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Who is who and why. Implications of tooth-marks identification at two sites in the Orce Basin Archaeological Zone (OBAZ; southern Spain) [☆]

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ABSTRACT

The Orce Basin Archaeological Zone (OBAZ; Granada, Spain) is well known because it contains some of the most important Early Pleistocene archaeo-palaeontological sites for understanding the earliest human settlement in the westernmost part of Eurasia and its ecological context. Among those are Venta Micena (VM), Barranco León (BL) and Fuente Nueva 3 (FN3). The role played by the extinct *Pachycrocuta brevirostris* present at the OBAZ sites has long been recognised in the literature. However, little or nothing is known about the agency of the other documented carnivore species. Nevertheless, the development of technologies such as 3D modelling, geometric morphometrics, robust data modelling and artificial intelligence algorithms makes it possible to characterise a type of tooth mark (pits) and its assignment to a taxon. Moreover, such a combination of methodologies allows us to infer novel aspects related to the behaviour of carnivores, to establish interpretative differentiation between the carnivore agents at VM3 and BL, to point to the interactions among them and with *Homo*, and to review some proposals on the first human dispersal outside Africa.

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1. Introduction

During the Pleistocene, large carnivores belonging to diverse families and subfamilies roamed the European continent, most of which are extinct, except for ursines (i.e., bears). Thus, machairodontines, pantherines, canids and hyaenids coexisted with the first human inhabitants of western Eurasia. Although they

all feed on the carcasses of herbivores, there has been much debate about the ability of each taxon to leave tooth marks on bones. One of the most persistent and paradigmatic issues is whether large sabre-tooth cats ate only the soft viscera and muscle packets (Arribas and Palmqvist, 1999; Palmqvist et al., 2023) or if they made further exploitation of the carcasses by unintentionally modifying with their delicate teeth the bones of the animals on which they fed.

Until quite recently, it has been difficult to establish analytically which taxon was responsible for tooth marks such as pits. At most it was possible to say whether it was small or large. This has not

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been the case for other types of markings such as furrowing or fracturing that have been readily attributed to the large short-snouted hyaena, *Pachycrocuta brevirostris* (Arribas and Palmqvist, 1998; Palmqvist et al., 2011). Nevertheless, the ongoing development of new techniques applied to taphonomical research has recently led to a massive improvement in terms of resolution in the identification, documentation, and interpretation of taphonomical agencies (Courtenay et al., 2019; Yravedra et al., 2017, 2019), specifically those related to carnivore feeding behaviour. These advances include the application of different techniques for the three-dimensional reconstruction of tooth marks (Aramendi et al., 2017; Courtenay et al., 2019; Yravedra et al., 2019), microphotogrammetrical and morphometrical analyses (Arriaza et al., 2017, 2019a, 2021; Yravedra et al., 2017; Aramendi et al., 2019), and the integration of computational learning algorithms and geometric morphometrics (Courtenay et al., 2019, 2020a, 2020b, 2021a; Yravedra et al., 2019, 2022a).

Most morphometrical research aspiring to characterise tooth marks has focused on the study of tooth marks left by extant carnivores (Arriaza et al., 2017, 2019a; Courtenay et al., 2019, 2020a, 2020b, 2021a, 2021b; Yravedra et al., 2017, 2019; Table 1). Such research has contributed to the development of a comprehensive and high-resolution, actualistic reference framework, developing some issues pointed out in the pioneering work of Selvaggio and Wilder (2001). These studies have shown that pit marks produced by a species of carnivore can be classified with a high degree of accuracy. In addition, other papers have provided evidence that pit morphology is not affected by the size of the prey (Courtenay et al., 2021a) or the wild or free state of the carnivores (Courtenay et al., 2021b). Pits are unaffected by the size, including sexual dimorphism of the markers (Herranz-Rodrigo et al., 2021).

Our next step was to try to identify those extinct taxa likely responsible for the tooth marks detected on fossil bone by morphological comparison of those marks inflicted on bone by different extant species. Even though such an approach has been applied to fossil assemblages a few times, the results are very promising. Thus, it has been possible to document the consumption of Olduvai Gorge hominins by felids (Aramendi et al., 2017, 2019), crocodiles (Aramendi et al., 2017), and by hyaenas at Sterkfontein, South Africa (Arriaza et al., 2021). In addition, such combination of techniques and methodologies has allowed us to establish the agency of different carnivores at two sites of the OBAZ: Venta Micena 3 (VM3; Yravedra et al., 2022a) and Barranco León (BL; Courtenay et al., 2023).

The taxonomical characterization of tooth marks has implications beyond the assignment to a specific taxon. It enables the setting of research questions through testable hypotheses that can be assessed quantitatively in order to: (i) to infer the behaviour of certain taxa, (ii) to discuss interactions between carnivores, (iii) to establish if there are differences between the OBAZ sites, and (iv) to discuss the causes of the first human dispersal out of Africa.

