

## 2. HOMININS, MAMMOTHS, SABER-TOOTHES AND GIANT HYENAS IN THE EARLY PLEISTOCENE OF THE BAZA BASIN (SE SPAIN)

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### ABSTRACT

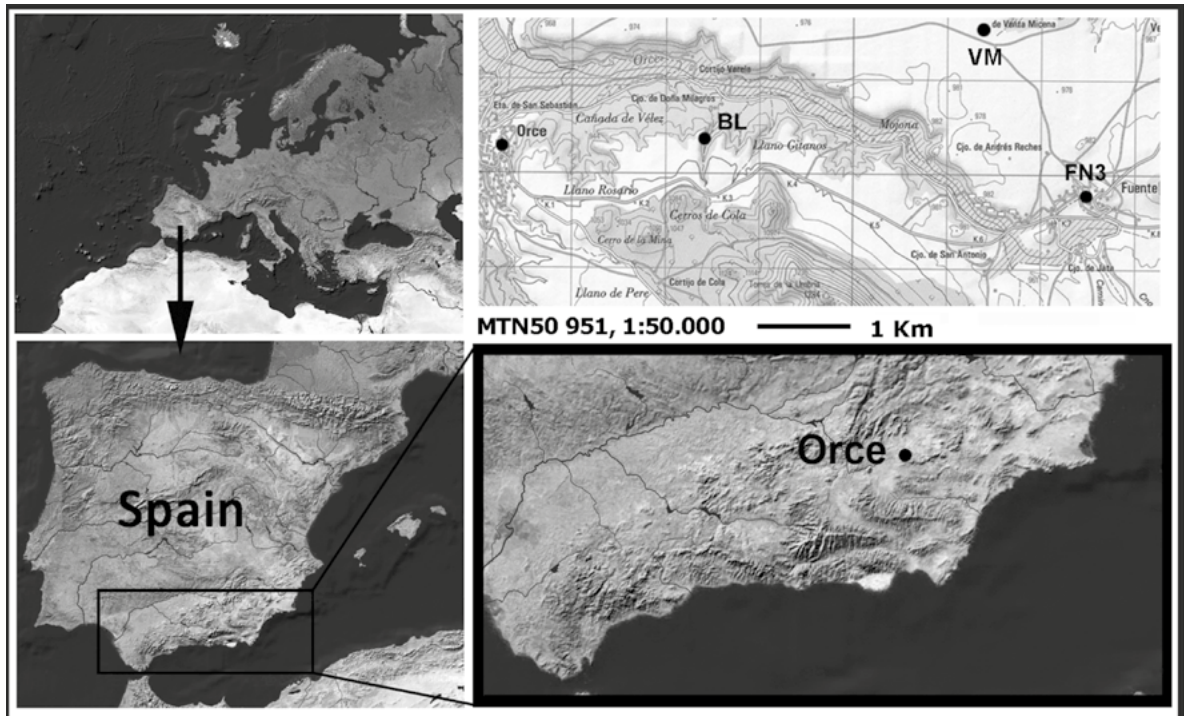
The Baza Basin preserves an exceptional Plio-Pleistocene palaeontological record, which includes the earliest evidence of human presence in western Europe, dated to ~1.4 Ma, coming from the sites of Barranco León and Fuente Nueva-3, in the vicinity of the town of Orce. In this geographical region, early *Homo* coexisted and likely competed with the giant, short-faced hyena *Pachycrocuta brevirostris* for the exploitation of prey carcasses abandoned by saber-tooth cats (*Megantereon* and *Homotherium*). The presence of these hypercarnivorous felids favored the surviving of both scavenging species (*Homo* and *Pachycrocuta*), as they exploited their prey to a lesser extent than the living pantherine

felids. In this context, proboscideans were an exploited food resource, as evidenced by the presence of a partial skeleton of the mammoth *Mammuthus meridionalis* in Fuente Nueva-3, which was surrounded by lithic artifacts and hyena coprolites. This association suggests that both hominins and hyenas fed on the mammoth carcass. Some paths for elucidating their pattern of access to these resources are also discussed.

### 2.1 INTRODUCTION

The Baza Basin (SE Spain; Fig. 2.1) is part of the Guadix-Baza Depression, a post-orogenic Neogene–Quaternary intramontane basin that was





**Figure 2.1:** Geographic location of Venta Micena, Barranco León and Fuente Nueva-3. Sources: software MapCreator 2.0 free edition and topographic map from MTN50, 951 Instituto Cartográfico Nacional.

subject to endorheic conditions from the latest Miocene to the Middle Pleistocene, which resulted in a wide swampy and lacustrine setting. The entire sedimentary depression experienced during the Early Pleistocene intense hydrothermal activity in an active tectonic system. This is evidenced by the presence of many hot springs in the basin, some of them currently active (García-Aguilar et al., 2014, 2015). The contribution of thermal waters helped to maintain a relatively permanent water table with warm and stable temperatures throughout the year. This allowed the development of a well-diversified mammalian community, whose fossil remains are found in many palaeontological sites with chronologies that range from the latest Miocene to the Middle Pleistocene.

