



Use of meat resources in the Early Pleistocene assemblages from Fuente Nueva 3 (Orce, Granada, Spain)

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Abstract

Over the last few decades, several types of evidence such as presence of hominin remains, lithic assemblages, and bones with anthropogenic surface modifications have demonstrated that early human communities inhabited the European sub-continent prior to the Jaramillo Subchron (1.07–0.98 Ma). While most studies have focused primarily on early European lithic technologies and raw material management, relatively little is known about food procurement strategies. While there is some evidence showing access to meat and other animal-based food resources, their mode of acquisition and associated butchery processes are still poorly understood. This paper presents a taphonomic and zooarchaeological analysis of the Fuente Nueva-3 (FN3) (Guadix-Baza, Spain) faunal assemblage, providing a more in-depth understanding of early hominin subsistence strategies in Europe. The present results show that hominins had access to the meat and marrow of a wide range of animal taxa, including elephants, hippopotami, and small- and medium-sized animals. At the same time, evidence of carnivore activity at the site suggests that these communities likely faced some degree of competition from large predators when acquiring and processing carcasses.

Keywords Early Pleistocene · Taphonomy · Hominin-carnivore interactions · Zooarchaeology · Cut marks · Palaeolithic archaeology

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Introduction

Recent publications have amply demonstrated that hominins inhabited Europe prior to the Jaramillo Subchron (1.07–0.98 Ma). Thus, sites such as Barranco León, Fuente Nueva 3 (FN3) (Barsky et al., 2010, 2015; Tifton et al., 2019, 2020; Toro-Moyano et al., 2009, 2010a, 2010b, 2011, 2013), and Sima del Elefante in Spain (Parés et al., 2006; Carbonell et al. 2008), Le Vallonnet (Michel et al., 2017), Bois-de-Riquet, and Pont-de-Lavaud in France (Bourguignon et al., 2015; Despriée et al., 2018; Lozano-Fernández et al., 2019), and Kozarnika cave in Bulgaria (Sirakov et al., 2010) as well as Pirro Nord in Italy (Arzarello et al., 2016; Pavia et al., 2012) have provided extensive evidence of hominin activities older than 1 Ma. The studies carried out so far in most of these early sites have focused on improving our understanding of the technological behaviours reflected in the lithic assemblages, documenting the use of Oldowan technocomplexes (Mode 1) at most of these sites (Carbonell et al., 2008; Barsky et al., 2010, 2015; Sirakov et al., 2010; Toro-Moyano et al., 2011, 2013; de Lombera-Hermida et al. 2015; Arzarello et al. 2016; Bourguignon et al. 2015). Nevertheless, comparatively little is still known about their food procurement strategies, which included both plant matter and animal resources. In addition to the material traces of their activities, the presence of these early human communities in the European subcontinent has been directly demonstrated through the discovery of hominin remains at sites such as Barranco León (Toro-Moyano et al. 2013) and Sima del Elefante (Carbonell et al., 2008).

With regards to the exploitation of animal resources, some evidence is known of cut-marked bones, providing direct evidence of hominin access to meat resources. In some cases, such as Kozarnika cave (Sirakov et al., 2010), Trlica (Vislobokova et al., 2020), or Pirro Nord (Cheheb et al., 2019), sample sizes are small and present ambiguous distribution patterns. This unfortunately limits the extent to which inferences can be inferred about procurement modalities and the order of which hominins had access to these carcasses (primary or secondary). The timing of hominin access to carcasses is nonetheless a fundamental issue for understanding the subsistence strategies of Early Pleistocene populations. When conceptualising carcass acquisition strategies, primary access implies that hominins processed the remains before any other predator, while secondary access implies that hominin consumption of animal resources took place after other predators had already been feeding upon the carcass.

Primary access is only possible in either of these scenarios: (1) when hominins hunted prey; (2) when hominins dispossessed another carnivore of its prey (confrontational

scavenging, as proposed by Bunn & Ezzo 1993); (3) when hominins encountered an animal carcass dead from natural causes. The first scenario entails a series of important behavioural capacities among early hominins, since hunting involves some degree of planning, cooperation, and the ability to kill prey. Scenarios 2–3 also entail some degree of landscape knowledge through the monitoring of suitable procurement spots (Clark and Linares-Matás 2021), although some authors have highlighted a series of issues associated with them. For example, Treves and Treves (1999) and Domínguez-Rodrigo (2002) have noted how scenario 2 is dangerous and unlikely, while the third scenario is highly reliant on trophic pressures and seasonality (Blumenshine, 1986, 1989; Tappen, 1995; Clark and Linares-Matás, 2021), which renders recurrent and reliable access to carcasses rather unlikely (Domínguez-Rodrigo (2002; Yravedra 2006: 162) beyond opportunistic exploitation of catastrophic carrion pulses. From the 1970s and 1980s, Binford (1981) challenged the “Man the Hunter” paradigm of human subsistence by proposing that hominins were scavengers, kickstarting an intense “hunting versus scavenging” debate that has generated a vast academic literature involving several hypotheses and the elaboration of models derived from actualistic reference frameworks (see Yravedra 2006; Parkinson 2018). After more than 30 years of debates, there is an emerging consensus that hominins had primary access to animal carcasses of different sizes at Early Stone Age sites in Africa such as FLK-Zinj and BK (Olduvai Gorge, Tanzania), St (Peninj, Tanzania), FwJj14A, FwJj14B, and GaJi14 (Koobi Fora, Kenya), KJS (Kanjera, Kenya), and Swartkrans (South Africa) (Monahan, 1996, Domínguez-Rodrigo (2002; Domínguez-Rodrigo et al. 2002, 2009; Pickering et al., 2008; Pobiner et al., 2008; Bunn & Pickering, 2010; Ferraro et al., 2013; Parkinson, 2018; Oliver et al., 2019; Clark & Linares-Matás 2021).

In Europe, Sima del Elefante (Atapuerca, Spain) is the only site older than 1 Ma with conclusive evidence of early human access to animal carcasses (Huguet et al., 2013, 2017). At this site, 5% of cervid, bovid, and equid remains from different anatomical parts possess cut marks, evidencing butchery activities such as skinning, dismembering, and defleshing (Huguet et al., 2017). Moreover, the presence of percussion marks in this highly fragmented assemblage evidences the exploitation of bone marrow. Alongside anthropogenic evidence, the Sima del Elefante faunal assemblage also has some taphonomic evidence of carnivore activity (5%), resulting from the action of medium-sized carnivores, i.e. wolves or hyenas, according to Huguet et al. (2017). In contrast with the distribution of cut marks, most tooth marks are found on fat-rich elements, such as vertebrae, ribs, and epiphyses/metadiaphyses, a pattern generally associated with secondary access, according to Huguet et al. (2017).

At Orce, a model of hominin-carnivore competition has been proposed for both Barranco León and FN3 (Rodríguez-Gómez et al., 2016; Espigares et al., 2019). At FN3, the discovery of an elephant carcass with nearby lithic implements and giant hyena (*Pachycrocuta brevirostris*) coprolites was interpreted as a place of encounter and competition between both agents (Espigares et al., 2013). The study of the bone assemblages from Barranco León and FN3 in Espigares et al. (2019) shows the remains from multiple animals modified by humans and carnivores, interpreted as hominins having secondary access to the carcasses. However, the results of Espigares et al. (2019) have been challenged by Domínguez-Rodrigo et al. (2020), who reassessed some of the evidence. In any case, it is unexpected for Espigares et al. (2019) to claim that hominins had secondary access to carcasses when they are documenting evisceration cut marks on the ventral side of the ribs and vertebrae, as well as defleshing cut marks on long bone diaphyses (Espigares et al., 2019, SF Table S12). Furthermore, carnivore tooth marks are relatively infrequent in these assemblages. As such, there is scope for putting forward alternative hypotheses to those presented by Espigares et al. (2019) and other authors (e.g. Martínez-Navarro et al. 2003, 2010; Palmqvist et al. 2005, 2011; Rodríguez-Gómez et al., 2016).

Through the present zooarchaeological and taphonomic study, which analyses the faunal remains excavated during the 2017–2020 fieldwork seasons at FN3, we expand the FN3 assemblage and assess the hypotheses put forward Espigares et al. (2013, 2019). The new data may enable us to

provide a more developed understanding of the subsistence strategies employed by the Early Pleistocene populations at FN3.

The FN3 archaeological site

FN3 is an Early Pleistocene archaeological site located 7 km west of the town of Orce (Granada, southern Spain), situated in the northeasternmost part of the Guadix-Baza Basin (Toro-Moyano et al., 2010a, 2010b) (Fig. 1). This intermontane basin was formed in the upper-middle Miocene after the closure of one of the Betic corridors between the Mediterranean and the Atlantic (Hüsing et al. 2010). From the Upper Miocene to the Middle-Upper Pleistocene, this area has been interpreted as an endorheic continental basin, that is, a closed drainage basin, which eventually formed the saline Baza lake (Anadón et al., 1994; Anadón and Gabàs, 2009), around which various archaeopalaeontological localities such as Barranco León, Fuente Nueva, or Venta Micena have been observed (Fig. 1). The waters of this endorheic system were drained by the changing course of the Guadalquivir River and its tributaries. Today, the basin preserves a succession of alluvial (Guadix) and colluvial deposits (Baza: lacustrine clays, silts, and sands with evaporitic limestone crusting), reaching up to 100 m thick and covering a timescale ranging from the Upper Miocene to the Upper Pleistocene. Over the

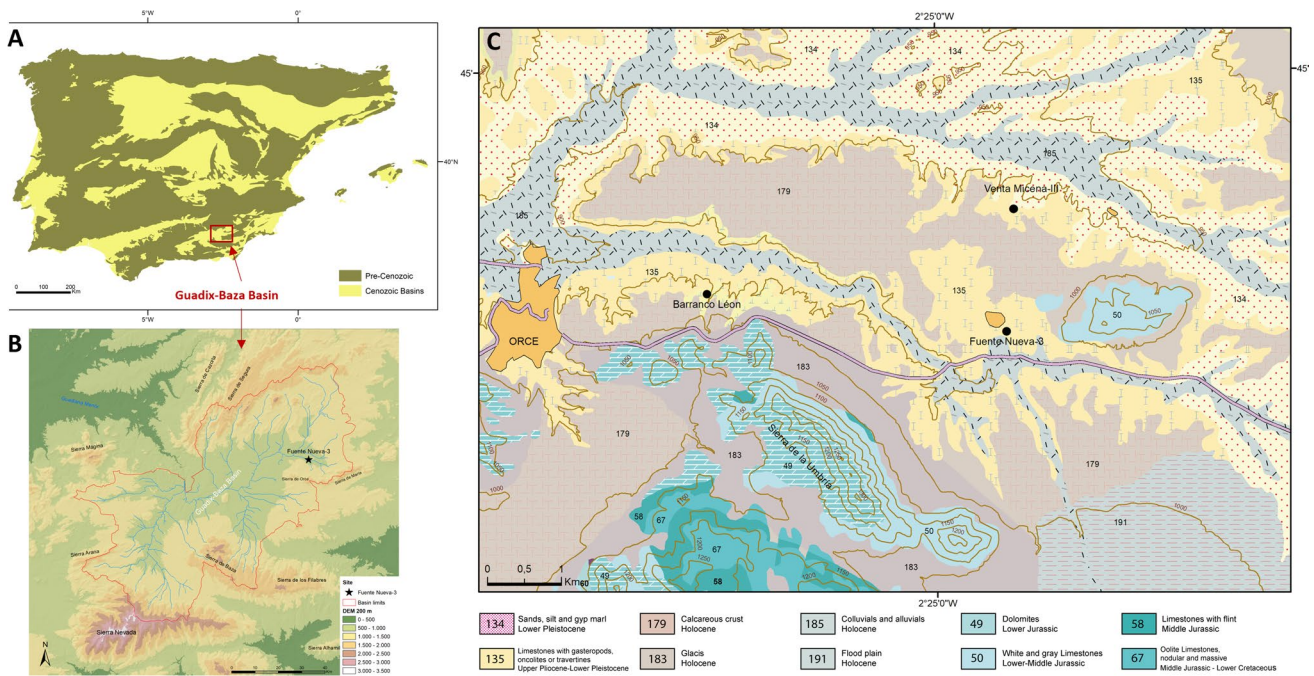


Fig. 1 Location of the FN3 archaeological site

last half-century, numerous fossiliferous and archaeological localities have been documented (Maldonado-Garrido et al., 2017).

