The Early Pleistocene assemblages of large mammals from Orce (Baza Basin, SE Spain) : an example of reciprocal illumination between taphonomy and paleoecology

Paul Palmqvist, M. Patrocinio Espigares

Departamento de Ecología y Geología, Facultad de Ciencias, Universidad de Málaga

1 Introduction

Orce is placed in the northeastern sector of the Guadix-Baza depression, South East Spain. This region preserves abundant Early Pleistocene localities with mammalian remains, including the Late Villafranchian (late Early Pleistocene, Calabrian) paleontological site of Venta Micena, which has been dated by biostratigraphy at 1.6-1.5 Ma [1, 2]. This site has provided a record of $>$ 17 000 fossils of large mammals unearthed from a surface of around 370 m^2, although there are more than a million fertile square meters with the potential to be excavated in the future. In addition, there are two archaeopaleontological sites, Barranco León-D and Fuente Nueva-3. The latter have provided the oldest evidence of human presence in Europe, including the finding of huge lithic assemblages of Oldowan (Mode 1) tradition, abundant cut marks on large mammals bones, a deciduous human tooth in Barranco León-D [3] and a partial elephant skeleton surrounded by flint flakes and hyena coprolites in Fuente Nueva-3 [4]. According to the results of the combined U-series / ESR dating method [3, 5] and an age estimate obtained from cosmogenic nuclides for Fuente Nueva-3 [6], these sites are slightly younger (*ca.* 1.4 Ma) than Venta Micena. Huge fossil assemblages of Early Pleistocene large mammals have been unearthed from the three sites. Taxonomically, there are some minor differences between Venta Micena, on the one hand, and Barranco León-D and Fuente Nueva-3, on the other, which mainly concern the record of bovids and, to a lesser extent, of equids (Table 1). As discussed below, the

main differences between the three assemblages involve the degree of preservation of skeletal elements and the relative abundance of bone parts.

Table 1 – Faunal list of Venta Micena, Barranco León and Fuente Nueva-3 in Orce [7, 8, 9, 10, 11, 12, 12, 13, 14, 15, 16, 17]. The numbers between brackets indicate MNI counts based on deciduous teeth for juveniles (left) and permanent teeth for adults (right). BM: estimated body mass, in kg [18, 19].

Order	**Species**	**BM**	**VM**	**BL**	**FN-3**
Carnivora	*Homotherium latidens*	200	(0/2)	?	(0/1)
	Megantereon whitei	100	(0/3)	(0/1)	?
	Panthera gombaszoegensis	100	(0/1)		
	Lynx cf. *pardinus*	18	(0/2)	(0/1)	(0/1)
	Pachycrocuta brevirostris	110	(9/9)	(0/1)	(0/3)
	Lycaon lycaonoides	30	(1/8)	(0/1)	(0/3)
	Canis mosbachensis	12	(1/8)	(0/1)	(0/2)
	Vulpes cf. *praeglacialis*	5	(0/2)	(0/2)	(0/3)
	Ursus etruscus	300	(1/3)	(0/1)	(0/4)
	Pannonictis sp.	5	(0/1)	(0/1)	(0/3)
	Meles meles	12	(0/1)	(0/1)	(0/1)
Proboscidea	*Mammuthus meridionalis*	6000	(4/1)	(0/1)	(8/2)
Perissodactyla	*Stephanorhinus hundsheimensis*	1000	(4/3)	(0/3)	(2/5)
	Equus altidens	350	(51/40)	(6/13)	(6/22)
	Equus sussenbornensis	565		(1/3)	(1/5)
	Equus altidens/sussenbornensis			(0/4)	(3/8)
Artiodactyla	*Hippopotamus antiquus*	3200	(2/3)	(2/6)	(2/4)
	Hemibos sp. cf. *gracilis*	300	(0/1)		
	Bison sp.	450	(0/1)	(1/4)	(2/8)
	Bison sp.+ *Hemibos* sp. cf. *H. gracilis*		(23/28)		
	Praeovibos sp.	315	(0/1)		
	Soergelia minor	225	(4/16)		
	Hemitragus albus	75	(2/14)	(0/3)	(1/8)
	Ammotragus europaeus	135		(0/1)	(0/1)
	Praemegaceros verticornis	385	(26/30)	(1/5)	(0/6)
	Metacervocerus rhenanus	95	(9/24)	(2/7)	(4/5)

2 An overview on the Early Pleistocene localities of Orce

2.1 Venta Micena

Venta Micena was discovered in the northeastern sector of the Baza basin during the late seventies and systematic excavations of the site started in the early eighties, continuing until the present decade. Chronologically, the site is situated in the Matuyama magnetic epoch and, more specifically, in the 1r2r chron between Jaramillo and Olduvai. It belongs to MNQ-2 biozone, which is characterized by the presence of *Allophaiomys pliocaenicus*, with an estimated age of 1.6-1.5 Ma.

Systematic excavations of this site have concentrated on Quarry III, although other parts of the fertile stratum have been occasionally excavated during the last decades. This quarry shows a very high density of fossils, which may reach up to 100 elements per squared meter, although the mean density is close to 50 fossils/m^2. The assemblage unearthed is basically composed of large mammal remains, mostly isolated teeth and bones of the appendicular skeleton of large sized species [20].

During the last decades, a number of skeletal elements from the assemblage, particularly skull cap VM-0, have been tentatively ascribed to the genus *Homo,* which has generated strong debate and controversy in the paleoanthropological community [2, 21, 22]. However, the paleobiological record of VM is exceptional, making it one of the most spectacular sites of the Quaternary of Europe.

Currently, most efforts are being undertaken in a new excavation area, Quarry IV, but in this paper we shall focus on the results obtained in the taphonomic study of the assemblage unearthed from Quarry III.

Six major lithological units can be distinguished from bottom to top in Venta Micena [23, 24, 25]. The fertile level is located in unit C, which thickness ranges from 2.3 to 3.4 m. It is composed of lutitic limestones that correspond to the level "Venta Micena 1", which locally shows sandy lutites at its base. Overlying it, there is a bed of micrite limestones that preserve the large mammal remains and is know as the VM stratum [26]. This stratum is 80-120 cm thick, stands out topographically in the ravines of the region and can be followed along 2.5 km. It is composed of 90-98% micrite limestone and is formed by two beds precipitated in a lacustrine system, which are separated by a 4-15 mm thick caliche paleosoil or hardpan.

The lower bed corresponds to a first lacustrine stage and its thickness varies between one third and half the stratum. It is azoic in vertebrate fossils and is composed of micrite with 5-20 cm thick carbonate nodules of edaphic origin, which preserve shells of freshwater mollusks (*e.g.*, *Melanoides tuberculata*, an eurythermal species that colonizes a wide range of biotopes). During this stage, micrite was precipitated in a shallow (< 10 m) and well-oxygenated water sheet not subject to eutrophic conditions, as indicated by the absence of pyrite and carbonate facies rich in organic matter [25]. The paleosoil is sub-parallel to the bedding plane and evidences the lowering of the water table in the lake. This resulted in emerged zones (approx. 4 km width), as evidenced by the presence of mud cracks and root marks, with small freshwater ponds (< 1 m depth, 2-20 m diameter) and swampy marginal zones that surrounded

the shallow lacustrine areas of the Baza basin. The bone assemblage is embedded in homogeneous and porous micrite sediments, which precipitated during a period of partial expansion of the ponds (restricted swampy biotope of carbonate facies, with plants colonizing the border of the ponds), and is capped by the massive precipitation of micrite that took place after a subsequent phase of uprising of the water table [26].

