duval et al., 2012). Nevertheless, such dating has been refined and extended through biochronology, on the basis of the presence of *Allophaiomys ruffoi*

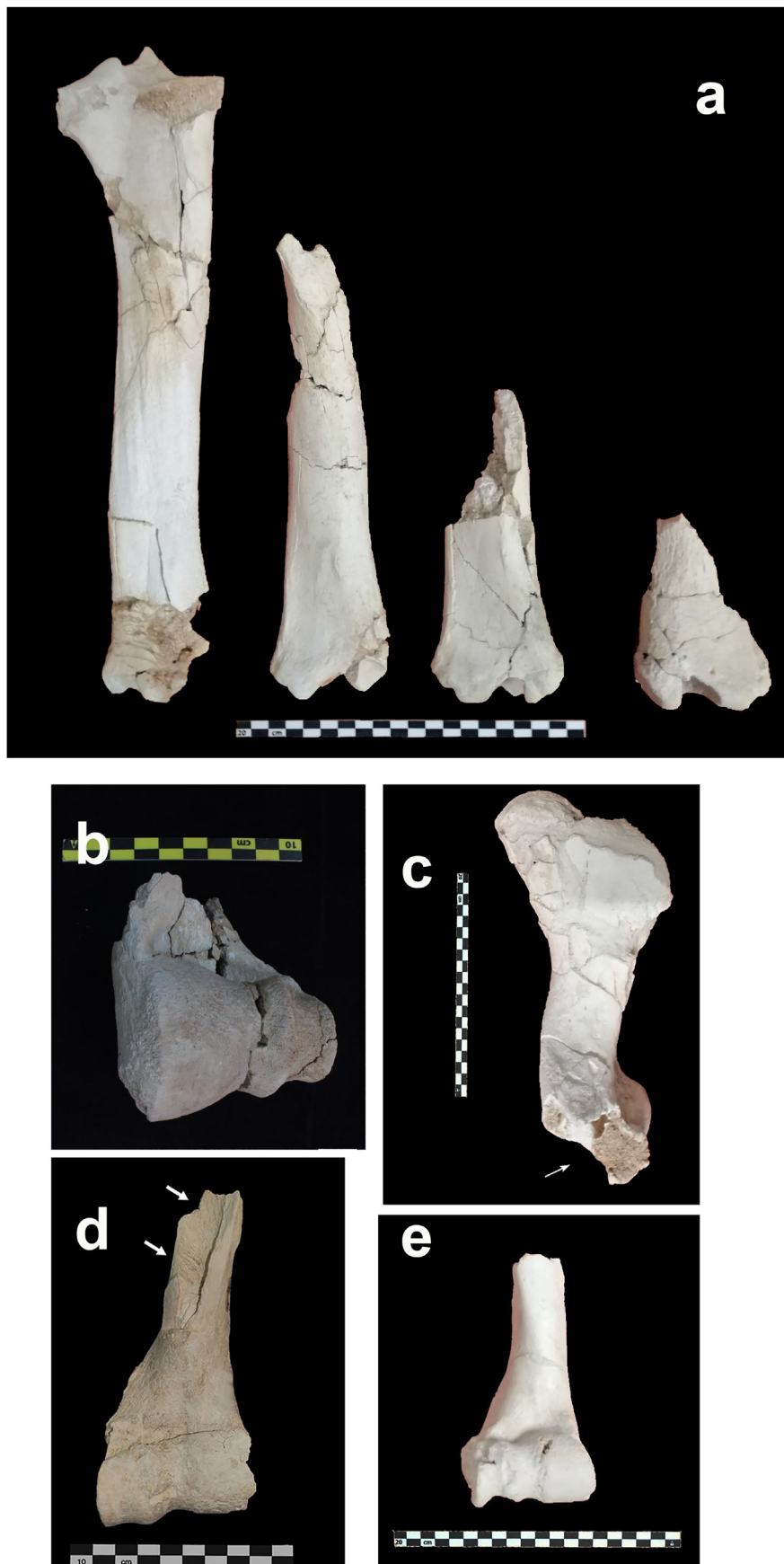
(Agustí et al., 2007, 2010), up to c.1.6 Ma.

Even though Espigares's Ph.D. dissertation (2010) doctoral thesis includes an analysis of the orientations and inclinations of fossil remains from Sondeo IV of VM (n = 211), Luzón et al. (2021) were the first to offer a comprehensive taphonomic study of VM4. Their research includes an analysis of the remains derived from the 2005, 2018 and 2019 field seasons (NISP = 1609). Despite the spatial proximity, stratigraphic correlation (Granados et al., 2021), and the existence of taxonomic parallels between VM3 and VM4 (Luzón et al., 2021; Palmqvist et al., 2022), these two sites show some notable differences, according to Luzón et al. (2021).

1. The VM4 faunal assemblage exhibits a lower degree of bone weathering than VM3, which suggests a more reduced environmental exposure timespan.
2. The VM4 faunal assemblage shows a lower intensity of carnivore damage.
3. VM4 should be interpreted as a fossil assemblage accumulated in the vicinity of a freshwater source where herbivores and carnivores interacted, albeit it is not possible to determine at this stage which carnivores intervened in the formation and modification of the assemblage, and to what extent.



**Fig. 1.** Left: Location of Venta Micena VM (Guadix Baza basin, Orce, Spain). Right: geospatial and stratigraphic relationship between the VM3 and VM4 palaeontological localities. A: Shows the spatial ubication of VM3 and VM4. B: Shows the stratigraphic correlation between VM3 and VM4. C: Satellite image (source: Google EARTH and Instituto Geográfico Nacional, Spain) indicating the location of the different Venta Micena palaeontological localities (VM1-VM4) (Figure modified from Granados et al., 2021).



**Fig. 2.** Feeding and furrowing sequences on long limb bones at VM4. 2a: Feeding sequence on equid tibiae. 2b-e distal humerus epiphyses of different species, b: artiodactyl, c: *Stephanorhinus*, d: Equid, e: *Metacervoceros*. Scarce furrowing is documented on the distal epiphysis, since it was only observed on the *Stephanorhinus*' latero-caudal condyle.

4. VM4 would not constitute a hyaena den or *Pachycrocuta* camp, on the basis of an absence of immature remains of *P. brevirostris*, the low frequencies of bones with tooth mark alterations, and the presence of multiple bones still in anatomical connection.
5. VM4 presents two depositional events, whereas VM3 has long been interpreted as being constituted by a single depositional process.

This proposal has recently been disputed by [Palmqvist et al. \(2022\)](#). Reinterpreting the results generated on the basis of the materials retrieved during the 2005 and 2013–2015 field seasons (NISP = 3961) and comparing them with the data from VM3, these authors claim that both sites have different sedimentological biographies but a shared functional nature as a *Pachycrocuta* den.

With the aim of addressing the debate surrounding the nature of VM4, we present in this paper the first comprehensive study of the totality of the VM4 faunal assemblage, including the remains retrieved from the 2005, 2013–2015 and 2017–2019 field seasons. Since the global taphonomic context of the VM4 assemblage has already been characterised by [Luzón et al. \(2021\)](#), this paper focuses on more specific aspects related to the biological processes that led to the accumulation of faunal remains in the two VM4 sublevels.

## 2. Materials and methods

In this paper, the sample has been analysed from a taphonomic perspective. The bone sample analysed at VM4 consists of 4898 remains from two levels, VM4-I with 1732 remains ([Table 2](#)) and VM4-II with 3166 remains ([Table 3](#)), spread over a surface area of 39 m<sup>2</sup> (see [Luzón et al., 2021](#)). Micromammal remains were excluded from this study. The 181 bones that were not assigned to either level VM4-I or VM4-II have not been included in the study, and neither have been included those currently undergoing restoration work.

The taxonomical profiles have been quantified on the basis of NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals). MNI estimates have taken into consideration element laterality as well as their ontogenetic age ([Brain, 1969](#)), epiphyseal fusion, long bone biometrics and, if applicable, dental wear. When the taxonomic attribution of individual bones could not be discerned but they were identifiable anatomically, these fossils were classified to weight/size classes using different categories. These follow the scheme provided in [Luzón et al. \(2021\)](#), where herbivores were assigned to 5 different size classes: Very Small Size (0) for species less than 25 kg of weight; Small Size (1), including species weighing 25–50 kg; Small-Intermediate Size (2), including species weighing 50–125 kg; Intermediate Size (3), including species weighing 125–500 kg, divided in 3a (125–250 kg) and 3b (250–500 kg); Large Size (4), including species weighing 500–1000 kg; and Very Large Size (5), species weighing >1000 kg. Carnivora were classified according to three groups; Small Carnivora (e.g. fox); Intermediate Carnivora (e.g. wolf); and Large Carnivora (e.g. lion). The mortality profiles were established by assigning suitable remains to one of four different ages classes (infantile, juvenile, prime adult-adult and senile), based on tooth eruption, crown wear and epiphyseal fusion.

Skeletal profiles were generated using the MNE (Minimum Number of Elements) following [Marean and Kim \(1998\)](#) for shaft classification. We have divided the skeleton into different anatomical sections, according to the scheme proposed by [Yravedra and Domínguez-Rodrigo \(2009\)](#), namely: cranial (horns, crania, maxillae, mandibles and teeth), axial (vertebrae, ribs, pelvises and scapulae); appendicular limbs were subdivided into upper elements (humerii, femora), intermediate appendicular (radii, ulnae, tibiae, patellae, fibulae), lower appendicular elements, and

posterior portions (carpals, tarsals, and metapodials).

The nature and extent of bone fragmentation was assessed based on three variables. First, bones were divided into several size categories based on their length: ≤ 3 cm, 3.1–5.0 cm, 5.1–10 cm and ≥ 10 cm. Second, long bones were classified according to whether they present green or dry fractures, following the criteria outlined in [Villa and Mahieu \(1991\)](#). Third, the percentage of preserved shaft circumference was defined as follows: Type 1 are specimens that preserve <50% of the shaft circumference intact; Type 2 are specimens with >50% of the shaft circumference; and Type 3 are specimens with >75% of shaft circumference, following [Bunn \(1982\)](#).

Bone alteration patterns were quantified using NISP values, and the observation of bone surface modifications was carried out using both binocular and hand-held lenses. The nature and intensity of hydric activity and other waterborne alterations was characterised basing on the frequencies of bones with abrasion, polishing and rounding. Abrasion is produced in situations where water may have transported small sedimentary particles which erode bone surfaces, according to [Lyman \(1994\)](#) and [Thompson et al. \(2011\)](#), hydric polishing and rounding are produced in contexts where bones experience movement or transportation by water flows ([Shipman, 1981](#); [Lyman, 1994](#); [Fernández-Jalvo and Andrews, 2016](#)), although sometimes the action of water-suspended particles can also result in the erosion of bone surfaces, producing rounding without the bone having experienced displacement ([Thompson et al., 2011](#)). These waterborne alterations were each subdivided into three different stages: light (the bone surface very little; the bones do not have rounded edges, the bone surface can be seen very well, and polish is only reflected in a slight shine on the bone), intermediate (when rolling edges are already appreciated, the polishing is greater, with shine across the entire bone surface, but bone surface modifications can still be observed, although with difficulty), and intense (when the bones are very rolled and eroded, which prevents the documentation of bone surface modifications).

Bone weathering was classified following [Behrensmeier \(1978\)](#). Other processes such as manganese staining, oxidation and biochemical alterations were also quantified as presence/absence. Finally, carnivore activity was analysed through the frequency and anatomical distribution of tooth marks, the pit/score ratio and the quantity of tooth marks tooth marks per bone. Tooth marks were divided into pits, scores, and punctures, and their identification was made following [Binford \(1981\)](#) and [Blumenschine \(1995\)](#). According to [Capaldo and Blumenschine \(1994\)](#) and [Moclán et al. \(2019\)](#), notches were classified into the following types (see Suppl. Data, [Fig. 1](#)): Type 1 (complete single notches); Type 2 (double opposing complete notches); Type 3a (incomplete notches where inflection points are missing); Type 3b (complete and other incomplete notches where one inflection points is missing); Type 4 (double overlapping notches); Type 5 (notches with other double opposing notches); Type 6 (pseudo notches); and Type 7 (notches smaller than 1 cm). Moreover, we have also analysed the angles of green bone fractures, following [Alcántara García et al. \(2006\)](#), for they can offer insights into the nature of the force that led to the fracture, namely dynamic or static load; the latter is typical of carnivore bone breaking activities. To discriminate between the agency of different carnivores, particularly between hyaenas and canids, we have followed [Moclán et al. \(2019\)](#). Lastly, we have also measured furrowing intensity following the taphotype typology of [Domínguez-Rodrigo et al. \(2015\)](#).

In order to evaluate the dependence of a given variable (percentage of immature individuals) respect to an independent variable (adult body mass), we have carried out regression analyses by the adjustment technique of Ordinary Least Square (OLS). If the null hypothesis [ $H_0$  (slope = 0)] cannot be rejected (that is,  $p$ -value

**Table 2**  
Taxonomical profiles (VM4-I). S: Senile; A: Adults; J: Juvenile; I: Infants.

VM4-I	NISP	% Herbivores	% total	MNI	% Herbivores	% total	S/A/J/I	% non-adults
<i>Mammuthus meridionalis</i>	3	1.01	0.17	1	3.57	2.50	0/0/0/1	100
<i>Stephanorhinus etruscus</i>	13	4.36	0.75	4	14.29	10.00	0/1/1/2	75
<i>Equus altidens</i>	126	42.28	7.27	7	25.00	17.50	1/4/1/1	28.7
<i>Hippopotamus antiquus</i>	17	5.70	0.98	2	7.14	5.00	0/1/0/1	50
<i>Bison</i> sp.	20	6.71	1.15	2	7.14	5.00	1/1/0/0	0
<i>Soergelia minor</i>	8	2.68	0.46	1	3.57	2.50	0/1/0/0	0
<i>Capra alba</i>	16	5.37	0.92	3	10.71	7.50	1/2/0/0	0
<i>Praemegaceros verticornis</i>	39	13.09	2.25	4	14.29	10.00	1/1/1/1	50
<i>Metacervoceros rhenanus</i>	33	11.07	1.91	4	14.29	10.00	1/1/1/0	33.3
Bovidae	23	7.72	1.33					
Total Herbivore determinable	298		17.21					
Herbivore indet. size 0	5		0.29					
Herbivore indet. size 1	1		0.06					
Herbivore indet. size 2	60		3.46					
Herbivore indet. size 3	97		5.60					
Herbivore indet. size 3a	42		2.42					
Herbivore indet. size 3b	151		8.72					
Herbivore indet.	956		55.20					
Total Herbivore	1610		92.96	28	100	70.00		
	NISP	% Carnivora	% total	MNI	% Carnivora	% total	S/A/J/I	% non-adults
<i>Canis mosbachensis</i>	7	9.72	0.40	2	22.22	5.00	0/2/0/0	0
<i>Xenocyon (= Lycaon) lycaonoides</i>	13	18.06	0.75	1	11.11	2.50	0/1/0/0	0
<i>Vulpes alopecoides</i>	2	2.78	0.12	1	11.11	2.50	0/1/0/0	0
<i>Pachycrocuta brevirostris</i>	16	22.22	0.92	2	22.22	5.00	1/1/0/0	0
<i>Homotherium latidens</i>	1	1.39	0.06	1	11.11	2.50	0/1/0/0	0
<i>Ursus etruscus</i>	4	5.56	0.23	2	22.22	5.00	1/1/0/0	0
Canidae	13	18.06	0.75					
Felidae	4	5.56	0.23					
Carnivora	12	16.67	0.69					
Total Carnivora	72		4.16	9	100.00	22.50		
	NISP	% other	% total	MNI	% other	% total	S/A/J/I	% not adults
Lagomorpha	7	14.00	0.40	1	2.50	2.50	0/1/0/0	0
Testudines	38	76.00	2.19	1	2.50	2.50	0/1/0/0	0
Aves	5	10.00	0.29	1	2.50	2.50	0/1/0/0	0
Total	1732	100.00	100.00	40	100	100.00		

>0.05), we will consider that there is no significant relationship between the variables used. Regression functions were estimated using the statistical package SPSS 28.0.

### 3. Results

#### 3.1. Taxonomical and mortality profiles

VM4-I (Table 2) comprises a faunal assemblage of 1732 remains, with herbivores representing 70% and carnivores 22.5% of the MNI (Table 2). Among the herbivore taxa, the equid *E. altidens* is the predominant species (25% of individuals), but cervids are the most abundant group (28.6%), represented by genera *Praemegaceros* and *Metacervoceros* (Table 2). Rhinocerotids and caprids are in third place (each accounting for 14% of the MNI), followed by large bovids, such as bison, hippopotamids with 7%, and lastly proboscideans with 3.5%. Among carnivores, *C. mosbachensis*, *P. brevirostris* and *U. etruscus* are represented by two individuals each, while the remaining carnivores are only represented by a single individual.