The early Pliocene is well represented in the Baza Basin, especially at the Ruscinian site of Baza-1, where two proboscidean species are present, the mammutid *Mammuth borsoni*, and the gomphothere *Anancus arvernensis*. These megaherbivores are associated with other large mammals, including *Stephanorhinus cf. jeanvireti*, *Hipparion* sp., *Alephis*

sp., cf. *Antelope* and Cervinae indet. In addition, there are microfaunal remains of 16 species of rodents, lagomorphs and insectivores, as well as reptiles, amphibians, fishes and birds (Piñero et al., 2017; Ros-Montoya et al., 2017).

The Early Pleistocene is well documented in many sites of the basin, especially in its north-eastern sector, in the vicinity of the town of Orce (Moyà-Solà et al., 1987; Martínez-Navarro, 1991; Arribas and Palmqvist, 1998; Palmqvist et al., 2011; García-Aguilar et al., 2014; Martínez-Navarro, 2018). Among these sites, Venta Micena (VM), Barranco León (BL) and Fuente Nueva-3 (FN-3) are particularly remarkable for the quality and quantity of their fossil record.

VM is a palaeontological site with an estimated chronology of ~1.6–1.5 Ma, which has provided a rich assemblage of large mammals of late Villafranchian age with an excellent preservation state. The faunal assemblage includes skeletal remains of 21 taxa of large (>10 kg) mammals. Taphonomic analysis has evidenced the involvement of the giant, short-faced hyena *Pachycrocuta*

*brevirostris* in the bone accumulating process (see details in Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Espigares, 2010; Palmqvist et al., 2011).

BL and FN-3 are two localities that provide some of the earliest records of human presence in western Europe (Espigares et al., 2019). The age of these sites has been estimated by a combination of biostratigraphy and the U-series/ESR dating method at  $1.43 \pm 0.38$  Ma for BL and  $1.19 \pm 0.21$  Ma for FN-3 (Duval et al., 2012; Toro-Moyano et al., 2013), and there is also an age estimation of  $1.50 \pm 0.31$  Ma for FN-3 derived from cosmogenic nuclides (Álvarez et al., 2015). In addition, the absence of suids suggests that both sites are older than 1.22 Ma (Martínez-Navarro et al., 2015). The evidence of human presence in BL and FN-3 includes the finding of a human deciduous tooth at BL (D Level), rich lithic Oldowan tool assemblages at both sites and abundant bones that show anthropogenic modifications, including cut and percussion marks related to carcass processing (Toro Moyano et al., 2011, 2013; Titton et al., 2018; Espigares et al., 2019). The faunal assemblages of these sites include 18 species of large mammals, 15 species of small mammals and 23 herpetofaunal taxa; some avian fossils have also been discovered (Table 2.1).

The presence of mammoths, saber-tooth felids and hyenas in the three sites, as well as the evidence of hominin occurrence at BL and FN-3, make these sites ideal case studies for their interactions during the Early Pleistocene in western Europe.

## 2.2 HOMININS

Early members of the genus *Homo* dispersed in the middle latitudes of Eurasia at  $\sim 2.0$  Ma. Out of Africa, the earliest hints of human presence come from Shangchen (China) and Riwat (Pakistan), based on the presence of lithic artifacts, dated to  $\sim 2.12$  Ma and  $\sim 1.9$  Ma, respectively. Slightly younger, but more abundant, are the findings from Dmanisi in Caucasus, where a rich assemblage of Old-

owan tools and skeletal remains of large mammals, including five hominin skulls, dated to  $\sim 1.8$  Ma have been discovered (Lordkipanidze et al., 2013 and references therein). At  $\sim 1.6$  Ma hominins are present in Majuangou III (Nihewan) and Gondwangling (Lantian), both in China, as well as in Mojokerto and Sangiran (Java, Indonesia) (Zhu et al., 2015, 2018). Later on, they arrive in western Europe, where their settlements are dated to  $\sim 1.5$ – $1.4$  Ma.

Evidence of early human presence in Europe is recorded in several sites, including Level TE9, Sima del Elefante in Atapuerca, Spain ( $\sim 1.2$  Ma), Pirro Nord in Italy (1.7–1.3 Ma), and Lézignan-la-Cèbe (1.3–1.1 Ma), Vallonnet (1.2–1.1 Ma) and Pont-de-Lavaud ( $\sim 1.1$  Ma) in France (Carbonell et al., 2008; Michel, et al., 2017; Cheheb et al., 2019). In this context, the two localities in the vicinity of the town of Orce, BL and FN-3, are very interesting, as they provide some of the earliest records of human presence in western Europe (Martínez-Navarro et al., 1997; Oms et al., 2000; Espigares et al., 2013, 2019; Toro-Moyano et al., 2013).

