

Human and carnivore behaviour in view of zooarchaeology and taphonomy at Orce (Guadix Baza, Orce, Spain) during the late Early Pleistocene

José Yravedra^{1,2,3,4,*}, Lloyd, A. Courtenay⁵, Gonzalo Linares-Matás^{6,7},
Verónica Estaca-Gómez¹, Darío Herranz-Rodrigo⁸, Alexia Serrano-Ramos⁸,
José A. Solano⁸ & Juan Manuel Jiménez-Arenas^{8,9,10,11}

¹) Department of Prehistory, Ancient History and Archaeology, Complutense University of Madrid, Faculty of Geography and History, Edificio B, Calle Profesor Aranguren, Ciudad Universitaria, ES-28040 Madrid, Spain (*corresponding author's e-mail: joyravedra@hotmail.com)

²) C.A.I. Archaeometry and Archaeological Analysis, Department of Prehistory, Ancient History and Archaeology, Complutense University of Madrid, Faculty of Geography and History, Edificio B, Calle Profesor Aranguren, Ciudad Universitaria, ES-28040 Madrid, Spain

³) Research Group 'Quaternary Ecosystems', Department of Prehistory, Ancient History and Archaeology, Complutense University of Madrid, Faculty of Geography and History, Edificio B, Calle Profesor Aranguren, Ciudad Universitaria, ES-28040 Madrid, Spain

⁴) Research Group 'Prehistoric Archaeology, Department of Prehistory, Ancient History and Archaeology, Complutense University of Madrid, Faculty of Geography and History, Edificio B, Calle Profesor Aranguren, Ciudad Universitaria, ES-28040 Madrid, Spain

⁵) Centre National de la Recherche Scientifique (CNRS) PACEA UMR 5199, Université de Bordeaux, Bât B2 Allée Geoffroy Saint-Hillaire CS 50023, FR-33615 PESSAC CEDEX, France

⁶) St. Hugh's College, University of Oxford, St Margaret's Road, Oxford OX2 6LE, United Kingdom

⁷) Emmanuel College, University of Cambridge, St Andrew's Street, Cambridge CB2 3AP, United Kingdom

⁸) Department of Prehistory and Archaeology, University of Granada, Faculty of Philosophy Humanities, Campus de Cartuja, ES-18071 Granada, Spain

⁹) Research Unit of Excellence "Archaeometrical Studies. Inside the Artefacts & Ecofacts", Campus de Cartuja, ES-18071 Granada, Spain

¹⁰) The Orce Prehistory and Palaeontology Museum, 'Josep Gibert' (Museo de Prehistoria y Paleontología de Orce — 'Josep Gibert'), Camino de San Simón, ES-18858 Orce, Granada, Spain

¹¹) The Gibraltar National Museum, 20 Bomb House Lane, Gibraltar GX11 1AA, Gibraltar

Received 28 Feb. 2024, final version received 18 Apr. 2024, accepted 6 May 2024

Yravedra, J., Courtenay, L. A., Linares-Matás, G., Estaca-Gómez, V., Herranz-Rodrigo, D., Serrano-Ramos, A., Solano, J. A. & Jiménez-Arenas, J. M. 2024: Human and carnivore behaviour in view of zooarchaeology and taphonomy at Orce (Guadix Baza, Orce, Spain) during the late Early Pleistocene. — *Ann. Zool. Fennici* 61: 343–355.

Since the discovery of Venta Micena in 1976 until now, the Orce archaeopalaeontological sites (Guadix Baza basin) in the northern part of Granada have contributed significantly to the body of knowledge on Early Pleistocene ecosystem dynamics. The exceptional fossil accumulation at Venta Micena stands out, housing important examples of early Pleistocene European faunas. Additionally, the discovery of new sites such as Bar-

rango León and Fuente Nueva 3 has yielded evidence of some of the oldest human presence in western Eurasia, alongside bones bearing cut and percussion marks made by stone tools. These discoveries were made by using novel techniques and methodology, allowing for new interpretations of the fossil record. Integration of artificial intelligence and geometric morphometrics applied to fossil studies contributed to better understanding of the genesis of the sites, and to unravelling the role of humans and other mammals in creating fossil accumulations at the Orce sites. At Barranco León, *Canis mosbachensis* was found to be the most active carnivore and not, as earlier thought, the large hyaena *Pachycrocuta brevirostris*. At Fuente Nueva 3, large saber-toothed cats seem to be the top consumers of carcasses. This evidence suggests the existence of more complex associations between humans and various carnivorous taxa.

Introduction

The Orce sites (Guadix Baza basin, Granada, Spain) were discovered in 1976 by a local farmer, Tomás Serrano. At that time, Björn Kurtén's book, *Pleistocene Mammals of Europe* (Kurtén 1968), was one of the must-have sources for any specialist in vertebrate palaeontology. From the outset, these sites yielded significant large mammal fossils on which species such as the bovids *Soergelia minor* and *Capra alba* were defined (Moyà-Solà 1987). However, it was the discovery of the fossil called VM-0 (the Orce Man) that brought this region to wide attention (Gibert et al. 1983). However, in 1984, the first taxonomical doubts about VM-0 had been raised, and a race to confirm the presence of humans at the Orce sites began (e.g., Gibert & Palmqvist 1995), the latest episode being a palaeoanthropological conference in 1995. Not long afterwards, lithic tools made by humans were discovered at two new sites near Orce, Barranco León (BL) and Fuente Nueva 3 (FN3), confidently shifting the human presence in western Eurasia back in time (Tixier et al. 1995, Turq et al. 1996).

Research conducted in Orce during the early 21st century was carried out under the guidance of several research teams successively led until 2015 by Isidro Toro-Moyano and Robert Sala. During those years, significant discoveries were made, such as the oldest known human evidence in Europe at that time (Gibert et al. 1999, Toro-Moyano et al. 2013, Ribot et al. 2015). Additionally, geology (e.g., Oms et al. 2000a, 2000b, 2010, 2011, Duval et al. 2011, 2012, Granados et al. 2021), stone knapping techniques (e.g., Toro-Moyano et al. 2009, 2011, Barsky et al. 2010,

2014, 2022, Tifton et al. 2018, 2020, 2021), and palaeontology (e.g., Moyà-Solà 1987, Martínez-Navarro 1991, Martínez-Navarro & Palmqvist 1995, Palmqvist et al. 1996, 2011, Agustí et al. 2010, 2022, Martínez Navarro et al. 2010, 2021, Blain et al. 2011, 2016, Espigares et al. 2013, 2019, Ros-Montoya et al. 2021, Saarinen et al. 2021) were also studied.

Inspired by Turner's hypothesis (1992), Palmqvist et al. (1996, 2011), Arribas and Palmqvist (1998, 1999) and Palmqvist and Arribas (2001) suggested that the human exodus from Africa and human dispersal throughout Europe occurred by taking advantage of the prey of the large sabretooth cats. These authors proposed that large prey killed by large felines, which left Africa, was then scavenged by the large short-snouted hyaena (*Pachycrocuta brevirostris*) and humans. According to this hypothesis, as exemplified at FN3, humans and hyaenas must have competed for the carrion left by the sabretooth cats. The evidence would rest on the spatial grouping of hyaena coprolites with lithic tools, all associated with the remains of an almost complete skeleton of a mammoth (Espigares et al. 2013, 2019, Palmqvist et al. 2023). However, the Paleolithic peopling of Europe is a much more complex process that is not limited to the interaction between humans, carnivores and their prey. Recent studies show how the Paleolithic settlement of Europe could have been affected e.g., by climate (Margari et al. 2023, Muttoni & Kent, 2024, Sánchez Bandera et al. 2023), palaeoenvironment (Ochando et al. 2020, Saarinen et al. 2021, Sánchez Bandera et al. 2020, 2023), or the combination of different factors that may have led to the discontinuous settlement of the



Fig. 1. Location of Venta Micena 3, Barranco León and Fuente Nueva 3 sites. Base image from Google Earth Pro.

westernmost part of Eurasia (e.g. Dennell, 2009, MacDonald *et al.* 2012, Margari *et al.* 2023).