FN3 is located near the margins of the lake (Fig. 1). The age of FN3 has been determined using both relative and absolute dating methods, employing both micro- and macro-vertebrate biochronological calibrations with magneto-stratigraphical data (Agustí et al., 1987, 1996, 2007, 2010; Martínez-Navarro et al., 1997, 2003, 2010; Oms et al., 1999, 2000a, 2000b; Agustí and Madurell, 2003; Scott et al., 2007; Lozano-Fernández et al., 2015a), as well as combined U-series/ESR dating of quartz grains and tooth enamel (Duval et al., 2011, 2012a, 2012b). The stratigraphical sequence at the site (Fig. 2) correlates to the Matuyama Chron, situated between the Olduvai and Jaramillo subchrons (1.78–1.48 Ma 1.07–0.98 Ma, Gradstein et al., 2005). In particular, an age of around 1.2 Ma is accepted for the site of FN3, on the basis of the derived features of the rodents *Allophaiomys* aff. *lavocati* (Agustí and Madurell, 2003; Lozano-Fernández et al., 2015b).

Since the discovery of FN in 1991 by Alain Bocquet, and until 2016, several research projects have demonstrated important associations between the faunal remains and the lithic industries from this locality (Gibert et al., 1992, 1998; Roe, 1995; Tixier et al., 1995; Turq et al., 1996; Martínez-Navarro et al., 1997, 2010; Toro-Moyano et al., 2003). Since 2017, a new research project under the direction of the University of Granada has undertaken fieldwork at the site. The present study explores the zooarchaeological and taphonomic insights from the faunal assemblage retrieved from field campaigns carried out between 2017 and 2020.

The taxonomy of the faunal assemblages represented in the archaeo-palaeontological sites of Orce has undergone numerous changes over the last five decades (see Luzón et al., 2021, Supplementary Notes S2 for a further discussion). Nevertheless, we present an updated list of the site of FN3. These include carnivores, such as the bear *Ursus etruscus* (Medin et al., 2017), the canids *Canis mosbachensis* (Luzón et al., 2021, Supplementary Notes S2), *Xenocyon* (*Lycaon*) *lycaonoides* (Luzón et al., 2021, Supplementary

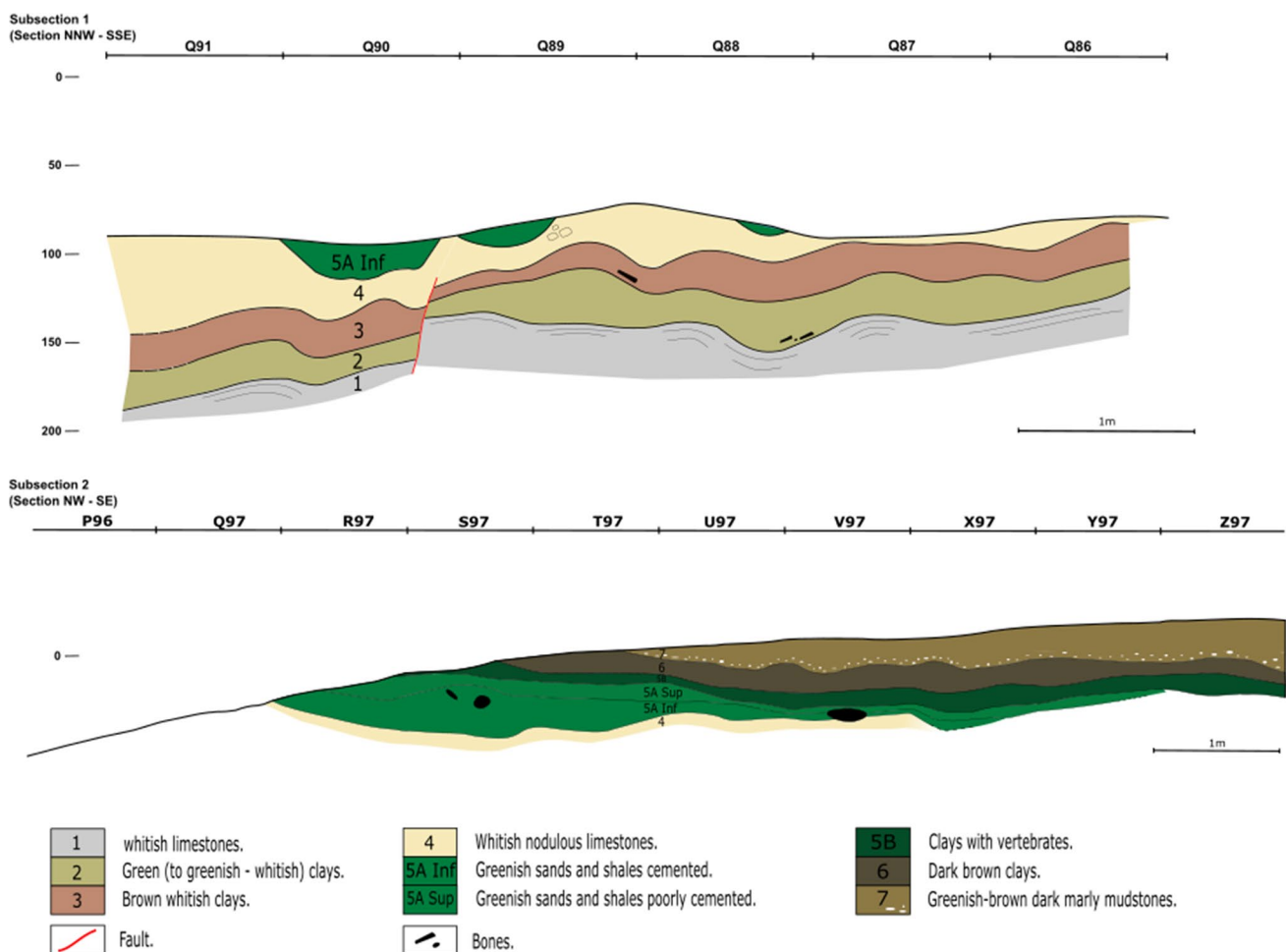


Fig. 2 Stratigraphic sequence of FN3 (after Oms et al., 2011; Reinoso-Gordo et al., 2020)

Notes S2), and *Vulpes alopecoides* (Bartolini-Lucenti & Madurell-Malapeira, 2020), the hyena *Pachycrocuta brevirostris* (Martínez-Navarro et al., 2010), Felidae indet. (Martínez-Navarro et al., 2010), the small felid *Lynx cf. pardinus* (Boscaini et al., 2015), the badger *Meles meles* (Madurell-Malapeira et al., 2011), and the mustelid *Martellictis ardea* (Ros-Montoya et al., 2021); and large herbivores, such as the proboscidean *Mammuthus meridionalis* (Ros-Montoya, 2010), the rhino *Stephanorhinus cf. etruscus* (Luzón et al., 2021, Supplementary Notes 2), two horses *Equus altidens* and *E. sussenbornensis* (Alberdi, 2010), the hippo *Hippopotamus antiquus* (Martínez-Navarro et al., 2010), the bovid *Bison* sp. (Martínez-Navarro et al., 2010), the caprids *Ammotragus europaeus* (Martínez-Navarro et al., 2010) and *Capra cf. alba* (van der Made et al., 2008), and the cervids *Praemegaceros cf. verticornis* and *Metacervoceros rhenanus* (Abbazzi, 2010). From a paleoecological point of view, two variables have been calculated both based on dental ecometrics in large herbivorous mammal guilds of FN3 and Barranco León: Mean Annual Precipitation (MAP) and Net Primary Production (NPP). Results have provided equal values for MAP (602 mm) and NPP (914 g(C)/m²/a) in both sites (Saarinen et al., 2021). It is worth noting that the MAP calculation on dental ecometrics is slightly lower than such calculated by Mutual Ecogeographic Range (FN3 MAP: 738 mm; Blain et al., 2016). In addition, drier climatic conditions (MAP: 449 mm) and lesser productivity (NPP: 747 g(C)/m²/a) have been calculated from the dental features of the Venta Micena herbivore community (Saarinen et al., 2021).

The micromammals from FN3 include the insectivores Erinacena indet., *Crocidura* sp., *Sorex minutus*, *Sorex* sp., *Asoriculus gibberodon*, and *Galemys* sp. (Agustí et al., 2010); and the rodents, *Allophaiomys* aff. *lavocati*, *Allophaiomys* sp., *Mimomys savini*, *Castillomys crusafonti*, *Apodemus* aff. *mystacinus*, and *Hystrix* sp. (Agustí and Madurell, 2003; Agustí et al., 2007, 2010).

The herpetofaunal list of FN3 is somewhat poorer (13 taxa in total) than the nearby site of Barranco León with four anurans (*Discoglossus cf. jeanneae*, *Pelobates cultripes*, *Bufo bufo* s.l., and *Pelophylax cf. perezii*), four lizards (*Chalcides cf. bedriagai*, *Timon* sp., indeterminate small lacertids, and cf. *Ophisaurus*), and five snakes (*Coronella girondica*, *Natrix maura*, *Natrix natrix* s.l., *Zamenis scalaris*, and *Malpolon monspessulanus*) (Blain, 2005, 2009; Blain and Bailon, 2010; Blain et al., 2011, 2016; Sánchez-Bandera et al., 2020). Some fish and chelonian remains are also present in the faunal assemblage.

The stratigraphic sequence of FN3 was first described by Turq et al. (1996). Nevertheless, it has since been redefined by Oms et al. (2010), recognizing 12 stratigraphic levels (Fig. 2), among which level 5 stands out as it contains most of the macro-vertebrate and lithic remains.

