

## Taphonomic decoding of the paleobiological information locked in a lower Pleistocene assemblage of large mammals

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**Abstract.**—The processes of fossilization have usually been perceived by paleontologists as destructive ones, leading to consecutive (and in most cases irretrievable) losses of paleobiological information. However, recent developments of conceptual issues and methodological approaches have revealed that the decrease in paleobiological information runs parallel to the gain of taphonomic information. This taphonomic imprinting often makes it possible to decode the fraction of paleobiological information that was lost during fossilization, and may also contribute new data for deciphering paleobiological information that was not originally preserved in the assemblage, such as paleoethology. A good example is the study of the macrovertebrate assemblage from the lower Pleistocene site at Venta Micena (Orce, southeastern Spain). Taphonomic analysis showed that the giant, short-faced hyenas (*Pachycrocuta brevirostris*) selectively transported ungulate carcasses and body parts to their maternity dens as a function of the mass of the ungulates scavenged. The fracturing of major limb bones in the dens was also highly selective, correlating with marrow content and mineral density. Important differences in bone-cracking intensity were related to which species the bones came from, which in turn biased the composition of the bone assemblage. The analysis of mortality patterns deduced for ungulate species from juvenile/adult proportions revealed that most skeletal remains were scavenged by the hyenas from carcasses of animals hunted by hypercarnivores, such as saber-tooths and wild dogs. Analytical study of the Venta Micena assemblage has unlocked paleobiological information that was lost during its taphonomic history, and has even provided paleobiological information that was not preserved in the original bone assemblage, such as the paleoethology of *P. brevirostris*, which differed substantially from modern hyenas in being a strict scavenger of the prey hunted by other carnivores.

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### Introduction

Prior to the 1980s most vertebrate taphonomists emphasized the incompleteness of the fossil record, because the processes of fossilization were envisioned as destructive, leading to loss of paleobiological information. As a result, taphonomy came to be associated with the documentation of information loss and bias in the transition of organic remains from the biosphere to the lithosphere. However, in their important paper Behrensmeyer and Kidwell (1985) envisioned taphonomy as “the study of processes of preservation and how they affect information in the fossil record.” They were following the approach of numerous invertebrate paleontologists who were engaged since the mid-1980s in more “positive” aspects of comparative taphonomic research intended to establish that postmortem processes (e.g., weathering, transport, and

sorting) leave signatures that are useful and diagnostic of various paleoenvironmental and sedimentary conditions (Kidwell and Bosence 1991; Kidwell and Flessa 1995). Additionally, time-averaging—viewed negatively by most paleontologists in the past—is widely recognized as advantageous, because short-term ecological “noise” is dampened and longer-term signals from a biological community are preserved. In fact, bone assemblages from surface environments are considered comparable in some respects to repeated ecological surveys in assessing the long-term dynamics of the potentially preservable fraction of terrestrial communities (for review and references, see Behrensmeyer and Hook 1992; Cutler et al. 1999; Martin 1999).

Our analysis of large mammals preserved at Venta Micena shows that it is possible to recover significant paleobiological information from a taphonomically altered assemblage.

Such information is obtainable from quantitative study of the preservational bias introduced by the behavior of the large, extinct hyena *Pachycrocuta brevirostris*, the bone-collecting agent at this site (Palmqvist et al. 1996; Arribas and Palmqvist 1998). Until now little has been known about the relative importance of hunting and scavenging for this extinct bone-cracking carnivore, its role as a bone-accumulating agent during the lower Pleistocene, and the bias it introduced in the composition of the assemblages of large mammals. Here we evaluate the nature and consequences of such bias for the composition of the Venta Micena assemblage, paying special attention to several aspects not reported in detail before, such as the transport by hyenas of carcasses and bone remains to their maternity dens and the differential breakage of limb bones from various ungulate species.

### The Venta Micena Site

Venta Micena (Orce, Granada, southeastern Spain) is located in the eastern sector of the Guadix-Baza intramontane basin. The basin was endorheic (i.e., characterized by interior drainage) until late Pleistocene times, thus facilitating an exceptional record of Plio-Quaternary taphocenoses of large mammals preserved in swampy and lacustrine sediments (Fig. 1A). This site is dated by biostratigraphy to the early Pleistocene, with an estimated age of  $1.3 \pm 0.1$  Ma (Arribas and Palmqvist 1999). The 80–120-cm-thick Venta Micena stratum (VM-2, Fig. 1A) is one of the various fossiliferous units in the Plio-Pleistocene sedimentary sequence of Orce, whose surface can be followed along ~2.5 km and stands out topographically in the ravines of the region. This stratum has the following vertical structure from bottom to top (Arribas and Palmqvist 1998: Fig. 2):

1. A basal unit (first lacustrine stage) that is one-third to one-half the total thickness, formed by homogeneous micrite with some carbonate nodules (5–20 cm thick) and small mud banks. The sediment preserves abundant shells of freshwater mollusks and is sterile in vertebrate fossils, thus attesting to a first generalized lacustrine stage in the

region, in which the micrite was precipitated in water of variable depth; the absence of pyrite and carbonate facies rich in organic matter are evidence that the lake was not eutrophic.

2. A 4–15-mm-thick calcrete paleosol (hardpan) developed on the surface of the micrite sediments deposited during the previous lacustrine stage. The calcrete forms an irregular surface, subparallel to the bedding plane, following the preexisting limnic microtopography, and is thicker at topographic highs. This surface defines a stratigraphic unconformity, indicating a major drop of the Pleistocene lake level and thus the emergence of an extensive plain around the lake.
3. An upper unit of micrite (second lacustrine stage) deposited in a subsequent rise of the lake level, which continues up to the top of the stratum, showing root marks, mud cracks, and a high density of fossil bones of large mammals resting on the paleosol.

The sedimentary environment of the fossil assemblage was characterized by wide emerged zones (~4 km width) around the lake, with small shallow ponds (<1 m depth, 2–20 m diameter) (Arribas 1999). The bones are embedded in a porous micrite matrix (98–99%  $\text{CaCO}_3$ ) with mud cracks and root marks, which precipitated during a period of partial expansion of the ponds (i.e., restricted swampy biotope of carbonate facies, with plants colonizing the border of the ponds). It is capped by a massive micritic limestone, produced during a subsequent phase of water level rise (i.e., second lacustrine stage) that was rather slow, as indicated by the absence of terrigenous, erosive structures and of any evidence of sediment traction.

The Venta Micena quarry has an area of ~300 m<sup>2</sup> (Fig. 1B,C). This surface was divided in square meters and excavated systematically from 1979 to 1995, providing a rich collection composed of 5798 identifiable skeletal remains from 225 individuals belonging to 19 taxa of large ( $\geq 5$  kg) mammals, 655 anatomically identifiable bones of mammals that could not be determined taxonomically (e.g., diaphyses and small cranial fragments), and