VM4-II has a faunal assemblage of 3166 remains, with herbivores representing 69% of the MNI (Table 3). The most represented species are *E. altidens* and *P. verticornis*, each with 22.5% of the MNI. Cervids (both *Praemegaceros* and *Metacervoceros*) are also the predominant group with 37.5% of the total herbivore assemblage and 26% of the total MNI. Bovids comprise the third most numerous group, followed by the caprids *C. alba* and *S. minor*, and mega-herbivores

*M. meridionalis*, *S. etruscus*, and *H. antiquus* are the scarcest group. Regarding carnivores, canids are the most representative group (50% of the carnivore MNI sample), followed by hyaenids, ursids, and felids, all of which exhibit similar frequencies.

The mortality profiles of both palaeosurfaces (VM4-I and VM4-II) show a predominance of adult individuals in all species except for Size 5 animals. Additionally, we have noticed some differences on which taxa are better represented by immature individuals: rhinoceroses, elephants and hippopotamuses for VM4-I (Table 2) and elephants for VM4-II (Table 3). Among size 2–3 herbivores, only *P. verticornis* (VM4-I: 50% and VM4-II: 55.5%) and *M. rhenanus* (VM4-II: 50%) exhibit an important representation of immature individuals, while adults dominate the mortality profiles of all other taxa. Thus, we can establish that at VM-4 the largest species are dominated by infant-juvenile individuals, while small and medium species are dominated by adults. Concerning bone pathologies, only a horse metatarsal and a bear phalanx have been identified with signs of osteoarthritis, as well as some cranial fragments (Suppl. Data, Fig. 2).

#### 3.2. Skeletal profiles

Size 3 species show the most representative skeletal profiles at both VM4-I (Table 4) and VM4-II (Table 5), while other species are less abundant. Size 2 taxa present lower frequencies than Size 3 species, though bones from every anatomical portion have been recorded. However, very few remains can be attributed to Sizes 1 and 5.

There is a balanced representation of the different anatomical

**Table 3**  
Taxonomical profiles (VM4-II). S: Senile; A: Adult; J: Juvenile; I: Infant.

VM4-II	NISP	% Herbivores	% total	MNI	% Herbivores	% total	S/A/J/I	% non-adults
<i>M. meridionalis</i>	6	1.16	0.19	3	7.50	5.36	0/1/1/1	66.6
<i>S. etruscus</i>	14	2.70	0.44	2	5.00	3.57	0/2/0/0	0
<i>E. altidens</i>	177	34.17	5.59	9	22.50	16.07	1/5/2/1	33.3
<i>H. antiquus</i>	4	0.77	0.13	1	2.50	1.79	0/1/0/0	0
<i>Bison</i> sp.	70	13.51	2.21	5	12.50	8.93	0/3/1/1	40
<i>H. cf. gracilis</i>	7	1.35	0.22	1	2.50	1.79	0/1/0/0	0
<i>S. minor</i>	18	3.47	0.57	1	2.50	1.79	0/1/0/0	0
<i>C. alba</i>	23	4.44	0.73	3	7.50	5.36	1/1/1/0	33.3
<i>P. verticornis</i>	89	17.18	2.81	9	22.50	16.07	1/3/1/4	55.5
<i>M. rhenanus</i>	73	14.09	2.31	6	15.00	10.71	1/2/2/1	50
Cervidae	2	0.39	0.06					
Bovidae	35	6.76	1.11					
Total Herbivore determinable	518		16.36					
Herbivore indet. Size 0	8		0.25					
Herbivore indet. Size 1	2		0.06					
Herbivore indet. Size 2	74		2.34					
Herbivore indet. Size 3	91		2.87					
Herbivore indet. Size 3a	9		0.28					
Herbivore indet. Size 3b	112		3.54					
Herbivore indet.	2095		66.17					
Total Herbivore	2909	100.00	93.39	40	100	71.43		
	NISP	% Carnivora	% total	MNI	% Carnivora	% total	S/A/J/I	% non-adults
<i>C. mosbachensis</i>	26	11.98	0.82	3	25.00	5.36	1/2/0/0	0
<i>X. (= Lycaon) lycaonoides</i>	71	32.72	2.24	3	25.00	5.36	1/2/0/0	0
<i>P. brevirostris</i>	7	3.23	0.22	2	16.67	3.57	1/1/0/0	0
<i>H. latidens</i>	2	0.92	0.06	1	8.33	1.79	0/1/0/0	0
<i>M. cultridens</i>	3	1.38	0.09	1	8.33	1.79	0/1/0/0	0
<i>U. etruscus</i>	11	5.07	0.35	2	16.67	3.57	1/1/0/0	0
Canidae	77	35.48	2.43					
Felidae	2	0.92	0.06					
Carnivora	18	8.29	0.57					
Total Carnivora	217	100.00	6.85	12	100.00	21.43		
	NISP	% other	% total	MNI	% other	% total	S/A/J/I	% non-adults
Lagomorpha	21	44.68	0.66	2	3.57	3.57	0/2/0/0	0
Testudines	3	6.38	0.09	1	1.79	1.79	0/1/0/0	0
Aves	16	34.04	0.51	1	1.79	1.79	0/1/0/0	0
Total	3166	100	100.00	56	100	100.00		

portions among Size 3 species at VM4-I: axial remains are represented by 32 elements, upper and intermediate limb bones have 31 elements each, and there are 37 lower appendicular elements (Table 4). The only notable difference is documented between forelimb and hindlimb bones, with the latter being more abundant among Size 3 animals; this trend is reversed for Size 2 animals, with forelimbs being more commonly depicted (Table 4).

At VM4-II, the faunal sample is larger and more representative, even though it is still dominated by teeth (Table 5). Species from Sizes 2–3 are the most abundant, with all skeletal portions represented, although there are some notable biases. For example, upper limb bones are poorly represented (N = 4) while other portions reach MNE values of 11 (Table 5). Both forelimbs and hindlimbs are represented, although the former are slightly more common. Metacarpals are particularly well represented among Size 3 animals. For species from Sizes 4–5, the sample is limited, and only forelimbs are present.

When comparing VM4-I and VM4-II, the skeletal part profiles are biased for all species, particularly when comparing MNEs (Tables 4 and 5) with the MNI values for Sizes 2, 3 and 5 (Tables 2 and 3). In this regard, Size 3 animals at VM4-I would be represented on average by 17.3 elements per individual, Size 2 species by 8.6 elements per individual, and Size 5 by 1.6 elements per individual. At VM4-II, these ratios are still rather biased, with 16.1 elements per individual for Size 3 species, 17.4 elements per individual for Size 2 animals, and 3.3 elements per individual for Size 5 animals.

This bias is further documented in the low representativity

ratios exhibited by limb bone epiphyses, since they are far removed from the value of 1 that would indicate a complete representation. When measuring the relative abundance of the less dense epiphyses (proximal humerus plus distal radius)/(distal humerus plus proximal radius) we obtain values of 0.125 for VM4-I and 0.24 for VM4-II, evidencing the skeletal bias of the sample. Similar levels of skeletal bias are documented based on the predominance of diaphysary elements over epiphyses (Supp. Data, SF6). Despite these biases, the representation of all skeletal parts among Size 2 and Size 3 animals may indicate that some animals were perhaps initially complete at the site.

### 3.3. Taphonomic evidence

Bone surface preservation is generally good both at VM4-I (76%) and VM4-II (84%) (Table 6). Weathering alterations are low at both levels, which implies that bones were not subjected to subaerial exposure. The frequencies of manganese or other oxide staining, as well as bone concretions, are very low (Table 6). Lastly, in relation to waterborne alterations, rounding and polishing have not been observed, while abrasion is documented on 29% of the bone assemblage from VM4-I and 22% at VM4-II. However, intense abrasion is only documented on 8,6% and 5,9% of the sample (Table 6). Moreover, biochemical alterations affect 17,6% and 11,2% of VM4-I and VM4-II, respectively (Table 6).

VM4-I and VM4-II present a moderate degree of fragmentation, with over 50% of remains being larger than 3 cm (Table 6). This

**Table 4**  
Skeletal part profiles at VM4-I in relation to the MNE.

MNE VM4-I	0	1	2	%	3	%	3a	%	3b	%	Total 3	%	4	5	Carniv 1	Carniv 2	Carniv 3	Indet.
Horn-antler			1	1.45		0.00		0.00		0.00	0	0.00						
Cranial				0.00	1	2.94		0.00		0.00	1	0.53						7
Maxillar				0.00		0.00	1	3.85		0.00	1	0.53						
Mandible			5	7.25	1	2.94	1	3.85	2	1.54	4	2.11						
Tooth	1	29	42.03	12	35.29	14	53.85	41	31.54	67	35.26	3	5	2	18	21	236	
Vertebra		1	1.45	6	17.65	1	3.85	4	3.08	11	5.79						4	
Rib		6	8.70	10	29.41	1	3.85	1	0.77	12	6.32						5	
Scapula				0.00		0.00		0.00	2	1.54	2	1.05						
Humerus	1	3	4.35		0.00	2	7.69	4	3.08	6	3.16			1				
Radius	0	5	7.25	1	2.94	1	3.85	2	1.54	4	2.11							
Ulna		2	2.90		0.00		0.00	2	1.54	2	1.05		2			1		
Carpal		1	1.45	1	2.94		0.00	2	1.54	3	1.58							
Metacarpal		2	2.90		0.00	2	7.69	15	11.54	17	8.95			1		1		
Pelvis		1	1.45	2	5.88		0.00	5	3.85	7	3.68							
Femur	1	1	1.45		0.00	1	3.85	5	3.85	6	3.16		1					
Patella				0.00		0.00		0.00		0	0.00							
Tibia	1	1	1.45		0.00		0.00	13	10.00	13	6.84		1			2		
Tarsal		5	7.25		0.00	1	3.85	11	8.46	12	6.32		1	2				
Metapodial	2	1	1.45		0.00	1	3.85	6	4.62	7	3.68						2	
Metatarsal		1	1.45		0.00		0.00	13	10.00	13	6.84		1			1		
Phalange	3	2	2.90		0.00		0.00	1	0.77	1	0.53					3		
Sesamoid		2	2.90		0.00		0.00	1	0.77	1	0.53							
Carapace plate	25			0.00		0.00		0.00		0	0.00							
<b>Total</b>	<b>33</b>	<b>1</b>	<b>69</b>	<b>100</b>	<b>34</b>	<b>100</b>	<b>26</b>	<b>100</b>	<b>130</b>	<b>100</b>	<b>190</b>	<b>100</b>	<b>3</b>	<b>11</b>	<b>6</b>	<b>28</b>	<b>21</b>	<b>253</b>
Cranial	0	1	35	50.72	14	41.18	16	61.54	43	33.08	73	38.42	3	5	2	18	21	243
Cranial (excluding tooth)	0	0	6	8.70	2	5.88	2	7.69	2	1.54	6	3.16	0	0	0	0	0	7
Vert. + rib	0	0	7	10.14	16	47.06	2	7.69	5	3.85	23	12.11	0	0	0	0	0	9
Girdle	0	0	1	1.45	2	5.88	0	0.00	7	5.38	9	4.74	0	0	0	0	0	0
Total Axial	0	0	8	11.59	18	52.94	2	7.69	12	9.23	32	16.84	0	0	0	0	0	9
Upper appendic.	2	0	4	5.80	0	0.00	3	11.54	9	6.92	12	6.32	0	1	1	0	0	0
Intermed. appendic.	1	0	8	11.59	1	2.94	1	3.85	17	13.08	19	10.00	0	3	0	3	0	0
Lower appendic.	2	0	4	5.80	0	0.00	3	11.54	34	26.15	37	19.47	0	1	1	4	0	1
Carpal+tarsal+phal.	3	0	10	14.49	1	2.94	1	3.85	15	11.54	17	8.95	0	1	2	3	0	0
Forelimb	1	0	13	59.09	2	50.00	5	71.43	27	36.49	34	40.00	0	2	2	2	0	0
Hindlimb	2	0	9	40.91	2	50.00	2	28.57	47	63.51	51	60.00	0	4	2	3	0	1

moderate degree of fragmentation can also be observed in relation to the degree of shaft preservation, since 54% and 66% of diaphyses in VM4-I and VM4-II preserve over 50% of the shaft circumference. Limb bone length index also reflects a moderate degree of fragmentation, since over 21% of bones from VM4-I and 36% from VM4-II still have over 50% of their expected length. Lastly, around 30% of shaft remains show green fractures, but dry fractures of diagenetic origin are still more common in the VM4 assemblage (Table 6).

In relation to carnivore alterations, we have identified tooth marks (Tables 7–9), furrowing (Table 11) green fractures associated with notches (Tables 12 and 13) and taphotypes (Table 14).

Tooth marks have been observed on 4.4% of bones with well-preserved cortical surfaces at VM4-I and 1.9% at VM4-II (Table 7). Only 5% of tooth-marked bones exhibit more than 5 tooth marks per bone, indicating a relatively low intensity of carnivore ravaging (Table 8). Regarding the pit to score ratio, there is a clear predominance of pits over scores (Table 7). Other alterations, such as digested bones (n = 2) or bones polished due to saliva damage (n = 6), are minimally present.

At VM4-I, medium-sized (equids) and small-sized species, such as *Metacervoceros*, present tooth marks. At VM4-II, in addition to these species, *Soergelia* and very large sized animals, such as elephants, rhinoceroses, and hippopotamuses, also show tooth marks (Table 8). All the remains with tooth marks belong to adult individuals, except for an immature *Metacervoceros* and a juvenile *Mammuthus*, both from VM4-II.

The anatomical distribution of tooth marks is outlined in Table 9. At VM4-I, tooth marks are found on limb bones, compact bones such as astragali or calcanei, as well as axial bones, such as pelvises.

Even though the number of bones with carnivore damage is limited, tooth marks are more abundant on high meat yield skeletal parts, such as upper limb bones. At VM4-II, all anatomical portions exhibit tooth marks, though they are more frequent on upper limb diaphyses. This pattern can be observed for Sizes 2 and 3 at VM4-I and among Sizes 2, 3, and 5 at VM4-II (Table 10).

Furrowing consists in the deletion of bone portions due to carnivore ravaging. This alteration has been documented on 13 bones from VM4-I and 27 bones from VM4-II, spanning a wide range of anatomical parts, including compact bones, mandibles, and primarily on limb bones (Table 11; Figs. 2c, 3f and 3h). Despite the low numbers, it complements the tooth mark distribution data for a more accurate depiction of carnivore alteration of the faunal assemblage, since there are some bones that show furrowing even though no tooth marks are found on their cortical surfaces, such as among some upper limb bones from Size 5 species (see Suppl. Data, SF5 and SF7; and Fig. 2e). Furthermore, their distribution frequencies can reach high levels for some size classes. For example, the percentage of furrowing on Size 3b humeri (20%) or on Size 5 limb bones (100%) at VM4-II is notable (see Suppl. Data, SF7 and SF8).