The lithic industry of FN3 has been studied in detail by Toro-Moyano et al. (2003, 2010a, 2010b, 2011, 2013) and Barsky et al. (2010, 2013, 2015), presenting typical Oldowan (Mode 1) artefacts. The lithic industry recovered in FN3 level 5 represents 5% of the archaeological material recovered at the site, compared to the fauna that comprises 95%. Flint is the predominant raw material, followed by limestone, both of which were obtained from local sources (Barsky et al., 2010, 2015). The predominant knapping techniques include bipolar knapping on anvil, as well as direct percussion knapping, used to produce small-sized flakes and choppers (Zaidner, 2013; Barsky et al., 2010, 2015). Limestone blocks and some cobbles were mainly used as heavy-duty tools. Although both flint and limestone were used to knap small flakes, the abundance of limestone percussion tools indicates a clear, task-related differentiation between the two materials (Toro-Moyano et al., 2010a; Barsky et al., 2015). As in other Oldowan assemblages, the toolkit is non-standardized and contains few retouched items. In addition, some heavy-duty scrapers have been identified in the macro-toolkit (Barsky et al., 2018). Stone tool production was carried out with hard hammers, using both bipolar-on-anvil and free-hand percussion methods.

Materials and methods

The materials analysed for this study were retrieved from levels 1–6 of FN3 during the 2017–2020 field seasons, with most remains coming from level 5 (Table 1). This faunal assemblage encompasses the fossils bones obtained during the new field seasons from 2017 to 2020, retrieved from 44 m² in level 5, and 51 m² in all other levels. This material expands the faunal assemblages discussed by previous research.

Faunal remains were quantified by the number of identifiable specimens (NISP), minimum number of elements (MNE), and minimum number of individuals (MNI). MNI estimates considered element side and ontogenetic age (Brain, 1969). Mortality profiles were developed by assigning relevant elements/individuals to one of four categories: infant, juvenile, prime adult-adult, and senile, based on tooth eruption and crown wear.

Skeletal part profiles were based on a division of the skeleton into the following anatomical regions: cranial (i.e. horn, cranium, mandible, and teeth); axial (vertebrae, ribs, pelvis, and scapulae, according to Yravedra and Domínguez-Rodrigo (2009)); upper appendicular elements (humerii, femora); intermediate appendicular limbs (radii, tibiae, patellae, ulnae); and lower appendicular elements (metapodials, carpals, tarsals, phalanges, and sesamoids). Long limb bones were further divided into anterior elements (scapulae, humerii, radii, ulnae, carpals, and metacarpals), as well

Table 1 Taxonomic representation in the zooarchaeological assemblages of FN3, based on the faunal remains retrieved from the 2017–2020 field seasons, quantified in terms of NISP and MNI. Age classes: S: seniles; A: adults; J: juveniles; I: infants. The Bold entries reflected the total

| Layer | NISP | | | | | MNI | | | | | |
|---|------------|------------|-------------|-----------|-------------|-----|---|---|---------|---|----------|
| | 2 | 3 | 5 | 6 | Total | 2 | 3 | 5 | S/A/J/I | 6 | Total |
| <i>Mammuthus meridionalis</i> | | 1 | 389 | 3 | 393 | | 1 | 4 | 0/2/1/1 | 1 | 6 |
| <i>Stephanorhinus etruscus</i> | 1 | | 18 | 1 | 20 | 1 | | 1 | 0/1/0/0 | 1 | 3 |
| <i>Equus altidens</i> | | | 5 | | 5 | | | 1 | 0/1/0/0 | | 1 |
| <i>Equus</i> sp. | 2 | 1 | 27 | | 30 | 1 | 1 | 2 | 0/2/0/0 | | 4 |
| <i>Hippopotamus antiquus</i> | | | 53 | | 53 | | | 3 | 0/1/1/1 | | 3 |
| <i>Bison</i> sp. | | | 8 | | 8 | | | 2 | 0/2/0/0 | | 2 |
| Bovidae | 3 | 1 | 18 | | 22 | 1 | 1 | 2 | 0/2/0/0 | | 4 |
| <i>Praeovibos</i> sp. | | | 1 | | 1 | | | 1 | 0/1/0/0 | | 1 |
| <i>Capra alba</i> | | | 6 | | 6 | | | 1 | 0/1/0/0 | | 1 |
| <i>Sorgelia minor</i> | | | 1 | | 1 | | | 1 | 0/1/0/0 | | 1 |
| Cervidae | | 1 | 36 | | 37 | | 1 | 3 | 0/2/1/0 | | 4 |
| <i>Metacervocerus rhenanus</i> | | 1 | 2 | | 3 | | 1 | 1 | 0/1/0/0 | | 2 |
| <i>Praemegaceros</i> cf. <i>verticornis</i> | | 1 | 5 | | 6 | | 1 | 1 | 0/1/0/0 | | 2 |
| Artiodactyla size 2 | | 1 | 3 | | 4 | | | | | | |
| Artiodactyla size 3 | | | 1 | | 1 | | | | | | |
| Artiodactyla size 3b | | | 6 | | 6 | | | | | | |
| <i>Oryctolagus lacosti</i> | | | 6 | | 6 | | | 1 | 0/1/0/0 | | 1 |
| <i>Ursus etruscus</i> | | | 3 | | 3 | | | 1 | 0/1/0/0 | | 1 |
| Carnivore indet | | | 3 | | 3 | | | 1 | | | 1 |
| Carnivore size 2 | | 1 | | | 1 | | 1 | | 0/1/0/0 | | 1 |
| Chelonia | | | 35 | | 35 | | | 1 | 0/1/0/0 | | |
| Ave | | | 1 | | 1 | | | 1 | | | |
| Mammalia indet size 0 | | | 4 | | 4 | | | | | | |
| Mammalia indet size 1 | | | 6 | | 6 | | | | | | |
| Mammalia indet size 2 | | 6 | 59 | | 65 | | | | | | |
| Mammalia indet size 3 | 1 | 6 | 47 | 1 | 55 | | | | | | |
| Mammalia indet size 3a | 1 | 1 | 14 | | 16 | | | | | | |
| Mammalia indet size 3b | 2 | 3 | 118 | | 123 | | | | | | |
| Mammalia indet size 4 | 1 | | 9 | | 10 | | | | | | |
| Mammalia indet size 5 | 5 | 2 | 99 | | 106 | | | | | | |
| Indet | 84 | 81 | 3567 | 39 | 3771 | | | | | | |
| Total | 100 | 107 | 4550 | 44 | 4801 | | | | | | |

as posterior elements (pelves, femora, tibiae, patellae, tarsals, and metatarsals). Herbivore and carnivore specimens that could not be identified at a species level, but were not entirely considered indeterminable, were assigned a weight/size class. The categories used for herbivores follow the adaptation made by Espigares et al. (2019) of the classification system developed by Bunn (1982): microfaunal (0), including species weighing less than 25 kg; very small size (1), including macro-vertebrates species weighing 25–50 kg; small size (2), including species weighing 50–125 kg; intermediate size (3), including species weighing 125–500 kg, with an additional division between 3a (125–250 kg) and 3b (250–500 kg); large size (4), including species weighing 500–1000 kg; and very large size (5) for species weighing > 1000 kg. Carnivores were classified according to three size classes: small carnivores (e.g. foxes); intermediate

carnivores (e.g. wolves); and large carnivores (e.g. lions, hyenas), following Espigares et al. (2019).

Several procedures were followed to reconstruct site formation processes, assessing and evaluating both site integrity and the contribution of various biological agents to the faunal assemblage. Bone fragmentation was analysed according to three variables; first, bones were divided into several categories according to their length: < 3 cm, 3.1–5.0 cm, 5.1–10 cm, and > 10 cm; secondly, bones were classified based on the nature of their breakage planes, i.e. green or dry fractures, following Villa and Mahieu (1991). Criteria used to diagnose dry breaks included the existence of abundant breaks that are longitudinal and/or transverse to the axis of the bone, as well as breakage planes that are uneven, rough, and in possession micro-step fractures. Dry breaks are further characterized by cortical medullary

surface angles that are close to 90°. In contrast, specimens broken when fresh frequently have smoother surfaces and more abundant oblique breakage planes. Lastly, bone diaphysis preservation was recorded according to the relative length of their fragments, as well as circumference types; where type 1 refers to specimens with < 25% of the shaft circumference intact; type 2 refers to specimens with 25–50% of the shaft circumference intact; and type 3 refers to specimens with > 50% shaft circumference.

The impact of fluvial alterations was estimated with fragment size distributions, as well as the presence of abrasion, polishing, and rounding on bone surfaces. Rounding and abrasion were additionally classified into different stages; light, intermediate, and intense. Weathering intensity was analysed following Behrensmeyer (1978). Bone surface modification analyses were carried out using hand-held lenses at 10–40× magnification. Tooth marks were classified as pits, scores, or punctures, while furrowing was also analysed following the criteria established by multiple authors (Binford, 1981; Blumenschine, 1995; Blumenschine et al., 1996). Cut and percussion marks were classified according to Binford (1981), Blumenschine and Salvaggio (1988), and Blumenschine et al. (1996). Modifications were quantified for specimens with well-preserved bone surfaces in terms of NISP values. Other processes, such as manganese staining or biochemical alterations, were recorded using the criteria outlined by Fernández Jalvo and Andrews (2017).

Results

Zooarchaeological analyses

The sample analysed comprises 4801 remains, with level 5 being the one that has provided the largest volume of remains ($n = 4550$), of which 14% were considered determinable remains (Table 1). The other levels have only provided a relatively small sample; in levels 2 and 3, hardly more than 100 remains per level have been found and only 6% of them could be determined. In level 6, the sample is even more limited, with only 44 remains documented. Remains identified at the site belong to several herbivore and carnivore taxa.

Among the herbivores, *Mammuthus meridionalis* stands out with 62% of the determinable remains, and 14% of the MNI. The second best-represented taxa is *Hippopotamus antiquus* with 8.5% of the remains and 10.7% of the individuals. Artiodactyla (cervids, caprids, and bovids) are better represented than equids. Finally, there are several carnivore remains, of which only an ursid (*Ursus etruscus*) could be identified at a species level. From a palaeoecological perspective, the species represented belong to a wide range of different ecological settings. Species associated with open environments, such as proboscideans, equids, and

rhinoceroses, are well represented, alongside animals better adapted to wooded environments (such as cervids), generalist animals adapted to rocky environments (such as caprids), and animals that tend to rely on watercourses (such as hippopotami). In relation to the latter, other non-herbivore species such as turtles are also present. Mortality patterns show a predominance of adults in all levels across all taxa, with only level 5 yielding infant or juvenile individuals, found among proboscideans, hippopotami, and cervids (Table 1).