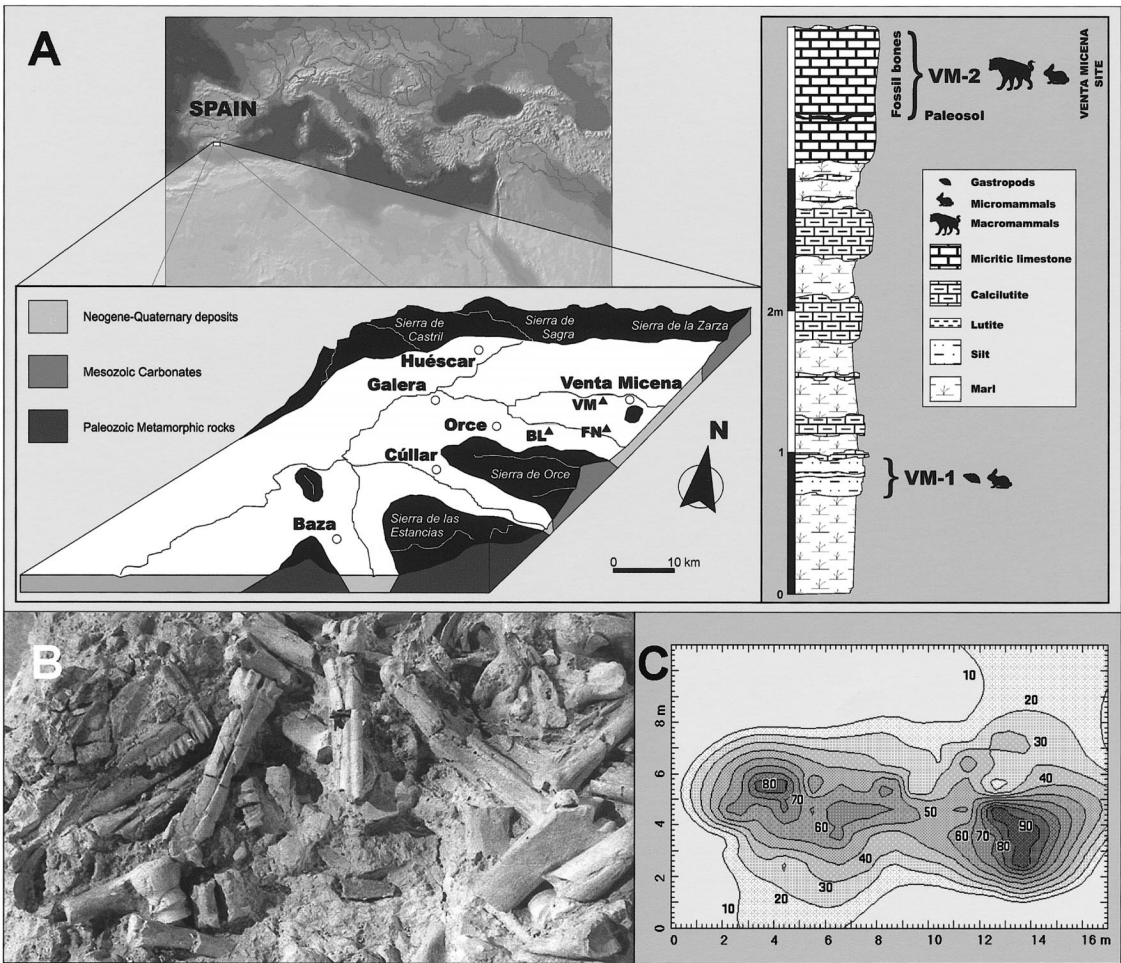


FIGURE 1. A, Geographic location of the paleontological site at Venta Micena (Orce, Granada, southeastern Spain) in the intramontane basin of Guadix-Baza, and stratigraphic section of the lower Pleistocene deposits in the Venta Micena (VM) sector. The location of two other paleontological and archaeological sites (BL = Barranco León, FN = Fuente Nueva) is also indicated. B, Bones outcropping at high density in one grid of the surface excavated at Venta Micena. C, Density plot for the abundance of skeletal remains per square meter (z-axis) in the quarry.

~10,000 unidentifiable bone shafts. Complete elements and bone fragments range in size from isolated premolars and third phalanges of *Vulpes* to complete mandibles of *Mammuthus*. Fossil remains of micromammals, including teeth and elements from the axial skeleton, are also present in small numbers and were not included in the taphonomic study; they were probably deposited as fecal droppings of small carnivores. Table 1 summarizes the raw data on the abundances of large-mammal taxa.

The longitudinal axes of major longbones show no preferred orientation, which suggests that the bones were not aligned by current.

The stratigraphy also indicates the absence of channelled currents in the area in which fossils were accumulated. The bones lie horizontally on the paleosurface, and there is no evidence of trampling, as no skeletal element was found in vertical or diagonal position (Arribas 1999). Surfaces of the bones are well preserved; no signs of abrasion or polish are present and only four elements show evidence of slight dissolution. The concentration of fossils on the excavated surface is very high, with a mean density of elements of ~60 bones/m<sup>2</sup> (Fig. 1C), and >90% of skeletal elements are in contact with other bones. Two areas had 80–90 bones/m<sup>2</sup> of up to 50 cm in length, such as tib-

TABLE 1. Abundance of taxa of large mammals ( $\geq 5$  kg) identified in the Venta Micena assemblage (data from Arribas and Palmqvist 1998). MNI = minimum number of individuals (juveniles/adults), based on counts of deciduous and permanent teeth. NISP = number of identifiable specimens (teeth/bones). C = carnivore (Hy = hypercarnivore,  $>70\%$  vertebrate flesh in diet; Co = carnivore/omnivore,  $<70\%$  flesh in diet; Bc = bone cracker). H = herbivore (Br = browser,  $<10\%$  grass in diet; Mf = mixed-feeder,  $10\text{--}90\%$  grass; Gr = grazer,  $>90\%$  grass). O = omnivore.

Species	Trophic habits	MNI (juv./adults)	% Juv.	NISP <sub>total</sub> (teeth/bones)	% Total	NISP <sub>sample</sub> (teeth/bones)	% Samples	Mass of adults (kg)
<i>Mammuthus meridionalis</i>	H (Mf)	5 (4/1)	80.0	48 (16/32)	0.8	21 (4/17)	2.1	6000
<i>Hippopotamus antiquus</i>	H (Gr)	5 (3/2)	60.0	58 (19/39)	1.0	14 (0/14)	1.4	3000
Bovini cf. <i>Dmanisibos</i>	H (Gr)	27 (16/11)	59.3	775 (382/393)	13.4	97 (48/49)	9.5	450
<i>Soergelia minor</i>	H (Mf)	13 (3/10)	23.1	334 (215/129)	5.8	74 (51/23)	7.3	225
<i>Praeovibos</i> sp.	H (Gr)	1 (0/1)	0.0	6 (3/3)	0.1	3 (2/1)	0.3	320
<i>Hemitragus alba</i>	H (Gr)	14 (2/12)	14.3	305 (209/96)	5.3	30 (12/18)	2.9	75
Caprini gen. et sp. indet.	H (Mf)	1 (0/1)	0.0	1 (0/1)	0.0	1 (0/1)	0.1	10
<i>Eucladoceros giulii</i>	H (Br)	36 (15/21)	41.7	962 (557/405)	16.6	121 (70/51)	11.9	380
<i>Dama</i> sp.	H (Mf)	20 (3/17)	15.0	417 (231/186)	7.2	55 (30/25)	5.4	95
<i>Stephanorhinus etruscus</i>	H (Br)	6 (2/4)	33.3	90 (55/35)	1.6	27 (16/11)	2.6	1500
<i>Equus altidens</i>	H (Gr)	70 (32/38)	45.7	2562 (1183/1379)	44.2	457 (210/247)	44.8	350
<i>Vulpes praeglacialis</i>	C (Co)	1 (0/1)	0.0	24 (19/5)	0.4	12 (10/2)	1.2	5
<i>Canis falconeri</i>	C (Hy)	3 (0/3)	0.0	65 (40/25)	1.1	33 (21/12)	3.2	30
<i>Canis etruscus</i>	C (Co)	4 (0/4)	0.0	33 (20/13)	0.6	16 (10/6)	1.6	10
<i>Lynx</i> aff. <i>issiodorensis</i>	C (Hy)	1 (0/1)	0.0	6 (2/4)	0.1	3 (1/2)	0.3	10
<i>Megantereon whitei</i>	C (Hy)	3 (0/3)	0.0	16 (7/9)	0.3	8 (3/5)	0.8	100
<i>Homotherium latidens</i>	C (Hy)	2 (0/2)	0.0	7 (6/1)	0.1	3 (2/1)	0.3	250
<i>Pachycrocuta brevirostris</i>	C (Bc)	10 (4/6)	40.0	62 (34/28)	1.1	31 (17/14)	3.0	100
<i>Ursus etruscus</i>	O	3 (1/2)	33.3	27 (15/12)	0.5	14 (8/6)	1.4	375

iae of *Equus* and metapodials of *Eucladoceros* (Arribas and Palmqvist 1998: Figs. 7, 8). Articulated bones are relatively scarce, representing less than 20% of all elements in the sample; however, there is a low degree of horizontal dispersion, with abundant groups of disarticulated but associated elements, such as skulls with mandibles and metapodials with phalanges. The most frequently preserved articulations are those formed by tibiae-tarsal-metatarsal-phalanges, humerus-radius/ulna, radius-carpal-metacarpal-phalanges, and vertebrae.

The age estimated for individuals preserved in the assemblage included two major groups: immature or juvenile individuals with deciduous teeth, and adults with fully erupted permanent dentition (Table 1). Body mass estimates for adults were obtained from Palmqvist et al. (1996), who used "taxon-free" regression equations of mass on craniodental/postcranial measurements from modern species (Damuth and MacFadden 1990).

Inspection of data in Table 1 shows that herbivore taxa dominate the assemblage in both number of identifiable specimens (NISP) and

estimates of minimum number of individuals (MNI). More common herbivorous species (those with higher NISP and MNI values), such as the horse *Equus altidens* and the large deer *Eucladoceros giulii*, have high percentages of juveniles,  $>40\%$  in both cases (32/70 and 15/36, respectively). Among carnivores, only adult individuals are recovered, with the exception of the hyaenid and the ursid. Forty percent (4/10) of the individuals of *P. brevirostris* are juveniles, represented by deciduous teeth contained within the maxilla or mandible, indicating that these cranial elements were produced not by tooth replacement but as a consequence of the death of immature individuals.

#### An Overview of the Taphonomy of Venta Micena

Previous research on the taphonomy of Venta Micena (Palmqvist et al. 1996; Arribas and Palmqvist 1998; Arribas 1999; Palmqvist and Arribas 2001) focused on the analysis of size/abundance patterns in ungulate species using the model of Damuth (1982), and on the abundance of preserved epiphyses and complete

TABLE 2. Abundance of skeletal elements of large mammals grouped according to their potential for water dispersal (Voorhies' groups) in the subset used for taphonomic analysis ( $n = 1231$ ), and in the three better-represented taxa in the assemblage, the horse (*Equus altidens*;  $n = 488$ ), the buffalo (Bovini cf. *Damanisibos*;  $n = 95$ ), and the megacerine deer (*Eucladoceros giulii*;  $n = 138$ ).