Studies at the Orce Archaeological Zone (OAZ) have continued since 2017 with participation of an international research team coordinated by the University of Granada and with a leading role of the University of Helsinki, represented amongst others by a disciple of B. Kurtén, Mikael Fortelius. Since then, new sites, such as Venta Micena 4 (VM4), have been included (Luzón *et al.* 2021), and new methods used in studying e.g., geology (Granados *et al.* 2021), palaeontology (Agustí *et al.* 2022), palaeoecology (Sánchez Bandera *et al.* 2020, 2023, Martínez Monzón *et al.* 2021, Blain *et al.* 2021, Ochando *et al.* 2022, Saarinen *et al.* 2021), and taphonomy (Luzón *et al.* 2021, Yravedra *et al.* 2021, 2022a, 2022b, 2023, 2024, Courtenay *et al.* 2023). From all these, new explanatory models have been proposed concerning the paleoenvironmental and palaeoecological conditions that may contribute to understanding the first human settlement across Europe. Alongside this, the latest advances in taphonomy have also enabled progress in understanding the behaviour of the early human populations that lived in the Orce area.

The Orce sites

Venta Micena 3 (VM3) and Venta Micena 4 (VM4), Barranco León (BL), and Fuente Nueva 3 (FN3) are situated within what we may term the Orce Archaeological Zone (OAZ) in

the northeast sector of the Guadix-Baza basin (GBB) in Granada (Fig. 1). This intramontane basin is located in the southern part of the Iberian Peninsula, covering an area of 4500 km² with a geological sedimentary fill reaching approximately 300 m deep. Notably, this basin boasts an exceptional abundance of Neogene–Quaternary fossil vertebrate sites distributed across a distinctive landscape of badlands sculpted by erosion (Maldonado *et al.* 2017).

The OAZ is a protected heritage area, comprised of a core (> 8.5 km²) and a buffer zone (> 18 km²), collectively encompassing around 20 Early Pleistocene localities (Solano *et al.* in press). These sites are integral to the GBB, with the northeastern sector, including Orce, bordered by the Sierra de la Umbria. The formation of this region and the location of the archaeopalaeontological sites originated on the edge of an endorheic basin, which eventually transformed into a large lake, resulting in the lacustrine alluvial sediments of the Upper Member of the Baza Formation. The seasonal fluctuations of the extensive saline Baza lake exposed freshwater streams (Granados *et al.* 2021), attractive to fauna, and forming wetlands (Martínez-Monzón *et al.* 2022) contributing to the formation of the sites under investigation today.

Subsequently, during the Middle Pleistocene, the Guadalquivir River diverted the waters of erstwhile Baza lake, along with some sediment, giving rise to the current landscape dominated by ravines and gullies where fossiliferous levels are exposed.

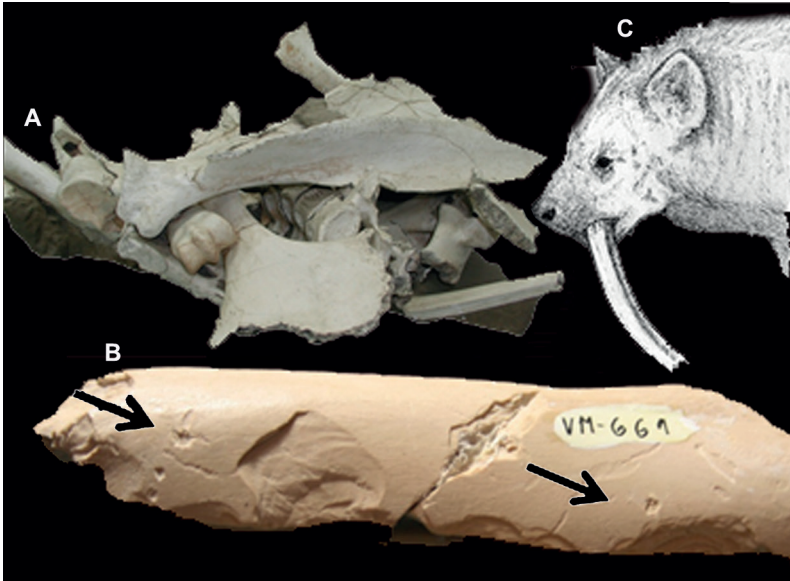


Fig. 2. — **A:** Bone accumulation from Venta Micena 3 (VM3, Orce, Granada, Spain). — **B:** Long-bone shaft with tooth marks of *Pachycrocuta brevirostris* from VM3. — **C:** *Pachycrocuta brevirostris* carrying a bone (drawn by Juan José Rodríguez-Alba).

Venta Micena (VM)

Venta Micena has served as a key reference site because of its abundant fossil assemblage of large vertebrates, essential for characterising the behaviour of the large hyaena *Pachycrocuta brevirostris* (e.g., Palmqvist *et al.* 1996, 2011, 2022, Arribas & Palmqvist 1998). It encompasses an extensive area representing an ancient palaeolandscape where several sites with independent taphonomic histories are located. Recently, Yravedra *et al.* (2023) discussed the differences between VM3 and VM4, two nearby sites with distinct but complementary histories. Furthermore, VM exhibits stratigraphic complexity, with two palaeosurfaces clearly identifiable based on the spatial distribution and taphonomic features of fossil remains within the lacustrine-palustrine sediments at the VM4 excavation site, stratigraphically assigned to “unit C” (Granados *et al.* 2021, Luzón *et al.* 2021, Yravedra *et al.* 2023).

Taphonomical analysis suggests that the VM3 site represents a hyaena den (e.g., Palmqvist *et al.* 1996, 2011, 2022, Arribas & Palmqvist 1998). It is thought that most tooth marks on fossilised bones were made by *P. brevirostris* (Yravedra *et al.* 2022a) (Fig. 2). Although VM4 is under excavation, preliminary studies suggest that it represents a more complex accumulation around freshwater ponds (Yravedra *et al.* 2023).

Barranco León (BL)

The sediments excavated at BL date back to approximately 1.4 million years ago (Toro-Moyano *et al.* 2013), whereas those at VM date back to around 1.6 million years ago (Duval *et al.* 2012). However, unlike VM, BL holds evidence of human presence and activity (e.g., Gibert *et al.* 1999, Ribot *et al.* 2015, Titton *et al.* 2018, 2020, 2021, Toro Moyano *et al.* 2013). Although the stratigraphic sequence of BL is extensive, human presence is confined to two levels, D1 and D2, with the former being much richer in archaeopalaeontological remains than the latter (e.g., Titton *et al.* 2021). Moreover, it has been established that D1 constitutes a mixed fluvial deposit (comprising primary and secondary fluvial sediments), although the transported remains appear to have been redeposited and not transported from a great distance (Titton *et al.* 2021, Yravedra *et al.* 2022b). Consequently, during this transport episode, a significant amount of raw material (limestone and flint) from the nearby mountain range was available at the site for knapping (Barsky *et al.* 2022, Titton *et al.* 2021).