The skeletal profiles analysed for levels 2, 3, and 6 are not very representative due to their small sample size (see Suppl. File). The level 5 sample is larger, but with the exception of size 3 animals, most size classes are generally poorly represented, and tend to show a predominance of cranial elements due to the overrepresentation of heavily fragmented teeth and ivory tusks. Small animals (sizes 0–2) also show some presence of axial and appendicular elements. Among medium-sized animals (size 3), all the skeletal portions are represented including the axial and appendicular elements, even if cranial remains are clearly overrepresented (see Tables 2–3 and Suppl. File). Among the appendicular elements, we observe that both forelimbs and hindlimbs have a fairly similar representation. Very few remains could be attributed to large animals (size 4), while very large animals (size 5) are also represented mainly by cranial elements (see Tables 2–3 and Suppl. File).

Taphonomic analyses

The faunal assemblage shows a very high degree of fragmentation across all levels, with a predominance of bones < 3 cm, rendering more than 86% of the analysed sample indeterminate (Table 4). Among long limb bones, the high level of fragmentation has considerably influenced their circumference index and relative length values. In this regard, more than 90% of long bones from level 5 have less than 25% of their shaft circumference and less than 25% of their relative length (Table 4). In levels 3 and 6, the sample is very small but also shows high fragmentation rates. This high degree of fragmentation is likely due to diverse biostratigraphic processes that have induced green fractures in > 40% of the level 5 bone assemblage, and in > 50% of the bone samples from levels 2, 3, and 6 (Table 4).

Although bone fragmentation is high, cortical surface preservation in the assemblage is very good (> 75% of the bones are in a good state of preservation), and only level 2 bones are poorly preserved (Table 5). This good state of cortical preservation is likely due to the rapid burial rates that the assemblage experienced, as indicated by the very low incidence of weathering alterations: over 99% of the sample exhibit slight or no weathering (Table 3). Furthermore, waterborne alterations (abrasion, polishing, or rounding) are not particularly common, with only 13% of bones from

Table 2 Skeletal profiles according to NISP of the level 5 of FN3 assemblage from the 2017–2020 field seasons. See complete information in SF. The Bold entries reflected the total

| NISP | Species size level 5 | | | | | | | | | | Carniv 1 | Carniv 3 | Indet | Total | |
|--------------|----------------------|----------|-----------|-----------|-----------|------------|----------|------------|----------|----------|----------|-------------|-------------|-------|-----|
| | 0 | 1 | 2 | 3 | 3a | 3b | 4 | 5 | | | | | | | |
| Ivory | | | | | | | | | | | 228 | | | | 228 |
| Cranial | | | 1 | 1 | | 2 | 1 | 3 | | | | | | | 8 |
| Mandible | | | 1 | | | 3 | | 1 | | | | | | | 5 |
| Tooth | 2 | | 31 | 18 | 1 | 55 | | 202 | | | 3 | | 120 | 432 | |
| Vertebrae | | | 4 | 3 | | 8 | | | | | | | 4 | 19 | |
| Rib | | 4 | 14 | 16 | 3 | 33 | 4 | 32 | 1 | | | | 122 | 229 | |
| Scapule | | | | 1 | | 1 | | 1 | | | | | 1 | 4 | |
| Humerus | | | 3 | 1 | 3 | 7 | | | | | | | | 14 | |
| Radius | | | 1 | | | 2 | | | | | | | | 3 | |
| Ulna | | | | | | | | | 1 | | | | | 1 | |
| Carpal | | | | 1 | 1 | 8 | | 4 | | | | | | 14 | |
| Metacarpal | | | | | | 3 | | | | | | | | 3 | |
| Pelvis | | | 3 | | | | | 1 | | | | | | 4 | |
| Femur | | 1 | 2 | 1 | 1 | 6 | | 3 | | | | | | 14 | |
| Tibia | 1 | | 1 | 6 | 1 | 10 | | | | | | | | 19 | |
| Metatarsal | | | 1 | | 1 | 4 | | 1 | | | | | | 7 | |
| Metapodial | 2 | | 1 | 6 | 1 | 7 | | | | | | | 1 | 18 | |
| Tarsal | | | 1 | | | | | 1 | | | | | | 2 | |
| Phalange | 1 | | | | | 5 | | 2 | | | | | | 8 | |
| Indet | 5 | 1 | 21 | 11 | 4 | 42 | 4 | 69 | | | | | 3302 | 3459 | |
| Placa | | | | | | | | | | | | | 35 | 35 | |
| Total | 11 | 6 | 85 | 65 | 16 | 196 | 9 | 548 | 2 | 3 | 3 | 3585 | 4526 | | |

Table 3 Skeletal profiles according to MNE of the level 5 of FN3 assemblage from the 2017–2020 field seasons. See complete information in SF. The Bold entries reflected the total

| MNE | Species size level 5 | | | | | | | | | | 4 | 5 | Carniv 1 | Carniv 3 | |
|--------------|----------------------|----------|-----------|-----------|----------|-----------|--------------|--------------|--------------|----------|-----------|----------|----------|----------|--|
| | 0 | 1 | 2 | 3 | 3a | 3b | Total size 3 | % with tooth | % no tooth | | | | | | |
| Ivory | | | | | | | | | | | | 5 | | | |
| Cranial | | | 1 | 1 | | 1 | 2 | 1.6 | 2.7 | 1 | 1 | | | | |
| Mandible | | | 1 | | | 2 | 2 | 1.6 | 2.7 | | 1 | | | | |
| Tooth | 2 | | 20 | 12 | 1 | 39 | 52 | 40.9 | | | 23 | | | 3 | |
| Vertebrae | | | 2 | 1 | | 3 | 4 | 3.1 | 5.3 | | | | | | |
| Rib | | 1 | 3 | 3 | 1 | 10 | 14 | 11.0 | 18.7 | 2 | 8 | 1 | | | |
| Scapule | | | | 1 | | 1 | 2 | 1.6 | 2.7 | | 1 | | | | |
| Humerus | | | 1 | 1 | 1 | 2 | 4 | 3.1 | 5.3 | | | | | | |
| Radius | | | 1 | | | 1 | 1 | 0.8 | 1.3 | | | | | | |
| Ulna | | | | | | | | 0.0 | 0.0 | | | 1 | | | |
| Carpal | | | | 1 | 1 | 8 | 10 | 7.9 | 13.3 | | 4 | | | | |
| Metacarpal | | | | | | 3 | 3 | 2.4 | 4.0 | | | | | | |
| Pelvis | | | 1 | | | | | 0.0 | 0.0 | | 1 | | | | |
| Femur | | 1 | 1 | 1 | 1 | 4 | 6 | 4.7 | 8.0 | | 1 | | | | |
| Tibia | 1 | | 1 | 5 | 1 | 7 | 13 | 10.2 | 17.3 | | | | | | |
| Metatarsal | | | 1 | | 1 | 4 | 5 | 3.9 | 6.7 | | 1 | | | | |
| Metapodial | 1 | | 1 | 2 | 1 | 2 | 5 | 3.9 | 6.7 | | | | | | |
| Tarsal | | | 1 | | | | | 0.0 | 0.0 | | 1 | | | | |
| Phalange | 1 | | | | | 4 | 4 | 3.1 | 5.3 | | 2 | | | | |
| Total | 5 | 2 | 35 | 28 | 8 | 91 | 127 | 100.0 | 169.3 | 3 | 49 | 2 | 3 | | |

Table 4 Fragmentation patterns of the FN3 bone assemblage (levels 2, 3, 5, and 6). The Bold entires reflected the total of NISP of sample

| Taphonomic features | | Lev-2 | Lev-3 | Lev-5 | Lev-6 |
|---------------------|---|------------|------------|-------------|-----------|
| Fragmentation | Sample NISP | 100 | 107 | 4550 | 44 |
| | Bones < 3 cm | 82 | 87 | 3843 | 40 |
| | Bones 3.1–5 cm | 12 | 10 | 416 | 3 |
| | Bones > 5.1–9.9 cm | 6 | 10 | 218 | 1 |
| | Bones > 10 cm | | | 73 | |
| | % long bone with | | | | |
| | % long bone with green fracture | 60 | 50 | 41 | 100 |
| | % Long bone with dry fracture | 40 | 50 | 18.4 | |
| | % long bone with indet fracture | | | 40.6 | |
| | % degree of long bone shaft circumference | | | | |
| | < 25% | | 75 | 91.1 | 100 |
| | 26–50% | | 12.5 | 5.48 | 0 |
| | > 51% | | 12.5 | 3.42 | 0 |
| | % shaft length of long bones | | | | |
| | < 25% | | 87.5 | 95.9 | 100 |
| | 26–50% | | 12.5 | 2.72 | 0 |
| | > 51% | | | 1.4 | |

levels 3 and 5 showing evidence of these alterations, always of low or moderate intensity (Table 5). These alterations indicate that the assemblage did not experience considerable water transport and that these different waterborne alterations were produced by small sedimentary particles sliding over the bone surface during processes of site formation. Very few specimens show calcitic concretions, and surface staining by manganese or oxides, which affects around 15% of the assemblage although it has not impacted bone preservation (Table 5). Biochemical alterations, such as root-etching or rodent damage, were relatively unimportant in the FN3 assemblage.

Carnivore activity has been recorded for levels 2, 3, and 5, and if we exclude bone fragments < 2 cm, tooth-marked bones can reach up to 11% in the smaller samples (levels 2–3). Nevertheless, overall tooth mark frequencies are lower than 3%, with very few digested bones or instances of furrowing are present. Similarly, only one bone exhibited 5 or more tooth marks, suggesting that the incidence of carnivore activity at the site is low. Tooth marks are usually 2–3 mm in diameter (with only one instance reaching 5 mm), and these traces of carnivore activity are mostly found on the edges of ribs and long bones of small-, medium-, and large-sized animals (see Suppl. File).

Hominins also contributed to the accumulation and modification of the faunal assemblage, as evidenced by the presence of cut and percussion marks on bone elements. Cut mark frequencies are lower than 1% (Table 5), although they are found across all carcass sizes, including very large animals, such as hippopotami or elephantids (Table 6). The distribution patterns of cut marks show that these anthropogenic alterations appear on ribs, diaphysis of femur of very

large species, and ribs, vertebrae, and shafts of intermediate size species. Furthermore, the presence of percussion marks on long bones indicates that these bones were intentionally fractured in order to access energy-dense within-bone resources, such as marrow (Table 5).

Discussion and conclusions

The evidence reported in this study resembles the previous analyses of FN3 presented by Espigares et al. (2019). Both studies show similarly diverse taxonomic profiles with species from different ecological settings, with a predominance in the MNI of very large animals, such as elephants and hippopotami. The mortality patterns are also consistent, highlighting that the mortality profiles of sizes 1, 2, and 3 show a predominance of adult individuals, whereas larger animals present a higher percentage of infants and juveniles. Skeletal part profiles also show a similar scarcity of axial elements and an overrepresentation of cranial elements, with teeth playing a major role in this regard. The presence of bones from all skeletal portions suggests that some carcasses may have arrived complete at the site.