Voorhies' groups	Skeletal element	$n_{total}$	%	$n_{horse}$	%	$n_{buffalo}$	%	$n_{deer}$	%
Group I	Isolated teeth	168	13.7	47	9.6	3	3.2	13	9.4
	Fragments of deer antlers	19	1.5	—	—	—	—	14	10.1
	Vertebrae	178	14.5	51	10.5	21	22.1	13	9.4
	Ribs	36	2.9	16	3.3	0	0.0	0	0.0
	Scapulae	31	2.5	12	2.5	2	2.1	11	8.0
	Ulnae	8	0.6	3	0.6	0	0.0	0	0.0
	Calcanei	36	2.9	14	2.9	8	8.4	8	5.8
	Astragali	51	4.1	23	4.7	10	10.5	8	5.8
Phalanges	72	5.9	38	7.8	7	7.4	5	3.6	
Group II	Humeri	78	6.3	24	4.9	12	12.6	9	6.5
	Radii	34	2.8	7	1.4	2	2.1	7	5.1
	Pelvis fragments	23	1.9	12	2.5	2	2.1	2	1.5
	Femora	32	2.6	25	5.1	0	0.0	0	0.0
	Tibiae	87	7.1	47	9.6	7	7.4	12	8.7
	Metapodials	258	21.0	145	29.7	11	11.6	25	18.1
Group III	Cranial elements	120	9.7	24	4.9	10	10.5	11	8.0

limb bones of ruminants. The results obtained indicated that most losses of paleobiological information during the taphonomic history of the assemblage were a consequence of the selective destruction of skeletal remains during the period when the bones were exposed on the surface before burial, and that the effect of this preservational bias was more pronounced in those species of smaller body size (Arribas and Palmqvist 1998; Arribas 1999).

The role of hyenas in the bone accumulation process at Venta Micena was determined by comparing the frequencies of different types of postcranial bones in this assemblage (e.g., vertebrae, ribs, limb and girdle bones, phalanges) with the corresponding figures for several recent and archaeological deposits accumulated by carnivores, rodents and hominids (Arribas and Palmqvist 1998: Table 2). Results indicated that *P. breivrostris* was the main agent responsible for the bone accumulation at Venta Micena, because the composition of the fossil assemblage is strikingly similar to bone accumulations produced by modern hyenas in which major limb bones predominate whereas ribs and vertebrae are comparatively scarce. Specifically, the relative abundances of limb bones and vertebrae/ribs in Venta Micena (79.3% and 14.3%, respectively) are similar to the frequencies of these elements in as-

semblages collected by spotted hyenas (*Crocuta crocuta*), 69.4–76.2% and 12.2–24.2%, respectively (Behrensmeyer and Dechant Boaz 1980; Brain 1981; Skinner and Van Aarde 1981; Bunn 1982; Skinner et al. 1986), but different from those accumulated by striped hyenas (*Hyaena hyaena*) and brown hyenas (*Parahyaena brunnea*), in which higher frequencies of limb bones (90.8–93.2%) and lower frequencies of vertebrae/ribs (4.2–7%) are found (Maguire et al. 1980; Skinner et al. 1980, 1995; Skinner and Van Aarde 1981, 1991; Kerbis Petherhans and Kolska-Horwitz 1992). However, Venta Micena resembles assemblages from dens of brown and striped hyenas in its high density of bones (Leakey et al. 1999). Spotted hyenas are efficient hunters, owing to their greater body size and strong social behavior, and produce a highly enriched milk; thus, they do not regularly carry carrion to their maternity dens to feed their cubs (Kruuk 1972; Ewer 1973; Mills 1989). Nonetheless, there are some reported cases of spotted hyenas accumulating huge amounts of skeletal remains (e.g., see Hill 1981 for a dense accumulation of bones within a breeding den in Amboseli National Park, Kenya), and this was certainly the case with the cave hyena (*Crocuta crocuta spelaea*) in the late Pleistocene of Europe (Fosse 1996). The differences in composition between the

assemblage accumulated by *Pachycrocuta* at Venta Micena and those collected by other species suggest that the life habits of the short-faced hyenas were not identical to those of any living hyaenid.

The quantitative study of differential preservation of major limb bones of ruminants in the assemblage (Palmqvist et al. 1996; Arribas and Palmqvist 1998) showed that bone-gnawing and -crushing behavior by hyenas of those ruminant carcasses transported to the maternity den resulted in the preferential consumption of longbone epiphyses with high fat contents, and thus the differential breakage of major limb bones according to their marrow yields. Such a selective pattern rules out the possibility that other processes (e.g., ungulate trampling) were responsible for bone fracturing.

The recovery of several deciduous teeth of *P. brevirostris* belonging to four individuals also suggests that the assemblage originated through accumulation of skeletal parts near shallow breeding dens excavated by the hyenas in the plains surrounding the Pleistocene lake (Arribas and Palmqvist 1998). The abundance of unworn deciduous hyena teeth rules out the possibility that bones were accumulated in open feeding places located at hunting sites distant from maternity dens, if we presume that, like modern hyenas, the cubs did not accompany adults on their search for ungulate carcasses.

A comparison of the Venta Micena assemblage with those from other Plio-Pleistocene lacustrine sites from the Guadix-Baza Basin (Arribas 1999) revealed that Venta Micena shows the highest diversity of large mammals, mainly because of the high diversity of carnivores, from opportunistic scavengers to large predators. The taxonomic richness of large mammals at Venta Micena (19 taxa) is similar to that recorded from a modern spotted hyena den developed on a calcrete paleosol in Amboseli (18 taxa) (Hill 1981). Similarly, Leakey et al. (1999) identified 15 species of mammals from skeletal remains collected by striped hyenas in Lothagam, Kenya, and Skinner et al. (1991, 1998) identified 11 mammalian taxa at two maternity den sites of brown hyenas from the west coast of Namibia. These

counts of taxonomic richness from hyena accumulations accurately reflect the composition of the available vertebrate prey community in these areas.

### Biostratinomic Analysis of the Assemblage

We have used here several biostratinomic variables to further characterize the bone assemblage from Venta Micena, following in part the procedure described by Behrensmeyer (1991) for studying vertebrate assemblages. Descriptive analysis was based on a subset of 1339 specimens, which includes 1020 identifiable skeletal remains (distributed among taxa in Table 1) as well as 211 bones and 108 bone shafts that could not be determined taxonomically. This sample comprises the well-restored specimens housed at the Museum of Paleontology of Orce (Palmqvist et al. 1996). The high value obtained for the Pearson product-moment correlation between the relative frequencies of taxa in the whole assemblage and in the subset (Table 1;  $r = 0.985$ ;  $p < 0.0001$ ) indicates that the latter represents a random sample of the entire assemblage.

Table 2 shows the abundances of different skeletal elements in the subset of large mammals and in the three most abundant taxa, the horse (*E. altidens*), the buffalo (Bovini cf. *Dmanisibos*), and the megacerine deer (*E. giulii*).

The ratio of isolated teeth to vertebrae (0.94:1) is close to the value expected in the absence of hydrodynamic sorting (1:1), indicating that the skeletal remains were not transported by fluvial processes prior to deposition (Behrensmeyer and Dechant Boaz 1980; Shipman 1981). The frequencies of bones grouped according to their potential for dispersal by water (i.e., Voorhies' groups) are as follows: 48.6% for Group I (isolated teeth, deer antlers, vertebrae, ribs, scapulae, ulnae, calcanei, astragali, phalanges), 41.7% for Group II (femora, tibiae, humeri, metapodials, pelvis, radii), and 9.7% for Group III (cranial elements); such a degree of skeletal completeness rules out the possibility of hydraulic sorting (Voorhies 1969).

Limb elements clearly dominate (57.7%) the sample, followed by vertebrae, cranial elements (cranial vaults, maxillae, and mandi-

bles; Fig. 2G–I), and ribs. Scapulae are mostly represented by proximal fragments. Diaphyses and distal epiphyses predominate among humeri (Fig. 2A). Femora are mainly preserved as fragments of diaphyses, and tibiae as distal epiphyses (Fig. 2B). The pelvis is represented only by fragments that preserve the acetabulum.

Analysis of weathering stages for the bones in the subset indicates exposure to the elements for only a relatively short time: 89.3% (784/878) of the skeletal elements show weathering stage 0 (Behrensmeyer 1978) and only 10.7% of the bones (of which two-thirds are metapodials) show weathering stage 1, with a few, shallow, small split-line cracks due to insolation (Fig. 2C) and without flaking of the outer surface (Arribas and Palmqvist 1998; Arribas 1999). Although low degrees of physico-chemical weathering could reflect protection by vegetation in moist conditions until burial, this was not the case here because most bones show no evidence of root marks. On the other hand, bones that were preserved complete lack sedimentary infilling, even in areas of the medullary cavity that are close to nutrient foramina, indicating that they were buried in fresh condition, with the periosteum intact (Arribas and Palmqvist 1998). Thus, these results suggest a very short period of subaerial exposure before burial (less than one year in most cases).