Although the fauna of BL and VM share many taxa, there are notable differences. For instance, BL is characterised by the presence of two arvicolid rodents (*Allophaiomys* aff. *lavocati* [formerly *A. burgondiae*] (Agustí *et al.* 2010)

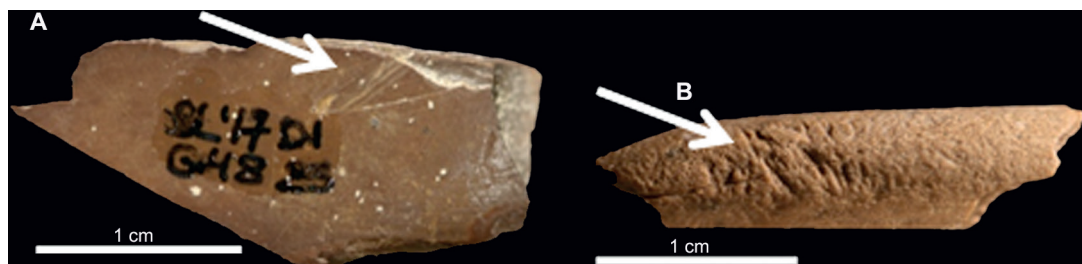


Fig. 3. Cut marks (indicated by arrows) on two fragments of herbivore long-bone diaphyses from level D1 at Barranco León (Orce, Granada, Spain).

and the newly identified taxon *Manchenomys orcensis* (Agustí *et al.* 2022), which are absent from VM. Additionally, *A. ruffoi* (formerly *A. pliocaenicus*) was recorded at VM but not at BL (Agustí *et al.* 2010). The lithic assemblage knapped at BL is attributed to the Oldowan techno-complex (e.g., Titton *et al.* 2018, 2021), although the presence of subspheroids (Titton *et al.* 2020) suggests a relation to the ‘late Oldowan’, as identified from the African record (De la Torre & Mora 2014). Regarding fauna, cut marks and percussion marks associated with carcass manipulation have been observed at BL (Fig. 3) (Courtenay *et al.* 2023, Espigares 2010, Espigares *et al.* 2019, Yravedra *et al.* 2022).

Fuente Nueva 3 (FN3)

Fuente Nueva 3 is an open-air site with an excavated surface area of 104 m². It is characterised by distal fluvial/alluvial sedimentation and carbonate formations of biogenic and paedogenic origin. Invertebrate fauna associations also indicate the alternation between shallow aquatic environments (Anadón *et al.* 2003). FN3 comprises two rich archaeopalaontological units: FN3-2 and FN3-5.

The age of FN3-5 has been dated to approximately 1.2 million years ago, by using a combination of magnetostratigraphy, biochronology, and U-series/ESR methods (Duval *et al.* 2012). FN3-5 consists of fine-grained greenish sands and mudstones, further subdivided into five facies (Yravedra *et al.* 2024). No taphonomic attributes indicative of re-sedimentation or reworking processes have been identified. FN3 is characterised by an abundant faunal collection,

represented by megafauna, including a partial skeleton of *Mammuthus meridionalis* in anatomical connection (Espigares *et al.* 2013, Palmqvist *et al.* 2023, Yravedra *et al.* 2024). Moreover, it includes fauna dominated by medium- to large-sized large mammals such as equids (*Equus altidens* and *E. suessenbornensis*), deer (*Metacervoceros* and *Praemegaceros*), large bovines (*Bison* sp.), rhinoceroses (*Stephanorhinus etruscus*), hippopotamuses (*Hippopotamus antiquus*) and mammoths (*M. meridionalis*).

Dental ecometrics and mesowear data suggest a predominantly browsing herbivorous diet for the ungulate species at FN-3 (Saarinen *et al.* 2021). Faunal remains and pollen from FN3-5 indicate relatively dryer and somewhat cooler climatic conditions compared with those at BL, with the presence of open areas interspersed with wooded areas (Sánchez-Bandera *et al.* 2020, 2023, Agustí *et al.* 2022, Ochando *et al.* 2022).

FN3 has yielded one of the richest knapped lithic assemblages associated with the European Oldowan techno-complex (Toro-Moyano *et al.* 2010, 2011, Barsky *et al.* 2010, 2014, 2022), characterised by the abundance of small flakes of flint and limestone of local origin near the site (Barsky *et al.* 2010). Espigares *et al.* (2019), and Yravedra *et al.* (2021) found an accumulation of fauna with cut marks and percussion marks on bones, suggesting that the animal resources at the site were also used by humans.

Bone marker agents at the Orce Archaeological Zone

Diverse hypotheses have driven the research at the sites of the OAZ (e.g. Arribas & Palmqvist

1999, Espigares *et al.* 2013, 2019, Palmqvist *et al.* 2022, 2023). The first was that to protect their long canines, sabretooth cats did not bite bones of the animals they fed on, thus they did not leave tooth marks on the surfaces of the bones (e.g., Palmqvist *et al.* 2023). The second was that if sabretooth cats consumed only soft parts of the carcasses, a lot of the carrion were left available to other carnivores, especially scavengers (Palmqvist *et al.* 2023). The third was that hyaenas played a pivotal role in the formation of all three major sites: VM (3 and 4), BL and FN3 (Arribas & Palmqvist 1999, Espigares *et al.* 2013, 2019, Palmqvist *et al.* 2023). The fourth, suggested that the humans living in Orce during the Early Pleistocene were opportunistic scavengers, competing with hyaenids such as *P. brevirostris* for access to carcasses (Espigares *et al.* 2013, 2019, Palmqvist *et al.* 2023). However, as of 2019, new taphonomical analyses have allowed for new interpretations of the role of different bone-modifying agents.

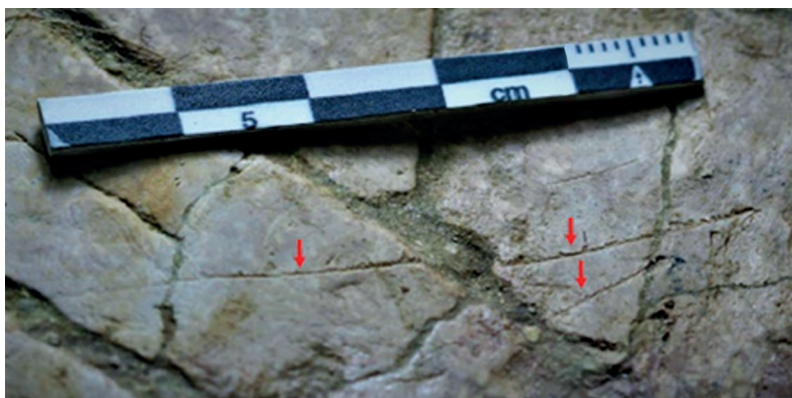
Owing to the results of the new taphonomical analyses by Yravedra *et al.* (2021, 2022b) of Fuente Nueva 3 and Barranco León, focusing on medium-sized ungulates such as equids, bovids, and cervids, as well as small-sized ungulates like caprines and small cervids, the above-mentioned hypotheses have been revised. The new studies have shown that when comparing various frequencies of bone alteration with reference material, ambiguous and inconclusive results may be obtained regardless of whether analysing cut marks and percussion marks produced by humans or tooth marks produced by carnivores. The reason for this ambiguity lies in the very low frequencies of tooth marks found on bones from BL and FN3, which do not align with the frequencies of tooth marks typically produced by carnivores when they are the primary agents interacting with carcasses (e.g., Blumenschine 1988, 1995, Blumenschine *et al.* 1994, Capaldo, 1997, Pobiner 2007, Pante 2013). These frequencies of tooth (or cut) marks, however, fall within the variability typical in cases where humans compete for access to carcasses with carnivores (Blumenschine 1988, 1995, Blumenschine *et al.* 1994, Capaldo 1997, Pante 2013). This could be used to argue that humans were the first to prey on herbivores. The above-mentioned frequencies of marks are, however, too low to be typical for

the situation when humans are the first to interact with a carcass (Capaldo 1997, Lupo & O'Connell, 2002, Pante 2013). Instead, the frequencies of cut marks fall within the variability described for secondary anthropic access. In essence, the frequencies of tooth marks suggest one pattern of interactions between humans and carnivores, while the frequencies of cut and percussion marks indicate another. To resolve this, we ought to seek alternative methodological solutions.

In recent years, several solutions have been proposed. One involved measuring the fracture angles of long bones (Alcántara *et al.* 2006), or applying machine learning to fracture patterns, as suggested by Yezzi-Woodley *et al.* (2024). Alternatively, Maté-González *et al.* (2019) developed and applied a different set of techniques, focused on the morphometric and photogrammetric analysis of bone alterations, and Courtenay *et al.* (2019) carried out digital scanning of bone alterations using DAVID SLS Slice scanner. We applied these methods to study tooth marks found on fossil remains from BL and FN3, following the procedures described in Yravedra *et al.* (2019) and Courtenay *et al.* (2019, 2021a, 2021b) with the aim to determine the origin of tooth marks, and thus verify whether there was indeed competition between hyaenids and hominids for carcasses.