2. The Orce Basin Archaeological Zone (OBAZ)

The OBAZ is in the NE sector of the Guadix-Baza Basin (GBB), Granada, an important intramontane basin in the south of the Iberian Peninsula with an area of 4,500 km² and a depth of ca. 300 m of geological sedimentary fill (Fig. 1). This basin is exceptionally rich in Neogene-Quaternary fossil vertebrate sites (Maldonado-Garrido et al., 2017) distributed across a unique landscape of badlands sculpted by erosion (Arribas-Herrera et al., 2021).

The OBAZ is a protected heritage area consisting of a core area (>8.5 km²) and a buffer zone (>18 km²) that together contain some 20 locations that have been object of Early Pleistocene research. They form part of the GBB, the NE sector of which at Orce is

Table 1

Main analyses on tooth marks of carnivores using three-dimensional reconstruction techniques analyzing tooth marks.

Reference	Taxon/Taxa	Number of observations (by type)
Aramendi et al. (2017)	<i>Crocota crocuta</i>	20 pits
Aramendi et al. (2017)	<i>Panthera onca</i>	20 pits
Aramendi et al. (2017)	<i>Panthera leo</i>	20 pits
Aramendi et al. (2017)	<i>Canis lupus</i>	20 pits
Aramendi et al. (2017)	<i>Crocodylus niloticus</i>	9 pits
Arriaza et al. (2017)	<i>P. leo</i>	30 scores
Arriaza et al. (2017)	<i>C. crocuta</i>	33 scores
Yravedra et al. (2017)	<i>P. leo</i>	30 scores
Yravedra et al. (2017)	<i>P. onca</i>	34 scores
Yravedra et al. (2017)	<i>C. crocuta</i>	33 scores
Yravedra et al. (2017)	<i>C. lupus</i>	30 scores
Aramendi et al. (2019)	<i>C. crocuta</i>	21 pits
Aramendi et al. (2019)	<i>P. onca</i>	20 pits
Aramendi et al. (2019)	<i>P. leo</i>	24 pits
Arriaza et al. (2019a)	<i>P. leo</i>	24 pits
Arriaza et al. (2019b)	<i>Panthera pardus</i>	28 scores/41 pits
Arriaza et al. (2019b)	<i>C. crocuta</i>	21 scores
Courtenay et al. (2019)	<i>C. crocuta</i>	33 scores/21 pits
Courtenay et al. (2019)	<i>P. onca</i>	34 scores/20 pits
Courtenay et al. (2019)	<i>P. leo</i>	30 scores/24 pits
Courtenay et al. (2019)	<i>C. lupus</i>	30 scores/24 pits
Yravedra et al. (2019)	<i>Vulpes vulpes</i>	41 scores/29 pits
Yravedra et al. (2019)	<i>C. lupus</i>	30 scores/24 pits
Yravedra et al. (2019)	<i>Canis familiaris</i>	34 scores/30 pits
Courtenay et al. (2020a)	<i>C. lupus</i>	156 pits/163 scores
Courtenay et al. (2020b)	<i>C. lupus/C. familiaris</i>	30 pits/30 pits
Courtenay et al. (2021b)	Wild and captive <i>C. lupus</i>	288 score/283 pits
Courtenay et al. (2021a)	<i>P. leo</i>	82 pits
Courtenay et al. (2021a)	<i>P. pardus</i>	84 pits
Courtenay et al. (2021a, 2023)	<i>P. onca</i>	77 pits
Courtenay et al. (2021a, 2023)	<i>C. crocuta</i>	86 pits
Courtenay et al. (2021a, 2023)	<i>Ursus arctos</i>	69 pits
Courtenay et al. (2021a, 2023)	<i>Lycaon pictus</i>	89 pits
Courtenay et al. (2021a, 2023)	<i>C. lupus</i>	80 pits
Courtenay et al. (2021a, 2023)	<i>V. vulpes</i>	53 pits
Yravedra et al. (2021b)	<i>C. lupus/C. familiaris</i>	80 pits/80 pits
Herranz-Rodrigo et al. (2021)	<i>Panthera tigris</i>	104 pits
Herranz-Rodrigo et al. (2021)	<i>P. pardus</i>	96 pits
Arriaza et al. (2021)	<i>Parahyaena brunnea</i>	48 scores/24 pits
Arriaza et al. (2021)	<i>C. crocuta</i>	33 scores/21 pits
Arriaza et al. (2021)	<i>P. leo</i>	30 scores/24 pits
Arriaza et al. (2021)	<i>P. pardus</i>	28 scores/28 pits

bounded by the Sierra de la Umbría. Three well-known locations, where ongoing excavation commenced several years ago, are Venta Micena, Barranco León and Fuente Nueva 3 (Fig. 1).

