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## The giant hyena *Pachycrocuta brevirostris*: Modelling the bone-cracking behavior of an extinct carnivore

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## ABSTRACT

The giant hyena *Pachycrocuta brevirostris* was the largest bone-cracking carnivore that ever existed. With the mass of a lioness, it had massive limbs with shortened distal bones and a heavy, powerfully built mandible with robust, well-developed premolars. All these features reflect its adaptation for dismembering ungulate carcasses, transporting large pieces of them without dragging to the denning site and fracturing bones. This paper estimates the relative contribution of hunting and scavenging to the diet of this extinct hyena, using a combined biomechanical and taphonomic approach. Analysis of the bone-cracking behavior of *P. brevirostris* was based on the abundance of skeletal elements in the large mammals assemblage from Venta Micena (Guadix-Baza basin, southeast Spain), a locality currently interpreted as an early Pleistocene hyena den. The distribution of major limb bones of ungulates among complete elements, isolated epiphyses and diaphyses were analyzed using contingency tables and correspondence analysis. Results obtained showed that the bones with greater marrow contents (femur, humerus and tibia) were preferentially fractured by the hyenas, while those others with less nutritional value (radius and metapodials) were better represented as complete elements in the assemblage. The quantitative analysis of the preservational state of skeletal elements allowed testing specific patterns of bone modification by the giant hyenas, such as a proximodistal sequence of consumption for humerus and tibia, thus revealing the highly specialized bone-cracking behavior of *P. brevirostris*. Regression equations adjusted with modern carnivores for body size on craniodental and postcranial measurements provide an average estimate of mass of ~110 kg for the giant hyena. The high moment arms for masseter and temporalis muscles indicate a substantial strength for bone fracturing with the well-developed premolar teeth. Jaw depth provided resistance against dorsoventral loads during bone-cracking activities. However, the moment arm of resistance for an object positioned at the canines reveals a loss of bite strength compared with spotted hyenas and thus less predatory abilities. These results are in agreement with the scavenging niche deduced for *P. brevirostris* from taphonomic analysis.

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## 1. Introduction

*Pachycrocuta brevirostris* (Aymard) (Mammalia, Carnivora, Hyae-nidae) was the largest hyaenid that ever existed, with a body size 20% larger than that of the modern spotted hyena (*Crocuta crocuta*) and was well adapted for dismembering carcasses and consuming bone (Fig. 1) (Werdelin and Solounias, 1991; Turner and Antón, 1996; Arribas and Palmqvist, 1998; Saunders and Dawson, 1998; Werdelin, 1999; Palmqvist and Arribas, 2001). The basal lengths of

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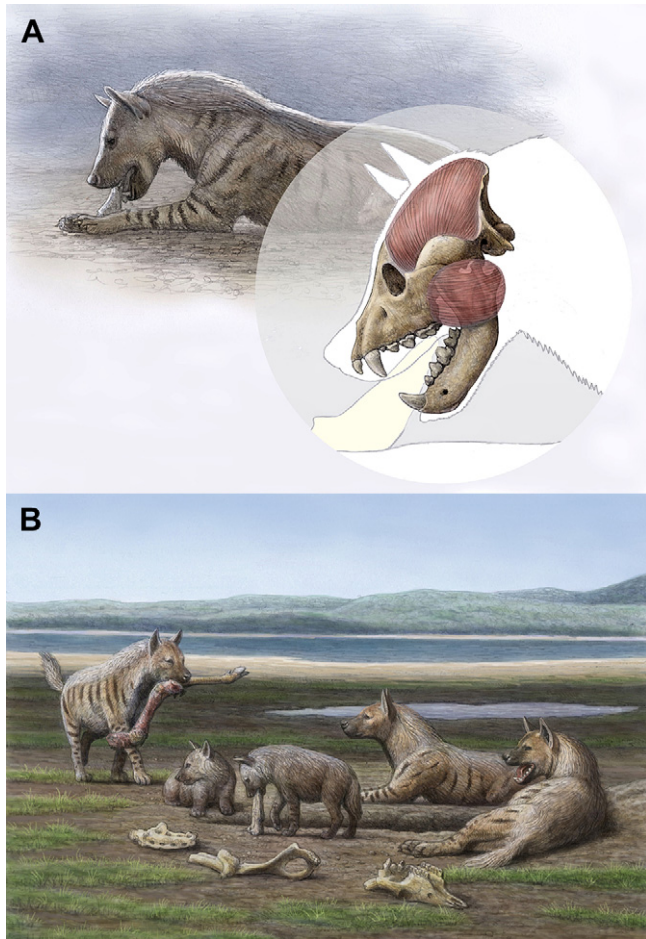