Insights on the subsistence strategies of the populations of early *Homo* suggest that their diet included probably a broad spectrum of resources, where meat and other animal products (e.g., bone marrow and viscera) constituted perhaps an important fraction of the daily caloric intake (Stanford, 1999; Bunn, 2007; Hardy, 2010; Bunn et al., 2017; Hardy et al. 2017; Prado-Nóvoa et al., 2017). The evolutionary trend in humans towards an increase of encephalization in parallel to a decrease in the size of the post-canine teeth is usually envisioned as evidence of the progressive adaptation of *Homo* to a higher quality, more carnivorous and more easily digestible diet than in other hominins, such as the australopithecines (Aiello and Wheeler, 1995; Bunn, 2001; Dunsworth and Walker, 2002; Jiménez-Arenas et al., 2012; Espigares et al., 2019). The adaptation to meat eating, which probably arose in Africa at the origin of the genus *Homo* at  $\sim 2.6$  Ma, allowed the expansion of the dietary niche of these early populations (Speth,

TAXON	VENTA MICENA	BARRANCO LEÓN	FUENTE NUEVA-3	REFERENCE
Aves indet.		x	x	Espigares, 2010
<i>Discoglossus cf. jeanneae</i>		x	x	Blain et al., 2016
<i>Pelobates cultripes</i>		x	x	Blain et al., 2016
<i>Bufo bufo</i>		x	x	Blain et al., 2016
<i>Epidalea calamita</i>		x		Blain et al., 2016
<i>Bufo</i> sp.		x	x	Blain et al., 2016
<i>Hyla</i> sp.		x		Blain et al., 2016
<i>Pelophylax cf. perezi</i>	x	x	x	Blain et al., 2016
Anura indet.		x	x	Blain et al., 2016
<i>Chalcides cf. bedriagae</i>			x	Blain et al., 2016
cf. <i>Chalcides</i>		x		Blain et al., 2016
<i>Timon cf. lepidus</i>	x	x	x	Blain et al., 2016
<i>Dopasia</i> sp.		x	x	Blain et al., 2016
<i>Ophisaurus</i> sp.		x		Blain et al., 2016
<i>Coronella girondica</i>		x	x	Blain et al., 2016
<i>Natrix maura</i>	x	x	x	Blain et al., 2016
<i>Natrix natrix</i>		x	x	Blain et al., 2016
<i>Rhinechis scalaris</i>		x	x	Blain et al., 2016
<i>Malpolon monspessulanus</i>		x	x	Blain et al., 2016
Colubridae		x	x	Blain et al., 2016
Ophidien indet.		x		Blain et al., 2016
<i>Emys cf. orbicularis</i>		x		Blain et al., 2016
<i>Mauremys cf. leprosa</i>		x		Blain et al., 2016
<i>Testudo</i> sp.	x	x	x	Blain et al., 2016
<i>Asoriculus gibberodon</i>	x	x	x	Furió, 2010
<i>Sorex minutus</i>		x	x	Furió, 2010
<i>Sorex</i> sp.		x	x	Furió, 2010
<i>Crocidura</i> sp.		x	x	Furió, 2010
<i>Erinaceus cf. praeglacialis</i>		x	x	Furió, 2010
<i>Galemys</i> sp.	x	x	x	Furió, 2010
<i>Mimomys savini</i>		x	x	Agustí et al., 2010
<i>Allophaiomys ruffoi</i>	x			Agustí et al., 2010
<i>Allophaiomys lavocati</i>		x	x	Agustí et al., 2010
<i>Allophaiomys</i> sp.		x	x	Agustí et al., 2010
<i>Castillomys rivas</i>	x	x	x	Agustí et al., 2010
<i>Apodemus sylvaticus</i>	x			Agustí et al., 2010
<i>Apodemus flavicollis</i>		x		Agustí et al., 2010
<i>Apodemus mystacinus</i>	x		x	Agustí et al., 2010
<i>Oryctolagus cf. lacosti</i>	x	x	x	Agustí et al., 2010

<i>Prolagus</i> sp.	x	x		Agustí et al., 2010
<i>Hystrix</i> sp.	x	x	x	Agustí et al., 2010
<i>Homotherium latidens</i>	x			Martínez-Navarro, 1991
<i>Megantereon whitei</i>	x			Martínez-Navarro and Palmqvist, 1995
<i>Panthera gombaszoegensis</i>	x			Pons-Moyà, 1987
<i>Lynx</i> cf. <i>pardinus</i>	x		x	Boscaini et al., 2015
<i>Pachycrocuta brevirostris</i>	x	x	x	Pons-Moyà, 1987
<i>Lycaon lycaonoides</i>	x	x	x	Martínez-Navarro and Rook, 2003
<i>Canis mosbachensis</i>	x	x	x	Martínez Navarro, 2002
<i>Vulpes</i> cf. <i>praeglacialis</i>	x	x	x	Pons-Moyà, 1987
<i>Ursus etruscus</i>	x	x	x	Torres Pérez-Hidalgo, 1992; Medin et al., 2017
<i>Pannonictis</i> cf. <i>nestii</i>	x	x	x	Martínez Navarro et al., 2010
<i>Meles meles</i>	x	x	x	Madurell-Malapeira et al., 2011
<i>Mammuthus meridionalis</i>	x	x	x	Ros-Montoya et al., 2010
<i>Stephanorhinus hundsheimensis</i>	x	x	x	Lacombat, 2010
<i>Equus altidens</i>	x	x	x	Guerrero-Alba and Palmqvist, 1997; Alberdi, 2010
<i>Equus sussenbornensis</i>		x	x	Alberdi, 2010
<i>Hippopotamus antiquus</i>	x	x	x	Alberdi and Ruiz-Bustos, 1985
<i>Bison</i> sp.	x	x	x	Moyà-Solà, 1987
<i>Hemibos</i> cf. <i>gracilis</i>	x			Martínez Navarro et al., 2011
<i>Soergelia minor</i>	x			Moyà-Solà, 1987
<i>Praeovibos</i> sp.	x			Moyà-Solà, 1987
<i>Hemitragus albus</i>	x	x	x	Crégut-Bonnoure, 1999
<i>Ammotragus europaeus</i>			x	Moullé et al., 2004; Martínez-Navarro et al., 2010
<i>Praemegaceros</i> cf. <i>verticornis</i>	x	x	x	Abazzi, 2010
<i>Metacervoceros rhenanus</i>	x	x	x	Abazzi, 2010