In relation to taphotypes, which characterise the nature and distribution of furrowing, there is a predominance of Type 15 (both epiphyses deleted), with 33% at VM4-I and 35% at VM4-II (Table 14; Fig. 3h). Most bones presenting a Type 15 taphotype are upper limbs, such as humeri and femora, which have a lower density than intermediate and lower limbs. This characteristic makes them more vulnerable to carnivore ravaging. In contrast, denser elements, such as metapodials and tibiae, are more complete, even exhibiting type



**Table 5**  
Skeletal part profiles at VM4-II in relation to MNE.

MNE VM4-II	0	1	2	%	3	%	3a	%	3b	%	Total 3	%	4	5	Carniv 1	Carniv 2	Carniv 3	indet
Horn-antler			4	2.30	1	4.76		0.00	1	0.42	2	0.65						
Cranial			2	1.15		0.00		0.00		0.00	0	0.00				1		15
Maxillar			1	0.57		0.00	1	2.13	5	2.10	6	1.96					2	
Mandible		2	12	6.90		0.00	4	8.51	3	1.26	7	2.29				6		
Teeth	9	9	98	56.32	3	14.29	33	70.21	109	45.80	145	47.39	2	4	4	57	21	305
Vertebra	2		8	4.60	4	19.05		0.00	10	4.20	14	4.58						5
Rib	4	1	10	5.75	7	33.33		0.00	1	0.42	8	2.61		1				13
Scapula			2	1.15	1	4.76		0.00	2	0.84	3	0.98					1	
Humerus	5		4	2.30		0.00		0.00	9	3.78	9	2.94	2			5		
Radius			5	2.87	2	9.52	1	2.13	9	3.78	12	3.92	1			3		1
Ulna			3	1.72		0.00		0.00	3	1.26	3	0.98	1			4		
Carpal			2	1.15		0.00		0.00	3	1.26	3	0.98	1			1		1
Metacarpal			2	1.15		0.00		0.00	29	12.18	29	9.48	5			6		
Pelvis	1		1	0.57	1	4.76		0.00	5	2.10	6	1.96						
Femur	1			0.00		0.00	2	4.26	4	1.68	6	1.96	1					
Patella				0.00		0.00		0.00		0.00	0	0.00	1					
Tibia	2	1	2	1.15		0.00	2	4.26	7	2.94	9	2.94	1				1	
Tarsal			6	3.45		0.00	1	2.13	19	7.98	20	6.54	1			4		
Metapodial	3		4	2.30	2	9.52		0.00	6	2.52	8	2.61				16		
Metatarsal			5	2.87		0.00	1	2.13	8	3.36	9	2.94	1					
Phalange	2		3	1.72		0.00	2	4.26	2	0.84	4	1.31				23	1	
Sesamoid				0.00		0.00		0.00	3	1.26	3	0.98				10		2
Carapace plate	3			0.00		0.00		0.00		0.00	0	0.00						
Total	32	13	174	100	21	100	47	100	238	100	306	100	2	20	4	140	26	342
Cranial	9	11	117	67.24	4	19.05	38	80.85	118	49.58	160	52.29	2	4	4	64	23	320
Cranial (excluding tooth)	0	2	19	10.92	1	4.76	5	10.64	9	3.78	15	4.90	0	0	0	7	2	15
Vert. + Rib.	6	1	18	10.34	11	52.38	0	0.00	11	4.62	22	7.19	0	1	0	0	0	18
Girdle	1	0	3	1.72	2	9.52	0	0.00	7	2.94	9	2.94	0	0	0	0	1	0
Total Axial	7	1	21	12.07	13	61.90	0	0.00	18	7.56	31	10.13	0	1	0	0	1	18
Upper appendic.	6	0	4	2.30	0	0.00	2	4.26	13	5.46	15	4.90	0	3	0	5	0	0
Intermed. appendic.	2	1	10	5.75	2	9.52	3	6.38	19	7.98	24	7.84	0	4	0	11	1	1
Lower appendic.	3	0	11	6.32	2	9.52	1	2.13	43	18.07	46	15.03	0	6	0	22	0	0
Carpal+tarsal+phal.	2	0	11	6.32	0	0.00	3	6.38	27	11.34	30	9.80	0	2	0	38	1	3
Forelimb	5	0	18	56.25	3	75.00	1	25.00	55	56.12	59	55.66	0	10	0	19	1	2
Hindlimb	4	1	14	43.75	1	25.00	6	150.00	43	43.88	50	47.17	0	5	0	8	1	0

**Table 6**

General taphonomic alterations in VM4 site. \*% respect to total amount of specimens. \*\*% with respect to long bones. \*\*\*% respect to total amount of specimens excluding teeth.

		VM4-I	%	VM4-II	%
	All sample	1732		3166	
	NISP excluding teeth	1272		2459	
Fragmentation	Bone length <3 cm*	742	42.8	1142	36.1
	Bone length 3.1 cm–5cm*	436	25.2	930	29.4
	Bone length 5.1–9.9 cm*	359	20.7	647	20.4
	Bone length >10 cm*	195	11.3	447	14.1
Long bone fracture	NISP of long bone with green fracture**	46	23	30	21
	NISP of long bone with dry fracture**	118	59	31	21.7
	NISP of long bone with green & dry fracture**	18	9	12	8.3
	NISP of long bone with indet fracture**	19	9	70	49
Circumference	NISP shaft circumference <50%**	89	46.4	40	34.2
	NISP shaft circumference >50%**	32	16.7	24	20.5
	NISP shaft circumference >75–100%**	71	37.0	53	45.3
Length respect to total long bone	NISP % length respect the total of long bone >50%**	157	78.5	84	63.6
	NISP % length respect the total of long bone <50%**	13	6.5	25	18.9
	NISP % length respect the total of long bone 75–100%**	30	15.0	23	17.4
Alterations	NISP good surface preservation, excluding tooth***	965	75.9	2073	84.3
	NISP weathering 1–2 stage*	137	7.9	224	7.1
	NISP weathering 3–4 stage*	0	0.0	0	0.0
	NISP with concretion*	151	8.7	188	5.9
	NISP manganese or oxide staining*	287	16.6	319	10.1
Abrasion	NISP with abrasion*	516	29.8	706	22.3
	NISP light abrasion*	157	9.1	212	6.7
	NISP moderate abrasion*	210	12.1	302	9.5
	NISP intense abrasion*	149	8.6	188	5.9
	NISP with biochemical*	304	17.6	354	11.2

**Table 7**

Tooth mark frequencies. Tooth mark type and number of marks per bone. \*: NISP frequencies excluding teeth and bones with poor surface preservation; \*\*: Frequencies in relation to bones with tooth marks.

NISP excluding tooth and bones with bad surface preservation	VM4-I	%	VM4-II	%
	965		2078	
Bones with tooth marks	42	4.4*	40	1.9*
Bones with pits	30	71.4**	26	65.0**
Bones with scores	8	19.0**	5	12.5**
Bones with pit and scores	4	9.5**	8	20.0**
Bones with punctures	0	0.0**	1	2.5**
N° tooth mark for specimen (5-10)	2	4.8**	2	5.0**
N° tooth mark for specimen (2-4)	20	47.6**	26	65.0**
N° tooth mark for specimen (1)	20	47.6**	12	30.0**

**Table 8**

Distribution of bones with tooth marks (TM) per species.

Level	VM4-I			VM4-II		
	NISP excluding teeth and bones with bad surface preservation	NISP with TM	%TM	NISP excluding teeth and bones with bad surface preservation	NISP with TM	%TM
<i>M.meridionalis</i>				3	1	33.3
<i>S. etruscus</i>	3		0.0	10	2	20.0
<i>H. antiquus</i>	16		0.0	1	1	100.0
Bovinae	6	1	16.7	10		0.0
<i>E. altidens</i>	48	8	16.7	104	4	3.8
<i>M. rhenanus</i>	14	2	14.3	22	2	9.1
<i>P. verticornis</i>	11	1	9.1	25	4	16.0
<i>S. minor</i>	5		0.0	6	2	33.3
Herbivore indet. Size 2	47	1	2.1	60	3	5.0
Herbivore indet. Size 3	40	5	12.5	69	4	5.8
Herbivore indet. Size 3a	22	3	13.6	6	2	33.3
Herbivore indet. Size 3b	109	18	16.5	71	11	15.5
Herbivore indet.	544	3	0.6	1498	4	0.3

**Table 9**

Anatomical distribution of bones with tooth marks in VM4-I and VM4-II.

	Anatomical distribution of tooth marks												
	VM4-I					VM4-II							
Animal Size	2	3	3a	3b	Indet.	1	2	3	3a	3b	5	Indet.	
Mandibles						1				1			
Ribs								1					
Vertebrae										1			
Scapulae							1						
Humeri	1	1		3			1			5	2		
Radii									1	2			
Pelvises				1						2			
Femurs			1	1						1			
Tibiae				10									
Metacarpals				1						2	1		
Metatarsals				1			2						
Tali	1									1			
Calcanei	1						1				1		
Shafts		1	1	7	3					1		3	
Indet.		3	1	4			1	3	1	3		1	
Total	3	5	3	28	3	1	6	4	2	19	4	4	

0 taphotypes, which means that they are complete (Table 13; Fig. 2a) Proximal epiphyseal deletion has also been observed in over 36% of limb bones at VM4-II and 48% at VM4-I (taphotypes 2–7), while several examples of distal epiphysis deletion corresponding to taphotypes 9–12 have also been documented (Table 14; Fig. 2a).

Regarding bone fracture angles, there is a predominance of angles with values between 75 and 110° among bones with green fractures (Table 13).

At VM4-I, notches have only been documented among Size 2 and 3 animals (Table 12). Single notches comprise 47% of the sample (Figs. 3 and 4d), followed by double or opposing notches

**Table 10**

Frequencies of tooth marks respect bones with good cortical surface according to appendicular limbs where upper: Humerus + Femur; intermediate: Radius + Tibia + Ulna; and lower (metapodials). Size 3 included (3a, 3b and 3).

Animal Size	VM4-I				VM4-II					
	2		3		2			3		
	NISP with Tooth marks	% tooth marks	NISP with Tooth marks	% Tooth marks	NISP with Tooth marks	% Tooth marks	NISP with Tooth marks	% Tooth marks	NISP with Tooth marks	% Tooth marks
Upper limbs	1	6	25	46.2	1	6	2	16.7	31.6	66.7
Intermediate limbs	10	0	40		2	0	0	8.6	0	
Lower limbs	2	0	7.7		1	2	1	20	3.7	20

(Types 2, 3b, 4 and 5; Fig. 4b and c); and then by micro-notches and pseudo-notches. At VM4-II, notches are also mostly found among Size 2–3 animals (Table 12), although micro-notches and pseudo-notches predominate in this level, followed by single notches, with double and opposing notches being less well represented.

## 4. Discussion

### 4.1. Comparing VM4-I and VM4-II

In this paper we have presented the first comprehensive analysis of the faunal assemblage retrieved from VM4 during the 2005, 2013–2015 and 2017–2019 field seasons. Contrary to Palmqvist et al. (2022), there are no data from the 2020 field season as no excavations were carried out at VM4 that year.

As outlined in previous works (Granados et al., 2021; Luzón

**Table 11**  
Bones exhibiting furrowing from VM4.

VM4-I	Bovinae	Equus	Praemegaceros	Indet.				
Talus		3						
Femur			1	1				
Humerus	1	1		2				
Tibia		3						
Pelvis		1	1	1				
Total	1	6	2	4				
VM4-II	Stephanorhinus	Hippopotamus	Mammuthus	Bison	Equus	Praemegaceros	Sorgelia	Indet.
Mandible				2		1	1	
Humerus	2						1	3
Femur	1				3			1
Radio					1			2
Tibia					2			1
Pelvis					2			
Calcaneous		1						
Carpal-tarsal			1					
Indet.								2
Total	3	1	1	2	8	1	2	9

**Table 12**  
Notches identified at VM4. Type 1: complete single notches; Type 2: double opposing complete notches; Type 3a: incomplete notches where inflection points are missing; Type 3b: complete and other incomplete notches where one inflection points is missing; Type 4: double overlapping notches; Type 5: a notch and other double opposing notches; Type 6: pseudo notch; Type 7: micronotch (< 1 cm) (See Suppl. Data, Fig. 1).

	VM4-I	%	VM4-II	%	Total	%
Type 1	8	20.0	13	16.7	21	17.8
Type 2	3	7.5	4	5.1	7	5.9
Type 3a	11	27.5	16	20.5	27	22.9
Type 3b	5	12.5	4	5.1	9	7.6
Type 4	2	5.0	4	5.1	6	5.1
Type 5	2	5.0	3	3.8	5	4.2
Type 6	1	2.5	10	12.8	11	9.3
Type 7	8	20.0	24	30.8	32	27.1
Total	40		78		118	

**Table 13**  
Descriptive statistics for green fracture angles on bones from size 3 animals, based on the nature of the fracture plane: oblique and longitudinal.

	VM4-I		VM4-II	
	Oblique	Longitudinal	Oblique	Longitudinal
Average < 90°	76.6	74.7	77.3	76
Average > 90°	99.7	102.6	104.5	102

et al., 2021), geoarchaeological and taphonomic evidence proves the existence of at least two palaeosurfaces at VM4, resulting from at least two depositional events. Accordingly, it is relevant to start by outlining the similarities and differences between both sub-levels. The species represented at VM4-I and VM4-II are essentially identical, except for *Hemibos* and *Megantereon*, which are only present in VM4-II. The proportion of herbivores and carnivores on both levels is remarkably similar (70/30 in VM4-I vs. 69/31 in VM4-II). Among the herbivore taxa, Cervidae (*Metacervoceros* and *Praemegaceros*) is the best represented family in both sublevels, although the most abundant species is *E. altidens*.

Despite their similarities, there are some slight differences in the assemblage composition that might indicate some sort of palaeoecological change in the landscape of Venta Micena. In VM4-II, species associated with open habitats, such as horses and rhinos, are less frequent than in VM4-I, with a corresponding increase in the proportion of cervids from 28% of MNI in VM4-I to 37% in VM4-II. These variations may indicate a more humid environment during

the formation of VM4-II, an interpretation that would be supported by the geochemical data discussed in Granados et al. (2021). However, more data from tooth wear, archaeobotanical remains and stratigraphic micromorphology are needed for a more accurate depiction of the palaeoenvironmental changes that seem to have occurred between the formation of VM4-I and VM4-II.

From a taphonomic perspective, VM4-I and VM4-II faunal assemblages share several similarities, since both are characterised by good preservation conditions, reflected in a limited incidence of weathering. While carnivore action is present in both levels, there is a greater incidence at VM4-I than at VM4-II. At VM4-I there is a greater degree of fragmentation, as shown by the proportion of bones smaller than 3 cm (43% NISP < 3 cm in VM4-I vs. 36% NISP < 3 cm in VM4-II) and the greater proportion of bones with shaft circumference preservation under 50% (46% in VM4-I vs. 34% in VM4-II) (Table 6). There is also a greater degree of skeletal bias at VM4-I, with 8 elements per individual among Size 2 animals, 17 elements among Size 3 animals, and 1.5 elements among Size 5 animals; by contrast, at VM4-II the values are higher, with 17 elements per individual among Size 2 animals, 16 elements per individual among Size 3 animals and 3.3 elements per individual among Size 5 animals. This skeletal bias may be related to the greater proportion of carnivore damage observed within the VM4-I faunal assemblage, as noted in Table 7. 4.4% of bones from VM4-I show tooth marks versus 1.9% at VM4-II (Table 7). In relation to bone fracture angles, no appreciable differences are observed between the two levels (Table 13), although they are consistent with carnivore bone breakage patterns (Alcántara García et al., 2006; Suppl. Data, SF7), particularly in relation to canid and hyaenid feeding behaviour (cf. Moclán et al., 2019). Both levels also exhibit similar proportion of Type 15 taphotypes (shaft cylinders; Table 14).

Expanding the sample size will provide additional data to assess the extent to which these differences between sublevels are replicated or ought to be discarded.

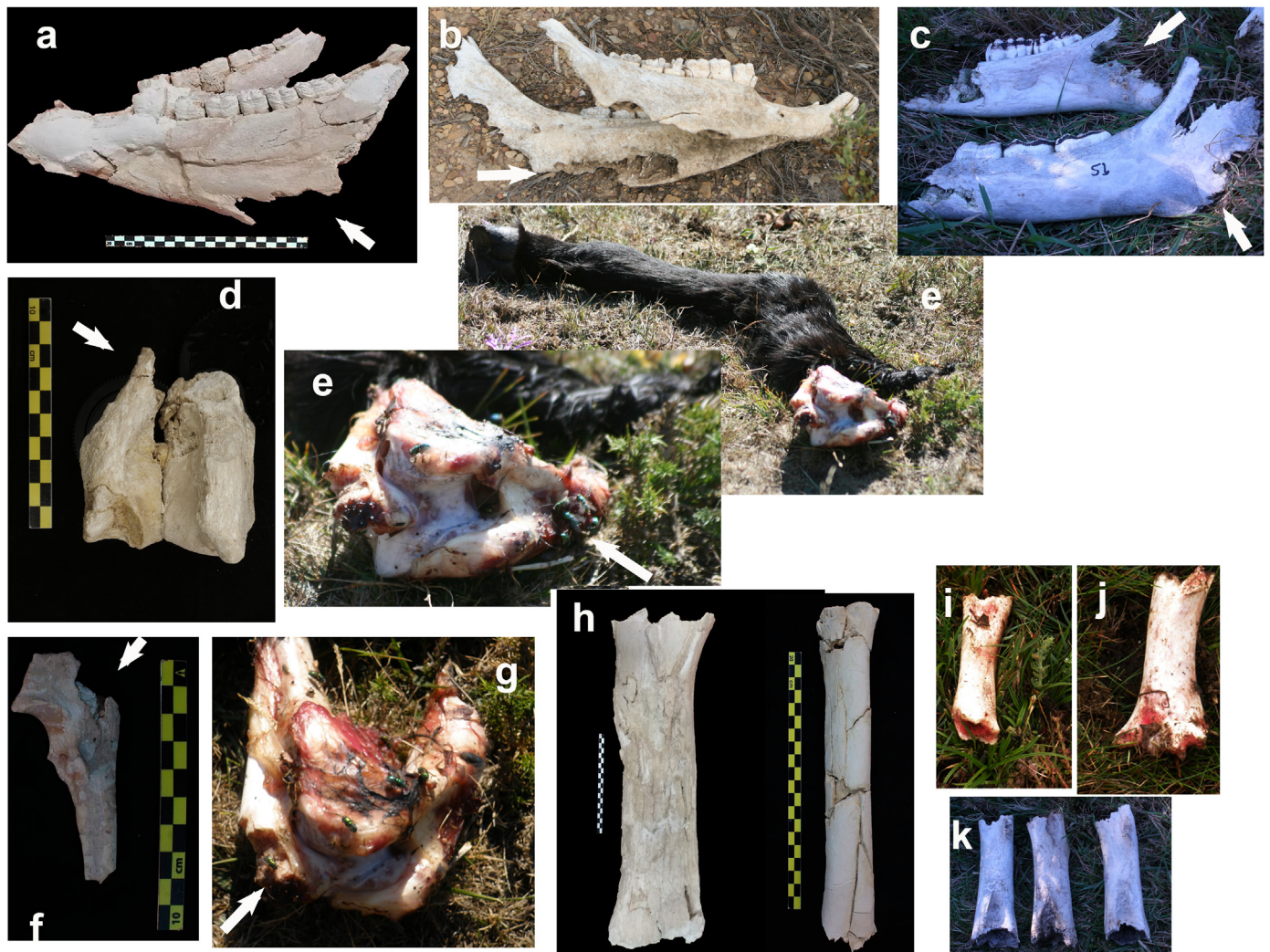
#### 4.2. Relationship and comparative assessment between VM4 and VM3

Comparing our results with those provided by Arribas and Palmqvist (1998, 1999), Palmqvist and Arribas (2001), Espigares (2010) and Palmqvist et al. (2022), it is true that VM3 and VM4 exhibit some similarities (Table 16). However, there are also clear differences (Table 16 and 17).