The detailed study of horse remains has shown that biostratinomic fractures are very abundant (Fig. 2), as only 29.1% of major limb bones are complete; metapodials are the most abundant bones preserved as complete elements, 82.2%. Among the fractured elements, type II spiral fractures (Shipman 1981; Lyman 1994) predominate (100% of fragmented humeri, femora, and radii; 74.4% of tibiae). Other types are longitudinal fractures in tibiae, undifferentiated fractures (all ribs and vertebrae, with the exception of some vertebrae that lack only apophyses), and maxillary bones with both cheek-tooth rows (33.3% of cranial elements). Gnaw-marks are very frequent on the horse remains: all cranial fragments, scapulae, humeri, radii, pelvis, femora, and tibiae show striations and gnaw-marks produced by carnivores; the preserved epiphyses have fur-

rows and punctures; and the diaphyses, as well as the skull bones, show scoring and pitting. These marks are also observed in all other taxa identified at Venta Micena. Coprolites (3–6 cm thick) are relatively common.

### Evaluation of Taphonomic Bias in the Assemblage

The taphonomic analysis of the large-mammal assemblage preserved at Venta Micena has revealed the existence of the following preservational biases, which took place consecutively during the biostratinomic stage and affected its original composition (Palmqvist et al. 1996; Arribas and Palmqvist 1998; Palmqvist and Arribas 2001): (1) scavenging by hyenas of ungulate prey hunted by hypercarnivores; (2) selective transport of carcasses and bone remains to their maternity dens; and (3) differential breakage of major limb bones within the dens. In the following sections we evaluate the importance of these biases and their consequences for the composition of the assemblage, with a special focus on the transport of carcasses and the breakage of bones from horse (*E. altidens*) and buffalo (Bovini cf. *Dmanisibos*), which are two of the better-represented ungulate taxa in the assemblage.

*Bias 1: Scavenging of Ungulate Prey Selectively Hunted by other Predators.*—Previous research on the composition of the bone assemblage (Palmqvist et al. 1996; Arribas and Palmqvist 1998) has shown that the overwhelming majority of skeletal remains preserved in Venta Micena were scavenged by hyenas from carcasses of ungulates preyed upon by hypercarnivores (i.e., species in which vertebrate flesh represented >70% of diet). The selection by hypercarnivores of specific ungulates was basically a function of differences in the body mass of the prey—between juveniles and adults as well as between the sexes.

The evidence of prey selection at Venta Micena is the following: (1) U-shaped (i.e., bimodal) attritional mortality profiles deduced from crown height measurements for those herbivore species that are well represented in the assemblage, indicating a strong selection by predators of very young and old individuals (Palmqvist et al. 1996: Fig. 8); (2) the interspecific analysis of the relative abundance

of juveniles with deciduous teeth, and adults with permanent dentition, which shows that juveniles represent 16.7% (8/48) of all individuals in ungulate species <300 kg, yet the proportion of juveniles increases to 48.0% (72/150) in those species >300 kg (these percentages are significantly different according to a one-tailed *t*-test:  $t = 4.63$ ;  $p < 0.0001$ ); (3) the presence of many metapodials with severe osteopathologies (Palmqvist et al. 1996: Fig. 11A,B), such as arthrosis, which limited the locomotor capabilities of the ungulates and therefore their ability to escape from predators; and (4) the sex ratio deduced from the size distribution of metapodials in large prey species, such as horse and buffalo, which is biased in favor of females in both cases (approximately 1 male : 3–4 females [Palmqvist et al. 1996: Fig. 11C]). This sex ratio suggests that females were more vulnerable to predation because of their smaller body size.

Given that most carnivores usually hunt herbivores within a narrow range of body mass around the same size as that of the predator (Kruuk 1972; Schaller 1972 and references therein), the wide range of body mass represented by the ungulate taxa preserved in the assemblage (10–6000 kg) suggests that in most cases these animals were preyed upon by different carnivore species (Palmqvist et al. 1996).

Hypercarnivores are represented in the assemblage by four species—two saber-tooths (*Homotherium latidens* and *Megantereon whitei*), a felid (*Lynx* aff. *issiodorensis*), and a wild dog (*Canis falconeri*).

*M. whitei* (Fig. 3) had an intermediate body size (~100 kg), similar to that of a jaguar, *Panthera onca* (Martínez-Navarro and Palmqvist 1995, 1996). Judging from the low value estimated for the brachial index (i.e., radius length : humerus length, ~80%) it was an ambush predator, hunting in closed, forested habitats and presumably preying on browsing and mixed-feeding ungulates of intermediate to large body mass (Lewis 1997). This reconstruction of its predatory behavior is corroborated by the fact that the metapodials were comparatively shorter than those of large modern felids and other saber-tooths. This dirk-toothed machairodont had a strong body

with a short back, powerfully developed forelimbs with large claws, and extremely long, sharp, laterally compressed (and inherently fragile) upper canine teeth. The brain was small in relation to *Homotherium*'s, showing olfactory lobes that were well developed. All these features give the strong impression of an animal built for capturing prey using a short rush and then using its considerable strength to bring down and hold prey with the forelimbs, before killing with a slashing bite to the throat (Turner and Antón 1998; Arribas and Palmqvist 1999). A similar hunting behavior was inferred by Anyonge (1996) for the closely related genus *Smilodon*, a possible descendant of *Megantereon* in the New World.

*Homotherium* (Fig. 3) was a scimitar-toothed machairodont with relatively long and slender limbs, which provided considerable leverage (Turner and Antón 1998; Martin et al. 2000). According to regressions of body mass against postcranial measurements in modern carnivores (Anyonge 1993), it was similar in size to a modern male lion, *Panthera leo* (150–220 kg). The regression of body mass on lower carnassial length in modern felids (Van Valkenburgh 1990), however, provides a larger size estimate for the Venta Micena *H. latidens* (Palmqvist et al. 1996), 250 kg. The upper canines were comparatively shorter and broader than those of *Megantereon*, bearing coarse serrations in the enamel of the posterior margin. The forelimb was more elongated than the hindlimb, indicating that the animal probably had a sloping back. The claws of *Homotherium* appear to have been small, with the exception of a well-developed dewclaw in the first digit of the forefoot. The elongated forelimb and smaller claws suggest increased cursoriality and less prey-grappling capability than other saber-tooths (Rawn-Schatzinger 1992; Turner and Antón 1998; Arribas and Palmqvist 1999). Both the comparatively high brachial index ( $\geq 100\%$  [Lewis 1997]) and the results obtained by Anyonge (1996) in a multivariate analysis of the postcranial skeleton of extant and extinct felids, indicate that *Homotherium* was a pursuit predator, which presumably hunted very large grazing and mixed-feeding ungulates in open habitats. *Homotherium* had a large brain relative to other saber-tooths, with