**Table 2.1:** Vertebrate assemblages from Venta Micena (VM), Barranco León (BL) and Fuente Nueva-3 (FN-3).

1989; Bunn and Ezzo, 1993; Milton, 1999, 2000) and, as a consequence, their dispersal outside of Africa.

Herbivorous animals rely on plant biomass in the ecosystems, which ultimately depends on climate. Tropical latitudes are productive through the entire year with different kinds of plants, which in the past hominins could consume. However, when our ancestors arrived in the middle latitudes of Eurasia, they faced more seasonal conditions, where they relied possibly more on ani-

mal resources, especially during the cold season, when fruits and leaves were less available (Speth and Spielmann, 1983; Martínez-Navarro, 2010; Martínez-Navarro et al., 2014). Meat consumption by early *Homo* is evidenced by the finding in several Early Pleistocene localities of cut marks, percussion marks and fractures on bones, mostly belonging to large mammals, highlighting the importance of animal food for these populations.

Evidence of butchery can be confidently traced back to the origin of our genus or even earlier. In

Africa, the oldest cut marks associated with stone tools are recorded at Gona (Ethiopia) and are dated to 2.6–2.5 Ma (Semaw et al., 1997). Additionally, there are a number of Early Pleistocene localities from East and North Africa that preserve evidence of ancient anthropic activity, including Bouri (~2.5 Ma; de Heinzelin et al., 1999), Ain Boucherit (2.4–1.9 Ma; Sahnouni et al., 2018), Koobi Fora (~1.9 Ma; Bunn, 1997), FLK Zinj (Olduvai Gorge, ~1.8 Ma; Bunn and Kroll, 1986) and Ain Hanech (1.8 Ma; Sahnouni et al., 2013). However, the record of such evidence is not frequent. In Europe, the presence of cut marks and intentionally broken bones in BL and FN-3 provide key information on the dietary behavior of the first human settlers of western Europe (Espigares et al., 2013, 2019). Evidence of human presence in FN-3 and BL is well documented by the occurrence of rich assemblages of Oldowan artifacts (Turq et al., 1996; Martínez-Navarro et al., 1997), which include small-sized flakes (usually <2 cm), as well as cores and debris, made by flint and to a lesser extent by limestone (Toro-Moyano et al., 2011; Tilton et al., 2018). These artifacts are associated to skeletal remains of large mammals (Table 2.1), of which a number preserve evidence of anthropogenic damage, such as cut marks (incisions, scrapes, sawing marks and chop marks) and percussion marks, related to the exploitation of carcasses for obtaining meat, fat and marrow (Espigares et al., 2019).

A subsistence strategy that included the consumption of animal resources obtained from the scavenging of ungulate carcasses, partially defleshed and abandoned by saber-tooth cats, has been proposed for the Early Pleistocene hominin populations that inhabited the Baza Basin (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Martínez-Navarro, 2004, 2010; Martínez-Navarro et al., 2014; Palmqvist et al., 2005, 2007, 2011; Espigares et al., 2013, 2019; Rodríguez-Gómez et al., 2016, 2017). This interpretation is based on the technological features of the lithic artifacts, which make it difficult to conceive that these populations had

a direct impact on medium-to-large and very large ungulate prey using their small-sized Oldowan flakes (Blumenschine and Pobiner, 2007). Moreover, a scavenging behavior is supported by a mathematical model that estimates the meat that was available for the members of the carnivore guild, including the genus *Homo*, which in turn allows to evaluate the sustainability of the community of secondary consumers. After modelling three scenarios, the results obtained suggested a passive scavenging behavior as optimal for this population (Rodríguez-Gómez et al., 2016). However, this does not exclude other strategies of acquisition of animal foods, such as the opportunistic hunting of smaller mammals, the power scavenging of the prey of hypercarnivores (i.e., kleptoparasitism) or the scavenging of animal carcasses died from natural causes.