On the basis of the presence and distribution of cut marks, percussion marks, and tooth marks, both studies also agree that humans and carnivores had access to the meat and within-bone nutrients of several animal species at FN3. The identification of cut marks on small-, medium-, and very large-sized animals such as elephantids or hippopotami also indicate that hominins exploited multiple animal taxa. Carnivores have also left feeding traces on a wide range of

Table 5 Taphonomical alterations for FN 3

| Taphonomic characteristics | | Lev-2 | Lev-3 | Lev-5 | Lev-6 | % lev-2 | % lev-3 | % lev-5 | % lev-6 |
|---|---|----------------------|-------|-------|-------|---------|---------|---------|---------|
| | Sample NISP | 100 | 107 | 455 | 44 | | | | |
| | Sample excluding teeth and Ivory | 94 | 97 | 3821 | 37 | | | | |
| Bone surfaces | Samples with bad preservation | 68 | 16 | 1101 | 7 | 68.0 | 15.0 | 24.2 | 15.9 |
| | Samples with good preservation | 26 | 81 | 272 | 30 | 32.0 | 85.0 | 75.8 | 84.1 |
| Weathering | Weathering stage 0 | 97 | 105 | 4378 | 44 | 97.0 | 98.1 | 96.2 | 100 |
| | Weathering stage 1–2 | 2 | 2 | 162 | 0 | 2.0 | 1.9 | 3.6 | 0.0 |
| | Weathering stage 3–4 | 1 | | 10 | | 1.0 | 0.0 | 0.2 | 0.0 |
| Water alteration | Hydrolic alteration | 4 | 14 | 605 | 4 | 4.0 | 13.1 | 13.3 | 9.1 |
| | Abrasion | 4 | 10 | 293 | 2 | 4.0 | 9.3 | 6.4 | 4.5 |
| | Light stage abrasion | 2 | 5 | 222 | 2 | 50.0 | 50.0 | 75.8 | 100 |
| | Intermediate stage abrasion | 2 | 3 | 54 | | 50.0 | 60.0 | 18.4 | |
| | Intense stage abrasion | | | 16 | | 0.0 | 0.0 | 5.5 | |
| | Polishing | 3 | 5 | 154 | | 3.0 | 4.7 | 3.4 | 0 |
| | Rounding | 2 | 5 | 379 | 3 | 2.0 | 4.7 | 8.3 | 6.8 |
| | Light stage rounding | 1 | 3 | 270 | 1 | 50.0 | 60.0 | 58.2 | 33.3 |
| | Intermediate stage rounding | 1 | 1 | 116 | 1 | 50.0 | 20.0 | 25.0 | 33.3 |
| | Intense stage rounding | | 1 | 78 | 1 | 0.0 | 20.0 | 16.8 | 33.3 |
| Carnivore activity | Calcitic concretions | 1 | | 14 | | 1.0 | 0.0 | 0.3 | 0.0 |
| | Oxides (MN, FE) | 8 | 18 | 681 | 13 | 8.0 | 16.8 | 15.0 | 29.5 |
| | Trampling alterations | 2 | 2 | 99 | 1 | 7.7 | 2.5 | 3.6 | 3.3 |
| | Biochemical and root alterations | 6 | 12 | 183 | 1 | 6.0 | 11.2 | 4.0 | 2.3 |
| | Bones with rodent tooth marks | | 1 | | | | 0.9 | | |
| | Bones with carnivore tooth marks | 1 | 2 | 21 | 0 | 3.8 | 2.5 | 0.8 | 0 |
| | Bones with carnivore tooth marks (excluded bone fragments < 2 cm) | 1 | 2 | 21 | 0 | 11.1 | 11.1 | 2.6 | 0 |
| | Bones with tooth pits | 1 | 1 | 15 | | 100 | 100 | 71.4 | |
| | Bones with tooth scores | | | 10 | | | | 47.6 | |
| | Bones with punctures | | | 1 | | | | 4.8 | |
| | Bones with both pits and scores | | 1 | 3 | | | 50 | 14.3 | |
| | Digestive alterations | | | 1 | | | | | |
| | Human activity | Bones with cut marks | 1 | 2 | 22 | | 3.8 | 2.5 | 0.8 |
| Bones with cut marks (excluded bone fragments < 2 cm) | | 1 | 2 | 22 | | 11.0 | 11.0 | 2.7 | |
| Bones with peeling | | | | 1 | | | | | |
| Bones with percussion marks | | | 1 | 14 | 1 | 0.0 | 1.2 | 0.5 | 3.3 |

carcass sizes, from smaller animals such as rabbits to very large animals, including elephants.

The butchery activities inferred from the distribution patterns of cut marks (Table 6) appear to be related to evisceration and defleshing activities, which, alongside the evidence for percussion marks, suggests that hominins were accessing the meat and marrow from different carcass sizes. However, the presence of tooth marks also indicates that carnivores played a role in the alteration of the faunal assemblage at the site. These taphonomic data are all consistent with the results described by Espigares et al. (2019). In order to ascertain the temporality of carcass access, we have subsequently compared the cut and tooth mark frequencies

documented at FN3 with the results of several actualistic frameworks.

These actualistic reference frameworks were developed by different authors (see SF 2) with the aim of establishing empirically the order in which hominins and carnivores accessed animal carcasses. Carcasses of different sizes were made available to different human and carnivore agents in different experimental settings, in order to quantify the frequencies of taphonomic alterations that they generated. It was noted that the frequency and distribution of cut marks, percussion marks, and tooth marks varied depending on which agent(s) accessed the carcass first, which allowed researchers to empirically establish the relative temporality

Table 6 Cut-marked bones identified among the FN3 assemblage from the 2017–2020 field seasons

| Taxon | Species size | Skeletal bone | Function |
|------------------------------|--------------|---------------------|-----------------|
| Bovidae | 3b | Rib | Disarticulation |
| Mammalia indet | 1 | Rib | Defleshing |
| Mammalia indet | 5 | Rib | Defleshing |
| Mammalia indet | 5 | Rib | Defleshing |
| <i>Hippopotamus antiquus</i> | 5 | Femur diaphysis | Defleshing |
| Mammalia indet | 3b | Femur diaphysis | Defleshing |
| Mammalia indet | 3 | Long bone diaphysis | Defleshing |
| Mammalia indet | 5 | Long bone | Indet |
| Mammalia indet | 3b | Long bone | Indet |
| Mammalia indet | 3b | Long bone diaphysis | Defleshing |
| Mammalia indet | 3b | Long bone diaphysis | Defleshing |
| Mammalia indet | Indet | Indet | Defleshing |
| Mammalia indet | 2 | Indet | Defleshing |
| Mammalia indet | 3a | Indet | Defleshing |
| Mammalia indet | Indet | Indet | Indet |
| Indet | Indet | Indet | Indet |
| Mammalia indet | 2 | Pelvis | Defleshing |
| Mammalia indet | 5 | Pelvis | Evisceration |
| Mammalia indet | 3b | Tibia diaphysis | Indet |
| Mammalia indet | 3 | Tibia diaphysis | Defleshing |
| Mammalia indet | 3b | Tibia diaphysis | Defleshing |
| Mammalia indet | 3b | Vertebrae | Defleshing |
| Mammalia indet | 3b | Vertebrae | Defleshing |

of animal resource acquisition. This approach has generally yielded positive results in taphonomic studies of Early Pleistocene sites in Africa (Domínguez-Rodrigo, 2002; Domínguez-Rodrigo et al. 2002, 2009; Pickering et al., 2008; Pobiner, 2007; Pobiner et al., 2008; Pante, 2013; Parkinson, 2018; Yravedra et al., 2020).

Nevertheless, it is worth noting that the comparative assessment of bone surface modifications for interpreting the order of carcass intervention at FN3 using experimental or actualistic frameworks is hindered by small sample sizes (Figs. 3–7).

The very low frequencies of carnivore tooth marks documented at FN3 are not consistent with the percentage ranges generated by carnivore-hominin models (Fig. 3), with the exception of cheetah or leopard accumulations of size 1–2 animals. However, the FN3 assemblage has a considerable representation of animals > 150 kg, a size range that neither cheetahs nor leopards target, which suggests that carnivores were not the main accumulation agents at FN3 (Fig. 3).

Across all three categories of appendicular elements, tooth mark frequencies are considerably lower than those that would be expected in episodes of primary access by carnivores (Fig. 4). ULB and ILB in particular have very low tooth mark frequencies, a pattern inconsistent with the observations of carnivore feeding when they have access to the most nutritious portions of the carcasses. The same

happens when analysing the frequency of tooth marks on limb bone diaphyses: the results obtained are well below the outcomes of actualistic observations of carnivore-first models. Instead, the low tooth mark frequencies fit much better the patterns left by carnivores when they engage with carcasses after human intervention, including those instances when carcasses were initially modified by vultures (Fig. 5).

While tooth mark data seems to indicate that carnivores were not the primary agent responsible for the accumulation of the faunal assemblage at FN3, it is still necessary to conclusively prove the degree of human intervention through the analysis of the cut mark and percussion mark frequencies at the site.

When the frequencies of percussion marks left by humans are compared with the actualistic framework, the very low percentages found at FN3 do not readily fit any of the proposed models (Fig. 6), leading to a somewhat inconclusive result.

Neither do the very low cut mark frequencies seem to correspond to primary anthropogenic accumulations either (Fig. 7), resembling more closely the profiles that result from secondary hominin access to carcasses previously consumed by carnivores. Breaking down cut mark frequencies by upper, intermediate, and lower appendicular elements, ULB frequencies would match those associated with secondary access, while cut mark frequencies on diaphyses/bone shafts,

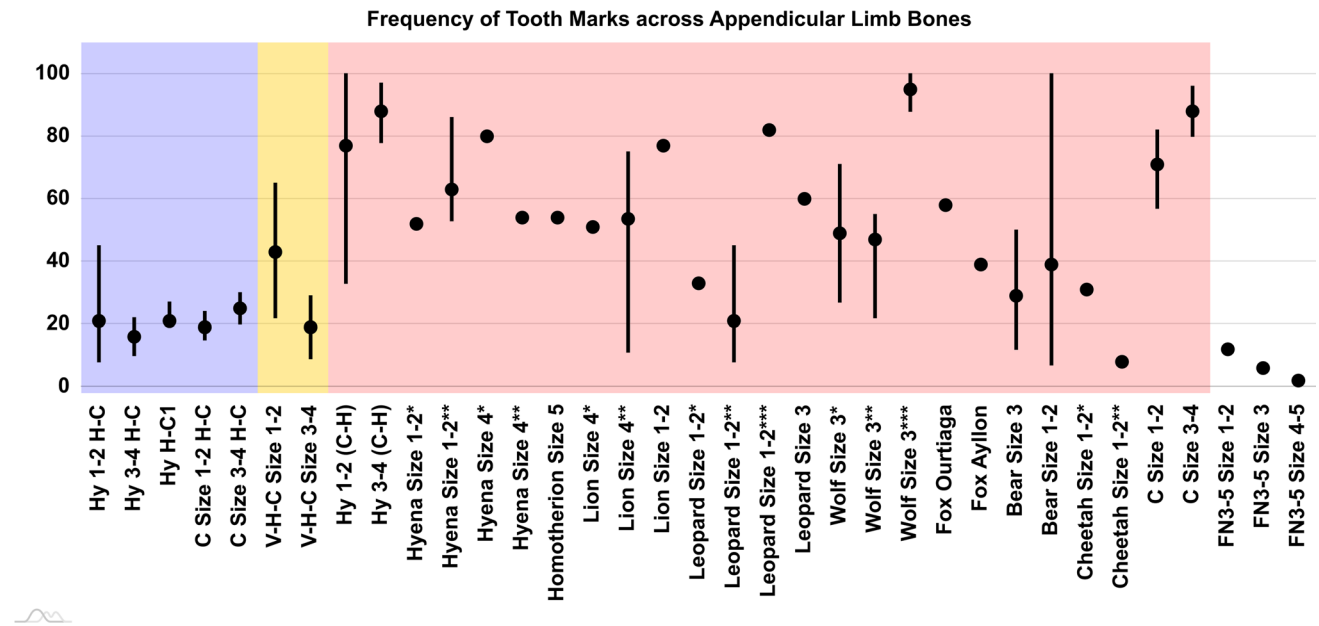


Fig. 3 Tooth mark frequencies on appendicular elements from FN3 by size classes (1–2, 3, 4–5) in relation to the actualistic framework derived from carnivore feeding behaviours documented in different contexts. The blue box highlights the range of tooth mark frequencies that carnivores tend to leave on bones during secondary scavenging activities after human abandonment of the carcasses. The

yellow box shows the tooth mark frequencies resulting from a model in which vultures accessed first the carcasses, followed by humans and then carnivores, while the red box documents the main range of tooth mark frequencies associated with primary carnivore accumulations. See Suppl. file 2 for the full bibliographic details of the relevant sources