Fig. 1. Reconstruction of the life appearance of the giant hyena *P. brevirostris* during bone-cracking activities (A) and transporting anatomical portions of ungulate carcasses to the Venta Micena denning site (B). Drawings by Mauricio Antón.

the skull of the Sainzelles type specimen (322 mm; Turner and Antón, 1996) and the skull from Zhoukoudian (315 mm; estimated from Pei, 1934) provide an appropriate picture of the enormous size of this extinct carnivore, as they parallel those of the largest southern African male lions (range: 241–328 mm; Turner and Antón, 1996).

The *Pachycrocuta* lineage evolved from the late Miocene *Hyaenictitherium* (Howell and Petter, 1980) and is first recorded in Africa during late Pliocene times (Hadar, ~3.0 Ma; Turner, 1990). Later, close to the Plio-Pleistocene boundary (recently redefined at 2.588 Ma; Gibbard et al., 2010) and coincident with the appearance in the archaeological record of the first stone tools and evidence of human activity on large mammal bones (de Heinzelin et al., 1999; Semaw et al., 2003), *Pachycrocuta* was extinct in East Africa but dispersed into southern Africa (e.g., Makapansgat Member 3) (Toerien, 1952; Randall, 1981; Werdelin, 1999), where it is represented by *Pachycrocuta bellax*. By these times, two hyaenid species, the large bone destroying *Pliocrocuta perrieri* and the gracile pack-hunting *Chasmaporthetes lunensis*, reached Eurasia within the “Elephant–Equus” dispersal event (Azzaroli et al., 1988). During the Early Pleistocene, both species were replaced by the giant form *P. brevirostris*, although *P. perrieri* re-appeared in Europe in the Middle Pleistocene (Turner and Antón, 1996; Turner et al., 2008). *Pachycrocuta* inhabited Asia from the end of the Pliocene to middle Pleistocene times (Nihowan, ~3 Ma; Upper Siwaliks, 1.8–1.2 Ma; Dmanisi, ~1.8 Ma; Zhoukoudian Locality I, ~0.4 Ma; Turner and Antón, 1996; Boaz et al., 2000, 2004; Dennell et al., 2008). In

Western Europe, *P. brevirostris* is first recorded in Early Pleistocene deposits of Italy (Olivola Faunal unit, ~1.99 Ma; Napoleone et al., 2003; Pirro Nord, 1.7–1.3 Ma; Arzarello et al., 2007) and its latest appearances are in the late-Early Pleistocene (1.0–0.8 Ma) (Süssenborn, Stranska Skala, Untermassfeld, Vallonnet, Cueva Victoria, Slivia, Incarcari) (Turner and Antón, 1996; Arribas and Palmqvist, 1999; Turner et al., 2008). The dispersal of *P. brevirostris* in Europe would in all probability be from Asia, as this species was extinct in East Africa by late Pliocene time (Werdelin, 1999).

The disappearance of the giant hyena in Europe was probably linked to the decline and subsequent extinction of saber-tooth cats, particularly *Megantereon whitei* (Martínez-Navarro and Palmqvist, 1996; Palmqvist, 2002a), which implied the loss of an important source of partly consumed carcasses and thus a change in the interactions between flesh-eating and bone-cracking species of the carnivore guild. During the early middle Pleistocene transition (~0.8 Ma), *P. brevirostris* was replaced by the spotted hyena, as recorded at the Gran Dolina of Atapuerca deposits in Spain (García, 2003).

Apart from its enormous size, *P. brevirostris* differed from the modern hyenas in the shortening of the radius and the tibia relative to the humerus and the femur, respectively. As a result, the overall height of the giant hyenas (shoulder height between 90 and 100 cm) was not much greater than that of a large spotted hyena (85 cm), as the skull size alone would suggest (Turner and Antón, 1996). The shortening of the distal limb segments indicates a less cursorial life style for *P. brevirostris* compared to the living hyenas, although it certainly provided greater power and more stability to dismember and carry large pieces of ungulate carcasses to the denning sites (Palmqvist and Arribas, 2001). This agrees with the scavenging behavior deduced from taphonomic analysis of bone assemblages collected by this extinct hyena (Arribas and Palmqvist, 1998; Palmqvist, 2002b).