Applying these techniques to the bone samples of medium-sized animals from BL (as in Courtenay *et al.* 2023) yielded interesting results that highlight contradictions with the studies of Palmqvist *et al.* (1996, 2011, 2021, 2023) and Espigares *et al.* (2019). We concluded that most of the tooth marks found at BL were probably made by *Canis mosbachensis* rather than *Pachycrocuta*. This is surprising since *C. mosbachensis* was a small-sized carnivore whose prey ranged from micromammals to small ungulates, representing only 10% of the individuals and remains found at BL (Yravedra *et al.* 2022b). This mismatch suggests that humans likely played a more active role in the fossil accumulation of medium-sized prey than previously thought. This increased human involvement is supported by some of the evisceration marks identified by Espigares *et al.* (2019), as well as the presence of defleshing marks on upper limb bones such as the humerus and femur, ribs and vertebrae (Yravedra *et al.* 2022b).

Fig. 4. Cut marks (indicated by arrows) on the pelvis of a female *Mammuthus meridionalis* (FN3-5-MPS) from level 5B at Fuente Nueva 3 (Orce, Granada, Spain).



Courtenay *et al.* (2023) also found a few tooth marks made by other carnivores including hyaenids (6 marks), ursids (5 marks), and large felids (8 marks). This indicates that hyaenids played a less active role in the fossil accumulation at BL. Furthermore, it shows that sabretooth cats did indeed make tooth marks on the bones. Such sabretooth cat tooth marks have been observed at VM3 (Yravedra *et al.* 2022a), BL (Courtenay *et al.* 2023), and FN3 (Yravedra *et al.* 2024), and other sites in the Early Pleistocene of Africa (Domínguez Rodrigo *et al.* 2007) and the Late Pleistocene of the Americas (Marean & Ehrhardt 1995, Scanferla *et al.* 2013, Labarca *et al.* 2014, Domínguez Rodrigo *et al.* 2022). This evidence indicates a complexity of interactions among humans and large felids at large mammal carcasses, where small canids likely acted as scavengers, while *Pachycrocuta* had a minor role in the bone accumulation at BL.

Until now it was not possible to analyse tooth marks left by different carnivores on bones found at FN3, as was also the case at BL. Therefore, we could not reach conclusions as to their origin until Yravedra *et al.* (2024) found that cut marks on two bones of the partial mammoth (*M. meridionalis*) skeleton (specimen FN3-5-MPS) exhumed at FN3 were of human origin (Fig. 4). They also found that tooth marks on the rib and pelvis of FN3-5-MPS were made by large sabretooth cats. This shows that both humans and felids utilised the mammoth carcass. Furthermore, microstratigraphic evidence (Yravedra *et al.* 2024) casts doubt on the stratigraphic association of the coprolites with the mammoth

skeleton suggested by Espigares *et al.* (2013) and Palmqvist *et al.* (2022).

Hyaenas are well known for leaving frequent tooth marks on bones. This is not the case with the FN3-5-MPS skeleton of mammoth from FN3. The absence of modifications such as furrowing, gnawed bones, or collapsed bones should be interpreted as absence or low activity of hyaenas. Palmqvist *et al.* (2023) justified the absence of tooth marks by suggesting that adult hyaenids do not bite bones unless they can fracture them. However, this does not seem likely, because there are sabretooth cat bite marks and human-made cut marks, but no hyaena bite marks on the specimen, although those have been found on several cases of extant and fossil proboscidean carcasses (Haynes & Klimowitzh 2015, Haynes & Hutson 2020, Yravedra *et al.* 2010).

Although a high-resolution study applying morphometric techniques to the bone alterations of medium-sized animals at FN3 is still pending, the evidence described for the mammoth skeleton at that site (Yravedra *et al.* 2024), combined with the evidence described in Yravedra *et al.* (2021), seems to indicate that, as in Barranco León, hyaenids were not significant agents in the bone accumulation at FN3.

The presence of tooth marks made by large felids on bones of large animals such as the mammoth at FN3, and on large and medium-sized animals such as those from BL, suggests that these carnivores likely made more intense use of carcasses than traditionally thought, inviting a reassessment of the effects sabretoothed cats

may have had on the carcasses of animals found at the sites. Furthermore, the presence of cut marks on upper appendicular elements such as the humerus and femur, and axial bones at FN3 (Yravedra *et al.* 2021) and BL (Yravedra *et al.* 2022b) indicates that butchering activities practiced on these animals were independent of the actions of large felids and that probably human populations at BL and also FN3 had early access to certain meat resources. If this is confirmed, the evidence from the Orce sites would align with what other authors observed at other Early Pleistocene sites, where human groups could access carcasses earlier than other predators or scavengers (Domínguez Rodrigo *et al.* 2007, Pobiner 2007, Hugué *et al.* 2013, 2017, Linares-Matás & Yravedra 2021, Cáceres *et al.* 2023).

Conclusions

We provided a brief overview of the research conducted at the Orce sites, with particular attention to the archaeological sites of BL and FN3. Although the research is still ongoing, we highlighted how novel methodologies can help overcome limitations of previous analysis techniques where they offered ambiguous or inconclusive results (Yravedra *et al.* 2021, 2022b); thus, helping to clarify the role of humans in the formation of the Orce fossil assemblages.

On one hand, it has been shown that evidence of direct competition between hyaenas and humans for carcasses is not present at BL and FN3. Instead, it has been found that hyaenas played a modest role (Courtenay *et al.* 2023) in the accumulation of medium-sized large mammal remains at BL. Also, no hyaena activity was found on FN3-5-MPS specimen of *Mammuthus meridionalis* (Yravedra *et al.* 2024). The evidence uncovered at BL indicates that probably the main carnivore involved in the bone remain modifications was *Canis mosbachensis* (Courtenay *et al.* 2024), suggesting a lesser role of carnivores in the fossil accumulation at BL than previously assumed and, conversely, enhancing the relevance of humans, especially considering that the type of prey hunted by *Canis mosbachensis* represented only 10% of the bone sample from the site (Yravedra *et al.* 2022).

The studies by Yravedra *et al.* (2021, 2024) and Courtenay *et al.* (2023) showed that machairodontine sabretooth cats left tooth marks on the bones, suggesting that they processed the carcasses more thoroughly than initially proposed. The proof of mammoth consumption by sabretooth cats and humans suggests that both humans and felids may have utilised mammoths as prey. However, this is currently a hypothesis that is being tested in ongoing analyses. For now, we can only say that humans and felids accessed an adult mammoth that appears to have died naturally (Yravedra *et al.* 2024). Regarding other animals, the evidence in Yravedra *et al.* (2021) should be reassessed with higher-resolution analyses as currently the studies demonstrating low incidence of tooth marks and furrowing indicate a lesser role of hyaenas.

Finally, we would like to emphasize that just as Björn Kurtén closely collaborated with Spanish paleontologists, in particular with Miquel Crusafont, more than 50 years later, the collaboration between Finnish and Spanish scientists has been strengthened thanks to ProjectORCE. Miquel Crusafont was the director of the Paleontological Institute of the Diputació de Barcelona when Josep Gibert and Jordi Agustí, researchers at this institute, unveiled the Venta Micena site, initiating the research in this region. Orce, as it could not be otherwise, also caught the attention of Finnish paleontologist Mikael Fortelius, who wrote in a *Seura* magazine about the importance of Venta Micena (Orce) to understand a very ancient human settlement in this part of Europe. That is why the spirit of Kurtén, in a way, is present in the current research at Orce.