### 2.3 SABER-TOOTH CATS

The predator guild in the Early Pleistocene of Europe was dominated by two species of saber-tooth cats, *Megantereon whitei* and *Homotherium latidens* (Felidae, Machairodontinae). Martínez-Navarro and Palmqvist (1995, 1996) proposed that the arrival of *M. whitei* from Africa was the key factor that allowed the first hominin dispersal in Eurasia. This predator had a number of craniodental features, such as its relatively enlarged sabers and powerful forearms, as well as the extreme reduction of the premolar teeth and the short coronoid process (which indicates an increase in gape angle at the expense of a reduction in bite force), that suggest a capability to kill efficiently ungulate prey larger in relation to its own size in contrast to the extant pantherine felids of similar size. However, its highly specialized dentition for meat slicing suggests that this predator consumed only the soft tissues of its prey, leaving thus significant amounts of flesh on the prey carcasses and all within-bone nutrients. Compared to the living large felids, which are less hypercarnivorous than the saber-tooth cats, this would result

in greater quantities of animal resources available for the scavengers, including hominins and the giant, short-faced hyenas (Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999; Martín-Serra et al., 2017; Palmqvist and Arribas, 2001; Palmqvist et al., 2003, 2007, 2008a, b, 2011; Ripple and Van Valkenburgh, 2010; Espigares et al., 2013, 2019; Martínez-Navarro, 2010; Martínez-Navarro et al., 2014; Van Valkenburgh et al., 2016).

The survival of saber-tooth cats in Europe helps to explain the persistence of Oldowan tools for nearly one million years more than in Africa (Palmqvist et al., 2005), as the sharp flakes were fully appropriate for scavenging the ungulate carcasses, partially defleshed by these felids, while the cores would have been useful for heavy-duty activities, such as bone-fracturing for accessing their marrow content (Plummer, 2004).

This scene changed during the Middle Pleistocene with the arrival of pantherine cats, which exploited their prey more intensively than saber-tooths. The new conditions implied a substantial change for the scavengers, the loss of a regular source of scavengable animal foods and the replacement of the Oldowan technology by the more derived Acheulean tools (Arribas and Palmqvist, 1999).

## 2.4 PACHYROCUTA BREVIROSTRIS

The Plio-Pleistocene short-faced hyena *Pachyrocuta brevirostris* was the largest bone-cracking carnivore mammal that ever existed. This giant hyena shows massive limbs with shortened distal bones (especially evident in the length of the tibia in relation to the length of the femur), and a heavy, powerfully built mandible with robust and well-developed premolars. The features of the postcranial skeleton suggest a less cursorial life style for *P. brevirostris* than the modern spotted hyena *Crocuta crocuta* as a result of its adaptation towards greater power and stability for dismembering animal carcasses and transporting large portions of them to

the denning area (Turner and Antón, 1996), as evidenced in VM (Palmqvist and Arribas, 2001; Palmqvist et al., 2011).

The analysis of the preservation state of the skeletal elements modified by the giant hyenas evidences their highly specialized bone-cracking behavior, in agreement with the scavenging niche deduced for this species from the taphonomic analysis at VM. This site was interpreted as an accumulation by hyenas of portions of prey of flesh-eating carnivores in the surroundings of their maternity den (Palmqvist et al., 1996). The activity of *P. brevirostris* inserted a number of taphonomic biases in the bone assemblage. These resulted from the selective transport of ungulate carcasses and body parts, as a function of their body size, and also from the preferential consumption of those skeletal parts with lower density and greater marrow contents. This allows to define sequences of bone consumption for the different anatomical elements (i.e., a proximodistal sequence for humerus and tibia, a distoproximal sequence for radius and metapodials, and a less clearly defined pattern of consumption in the case of femur, which involves the fracturing of both bone epiphyses). Moreover, the high abundance of femoral diaphyses, and distal fragments of humeri and tibiae compared to other elements, is related with their marrow contents, which are greater than in the case of metapodials. The latter explains why these bones are more frequently preserved as complete elements (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001; Espigares, 2010; Palmqvist et al., 2011).

The bone accumulations made by extant striped hyenas (*Hyaena hyaena*) show a similar preservation completeness of the ungulate skeletal remains to that recorded at VM (Skinner et al., 1980; Kerbis-Peterhans and Horwitz, 1992; Leakey et al., 1999) and this basic pattern applies to some extent also for those of spotted hyenas (Sutcliffe, 1970). This reveals an optimization of the benefit/cost ratio in the pattern of bone consumption by both extant and extinct bone-cracking hyenas. The dietary habits of *Pachyrocuta*

may have been more similar to those of the brown (*Hyaena brunnea*) and striped hyenas, whose subsistence relies mainly on carrion, including a high percentage of bones, as evidenced by the huge accumulation of bones preserved at VM, and also by the relative dimensions of the bone-cracking premolars and carnassials (Palmqvist et al., 2008b). Moreover, in VM the taphonomic evidence suggests that the hyenas scavenged selectively the prey hunted by the hypercarnivorous saber-tooths and the painted dog *Lycaon lycaonoides* (Palmqvist et al., 1996). In summary, *P. brevirostris* exhibited a combination of body size and craniodental features, which suggests a mode of life based more on scavenging compared to the spotted hyenas (Palmqvist et al., 2011).

This interpretation, however, may have some problems. Striped and brown hyenas rely heavily on carrion (Rieger, 1981; Mills, 1982). Their postcranial skeleton is more lightly built than the spotted hyena one, owing to their need to prospect great distances in search of scavengeable carcasses. However, in the case of *P. brevirostris*, the large and robust body and the shortened distal limb segments represented probably a disadvantage for this mode of life. A plausible explanation for the strict scavenging behavior in this species is that *P. brevirostris* pursued other predators, for example *Megantereon whitei*, and exploited their prey acting as a kleptoparasite (Palmqvist et al., 1996, 2011; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001).