However, Turner and Antón (1996), Galobart et al. (2003) and Dennell et al. (2008) have argued that the large size of *P. brevirostris* could have been advantageous for the capture and subduing of medium-to-large-sized ungulate prey under concerted action within a pack, as well as in any contest with other predators in defence of a kill or during aggressive scavenging (i.e., kleptoparasitism). While acknowledging that the giant hyenas may have operated as less of a hunter than modern spotted hyenas, Turner and Antón (1996) point to several aspects of the morphology of spotted hyenas that in their opinion only make sense in relation to their hunting ability when viewed within the context of group activity. These features include their body and limbs more heavily built and massive than in both the extant brown hyena (*Parahyaena brunnea*) and striped hyena (*Hyaena hyaena*), species that need to cover longer distances searching for scavengable carcasses.

Scavenging and hunting are simply part of a continuous spectrum (Turner et al., 2008), which means that the behavior of many extant carnivores cannot be extrapolated directly from the study of a single living population (e.g., there are marked differences between the predatory habits of spotted hyenas in Serengeti and Ngorongoro National Parks; Kruuk, 1972). This situation is even worse in the case of extinct carnivores, because the fossil record usually does not provide clear evidence on which particular predator made a kill. At best, researchers can only make inferences on which carnivore consumed the carcass and at what stage it might have gained access to it (Dennell et al., 2008). For these reasons, the question of whether an extinct predator habitually killed its own prey or scavenged the prey captured by others will be always a difficult one to address.

This paper tries to decipher the paleobiology of *P. brevirostris* using a combined biomechanical and taphonomic approach. The biomechanical study focuses on features of the craniodental and postcranial morphology of this extinct hyena related to feeding

preferences and locomotive performance, including new body mass estimates. The taphonomic analysis concentrates on the preservational bias introduced by the bone-cracking behavior of *P. brevirostris* in the large mammal assemblage of Venta Micena, a locality currently interpreted as an early Pleistocene denning site of this giant hyena (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001).

## 2. The early Pleistocene large mammal fauna from Venta Micena

Venta Micena is located near the village of Orce in the Guadix-Baza intramontane basin (Granada, southeast Spain). This sedimentary basin was endorheic (i.e., characterized by interior drainage) from the end of the Miocene to late Pleistocene times, which facilitated an exceptional record of Plio-Quaternary taphocoenoses of large mammals in swampy and lacustrine sediments (Arribas and Palmqvist, 1999). The large mammal assemblage from Venta Micena shows close affinities to the one preserved at the Georgian site of Dmanisi, a locality dated at 1.81 Ma (Lumley et al., 2002), although the absence in Venta Micena of *Canis etruscus* and the presence of both *Canis mosbachensis* and *Lycaon lycaonoides* (Martínez-Navarro et al., 2003; Martínez-Navarro and Rook, 2003; Martínez-Navarro, 2004) indicate that Venta Micena is somewhat younger ( $\sim 1.5 \pm 0.1$  Ma).

The excavated surface (VM-3 quarry,  $\sim 220$  m<sup>2</sup>) has provided  $\sim 5800$  identifiable skeletal remains from 225 individuals belonging to 21 taxa of large ( $>5$  kg) mammals,  $\sim 650$  anatomically identifiable bones that could not be determined taxonomically (e.g., diaphyses and small cranial fragments) and  $\sim 10\,000$  unidentifiable bone shafts (for details, see Martínez-Navarro, 1991; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). Complete elements and bone fragments range in size from isolated teeth and phalanges of small carnivores to mandibles of elephants. Herbivore taxa dominate the bone assemblage in both number of identifiable specimens (NISP) and estimates of minimal number of individuals (MNI). The age estimated for individuals preserved in the assemblage includes juveniles with deciduous teeth and adults with fully erupted permanent dentition. More common herbivores, such as horse (*Equus altidens*) and megacerine deer (*Praemegaceros verticornis*) have high percentages of juveniles,  $>40\%$  in both cases. Among carnivores, only adult individuals are recovered, with the exception of *P. brevirostris* and the Etruscan bear (*Ursus etruscus*) (for details, see Palmqvist and Arribas, 2001: Table 1).