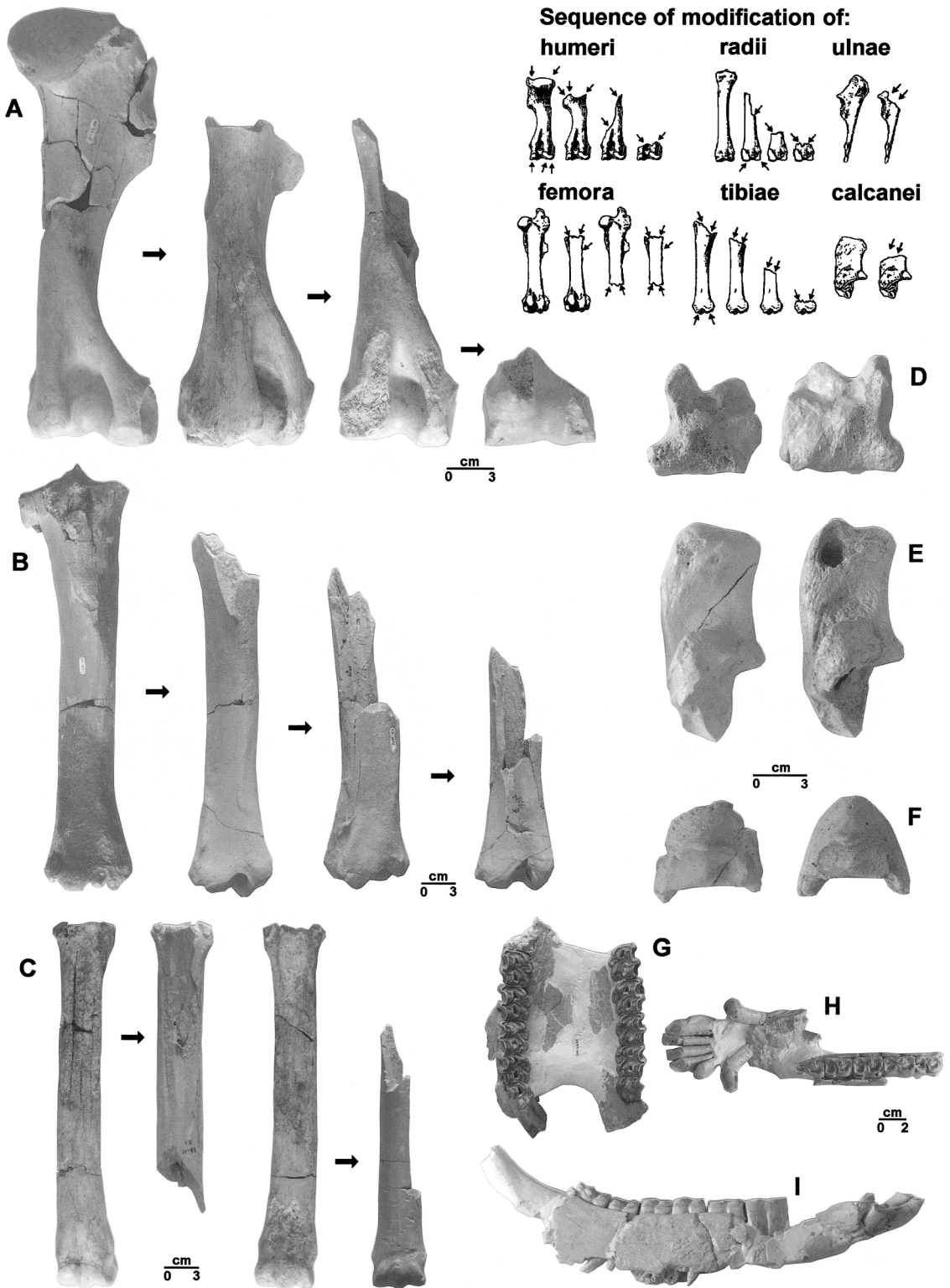


FIGURE 2. Selected examples of equid bones from Venta Micena, with evidence of modification by hyenas: A, B, Humeri and tibiae, respectively, showing gnawing of epiphyses, spiral and longitudinal fractures. C, Third metatarsals, complete and fractured, showing longitudinal and spiral fractures made by hyaenid crushing, and orthog-

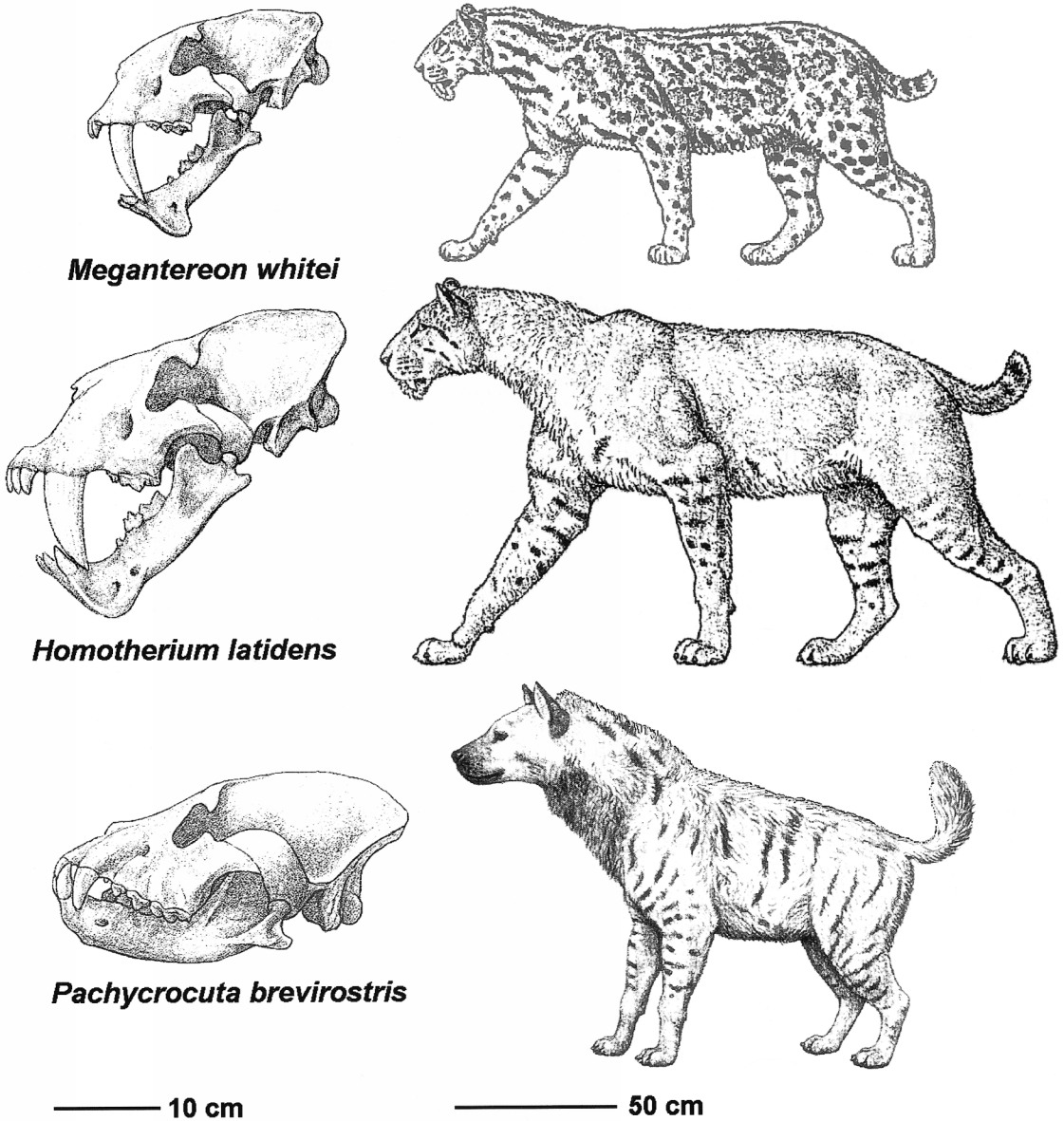


FIGURE 3. Skulls and reconstructions of the life appearance of the three largest carnivore species preserved at Venta Micena, the dirk-tooth *Megantereon whitei*, the scimitar-tooth *Homotherium latidens*, and the giant hyena *Pachycrocuta brevirostris*. All drawn to scale, with a typical height at shoulder of 110 cm for *Homotherium*. Specific coat patterns are unknown but typical of those seen across the range of living felids and hyaenids. Drawings by Mauricio Antón.

onal diagenetic fractures in the diaphyses due to sediment compaction. D, Astragali. E, Calcanei; one calcaneum shows marks made by insect larvae. F, Third phalanges; one phalanx is partially gnawed by hyenas. G, Maxillae gnawed by hyenas, indicating an extreme destruction of the splanchnocranium. H, I, Mandibles gnawed and fragmented by hyenas. Typical sequences of bone modification by hyenas for postcranial elements of *Equus* (Arribas 1999; Arribas and Palmqvist 1998) are also indicated.

an enlargement of the optic center, a condition similar to that of the cheetah, *Acinonyx jubatus* (Rawn-Schatzinger 1992). Turner and Antón (1998) suggest that such a cursorial lifestyle and hunting strategy would imply some degree of group activity to bring down and restrain prey. In addition, given that a pursuit strategy for hunting can be deployed only in relatively open terrain, group behavior may be needed to repel the inevitable attention of scavengers. The likelihood of group activity is suggested by the similarly proportioned American species, *H. serum*, which is known in some numbers (NISP >250, MNI = 33) from the late Pleistocene site of Friesenhahn cave, Texas. At this site, *H. serum* is associated with numerous remains (NISP >900 [Rawn-Schatzinger 1992: Table 38]; MNI = 34 [Marean and Ehrhardt 1995: Fig. 1]) of mammoths—one adult and the remainder juveniles—and it has been suggested that successful predation of mammoths most likely would require group hunting.

*C. falconeri* was a hypercarnivorous canid of ~30 kg, according to the results of multivariate analysis and multiple regression of body mass on craniodental measurements in modern canids (Palmqvist et al. 1999). The second metacarpal has a very reduced articular facet with the first metacarpal, which indicates that the latter bone was vestigial if not absent, a condition similar to that of African painted dogs (*Lycaon pictus*); this suggests increased cursoriality for *C. falconeri*. This predator probably hunted small to medium-sized grazing ungulates (50–300 kg) in open to intermediate forested country.

*Pachycrocuta brevirostris* (Fig. 3) was a bone-cracking carnivore with a body 10–20% larger than the modern spotted hyena and was well adapted for dismembering carcasses and consuming bone (Palmqvist et al. 1996; Turner and Antón 1996; Arribas and Palmqvist 1998; Saunders and Dawson 1998). Apart from its size, this short-faced hyena differed from other species in the relative shortening of its distal limb segments (Turner and Antón 1996): the brachial index is close to 88%, whereas in modern hyaenids the values range between 99% and 106%; the crural index (i.e., tibia length : femur length) is 74%, whereas the cor-

responding figures for modern species range between 80% and 89%. These differences suggest a less cursorial lifestyle for *P. brevirostris*. It is also possible that the shortening of the distal limb segments could provide greater power and more stability to dismember and carry large pieces of carcasses, which perhaps could be obtained from aggressive scavenging (i.e., kleptoparasitism).