Petrographic, mineralogical and geochemical analyses [25, 26, 27] allow to describe with greater precision the evolution of the paleolake, from a restricted, stagnated and well stratified water table with elevated salinity and decreased oxygen levels at the base of the sequence to a more open, well-oxygenated water column with decreased salinity at the top of the sequence, which resulted from increased water supply and circulation. Interestingly, the salinity level dramatically increased just prior to paleosoil development, thus evidencing the lowering of the water table.

2.2 Barranco León-D

Barranco León-D is 3 km distant from Orce in the direction to the town of María. It is a N-S oriented ravine that originates at the foot of "Sierra de la Umbría" mountains and flows to the Vélez gorge. Although this site is known from the eighties, the first excavation took place in 1995. The site records an archaeological level, which was originally named as Barranco León-5 [28] and is now designated as Bed D [4].

Barranco León-D and Fuente Nueva-3 are both placed within the biozone of *Allophaiomys* aff. *lavocati* [7, 24, 29, 31, 32]. The combination of biostratigraphic data and paleomagnetic analyses indicates that both sites are within a section that shows reversed polarity, which allows estimating for them an age prior to the Bruhnes normal polarity chron. The composition of the micro- and macrofaunal assemblages, which are slightly older than those recorded in the site of Le Vallonet (France), dated at 1 Ma, and more derived than those from Dmanisi (Georgia), dated at 1,81 Ma [33], and Venta Micena (*ca.* 1.6-1.5 Ma), allow to infer that Barranco León-D and Fuente Nueva-3 are both older than the Jaramillo normal polarity subchron and younger than the Olduvai normal polarity subchron These data, combined with the relative development of the anteroconid complex in the first lower molar tooth (M_1) of the microtine rodents unearthed in these sites, suggest an age of 1.4-1.3 Ma for them. Similarly, an age of 1.26 ± 0.13 Ma has been calculated for Barranco León-D using an equation of rectilinear change for the length of M_1 in the arvicolid *Mimomys savini* [34, 35]. However, it is worth noting that this chronometric tool, based on an orthogenetic approach, has severe problems that discourage its use for deriving "biometric ages" in biostratigraphy [36, 37]. Finally, an age estimate of 1.46 ± 0.17 Ma has been also obtained for the site using the Electron Spin Resonance (ESR) method [5].

The stratigraphic sequence of the Barranco León gorge, from the bottom of the ravine to the top at the plain that corresponds to the glacis level, shows a predominance of reddish and whitey lutitic marls (Middle Member or red detritic), which outcrop at the lower part of the ravine, and a set of carbonated sediments interspersed with layers of quartz sands and lutites, which constitute the most pronounced escarpments of the ravine [38, 39, 40]. Bed D (formerly level 5), the main archaeopaleontological level of the site, consists of two parts [28] : the lower (level D1) has variable thickness

and shows sandy conglomerates and gravels with an irregular basal contact of erosive nature; the upper (level D2) has a mean thickness of 0.22 m and is composed of grey bioclastic quartz sands that show irregular yellowy patches at its base and ends in a level of white limestone. These levels preserve a relatively diverse mollusk fauna, but the diversity of ostracods is very low, which indicates the presence of oligosaline waters. The sedimentological features of the lower level suggest that the faunal remains were redeposited, while in the upper level they seem to have been accumulated "*in situ*", or to come from zones close to their final depositional environment.

2.3 Fuente Nueva-3

The site of Fuente Nueva-3 is 7 km East from the town of Orce, in the village of Fuente Nueva, from which it takes its name, and outcrops in one of the catchment areas of the headwaters that discharge in the fluvial valley of the Vélez gorge. The late Alain Bocquet discovered this site in 1991. It belongs to the same biozone than Barranco León-D and shows a similar chronology. The age estimate obtained with the combined U-series/ESR method is 1.19 ± 0.21 Ma [5] and there is a recent estimate of 1.50 ± 0.31 Ma from cosmogenic nuclides [6]. This site shows two sedimentary cycles, both with limestone deposits at the top and intermediate levels of detritic sediments (clays, marls, marly limestones and sands). This stratigraphic sequence is basically composed of carbonate rocks and corresponds to a shallow lacustrine environment with a source of terrigenous inputs that evidences frequent emersions of the lake floor [40].

Fuente Nueva-3 preserves two archaeological levels. The Lower level is composed of a basal deposit of limestones overlapped by clays, marls and marly limestones, and has provided 88% of the lithic tools unearthed in the site. There are abundant faunal remains in this level, which use to be fractured. In the Upper level tools are scarce, but the density of fossils is very high and their state of preservation is excellent.

3 Descriptive taphonomic attributes

3.1 Spatial distribution

Skeletal elements in anatomical connection are relatively scarce in the three assemblages, with a few exceptions, including a partial elephant skeleton in Fuente Nueva-3 [3, 7]. In the case of Venta Micena, skeletal elements from the same individual are frequently found. Although these elements are not anatomically connected, they are not very dispersed. In which concerns the spatial distribution of bones, there are not spatial concentrations of elements from a given species except for the upper archaeological level of Fuente Nueva-3, in which proboscidean remains are very abundant. Similarly, there are no differences in the spatial distribution of anatomical elements, with the only exception of an accumulation in one square meter of Venta Micena that includes cranial remains of *Homotherium latidens*, *Mammuthus meridionalis*, *Stephanorhinus hundsheimensis*, *Equus altidens*, *Bison* sp. and *Hystrix major*.

The spatial orientation of fossils does not show preferential directions in Venta Micena and Fuente Nueva-3, which discards that the bones were aligned by currents [20]. This

is also evidenced by the finding of skeletal remains from the same individual that are spatially associated and by the absence of bones with signs of abrasion or polish in their cortical surface. In which concerns Barranco León-D, however, the bones of the lower part of Level D (Sublevel D1) are NE-SW aligned to a certain degree, which coincides with the direction of the paleo-currents estimated in this zone [41], and the skeletal elements from this level show their borders rounded and polished. This indicates that they were, at least in part, subject to transport by fluvial processes prior to deposition, which opens the possibility of hydraulic sorting.

3.2 Age classes

Only adult individuals represent most carnivore species in the three assemblages. The exception is *Pachycrocuta brevirostris* in Venta Micena, where half the individuals of this species are juveniles (Table 1). Among herbivores, juveniles are abundantly preserved and their percentage with respect to adults shows a direct correlation with the body size estimated for the ungulate species, as discussed below. Specifically, the largest sized species, like the hippo *Hippopotamus antiquus* and the elephant *M. meridionalis,* are represented by percentages of juveniles in excess of 50%. This pattern is particularly interesting in the assemblage from Venta Micena, in which the number of remains unearthed and the estimates of minimal number of individuals obtained from them are very high.

3.3 Body size

Mean size estimates of adult individuals [18, 19] were obtained for the species of large mammals identified in the sites of Orce using least-squares regression equations for body mass on craniodental and postcranial measurements derived from living species [42]. The estimates obtained showed that these Early Pleistocene taxa covered a wide size spectrum, from 5 kg in the small fox *Vulpes cf. praeglacialis* to 6 000 kg in elephant *M. meridionalis* (Table 1).

3.4 Preservational completeness according to anatomical elements

The skeletal elements better preserved in the three taphocoenoses are teeth isolated from the jaw or maxilla. Cranial remains are poorly preserved, generally as skullcaps that in the case of ruminants preserve the pedicles or horn cores, and fragments of hemimaxillae and hemimandibles in which the osseous tissue is consumed to the base of the cheek teeth. The elements of the axial skeleton are also scarce, being composed of rib fragments, vertebral bodies, and fragments of scapulae and pelvis that use to preserve the glenoid cavity or the acetabulum, respectively. Of the elements of the appendicular skeleton, tibiae and humeri are usually preserved by their distal epiphyses, radii tend to appear represented by proximal epiphyses and femora use to be preserved as isolated diaphyses. In contrast, carpal and tarsal elements, metapodials and phalanges tend to be recorded as complete elements.