The longitudinal axes of long bones in the assemblage show no preferred orientation, indicating that the currents did not align them (Arribas and Palmqvist, 1998). The ratio of isolated teeth to vertebrae (0.94:1) is close to the value expected in the absence of hydrodynamic sorting (1:1). Similarly, the frequencies of bones grouped according to their potential for dispersal by water (i.e., Voorhies groups) are similar to those in the mammalian skeleton, ruling out the possibility of fluvial transport. Analysis of weathering stages indicates exposure to the elements for a very short time, less than one year in most cases (89% of the bones show weathering stage 0; Palmqvist et al., 1996). The scarcity of root-marks eliminates the possibility of delayed burial in a moist environment where the bones would be protected from weathering by the vegetation (Palmqvist and Arribas, 2001).

Previous research on the taphonomy of VM-3 quarry has revealed that the hyena *P. brevirostris* was the biotic agent responsible of accumulating the huge bone assemblage, and that most losses of paleobiological information were a consequence of the selective destruction of skeletal remains by hyenas during the period when the bones were exposed on the surface before burial (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). In

addition, the analysis of mortality patterns deduced for ungulate species from juvenile/adult proportions and tooth-wearing classes (Palmqvist et al., 1996) indicates that most skeletal remains were scavenged by the hyenas from carcasses of animals hunted by hypercarnivores such as saber-tooth cats (*Homotherium latidens* and *M. whitei*) and hunting dogs (*L. lycaonoides*).

Paleoautecological inferences for the large mammal species have been obtained from biogeochemical and ecomorphological approaches (Palmqvist et al., 1999, 2002, 2003, 2008a,b). Specifically, analysis of stable-isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ,  $\delta^{18}\text{O}$ ) and trace elements (Sr, Zn) from bone collagen and tooth enamel allowed estimation of the dietary niches and habitat preferences of carnivores and ungulates, providing clues on predator–prey relationships within this early Pleistocene community. For example, saber-tooths *H. latidens* and *M. whitei* show quite distinct isotopic signatures, which indicates that both species preyed on different ungulate prey. This is also suggested by the anatomy of their postcranial skeletons (Turner and Antón, 1998; Arribas and Palmqvist, 1999; Palmqvist and Arribas, 2001), which suggests that *Homotherium* pursued grazing ruminants and juveniles of megaherbivores in open habitat, while *Megantereon* ambushed browsing ungulates in forest. Of interest to this study, *P. brevirostris* shows isotopic values that match those expected from isotopic enrichment from prey to predator for a carnivore consuming all ungulate species preserved in the faunal assemblage. This suggests that the hyenas specialized in scavenging the kills of these hypercarnivores in the proportions in which they were available (Palmqvist et al., 2008b).

Analysis of skeletal representation for ungulate taxa in Venta Micena has shown that the hyenas selectively transported herbivore carcasses and body parts to their maternity dens as a function of the mass of the ungulates scavenged (Palmqvist and Arribas, 2001). The fracturing of major limb bones in the dens was also highly selective, correlating well with their marrow content and mineral density. As a consequence, important differences were recorded among the skeletal elements of each ungulate species as well as among taxa (Arribas and Palmqvist, 1998). The importance of this taphonomic bias for the final composition of the bone assemblage is further evaluated here, with emphasis on the specific patterns followed by the hyenas in the consumption of skeletal elements of those ungulates better represented in the taphocoenosis. Such inferences are tested with a comparative analysis of the bone-cracking abilities of *P. brevirostris*, using a biomechanical approach. In doing so, this study contributes to the debate on the relative importance of hunting (Turner and Antón, 1996; Galobart et al., 2003; Dennell et al., 2008) and scavenging (Palmqvist et al., 1996, 2008b; Palmqvist and Arribas, 2001) in the diet of this extinct hyena.

## 3. Materials and methods

The original abundance of skeletal remains of each ungulate species in the assemblage transported by the hyenas (i.e., the bone frequencies prior to destruction of skeletal elements within the maternity dens) was estimated using the minimal number of individuals (MNI) calculated from teeth counts and cranial elements (mandibles, maxillae and cranial vaults), as well as from minimal number of elements (MNE) estimated for each major limb bone (i.e., complete elements and those represented by isolated epiphyses and diaphyses). These estimates were obtained using data updated from Martínez-Navarro (1991) and following the procedure described in Palmqvist and Arribas (2001). MNE counts were estimated combining complete bones and the most abundant bone portion for right and left sides separately. This allowed the calculation of minimal numbers of fore- and hind-limbs, and thus MNI estimates for the postcranial skeleton.