Lacustrine alluvial sediments of the Upper Mb. of the Baza Fm. (Vera et al., 1985) have been explored by excavation at all three locations. Levels with presence of extinct large mammals, including humans, correspond to episodic regression of the erstwhile vast saline 'Baza' lake and consequent upwelling of fresh groundwater attractive to fauna, and formation of the Orce wetlands (Granados et al., 2021; Martínez-Monzón et al., 2021). Subsequently, during the Middle Pleistocene, the Guadalquivir River captured the waters of the erstwhile vast saline 'Baza' lake as well as part of the sediments (Medina-Cascales et al., 2021), giving rise to the present landscape dominated by ravines and gullies where fossiliferous levels are exposed. Although there are three main sites, we will focus in this study on only two of them: Venta Micena and Barranco León.

2.1. Venta Micena (VM)

VM (Fig. 1) has been a reference site for its rich fossil record of large vertebrates (Arribas, 1999; Arribas and Palmqvist, 1998;



Fig. 1. A. Location of the Archaeological Zone (Orce Basin) in the Iberian Peninsula. B. Location of the Venta Micena (VM) and Barranco León (BL) sites.

Luzón et al., 2021; Palmqvist et al., 2022) and for the characterisation of the behaviour of the large short-snouted hyaena, *P. brevirostris* (Palmqvist et al., 1996, 2011, 2022; Arribas and Palmqvist, 1998). Both the faunal lists and stratigraphy have been extensively published (Granados et al., 2021; Luzón et al., 2021; Martínez-Navarro et al., 2021; Palmqvist et al., 2022). However, there are two matters that, because of their novelty, demand to be highlighted. First, VM is not a single site but a location where diverse numbered test-pits and extensively excavated sites provide cross-sections of the VM stratigraphical sequence (Yravedra

et al., 2023). Secondly, two paleosurfaces are clearly identifiable from the spatial distribution and taphonomical features of fossil remains from the lacustrine-palustrine sediments at the VM4 excavation site, which are assigned stratigraphically to “unit C” (Granados et al., 2021; Luzón et al., 2021; Yravedra et al., 2023).

In relation to the computational approach for the identification of tooth marks on fossil bones described above, we focused in a previous study on a sample of bones from VM3 that showed traces of having been bitten by carnivores. Because this site has been interpreted as a hyaena den (Palmqvist et al., 1996, 2011, 2022;

Arribas and Palmqvist, 1998), it is to be expected that most of the tooth marks were inflicted by *P. brevirostris*. The results provided by Yravedra et al. (2022a) confirm this.

2.2. Barranco León (BL)

Sediments excavated at BL (Fig. 1) date from ca. 1.4 Ma (Moyano et al., 2013) whereas sediments excavated at VM date from ca. 1.6 Ma (Duval et al., 2012), but unlike VM, BL has unquestionable evidence of human presence and activity (Gibert et al., 1999; Ribot et al., 2015; TITTON et al., 2018, 2020, 2021; Toro Moyano et al., 2013). Excavations at BL shed light on the earliest human settlement of western Eurasia. The stratigraphical sequence of BL is long, although human presence is limited to two levels, D1 and D2, the former being much richer in archaeo-palaeontological remains than the latter (TITTON et al., 2021). In addition, it has been possible to establish that D1 is a mixed fluvial deposit (of primary and secondary fluvial sediments) although the transported remains seem to have been redeposited and not to have come from very far away (TITTON et al., 2021; Yravedra et al., 2022b). Thus, during that transport episode, much raw material (limestone and flint) from the nearby mountain range was available in the site for knapping (Barsky et al., 2022; TITTON et al., 2021).

Although BL and VM faunal lists contain many taxa in common, there are some significant differences. For example, the presence in BL of two arvicolid rodents (*Allophaiomys* aff. *lavocati* [formerly *A. burgondiae*] and the new taxon *Manchenomys orcensis*; Agustí et al., 2010, 2022) absent in VM. In addition, *A. ruffoi* (formerly *A. pliocaenicus*) is recorded in VM but not in BL (Agustí et al., 2010).

The BL knapped lithic assemblage is attributable to the Oldowan techno-complex (TITTON et al., 2018, 2021), although it presents some particularities with respect to European assemblages elsewhere. The most conspicuous is the presence of subspheroids (TITTON et al., 2020) that, in African contexts are considered 'late Oldowan' (De la Torre and Mora, 2014).

Our integrated application of 3D modelling, geometric morphometrics, robust data modelling, and artificial intelligence algorithms, to the characterisation of the tooth marks (pits) on the fossil bones from BL highlights the predominance of modifications by canids, especially *Canis mosbachensis* (Courtenay et al., 2023).

3. Implications of the characterization of carnivore tooth marks

Recent taphonomical studies conducted at BL (Yravedra et al., 2022b; Courtenay et al., 2023) and VM3 (Yravedra et al., 2022a), VM4 (Luzón et al., 2021; Yravedra et al., 2023), and FN3 (Yravedra et al., 2021a, 2023, submitted), give good grounds not only for reflecting on the respective parts played by carnivores and humans in the OBAZ, but also for reconsidering previous

hypotheses (Arribas and Palmqvist, 1998; Palmqvist et al., 2011; Rodríguez-Gómez et al., 2016).