3.5 Species abundance

The large mammals assemblage from Venta Micena includes 22 taxa from the orders Carnivora, Proboscidea, Perissodactyla and Artiodactyla, which are represented

by members of the families Felidae, Hyaenidae, Canidae, Ursidae, Mustelidae, Elephantidae, Rhinocerotidae, Equidae, Bovidae and Cervidae (Table 1). In addition, there is also a large sized rodent, the porcupine *Hystrix major*, and a number of small mammals (rodents and insectivores). Finally, there are also remains from lagomorphs, chelonians and birds. Herbivore taxa represent 86.4% of the assemblage, carnivores constitute 6.7% and the remaining 6.9% are bone remains that could not be ascribed taxonomically [18, 20].

Barranco León-D and Fuente Nueva-3 show minor differences in faunal composition with Venta Micena. In the case of the record of carnivore taxa, several remains can be attributed to machairodontine cats, although most of them have not been determined at the genus and species level. Similarly, no bone remain has been unequivocally attributed to a large sized pantherine cat. However, the main differences between these sites concern the record of equids and bovids. Remains of a large sized horse ascribed to *Equus sussenbornensis* and of a caprine identified as *Ammotragus europaeus* have been identified in both Barranco León-D and Fuente Nueva-3, while these taxa are not present in VM. Conversely, the bovids *Soergelia minor*, *Praeovibos* sp. and *Hemibos* sp. *cf. H. gracilis,* represented in Venta Micena, are all absent from Barranco León-D and Fuente Nueva-3 (Table 1).

Equids are the family best represented by far in the three assemblages. In general terms, there is a predominance of large sized taxa, equids, bovids and cervids among them, although it is outstanding the abundance of proboscideans in Fuente Nueva-3 and hippos in Barranco León-D [20].

4 Osseous modification

In general terms, the skeletal elements preserved complete are scarcely represented in the three assemblages and correspond to isolated teeth and autopodial bones, which are highly mineralized and have a low nutritional value. Analyses of bone fracturing patterns evidence that biological agents fractured the bones in fresh state in most cases.

Quarry III of Venta Micena has been interpreted as a bone accumulation generated by the activity of the giant, short-faced hyena *Pachycrocuta brevirostris.* Up to date, there are no evidence of human presence in the site and anthropic patterns of bone modification are also absent from the cortical surface of the skeletal elements.

Most bones unearthed from this excavation quarry have an excellent preservation of their cortical surface, in most cases showing a weathering stage 0 according to the criteria of Behrensmeyer [43], which evidences a very short period of subaerial exposure before their definitive burial, less than one year in most cases [18, 20, 26]. This allowed the preservation of most modifications that took place during the biostratinomic stage, which study has shown the presence of abundant tooth marks produced by hyaenids, including pits, scores, furrowing and crenulated edges.

Mandibles use to preserve the bone portion of the horizontal ramus with the cheek teeth, which uses to be gnawed up to the tooth roots, while the ascending ramus with the gonial process and the coronoid tend to be absent. The preservation of maxillae

is similar. Scapulae use to be preserved as distal portions that preserve the glenoid cavity and pelves use to preserve the acetabulum. Ribs are preserved at their medial shafts and vertebrae use to be represented by vertebral bodies with the apophyses destroyed.

The major limb bones use to be highly modified, preserving those anatomical portions that have a lower nutritional value, which provides information on the bone-consuming pattern of hyenas. Specifically, humeri and tibiae are consumed following a proximal-distal sequence, which results in the overrepresentation of these bones as isolated distal epiphyses. In the case of radii, they are fractured in a distal-proximal pattern, which means that these elements are mostly represented by proximal epiphyses. In contrast, femora use to be preserved as diaphyseal bone cylinders, which indicate that the hyenas consumed these skeletal elements both distally and proximally. Finally, autopodial elements use to be more represented as complete elements with a slight overrepresentation of proximal epiphyses in the case of metapodials, which suggests that the hyenas use to fracture them distally for consuming the phalanges. In the case of the carpal and tarsal bones of proboscideans, which in almost all cases correspond to juvenile individuals, these elements are preserved heavily gnawed by the hyenas.

Patterns of bone preservation in Barranco León and Fuente Nueva-3 are quite different from those described for Venta Micena. These sites preserved the oldest evidence of human presence in Western Europe, as noted above, including a deciduous tooth from Barranco León [4] and huge tool assemblages of Oldowan tradition made of flint and limestone in both sites, in which the whole lithic chain is represented. These tools are directly related with the faunal remains by the presence of abundant cut marks on bones that can be related with different stages of carcass processing, including disarticulation, filleting, skinning, evisceration and removal of periosteum [20]. Percussion stigma related to bone fracturing for accessing the medullary cavities are also frequent.

Evidence of bone modification by carnivores has been also identified in these sites, although their intensity is much lower than in Venta Micena. This activity is restricted to the presence of pits and scores, which are usually found on the major limb bones of large ungulates. Apart from the modifications produced by hyenas, there is evidence of the activity of a small-sized carnivore in Barranco León and Fuente Nueva-3, which probably corresponds to one of the canids present in the assemblages.

In any case, the percentage of bones in these sites that show modifications produced by biological agents during the biostratinomic stage is remarkably lower than in Venta Micena, because the preservation of the cortical surface of bones is not as good as in the latter site. In addition, root activity of modern plants in the current topography has deteriorated the bones and the presence of calcareous crusts resulted in the loss of the outermost surface of the bones, which erased the potential marks that they could have preserved.

5 Taphonomic biases

The site of Venta Micena is by far the locality of the Orce region in which most extensive taphonomic analyses have been developed. The first studies of this bone assemblage, accumulated by *P. brevirostris*, evidenced the presence of a number of taphonomic biases that affected its record, including : (1) the selection of ungulate prey by hypercarnivores ; (2) the selective scavenging of ungulate carcasses by the hyenas ; (3) the selective transport of carcasses and anatomical portions ; and (4) the selective fracturing of bone elements [18, 26, 44]. Each of these biases was identified using a number of taphonomic evidences that are discussed in further depth below, as the interpretation of some of them has changed after the studies developed during the last years [20].

5.1 Selection of prey by hypercarnivores

Mortality patterns among ungulates (Figure 1) : the mortality profiles deduced for the two ungulate species better represented in the assemblage, the horse *Equus altidens* and the large-sized megacerine deer *Praemegaceros verticornis*, show U-shaped patterns. This suggests that most deaths resulted from predation pressure, which would be focused on very young individuals with deciduous teeth and past prime adults with heavily worn permanent teeth. In the case of *P. verticornis*, the peak that corresponds to the first ten percent of the potential lifespan is very marked [18].

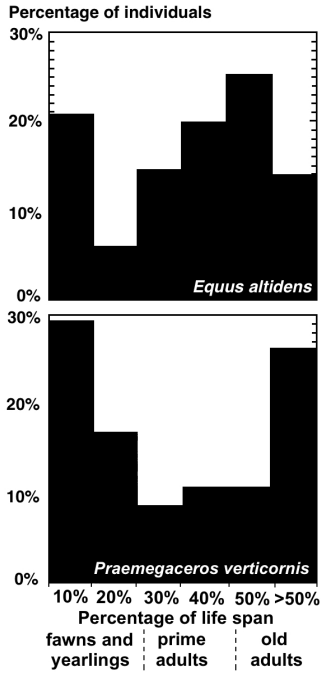


Figure 1 – Mortality profiles deduced from crown height measurements in the horse *Equus altidens* and the megacerine deer *Praemegaceros verticornis* of Venta Micena. (Data from ref. [18].)