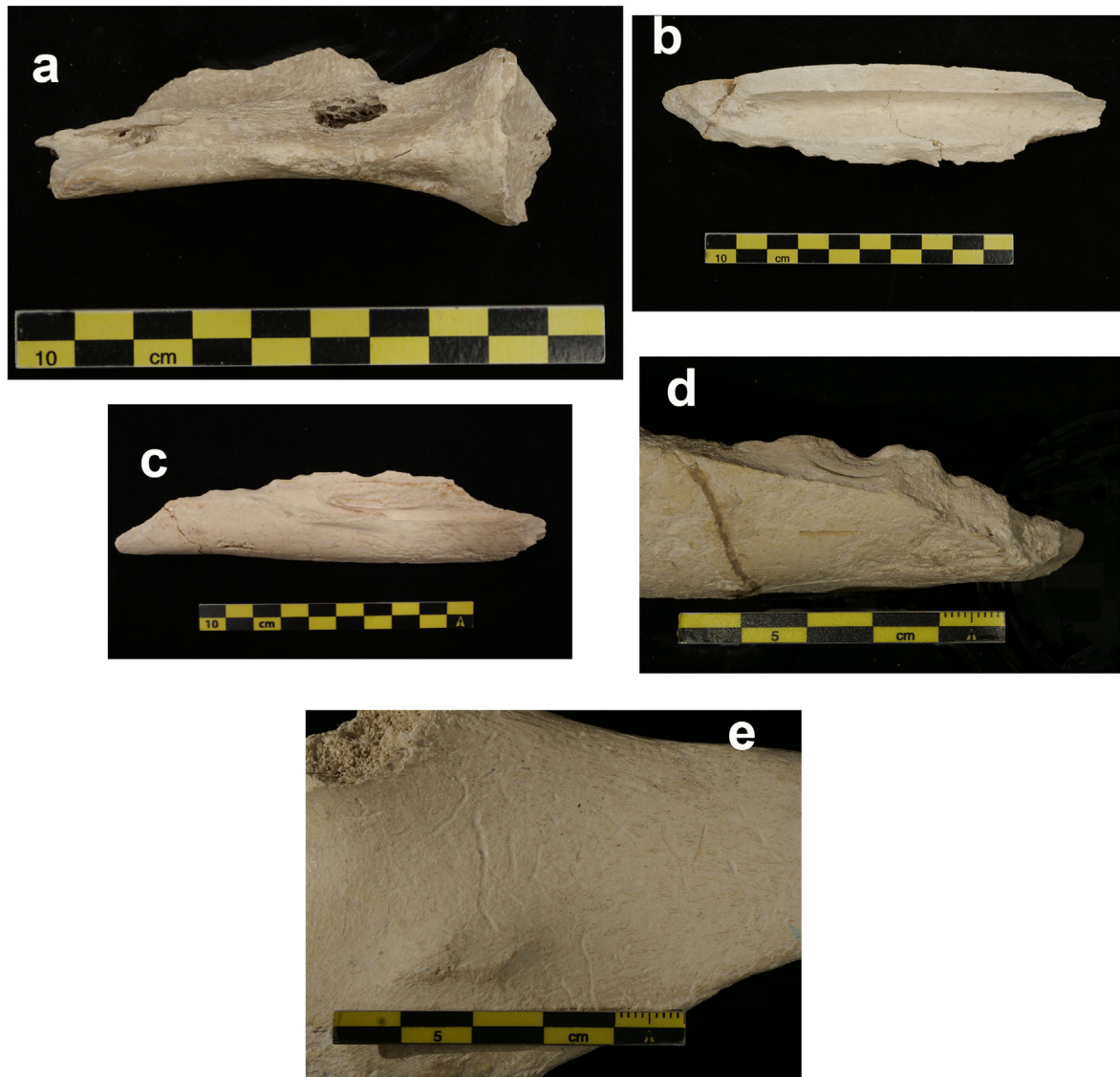
The first difference is in the origin of the materials. We know the

**Table 14**  
Taphotypes identified at VM4, following the criteria outlined by Domínguez Rodrigo et al. (2015).

VM4-I											
Taphotype	0	1	3	4	5	6	9	10	11	12	15
Femur											2
Humerus				1	2						3
Metatarsal								1			
Radio-ulna	1										
Tibia	1		5		1						1
Total	2		5	1	3			1			6
%	11.1		27.8	5.55	16.7			5.55			33.3
VM4-II											
Taphotype	0	1	3	4	5	6	9	10	11	12	15
Femur				1			1				4
Humerus		1	1		2						3
Metacarpal	1									1	
Metatarsal	1										
Radio					1	1			1	1	2
Tibia	1		2	1		1					1
Total	3	1	3	2	3	2	1		1	2	10
%	10.71	3.57	10.71	7.14	10.71	7.14	3.57		3.57	7.14	35.71



**Fig. 3.** Bones from VM4 compared with bones retrieved from actualistic open-air sites. 4a: Horse mandible with furrowing on the mandibular ramus. 4b-c: neotaphonomic examples of mandibles ravaged by wolves at a kill site in El Campelo (Galicia). 4d: distal humerus epiphysis from VM4. 4e: distal humerus epiphysis from a horse hunted by wolves at a kill site in El Campelo (Galicia). 4f: proximal ulna epiphysis with furrowing. 4g: similar feeding sequence documented by wolves at a kill site in El Campelo (Galicia). 4h: two equid shaft cylinders on a tibia and a metatarsal from VM4. 4i-k: immature equid femoral shafts from El Campelo (Galicia).



**Fig. 4.** Tooth-marked bones from VM. 4a: Scapula with a puncture; 4 b-d: long bones with different notch types. 4e: pelvis with biochemical alterations.

stratigraphic and spatial provenance for the VM4 sample: 39 m<sup>2</sup> located at 552462 E, 4176355 N. On the contrary, the provenance of the VM3 sample is heterogeneous, with almost half of the materials lacking a clear origin. Espigares ph.D. dissertation (2010) (supervised by B. Martínez-Navarro and P. Palmqvist) states that 3603 of 7171 elements come from known areas (Table 15). The remaining 3568 elements come from indeterminate localities (Espigares, 2010: 114, Table 7.2.). Moreover, for the remains coming from known emplacement, 723 elements come from fossil outcrops other than VM3. These fossils account for 20% of the known provenance material and 10% of the total. The significance of this lies in the fact that Palmqvist et al. (2022) have based their study on the materials studied by Espigares (2010), mistakenly attributing them all to VM3 (Palmqvist et al., 2022: p. 4, Table 2).

To sum up, around 50% of the remains cannot be associated with any specific VM sector, and 20% of the subsample with known origin does not come from VM3. The VM3 fossil assemblage *sensu stricto* is thus reduced to 2880 specimens (Espigares, 2010; Table 15; Fig. 5). For those reasons, until this smaller sample is restudied separately, all previously reported results should be

treated with caution. Despite the above, we will compare our results for VM4 with those previously published for VM3 because up to this point it is the major reference when it refers to VM. Any future taphonomic study involving VM assemblages must be carried out on remains with known provenance and stratigraphic position, because the provenance of several samples published by Espigares (2010) and Palmqvist et al. (2022) remains unknown.

Taxonomic representation also differs between VM3 and VM4, even if their taxonomic composition is similar (Luzón et al., 2021; Arribas and Palmqvist, 1998, 1999; Palmqvist and Arribas, 2001). According to MNI values, equids are the most represented herbivores at VM3 (35%), a higher frequency than in VM4-I (25%) and VM4-II (22.5%). Megafaunal remains (elephants, rhinos and hippos) are more abundant at both VM4-I (25%) and VM4-II (15%) than at VM3 (8%) (Tables 2 and 3). However, other taxa show similar values in VM3 and VM4. Cervids represent 28.6% of the MNI at VM4-I and 28.3% at VM3, increasing to 37% at VM4-II. Caprids also have similar frequencies in the VM3 assemblage (13.6%) to those found at VM4-I (14.3%) and VM4-II (10%). In summary, very large mammals are more frequent at VM4, while equids are better represented at VM3.

**Table 15**  
Number of studied remains by Espigares, (2010: Table 7.2), with a breakdown of their source provenance. "Corte": large-scale excavation; "Sondeo": test-pit.

Location	Number of remains	%
Corte I	403	5.62
Corte II	51	0.71
<b>Corte III</b>	<b>2.880</b>	<b>40.16</b>
Corte IV	16	0.22
Corte V	1	0.01
Sondeo I	199	2.78
Sondeo II	33	0.46
Sondeo III	12	0.17
Sondeo IV	2	0.03
Sondeo V	6	0.08
<b>Indeterminate</b>	<b>3.568</b>	<b>49.76</b>

There are also some differences in the carnivore palaeoguild represented at both localities. The giant hyaena *P. brevirostris* constitutes 34% of carnivore MNI at VM3 (Arribas and Palmqvist, 1998, 1999; Palmqvist and Arribas, 2001), a higher value than those reported for VM4-I (22.2%) and VM4-II (16.7%). This trend become even more striking when we assess their representation using NISP values (26.9% at VM3 vs. 3.2% at VM4-II). *P. brevirostris* is decidedly more abundant at VM3.

Mortality profiles constitute a third area in which VM3 and VM4 differ, particularly regarding non-adult age groups. At VM4-I and VM4-II, only *P. verticornis* and the very large taxa exhibit non-adult values over 45%, while all medium, large, and very large-sized animals at VM3 exhibit non-adult values over 45%. A borderline example are equids, of which there are 46% of non-adult individuals at VM3 according to Arribas and Palmqvist (1998, 1999), Palmqvist and Arribas (2001) and Palmqvist et al. (2011), or 55% according to Palmqvist et al. (2022). In contrast, their percentage decreases to 28.7% at VM4-I and 33% at VM4-II. These divergences in terms of mortality profiles increase when we assess the data reported for *Pachycrocuta brevirostris*, since 40–50% of MNI corresponds to non-adults at VM3, according to Arribas and Palmqvist (1998, 1999),

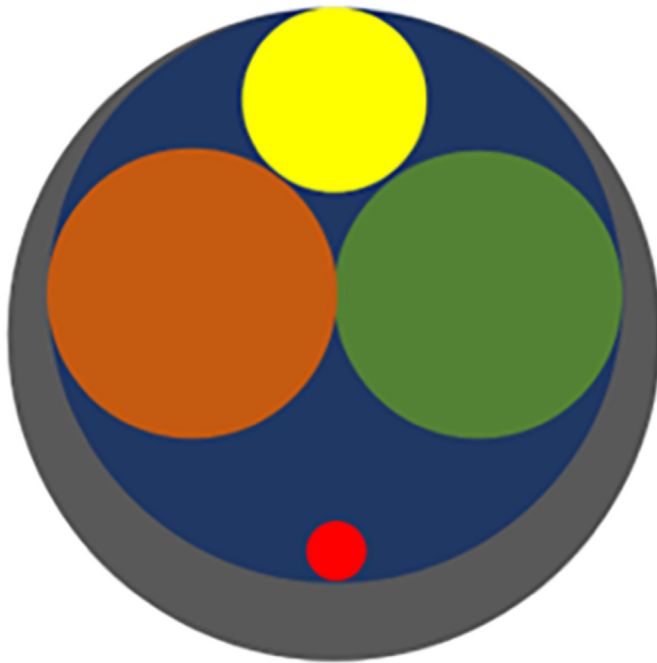
Palmqvist and Arribas (2001), Palmqvist et al. (2011) and Palmqvist et al. (2022); meanwhile, only adult individuals are represented at VM4-I and VM4-II (Tables 2 and 3).

A direct correlation between the size of the species and the proportion of non-adult specimens at VM3 has been claimed repeatedly (Palmqvist et al. 1996; Arribas and Palmqvist, 1998; Palmqvist et al., 2022). Applying the same linear regression method employed by Palmqvist et al. (2022), we note that no such correlation between size class and proportion of non-adult individuals is observed for the faunal assemblages of VM4-I, VM4-II, VM4 (this study) or VM4 [in Palmqvist et al. (2022)]. This lack of correspondence further reinforces the notion that VM3 and VM4 constitute different locations in a complex landscape, without evidence at VM4 of the same prey selection strategies proposed for VM3 (Table 17). Moreover, in terms of skeletal part profiles, Arribas and Palmqvist (1998), Palmqvist and Arribas (2001), Espigares (2010) and Palmqvist et al. (2011) propose that smaller animals (Size 2), such as *S. minor*, *C. alba* or *M. rhenanus*, were transported as complete carcasses to VM3, while medium-sized animals (Size 3), such as equids, would have been the subject of a more specialised strategy, characterised by the preferential transport of appendicular elements. In contrast, we note that both Size 2 and Size 3 animals show a similar pattern of skeletal part representation at VM4-I and VM4-II (Tables 4 and 5). All skeletal portions are represented for both size classes and they show similar biases in skeletal part proportions, which suggests a lower incidence of preferential prey selection than at VM3.

The notion of a less selective depositional strategy is supported by the existence of several joints, ribs, and vertebrae in natural anatomical connection for Size 2, 3, and 5 animals, as discussed here and previously described by Luzón et al. (2021) and Palmqvist et al. (2022, Fig. 6), while only cranial and lower appendicular elements are found in anatomical connection at VM3 (Palmqvist et al., 2022). The pattern observed at VM4 suggests that some carcasses accumulated on the site itself, without experiencing any transport by large carnivores or other biological agents as inferred for VM3.

**Table 16**  
Summary of differences reported for the two main Venta Micena sites (VM3 and VM4).

Features	Similarities	Differences
Sample provenance		The published VM3 samples are heterogeneous in origin; VM4 sample is well recorded and spatially located.
Sedimentological evidence	Similar sedimentological processes	
Stratigraphy	Similar strata present at VM3 and VM4	Two sublevels have been identified at VM4
Biostratigraphy	Similar species	
Water transport	Absent in both	
Weathering		More prolonged subaerial exposure at VM3 Very fast burial rate at VM4
Herbivore frequencies		Size 5 animals comprise 25–17.5% of MNI at VM4 vs. 6% at VM3
Carnivore frequencies		<i>Pachycrocuta</i> comprises 34.6% of carnivore MNI at VM3 vs. 22.2% at VM4-I and 16.7% at VM4-II
Mortality Profiles		VM3 >45% non-adults in Size 3 and 5 animals
Herbivores		VM4 >50% non-adults in Size 5 animals
		VM4 <33% non-adults in Size 2 and 3 animals
<i>Pachycrocuta mortality profile</i>		VM3 50% non-adults
Skeletal part profiles	Anatomical bias	0% of non-adults at both VM4-I and VM4-II
Anatomical connections		VM3: Size 3 animals are preferentially transported selective, size 2 animals are complete
		VM4: Both Size 2 and 3 are similarly represented.
		VM3: Only cranial bones and basipodial elements
		VM4: Abundant (including axial and appendicular elements)
Tooth marks		VM3: High frequencies (29.4%; Arribas, 1999)
		VM4: Low frequencies (4.4% at VM4-I, 1.9% at VM4-II)
Bone fractures		VM3: Predominance of green fractures over dry fractures.
		VM4: Predominance of dry fractures over green fractures.
Taphotypes	Presence of bone cylinders (Type 15) at both sites.	