## 2.5 MAMMOTHS AND THEIR INTERACTIONS WITH HOMININS AND HYENAS

The Baza Basin preserves one of the best Plio-Pleistocene records of proboscideans in Europe. Four species are documented: *Mammot borsoni* and *Anancus arvernensis*, and two mammoth species, *Mammuthus meridionalis* and *M. trogontherii* (Ros-Montoya, 2010). Moreover, in the nearby basins of Guadix and Granada, *Palaeoloxodon an-*

*tiquus* and *Mammuthus primigenius*, are also respectively recorded (Ros-Montoya, 2010).

*Mammot borsoni* and *A. arvernensis* appear together in the Ruscinian site of Baza-1, dated to 4.5–4.0 Ma (Ros-Montoya et al., 2017). The latter species is also documented in the sites of Huéscar 3 and Canal de San Clemente (late Pliocene). Concerning the genus *Mammuthus*, *M. trogontherii* is recorded in the Middle Pleistocene site of Cúllar-Baza-1, whereas *M. meridionalis* is the best recorded proboscidean in the Baza Basin; remains of this species are present in at least eight sites, including VM, BL, FN-3, Barranco del Paso, Cañada de Vélez, Huéscar-1, Zújar and Cortes de Baza (Early Pleistocene) (Ros-Montoya et al., 2010, 2017, 2018).

Although there are several localities in the Baza Basin, where human presence has been documented, evidence of coexistence of hominins with proboscideans is recorded to date in only four of them: BL, FN-3, Huéscar-1 and Cúllar Baza-1. Among them, the site of FN-3 deserves a special attention, because it has provided remains of at least 10 *M. meridionalis* individuals of different ontogenetic ages, including neonates, juveniles, prime adults, adults and senile individuals (Ros Montoya, 2010).

One of the most remarkable findings in this site is a partial skeleton of an old female *M. meridionalis* individual, buried in a thick layer of fine sands that were deposited during a short sedimentary event. The skeleton preserves in anatomical connection the vertebral column, the pelvis, a scapula, some ribs and the mandible. In contrast, the fore- and hindlimbs, and the cranium are absent (Espigares et al., 2013). During the excavation of the skeleton, 17 lithic artifacts and 34 carnivore coprolites surrounding it were unearthed from the same stratigraphic level (Fig. 2.2).

The spatial and stratigraphic association of coprolites and flakes suggest that both hominins and hyenas fed possibly on the mammoth carcass. Although cut and tooth marks are absent from the preserved bones, their absence is not strange. Experiments on elephant bones show that butchery traces are rare and, in particular, cut marks on

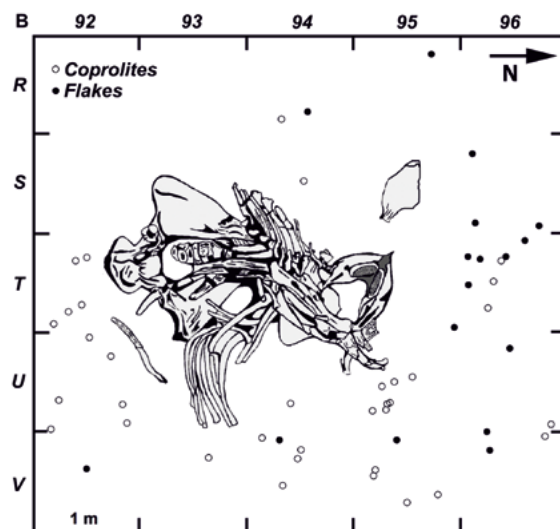


fossil proboscideans bones are scarce due to the thickness of the periosteum cover (Crader, 1983; Shipman and Rose, 1983; Haynes, 1991; Villa et al., 2005; Yravedra et al., 2010; Rabinovich et al., 2012). Similarly, evidence of carnivore tooth marks is also scarce in elephant bones (Haynes, 1988). For this reason, the absence of marks of biological origin, including those made by hominins and carnivores, does not imply that this type of resource was only used occasional. In fact, there are a number of sites in which human consumption of elephant carcasses has been proposed based on the presence of lithic tools associated to proboscidean remains with or without anthropogenic modifications on proboscidean bones, including Barogali in Djibuti (Chavaillon et al., 1987; Berthelet and Chavaillon, 2001), Olduvai in Tanzania (Leakey, 1971), Gombore II in Ethiopia, Mwanganda's Village in Malawi (Clark and Haynes, 1970), Revadim Quarry in Israel (Rabinovich et al., 2012), Notarchirico and la Polledrara di Cecanabbio in Italy (Piperno and Tagliacozzo, 2001; Mussi and Villa, 2008; Santucci et al., 2016), or Barranc de la Boella (Mosquera et al., 2015), Áridos and Torralba (Villa et al., 2005), and FN-3 in Spain (Espigares et al., 2013). In addition, the presence of elephant remains in caves, such as Bolomor cave in Spain, Ma'anshan cave in China and Spy cave in Belgium (Zhang et al., 2010; Blasco et al., 2013; Germonpré et al., 2014; Blasco and Fernández Peris, this volume), constitutes undisputed evidence of transport of selected anatomical portions of proboscideans by hominins.