Relationship between the minimal number of individuals (NMI) deduced for juvenile and adult individuals and the body mass estimated for the ungulate species : the interspecific analysis of the relative abundance of juvenile individuals with deciduous teeth and adults with permanent dentition developed in the earlier taphonomic studies of this site [18, 26, 44] showed that juveniles represent 16.7% (8/48) of the MNI counts of ungulate species weighing $<$ 300 kg, while for those of $>$ 300 kg their percentage increased to 48.0% (72/150). The updating of these data during the last years [20] does not show significant differences in these proportions, although there is a greater abundance of juveniles from both size categories, 22.8% (13/44) for ungulates $<$ 300 kg and 50.7% for those of $>$ 300 kg (105/207). Figure 2 shows that there is a direct, statistically significant relationship between the MNI's of juveniles (Y-axis) and the body masses estimated for the adults (X-axis). As a result, larger ungulates are represented by higher percentages of immature individuals, which reach 80% in the case of elephant *M. meridionalis*, the largest-sized species of the assemblage.

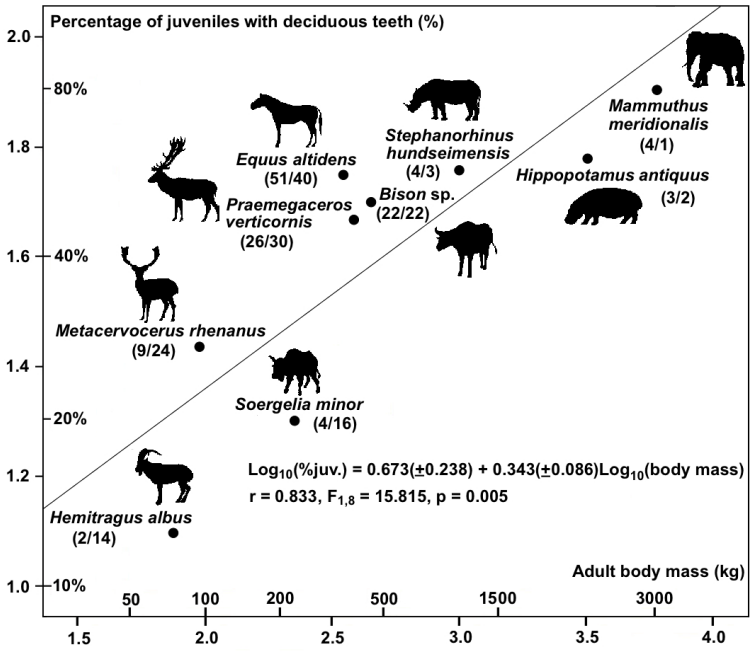


FIGURE 2 – Least-squares regression between the logarithms of the mean body masses (X-axis) estimated from postcranial measurements for the ungulate species of Venta Micena (data from refs. [18, 19]) and the logarithms of the percentage of juvenile individuals over the MNI estimates of each species (Y-axis) calculated from teeth counts (MNI juv./ad. for each species in brackets, values updated from ref. [20] ; mean body masses of species from Table 1).

Presence of osteopathologies : the abundance of bone elements that show evidence of osseous pathology, specially those of the appendicular skeleton that affect the ability of ungulates to escape from their predators, is also an evidence of the strong selection of prey by hypercarnivores. Palmqvist and colleagues [18] mentioned the presence of pathological bones, mostly metapodials, which were affected of degenerative processes

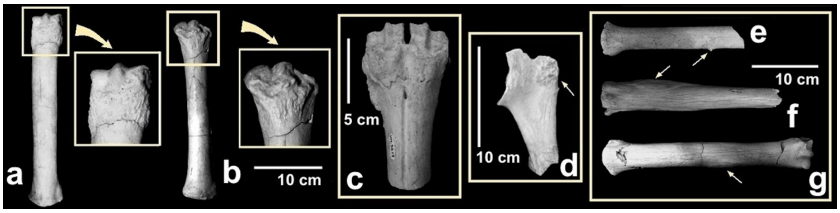


Figure 3 – Examples of osteopathologies detected in the Venta Micena assemblage. (a) horse metatarsal with osteophytic overgrowths in the distal epiphysis ; (b) horse metacarpal showing an intense deformation of its proximal epiphysis ; (c) severe osteoarthritis in a third-four metacarpal of megacerine deer ; (d) pelvis fragment of horse showing abundant osteophytes below the acetabulum ; (e) horse metacarpal showing a spur-shaped bony overgrowth (exostosis) ; (f) horse metatarsal showing a huge diaphyseal overgrowth in its dorsal face, close to the proximal epiphysis ; (g) horse metacarpal with a circular overgrowth in its diaphysis.

such as arthritis. This would diminish the ability of these individuals to flee from their predators, which would result in an increase in the number of pathological bones in the assemblage compared to their abundance in the living community (where they would be less abundant in relative terms). During the last years, new pathological bones have been identified in Venta Micena. These pathologies are mainly related to degenerative processes in individuals of old age and to infections that resulted in anomalous bony overgrowths (Figure 3).

Although the frequency of pathology is low in relative terms, especially for those affecting the postcranial skeleton, it is not negligible. For example, in the case of *E. altidens,* the species that is more abundant in the assemblage and shows the greatest incidence of pathology, the percentage of anomalous metapodials is 3.7%. Obviously, this percentage would increase fourfold if we translate it into the proportion of horses with diminished abilities for locomotion, as an individual with one of its four limbs affected of pathology would be functionally disabled. This would increase the percentage of handicapped individuals to nearly 15%. Although there are no data available on the frequency of pathology in wild populations of ungulates, except for some cases that can not be considered as representative (*e.g.*, the moose population of Isle Royale, which is subject to inbreeding and shows a disproportionate abundance of arthritis), there are abundant examples of pathologic bones in Venta Micena, which suggests a selection of these individuals by predators. Moreover, the difference between the percentages of third metacarpals and metatarsals of *E. altidens* that show pathology, 1.3% (3/238) and 7.1% (18/252), is statistically significant ($t = 4.49$, $p < 0.001$). Given that the hindquarters make most of the effort propelling forward the horse's body during the run, as happens in all ungulates with the only exception of proboscideans, the higher percentage of pathologic metatarsals indicates greater predator success against individuals with hind limb afflictions.

Sex ratio in large bovids : this evidence of prey selection was based on the presence of a bimodal size distribution for the metapodials of the large sized bovids, which bone remains were initially attributed to a single species, *Bison* sp. (formerly assigned to Bovini *cf. Bubalus* and Bovini *cf. Dmanisibos*). Such size differences were interpreted as reflecting a high degree of sexual dimorphism in this large bovid and suggested

a biased proportion of sexes (74 ♀ / 26 ♂) [18], which was interpreted as resulting from a selection by hypercarnivores of female individuals given their smaller body size. However, this evidence must be re-evaluated, because the presence of two large bovids in Venta Micena, *Bison* sp. and *Hemibos* sp. aff. *Hemibos gracilis*, was published in the year 2011 [9], which could explain in part the difference in size among the metapodials.

5.2 Scavenging and selective transport of carcasses by the hyenas

Palmqvist and colleagues [18] showed that the distribution of specimens among ungulate size classes in the assemblage unearthed from Venta Micena Quarry III differs from the frequencies of ungulates hunted by modern spotted hyenas, but is remarkably similar to those in which spotted hyenas scavenge carcasses of animals killed by lions and wild dogs. The only significant difference between the distribution of ungulate size classes in Venta Micena and in the prey scavenged by spotted hyenas is the proportion of small species, which are underrepresented in the fossil assemblage. This indicates that : (1) the predatory behavior of *P. brevirostris* differed from that of the spotted hyena, because that latter both hunts and scavenges ungulates, whereas the former seems to have relied more heavily on prey hunted by other predators such as saber-tooth felids *H. latidens* and *Megantereon whitei*, being its behavior more similar to that of the scavenging brown and striped hyenas ; and (2) the short-faced hyenas preferentially consumed small ungulates *in situ* and selectively transported carcasses and body parts of larger species to the surroundings of their maternity dens.