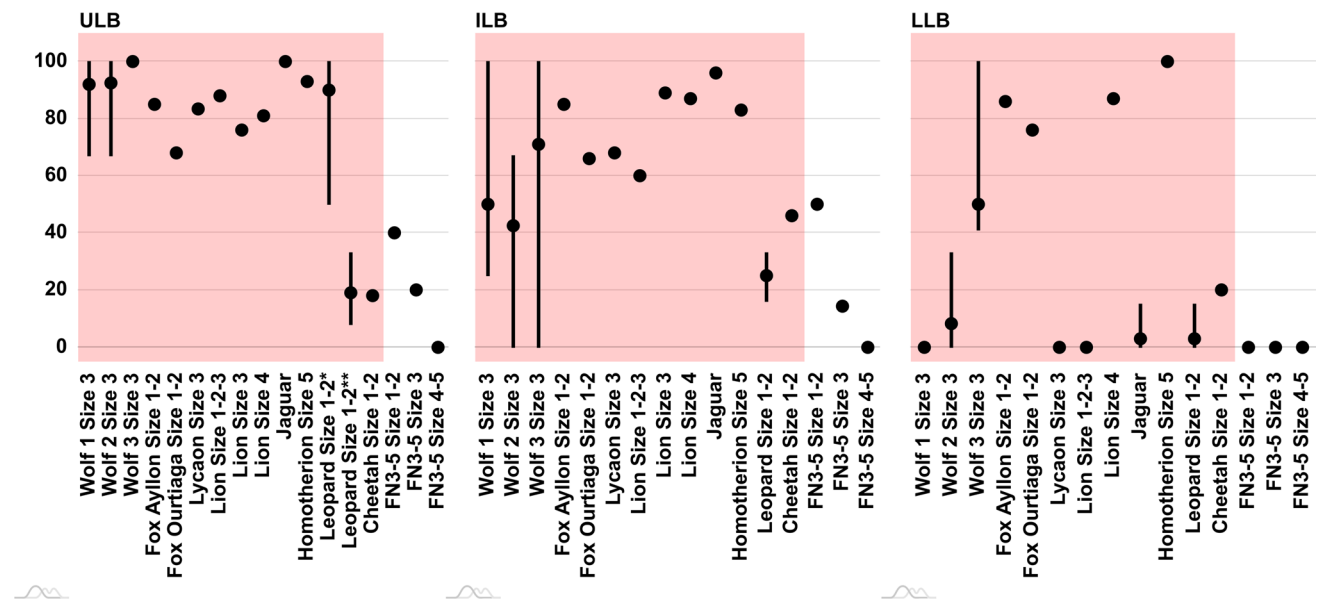


Fig. 4 Tooth mark frequencies on appendicular remains from FN3 on animal size classes 1–2, 3, and 4–5, in relation to the actualistic framework derived from carnivore feeding behaviours documented in different contexts. ULB refers to tooth marks on upper limb bones,

such as humeri and femoral remains, ILB refers to intermediate limbs (tibiae, radii), while LLB stands for lower limb bones (i.e. metapodials). See suppl. file 2 for more information on the comparative samples and their full bibliographic details

intermediate, and lower elements are inconclusive since they overlap with models of both primary and secondary accesses (Fig. 8). Consequently, the taphonomic evidence currently

available does not allow us to determine with certainty the temporality of hominin access to animal carcasses at FN3,

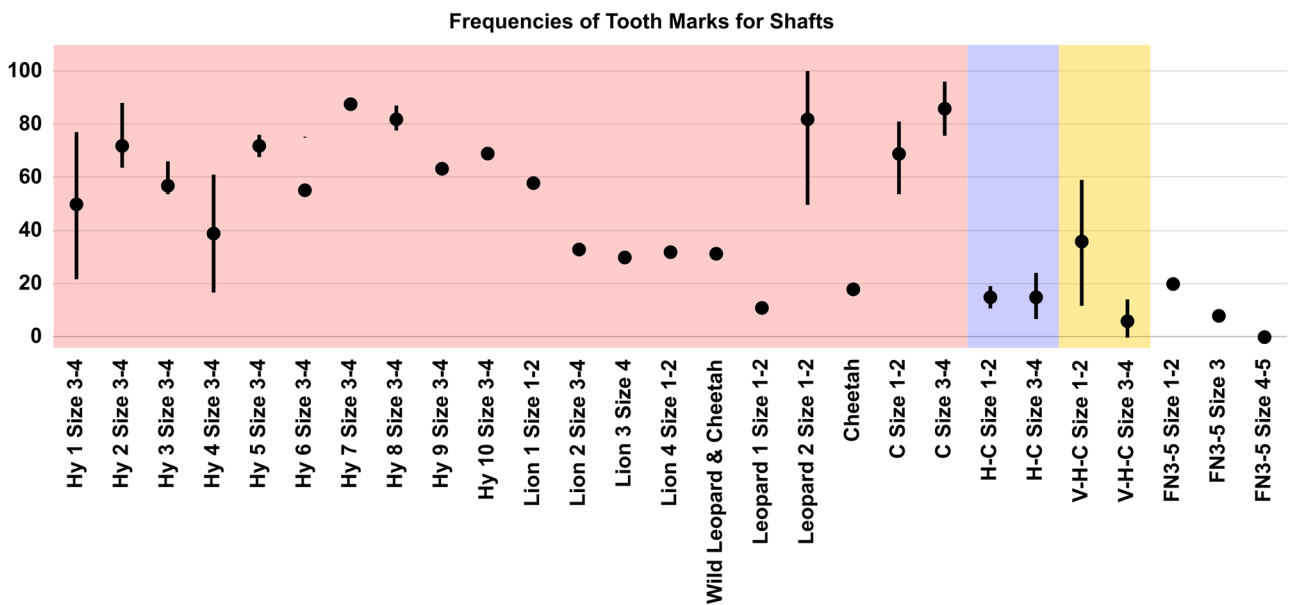
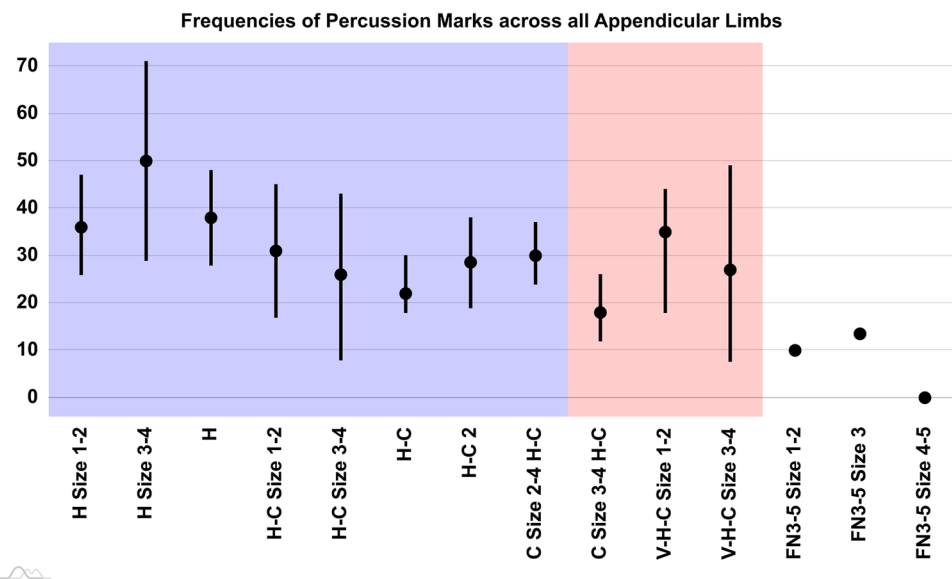


Fig. 5 Tooth mark frequencies on limb bone diaphyses from FN3 on animal size classes 1–2, 3, and 4–5, in relation to the actualistic framework derived from carnivore feeding behaviours documented in different contexts. The blue box highlights the range of tooth mark frequencies that carnivores tend to leave on bones during secondary scavenging activities after human abandonment of the carcasses. The

yellow box shows the tooth mark frequencies resulting from a model in which vultures accessed first the carcasses, followed by humans and then carnivores, while the red box documents the main range of tooth mark frequencies associated with primary carnivore accumulations. See the Suppl. file 2 for the full bibliographic details of relevant sources

Fig. 6 Percussion mark frequencies on appendicular elements from FN3 on the basis of carcass size (1–2, 3, and 4–5) in relation to a comparative actualistic framework. The blue box represents the percussion mark frequencies generated by humans when they have early access to carcasses, and the red box encompasses the percussion mark frequencies in contexts of secondary access. See Suppl. File 2 for bibliographic details of the reference samples employed



a problem of ambiguity further compounded by the small sample sizes of bone surface modifications.

With respect to the temporality of carcass access, the comparative assessment of cut mark, percussion mark, and tooth mark frequencies in the FN level 5 bone assemblage with actualistic framework returned ambiguous and inconclusive results. The low frequency of cut marks (Fig. 7 and 8) resemble more a pattern of secondary hominin access,

while the low frequency of tooth marks does not match the expectations of primary carnivore access (Figs. 3–5).