3.1. Eppure si muove. Sabre-tooth cats as bone markers

Results by Yravedra et al. (2022a) for VM3 indicate that 6 of the 26 (23.1%) documented tooth pit marks were generated by a large felid (Figs. 2, 3). Courtenay et al. (2023) show that at Barranco León Level D1, 8 of the 64 (12.5%) tooth pit marks were made by the same taxon (Figs. 2, 3). These modifications could be attributed with high probability to the sabre-tooth cat *Homotherium latidens*. Moreover, in both deposits Felidae (viz. *Homotherium*) were the second most common modifying agent, as identified from our study of pits (Fig. 3).

The evidence of pits should be sufficient to affirm that sabre-tooth cats left marks on the bones, despite their biomechanics (Palmqvist et al., 2011, 2023; Espigares et al., 2019; DeSantis et al., 2021). However, this statement does not mean that *H. latidens* displayed a durophagous diet, as Palmqvist et al. (2023) have claimed from an erroneous interpretation of Yravedra et al. (2021a). The production of tooth marks is, generally, an unintentional accident that occurs when a carnivore is killing its prey or consuming it, either by sliding its teeth to score the bone surface while extracting meat, or gripping the bone and, depending on the pressure applied, creating pits. Moreover, it is possible to puncture the bones by biting through soft tissue. Furthermore, presence of tooth marks caused by machairodontines at VM3 (Yravedra et al., 2022a) and BL (Courtenay et al., 2023) is consistent with results from tooth wear (Binder and Van Valkenburg, 2010), cranial morphology (Prevosti et al., 2010), and tooth marks identified in several taphonomical accounts (Marean and Ehrhardt, 1995; Domínguez-Rodrigo and Barba, 2007; Domínguez-Rodrigo et al., 2022; Scanferla et al., 2013; Labranca et al., 2014).

In addition, our results are also consistent with observations of feeding and taphonomical signals left by a wide range (with regard to size, hunting and social strategies) of modern felids, e.g., lynxes (Rodríguez-Hidalgo et al., 2013), pumas (Borrero et al., 2005; Muñoz et al., 2008), leopards (Pickering et al. 2004; Domínguez-Rodrigo et al., 2007; Pobiner, 2007; Herranz-Rodrigo et al., 2021), jaguars (Rodríguez-Alba et al., 2019), tigers (Parkinson et al., 2015; Herranz-Rodrigo et al., 2021), lions (Pobiner, 2007; Parkinson et al., 2015; Arriaza et al., 2016), and cheetahs (Pickering et al., 2004; Domínguez-Rodrigo et al., 2007; Horwitz et al. 2018). Similarly, some extant canids such as African wild dogs also leave tooth marks (Harstone-Rose, 2008; Yravedra et al., 2014; Fourvel et al., 2020).

The fact that sabre-tooth cats left marks on the bones ought to be evidence of intensive exploitation by those felids, following the logic applied in previous publications (Espigares et al., 2019;



Fig. 2. Some examples of tooth marks on herbivore diaphysis from the sites of Venta Micena 3 (upper part; specimen VM3 661) and Barranco León (lower part; left specimen BL-19-K48-D1-172, right specimen BL-13-D1-29-156 (28.80.133)).