**Fig. 5.** Comparison among reported NISP values for VM3: grey circle, NISP (total) provided by Palmqvist et al. (2022); blue circle, NISP (total) provided by Espigares (2010); green circle, NISP from known quarries/outcrops provided by Espigares (2010); orange circle, NISP from indeterminate location materials provided by Espigares (2010); yellow circle, NISP from VM3 provided by Espigares (2010); red circle, NISP of known quarries/outcrops other than VM3 provided by Espigares (2010). All circles are to scale.

Carnivore alterations are also far more frequent at VM3 than at VM4 (Arribas and Palmqvist, 1998; Espigares, 2010). Over 1555 remains (>30%) are described to exhibit *Pachycrocuta* tooth marks (Arribas, 1999; Espigares, 2010), whereas neither of the sublevel assemblages at VM4 has more than 5% of remains with tooth marks.

The last factor to consider in a comparative assessment between VM3 and VM4 is the time span in the biostratigraphic phase, the taphonomic stage between death and definitive burial. Weathering rates, which are useful for understanding the degree of subaerial exposure, are low for both levels of VM4 (Table 6), which would suggest a quick burial rate, favouring the preservation of the anatomical connections documented at the site (Palmqvist et al., 2022). Palmqvist et al. (2022) argue that the proportion of abraded remains at VM4 reported by Luzón et al. (2021) (29.8% at VM4-I and 22.3% at VM4-II, respectively) must be in error since no abrading substances are present in the VM4 sediment. However, we highlight that the abrasion is predominantly light in nature and could have been generated by the contact of suspended silt and clay particles with bone surfaces in the context of low energy water flows during deposition (cf. Thompson et al., 2011).

On the basis of all the differences observed between VM3 and VM4 (summarised in Tables 16 and 17), we argue that these two neighbouring and pencontemporaneous sites experienced

somewhat different assemblage formation processes (Luzón et al., 2021; Granados et al., 2021).

### 4.3. Site function at VM4

After establishing that VM3 and VM4 are the result of different site formation processes, we now need to discern the functionality of VM4, which we will interpret through the data presented in the Results section.

As a starting point, we can confirm that VM4 is not an accumulation generated by felids, canids, or ursids, since, apart from foxes, canids are generally agents of dispersal rather than accumulation (see Yravedra et al., 2012). A similar pattern towards favouring dispersion is observed among ursids (Arilla et al., 2014). Felids, such as leopards, can generate bone accumulations (Brain, 1981; Ruiter and Berger, 2000), although their prey tends to be considerably smaller than most of the species represented at VM4; additional differences are observed in terms of the expected mortality and skeletal part profiles of felid-generated accumulation and those described for VM4. Other large felids, such as lions, only rarely produced bone accumulations, often due to exceptional circumstances (Arriaza et al., 2019).

Hyaenas are one of the main biological agents of bone accumulation at a wide range of Pleistocene sites. One of the core features of hyaenid den sites is a high frequency of tooth marks, often above 50%, a pattern observed at both modern assemblages (Bearder, 1977; Skinner et al., 1986; Blumenschine, 1988; Hill, 1989; Cruz-Uribe, 1991; Lam, 1992; Capaldo, 1995; Marean and Kim, 1998; Pickering, 2002; Lacruz and Maude, 2005; Faith, 2007; Egeland et al., 2008; Prendergast and Rodrigo, 2008; Kuhn et al., 2009), as well as in Pleistocene contexts (Brugal et al., 1997; Marra et al., 2004; Michel, 2004; Andrews, 2008; Villa et al., 2010). While there are several examples of hyaenid accumulations with tooth mark frequencies falling below 50% (likely due to external factors that can play a role in reducing the intensity of bone ravaging, such as reduced ecosystem competition) tooth marks are generally still present in over 20% of bones (Faith, 2007; Pokines and Kerbis Peterhans, 2007; Kuhn et al., 2008; Fourvel et al., 2015; Mwebi and Brugal, 2018; Linares-Matás et al., 2021). Per contrary, the VM4 assemblage is far from those values, with barely 4.4% of bones exhibiting tooth marks in VM4-I, and only 1.9% for VM4-II. Furrowing also has a relatively low incidence (<6%) throughout the assemblage.

Tooth mark frequencies in *Pachycrocuta*-generated assemblages are high (Saunders and Dawson, 1998; Espigares, 2010; Garrido et al., 2010; Madurell-Malapeira et al., 2017; Gibert and Ferrández-Cañadell, 2015) to moderate (Mazza et al., 2004; Tappen et al., 2007; Bourguignon et al., 2016; Cheheb et al., 2019; Coil et al., 2020). In either case, these frequencies are higher than the values reported by Palmqvist et al. (2022) (5.5%) and in this study. The lower % of tooth marks in our study compared to Palmqvist et al. (2022) may be due to the fact that no biochemical marks were observed in the latter while 59 have been reported in this study (e.g., Fig. 4e). A mistaken characterisation of biochemical alterations as representing tooth marks has several precedents in Early Pleistocene taphonomy, including at Olduvai Bed I sites

**Table 17**

Regression analysis using the log10 of estimated adult body mass (BM) of herbivore taxa at VM3 and VM4 as independent variable and log10 of non-adult individuals at each locality as dependent variable. The only slope with a p-value <0.05 for which the null hypothesis (H<sub>0</sub>: slope = 0) is the linear regression of log immature on logBM at VM3.

	VM3 Palmqvist et al. (2022)			VM4 Palmqvist et al. (2022)			VM4-I (This study)			VM4-II (This study)			VM4 (This study)		
	R <sup>2</sup>	slope	p-value	R <sup>2</sup>	Slope	p-value	R <sup>2</sup>	slope	p-value	R <sup>2</sup>	slope	p-value	R <sup>2</sup>	slope	p-value
log%immature on logBM	0.694	0.340	<0.01	0.005	0.076	0.860 (ns)	0.060	-0.318	0.525 (ns)	0.329	0.779	0.106 (ns)	0.151	0.338	0.301 (ns)



**Fig. 6.** Neotaphonomic examples of carcasses found at open-air sites. a-c: Wildebeest carcass hunted by lions and scavenged by hyaenas, with some bones in anatomical connection. d: Complete limb bones in anatomical connection from a wildebeest carcass. e-f: Exposed wildebeest carcass at a lion kill site. g: Wildebeest carcass at a kill site with basipodium in anatomical connection. h-o: Young horse carcasses at wolf kill sites; note the presence of articulated remains and complete limb bones. h, i: Pictures taken 1h after a wolf feeding bout, j: Picture taken 4 days after the kill, k-o: Pictures taken 1–2 months after the kill (see Yravedra et al., 2011, 2012 for more details pertaining to the carcasses shown here).

(Domínguez-Rodrigo and Barba, 2006). Even if we consider the VM3 data reported by Espigares (2010) and Palmqvist et al. (2022) to be accurate (29% of bones with tooth marks), the values for this locality are considerably higher than those present at both VM4 sublevels. Furthermore, we can discard the notion that VM4 tooth mark values are underrepresented due to the incidence of other taphonomic processes causing high levels of bone fragmentation or affecting the preservation of bone surfaces (Cruz-Urbe, 1991; Brugal et al., 1997; Pickering, 2002; Kuhn et al., 2008), since cortical bone surfaces are very well preserved at both VM4 sublevels.

Several additional circumstances that may influence the variability observed in tooth mark frequencies within hyaenid accumulations include the presence of often underreported “inconspicuous” tooth marks caused by young individuals (Domínguez-Rodrigo and Pickering, 2010; Linares-Matás et al., 2021), the number of feeders, (Fourvel et al., 2015), bone density, or prey size, whereby the bones of larger animals tend to exhibit more tooth marks (Faith, 2007; Kuhn et al., 2009). This prey size-dependent pattern is indeed replicated at VM4-I and VM4-II (Tables 8 and 9), although the overall number of tooth marks per

bone specimen is consistently low (100% of bones with carnivore alterations exhibit <5 tooth marks: Table 7). This pattern is simply inconsistent with the values reported for hyaenid accumulations (Brugal and Fosse, 2004; Domínguez-Rodrigo and Pickering, 2010).

Several other lines of evidence further indicate that it is very unlikely that any of the VM4 sublevels could be a *Pachycrocuta* den site. There is an absence of immature *Pachycrocuta* remains—their presence is considered a strong indicator of hyaena denning activities, as reported for VM3 (Kruuk, 1972; Mills, 1989; Arribas and Palmqvist, 1998; Brugal and Fosse, 2004); besides, there is a much lower proportion of digested bone remains at VM4 than at other den sites (Kruuk, 1972; D’Errico and Villa, 1997; Marra et al., 2004; Michel, 2004; Brugal and Fosse, 2004; Villa et al., 2010; Gibert and Ferràndez-Cañadell, 2015). The pit/score ratio, with the clear predominance of the former over the latter at VM4 (Table 7), also diverge from the usual expectations and values reported for hyaenid-accumulated assemblages, where either scores predominate or scores exhibit similar values to pits (Egeland et al., 2008; Domínguez-Rodrigo et al., 2012; Arriaza et al., 2019). The low incidence of furrowing at VM4-I and VM4-II is reflected in the large



amount of epiphyses found at the site. The presence of bones in anatomical connection and the green bone fragmentation patterns in limb bones (23%; Table 6) reported for VM4 do not match the patterns observed for hyaenid-accumulated assemblages (Kruuk, 1972; Cruz-Urbe, 1991; Brugal and Fosse, 2004; Domínguez-Rodrigo and Pickering, 2010; Mwebi and Brugal, 2018). Lastly, the VM4 mortality profiles for Size 3 animals, with a predominance of adult individuals, also contrast to hyaenid-accumulated assemblages, which show a higher number of non-adult specimens (Kruuk, 1972; Cruz-Urbe, 1991; Brugal and Fosse, 2004; Arribas, 1999; Domínguez-Rodrigo and Pickering, 2010; Linares-Matás et al., 2021).

Other accumulation dynamics at open-air sites resemble more closely than a den site the patterns observed at VM4. Skeletal parts in anatomical connection, complete bones, and low tooth mark frequencies are commonly found at these sites (Sept, 1994; Coumont, 2009; Hutson and Cain, 2008; Yravedra et al., 2013). Lion-hunted carcasses exposed to the feeding behaviour of other scavengers, such as hyaenas and jackals, tend to exhibit complete limb bones and axial elements in anatomical connection (Fig. 6). Domínguez-Rodrigo et al., 2007 have observed that hyaenid ravaging is more intense at den sites than at open air sites, which correspondingly have lower tooth mark frequencies. Neotaphonomic research on wolf kill sites show that bones present different degrees of anatomical connectivity depending on the nature and intensity of consumption (Fig. 6h-o). We have observed that axial remains and limb bones tend to preserve a considerable degree of anatomical connection when wolves engage with the hunted carcasses of young horses for just one feeding bout (Fig. 6d and h), retaining those connections for several months after such consumption episodes (Fig. 6k-o). Foxes also tend to leave behind articulated remains, with lower tooth mark frequencies and bone fragmentation at open air sites than at den sites (Krajcarz and Krajcarz, 2014; Yravedra et al., 2014; Young et al., 2015; Arilla et al., 2019).

At some open-air waterholes, Hutson (2012) noted very high tooth mark frequencies (c.50%) during the dry season, although most tooth marks are found on axial remains, particularly vertebrae and ribs. Arilla et al. (2019) have also shown that girdle and axial bones tend to present more tooth marks than limb bone diaphyses at open air sites. However, the lower density of these remains in comparison to bone shafts and other anatomical parts (Lam et al., 1998, 1999) often leads to their disappearance from the fossil record due to a wide range of potential density-mediated attritional processes, which may explain why fossil assemblages from open-air sites tend to have low tooth mark frequencies (Hutson and Cain, 2008).

While carnivore predation often occurs at open-air sites, natural mortality can also lead to the accumulation of faunal remains in these localities (Haynes, 1981, 1987, 1988, 1991). Ecological and neotaphonomic studies have noted how carnivore feeding behaviour, such as the intensity of carcass consumption and bone ravaging, as well as scavenging opportunities, are influenced by seasonality and associated factors, such as the levels of carnivore competition or resource limitation (Blumenschine, 1986; Tappen, 1992; Sinclair et al., 2003; Pereira et al., 2014; Arilla et al., 2019; Linares-Matás and Yravedra, 2021; Linares-Matás and Clark, 2022; Clark and Linares-Matás, 2023). These patterns have been observed in the field by Yravedra et al. (2011), who noted how wolf-consumed carcasses in autumn exhibit a greater degree of alteration than those consumed during winter. In Africa, we noted how wet season carcasses (Fig. 6c-f) tend to exhibit more complete limb bones than those hunted by lions and scavenged by hyaenas during the dry season (Fig. 6b). Open-air sites tend to have skeletal elements in anatomical connection, resembling the patterns described

for accumulations generated by felids such as leopards (Ruiter and Berger, 2000) or lions (Arriaza et al., 2016) but not those for hyaenid den assemblages.

Based on the contextualisation of the results discussed above, it is very plausible to argue that VM4 constitutes an open-air locality where multiple agents and depositional processes were at play, leading to a complex set of accumulation episodes, which may also include some instances of natural deaths. The hunting and scavenging of herbivore carcasses by carnivores are reflected in the presence of tooth marks on bone surfaces and the biases of the skeletal part profiles in the absence of any substantial water transport (Tables 2–5). It is not implausible that some of the Size 5 animals (c.20% of MNI at VM4) present at the site, namely elephants, rhinoceroses, and hippopotamuses, may correspond to individuals killed by large sabre-toothed felids, who are considered to have targeted megafaunal species quite consistently (e.g. Palmqvist et al., 2003, 2008a, b). Alongside the predominance of non-adult individuals among Size 5 species, there are other lines of evidence that support the notion that felids played a relevant role in the accumulation and alteration of the faunal assemblage. The pit/score ratio more closely resembles the taphonomic patterns of felids than those of hyaenids (Pickering et al., 2011; Arriaza et al., 2019) and the number of tooth marks per bone is lower than 5 for VM4-II and lower than 7 tooth marks for VM4-I (see Suppl. Data, SF8), which fits more closely the patterns described for felids than those described for hyaenids or canids, which can leave more than 10 tooth marks per bone (Yravedra et al., 2011; Domínguez-Rodrigo et al., 2012) with the exception of lycans (Yravedra et al., 2014).

In addition to felids, hyaenids also interacted with carcasses at VM4, likely acting as scavengers; their activity is illustrated by the presence of diaphysary cylinders on limb bones from Size 3 adult individuals (Fig. 2; see also Sutcliffe, 1970; Cruz-Urbe, 1991; Fosse, 1994; Pokines and Kerbis Peterhans, 2007; Fosse et al., 2011; Domínguez-Rodrigo et al., 2012, 2015). Other carnivores, such as jaguars, can crush and collapse some bone epiphyses but do not produce such diaphysary cylinders (Domínguez-Rodrigo et al., 2012; Rodríguez-Alba et al., 2019). Lions are also not known to produce these alterations on the limb bones of medium- or large-sized species (Gidna et al., 2013; Pobiner and Blumenschine, 2003). Wolves have been observed to generate shaft cylinders when consuming deer bones or immature horse individuals (Fig. 4) or collapse some epiphyses of adult horses (Fig. 2; Yravedra et al., 2011) or even bison (Fosse et al., 2012), but they generally do not generate diaphysary cylinders on large adult prey. The presence of these taphonomic alterations at both VM4-I and VM4-II (Table 14) can more likely be attributed to the feeding behaviour of *P. brevirostris*, which may have even hunted some of these carcasses, a proposition which cannot be ruled out either (Turner and Antón, 1996; Dennell et al., 2008; Vinuesa et al., 2016; Iannucci et al., 2021).