When analysing the distribution and inferred functionality of cut marks (Table 6, Fig. 8), we note their presence on the diaphyses of long bones such as the femur or tibia (Figs. 9, 10, 11), as well as on axial elements such as ribs or the pelvis (Fig. 11). This pattern would be consistent with defleshing and evisceration activities on carcass elements

Fig. 7 Cut mark frequencies on appendicular elements from FN3 (level 5) on the basis of carcass size (1–2, 3, and 4–5) in relation to the comparative framework generated by several experimental and actualistic studies. The blue box represents the cut mark frequencies generated by humans when they have early access to carcasses, the yellow box corresponds to cut mark frequencies when human access followed the presence of vultures but preceded carnivore access, while the red box encompasses cut mark frequencies from contexts of secondary access. See suppl. File 2 for the full bibliographic details of the comparative samples employed

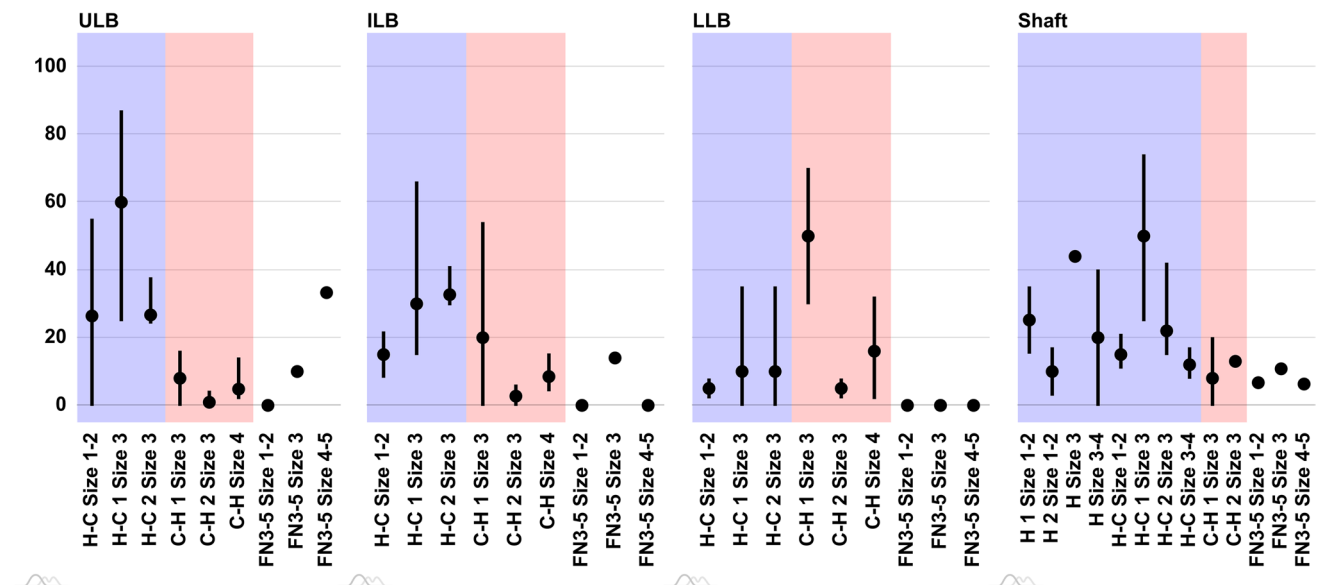
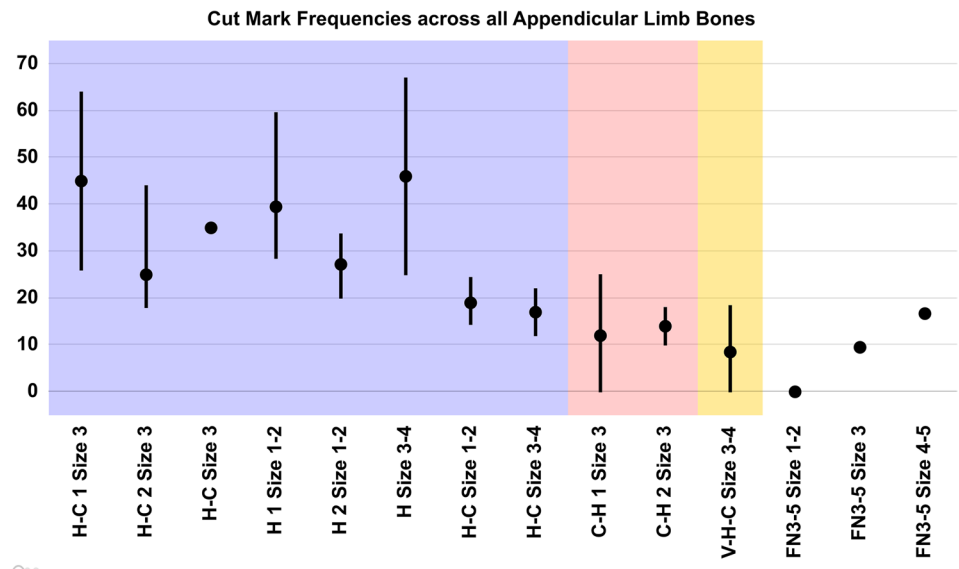


Fig. 8 Cut mark frequencies on appendicular remains from FN3 (level 5) on animal size classes 1–2, 3, and 4–5. ULB refers to tooth marks on upper limb bones, such as humerii and femoral remains, ILB refers to intermediate limbs (tibiae, radii), while LLB stands for lower limb bones (i.e. metapodials). The blue box represents cut mark

frequencies left by humans in early carcass access contexts, while the red box shows cut mark frequencies in contexts of secondary access. Cut mark frequencies on diaphyses are shown on the right hand side of the graph. See suppl. file 2 for more information on the comparative samples and their full bibliographic details

with high nutritional values, which may indicate early access to at least some of the carcasses, rather than secondary scavenging. This is especially relevant when considering actualistic reports of carnivore feeding patterns to first consume the visceral packages. This pattern is documented among a wide range of wild carnivores, such as felines (Schaller, 1972; Blumenschine, 1986; Blumenschine & Cavallo, 1992), canids (Mech, 1970; Stahler et al, 2006; Yravedra et al., 2011), and hyenas (Kruuk, 1972; Blumenschine, 1995; Faith, 2007).

At the same time, the low frequencies of anthropogenic traces do not allow to conclusively establish the nature of carcass acquisition strategies. The sample analysed in the present study thus experiences similar limitations than the work conducted by Espigares et al. (2019): both have few bones with anthropogenic and carnivore alterations, and thus neither can determine in which order did humans and carnivores access prey carcasses at the site. As such, there is little evidence to support previous models of hominin acquisition of animal resources at Orce consisting in the secondary

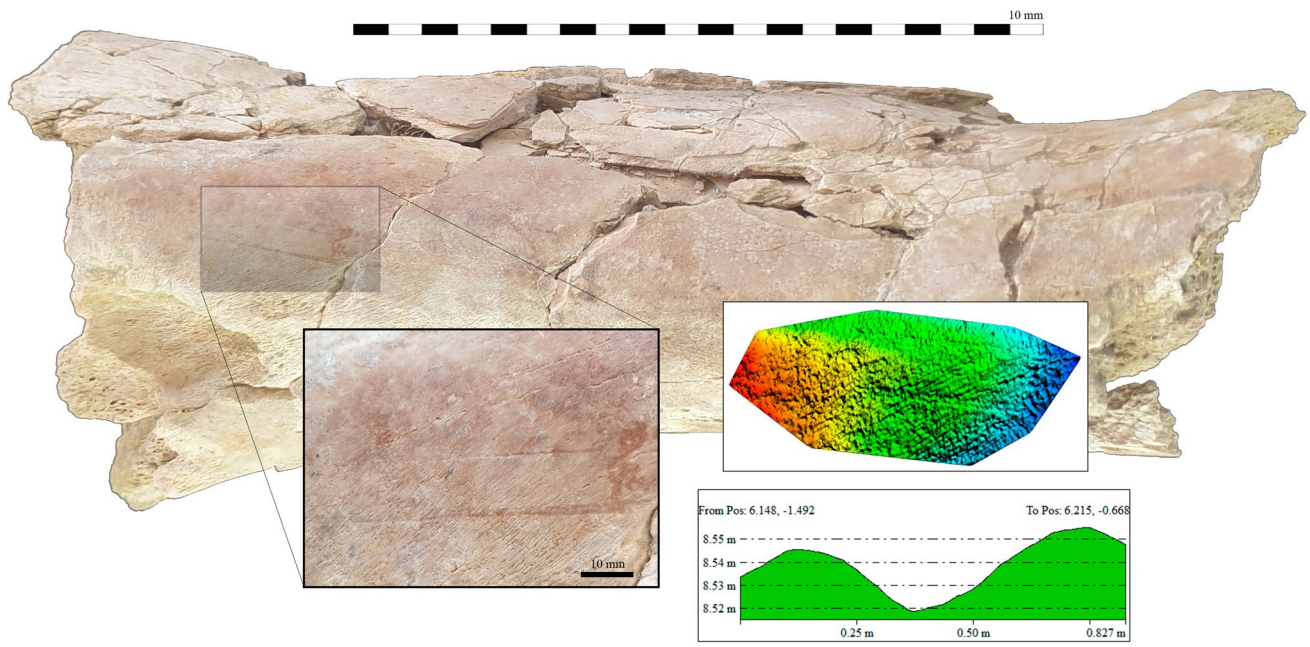


Fig. 9 Shaft of femur of hippopotamus with cut marks in FN3 level 5

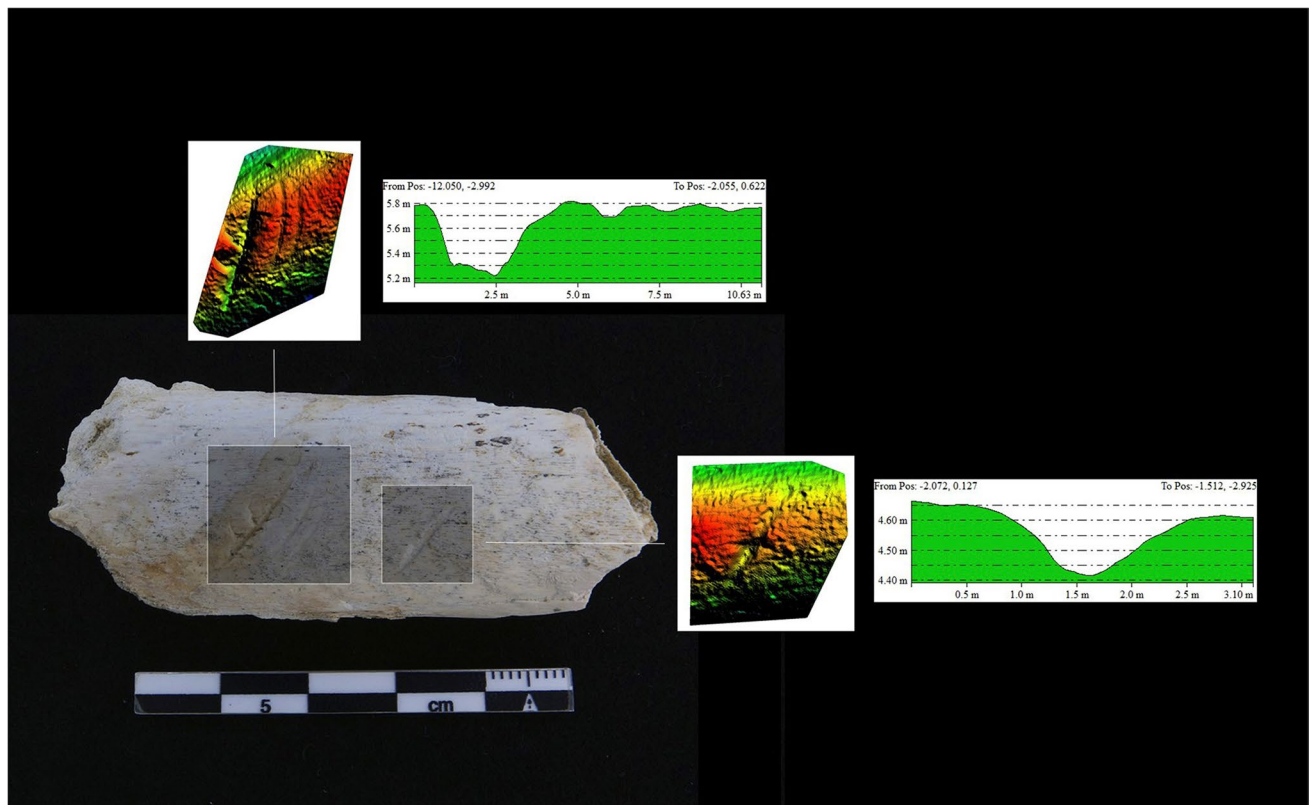


Fig. 10 Shaft with cut marks and 3D modelled of FN3 level 5



Fig. 11 Several cut marks of FN3 level 5 on animal size level 3, pelvis of animal size level 5, and indeterminate fragment of level 5