At FN-3, flakes and coprolites surround the mammoth carcass and partly overlap, although both distributions are displaced (Fig. 2.2): the lithic artifacts are slightly more distant from the mammoth carcass than the coprolites, and most of them group in the front area of the skeleton; in contrast, the coprolites show a more homogeneous distribution around the mammoth, although they tend to concentrate on the right and back sides of the skeleton. These distributions were statistically tested (Espigares et al., 2013), and evidenced that

coprolites and artifacts do not distribute randomly around the carcass.

An additional evidence that reinforces the argument that hyenas fed on the mammoth carcass is the color of these coprolites, which are darker than others unearthed in the site. This indicates that they were produced when the hyenas ate large quantities of meat and grease (Matthews, 1939; Bearder, 1977). In this regard, it is interesting to keep in mind that a spotted hyena can ingest one third of its body mass in only one meal (Kruuk, 1972).



**Figure 2.2:** Partial skeleton of *Mammuthus meridionalis* from Fuente Nueva-3, and spatial distribution of coprolites and lithic artifacts surrounding it (modified from Espigares et al., 2013).

## 2.6 DISCUSSION AND CONCLUSIONS

Europe was characterized by a marked seasonality during most of the Pleistocene, with cooler and drier conditions than those of tropical Africa. For this reason, the availability of large carcasses constituted a critical resource for species with scavenging behavior, including the two major agents responsible for modifying and accumulating the skeletal remains of large mammals during this period: the giant, short-faced hyena *Pachycrocuta brevirostris* and early *Homo* (Turner, 1990, 1992; Turner and Antón, 1998; Arribas and Palmqvist, 1999). In this setting, the two

species of saber-tooth cats (*Homotherium latidens* and *Megantereon whitei*) recorded in Early Pleistocene European assemblages, represented a fundamental component of the trophic chain, as their kills probably retained great amounts of flesh given their highly specialized dentition, thus opening broad opportunities for the scavengers (Martínez-Navarro and Palmqvist, 1996; Palmqvist et al., 2007).

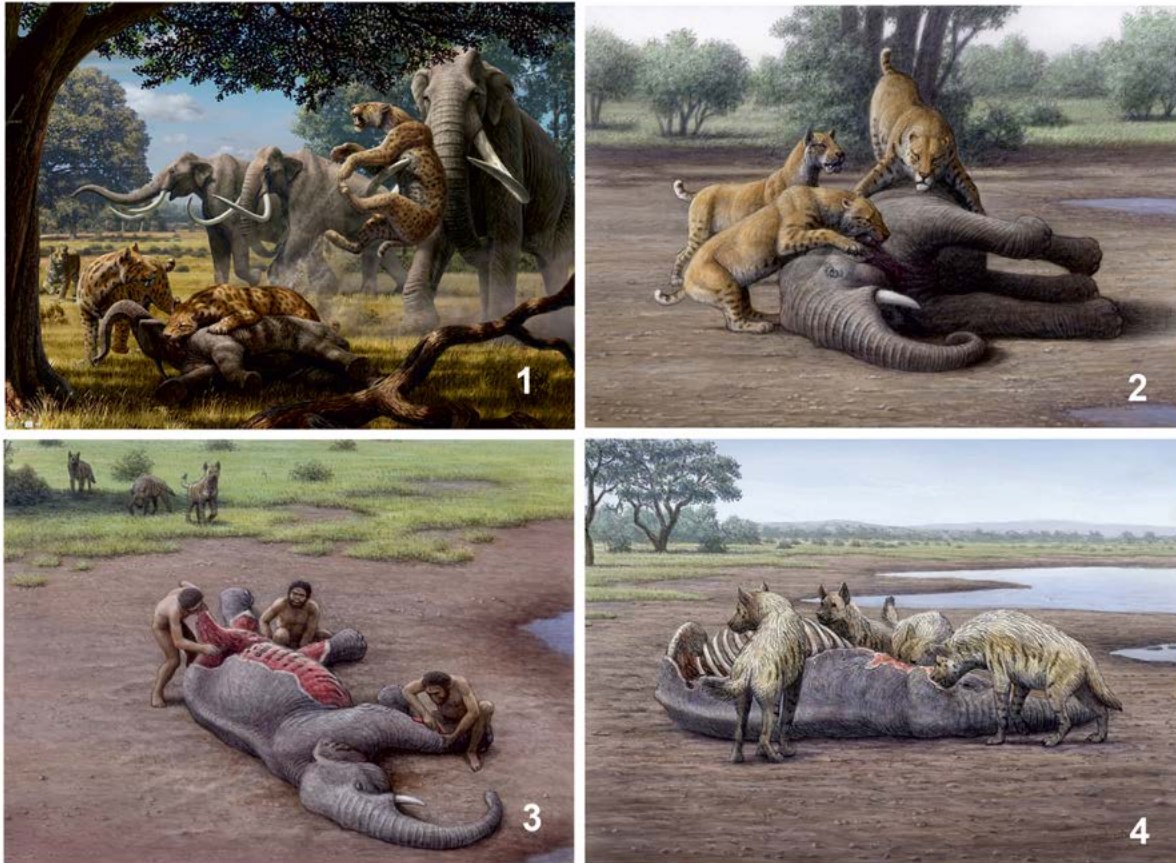
In this context, the mammoth carcass from FN-3 described above represents possibly the first documented evidence of direct competition between *Homo* and *Pachyrocuta* for access to scavengeable resources (Espigares et al., 2013). The data obtained in the analysis of the spatial distribution of the lithic artifacts and coprolites that surround this skeleton, as well as the absence of some anatomical parts, such as the limbs and the cranium, allow us to speculate on the sequence of access of hominins and hyenas to the mammoth remains.