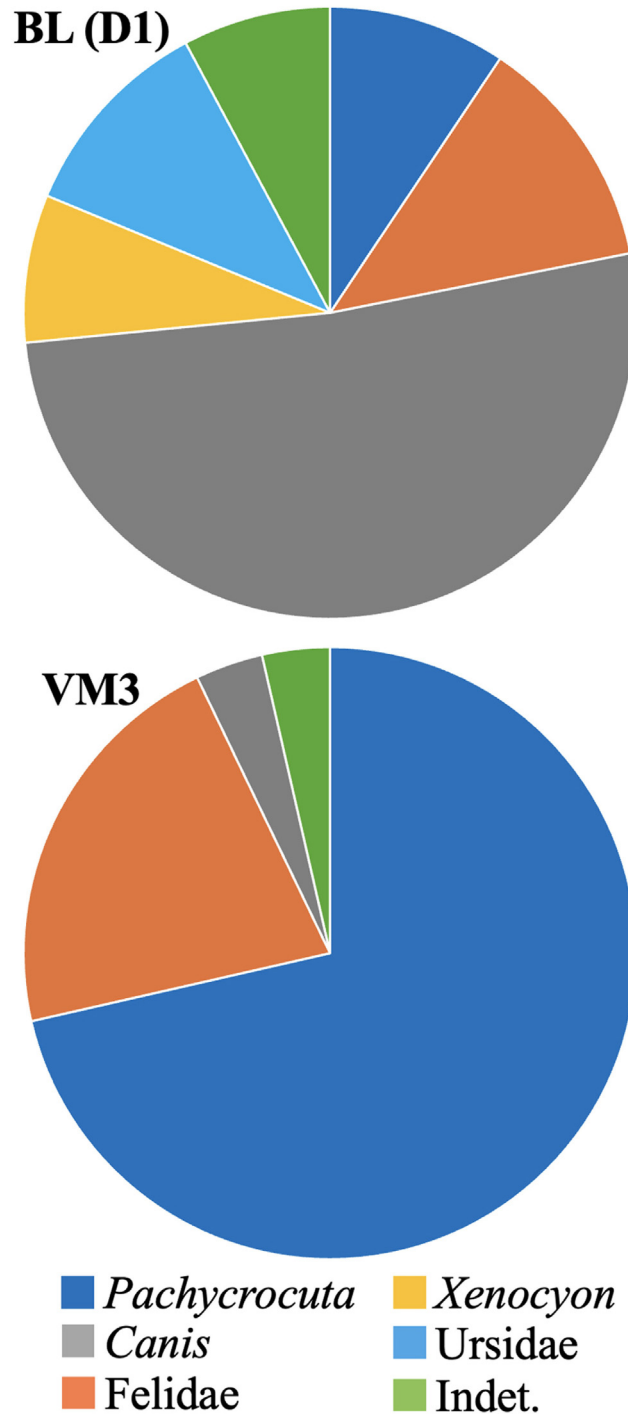


Fig. 3. Pie chart showing the number of pits found in Level D1 at Barranco León and Venta Micena 3. Data from Courtenay et al. (2023) and Yravedra et al. (2022a).

Palmqvist et al., 2023) whose principal authors, nevertheless, have insisted repeatedly that because, in their view, machairodontines did not leave marks on bones, it should be inferred that they would have left uneaten a large amount of carrion that ought to have been available for other meat eaters, including humans. Moreover, their view and assumption about feeding behaviour have prompted Espigares et al. (2019) and Palmqvist et al. (2023) to claim that humans had only secondary access to the carcasses. We will discuss this issue below, in Section 3.3.

To sum up, the combination of 3D modelling, geometric morphometrics, robust data modelling and artificial intelligence algorithms shows it to be highly likely that large felids (*Homotherium*) left pits on the bone surface of their captured prey. In both sites (VM3 and BL), machairodontines come second as carnivore modifying agents by number of pits. This implies, theoretically, a greater exploitation of carcasses by machairodontines than previously assumed.

3.2. Canids in Barranco León

One of the main novelties of the paper by Courtenay et al. (2023) is that the agent that left the most pits on the surface of the bones at Barranco León was the canid *Canis mosbachensis*, with 33 of the 64 identified tooth marks (51.6%) reliably assigned to this small canid (Fig. 3). *Pachycrocuta* tooth marks are reduced to 6 (9.4%), indicating a low incidence of this carnivore (Fig. 3).

To counter the evidence presented in the paper by Courtenay et al. (2023), Palmqvist et al. (2023) suggest that the small bite-marks in BL were produced by *Pachycrocuta* cubs. The question of the influence of age is relevant in assessing the marks left by teeth. While we have not yet been able to test this variable in hyaenids, a recent paper has pointed out that there are no significant differences with regard to age or semi-wild or wild status for extant wolves (Courtenay et al., 2021b). Additionally, it is worth recalling that Arribas and Palmqvist (1998: 30) stated that “The recovery of relatively high numbers of deciduous teeth of *P. brevirostris* reinforces this hypothesis” – [i.e., that VM was a feeding places for nearby dens] – “(as other carnivores are represented in the assemblage only by adult individuals) and helps to reject the possibility that bones were accumulated in open feeding-places located at hunting sites distant from dens, since it can be presumed that infant individuals would not accompany adults on their hunts, but would stay near the dens, as occurs in modern spotted hyaenas.” Following this premise, if the tooth marks attributed to *C. mosbachensis* were from *Pachycrocuta* cubs, we then ought to be in a den of this taxon, and not in an open feeding spot. The question now is: was BL a hyaena den, or is it best characterized as an open feeding place instead?

From standpoints of sedimentology and the type of materials that appear at each site, VM3 (Yravedra et al., 2023) and BL (Titton et al., 2021) present a very different genesis. BL (Level D1) is the result of a high-energy episode that transported materials from the nearby Sierra de la Umbría. They included knappable rocks that were knapped by humans in situ (Titton et al., 2021). The resulting stone tools were used on herbivore carcasses, among other activities (Espigares et al., 2019; Yravedra et al., 2022b). On the other hand, VM3 was a hyaena den (Arribas and Palmqvist, 1998). Moreover, although the sample analyzed in VM3 is small, the results of the morphometrical analysis of the tooth marks indicate that the hyaena action must have been very intense at this site (20/28; 71.4%) (Fig. 3). Meanwhile, a single mark classified as *Canis* (3.6%) has been found (Fig. 3). Although more research is needed, the present results indicate a very different participation of carnivores at VM and BL (Fig. 3).