The bias produced by the selective transport of ungulate remains by the adult hyenas is evidenced by the differential representation of preserved skeletal parts in the bone assemblage. Palmqvist and Arribas [26] estimated the abundance of adult individuals from each ungulate species by MNI counts obtained from teeth and cranial elements (antlers and horn bases in the case of ruminants), as well as from MNI counts based on minimum number of elements (MNE) of the postcranial skeleton (estimates obtained separately for forelimb and hind limb bones, which can be preserved as complete elements or as isolated proximal/distal epiphyses). In the case of the small-sized ungulates, *Hemitragus albus* and *Metacervocerus rhenanus,* the abundance estimates for adult individuals based on teeth are higher than those based on limb bones, with MNI_{teeth} : MNI_{bones} ratios of 2.8 :1 and 2.0 :1, respectively. In contrast, ungulate taxa of larger size, such as *E. altidens* and *Bison* sp., are better represented by postcranial elements and their MNI_{teeth} : MNI_{bones} ratios are reversed to 1 :1.8 and 1 :1.3, respectively (Table 1 ; estimates updated from refs. [18, 20, 26]).

These differences are in large part an indication of how the hyenas handled the carcasses they scavenged. Specifically, the abundances based on teeth and bones would be approximately the same in the accumulated assemblage for those ungulate species of small size that were transported to the maternity dens as complete carcasses. However, because hyenas selectively fractured major limb bones and destroyed their epiphyses to get at the marrow and fat, estimates based on teeth should be higher than those based on postcranial elements in the preserved assemblage. In the case of larger species, however, selective transport of marrow-rich body parts would led to an overrepresentation of limb bones for these ungulates, which resulted in the reversed MNI_{teeth} : MNI_{bones} ratios in the accumulated assemblage.

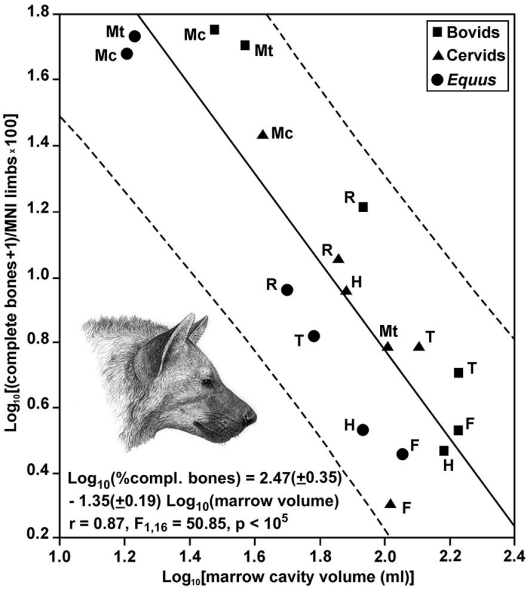


FIGURE 4 – Bilogarithmic least-squares regression of the percentage of major limb bones preserved complete (estimated as the number of complete elements plus one, divided by the minimum number of fore- or hind limbs, respectively) on their estimated medullary cavity volume (data from ref. [45]). Dashed lines represent the 95% confidence intervals for observations.

5.3 Fracturing of major limb bones

The fourth taphonomic bias introduced by the hyenas in the composition of the Venta Micena assemblage is the selective fracturing and consumption of those appendicular elements that provided higher yields of within-bone nutrients. Figure 4 shows the raw abundance in which major limb bones of horse *E. altidens,* cervids and bovids are preserved in the fossil assemblage, as a function of their mean marrow content (estimated from their marrow cavity volumes in modern horse, caribou and bison; data from ref. [45]). A least-squares regression shows an inverse relationship between both variables, which is statistically very significant. This indicates that hyenas selectively fractured those elements that provided higher within-bone nutrient contents (*e.g.*, femur, humerus and tibia) and acted less intensely on those yielding lower marrow values (*e.g.*, metapodials, and, to a lesser extent, radius), which biased the skeletal completeness of the assemblage.

These results were further corroborated by a contingency table [45], which revealed a heterogeneous distribution of major limb bones of horse among preservational categories (*i.e.*, complete elements, proximal epiphyses, diaphyses and distal epiphyses). Specifically, complete elements were underrepresented as humeri, femora and tibiae, while metapodials showed higher frequencies than those expected from a random distribution. Proximal epiphyses were overrepresented as radii and metapodials, while proximal humeri and tibiae were less abundantly preserved than expected. Diaphyses were better represented in the case of femora, while radii and tibiae were preserved

as isolated diaphyseal portions in lower proportions than expected. Finally, distal humeri and tibiae were clearly overrepresented in the assemblage, while all other limb bones show lower frequencies of this epiphyseal region than expected. This indicates the existence of three different bone-fracturing sequences by the hyenas, depending on the element considered : (1) in the case of radii and metapodials, which tend to be more frequently preserved as complete bones or proximal epiphyses, their reduction starts at the distal end ; (2) in contrast, tibiae and humeri are better represented by distal epiphyses, which means that the hyenas destroy these elements starting at their proximal ends ; and (3) femur is the only element that tends to be crushed at both ends and, consequently, it is mainly represented by isolated diaphyses.

6 Paleoecological inferences

Paleoautecological inferences for the large mammal species of Venta Micena have been obtained using combined biogeochemical and ecomorphological/biomechanical approaches [45, 46, 47, 48, 49, 50, 51]. Specifically, analysis of stable-isotopes ($\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$) and trace elements (Sr, Zn) from bone collagen and tooth enamel (hydroxylapatite) allowed estimation of the dietary niches and habitat preferences of carnivores and ungulates, providing clues on predator/prey relationships within this early Pleistocene community.

The hypsodonty index and the relative length of the lower premolar tooth row allow classifying the ungulates among grazers (*E. altidens, Bison* sp., *Praeovibos* sp., *H. albus, H. antiquus* and *M. meridionalis*), mixed-feeders (*Soergelia minor* and *M. rhenanus*) and browsers (*Stephanorhinus hundsheimensis* and *P. verticornis*). However, the range of $\delta^{13}C$ values from bone collagen show that these ungulates consumed exclusively C3 plants (Figure 5). For this reason, significant differences in isotopic values between perissodactyls (monogastric, hindgut fermenters) and ruminants (foregut fermenters) reflect physiological differences related to their rates of methane production and digestive efficiency. $\delta^{18}O$ ratios measured in tooth enamel allow the interpretation of the dietary water source of these species, suggesting that fallow deer *M. rhenanus*, goat *H. albus* and ovibovine *S. minor* obtained a significant fraction of their metabolic water from the vegetation consumed.

Carnivore species show higher $\delta^{15}N$ values of bone collagen than herbivores, which records the isotopic enrichment expected with an increase in trophic level. However, the unexpectedly high $\delta^{15}N$ values of hippo *H. antiquus* and muskoxen *Praeovibos* sp. (Figure 5) suggest that these ungulates predominantly consumed aquatic plants and lichens, respectively. It is worth noting here that a recent study showed that algae and aquatic macrophytes from a couple of hypersaline endorheic pools showed higher $\delta^{15}N$ values than the terrestrial grasses that surround these pools [52] ; given the saline nature of the Early Pleistocene lacustrine systems of the Baza basin, which were subject to hydrothermal feeding [53], this confirms that the extinct *H. antiquus* fed predominantly on aquatic vegetation unlike the modern hippo *H. amphibious,* which grazes during the night or early morning on river banks located close to watercourses and shows $\delta^{15}N$ values that are similar to those of other ungulates that feed on terrestrial vegetation.