Acknowledgements

This research is currently possible thanks to the support and approval of the Consejería de Turismo, Cultura y Deporte (Junta de Andalucía, Spain) through the General Research Project (2023-2026) Evolución humana y paleoecología a partir de los yacimientos pleistocenos de la Zona Arqueológica ‘Cuenca de Orce’. Retos y desafíos (Ref. SIDPH/DI/MCM). In addition, it has been carried out thanks to project PID 2021.125098NB.I00 funding by MCIN/AEI/10.13039/501100011033/FEDER Una manera de hacer Europa and ProyExcel_00274 funding by Dirección General de Planificación de la Investigación (Consejería de Universidad, Investigación e Innovación, Junta de Andalucía). Also

we acknowledge to Consejería de Universidad, Investigación e Innovación de la Junta de Andalucía for the Project Ref. P21_00168, and to the PALARQ Foundation with the convocatory of Analitics 2019: “Identificando Carnívoros a partir de análisis Tafonómicos de última generación aplicando Fotogrametría y Morfometría Geométrica de las Marcas de Diente. Aplicación a Yacimientos del Pleistoceno Inferior Ibérico: Fuente Nueva 3, Venta Micena 3 y 4 (Granada), Pontón de la Oliva (Patones, Madrid)”. Research at OAZ was made possible thanks to a large interdisciplinary research team and the collaboration of numerous student volunteers. DHR was supported by the contract ref. PRE2022-104179, funded by the Ministry of Science and Innovation, the State Research Agency (10.13039/501100011033) and the European Social Fund Plus.

References

- Agustí, J., Blain, H. A., Furio, M., De Marfa, 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. — *Quaternary International* 223–224: 162–169.
- Agustí, J., Piñero, P., Lozano-Fernández, I. & Jiménez-Arenas, J. M. 2022: A new genus and species of arvicolid rodent (Mammalia) from the Early Pleistocene of Spain. — *Comptes Rendus Palevol* 21: 847–858, <https://doi.org/10.5852/cr-palevol2022v21a39>.
- Alcántara-García, V., Egado, R. B., Barral del Pino, J. M., Ruiz, A. B. C., Vidal, A. I. E., Aparicio, A. F., Calleja, S. H., Jiménez, A. I., González, M. M., Gil, M. P., Tello, V. P., Calvo, J. R., Yravedra, 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. — *Trabajos de Prehistoria* 63: 37–45, <https://doi.org/10.3989/tp.2006.v63.i1.3>.
- Anadón, P., Julià, R. & Oms, O. 2003: Estratigrafía y estudio sedimentológico preliminar de diversos afloramientos en Barranco León y Fuente Nueva (Orce, Granada). — *Monografías de Arqueología* 17: 47–72.
- Arribas, A. & Palmqvist, P. 1998: Taphonomy and paleoecology 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. & Palmqvist, P. 1999: On the ecological connection between sabretooths and hominids: Faunal dispersal events in the lower Pleistocene and a review of the evidence for the first human arrival in Europe. — *Journal of Archaeological Science* 26: 571–585.
- 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). — *Quaternary International* 223–224: 201–219, <https://doi.org/10.1016/j.quaint.2009.12.004>.
- Barsky, D., Sala, R., Menéndez, L. & Toro-Moyano, I. 2014: Use and re-use: re-knapped flakes from the mode 1 site of Fuente Nueva 3 (Orce, Andalucía, Spain). — *Quaternary International* 361, 1–13, <https://doi.org/10.1016/j.quaint.2014.01.048>.
- Barsky, D., Titton, S., Sala-Ramos, R., Bargalló, A., Grégoire, S., Saos, T., Serrano-Ramos, A., Oms, O., Solano-García, J. A., Toro-Moyano, I. & Jiménez-Arenas, J. M. 2022: The significance of subtlety: contrasting lithic raw materials procurement and use patterns at the Oldowan sites of Barranco León and Fuente Nueva 3 (Orce, Andalusia, Spain). — *Frontiers in Earth Science* 10, 893776, <https://doi.org/10.3389/feart.2022.893776>.
- Blain, H. A., Bailon, S., Agustí, J., Martínez-Navarro, B. & Toro, I. 2011: Paleoenvironmental and paleoclimatic proxies to the Early Pleistocene hominids of Barranco León D and Fuente Nueva 3 (Granada, Spain) by means of their amphibian and reptile assemblages. — *Quaternary International* 243: 44–53, <https://doi.org/10.1016/j.quaint.2010.12.031>.
- Blain, H. A., Lozano-Fernández, I., Agustí, J., Bailon, S., Menéndez, L., Espigares-Ortiz, M. P., Ros-Montoya, S., Jiménez-Arenas, J. M., Toro-Moyano, I., Martínez-Navarro, B. & Sala, R. 2016: Refining upon the climatic background of the Early Pleistocene hominid settlement in Western Europe: Barranco León and Fuente Nueva-3 (Guadix-Baza Basin, SE Spain). — *Quaternary Science Review* 144: 132–144, <https://doi.org/10.1016/j.quascirev.2016.05.020>.
- Blain, H. A., Fagoaga, A., Ruiz-Sanchez, F. J., García-Medrano, P., Ollé, A. & Jiménez-Arenas, J. M. 2021: Coping with arid environments: a critical threshold for human expansion in Europe at the Marine Isotope Stage 12/11 transition? The case of the Iberian Peninsula. — *Journal of Human Evolution* 153, 102950, <https://doi.org/10.1016/j.jhevol.2021.102950>.
- Blumenschine, R. J. 1988: An experimental model of the timing of hominid and carnivore influence on archaeological bone assemblages. — *Journal of Archaeological Science* 15: 483–502, [https://doi.org/10.1016/0305-4403\(88\)90078-7](https://doi.org/10.1016/0305-4403(88)90078-7).
- Blumenschine, R. J. 1995: Percussion marks, tooth marks and the experimental determinations of the timing of hominid and carnivore access to long bones at FLK Zinjanthropus, Olduvai Gorge, Tanzania. — *Journal of Human Evolution* 29: 21–51, <https://doi.org/10.1006/jhev.1995.1046>.
- Blumenschine, R. J., Cavallo, J. A. & Capaldo, S. 1994: Competition for carcasses and early hominid behavioural ecology: a case study and conceptual framework. — *Journal of Human Evolution* 27: 94–214, <https://doi.org/10.1006/jhev.1994.1042>.
- Cáceres, I., Chelli Cheheb, R., van der Made, J., Harichane, Z., Boulagraief, K. & Sahnouni, M. 2023: Assessing the subsistence strategies of the earliest North African inhabitants: evidence from the Early Pleistocene site of Ain Boucherit (Algeria). — *Archaeological, Anthropological Science* 15, 87, <https://doi.org/10.1007/s12520-023-01783-8>.
- Capaldo, S. D. 1997: Experimental determinations of carcass