The proportion of juveniles in a population of a given species depends on two factors (Palmqvist et al. 1996): the reproduction rate (i.e., the annual birthrate) and the duration of infancy (i.e., the time spent as a juvenile individual). Rates of birth and death scale to the  $-0.3$  power of adult body mass ( $M$ ), whereas generation time (measured by life expectancy at birth, duration of infancy, or age at death) is interspecifically related to body mass by a power of 0.3 (Damuth 1982; Peters 1983; Calder 1984). As a result, larger species have lower birth and mortality rates per unit of absolute time but not per unit of biological time (i.e., relative to maximum life span), because rates of birth and death per generation are size independent. A third factor, differences in age-specific mortality rate, could be relevant here, as high adult mortality would increase the proportion of juveniles in the population and vice versa. However, data on cohort analysis and survivorship curves for African herbivores ranging in adult body mass between <50 kg and >3500 kg (Western 1979, 1980) show no differences among species in the age-specific mortality rate (e.g., the life expectancy at birth fluctuates around 30% of total life span, with small variations not related to body size). Moreover, several studies on the timing of ontogeny in eutherian mammals (summarized in Peters 1983) indicate that, regardless of size, a given developmental phase requires a constant proportion of the mammal's life; thus, the relative time spent as a juvenile individual does not scale with body mass.

The ratio of juvenile to adult individuals in a population would be the product of annual birthrate ( $B_r$ ) and duration of infancy ( $D_i$ ):

$$\% \text{ juveniles} \sim B_r D_i = M^{-0.3} M^{0.3} = M^0.$$

This relationship implies that the proportion

TABLE 3. Differences between primary bone assemblages collected by predators, such as leopards, and non-primary, secondary assemblages accumulated by scavenger carnivores, such as hyenas (Maguire et al. 1980; Richardson 1980; Skinner et al. 1980, 1986, 1995; Skinner and Van Aarde 1981, 1991; Vrba 1980; Brain 1980, 1981; Hill 1981; Shipman 1981; Klein and Cruz-Urbe 1984; Behrensmeier 1991; Kerbis Petherhans and Kolska-Horwitz 1992; Palmqvist et al. 1996; Arribas and Palmqvist 1998). Data for Venta Micena also shown (a = estimated from the whole collection, b = estimated from the subset used for taphonomic analysis).

Characteristics of the bone assemblage	Primary assemblage, collected by predators	Secondary assemblage, collected by scavengers	Venta Micena assemblage
Proportion of vertebrae and ribs in relation to girdle and limb bones	High, 1:4 (range = 1:3–5)	Low, 1:9 (range = 1:4.5–25)	16.9% (429/2544) <sup>a</sup>
Abundance of articulated bones, in anatomical connection	Articulated elements are quite abundant	Articulated bones are scarce (exceptions: metapodials and phalanges, vertebrae)	20.0% (204/1020) <sup>b</sup>
Abundance of major longbones preserved complete	High and not related to their marrow content	Low, inversely related to marrow yield; spiral and longitudinal fractures are abundant	27.6% (137/497) <sup>b</sup>
Abundance of limb bone epiphyses in relation to diaphyses	High (2:1), without preferential destruction of skeletal parts of low structural density	Comparatively low (1.5–1:1), with evidence of preferential consumption of low-density epiphyses	139.4% (693/497) <sup>b</sup>
Carnivore/ungulate index, calculated from MNI counts	High (25–50%) or very high (>50%, in death traps)	Low (5–15%), similar to that found in modern communities	13.6% (27/198) <sup>a</sup>
Relative abundance of juvenile ungulates, with deciduous teeth	High proportion (>25%)	Low proportion (<25%)	40.4% (80/198) <sup>a</sup>
Proportion of young/adult individuals for ungulate species	Increases as a function of species body mass	Not related with the size of species	Positively correlated with species mass
Range of body mass covered by the species preserved in the assemblage	Narrow, usually around the same size as that of the predator	Wide, in general more than two orders of magnitude (from <10 kg to >1000 kg)	5–6000 kg <sup>a</sup>
Richness of species (large mammals)	Comparatively low (only prey species)	High diversity (all scavenged species)	19 <sup>a</sup>

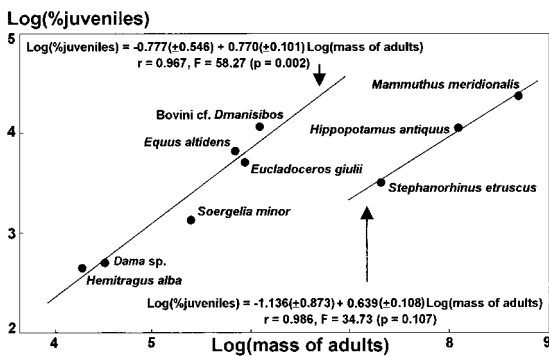


FIGURE 4. Least-squares regression analysis of the proportion of juvenile individuals (estimated from MNI counts) on adult body mass (in kg) for ungulate species ( $n = 9$ ) of the Venta Micena assemblage (data from Table 1). Separate analyses were conducted for two groups of prey species, the first of which (<1000 kg of estimated mass for the adult individuals) were presumably hunted by *Megantereon whitei* and *Canis (Xenocyon) falconeri*, and the second one (>1000 kg) by the large saber-tooth *Homotherium latidens*.

of juveniles in any ungulate population is approximately constant (30–40%) and independent of species body size (Palmqvist et al. 1996).

As previously indicated, in the Venta Micena assemblage the juvenile/adult ratios of ungulates (estimated from MNI counts based on deciduous and permanent teeth) as a function of adult body mass suggests that mortality age profiles differed depending on the size of the prey. This would be the consequence of selection by predators, which increased the proportion of young and more vulnerable individuals of those ungulate species of larger size. This interpretation is in accordance with available data on prey selection by Recent carnivores as a function of size and age of their preferred prey (Palmqvist et al. 1996: Fig. 7; Arribas and Palmqvist 1998: Table 3). Figure 4

shows the increase in the value of the juvenile/adult ratio in relation to the mass estimated for the ungulate species from Venta Micena.

Therefore, the positive slope for the relationship between the proportion of juveniles and the mass estimated for the adults indicates that the Venta Micena assemblage was not formed through catastrophic mortality events during droughts (in such case the abundance of juveniles of different species would be approximately constant and size-independent). We can conclude that the vast majority of skeletal elements accumulated by hyenas came from attritional mortality in ungulate populations, caused by selective choice of carnivores.

*Bias II: Selective Transport of Carcasses and Skeletal Parts.*—According to field data collected by Kruuk (1972) in the Serengeti and Ngorongoro National Parks (Tanzania), modern spotted hyenas are efficient hunters that hunt their prey in 58.3% of cases and scavenge ungulate carcasses in the remaining 41.7% of cases. Of those ungulates scavenged, individuals dead by illness or accident represent 19.4%, whereas the rest are carcasses of prey hunted and partially defleshed by lions and painted dogs. The relative abundances of ungulate prey of different body size classes hunted by lions and painted dogs correlate well with the frequencies of ungulate populations (Kruuk 1972; Schaller 1972).

The distribution of specimens among size classes in the ungulate assemblage from Venta Micena (Fig. 5; frequencies estimated from MNI counts in Table 1) is different from the frequencies of ungulates hunted by spotted hyenas according to a  $\chi^2$  test for the cumulative differences ( $\chi^2 = 148.2$ ;  $df = 4$ ;  $p < 0.0001$ ), but remarkably similar to those in which spotted hyenas scavenge carcasses of animals killed by lions and wild dogs ( $\chi^2 = 17.8$ ;  $p < 0.01$  for all size classes;  $\chi^2 = 4.3$ ;  $df = 3$ ;  $p > 0.1$  for ungulates weighing  $>50$  kg). 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 ( $<50$  kg), which are underrepresented in the fossil assemblage (one individual of *Caprini* indet.,

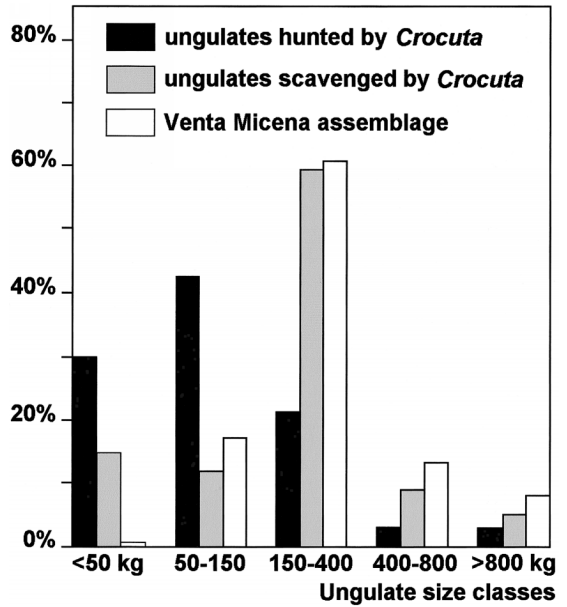


FIGURE 5. Comparison between the relative abundances of ungulate size classes in the prey hunted and scavenged by modern spotted hyenas (*Crocota crocuta*) in the Serengeti National Park (data from Kruuk 1972) and the frequencies of such categories in the ungulate assemblage preserved at Venta Micena (data from Table 1, MNI counts).