exploitation of carcasses left by large felids, and prior to the intervention of the giant hyena.

Several authors, including Martínez-Navarro and Palmqvist (1995), Palmqvist et al. (1996, 1999, 2005, 2011), Arribas and Palmqvist (1999, 2002), Espigares et al. (2013, 2019), and Rodríguez-Gómez et al. (2016), suggest, on the basis of skeletal part profiles, mortality patterns, and taphonomic evidence, that large felids, such as *Megantereon whitei*, would have had primary access to animal carcasses at FN3. They assume that *M. whitei* individuals would have only accessed part of their prey's visceral package, since the size and fragility of their canines may have prevented them from consuming much meat (Palmqvist et al., 1996, 1999, 2005, 2011; Espigares et al., 2013; Rodríguez-Gómez et al.,

2016, according to Van Valkenburgh and Ruff, 1987). This circumstance would provide hominins with opportunities to scavenge sizeable chunks of muscle tissue before giant hyena individuals accessed the carcasses. This passive scavenging scenario might help explain the cut mark distribution patterns and the scarcity of tooth marks that is observed by Espigares et al. (2019) documented at FN3.

However, there are multiple lines of evidence that prompt a reconsideration of the interpretations proposed by Martínez-Navarro and Palmqvist (1995), Palmqvist et al. (1996, 1999, 2005, 2011), Arribas and Palmqvist (1999, 2002), Espigares et al. (2013, 2019), and Rodríguez-Gómez et al. (2016) regarding the *Megantereon*-Hominins-*Pachyroculta* model of carcass acquisition at FN3.

Several authors have already shown in different publications that skeletal parts and mortality profiles are generally inconclusive when modelling the behaviour of humans and carnivores, since the resulting outcomes can experience issues of equifinality (see discussion in Domínguez-Rodrigo (2002)).

From a taphonomic perspective, it is worth bearing in mind that there are no empirical studies of the feeding behaviour of *M. whitei*, which precludes reliable interpretations and inferences regarding their role in the alteration of fossil assemblages. The only available taphonomic study of an accumulation altered by machairodonts is described by Marean and Ehrhardt (1995). While the assemblage corresponds to *Homotherium* rather than *M. whitei*—which may have generated slightly different patterns—the high frequencies of bone damage, particularly in relation to those documented at FN3, are noteworthy, indicating that some sabretooth felids were capable of inflicting considerable damage to the bones of their prey. Moreover, Harstone-Rose (2008, 2011) has argued that *Megantereon* would have had carcass processing behaviours no more hypercarnivorous than extant felids, which have been shown to generate considerable tooth mark damage (see e.g. Rodríguez-Alba et al. 2019 for jaguars; Brain 1969 and Arriaza et al. 2019 for leopards; or Arriaza et al. 2016, Haynes & Klimowicz 2015, and Haynes & Hutson 2020 for lions). Furthermore, bio-mechanical studies of sabretooth dentition suggest that these carnivores would have had no issue making contact with bone surfaces when they were feeding on animal carcasses (Bryant et al., 1995; Harstone-Rose, 2008; 2011; Desantis et al. 2012). Therefore, the teeth of *Megantereon whitei* were neither as fragile nor as inefficient as Van Valkenburgh and Ruff (1987) and Palmqvist et al. (1996, 1999, 2005, 2011) have proposed.

Regarding the action of the giant hyena, the low tooth mark frequencies documented at FN3 are in stark contrast with the damage generated by hyenas when they are the primary agent of carcass modification documented by different authors (Kruuk 1972; Blumenshine, 1986; Villa & Bartram,

1996; Villa & Soresi, 1998; Faith, 2007; Domínguez-Rodrigo et al., 2015; Haynes & Klimowicz, 2015; Fernández-Jalvo & Andrews, 2017; Haynes & Hutson 2020). This divergence suggests that the action of giant hyena at FN3 was likely more limited than previously envisioned.

Espigares et al. (2013) describe a *M. meridionalis* carcass surrounded by lithic industry and giant hyena coprolites at FN3, which indicate the presence of these carnivores at the site. Nevertheless, no tooth marks or anthropogenic marks were observed on the elephantid bones, thus not conclusively proving the interaction of humans or carnivores with the proboscidean carcass.

Cut marks demonstrating direct hominin engagement with the remains have been found on Middle Pleistocene elephant carcasses (e.g. Yravedra et al. 2010), and this absence of taphonomic alterations is also in stark contrast with actualistic reports of carnivore engagement with elephant carcasses, which tend to present a high number of tooth marks (Haynes & Klimowicz, 2015; Haynes & Hutson 2020). Therefore, this spatial association of lithic finds and coprolites in association with these elephant carcasses may have been fortuitous, resulting from independent episodes that coalesced into a palimpsest through complex site formation processes. Such coincidental associations of stone tools and faunal remains are not infrequent in the Palaeolithic record. At Bois Roche, lithic artefacts were found inside a hyena den, product of fluvial transportation (Villa & Bartram, 1996; Villa & Soresi, 1998). Likewise, associations of lithic artefacts with proboscidean remains are not uncommon (Gaudzinski et al 2005). Nevertheless, many of these associations have been shown to be the result of spatial processes unrelated to human subsistence strategies (Yravedra et al., 2014; Haynes et al 2020).

On the basis of the evidence documented at FN3, there are several important inferences that can be made regarding the role of hominins and carnivores at the site. The low tooth mark frequencies at the site (Table 5, Figs. 3–5) suggest that carnivore impact on the FN3 bone assemblage was relatively unimportant. The scarcity of digested bones, the absence of diaphysary cylinders, bones with pit tooth marks > 5 mm, or individual bones with more than 5 tooth marks all suggest that the role of the giant hyena was rather limited in the formation of the FN3 faunal assemblage. In the future, a geometric morphometric assessment of tooth marks (cf. Aramendi et al., 2017; Courtenay et al., 2021) could provide valuable insights into the specific carnivore(s) that played a role in the accumulation and/or alteration of the bone assemblage at the site.

Regarding the role played by hominins, it is worth highlighting the considerable degree of bone sample fragmentation (Table 4) and the presence of cut marks associated with butchery practices such as disarticulation, defleshing, and evisceration (Table 6, Figs. 9–11), as well as percussion

marks derived from marrow extraction (Table 5). These patterns suggest that hominins had recurrent access to meat and marrow resources at FN3.

The lithic evidence described by Toro-Moyano et al. (2003, 2009, 2011, 2013) and Barsky et al. (2010, 2013, 2015) is also in support of these interpretations. The lithic analyses at FN 3 show a predominance of small-sized single flakes of flint and limestone obtained from local sources, and some choppers (Toro-Moyano et al., (2003, 2009, 2011, 2013; Barsky et al. 2010, 2013, 2015). These heavy-duty tools may be associated with percussive activities oriented in part to the fragmentation of bones, as suggested by the existence of bones with green fractures (Table 4) and percussion marks (Table 5). Furthermore, use-wear analyses of FN3 flakes conducted by Toro-Moyano et al. (2003) documented their use in butchery activities. Recent experimental studies have shown that small flakes are suitable for defleshing activities, even on very large carcasses, such as proboscideans (Starkovich et al., 2021; Marinellu et al., 2021). Lower Palaeolithic sites with small, simple flake lithic assemblages associated with cut-marked remains are indeed very common (see Marinellu et al., 2021 for a more in-depth discussion).

Based on these taphonomic arguments, the possibility that hominins at FN3 had early access to meat from fresh carcasses prior to carnivore engagement with the remains cannot be dismissed. However, low cut mark frequencies in relation to actualistic models (Figs. 6–8) hinder the robusticity of the conclusions that can be established regarding the timing of hominin carcass access at FN3. It is also worth considering the possibility that hominins may have followed different carcass procurement strategies on the basis of animal size (small, medium, large, or very large), given the diverse range of animal carcass sizes at FN3 level 5 presenting evidence of anthropogenic alterations.

A convergence of different processes at the site is also plausible, with some animal deaths by natural causes, several episodes of primary and/or secondary hominin access to prey, and sporadic carnivore feeding bouts. This hypothetical scenario would explain the low cut mark frequencies while also accounting for the small number of tooth marks documented in the faunal assemblage.

Nevertheless, until the limited evidence is complemented by a revision of the materials from previous excavations and sample sizes are enlarged with further newly excavated remains, it will not be possible to conclusively define what role did humans play in the accumulation of the faunal assemblage at FN3. Likewise, more advanced statistical techniques may be able to shine new light on the nature of this assemblage. Additionally, the incorporation of new technologies applied to the study of cut marks could help us develop new approaches. For example, recent approaches may allow the identification of which raw materials and

types of lithic implements were employed in the butchery activities documented at the site (Courtenay et al., 2019; Linares-Matás et al., 2019; Maté-González et al., 2019; Yravedra et al., 2017, 2019).

Lastly, the current study provides further zooarchaeological data on hominin subsistence strategies in the Early Pleistocene settlement of the European subcontinent. The present study demonstrates the complexities and issues inherent to the study and interpretation of Early-Middle Pleistocene assemblages, given the limitations imposed by the representativity of faunal samples. Nevertheless, FN3 joins other Early Pleistocene sites older than 1 Ma across Europe where hominins had access to animal carcasses, such as Kozarnika (Sirakov et al., 2010), Trilika (Vislobokova et al., 2020), or Pirro Nord (Cheheb et al., 2019), although there are still some unresolved questions related to the temporality of carcass access or whether hominins exhibited different acquisition strategies on the basis of carcass size.

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