- proceeding by Plio-Pleistocene hominids and carnivores at FLK 22 (Zinjanthropus), Olduvai Gorge, Tanzania. — *Journal of Human Evolution* 33: 555–598.
- Courtenay, L. A., Yravedra, J., Hugué, R., Aramendi, J., Maté-González, M. Á., González-Aguilera, D. & Arriaza, M. C. 2019: Combining machine learning algorithms and geometric morphometrics: a study of carnivore tooth marks — *Palaeogeography, Palaeoclimatology, Palaeoecology* 522: 28–39, <http://dx.doi.org/10.1016/j.palaeo.2019.03.007>.
- Courtenay, L. A., Herranz-Rodrigo, D., González-Aguilera, D. & Yravedra, J. 2021a: Developments in data science solutions for carnivore tooth pit classification. — *Scientific Reports* 11, 10209, <https://doi.org/10.1038/s41598-021-89518-4>.
- Courtenay, L. A., Herranz-Rodrigo, D., Yravedra, J., Vázquez-Rodríguez, J., Hugué, R., Barja, I., Maté-González, M. A., Fernández, M. & González-Aguilera, D. 2021b: 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, <https://doi.org/10.3390/ani11082323>.
- 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). — *Quaternary Science Reviews* 300, 107912, <https://doi.org/10.1016/j.quascirev.2022.107912>.
- De la Torre, I. & Mora, R. 2014: The transition to the Acheulean in East Africa: an assessment of paradigms and evidence from Olduvai Gorge (Tanzania). — *Journal of Archaeological Method and Theory* 21: 781–823.
- Dennell, R. 2009: *The Palaeolithic settlement of Asia*. — Cambridge University Press, Cambridge.
- Domínguez-Rodrigo, M., Barba, R. & Egeland, C. P. 2007: *Deconstructing Olduvai: a taphonomic study of the Bed I sites*. — Springer Science & Business Media, Dordrecht.
- Domínguez-Rodrigo, M., Egeland, C. P., Cobo-Sánchez, L., Baquedano, E. & Hulbert, R. C. Jr. 2022: Saber-tooth carcass consumption behavior and the dynamics of Pleistocene large carnivore guilds. — *Scientific Reports* 12, 6045, <https://doi.org/10.1038/s41598-022-09480-7>.
- Duval, M., Falguères, C., Bahain, J. J., Grün, R., Shao, Q., Aubert, M., Hellstrom, J., Dolo, J. M., Agustí, J., Martínez-Navarro, B., Palmqvist, P. & Toro-Moyano, I. 2011: The challenge of dating early Pleistocene fossil teeth by the combined uranium series — electron spin resonance method: the Venta Micena palaeontological site (Orce, Spain). — *Journal of Quaternary Science* 26: 603–615.
- Duval, M., Falguères, C., Bahain, J. J., Grün, R., Shao, Q., Aubert, M., 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). — *Quaternary Research* 77: 482–491.
- Espigares, M. P., Martínez-Navarro, B., Palmqvist, P., Ros-Montoya, S., Toro, I., Agustí, J. & Sala, R. 2013: *Homo* vs. *Pachyrocota*: earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). — *Quaternary International* 295: 113–125, <https://doi.org/10.1016/j.quaint.2012.09.032>.
- Espigares, M. P., Palmqvist, P., Guerra-Merchán, A., Ros-Montoya, S., García-Aguilar, J. M., Rodríguez-Gómez, G., Serrano, F. J. & Martínez-Navarro, B. 2019: The earliest cut marks of Europe: a discussion on hominin subsistence patterns in the Orce sites (Baza basin, SE Spain). — *Scientific Reports* 9, 15408, <https://doi.org/10.1038/s41598-019-51957-5>.
- Gibert, J. & Palmqvist, P. 1995: Fractal analysis of the Orce skull sutures. — *Journal of Human Evolution* 28: 561–575.
- Gibert, J., Agustí, J. & Moyá-Solá, S. 1983: Presencia de *Homo* sp. en el yacimiento del Pleistoceno inferior de Venta Micena (Orce, Granada). — *Paleontología i Evolució Publicación Especial*, 12 pp.
- 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). — *Human Evolution* 14: 3–19.
- Granados, A., Oms, O., Anadon, P., Ibáñez-Insa, J., Kaakinen, A. & Jiménez-Arenas, J. M. 2021: Geochemical and sedimentary constraints on the formation of the Venta Micena early Pleistocene site (Guadix-Baza Basin, Spain). — *Scientific Reports* 11, 22437, <https://doi.org/10.1038/s41598-021-01711-7>.
- Haynes, G. & Klimowicz, J. 2015: Recent elephant-carcass utilization as a basis for interpreting mammoth exploitation. — *Quaternary International* 359–360: 19–37.
- Haynes, G. & Hutson, J. 2020: African elephant bones modified by carnivores: implications for interpreting fossil proboscidean assemblages. — *Journal of Archaeological Science Reports* 34, 102596, <https://doi.org/10.1016/j.jasrep.2020.102596>.
- Hugué, R., Saladié, P., Cáceres, I., Díez, C., Rosell, J., Bennasar, M., Blasco, R., Esteban-Nadal, M., Gabucio, J., Rodríguez-Hidalgo, A. & Carbonell, E. 2013: Successful subsistence strategies of the first humans in south-western Europe. — *Quaternary International* 295: 168–182.
- Hugué, R., Valleverdú, J., Rodríguez-Álvarez, X. P., Terradillos, M., Lombera, A., Menéndez, L., Modesto-Mata, M., van der Made, J., Soto, M., Blain, H. A., García, N., Cuenca-Bescós, G., Gómez-Merino G., Pérez-Martínez, R., Expósito, I., Allué, E., Rofes, J., Burjachs, F., Canals, Bennasar, M., Nuñez-Lahuerta, C., Bermúdez de Castro, J. M., Carbonell, E. & Carbonell, E. 2017: Level TE9c of Sima del Elefante (Sierra de Atapuerca, Spain): a comprehensive approach. — *Quaternary International* 433: 278–295.
- Kurtén, B. 1968: *Pleistocene mammals of Europe*. — Weidenfeld & Nicolson, London.
- Labarca, R., Recabarren, O. P., Canales-Brellenthin, P. & Pino, M. 2014: The gomphotheres (Proboscidea: Gomphotheriidae) from Pilauco site: scavenging evidence in the Late Pleistocene of the Chilean Patagonia. — *Quaternary International* 352: 75–84.