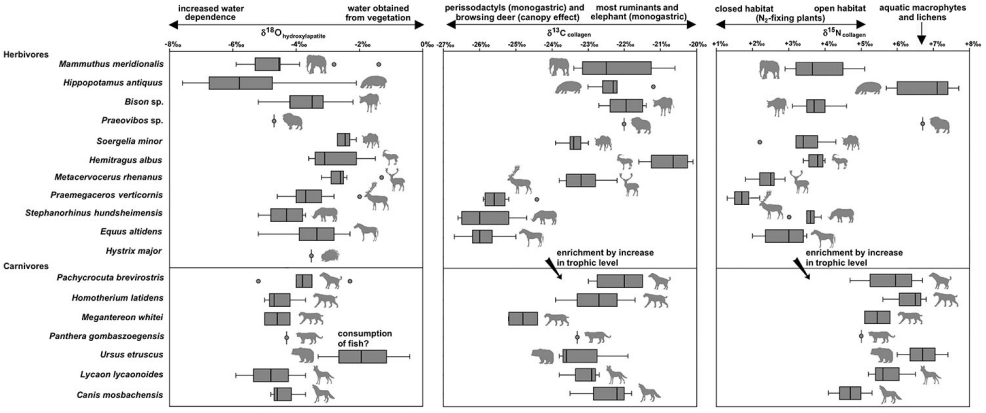


FIGURE 5 – Whiskers box plots of $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen and $\delta^{18}O$ values of enamel hydroxylapatite of large mammal species preserved at Venta Micena. Vertical line inside each box is the median. Box length is interquartile range and shows the difference between 25^{th} and 75^{th} percentiles. Horizontal bars enclose values of 5%-95% (the smallest and largest values that are not outliers). Circles are the outliers (*i.e.*, those values which lie more than 1.5 lower than the first quartile or 1.5 higher than the third quartile).

In the case of carnivores, their $\delta^{15}N$ values indicate resource partitioning among sympatric predators, suggesting that saber-tooth *M. whitei* and jaguar *Panthera cf. gombaszoegensis* were ambushers of forest environments while saber-tooth *H. latidens* and wild dog *Lycaon lycaonoides* were coursing predators in open habitat (Figure 5). The $\delta^{15}N$ values of *P. brevirostris* are in agreement with its role deduced from taphonomic analyses as the major scavenger of this paleocommunity, as they average the isotopic enrichment expected from the consumption of the prey of the four hypercarnivores.

The use of the dual isotope, three-source linear mixing model [50] has allowed the obtaining of inferences on predator-prey relationships within this ancient community, which help in identifying the three prey species more frequently consumed by each predator (Fig. 6). Specifically, the preferred prey of *H. latidens*, a large cursorial predator of open habitat, would be medium-to-large sized grazing herbivores from open habitat, such as adult *Bison* sp. and *E. altidens*, and juveniles of *M. meridionalis*. In the case of *M. whitei*, a medium-sized ambush predator in more closed habitat, the prey would consist of *E. altidens*, *P. verticornis* and *S. minor*. The other predator from forest, jaguar *P. gombaszoegensis*, would prey on browsing deer and ovibovines. Finally, the pack hunting, hypercarnivorous canid *L. lycaonoides* would focus on small-to-medium-sized ungulates such as adult goats and fallow deer, as well as juvenile horses.

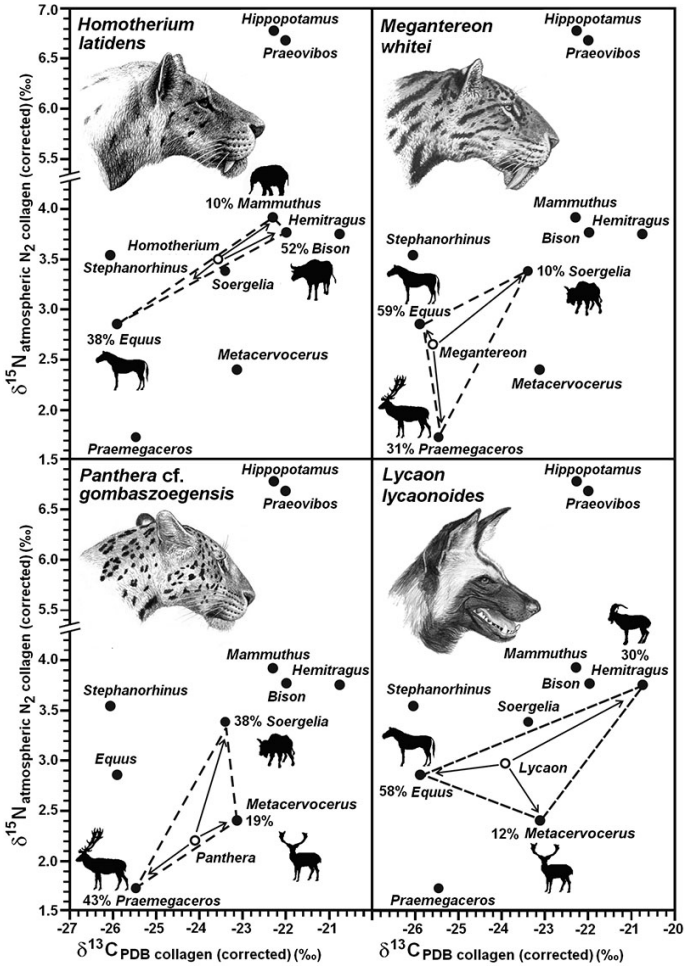


FIGURE 6 – Plot of $\delta^{13}C$ and $\delta^{15}N$ values for the four Venta Micena hypercarnivores and their ungulate prey, corrected for trophic fractionation. Each predator lies within the triangle defined by its three most probable prey species. According to the dual-isotope, three-source linear mixing model (see details in ref. [50]), the contribution to carnivore diet of each prey defining a vertex in the triangle is defined as the distance from this vertex to the opposite side in relation to its distance to the predator (both measured on the line connecting prey and predator).

References

[1] B. Martínez-Navarro, "Revisión sistemática y estudio cuantitativo de la fauna de macromamíferos del yacimiento de Venta Micena (Orce, Granada)", Ph.D. Thesis, Universidad Autónoma de Barcelona, 333 pages, 1991.

[2] Palmqvist, P., Martínez-Navarro, B., Toro, I., Espigares, M.P., Ros-Montoya, S., Torregrosa, V., Pérez-Claros, J.A., A re-evaluation of the evidence of human presence during Early Pleistocene times in southeastern Spain. L´Anthropologie, 109, 411-450, 2005.

[3] M.P. Espigares, B. Martínez-Navarro, P. Palmqvist, S. Ros-Montoya, I. Toro, J. Agustí, R. Sala, *Homo* vs. *Pachycrocuta* : Earliest evidence of competition for an elephant carcass between scavengers at Fuente Nueva-3 (Orce, Spain). Quaternary International, 295, 113-125, 2013.

[4] I. Toro, B. Martínez-Navarro, J. Agustí, C. Souday, J.M. Bermúdez de Castro, M. Martínón-Torres, B. Fajardo, M. Duval, C. Falguères, O. Oms, J.M. Parés, P. Anadón, R. Julià, J.M. García Aguilar, A.M. Moigne, M.P. Espigares, S. Ros-Montoya, P. Palmqvist, The oldest human fossil in Europe, from Orce (Spain). Journal of Human Evolution, 66, 1-9, 2013.