1/198, Table 1) but represent 14.5% (80/551 [Kruuk 1972: Table 26]) of the carcasses scavenged by spotted hyenas (one-tailed  $t$ -test:  $t = 9.68$ ;  $p < 0.0001$ ). This indicates that short-faced hyenas preferentially consumed small ungulates in situ and selectively transported carcasses and body parts of larger species to their maternity dens.

These results suggest that the predatory behavior of *Pachycrocota* differed from that of *Crocota*, because modern spotted hyenas both hunt and scavenge ungulates, whereas the short-faced hyenas seem to have relied more heavily on prey hunted by other predators; therefore, the behavior of *Pachycrocota* was probably more similar to that of modern brown and striped hyenas, which are predominantly scavengers (Mills 1989). This trophic dependence was facilitated by the fact that ungulate carcasses left by machairodonts and hypercarnivorous canids would retain variable amounts of flesh and all nutrients within the bones, given that the slicing dentition of these carnivores made them incapable of bone

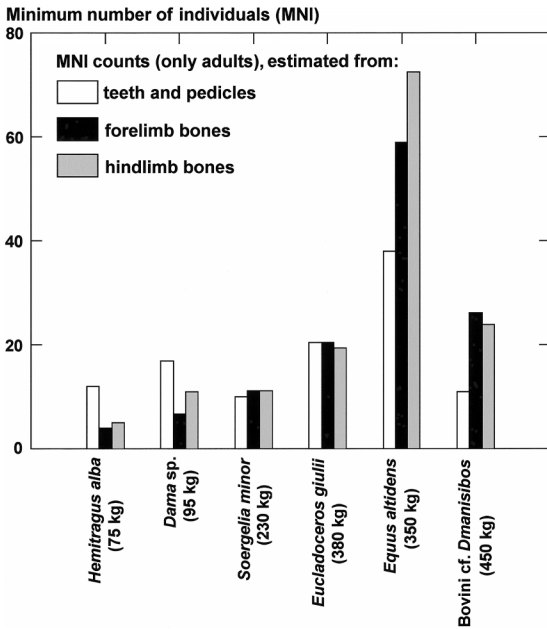


FIGURE 6. Abundance of ungulate species in Venta Micena, according to minimum number of adult individuals (MNI), calculated from craniodental elements (permanent teeth and antlers or horn bases) and from minimum number of elements (MNE) of postcranial bones (independent estimates for forelimb and hindlimb bones). Caprini indet., *Praeovibos* sp., and species >1000 kg were excluded from this analysis owing to their low sample sizes. Species ordered by decreasing values in the ratio  $MNI_{(teeth)} : MNI_{(bones)}$ .

cracking (Marean 1989; Arribas and Palmqvist 1999).

The bone assemblage of Venta Micena can thus be considered as mixed, showing some features typical of primary assemblages, collected by predators, and others that are characteristic of non-primary, secondary assemblages accumulated by scavenger carnivores (Table 3).

The bias produced by the selective transport of ungulate remains is particularly evidenced by the differential representation of preserved skeletal parts. The abundance of each taxon can be estimated by MNI counts obtained from teeth and cranial elements (i.e., antlers and horn bases in the case of ruminants), as well as from MNI counts based on minimum number of elements (MNE) estimated from postcranial remains (i.e., forelimb and hindlimb bones, complete elements or those represented by isolated epiphyses). Figure 6 shows that for small ungulates, such as the

goat (*Hemitragus alba*; 75 kg of estimated mass for adult individuals) or the fallow deer (*Dama* sp.; 95 kg),  $MNI_{(teeth)}$  gives a higher estimate of abundance than  $MNI_{(bones)}$  ( $\chi^2$ -test:  $\chi^2 = 5.33$  and 5.88;  $p < 0.05$  in both cases;  $MNI_{teeth}$  counts used as expected frequencies). For *Soergelia minor*, a bovine of intermediate mass (225 kg), the two MNI counts are similar ( $\chi^2 = 0.10$ ;  $p > 0.5$ ). Finally, ungulate taxa of larger size, such as the horse (*E. altidens*; 350 kg) and the buffalo (Bovini cf. *Dmanisibos*; 450 kg), are better represented by postcranial elements ( $\chi^2 = 30.42$  and 20.45, respectively,  $p < 0.0001$  in both cases).

These differences are in large part an indication of how the hyenas handled the carcasses they scavenged. In the case of species that were preferentially transported as complete carcasses, the original abundances, estimated from MNI counts based on teeth and bones, would be approximately the same as the abundances in the accumulated assemblage. However, because hyenas selectively fracture major longbones and destroy limb bone epiphyses to get at the marrow and fat, MNI estimates for the assemblage that are based on teeth should be higher than those based on postcranial elements. Therefore small ungulate species (<100 kg), which are represented by an  $MNI_{(teeth)} : MNI_{(bones)}$  ratio of approximately 2:1 in the Venta Micena assemblage (*H. alba* and *Dama* sp.), were probably transported in most cases as complete carcasses. In the case of larger species (>300 kg), selective transport of marrow-rich body parts (i.e., the forelimb in buffalo and the hindlimb in horse) is suggested by the reverse ratio ( $MNI_{teeth} : MNI_{bones} = 1:2$ ). Finally, for ungulate species of intermediate size (100–300 kg), such as *S. minor*, postcranial elements were transported by hyenas with a somewhat higher frequency than heads (after preferential consumption of major longbones, MNI counts calculated from teeth and bones are similar, 1:1).

The only exception to this trend is the large megacerine deer *E. giulii*. Although its body mass is estimated at 380 kg for adult individuals, MNI counts from teeth and bones are quite similar (Fig. 6;  $\chi^2 = 0.05$ ;  $p > 0.5$ ). This may be due to two reasons: (1) major limb bones are relatively slender in this species and

TABLE 4. Number of forelimbs and hindlimbs (calculated from MNE counts for each major limb bone) of *Equus altidens* and Bovini cf. *Dmanisibos* from Venta Micena. Total marrow yields and flesh weights of forelegs and hind legs estimated from values for modern *Equus caballus* (Outram and Rowley-Conwy 1998) and *Bison bison* (Brink 1997).

	<i>Equus altidens</i>		Bovini cf. <i>Dmanisibos</i>	
	Forelimbs	Hindlimbs	Forelimbs	Hindlimbs
Number of legs (right/left)	118 (59/59)	141 (72/69)	44 (18/26)	41 (24/17)
Total marrow yields (g)	77.1	115.4	622.0	558.4
Flesh content (kg)	14.0	46.2	13.0	43.9

were presumably more easily fractured by hyenas; and (2) the antlers of the males were particularly large (~1.5 m in width), and the hyenas might have transported the heads to their dens to exploit mineral phases and hemopoietic tissues supplied by the antlers; interestingly, fragments of deer antlers are well represented in the assemblage (Table 2).

The evidence that hyenas selectively transported certain parts from the carcasses of large ungulate species suggests that each short-faced hyena foraged alone in search of scavengeable carcasses, as do modern brown hyenas (Mills 1989). If they had foraged in groups, as spotted hyenas often do (Kruuk 1972; Mills 1989), the members of the hyena clan would have transported all the anatomical regions of each carcass scavenged to their maternity den; large ungulate taxa would then be represented in the assemblage by similar numbers of postcranial bones and craniodental elements, rather than the skewed ratio we observed.

Table 4 shows the number of forelimbs and hindlimbs calculated from MNE counts for each limb bone in two taxa well represented in the assemblage, the equid *E. altidens* and the buffalo Bovini cf. *Dmanisibos*. The corresponding values for flesh and marrow contents, estimated from data for major longbones in two modern, similarly sized herbivores—the horse, *Equus caballus* (Outram and Rowley-Conwy 1998) and the North American plain bison, *Bison bison* (Brink 1997), are also provided. The ratio of forelimbs to hindlimbs is 0.837 in the Venta Micena horse, which is clearly different from that of flesh yields provided by forelimbs and hindlimbs, 0.303, and closer to the corresponding ratio estimated for marrow contents, 0.668. In the case of the buf-

falo, the ratio of forelimbs to hindlimbs is 1.073, again a value different from that estimated for flesh contents, 0.296, but very close to the value obtained for marrow, 1.114. This suggests that marrow content was the main reason hyenas transported limb bones to their maternity dens.