Alongside felids and hyaenids, it is possible that other carnivores also intervened in the modification of the VM4 faunal assemblage. After comparing the fracture angles at the site with the patterns generated by hyaenids and canids (cf. Moclán et al., 2019), it seems that fracture angles at VM4 are closer to those left by canids, an observation that would also be consistent with the taxonomic profile at the site, with multiple species within the prey selection ranges of wolves and other canids (Kruuk and Turner, 1967; Pienaar, 1969; Mattioli et al., 1995; Jedrzejewski et al., 2000; Peterson and Ciucci, 2003; Hayward et al., 2006; Yravedra et al., 2011; Lagos-Abarzuza, 2013; Fourvel et al., 2018). However, the low tooth mark frequencies and the low number of tooth marks per bone does not fit the general pattern observed for canids (Haynes, 1980, 1983; Yravedra et al., 2011; Fosse et al., 2012). Future research employing geometric morphometrics and machine learning

approaches (Aramendi et al., 2017a; Courtenay et al., 2019, 2021; Maté-González et al., 2019; Yravedra et al., 2022b; Courtenay et al., 2023) may offer additional insights into the specific role of different carnivores in the formation and alteration of the two VM4 assemblages.

In addition to any carnivore-generated accumulation, it is plausible that natural deaths played also an important role in the formation of the VM4-II fossil assemblage, given the increase in the representation of Size 5 adult individuals (Table 3), including the presence of a rhinoceros carcass with articulated skeletal elements without tooth marks or any other bone surface modifications, suggesting that their remains were quickly buried prior to any carnivore interaction.

To summarize, and being cautious about the reliability and other issues associated with the VM3 sample, we can agree that VM3 could represent a *P. brevirostris* den site (Arribas, 1999; Arribas and Palmqvist, 1998, 1999; Palmqvist and Arribas, 2001). On the other hand, we can conclude that the nearby site of VM4 is best described as a complex open-air site where a multiplicity of biological processes, including the consumption of herbivore carcasses by carnivores as well as some natural deaths, constituting a diverse faunal assemblage represented by at least two sublevels.

The spatial proximity of two palaeontological sites with different accumulation processes and taphonomic biographies is not unprecedented, since this pattern has also been documented at other Early Pleistocene palaeolandscapes, such as Olduvai Bed I (Ashley et al., 2010; Arráiz et al., 2017). Some sites, such as FLK, were dry season camps (Leakey, 1971; Domínguez-Rodrigo et al., 2014; Linares-Matás and Clark, 2022), in the vicinity of other sites with relevant anthropogenic signatures, such as DS, PTK o AGS (Cobo, 2020), while others, such as AMK (Aramendi et al., 2017b) or FLKN (Domínguez-Rodrigo et al., 2007; Bunn et al., 2010) seem to have constituted carnivore accumulations, whereas others likely were kill sites near freshwater sources, such as FLKNN (Domínguez-Rodrigo et al., 2007; Ashley et al., 2010). This is therefore the first time that differences in the use of space can be proposed across penecontemporaneous sites within a relatively small area of the Orce basin (cf., Granados et al., 2021). However, further research must be carried out at the Venta Micena localities, considerably expanding the excavation area in order to unravel the complex palaeoecological dynamics unfolding at Orce.

## 5. Conclusions

The conclusions of this paper can be summarised as follows.

1. VM illustrates some of the complex site formation processes represented in the Early Pleistocene deposits of the Guadix-Baza Basin, where multiple and different taphonomic biographies are recorded vertically and horizontally. Therefore, it is paramount to dissect these palimpsests in order to study specific assemblages independently, isolating them from other diachronic or synchronic events taking place in the same landscape.
2. The VM4 faunal assemblage formed through the behaviour and input of multiple agents, rather than by the selective transport of any given taxon.
3. Based on the data gathered so far, it seems that VM4-is not a carnivore den site; instead, it resembles more closely an open-air site where multiple carnivores interacted with herbivore carcasses of different species, alongside some potential inputs from natural deaths at VM4-II of large animals, such as rhinoceros.

While only a relatively small excavation surface has been investigated at VM4 (39 m<sup>2</sup>), it is one of the largest Orce

assemblages with a known geospatial provenance *sensu stricto*. As such, the continuity of systematic and rigorous excavations at this relevant palaeontological site promises to expand our knowledge of Early Pleistocene ecosystem dynamics in the southern Iberian Peninsula. An aspect that we are particularly interested in is the seasonality of bone accumulation. This variable has a considerable impact in the formation of open-air sites, since predation cycles and carcass modification intensity are related to the spatio-temporal distribution of water sources. Periods of low water availability, such as Mediterranean summers, favour the concentration of prey around shrinking pools and waterholes, and the corresponding creation of predation opportunities. Therefore, understanding the impact of seasonality on inter-assemblage variability ought to become a future research priority at Early Pleistocene palaeontological localities.

## Author contributions statement

**JY:** Conceptualization, investigation, methodology, supervision, writing, formal analysis, original draft, review and editing. **CL:** Data curation, investigation in Taphonomy, methodology, editing, original draft, Visualization. **JAS:** Investigation in Taphonomy, Visualization. **GLM:** Writing, Review and Editing. **VEG:** Validation, formal analysis, **JJRA:** Investigation in Taphonomy, Visualization, Edition, **LAC:** Investigation in Taphonomy, review, Validation. **DHR:** Investigation in Taphonomy. **ASR:** Investigation, Project Administration. **JC:** Photography, Investigation. **JS:** Investigation and coordination in Macrovertebrates Taxonomy. **CSB:** Investigation in Microfauna Palaeontology. **H-AB:** Investigation in Microfauna Palaeontology. **SV-K:** Investigation in Macrovertebrates Taxonomy. **DdM:** Investigation in Macrovertebrates Taxonomy. **BA:** Investigation in Macrovertebrates Taxonomy. **OO:** Investigation and Supervision in Stratigraphy-Geology. **JA:** Investigation and Supervision in Microfauna Palaeontology. **MF:** Investigation and supervision in Macrovertebrates Taxonomy, Review. **JMJA:** Formal analysis, project administration, resources, supervision and writing, original draft, review and editing.

## Declaration of competing interest

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

## Data availability

All data is included in the text and supplementary files.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2023.108031>.

## References

- Agustí, J., 1985. Biostratigrafía de los depósitos Plio-Pleistocenos de la depresión de Guadix-Baza. (Prov. Granada). *Paleontología i Evolució* 18, 13–18.
- Agustí, J., Blain, H.A., Furió, M., De Marfà, R., Santos-Cubedo, A., 2010. The early Pleistocene small vertebrate succession from the Orce region (Guadix-Baza Basin, SE Spain) and its bearing on the first human occupation of Europe. *Quat. Int.* 223–224, 162–169.
- Agustí, J., Oms, O., Parés, J.M., 2007. Biostratigraphy, paleomagnetism and geology of the Orce ravine (Southern Spain). *Quat. Sci. Rev.* 26, 568–572.
- Alcántara García, V., Barba Egidio, R., Barral del Pino, J., Crespo Ruiz, A., Eiriz Vidal, A., Falquina Aparicio, Á., Herrero Calleja, S., Ibarra Jiménez, A., Megías González, M., Pérez Gil, M., Pérez Tello, V., Rolland Calvo, J., Yravedra Sáinz de los Terrenos, J., Vidal, A., Domínguez-Rodrigo, M., 2006. Determinación de procesos de fractura sobre huesos frescos: un sistema de análisis de los ángulos de los planos de fracturación como discriminador de agentes bióticos. *Trab. Prehist.* 63 (1), 37–45.
- Anadón, P., De Deckker, P., Julià, R., 1986. The Pleistocene lake deposits of the NE Baza Basin (Spain): salinity variations and ostracod succession. *Hydrobiologia* 143, 199–208.
- Anadón, P., Julià, R., De Deckker, E., Rosso, J.C., Soulié-Marsché, I., 1987. Contribución a la Paleolimnología del Pleistoceno inferior de la cuenca de Baza (sector Orce-Micena). *Paleontología i Evolució Mem. Esp.* 1, 35–72.
- Andrews, P., 2008. Cetaceans from a possible striped hyaena den site in Qatar. *Journal of Taphonomy* 6, 255–274.
- Aramendi, J., Maté-González, M.A., Yravedra, J., Ortega, M.C., Arriaza, M.C., González-Aguilera, D., Baquedano, E., Domínguez-Rodrigo, M., 2017a. Discerning carnivore agency through the three-dimensional study of tooth pits: revisiting crocodile feeding behaviour at FLK-Zinj and FLK NN3 (Olduvai Gorge, Tanzania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 93–102.
- Aramendi, J., Uribebarrea, D., Arriaza, M., Arráiz, H., Barboni, D., Yravedra, J., Ortega, M., Gidna, A., Mabulla, A., Baquedano, E., Domínguez-Rodrigo, M., 2017b. The paleoecology and taphonomy of AMK (Bed I, Olduvai Gorge) and its contributions to the understanding of the “Zinj” paleolandscape. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 35–49.
- Arilla, M., Rosell, J., Blasco, R., 2019. Contributing to characterise wild predator behaviour: consumption pattern, spatial distribution and bone damage on ungulate carcasses consumed by red fox (*Vulpes vulpes*). *Archaeological and Anthropological Sciences* 11, 2271–2291 (A).
- Arilla, M., Rosell, J., Blasco, R., Domínguez-Rodrigo, M., Pickering, T., 2014. The “bear” essentials: actualistic research on *Ursus arctos arctos* in the Spanish pyrenees and its implications for paleontology and archaeology. *PLoS One* 9 (7), e102457.
- Arráiz, H., Barboni, D., Ashley, G., Mabulla, A., Baquedano, E., Domínguez-Rodrigo, M., 2017. The FLK zinj paleolandscape: reconstruction of a 1.84 Ma wooded habitat in the FLK zinj-AMK-PTK-DS archaeological complex, middle bed I (Olduvai gorge, Tanzania). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 488, 9–20.
- Arriaza, M., Aramendi, J., Maté-González, M., Yravedra, J., Stratford, D., 2019. Characterising leopard as taphonomic agent through the use of micro-photogrammetric reconstruction of tooth marks and pit to score ratio. *Hist. Biol.* 33 (2), 176–185.
- Arriaza, M., Domínguez-Rodrigo, M., Yravedra, J., Baquedano, E., 2016. Lions as bone accumulators? Paleontological and ecological implications of a modern bone assemblage from Olduvai gorge. *PLoS One* 11, e0153797.
- Arribas, A., 1999. Análisis y modelización de la Tafonomía del yacimiento de Venta Micena (Orce, Granada) y su estudio comparativo con otras localidades españolas del Plio-Pleistoceno continental. Ph.D. Thesis. Universidad Complutense de Madrid.
- Arribas, A., Palmqvist, P., 1999. El modelo de actividad de *Pachycrocuta* en Venta Micena: Implicación de los hiénidos en el registro paleomastológico Plio-Pleistoceno español. *Temas Geológico-Mineros ITGE* 26, 173–181.
- Arribas, A., Palmqvist, P., 1998. Taphonomy and palaeoecology of an assemblage of large mammals: Hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). *Geobios* 31, 3–47.
- Arribas, A., Garrido, G., 2008. Hiénidos [*Pachycrocuta brevirostris* (Aymard, 1846) y *Hyaena brunnea* Thunberg, 1820] del yacimiento de Fonelas P-1 (cuenca de Guadix, Granada). In: Arribas, A. (Ed.), *Vertebrados del Plioceno superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas*. Instituto Geológico y Minero de España, serie Cuadernos del Museo Geominero 10, Madrid, pp. 201–230.
- Arsznov, B.M., Lundrigan, B.L., Holekamp, K.E., Sakai, S.T., 2010. Sex and the frontal cortex: a developmental CT study in the spotted hyena. *Brain Behav. Evol.* 76, 185–197.
- Ashley, G.M., Barboni, D., Dominguez-Rodrigo, M., Bunn, H.T., Mabulla, A.Z.P., Diez-Martín, F., Barba, R., Baquedano, E., 2010. A spring and woodland: new paleo-environmental reconstruction of FLK-Zinj, Olduvai Gorge, Tanzania. *Quat. Int.* 74, 304–314.
- Barsky, D., Celiberti, V., Cauche, D., Grégoire, S., Lebègue, F., de Lumley, H., Toro-Moyano, I., 2010. Raw material discernment and technological aspects of the Barranco León and Fuente Nueva 3 stone assemblages (Orce southern Spain). *Quat. Int.* 223–224, 201–219.
- Bearder, S., 1977. Feeding habits of spotted hyaenas in a woodland habitat. *Afr. J. Ecol.* 15, 263–280.
- Behrensmeier, A., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. New York Academic Press, p. 320.
- Blumenschine, R., 1988. An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. *J. Archaeol. Sci.* 15, 483–502.
- Blumenschine, R., 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., 1986. Early hominid scavenging opportunities; implications of carcass availability in the Serengeti and Ngorongoro ecosystems. *BAR International Series* No 283, 163.
- Borja, C., García-Pacheco, M., Olivares, E., Scheuenstuhl, G., Lowenstein, J., 1997. Immunospecificity of albumin detected in 1.6-million-year-old fossils from Venta Micena in Orce, Granada, Spain. *Am. J. Phys. Anthropol.* 103, 433–441.
- Bourguignon, L., Crochet, J., Capdevila, R., Ivorra, J., Antoine, P., Agustí, J., Barsky, D., Blain, H., Boulbes, N., Bruxelles, L., Claude, J., Cochard, D., Filoux, A., Firmat, C., Lozano-Fernández, I., Magniez, P., Pelletier, M., Rios-Garaizar, J., Testu, A., Valensi, P., De Weyer, L., 2016. Bois-de-Riquet (Lézignan-la-Cèbe, Hérault): a late Early Pleistocene archeological occurrence in southern France. *Quat. Int.* 393, 24–40.
- Brain, C., 1969. The probable role of leopards as predators of the swartkrans australopithecines. *S. Afr. Archaeol. Bull.* 24, 170–171.
- Brain, C.K., 1981. *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. University of Chicago Press, Chicago, p. 376.
- Brugal, J.P., Fosse, P., 2004. Carnivores et Hommes au Quaternaire en Europe de l’Ouest. *Rev. Paleobiol.* 23 (2), 575–595.
- Brugal, J.P., Fosse, P., Guadelli, J.L., 1997. Comparative study of bone assemblages made by recent and Pleistocene hyenids. In: *8<sup>th</sup> Meeting of Working Group 1 on Bone Modification*. Hot Springs: Augustana College, Archaeology Lab., pp. 158–187.
- Bunn, H.T., 1982. *Meat-eating and Human Evolution: Studies on the Diet and Subsistence Patterns of Plio-Pleistocene Hominins in East Africa*. Ph.D. Thesis. University of California.
- Bunn, H., Mabulla, A., Domínguez-Rodrigo, M., Ashley, G., Barba, R., Diez-Martín, F., Remer, K., Yravedra, J., Baquedano, E., 2010. Was FLK North levels 1–2 a classic “living floor” of Oldowan hominins or a taphonomically complex palimpsest dominated by large carnivore feeding behavior? *Quat. Res.* 74 (3), 355–362.
- Capaldo, S., Blumenschine, R., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *Am. Antiq.* 59 (4), 724–748.
- Capaldo, S.D., 1995. *Inferring Hominid and Carnivore Behavior from Dual-Patterned Archaeofaunal Assemblages*. Ph.D. Dissertation, Rutgers University.
- Carandell Baruzzi, M., 2020. *The Orce Man: Controversy, Media and Politics in Human Origins Research*. Brill, Leiden.
- Carandell Baruzzi, M., 2013. Homínidos, dudas y grandes titulares: la controversia del Hombre de Orce en la prensa española (1983–2007). *Dynamis* 33 (2), 365–387.
- Cheheb, R., Arzarello, M., Arnaud, J., Berto, C., Cáceres, I., Caracausi, S., Colopi, F., Daffara, S., Canini, G., Huguet, R., Karamatsou, T., Sala, B., Zambaldi, M., Berruti, G., 2019. Human behavior and Homo-mammal interactions at the first European peopling: new evidence from the Pirro Nord site (Apricina, Southern Italy). *Sci. Nat.* 106 (5–6).