[5] M. Duval, C. Falguères, J.J Bahain, R. Grün, Q. Shao, M. Auvert., J.M. Dolo, J. Agustí, B. Martínez-Navarro, P. Palmqvist, I. Toro, On the limits of ussing combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce área (Guadix-Baza basin, Spain). Quaternary Research, 77, 482-491, 2012.

[6] C. Alvarez, J.M. Parés, D. Granger, M. Duval, R. Sala, I. Toro, 2015. New magnetostratigraphic and numerical age of the Fuente Nueva-3 site (Guadix-Baza basin, Spain). Quat. Int., 389, 224-234.

[7] B. Martínez-Navarro, M.P. Espigares, S. Ros. "Estudio preliminar de las asociaciones de grandes mamíferos de Fuente Nueva-3 y Barranco Léon-5 (Orce, Granada, España) (Informe de las campañas de 1999-2002)", in El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria Científica Campañas 1999-2002, eds. I. Toro, J. Agustí, B. Martínez-Navarro, Junta de Andalucía, Consejería de Cultura, E.P.G. Arqueología Monografías, p.115-136, 2003.

[8] B. Martínez-Navarro, P. Palmqvist, J. Madurell, S. Ros-Montoya, M.P. Espigares, Torregrosa, V., Perez-Claros, J.A, "La fauna de grandes mamíferos de Fuente Nueva-3 y Barranco León-5 : Estado de la cuestión", in Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza, eds. I. Toro, B. Martínez-Navarro, J. Agustí, Junta de Andalucía, Consejería de Cultura, Arqueología Monografías, p.197-236, 2010.

[9] B. Martínez-Navarro, S. Ros-Montoya, M.P. Espigares, P. Palmqvist, Presence of the Asian origin Bovini, *Hemibos* sp. aff. *Hemibos gracilis* and *Bison* sp. at the early Pleistocene site of Venta Micena (Orce, Spain). Quaternary International, 243, 54-60, 2011.

[10] P.E. Moullé, A. Echassoux, B. Martínez-Navarro, Ammogragus europaeus : une nouvelle espèce de Caprini (Bovidae, Mammalia) du Pléistocène Inférieur à la grotte du Vallonnet (France). C.R. Palevol, 3, 663-673, 2004.

[11] M.T. Alberdi, "Estudio de los caballos de los yacimientos de Fuente Nueva-3 y Barranco León-5", in Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza, eds. I. Toro, B. Martínez-Navarro, J. Agustí, Junta de Andalucía, Consejería de Cultura, Arqueología Monografías, p.291-306, 2010.

[12] L. Abbazzi, "La fauna de cérvidos de Barranco León y Fuente Nueva-3", in Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza, eds. I. Toro, B. Martínez-Navarro, J. Agustí, Junta de Andalucía, Consejería de Cultura, Arqueología Monografías, p.273-290, 2010.

[13] Lacombat, F. "Estudio paleontológico de *Stephanorhinus hundsheimensis* de Fuente Nueva 3 y de Barranco León 5", in Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza, eds. I. Toro, B. Martínez-Navarro, J. Agustí, Junta de Andalucía, Consejería de Cultura, Arqueología Monografías, p.237-246, 2010.

[14] S. Ros-Montoya, Palombo, M.R., M.P. Espigares, B. Martínez-Navarro. "La sucesión de proboscídeos en el Plio-Pleistoceno de las Cuencas de Guadix-Baza y de Granada (España)", in Ocupaciones Humanas en el Pleistoceno inferior y medio de la Cuenca de Guadix-Baza, eds. I. Toro, B. Martínez-Navarro, J. Agustí, Junta de Andalucía, Consejería de Cultura, Arqueología Monografías, p.247-272, 2010.

[15] J. Madurell-Malapeira, B. Martínez-Navarro, S. Ros-Montoya, M.P. Espigares, I. Toro, P. Palmqvist, The earliest European badger (*Meles meles*), from the Late Villafranchian site of Fuente Nueva 3 (Orce, Granda, SE Iberian Peninsula). Comptes Rendus Palevol, 10, 609-615, 2010.

[16] A. Boscaini, J. Madurell-Malapeira, M. Llenas, B. Martínez-Navarro, The origin of the critically endangered Iberian lynx : Speciation, diet and adaptive changes. Quaternary Science Reviews. 123, 247-253, 2015.

[17] T. Medin, B. Martínez-Navarro, F. Rivals, J. Madurell-Malapeira, S. Ros-Montoya, M.P. Espigares, B. Figueirido, L. Rook, P. Palmqvist, Late Villafranchian *Ursus etruscus* and other large carnivorans from the Orce sites (Guadix-Baza basin, Andalusia, southern Spain) : Taxonomy, biochronology, paleobiology, and ecogeographical context. Quaternary International, in press 2015.

[18] P. Palmqvist, B. Martínez-Navarro, A. Arribas, Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity. Paleobiology, 22, 514-534, 1996.

[19] G. Rodríguez-Gómez, P. Palmqvist, J. Rodríguez, A. Mateos, J.A. Martín-González, M.P. Espigares, S. Ros-Montoya, B. Martínez-Navarro. On the ecological context of the earliest human settlements in Europe : Resource availability and competition intensity in the carnivore guild of Barranco León-D and Fuente Nueva-3 (Orce, Baza Basin, SE Spain). Quaternary Science Reviews, 143, 69-83, 2016.

[20] M.P. Espigares, "Análisis y modelización del contexto sedimentario y los atributos tafonómicos de los yacimientos pleistocénicos del borde nororiental de la Cuenca de Guadix-Baza", Ph.D. Thesis, Universidad Autónoma de Granada, 533 pages, 2010.

[21] P. Palmqvist, A critical re-evaluation of the evidence for the presence of hominids in Lower Pleistocene times at Venta Micena, southern Spain. Journal of Human Evolution, 33, 83-89, 1997.

[22] B. Martínez-Navarro, The skull of Orce : parietal bones or frontal bones ? Journal of Human Evolution, 42, 265-270, 2002.

[23] P. Anadón, R. Julià, E. De Deckker, J.C. Rosso, I. Soulié-Marsché, I. Contribución a la Paleolimnología del Pleistoceno inferior de lacuenca de Baza (sector Orce-Venta Micena). Paleontología i Evolució, Memoria Especial, Sabadell, 1, 35-72, 1987

[24] A. Turq, B. Martínez-Navarro, P. Palmqvist, A. Arribas, J. Agustí, J. Rodríguez-Vidal, J. Le Plio-Pléistocène de la région d'Orce, province de Grenada, Espagne : Bilan et perspectivas de Recherche. Paléo 8, 161-204, 1996.

[25] J.M. García-Aguilar, P. Palmqvist, A model of lacustrine sedimentation for the Lower Pleistocene deposits of Guadix-Baza basin (southeast Spain). Quaternary International, 243, 3-15, 2011.

[26] A. Arribas, P. Palmqvist. Taphonomy and palaeoecology of an assemblage of large mammals : hyaenid activity in the Lower Pleistocene site at Venta Micena (Orce, Guadix-Baza Basin, Granada, Spain). Geobios 31 (Suppl.) 3-47, 1998.

[27] A. Arribas, "Análisis y Modelización de la Tafonomía del Yacimiento de Venta Micena (Orce, Granada) y su estudio comparativo con otras localidades españolas del Plio-Pleistoceno continental" Unpub. Ph.D. Thesis, Universidad Complutense de Madrid. 344 pages, 1999.