In addition, the results published by Yravedra et al. (2022b) and by Courtenay et al. (2023) find no evidence at BL for high competition between hominins and hyaenids, contra Palmqvist et al. (2022, 2023) and Espigares et al. (2019). Furthermore, both Espigares et al. (2019) and Yravedra et al. (2022b) have shown that the impact of carnivores was minimal at BL-D1. According to Yravedra et al. (2022b), only 168 (4.7%) of the remains exhibited tooth marks. This amount is lower than that found in VM3, interpreted as a hyaena den (29.4% according to Arribas, 1999).

The high frequency of *C. mosbachensis* tooth marks at BL also allows us to draw inferences about its role in the trophic chain. The estimated body mass for this taxon is 12 kg according to Rodríguez-Gómez et al. (2016). Were *C. mosbachensis* to have a social behaviour like that of present-day wolves, its prey would not have exceeded size 2. In the total fauna recovered from BL level D1, this group represents 11.2% of the MNI (minimum number of individuals) and 10.8% of the NISP (number of identifiable specimens) (Yravedra et al., 2022b). However, considering the bones with pits analysed in Courtenay et al. (2023), 7 of the 17 bones whose size could be determined are size 2 (e.g., *Metacervoceros*, *Capra*; Fig. 4; Table 2). Of these, 5 bones (29.4%) show bite marks

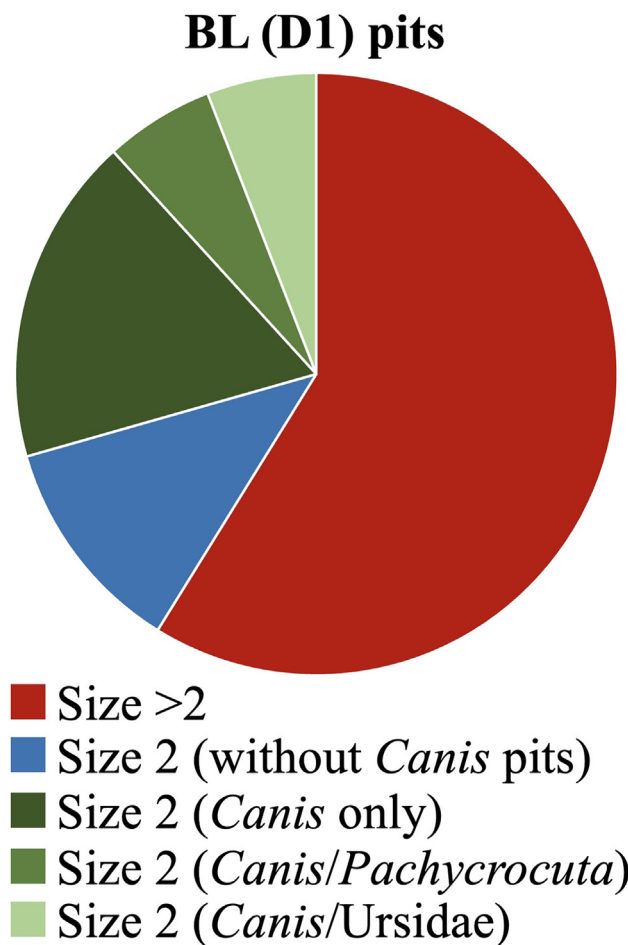


Fig. 4. Pie chart showing distribution of pits in Level D1 at Barranco León considering size and carnivore agency. Green portions: bones belonging to herbivores with size 2 and with *Canis* pits. Data from Courtenay et al. (2023). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

attributable to *Canis*: three have marks of *Canis* only (17.6%), one shows an accompanying hyaena mark, and another shows an accompanying bear mark (Fig. 4; Table 2). From these results it can be assumed that *C. mosbachensis* scavenged by acting as a secondary agent at least on 7 individuals (size >2) (Fig. 4; Table 2), although it cannot be ruled out that it also hunted smaller prey.

3.3. Interpreting the behaviour of the first humans outside of Africa

A recurrent topic in Human Evolution concerns the timing and causes of the first dispersal out of Africa (Arribas and Palmqvist, 1999; Carbonell et al., 2010; Timmermann et al., 2022). Before 2018, the oldest human presence outside Africa was recorded at Dmanisi (Georgia), dated to 1.8 Ma (Ferring et al., 2011). Nevertheless, the picture changed radically in 2018, when earlier human presence at the Chinese site of Shangchen (2.1 Ma) was published (Zhu et al., 2018).

The proposal put forward by Arribas and Palmqvist (1999) drew a scenario of major faunal dispersal in which humans were favored by certain biomechanical and functional limitations of two sabre-tooth cats (*H. latidens* and *Megantereon whitei*). Arribas and Palmqvist (1999: 579) stated that “the composition of the European carnivore guild was quite different from that of East Africa, including two species of saber-toothed cats (*Homotherium latidens* and *M.*

Table 2
Number of herbivore bones with tooth marks in Level D1 of Barranco León (BL). Indet.: Indeterminable.