- Clark, J., Linares-Matás, G.J., 2023. Seasonal resource categorisation and behavioral adaptation among chimpanzees: implications for early hominin carnivory. *J. Anthropol. Sci.* 101, 1–36.
- Cobo, L., 2020. *Estudio Tafonómico y Espacial del Yacimiento Arqueológico DS del Lecho I de la Garganta de Olduvai (Tanzania)*. Ph.D. Thesis. Universidad Complutense de Madrid.
- Coil, R., Tappen, M., Ferring, R., Bukhsianidze, M., Nioradze, M., Lordkipanidze, D., 2020. Spatial patterning of the archaeological and paleontological assemblage at Dmanisi, Georgia: an analysis of site formation and carnivore-hominin interaction in Block 2. *J. Hum. Evol.* 143, 102773.
- Coumout, M., 2009. Proposition d'un référentiel taphonomique fossile de faunes issues d'avens-pièges. *Ann. Paleontol.* 95 (1), 1–20.
- Courtenay, L.A., Herranz-Rodrigo, D., Yravedra, J., Vázquez-Rodríguez, J., Huguet, R., Barja, I., Maté-González, M., Fernández, M., Muñoz-Nieto, Á., González-Aguilera, D., 2021. 3D insights into the effects of captivity on wolf mastication and their tooth marks; implications in ecological studies of both the past and present. *Animals* 11 (8), 2323.
- Courtenay, L.A., Yravedra, J., Huguet, R., Aramendi, J., Maté-González, M.A., González-Aguilera, D., Arriaza, M.C., 2019. Combining machine learning algorithms and geometric morphometrics: a study of carnivore tooth marks. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 522, 28–39.
- Courtenay, L.A., Yravedra, J., Herranz-Rodrigo, D., Rodríguez-Alba, J.J., Serrano-Ramos, A., Estaca-Gómez, V., González-Aguilera, D., Solano, J.A., Jiménez-Arenas, J.M., 2023. Deciphering carnivore competition for animal resources at the 1.46 Ma early Pleistocene site of Barranco León (Orce, Granada, Spain). *Quat. Sci. Rev.* 300, 107912. <https://doi.org/10.1016/j.quascirev.2022.107912>.
- Cruz-Urbe, K., 1991. Distinguishing hyena from hominid bone accumulations. *J. Field Archaeol.* 18, 476–486.
- Dennell, R.W., Coard, R., Turner, A., 2008. Predators and scavengers in early Pleistocene southern Asia. *Quat. Int.* 192 (1), 88, 0. <https://doi.org/10.1016/j.quaint.2007.06.023>.
- D'Errico, F., Villa, P., 1997. Holes and grooves: the contribution of microscopy and taphonomy to the problem of art origins. *J. Hum. Evol.* 33 (1), 1–31.
- 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 (2), 170–194.
- Domínguez-Rodrigo, M., Pickering, T., 2010. A multivariate approach for discriminating bone accumulations created by spotted hyenas and leopards: harnessing actualistic data from East and Southern Africa. *Journal of Taphonomy* 8, 155–179.
- Domínguez-Rodrigo, M., Barba, R., Egeland, C.P., 2007. Deconstructing Olduvai: A Taphonomic Study of the Bed I Sites. Springer, New York, p. 292.
- Domínguez-Rodrigo, M., Bunn, H., Yravedra, J., 2014. A critical re-evaluation of bone surface modification models for inferring fossil hominin and carnivore interactions through a multivariate approach: application to the FLK Zinj archaeological assemblage (Olduvai Gorge, Tanzania). *Quat. Int.* 322–323, 32–43.
- Domínguez-Rodrigo, M., Gidna, A., Yravedra, J., Musiba, C., 2012. A comparative neotaphonomic study of felids, hyenids and canids: an analogical framework based on long bone modification patterns. *Journal of Taphonomy* 10, 147–164.
- Domínguez-Rodrigo, M., Yravedra, J., Organista, E., Gidna, A., Fourvel, J., Baquedano, E., 2015. A new methodological approach to the taphonomic study of paleontological and archaeological faunal assemblages: a preliminary case study from Olduvai Gorge (Tanzania). *J. Archaeol. Sci.* 59, 35–53.
- Duval, M., Falguères, C., Bahain, J., Grün, R., Shao, Q., Aubert, M., Dolo, J., Agustí, J., Martínez-Navarro, B., Palmqvist, P., Toro-Moyano, I., 2012. On the limits of using combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce area (Guadix-Baza basin, Spain). *Quat. Res.* 77 (3), 482–491.
- Egeland, A.G., Egeland, C., Bunn, H.T., 2008. Taphonomic analysis of a modern spotted hyena (*Crocuta crocuta*) den from Nairobi, Kenya. *Journal of Taphonomy* 6, 275–299.
- Espigares, M.P., 2010. Análisis y modelización del contexto sedimentario y los atributos tafonómicos de los yacimientos pleistocénicos del borde nororiental de la cuenca de Guadix-Baza. Universidad de Granada, Granada.
- Fernández-Jalvo, Y., Andrews, P., 2016. Atlas of Taphonomic Identifications. Springer. <https://doi.org/10.1007/978-94-017-7432-1>.
- Faith, J., 2007. Sources of variation in carnivore tooth-mark frequencies in a modern spotted hyena (*Crocuta crocuta*) den assemblage, Amboseli Park, Kenya. *J. Archaeol. Sci.* 34, 1601–1609.
- Fosse, P., 1994. Taphonomie paléolithique: Les grands mammifères de Soleilhac (Haute-Loire) et de Lunel-Viel 1 (Hérault). Ph.D. Thesis. Université de Provence Aix-Marseille, p. 257.
- Fosse, P., Avery, G., Selva, N., Smietana, W., Okarma, H., Wajrak, A., Fourvel, J.B., Madelaine, S., 2011. Taphonomie comparée des os longs d'ongulés dévorés par les grands prédateurs modernes d'Europe et d'Afrique (*C. lupus*, *P. brunnea*). In: Brugal, J.P., Gardeisen, A., Zuckler, A. (Eds.), *Prédateurs dans tous leurs états; évolution, biodiversité, interactions, mythes, symboles*. XXXI rencontres internationales d'archéologie et d'histoire d'Antibes, pp. 127–156.
- Fosse, P., Selva, N., Wajrak, A., Fourvel, J.B., Madelaine, S., et al., 2012. Bone modification by modern wolf (*Canis lupus*): a taphonomic study from their natural feeding places. *Journal of Taphonomy* 10 (3–4), 197–217.
- Fourvel, J., Fosse, P., Avery, G., 2015. Spotted, striped or brown? Taphonomic studies at dens of extant hyaenas in eastern and southern Africa. *Quat. Int.* 369, 38–50.
- Fourvel, J., Magniez, P., Moigne, A., Testu, A., Joris, A., Lamglait, B., Vaccaro, C., Fosse, P., 2018. Wild dogs and their relatives: implication of experimental feedings in their taphonomical identification. *Quaternaire* 29 (1), 21–29.
- Garrido, G., García-Solano, J.A., Viseras, C., Soria, J.M., Arribas, A., 2010. Taphonomic approach to Fonelas P-1 site (late Pliocene, Guadix basin, Granada): descriptive taphonomic characters related to hyaenid activity. In: *Proc. of "1ª Reunión de Científicos sobre Cubiles de Hiena (y otros grandes carnívoros) en los Yacimientos Arqueológicos de la Península Ibérica"*, pp. 132–146.
- Gibert, J., Palmqvist, P., 1995. Fractal analysis of the Orce skull sutures. *J. Hum. Evol.* 28, 561–575.
- Gibert, J., Agustí, A., Moyà-Solà, S., 1983. Presencia de Homo sp. en el yacimiento del Pleistoceno inferior de Venta Micena. *Paleontología i Evolució mem. esp.* 1–12.
- Gibert, J., Gibert, L., Iglesias, A., Maestro, E., 1998. Two 'Oldowan' assemblages in the Plio-Pleistocene deposits of the Orce region, southeast Spain. *Antiquity* 72, 17–25. <https://doi.org/10.1017/S0003598X00086233>.
- Gibert, J., Gibert, L., Albadalejo, S., Ribot, F., Sánchez, F., Gibert, P., 1999. Molar tooth fragment BL5-0: The oldest human remain found in the Plio-Pleistocene of Orce (Granada province, Spain). *Hum. Evol.* 14, 3–19.
- Gibert, L., Ferrández-Cañadell, C. (Eds.) 2015. *Geología y Paleontología de Cueva Victoria*. Mastia 11–13, 1–478.
- Gidna, A., Yravedra, J., Domínguez-Rodrigo, M., 2013. A cautionary note on the use of captive carnivores to model wild predator behavior: a comparison of bone modification patterns on long bones by captive and wild lions. *J. Archaeol. Sci.* 40, 1903–1910.
- Granados, A., Oms, O., Anadón, P., Ibáñez-Insa, J., Kaakinen, A., Jiménez-Arenas, J., 2021. Geochemical and sedimentary constraints on the formation of the Venta Micena early Pleistocene site (Guadix-Baza Basin, Spain). *Sci. Rep.* 11.
- Haynes, G., 1980. Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones. *Paleobiology* 6 (3), 341–351.
- Haynes, G., 1981. Bone Modifications and Skeletal Disturbances by Natural Agencies: Studies in North America. Unpublished Ph.D. Thesis, Catholic University of America.
- Haynes, G., 1983. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology* 9 (2), 164–172.
- Haynes, G., 1987. Proboscidean die-offs and die-outs: age profiles in fossil collections. *J. Archaeol. Sci.* 14 (6), 659–668.
- Haynes, G., 1988. Studies of elephant death and die-offs: potential applications in understanding mammoth bone assemblages. In: Webb, E. (Ed.), *Recent Developments in Environmental Analysis in Old and New World Archaeology*. BAR International Series No. 416, Oxford, pp. 151–169.
- Haynes, G., 1991. *Mammoths, Mastodonts, and Elephants: Biology, Behavior, and the Fossil Record*. Cambridge University Press, Cambridge, p. 428.
- Hayward, M., O'Brien, J., Hofmeyr, M., Kerley, G., 2006. Prey preferences of the African wild dog *Lycyon pictus* (canidae: carnivora): ecological requirements for conservation. *J. Mammal.* 87 (6), 1122–1131.
- Hill, A., 1989. Bone modification by modern spotted Hyenas. In: Bonnichsen, R., Sorg, M.H. (Eds.), *Bone Modification*. Center for the Study of the First Americans, Orono, pp. 169–178.
- Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007a. Social intelligence in the spotted hyena (*Crocuta crocuta*). *Phil. Trans. Roy. Soc. Lond. B* 362, 523–538.
- Holekamp, K.E., Sakai, S.T., Lundrigan, B.L., 2007b. The spotted hyena (*Crocuta crocuta*) as a model system for study of the evolution of intelligence. *J. Mammal.* 88, 545–554.
- Holekamp, K.E., Dantzer, B., Stricker, G., Yoshida, K.C.S., Benson-Amram, S., 2015. Brains, brawn and sociality: a hyaena's tale. *Anim. Behav.* 103, 237–248.
- Hutson, J., 2012. Neotaphonomic measures of carnivore serial predation at Ngamo Pan as an analog for interpreting open-air faunal assemblages. *J. Archaeol. Sci.* 39 (2), 440–457.
- Hutson, J.M., Cain, C.R., 2008. Reanalysis and reinterpretation of the kalkbalk faunal accumulation, limpopo province, South Africa. *Journal of Taphonomy* 6, 399–428.
- Iannucci, I., Mecozzi, B., Sardella, R., Iurino, D.A., 2021. The extinction of the giant hyena *Pachycrocuta brevirostris* and a reappraisal of the epivillafranchian and galerian hyaenidae in Europe: faunal turnover during the early–middle Pleistocene transition. *Quat. Sci. Rev.* 272, 107240. <https://doi.org/10.1016/j.quascirev.2021.107240>.
- Jedrzejewski, W., Jedrzejewska, B., Okarma, H., Schmidt, K., Zub, K., Musiani, M., 2000. Prey selection and predation by wolves in Bialowieza primeval forest, Poland. *J. Mammal.* 81, 197–212.
- Katsagoni, A., Konidaris, G.E., Giusti, D., Harvati, K., Kostopoulos, D.S., 2022. Bone modifications by the giant hyaena *Pachycrocuta brevirostris* on large-sized ungulate carcasses from the lower Pleistocene site of Tsiotira Vryssi (Mygdonia basin, Greece). *Hist. Biol.* <https://doi.org/10.1080/08912963.2022.2140424>.
- Krajcarz, M., Krajcarz, M., 2014. The red fox (*Vulpes vulpes*) as an accumulator of bones in cave-like environments. *Int. J. Osteoarchaeol.* 24 (4), 459–475.
- Kruuk, H., Turner, M., 1967. Comparative notes on predation by lion, leopard, cheetah and wild dog in the Serengeti Area, Tanzania. *Mammalia* 31 (1), 1–27.
- Kruuk, H., 1972. *The Spotted Hyena. A Study of Predation and Social Behavior*. The University of Chicago Press, Chicago, p. 335.
- Kuhn, B., Berger, L., Skinner, J., 2008. Examining criteria for identifying and differentiating fossil faunal assemblages accumulated by hyenas and hominins using extant hyenid accumulations. *Int. J. Osteoarchaeol.* 20 (1), 15–31. <https://doi.org/10.1002/oa.996>.