- Linares-Matás, G. J. & Yravedra, J. 2021: 'We hunt to share': social dynamics and very large mammal butchery during the Oldowan–Acheulean transition. — *World Archaeology* 53: 224–254, <https://doi.org/10.1080/00438243.2022.2030793>.
- Lupo, K. D. & O'Connell, J. F. 2002: Cut and tooth mark distributions on large animal bones: ethnoarchaeological data from the Hadza and their implications for current ideas about early human carnivory. — *Journal of Archaeological Science* 29: 85–109, <https://doi.org/10.1006/JASC.2001.0690>.
- Luzón, C., Yravedra, J., Courtenay, L. A., Saarinen, J., Blain, H.-A., DeMiguel, D., Viranta, S., Azanza, B., Rodríguez-Alba, J. J., Herranz-Rodrigo, D., Serrano-Ramos, A., Solano, J. A., Oms, O., Agustí, J., Fortelius, M. & Jiménez-Arenas, J. M. 2021: Taphonomical and spatial analyses from the Early Pleistocene site of Venta Micena 4 (Orce, Guadix-Baza, Basin, southern Spain). — *Scientific Reports* 11, 13977, <https://doi.org/10.1038/s41598-021-93261-1>.
- MacDonald, K., Martín-Torres, M., Denell, R. W. & Bermúdez de Castro, J. M. 2012: Discontinuity in the record for hominin occupation in south-western Europe: implications for occupation of the middle latitudes of Europe. — *Quaternary International* 271: 84–97, <https://doi.org/10.1016/j.quaint.2011.10.009>.
- Maldonado-Garrido, E., Piñero, P. & Agustí, J. 2017: A catalogue of the vertebrate fossil record from the Guadix-Baza Basin (SE Spain). — *Spanish Journal of Palaeontology* 32: 207–236.
- Marean, C. W. & Ehrhardt, C. L. 1995: Paleoanthropological and paleoecological implications of the taphonomy of a sabertooth's den. — *Journal of Human Evolution* 29: 515–547.
- Margari, V., Hodell, D. A., Parfitt, S. A., Ashton, N. M., Grimalt, J. O., Kim, H., Yun, K. S., Gibbard, P. L., Stringer, C. B., Timmermann, A. & Tzedakis, P. 2023: Extreme glacial cooling likely led to hominin depopulation of Europe in the Early Pleistocene. — *Science* 381: 693–699.
- Martínez-Monzón, A., Sánchez-Bandera, C., Fagoaga, A., Oms, O., Agustí, J., Barsky, D., Solano-García, J., Jiménez-Arenas, J. M. & Blain, H. A. 2021: Amphibian body size and species richness as a proxy for primary productivity and climate: the Orce wetlands (Early Pleistocene, Guadix-Baza Basin, SE Spain). — *Palaeogeography, Palaeoclimatology, Palaeoecology* 586, 110752, <https://doi.org/10.1016/j.palaeo.2021.110752>.
- 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.
- Martínez-Navarro, B. & Palmqvist, P. 1995: Presence of the African machairodont *Megantereon whitei* (Bromm, 1937) (Felidae, Carnívora, Mammalia) in the Lower Pleistocene Site of Venta Micena (Orce, Granada, Spain), with some considerations on the origin, evolution and dispersal of the genus. — *Journal of Archaeological Science* 22: 569–582, <https://doi.org/10.1006/jasc.1994.0054>.
- Martínez-Navarro, B., Palmqvist, P., Madurell, J., Ros-Montoya, S., Espigares, M. P., Torregrosa, V. & Pérez-Claros, J. A. 2010: La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5: estado de la cuestión. — In: Toro, I., Martínez Navarro, B. & Agustí, J. (eds.), *Ocupaciones humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza*: 197–236. Arqueología Monografía, Junta de Andalucía, Consejería de Cultura.
- Martínez-Navarro, B., Bartolini Lucenti, S., Palmqvist, P., Ros-Montoya, S., Madurell-Malapeira, J. & Espigares, M. P. 2021: A new species of dog from the Early Pleistocene site of Venta Micena (Orce, Baza Basin, Spain). — *Comptes Rendus Palevol* 20: 297–314.
- Maté-González, M. A., González-Aguilera, D., Linares-Matás, G. & Yravedra, J. 2019: New technologies applied to modelling taphonomic alterations. — *Quaternary International* 517: 4–15, <https://doi.org/10.1016/j.quaint.2018.12.021>.
- Moyá-Solà, S. 1987: Los bóvidos (Artiodactyla, Mammalia) del yacimiento del Pleistoceno inferior de Venta Micena (Orce, Granada, España). — *Paleontología i Evolució, Memoria Especial* 1: 181–236.
- Muttoni, G. & Kent, D. V. 2024: Hominin population bottleneck coincided with migration from Africa during the Early Pleistocene ice age transition. — *Proceedings of the National Academy of Sciences* 121(13), e2318903121, <https://doi.org/10.1073/pnas.2318903121>.
- Ochando, J., Carrión, J., Altolaguirre, Y., Munuera, M., Amorós, G., Jiménez-Moreno, G., Solano-García, J., Barsky, D., Luzón, C., Sánchez-Bandera, C., Serrano-Ramos, A., Toro-Moyano, I., Saarinen, J., Blain, H.-A., Bocherens, H., Oms, O., Agustí, J., Fortelius, M. & Jiménez-Arenas, J. M. 2022: Palynological investigations in the Orce Archaeological Zone, Early Pleistocene of southern Spain. — *Review of Palaeobotany and Palynology* 304, 10472, <https://doi.org/10.1016/j.revpalbo.2022.104725>.
- Oms, O., Agustí, J., Gabas, M. & Anadón, P. 2000a: Lithostratigraphic correlation of micromammal sites and biostratigraphy of the upper Pliocene to lower Pleistocene in the northeast Guadix-Baza Basin (southern Spain). — *Journal of Quaternary Science* 15: 43–50.
- Oms, O., Parés, J. M., Martínez-Navarro, B., Agustí, J., Toro, I., Martínez-Fernández, G. & Turq, A. 2000b: Early human occupation of Western Europe: paleomagnetic dates of two paleolithic sites in Spain. — *Proceedings of the National Academy of Sciences* 97: 10666–10670, <https://doi.org/10.1073/pnas.180319797>.
- Oms, O., Agustí, J. & Parés, J. M. 2010: Litoestratigrafía, magnetoestratigrafía y bioestratigrafía de los yacimientos de Barranco León 5 y Fuente Nueva 3 (Cuenca de Guadix-Baza, España). — In: Toro, I., Martínez-Navarro, B. & Agustí, J. (eds.), *Ocupaciones humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza*: 107–120. Arqueología Monografía, Junta de Andalucía, Consejería de Cultura.
- Oms, O., Anadón, P., Agustí, J. & Julià, R. 2011: Geology and chronology of the continental Pleistocene archaeological and paleontological sites of the Orce area (Baza basin, Spain). — *Quaternary International* 243: 33–43,

- https://doi.org/10.1016/j.quaint.2011.03.048.
- Palmqvist, P. & Arribas, A. 2001: Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. — *Paleobiology* 27: 512–530.
- Palmqvist, P., Martínez-Navarro, B. & Arribas, A. 1996: Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. — *Paleobiology* 22: 514–534.
- Palmqvist, P., Martínez-Navarro, B., Pérez-Claros, J. A., Torregrosa, V., Figueirido, B., Jiménez-Arenas, J. M., Espigares, P., Ros-Montoya, S. & De Renzi, M. 2011: The giant hyena *Pachycrocuta brevirostris*: modelling the bone-cracking behavior of an extinct carnivore. — *Quaternary International* 243: 61–79.
- 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). — *Scientific Reports* 12, 705, <https://doi.org/10.1038/s41598-021-04725-3>.
- Palmqvist, P., Rodríguez-Gómez, G., Martínez-Navarro, B., Espigares, M. P., Figueirido, B., Ros-Montoya, S., Guerra-Merchán, A., Granados, A., García-Aguilar, J. M. & Pérez-Claros, J. A. 2023: Déjà vu: on the use of meat resources by sabretooth cats, hominins, and hyaenas in the Early Pleistocene site of Fuente Nueva 3 (GuadixBaza Depression, SE Spain). — *Archaeological and Anthropological Sciences* 15, 17, <https://doi.org/10.1007/s12520-022-01712-1>.
- Pante, M. C. 2013: The larger mammal fossil assemblage from JK2, Bed III, Olduvai Gorge, Tanzania: implications for the feeding behavior of *Homo erectus*. — *Journal of Human Evolution* 64: 68–82.
- Pobiner, B. 2007: *Hominid–carnivore interactions: evidence from modern carnivore bone modification and Early Pleistocene archaeofaunas (Koobi Fora, Kenya; Olduvai Gorge, Tanzania)*. — Ph.D. thesis, Department of Anthropology, Rutgers University, New Brunswick.
- 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). — *Current Anthropology* 56: 134–142.
- Ros-Montoya, S., Bartolini-Lucenti, S., Espigares, M. P., Palmqvist, P. & Martínez-Navarro B. 2021: First review of Lyncodontini material (Mustelidae, Carnivora, Mammalia) from the Lower Pleistocene archaeo-palaeontological sites of Orce (southeastern Spain). — *Rivista Italiana de Paleontologia e Stratigrafia* 127: 33–47.
- Saarinen, J., Oksanen, O., Zliobaitė, I., Fortelius, M., DeMiguel, D., Azanza, B., Bocherens, H., Luzón, C., Solano-García, J., Yravedra, J., Courtenay, L., Blain, H. A., Sánchez-Bandera C., Serrano-Ramos, A., Rodríguez-Alba, J. J., Viranta, S., Barsky, D., Tallavaara, M., Oms, O., Agustí, J., Ochando, J., Carrión, J. & Jiménez-Arenas, J. M. 2021: Pliocene to Middle Pleistocene climate history in the Guadix-Baza Basin, and the environmental conditions of early *Homo* dispersal in Europe. — *Quaternary Science Reviews* 268, 107132, <https://doi.org/10.1016/j.quascirev.2021.107132>.
- Sánchez-Bandera, C., Oms, O., Blain, H. A., Lozano-Fernández, I., Bisbal-Chinesta, J. F., Agustí, J., Saarinen, J., Fortelius, M., Tittton, S., Serrano, A., Luzon, C., Solano-García, J., Barsky, D. & Jiménez-Arenas, J. M. 2020: New stratigraphically constrained palaeoenvironmental reconstructions for the first human settlement in Western Europe: the Early Pleistocene herpetofaunal assemblages from Barranco León and Fuente Nueva 3 (Granada, SE Spain). — *Quaternary Science Reviews* 243, 106466, <https://doi.org/10.1016/j.quascirev.2020.106466>.
- Sánchez-Bandera, C., Fagoaga, A., Serrano-Ramos, A., Solano-García, J., Barsky, D., DeMiguel, D., Ochando, J., Saarinen, J., Piñero, P., Lozano-Fernández, I., Courtenay, L. A., Tittton, S., Luzón, C., Bocherens, H., Yravedra, J., Fortelius, M., Agustí, J., Carrión, J.S., Oms, O., Blain, H.-A. & Jiménez-Arenas, J. M. 2023: Glacial/interglacial climate variability in southern Spain during the late Early Pleistocene and the climate backdrop for early *Homo* in Europe. — *Palaeogeography, Palaeoclimatology, Palaeoecology* 625, 111688, <https://doi.org/10.1016/j.palaeo.2023.111688>.
- Scanferla, A., Bonini R., Pomi, L., Fucks, E. & Molinari, A. 2013: New Late Pleistocene megafaunal assemblage with well-supported chronology from the Pampas of southern South America. — *Quaternary International* 305: 97–103.
- Tittton, S., Barsky, D., Bargalló, A., Serrano-Ramos, A., Vergès, J. M., Toro-Moyano, I., Sala-Ramos, R., García-Solano, J. A. & Jiménez Arenas, J. M. 2020: Sub-spheroids in the lithic assemblage of Barranco León (Spain): recognizing the late Oldowan in Europe. — *PLoS ONE* 15, e0228290, <https://doi.org/10.1371/journal.pone.0228290>.
- Tittton, S., Oms, O., Barsky, D., Bargalló, A., Serrano-Ramos, A., García-Solano, Sánchez-Bandera, C., Yravedra, J., Blain, H. A., Toro-Moyano, I., Jiménez-Arenas, J. M. & 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). — *Archaeological and Anthropological Science* 13, 108, <https://doi.org/10.1007/s12520-021-01353-w>.
- Tittton, S., Barsky, D., Bargallo, A., Vergés, J. M., Guardiola, M., García-Solano, J., Jimenez-Arenas, J. M., Toro-Moyano, I. & Sala-Ramos, R. 2018: Active percussion tools from the Oldowan site of Barranco Leon (Orce, Andalusia, Spain): the fundamental role of pounding activities in hominin lifeways. — *Journal of Archaeological Science* 96: 131–147, <https://doi.org/10.1016/j.jas.2018.06.004>.
- Tixier, J., Roe, D., Turq, A., Gibert, J., Martínez-Navarro, B., Arribas, A., Gibert, L., Gaete, R., Maillo, A. & Iglesias, A. 1995: Presence d'industries lithiques dans le Pleistocene inferieur de la région d'Orce (Grenade, Espagne): etat de la question. — *Current Research Academic Science Series* 11a 321: 71–78.
- Toro-Moyano, I., Lumley, H., de Fajardo, B., Barsky, D., Cauche, D., Celiberti, V., Grégoire, S., Martínez-Navarro, B., Espigares, M. P. & Ros-Montoya, S. 2009:

- L'industrie lithique des gisements du pléistocène inférieur de Barranco León et Fuente Nueva 3 à Orce, Grè-nade, Espagne. — *Anthropologie* 113: 111–124, <https://doi.org/10.1016/j.anthro.2009.01.006>.
- Toro-Moyano, I., Barsky, D., Cauche, D., Celiberti, V., Grégoire, S., Lebègue, F., Moncel, M. H. & Lumley, H. 2011: The archaic stone tool industry from Barranco León and Fuente Nueva 3, (Orce, Spain): evidence of the earliest hominin presence in southern Europe. — *Quaternary International* 243: 80–91, <https://doi.org/10.1016/j.quaint.2010.12.011>.
- Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J. M., Martínón-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J. M., Anadón, P., Julià Brugués, J., García-Aguilar, J. M., Moigne, A. M., Espigarrés, M. P., Ros-Montoya, S. & Palmqvist, P. 2013: The oldest human fossil in Europe, from Orce (Spain). — *Journal of Human Evolution* 65: 1–9, <https://doi.org/10.1016/j.jhevol.2013.01.012>.
- Turner, A. 1992: Villafranchian-Galerian larger carnivores of Europe: dispersions and extinctions. — *Courier Forschungsinstitut Senckenberg* 153: 153–160.
- Turq, A., Martínez-Navarro, B., Palmqvist, P., Arribas, A., Agustí, J. & Rodríguez-Vidal, J. 1996: Le Plio-Pleistocene de la région d'Orce, province de Grenada, Espagne: Bilan et perspectives de Recherche. — *Paleo Revista Archeologica Prehistorique* 8: 161–204.
- Yezzi-Woodley, K., Terwilliger, A., Jiafeng, B., Chen, L. E., Tappen, M., Calder, J. & Olver, P. 2024: Using machine learning on new feature sets extracted from three-dimensional models of broken animal bones to classify fragments according to break agent. — *Journal of Human Evolution* 187, 103495, <https://doi.org/10.1016/j.jhevol.2024.103495>.
- Yravedra, J., Domínguez-Rodrigo, M., Samntonja, M., Pérez-González, A., Panera, J. & Rubio-Jara, S. 2010: Cut marks on the MP elephant carcass of Aridos 2 (Madrid, Spain). — *Journal of Archaeological Science* 37: 2469–2476.
- Yravedra, J., Mate-González, M. A., Courtenay, L. A., González-Aguilera, D. & Fernández, M. F. 2019: The use of canid tooth marks on bone for the identification of live-stock predation. — *Scientific Reports* 9, 16301, <https://doi.org/10.1038/s41598-019-52807-0>.
- Yravedra, J., Solano, J. A., Courtenay, L. A., Saarinen, J., Linares-Matás, G. J., Luzón, C., Serrano-Ramos, A., Herranz-Rodrigo, D., Cámara, J. M., Ruiz, A., Tilton, S., Rodríguez-Alba, J. J., Mielgo, C., Blain, H. A., Agustí, J., 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., Courtenay, L. A., Herranz-Rodrigo, D., Linares-Matás, G. J., Rodríguez-Alba, J. J., Estaca-Gómez, V., Luzón, C., Serrano-Ramos, A., Maté-González, M. A., Solano, J. A., González-Aguilera, D. & Jiménez-Arenas, J. M. 2022a: Taphonomic characterization of tooth marks of extinct Eurasian carnivores through geometric morphometrics. — *Science Bulletin* 67: 1644–1648.
- 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., Tilton, 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. 2022b: Unravelling hominin activities in the zooarchaeological assemblage of Barranco León (Orce, Granada, Spain). — *Journal of Paleolithic Archaeology* 5, 6, <https://doi.org/10.1007/s41982-022-00111-1>.
- Yravedra, J., Luzón, C., Solano, J. A., Linares-Matás, G. J., Estaca-Gómez, V., Rodríguez-Alba, J. J., Courtenay, L. A., Herranz-Rodrigo, D., Serrano-Ramos, A., Cámara, J., Saarinen, J., Sánchez-Bandera, C., Blain, H. A., Viranta S., DeMiguel, D., Azanza, B., Oms, O., Agustí, J., Fortelius, M. & Jiménez-Arenas, J. M. 2023: To den or not to den. Contributions to the taphonomic history of the Early Pleistocene site of Venta Micena 4 (Orce, Guadix-Baza Basin). — *Quaternary Science Reviews* 308, 108031, <https://doi.org/10.1016/j.quascirev.2023.108031>.
- Yravedra, J., Courtenay, L. A., Gutiérrez-Rodríguez, M., Reinoso-Gordo, J. F., Saarinen, J., Égüez, N., Luzón, C., Rodríguez-Alba, J. J., Solano, J. A., Tilton, S., Montilla-Jiménez, E., Cámara-Donoso, J., Herranz-Rodrigo, D., Estaca, V., Serrano-Ramos, A., Amorós, G., Azanza, B., Boccherini, H., DeMiguel, D., Fagoaga, A., García-Alix, A., Jiménez-Espejo, F., Kaakinen, A., Munuera, M., Ochando, J., Piñero, P., Sánchez-Bandera, C., Viranta, S., Fortelius, M., Agustí, J., Blain, H.-A., Carrión, J., Barsky, D., Oms, O., Mallol, C. & Jiménez-Arenas, J. M. 2024: Not seen before. Unveiling depositional context and *Mammuthus meridionalis* exploitation at Fuente Nueva 3 (Orce, Southern Iberia) through taphonomy and microstratigraphy. — *Quaternary Science Reviews* 329, 108561, <https://doi.org/10.1016/j.quascirev.2024.108561>.