	All taxa	All taxa (size determinable)	Canis (only)	Canis/Pachycrocuta	Canis/Lyacon	Canis/Felidae	Canis/Ursus	Canis/Indet.	Canis/Total
Size 2	7	7	3	1	–	–	1	–	5
Size >2	10	9	3	2	1	1	–	–	7
Size indet.	11	–	4	–	–	1	1	1	7
Total	28	18	10	3	1	2	2	1	19

whitei), which presumably maximized the amount of flesh that remained on their kills, thus opening broad opportunities of scavenging for both hyaenas and hominids.” According to this view, machairodontines could consume only the softest and most nutritious parts of ungulate carcasses (viscera and more delicate muscle packets) on account of their gracile dentitions, and thus could not leave tooth marks on the surface of the bones (Palmqvist et al., 2023). Thus it was that a connection between machairodontines and humans, coupled with the specialization of large short-snouted hyaenas in breaking bones, became a landmark of the “Out of Africa 1” interpretation of initial human dispersal. The Orce sites played a fundamental role in supporting this idea, from the mid-1990s to the present day – an example can be found in the following quote: “[...] *M. whitei* [is] an African immigrant in Europe when the first hominin dispersal out of Africa took place, provided hominins and other scavengers access to ungulate carcasses with significant amounts of flesh and all within-bone nutrients intact” (Palmqvist et al., 2023: 12) – regardless of subsequent changes in our understanding of the archaeological record from Orce.

Alas, the numerical dating of Orce is too recent to be relevant to any “Out of Africa 1” notion (notwithstanding the assertions of, e.g., Palmqvist et al., 2023). Far older are Paleolithic assemblages dated to around 2.48 Ma from the Dawqara Fm. near Zarqa in Jordan (Scardia et al., 2019), and from the Chinese Shangchen Fm. dated to around 2.1 Ma (Zhu et al., 2018). By contrast, the relevant Orce deposits are much younger, namely, around 1.6 Ma at Venta Micena (Duval et al., 2012), 1.46 Ma at Barranco León (Toromoyano et al., 2013), and 1.2 Ma at Fuente Nueva 3 (Duval et al., 2011). Therefore, whereas the Orce sites provide fundamental knowledge of the first human settlement in southwestern Eurasia, they cannot be considered as examples of the first human dispersal out of Africa.

On the other hand, there is no consensus about whether western Eurasian *Megantereon* evolved from African *M. whitei* or Eurasian *M. cultridens* (Lewis and Werdelin, 2010). Moreover, the African-ness of human settlement in western Eurasia, not to mention its supposedly ecological relationship with machairodontines, has not gone unquestioned (O’Regan, 2008; Lewis and Werdelin, 2010; O’Regan et al., 2011). Similarly, the relationship between the development and persistence of the Oldowan technocomplex in Europe and the continuity of the machairodontines until the beginning of the Middle Pleistocene has also been questioned. Recovery from the North Sea (Reumer et al., 2003) and the Yukon (Barnett et al., 2020) of Late Pleistocene *Homotherium* remains, confirmed by DNA taxonomy, indicated that the genus survived until ~50 ka. Moreover, there is now clear morphometrical evidence of machairodontines tooth marks from the Orce sites. It is worth highlighting that this is not an isolated phenomenon. These marks have been documented at the three main sites. At both VM3 (Yravedra et al., 2022a) and BL (Courtenay et al., 2023), machairodontines are the secondmost detected modifying agent after *Pachycrocuta* and *Canis*, respectively. Research is still ongoing at the FN3 site, but the single example of the *M. meridionalis* carcass found at Level 5 indicates the action of a sabre-tooth cats (Yravedra et al., submitted). Undoubtedly, despite their biomechanical limitations, sabre-tooth cats left tooth marks

(mainly pits) on bones of some carcasses, as we have shown by combining 3D geometric morphometrics and artificial intelligence.

As we have seen above, one of the main arguments for interpreting “Out of Africa 1” is the supposedly commensal relationship of *Homo* with machairodontines because allegedly the latter never left tooth marks on bones. The presence of such signals requires us to caution against this conjecture, if not to reject it outright. Furthermore, Oldowan human groups were able to interact directly and on the same animal with machairodontines (Yravedra et al., 2024).

4. Final reflections

As we have observed, OBAZ represents a highly diverse ecosystem with different types of sites where various events took place. Instead of presenting a simplistic interpretation explained by accumulations of fauna preyed upon by sabre-tooth cats and scavenged by hyaenas (VM3 and VM4) and humans (FN3 and BL) (Palmqvist et al., 2011, 2023; Espigares et al., 2019), results produced by the combination of 3D modelling, geometric morphometrics, robust data modelling and artificial intelligence algorithms allow us to envisage a more complex scenario.