*Bias III: Consumption of Epiphyses and the Reduction of Major Limb Bones.*—Typical bone-consuming sequences for each postcranial element of *Equus* were described recently for Venta Micena by Arribas and Palmqvist (1998) and Arribas (1999). Three distinct types of bone-consuming activities by hyenas were established (Fig. 2), depending on the position of the bone in the horse skeleton (which is related to the hyenas' pattern of disarticulation), as well as on the amount of within-bone nutrients (i.e., grease and marrow content) and mineral density:

1. Humerus, radius, tibia, ulna, and calcaneum: these are consumed following an invariant proximodistal pattern. The reduction of these bones by hyenas starts with gnawing the proximal epiphysis, then is followed by fracturing the diaphysis, and is finished by gnawing of the distal epiphysis, which usually shows abundant tooth marks.

2. Femur: this is the only element in which the sequence of consumption follows a variable direction (i.e., from the proximal epiphysis to the distal epiphysis or vice versa) and both epiphyses are lost.

3. Third metacarpal and metatarsal: these bones are modified by crushing, with a variable direction of activity, and they tend to be more abundantly preserved as complete elements than other major limb bones, owing to their higher mineral density and lower marrow yields.

Therefore, these results indicate that the skeletal elements preserved in the fossil assemblage are those remaining once all within-bone nutrients were consumed by hyenas. To evaluate quantitatively this taphonomic bias on the preservational completeness of the bone assemblage, we performed a comparative analysis of the preservational state and abundance of postcranial elements in *E. altidens* and Bovini cf. *Dmanisibos*. We hypothesized that there would be differences in the abundance of postcranial elements because there are differences in their within-bone nutrients (Emerson 1990; Brink 1997; Arribas and Palmqvist 1998; Outram and Rowley-Conwy 1998). Figure 7A shows the raw abundance in which major limb bone epiphyses of horse are preserved in the assemblage, as a function of their mean marrow content (estimated from values for *E. caballus* in Outram and Rowley-Conwy 1998). A least-squares regression revealed an inverse relationship between both variables, which is statistically significant ( $r = -0.60$ ;  $p < 0.05$ ). This indicates that hyenas selectively consumed the epiphyses of bones having higher within-bone nutrient content (e.g., proximal and distal femur, proximal tibia), and acted less intensely on those yielding lower marrow values (e.g., metapodials, distal tibia).

The raw abundance of major longbone epiphyses of buffalo in relation to their marrow weight is shown in Figure 7B (data for *B. bison* in Brink 1997). The regression line also shows a negative slope ( $r = -0.85$ ,  $p < 0.0001$ ), which indicates that the skeletal parts better represented among the surviving epiphyses are those with lower marrow yields. However, the regression obtained for this species is statistically more significant than in the case of *E. altidens*, owing to the higher marrow contents of bovine epiphyses (six-fold on average). This suggests a great selectivity in the bone-cracking behavior of hyenas, which was in turn translated into a differential preservation of the skeletal elements of both taxa in the bone assemblage.

Three major factors therefore appear to have biased the composition of the Venta Micena assemblage: the scavenging by adult hyenas of ungulate prey hunted by hypercarni-

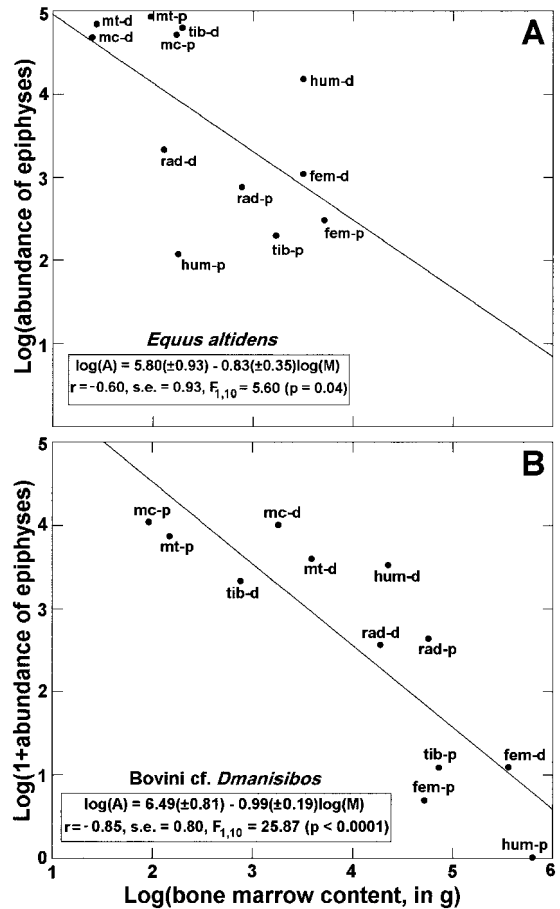


FIGURE 7. Least-squares regression analysis of the raw abundance at Venta Micena of preserved major limb bone epiphyses of horse (*Equus altidens*) (A) and buffalo (Bovini cf. *Dmanisibos*) (B) on their mean marrow content, estimated from data for modern horse (*Equus caballus*) by Outram and Rowley-Conwy (1998) and bison (*Bison bison*) by Brink (1997) (variables log-transformed).

vores (bias I); the selective transport of whole carcasses or certain anatomical parts, depending on the size of the ungulate species scavenged (bias II); and the preferential breakage in the dens of bones with higher marrow content (bias III). Although these biases decreased the amount of paleobiological information preserved in the assemblage, the representation of the original mammalian community is valid, thanks to the scavenging behavior of hyenas. A collection of bones from the prey of a single predator may differentially sample particular species because of the predator's prey preferences, and such accumulation would provide a poor estimate of standing diversity



in the paleocommunity (Vrba 1980; Brain 1981; Shipman 1981; Behrensmeyer 1991). This is not the case at Venta Micena, however, where the skeletal remains of a wide spectrum of ungulate prey hunted by several species of hypercarnivores in different habitats were collected by hyenas, thus providing a detailed picture of the diversity of large mammals that inhabited southern Spain during early Pleistocene times. This is corroborated by several studies of recent bone assemblages collected by hyenas (Maguire et al. 1980; Skinner et al. 1980; Hill 1981; Skinner and Van Aarde 1981, 1991; Skinner et al. 1980, 1986, 1995, 1998; Kerbis-Petherhans and Kolska-Horwitz 1992; Leakey et al. 1999), which indicate that the assemblages accurately reflect the composition of the mammalian fauna in areas adjacent to the maternity dens.

The assemblage from Venta Micena was probably accumulated over a very short time span; thus it is evidently not time-averaged and retains a relatively high degree of environmental resolution. The fact that most skeletal elements are unweathered suggests this, as do inferences on hyaenid mortality patterns. According to data on population densities of modern spotted hyenas obtained by Kruuk (1972), the mean numbers of adult and juvenile spotted hyenas per den in Serengeti are 55 and 12, respectively. With Kruuk's estimate of mean annual mortality at 16.7%, approximately 11 individuals of the hyena clan die each year, a figure remarkably similar to the MNI calculated for *P. brevirostris* in the fossil assemblage (10 individuals, 6 adults and 4 juveniles; Table 1). In fact, the juvenile short-faced hyenas from Venta Micena can be classified within two age groups: two newborn individuals, with unworn milk teeth, and another two that show deciduous dentition severely worn and being replaced by permanent teeth, indicating that they were at the end of their first year of life. This suggests that during a single season, probably summer, all four of these individuals died.

### Conclusions

Taphonomic processes have previously been interpreted as solely destructive forces. Information loss in terrestrial and fluvial bio-

tas results largely from such processes as transport, disarticulation, sorting, and breakage of skeletal parts by water, predators, scavengers, and trampling. However, such biostratigraphic processes imprint a taphonomic signature that often provides new data useful for decoding paleobiological information (Wilson 1988; Fernández-López 1991; De Renzi 1997). The assemblage of large mammals from Venta Micena constitutes a good example of how analytical studies can contribute toward re-creating a significant fraction of paleobiological information lost during the taphonomic history.

As we have discussed here, it is even possible to infer information that was *not* originally preserved in the bone assemblage, such as the behavior of the extinct hyena *P. brevirostris*, a species that differed from the modern spotted hyena in being a strict scavenger of ungulate carcasses selectively preyed upon by hypercarnivores. This inference was based on the quantitative study of the preservational bias introduced by the scavenging behavior of this giant hyena, which is shown to have been highly specialized.

However, similar paleobiological inferences may be obtained only in assemblages that were collected during the biostratigraphic stage by biological agents, like hyenas, hominids, or porcupines. Other types of terrestrial accumulations, where the bones were accumulated exclusively by physical agents (e.g., fluvial assemblages), would reveal useful sedimentological and paleoenvironmental data (e.g., strength and direction of water currents), but because the skeletal remains of such assemblages are frequently mixed, hydrodynamically sorted, and even reworked, decoding the taphonomic information locked in these assemblages would contribute little reliable paleobiological information about the structure and composition of the original paleocommunity from which they were derived. In this context, the macrovertebrate assemblage from Venta Micena constitutes an exceptional window for the detailed study of the mammalian communities that inhabited Western Europe during the early Pleistocene and the relationships among the species that lived within them.

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