We hypothesize that hominins arrived first, probably favored by their most diurnal foraging habits, in contrast to the preferably nocturnal lifestyle of hyenas. This probably gave them a time lapse sufficient to avoid a direct confrontation with the giant hyenas, given that their body size and technological skills would hardly have allowed them to succeed in this situation. In addition, stone-throwing by hominins could have helped them in a fateful encounter with the hyenas. This speculative scenario has been suggested by Ferring (2011) for Dmanisi (Georgia), based on the great amount of allochthonous cobbles recovered at this site. This reasoning could apply also to FN-3, because abundant limestone cobbles are present at the site that could have been transported by hominins (Espigares et al., 2013). In addition, the time elapsed between the death of the mammoth and its consumption by the hominins should not have been very long, because the human digestive system is not adapted to consume rotten meat, whereas hyenas do not require this condition (Jones et al., 2016).

After their arrival to the mammoth carcass, the available evidence suggests that hominins probably dismembered and transported the limbs to another place. Experimental studies demonstrate that after the meat has been removed, one person can easily detach an elephant limb (Haynes, 1991: p. 185). Moreover, Figure 2.2 shows that some coprolites are placed in the areas that were presumably covered by the limbs of the mammoth, when the carcass was complete with all skeletal elements in anatomical connection, which reinforces our interpretation of their arrival to the carcass after the hominins.

The cranium and tusks are absent, and no cranial or ivory fragments have been found in the level where the mammoth was discovered. For this reason, it is not clear what happened to these elements. The absence of the atlas and part of the axis could be interpreted as evidence of detachment of the cranium, and the mandible would have been also disarticulated after the detachment of the masseter muscles for extracting the tongue. After that, the cranium could have been transported to a safer place for accessing the resources within it, since the proboscidean head bears a considerable amount of edible tissues, including the brain, the trunk, the temporal gland and the edible fat inside the air cavities that divide the cranium (Byers and Ugan, 2005; Shoshani et al., 2006; Agam and Barkai, 2016). After this, the hyenas probably exploited the rest of the carcass, composed mainly of the axial skeleton (Fig. 2.3).

This scenario changed in the transition from the Early to the Middle Pleistocene, which is known as the Mid-Pleistocene Revolution, when a faunal turnover took place. The extinction of *Megantereon* and other felids, such as the European jaguar (*Panthera gombaszoegensis*), the European cougar (*Puma pardoides*) and the giant cheetah (*Acinonyx pardinensis*), was preceded by the arrival of the modern pantherine cats, such as lions (*Panthera leo*) and leopards (*Panthera pardus*). Probably these new felids exploited their kills more in depth than the saber-tooths, which implied the loss of a regular source of prey carcasses for the scaven-



**Figure 2.3:** Sequence of interactions during the exploitation of the carcass of *Mammuthus meridionalis*. **1**, Reconstruction of hunting of mammoth calves by a saber-tooth pack (in this case, a juvenile of the North American *Mammuthus columbi*, preyed upon by the saber-tooth cat *Smilodon fatalis*). Hunting of mammoth calves by *Homotherium latidens* has been evidenced by isotopic analysis of bone collagen at Venta Micena (Orce, Baza Basin, SE Spain), a site in which the remains of juveniles of *Mammuthus meridionalis* are well represented (Palmqvist et al., 2008a, b). **2**, Hunting of an individual of *Mammuthus meridionalis* by *H. latidens*. Although there is no evidence for this interaction, the only carnivore able to subdue a megaherbivore of this size was this saber-tooth; however, there is always the possibility that the female mammoth of FN-3 died from starvation, as suggested by its highly worn third molar teeth. **3**, Scavenging of the mammoth carcass by the hominins. **4**, Scavenging by the hyenas. Drawings kindly provided by Mauricio Antón; images 1 and 2 from Antón (2013); images 3 and 4 from Espigares et al. (2013).

gers. In this new setting, the fate of the giant hyena, constrained by its highly specialized anatomy and a strict scavenging behavior, was extinction (Palmqvist et al., 2007, 2011).

In the case of the Middle and Late Pleistocene hominins, their further technological developments and new hunting techniques ensured that proboscideans continued to be an important source of food (Konidaris and Turloukis, this volume), in addition as well of the use of their skeletal elements for other tasks (e.g., tusks and bones for dwelling structures) is well documented (Byers and Ugan, 2005; Demay et al. 2012; Iakovleva et al., 2012).

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