- Kuhn, B., Berger, L., Skinner, J., 2009. Variation in tooth mark frequencies on long bones from the assemblages of all three extant bone-collecting hyaenids. *J. Archaeol. Sci.* 36 (2), 297–307.
- Lacruz, R.S., Maude, G., 2005. Bone accumulations at brown hyena (*Parahyaena brunnea*) den sites in the Makgadikgadi Pans, Northern Botswana: taphonomic, behavioral and palaeoecological implications. *Journal of Taphonomy* 3, 43–53.
- Lagos-Abarzuza, L., 2013. Ecología del lobo (*Canis lupus*), del poni salvaje (*Equus ferus atlanticus*) y del ganado vacuno semiextensivo (*Bos taurus*) en Galicia. Ph.D. Thesis. Universidad de Santiago de Compostela, Santiago de Compostela.
- Lam, Y., 1992. Variability in the behaviour of spotted hyaenas as taphonomic agents. *J. Archaeol. Sci.* 19 (4), 389–406.
- Lam, Y., Chen, X., Pearson, O., 1999. Intertaxonomic variability in patterns of bone density and the differential representation of bovid, cervid, and equid elements in the archaeological record. *Am. Anthropol.* 64 (2), 343–362.
- Lam, Y., Chen, X., Marean, C., Frey, C., 1998. Bone density and long bone representation in archaeological faunas: comparing results from CT and photon densitometry. *J. Archaeol. Sci.* 25 (6), 559–570.
- Leakey, R., 1971. Further evidence of lower Pleistocene hominids from east rudolf, north Kenya. *Nature* 231, 241–245.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press.
- Linares-Matás, G.J., Fernández Ruiz, N., Haber Uriarte, M., López-Martínez, M., Walker, M.J., 2021. Hyaenas and early humans in the latest early Pleistocene of south-western Europe. *Sci. Rep.* 11, 24036. <https://doi.org/10.1038/s41598-021-03547-7>.
- Linares-Matás, G.J., Yravedra, J., 2021. 'We hunt to share': social dynamics and very large mammal butchery during the Oldowan–Acheulean transition. *World Archaeol.* 53 (2), 224–254. <https://doi.org/10.1080/00438243.2022.2030793>.
- Linares-Matás, G.J., Clark, J., 2022. Seasonality and oldowan behavioral variability in east africa. *J. Hum. Evol.* 164, 103070. <https://doi.org/10.1016/j.jhevol.2021.103070>.
- Luzón, C., Yravedra, J., Courtenay, L., Saarinen, J., Blain, H., DeMiguel, D., Viranta, S., Azanza, B., Rodríguez-Alba, J., Herranz-Rodrigo, D., Serrano-Ramos, A., Solano, J., Oms, O., Agustí, J., Fortelius, M., Jiménez-Arenas, J., 2021. Taphonomic and spatial analyses from the early Pleistocene site of Venta Micena 4 (Orce, Guadix-Baza Basin, southern Spain). *Sci. Rep.* 11.
- Madurell-Malapeira, J., Alba, D.M., Aurell-Garrido, J., Moyà-Solà, S., 2011. Taphonomic approach to the last villafranchian faunas of Europe. The layer 7 of the vallparadís estació local section (terrassa, NE iberian peninsula). In: IX Encuentro de Jóvenes Investigadores en Paleontología. Morella, Castellón.
- Madurell-Malapeira, J., Morales, J., Vinuesa, V., Boscaini, A., 2015. Úrsidos, hiénidos y félidos del Pleistoceno inferior de Cueva Victoria (Cartagena, Murcia). In: Gibert, L., Fernández Canadell, C. (Eds.), *Geología y Paleontología de Cueva Victoria*. Mastia: Revista del Museo Arqueológico Municipal de Cartagena. Ayuntamiento de Cartagena, Cartagena, pp. 401–432.
- Madurell-Malapeira, J., Alba, D.M., Espigares, M.P., Vinuesa, V., Palmqvist, P., Martínez-Navarro, B., Moyà-Solà, S., 2017. Were large carnivores and great climatic shifts limiting factors for hominin dispersals? Evidence of the activity of *Pachycrocuta brevirostris* during the Mid-Pleistocene Revolution in the Vallparadís Section (Vallés-Penedès Basin, Iberian Peninsula). *Quat. Int.* 431, 42–52. <https://doi.org/10.1016/j.quaint.2015.07.040>.
- Marean, C., Kim, S., 1998. Moustarian large-mammal remains from kobe cave (zagros mountains, Iran): behavioral implications for neanderthals and early modern humans. *Curr. Anthropol.* 39 (S1), S79–S114.
- Marra, A., Villa, P., Beauval, C., Laura, B., Goldberg, P., 2004. Same predator, variable prey: taphonomy of two Upper Pleistocene hyena dens in Sicily and SW France. *Rev. Paleobiol.* 23, 787–801.
- Martínez-Navarro, B., 1991. Revisión sistemática y estudio cuantitativo de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada). Ph.D. Thesis. Universitat Autònoma de Barcelona, Barcelona.
- Martínez-Navarro, B., 2002. The skull of Orce: parietal bones or frontal bones? *J. Hum. Evol.* 42, 265–270.
- Maté-González, M.A., González-Aguilera, D., Linares-Matás, G., Yravedra, J., 2019. New technologies applied to modelling taphonomic alterations. *Quat. Int.* 517, 4–15. <https://doi.org/10.1016/j.quaint.2018.12.021>.
- Mattioli, L., Apollonio, M., Mazzarone, V., Centofanti, E., 1995. Wolf food habits and wild ungulate availability in the Foreste Casentinesi National Park, Italy. *Acta Theriol.* 40, 387–402.
- Mazza, P., Bertini, A., Magi, M., 2004. The late pliocene site of poggio rosso (Central Italy): taphonomy and paleoenvironment. *Palaios* 19 (3), 227–248.
- Michel, P., 2004. La grotte d'Unikoté (Iholdy, Pyrénées Atlantiques, France): une grotte-repaire d'hyènes des cavernes avec des indices de présence humaine dans des niveaux würmiens. *Rev. Paléobiol.* 23, 741–760.
- Mills, M., 1989. The comparative behavioral ecology of hyenas: the importance of diet and food dispersion. In: Gittleman, J.L. (Ed.), *Carnivore Behavior, Ecology, and Evolution*. Springer, Boston, pp. 125–142.
- Moclán, A., Domínguez-Rodrigo, M., Yravedra, J., 2019. Classifying agency in bone breakage: an experimental analysis of fracture planes to differentiate between hominin and carnivore dynamic and static loading using machine learning (ML) algorithms. *Archaeol. Anthropol. Sci.* 11 (9), 4663–4680.
- Moyà-Solà, S., Köhler, M., 1997. The Orce skull: anatomy of a mistake. *J. Hum. Evol.* 33, 91–97.
- Mwebi, O., Brugal, J., 2018. Comparative taphonomical studies of sympatric hyenids (*Crocota crocuta* and *Hyaena hyaena*) bone assemblages, insights from modern dens in Kenya. *Quaternaire* 29 (1), 13–20.
- Oms, O., Anadón, P., Agustí, J., Julià, R., 2011. Geology and chronology of the continental Pleistocene archeological and paleontological sites of the Orce area (Baza basin, Spain). *Quat. Int.* 243, 33–43. <https://doi.org/10.1016/j.quaint.2011.03.048>.
- Palmqvist, P., 1997. A critical re-evaluation of the evidence for the presence of hominids in lower Pleistocene times at Venta Micena, Southern Spain. *J. Hum. Evol.* 33, 83–89.
- Palmqvist, P., Arribas, A., 2001. Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. *Paleobiology* 27 (3), 512–530.
- Palmqvist, P., Espigares, M., Pérez-Claros, J., Figueirido, B., Guerra-Merchán, A., Ros-Montoya, S., Rodríguez-Gómez, G., García-Aguilar, J., Granados, A., Martínez-Navarro, B., 2022. Déjà vu: a reappraisal of the taphonomy of quarry VM4 of the early Pleistocene site of Venta Micena (Baza Basin, SE Spain). *Sci. Rep.* 12 (1).
- Palmqvist, P., Gröcke, D., Arribas, A., Fariña, R., 2003. Paleoeological reconstruction of a lower Pleistocene large mammal community using biogeochemical ( $\delta^{13}C$ ,  $\delta^{15}N$ ,  $\delta^{18}O$ , Sr:Zn) and ecomorphological approaches. *Paleobiology* 29 (2), 205–229.
- Palmqvist, P., Martínez-Navarro, B., Arribas, A., 1996. Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. *Paleobiology* 22 (4), 514–534.
- Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J., Patrocinio Espigares, M., Ros-Montoya, S., De Renzi, M., 2011. The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. *Quat. Int.* 243 (1), 61–79.
- Palmqvist, P., Pérez-Claros, J., Janis, C., Gröcke, D., 2008a. Tracing the ecophysiology of ungulates and predator-prey relationships in an early Pleistocene large mammal community. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266 (1–2), 95–111.
- Palmqvist, P., Pérez-Claros, J., Janis, C., Figueirido, B., Torregrosa, V., Grocke, D., 2008b. Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. *Palaios* 23 (11), 724–737.
- Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. *Mamm. Rev.* 44, 44–55. <https://doi.org/10.1111/mam.12005>.
- Pérez-Claros, J.A., Coca-Ortega, C., 2020. Canines and carnassials as indicators of sociality in durophagous hyaenids: analyzing the past to understand the present. *PeerJ* 8, e10541. <https://doi.org/10.7717/peerj.10541>.
- Peterson, R.O., Ciucci, P., 2003. The wolf as a carnivore. In: Mech, D., Botani, L. (Eds.), *Wolves, Behavior, Ecology and Conservation*. The University of Chicago Press, Chicago, pp. 104–130.
- Pickering, T., 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *J. Osteoarchaeol.* 12 (2), 127–141.
- Pickering, T.R., Heaton, J.L., Zwodeski, S.E., Kuman, K., 2011. Taphonomy of bones from baboons killed and eaten by wild leopards in Mapungubwe National Park, South Africa. *J. Taphonomy* 9, 117–159.
- Pienaar, U., 1969. Predator-prey relationships amongst the larger mammals of the Kruger National Park. *Koedoe* 12 (1), 108–176.
- Pobiner, B., Blumenschine, R., 2003. A taphonomic perspective on Oldowan hominid encroachment on the carnivorous paleoguild. *J. Taphonomy* 1, 115–141.
- Pokines, J., Kerbis Peterhans, J., 2007. Spotted hyena (*Crocota crocuta*) den use and taphonomy in the Masai Mara National Reserve, Kenya. *J. Archaeol. Sci.* 34 (11), 1914–1931.
- Prendergast, M.E., Domínguez-Rodrigo, M., 2008. Taphonomic analyses of a hyena den and a natural-death assemblage near lake Eyasi (Tanzania). *J. Taphonomy* 6, 301–335.
- Ribot, F., Gibert, L., Ferrández-Cañadell, C., García-Olivares, E., Sánchez, F., Lería, M., 2015. Two deciduous human molars from the Early Pleistocene deposits of Barranco León (Orce, Spain). *Curr. Anthropol.* 56, 134–142.
- Rodríguez-Alba, J., Linares-Matás, G., Yravedra, J., 2019. First assessments of the taphonomic behaviour of jaguar (*Panthera onca*). *Quat. Int.* 517, 88–96.
- Ruiter, D., Berger, L., 2000. Leopards as taphonomic agents in dolomitic caves—implications for bone accumulations in the hominid-bearing deposits of South Africa. *J. Archaeol. Sci.* 27 (8), 665–684.
- Sakai, S.T., Arsznov, B.M., Lundrigan, B.L., Holekamp, K.E., 2011. Brain size and social complexity: a computed tomography study in Hyaenidae. *Brain Behav. Evol.* 77, 91–104.
- Saunders, J., Dawson, B., 1998. Bone damage patterns produced by extinct hyena, *Pachycrocuta brevirostris* (mammalia: carnivora) at the Haro River Quarry, northwestern Pakistan. In: Yomida, Y., Flynn, L.J., Jacobs, L.L. (Eds.), *Advances in Vertebrate Paleontology and Geochronology*, 14. National Science Museum Monographs, Tokyo, pp. 215–242.
- Sept, J., 1994. Bone distribution in a semi-arid riverine habitat in eastern Zaire: implications for the interpretation of faunal assemblages at early archaeological sites. *J. Archaeol. Sci.* 21 (2), 217–235.
- Shipman, P., 1981. *Life History of a Fossil. An Introduction to Taphonomy and Paleoecology*. University Press, Harvard.
- Sinclair, A., Mduma, S., Brashares, J., 2003. Patterns of predation in a diverse predator-prey system. *Nature* 425, 288–290. <https://doi.org/10.1038/nature01934>.
- Skinner, J., Henschel, J., van Jaarsveld, A., 1986. Bone-collecting habits of spotted hyaenas *Crocota crocuta* in the Kruger National Park. *S. Afr. J. Zool.* 21 (4), 303–308.

- Sutcliffe, A., 1970. Spotted Hyaena: crusher, gnawer, digester and collector of bones. *Nature* 227 (5263), 1110–1113.
- Tappen, M., 1992. Taphonomy of a central African savanna: natural bone deposition in Parc National des Virunga, Zaire. Ph.D. Thesis. Harvard University, Cambridge.
- Tappen, M., Lordkipanidze, D., Bukhianidze, M., Ferring, R., Vekua, A., 2007. Are you in or out (of Africa)? Site formation at Dmanisi and actualistic studies in Africa. In: Pickering, T., Schick, K., Toth, N. (Eds.), *Breathing Life into Fossils: Taphonomic Studies in Honor of C.K. Brain*. Stone Age Institution Press, Bloomington, pp. 119–135.
- Thompson, C., Ball, S., Thompson, T., Gowland, R., 2011. The abrasion of modern and archaeological bones by mobile sediments: the importance of transport modes. *J. Archaeol. Sci.* 38 (4), 784–793.
- Titton, S., Barsky, D., Bargalló, A., Vergès, J.M., Guardiola, M., García-Solano, J., Jiménez-Arenas, J.M., Toro-Moyano, I., Sala-Ramos, R., 2018. Active percussion tools from the Oldowan site of Barranco León (Orce, Andalusia, Spain): The fundamental role of pounding activities in hominin lifeways. *J. Archaeol. Sci.* 96, 131–147. <https://doi.org/10.1016/j.jas.2018.06.004>.
- Titton, S., Barsky, D., Bargalló, A., Serrano-Ramos, A., Vergès, J.M., Toro-Moyano, I., Sala-Ramos, R., García-Solano, J., Jiménez-Arenas, J.M., 2020. Subpheroids in the lithic assemblage of Barranco León (Spain): recognizing the late Oldowan in Europe. *PLoS One* 15 (1), e0228290. <https://doi.org/10.1371/journal.pone.0228290>.
- Titton, S., Oms, O., Barsky, D., Bargalló, A., Serrano-Ramos, A., García-Solano, J., Sánchez-Bandera, C., Yravedra, J., Blain, H., Toro-Moyano, I., Jiménez Arenas, J., Sala-Ramos, R., 2021. Oldowan stone knapping and percussive activities on a raw material reservoir deposit 1.4 million years ago at Barranco León (Orce, Spain). *Archaeol. Anthropol. Sci.* 13, 108.
- Tixier, J., Roe, D., Turq, A., Gibert, J., Martínez-Navarro, B., Arribas, A., Gibert, L., Maillo, A., Iglesias, A., 1995. Presence d'industries lithiques dans le Pléistocène inférieur de la région d'Orce (Grenade, Espagne): état de la question. *Comptes Rendus de la Academie des Sciences de Paris série Ila* 321, 71–78.
- Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J., Martínón-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J., Anadón, P., Julià, R., García-Aguilar, J., Moigne, A., Espigares, M., Ros-Montoya, S., Palmqvist, P., 2013. The oldest human fossil in Europe, from Orce (Spain). *J. Hum. Evol.* 65 (1), 1–9.
- Turner, A., Antón, M., 1996. The giant hyaena *Pachycrocuta brevirostris* (mammalia, carnivora, hyaenidae). *Geobios* 29, 455–468. [https://doi.org/10.1016/S0016-6995\(96\)80005-2](https://doi.org/10.1016/S0016-6995(96)80005-2).
- Turq, A., Martínez-Navarro, B., Palmqvist, P., Arribas, A., Agustí, J., Rodríguez-Vidal, J., 1996. Le Plio-Pleistocène de la région d'Orce, province de Grenade, Espagne: bilan et perspectives de recherche. *Paléo* 8, 161–204.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *J. Hum. Evol.* 21 (1), 27–48.
- Villa, P., Sánchez Goñi, M., Bescós, G., Grün, R., Ajas, A., García Pimienta, J., Lees, W., 2010. The archaeology and paleoenvironment of an Upper Pleistocene hyena den: an integrated approach. *J. Archaeol. Sci.* 37 (5), 919–935.
- Vinuesa, V., Madurell-Malapeira, J., Fortuny, J., Alba, D.M., 2015. The endocranial morphology of the Plio-Pleistocene bone-cracking hyena *Pliocrocuta perrieri*: behavioral implications. *J. Mamm. Evol.* 22, 421–434.
- Vinuesa, V., Iurino, D.A., Madurell-Malapeira, J., Liu, J., Fortuny, J., Sardella, R., Alba, D.M., 2016. Inferences of social behavior in bone-cracking hyaenids (Carnivora, Hyaenidae) based on digital paleoneurological techniques: implications for human-carnivoran interactions in the Pleistocene. *Quat. Int.* 413, 7–14. <https://doi.org/10.1016/j.quaint.2015.10.037>.
- Young, A., Stillman, R., Smith, M., Korstjens, A., 2015. Scavenger species-typical alteration to bone: using bite mark dimensions to identify scavengers. *J. Forensic Sci.* 60 (6), 1426–1435.
- 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 (1), 85–96.
- Yravedra, J., Andrés, M., Domínguez-Rodrigo, M., 2013. A taphonomic study of the African wild dog (*Lycan pictus*). *Archaeological and Anthropological Sciences* 6 (2), 113–124.
- Yravedra, J., Andrés, M., Fosse, P., 2014. Taphonomic analysis of small ungulates modified by fox (*Vulpes vulpes*) in southwestern Europe. *J. Taphonomy* 12 (1), 37–67.
- Yravedra, J., Lagos, L., Bârcena, F., 2011. A taphonomic study of wild wolf (*Canis lupus*) modification of horse bones in northwestern Spain. *J. Taphonomy* 9, 37–66.
- Yravedra, J., Lagos, L., Bârcena, F., 2012. The wild wolf (*Canis lupus*) as a dispersal agent of animal carcasses in northwestern Spain. *J. Taphonomy* 10, 227–248.
- Yravedra, J., Solano, J.A., Courtenay, L.A., Saarinen, J., Linares-Matás, G., Luzón, C., Serrano-Ramos, A., Herranz-Rodrigo, D., Cámara, J.M., Ruiz, A., Titton, S., Rodríguez-Alba, J.J., Mielgo, C., Blain, H.-A., Agustí, A., Sánchez-Bandera, C., Montilla, E., Toro-Moyano, I., Fortelius, M., Oms, O., Barsky, D., Jiménez-Arenas, J.M., 2021. Use of meat resources in the early Pleistocene assemblages from Fuente Nueva 3 (Orce, Granada, Spain). *Archaeological and Anthropological Sciences* 13, 213. <https://doi.org/10.1007/s12520-021-01461-7>.
- Yravedra, J., Solano, J.A., Herranz-Rodrigo, D., Linares-Matás, G., Saarinen, J., Rodríguez-Alba, J.J., Serrano-Ramos, A., Mielgo, C., Courtenay, L.A., Titton, S., Blain, H.-A., Luzón, C., Cámara, J.M., Agustí, A., Sánchez-Bandera, C., Montilla, E., Toro-Moyano, I., Fortelius, M., Oms, O., Barsky, D., Jiménez-Arenas, J.M., 2022a. Unravelling hominin activities in the zooarchaeological assemblage of Barranco León (Orce, Granada, Spain). *J. Palaeolithic Archaeol.* 5, 6. <https://doi.org/10.1007/s41982-022-00111-1>.
- Yravedra, J., Courtenay, L.A., Herranz-Rodrigo, D., Rodríguez-Alba, J.J., Linares-Matás, G., Serrano-Ramos, A., Solano, J.A., Jiménez-Arenas, J.M., 2022b. The first morphological characterization of an extinct carnivore's tooth marks from the Eurasian Early Pleistocene. *Sci. Bull.* <https://doi.org/10.1016/j.scib.2022.07.017>.