[28] A. Arribas, P. Palmqvist. The first human dispersal to Europe : remarks on the archaeological and palaeoanthropological record from Orce (Guadix-Baza basin, southeastern Spain). Human Evolution, 17, 55-78, 2002. Madurell

[29] J. Agustí, J. Madurell. "Los arvicólidos (Muroidea, Rodentia, Mammalia) del Pleistoceno inferior de Barranco León y Fuente Nueva 3 (Orce, Granada). Datos preliminares". in El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria Científica Campañas 1999-2002, eds. I. Toro, J. Agustí, B. Martínez-Navarro, Junta de Andalucía, Consejería de Cultura, E.P.G. Arqueología Monografías, p.137-146, 2003.

[30] O. Oms, J.M. Parés, B. Martínez-Navarro, J. Agustí, I. Toro, G. Martínez Fernández, A. Turq. Early human occupation of Western Europe : Paleomagnetic dates for two paleolithic sites in Spain. Proceedings of the National Academy of Sciences, 97 (19), 10666-10670, 2000.

[31] O. Oms, J.M. Parés, J. Agustí. "Datación Magnetoestratigráfica de los yacimientos de Fuente Nueva-3 y Barranco León (Orce, Granada)". in El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria Científica Campañas 1999-2002, eds. I. Toro, J. Agustí, B. Martínez-Navarro, Junta de Andalucía, Consejería de Cultura, E.P.G. Arqueología Monografías, p.105-114, 2003.

[32] B. Martínez-Navarro, A. Turq, J. Agustí, O. Oms. Fuente Nueva-3 (Orce, Granada, Spain) and the first human occupation of Europe. Journal of Human Evolution, 33, 611-620, 1997.

[33] H. Lumley de, D. Lordkipanidze, G. Féraud, T. García, C. Perrenoude, C. Falguères, J. Gagnepaind, T. Saose, P. Voinchet. Datation par la méthode 40Ar / 39Ar de la couche de cendres volcaniques (couche VI) de Dmanissi (Géorgie) qui a livré des restes d'hominidés fossiles de 1,81 Ma. C. R. Palevol 1, 181–189, 2002.

[34] I. Lozano-Fernández, G. Cuenca-Bescós, H.A. Blain, J.M. López-García, J. Agustí, *Mimomys savini* size evolution in the Early Pleistocene of south-western Europe and possible biochronological implications. Quat. Sci. Rev. 76, 96-101, 2013.

[35] I. Lozano-Fernández, H.A. Blain, J.M. López-García, J. Agustí, Biochronology of the first hominid remains in Europe using the vole *Mimomys savini :* Fuente Nueva 3 and Barranco León D, Guadix- Baza Basin, south-eastern Spain. Hist. Biol., 27, 1-8, 2014.

[36] Palmqvist, P., González-Donoso, J.M. & De Renzi, M., Rectilinear evolution in arvicoline rodents and numerical dating of Iberian Early Pleistocene sites. Quaternary Science Reviews, 98, 100-109, 2014.

[37] Palmqvist, P., Duval, M., Diéguez, A., Ros-Montoya, S. & Espigares, M.P. 2016. On the fallacy of using orthogenetic models of rectilinear change in arvicolid teeth for estimating the age of the first human settlements in Western Europe. Historical Biology, 28 : 734-752.

[38] J.A. Vera, J. Fernández, A.C. López-Garrido, J. Rodríguez-Fernández. Geología y estratigrafía de los materiales plioceno-pleistocenos de del sector Orce – Venta Micena (Prov. Granada). Paleont. i evolució, 18, 3-11, 1984.

[39] F.J. Soria, A.C. López-Garrido, J.A. Vera. Análisis estratigráfico y sedimentológico de los depósitos neógeno-cuaternarios en el sector de Orce (depresión de Guadix – Baza). Paleont. i evolució. Memoria Esp. 1, 11-34, 1987.

[40] P. Anadón, R. Julià. "Estratigrafía y estudio sedimentológico preliminar de diversos afloramientos de Barranco León y Fuente Nueva-3 (Orce, Granada)". in El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria Científica Campañas 1999-2002, eds. I. Toro, J. Agustí, B. Martínez-Navarro, Junta de Andalucía, Consejería de Cultura, E.P.G. Arqueología Monografías, p, 47-72, 2003.

[41] J.M. García-Aguilar. "Estratigrafía y Sedimentología del yacimiento paleontológico de Barranco León (Orce, Granada)". in El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Memoria Científica Campañas 1999-2002, eds. I. Toro, J. Agustí, B. Martínez-Navarro, Junta de Andalucía, Consejería de Cultura, E.P.G. Arqueología Monografías, p 73-105, 2003.

[42] J. Damuth, B.J. MacFadden, "Body Size in Mammalian Paleobiology. Estimation and Biological Implications". Cambridge University Press, pp. 409, Cambridge (UK), 1990.

[43] A.K. Behrensmeyer, Taphonomic and ecologic information from bone weathering. Paleobiology, 4(2), 150-162, 1978.

[44] P. Palmqvist, A. Arribas, Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals. Paleobiology, 27, 512-530, 2001.

[45] P. Palmqvist, B. Martínez-Navarro, J.A. Pérez-Claros, V. Torregrosa, B. Figueirido, J.M. Jiménez-Arenas, M.P. Espigares, S. Ros-Montoya, M. De Renzi, The giant hyena *Pachycrocuta brevirostris :* modeling the bone-cracking behavior of an extinct carnivore. Quaternary International, 243, 61-79, 2011.

[46] P. Palmqvist, A. Arribas, B. Martínez-Navarro, Ecomorphological study of large canids from southeastern Spain. Lethaia, 32, 75-88, 1999.

[47] P. Palmqvist, M. Mendoza, A. Arribas, D.R. Gröcke, Estimating the body mass of Pleistocene canids : discussion of some methodological problems and a new 'taxon free' approach. Lethaia, 35, 358-360, 2002.

[48] P. Palmqvist, D.R. Gröcke, A. Arribas, R. Fariña, Paleoecological reconstruction of a lower Pleistocene large mammals community using biogeochemical ((δ^{13}C, δ^{15}N, δ^{18}O, Sr :Zn) and ecomorphological approaches. Paleobiology, 29, 205-229, 2003.

[49] P. Palmqvist, J.A. Pérez-Claros, C.M. Janis, D.R. Gröcke. Tracing the ecophysiology of ungulates and predator-prey relationships in an early Pleistocene large mammal community. Palaeogeography Palaeoclimatology Palaeoecology 266, 95-111, 2008.

[50] P. Palmqvist, J.A. Pérez-Claros, C.M. Janis, B. Figueirido, V. Torregrosa, D.R. Gröcke, Biogeochemical and ecomorphological inferences on prey selection and resource partitioning among mammalian carnivores in an early Pleistocene community. Palaios, 23, 724-737, 2008.

[51] P. Palmqvist, V. Torregrosa, J.A. Pérez-Claros, B. Martínez-Navarro, A. Turner, A re-evaluation of the diversity of *Megantereon* (Mammalia, Carnivora, Machairodontinae) and the problem of species identification in extinct carnivores. Journal of Vertebrate Paleontology, 27, 160-175, 2007.

[52] J.M. García-Aguilar, A. Guerra-Merchán, F. Serrano, P. Palmqvist, A. Flores-Moya, B. Martínez-Navarro, Hydrothermal activity and its paleoecological implications in the latest Miocene to Middle Pleistocene lacustrine environments of the Baza Basin (Betic Cordillera, SE Spain). Quaternary Science Reviews, 96, 204-221, 2014.

[53] J.M. García-Aguilar, A. Guerra-Merchán, F. Serrano, A. Flores-Moya, A. Delgado-Huertas, M.P. Espigares, S. Ros-Montoya, B. Martínez-Navarro, P. Palmqvist, A reassessment of the evidence for hydrothermal activity in the Neogene-Quaternary lacustrine environments of the Baza basin (Betic Cordillera, SE Spain) and its paleoecological implications. Quaternary Science Reviews, 112, 226-235, 2015.