The interpretation of VM3 as a site produced by an accumulation by *Pachycrocuta* must be considered correct in the light of classical zooarchaeological (Arribas and Palmqvist, 1998) and new taphonomical results (Yravedra et al., 2022a). However, the first work presenting evidence that hyaenas consumed herbivore carcasses on which sabre-tooth cats also acted is that presented by Yravedra et al. (2022a). Because carrion would have to be transported by hyaenas to their dens, it can be reasonably surmised that machairodontines enjoyed primary access to the preys. Nevertheless, hunting cannot be ruled out as a way to obtain food by the large short-snouted hyaena because some herbivore bones accumulated in VM3 show only hyaenid tooth marks, or bones with tooth marks of canids and *Pachycrocuta*. Furthermore, from an actualist perspective, hunting is documented among carnivores that are habitual scavengers (Kruuk, 1972; Cooper, 1990; Henschel and Skinner, 1990; Mills, 1990).

BL is a site with a more complex taphonomical history involving stone tools and faunal remains accumulated in the same location (Espigares et al., 2019; Titton et al., 2021; Yravedra et al., 2022a). The faunal accumulation may have been produced and/or modified by different agents, including humans. *C. mosbachensis* was the main carnivore modificatory agent. We propose that these canids scavenged, at least partially, on some of the accumulated herbivores (>size 2). Nevertheless, we cannot rule out that *Canis* also hunted smaller animals (e.g., size 2).

The tooth marks observed at VM3 and BL reveal that, on several occasions, different carnivores interacted with bones. At VM3, circumstances are reflected where a bone was bitten by both a felid and a hyaena, and another by a hyaena and a canid. However, at BL this situation becomes more complex, with some specimens modified by bears and felines, canids and ursines, canids and felines, and canids and hyaenas, resembling what is observed in the current reference framework of contemporary multi-carnivore set-

tings, where a single carcass is exploited by different carnivores in various feeding events.

In any case, BL does not seem to have been a site where human and hyaenas compete, as proposed by Palmqvist et al. (2011, 2023) and Espigares et al. (2019). On the contrary, the low frequency of marks due to carnivores, the diversity of taphonomical agents that intervened in BL, and the low percentage attributable to *Pachycrocuta* point to a more complex scenario in which the great short-snouted hyaena did not play a predominant role.

The interpretation of the first human out of Africa must be reviewed in the light of older Eurasian sites discovered in recent years and their dating (Zhu et al., 2018; Scardia et al., 2019), and last but by no means least, the analytical contributions made by taphonomy and allied disciplines, which have reported significant advances in recent years.

In conclusion, the main contributions of this article are:

- The Orce Basin Archaeological Zone encompasses three outstanding sites important for the interpretation of the complex relationships between humans and a range of carnivores;
- The tooth marks identified in VM3 and BL reveal that sabretooth cats produced tooth marks on bones, providing new empirical information that challenges the notion that sabretooth cats did not modify the bone surfaces of their prey;
- Canids, in particular *C. mosbachensis*, played a relevant role in the bone modifications observed at BL. Interestingly, *Pachycrocuta* agency at this site appears to be low;
- Although it is likely that *C. mosbachensis* merely scavenged on the large prey sizes found at BL, we cannot discard the possibility of some hunting behaviors on smaller ones (size 2);
- Preliminary differences between VM3 and BL should be interpreted in relation to carnivore landscape use differences. In addition, we ought to consider the role of humans at BL when characterizing assemblage differences at these sites;
- The proposal of a direct dependence of humans on machairodontine kills to explain the first human out of Africa should be reassessed, based on both the new chronological framework and the presence of large felid tooth marks on bones, evidence that scavenging opportunities may not have been as bountiful as previously envisaged;
- The combination of 3D geometric morphometrics and artificial intelligence provides empirical evidence that brings into question entrenched theoretical proposals, streamlining interpretations, and opening new research avenues in human evolution and in taphonomy;
- Lastly, we need to continue developing these novel methodologies and techniques in order to unravel higher-resolution issues such as the specific roles played by each of the modificatory agents and to determine their order of access to the carcass.

CRediT authorship contribution statement

José Yravedra: Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Darío Herranz-Rodrigo:** Methodology, Formal analysis, Data curation. **Verónica Estaca-Gómez:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Idoia Claver:** Writing – original draft, Methodology, Investigation, Data curation. **Gonzalo Linares-Matás:** Writing – review & editing, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **Alexia Serrano-Ramos:** Resources, Project administration, Methodology, Formal analysis. **Carmen Luzón:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Data curation, Conceptualization. **Juan José Rodríguez-Alba:** Writing – review & editing, Validation, Supervision, Investigation, Formal analysis.

José A. Solano: Supervision, Software, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Juan Manuel Jiménez-Arenas:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Funding acquisition.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

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

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