**Table 1**  
Number of identifiable specimens (NISP; c: complete element, f: fragment, p: proximal epiphysis, m: medial diaphysis, d: distal epiphysis) and estimates of minimal number of elements (MNE) for the major bones of the skeleton (right/left/indeterminate side) in the three ungulate groups better represented in the assemblage of Venta Micena. The frequencies of preserved elements [MNE's and raw frequencies of preservational categories for each bone divided by number of forelimbs or hind limbs (data from Table 2), respectively] are shown between brackets. These percentages are a measure of the degree of skeletal completeness of each ungulate group.

Bone elements and portions		Horse		Cervids		Bovids	
		Abundance	%preserved	Abundance	%preserved	Abundance	%preserved
Cranial vaults	MNE	6	8.6	7	12.5	24	44.4
Antler pedicles	NISP	–	–	36 (16/20/0)	–	–	–
Maxillae	MNE	8	11.4	10	17.9	6	11.1
Hemimandibles	MNE	17 (9/8/0)	12.1	41 (19/22/0)	36.6	43 (27/16/3)	39.8
Atlas and axis	c	8	11.4	1	1.8	6	11.1
	f	9	12.9	1	1.8	1	1.9
	MNE	17	24.3	2	3.6	7	13.0
Cervical vertebrae	c	8	1.6	1	0.3	9	2.4
	f	0	0.0	1	0.3	1	0.2
	MNE	8	1.6	2	0.5	10	2.6
Dorsal vertebrae	c	16	1.3	2	0.2	1	0.2
	f	4	0.3	2	0.2	3	0.2
	MNE	20	1.6	4	0.4	4	0.4
Lumbar vertebrae	c	3	1.1	9	4.0	8	3.7
	f	4	1.4	8	3.6	14	6.5
	MNE	7	2.5	17	7.6	22	10.2
Scapula	c	1 (1/0/0)	0.9	0 (0/0/0)	0.0	0 (0/0/0)	0.0
	f	31 (12/19/0)	26.2	14 (7/6/1)	31.1	7 (2/5/0)	10.5
	MNE	32	27.1	14	31.1	7	10.5
Humerus	c	3 (2/1/0)	2.5	3 (2/1/0)	6.7	1 (0/1/0)	1.5
	p	4 (3/1/0)	3.4	1 (1/0/0)	2.2	0 (0/0/0)	0.0
	m	11 (4/7/0)	9.3	1 (1/1/1)	2.2	14 (5/9/0)	20.9
	d	65 (33/32/0)	55.1	42 (14/28/0)	93.3	43 (15/28/0)	64.2
	MNE	68	57.6	45	100.0	44	65.7
Radius	c	10 (6/4/0)	8.5	4 (1/3/0)	8.9	10 (6/4/0)	14.9
	p	13 (7/5/1)	11.0	24 (13/11/0)	53.3	17 (13/4/0)	25.4
	m	0 (0/0/0)	0.0	1 (0/1/0)	2.2	3 (1/2/0)	4.5
	d	18 (11/7/0)	15.3	14 (6/8/0)	31.1	12 (6/6/0)	17.9
	MNE	28	23.7	28	62.2	29	43.3
Ulnae	c	1 (0/1/0)	0.8	1 (0/1/0)	2.2	5 (3/2/0)	7.5
	p	10 (6/4/0)	8.5	4 (3/1/0)	8.9	7 (4/3/0)	10.4
	MNE	11	9.3	5	11.1	12	17.9
Metacarpal	c	55 (24/31/0)	46.6	11 (7/4/0)	24.4	38 (16/22/0)	56.7
	p	67 (28/28/11)	56.8	21 (8/12/1)	46.7	27 (16/9/2)	40.3
	m	26 (0/2/24)	22.0	5 (2/1/2)	11.1	2 (1/0/1)	3.0
	d	51 (35/15/1)	43.2	18 (4/5/9)	40.0	31 (5/6/20)	46.3
	MNE	118	100.0	31	68.9	63	94.0
Pelvis	c	1 (1/0/0)	0.7	2 (1/1/0)	4.0	0 (0/0/0)	0.0
	f	32 (2/2/28)	23.5	11 (0/0/11)	22.0	10 (0/0/10)	16.9
	MNE	33	24.3	13	26.0	10	16.9
Femur	c	3 (0/2/1)	2.2	0 (0/0/0)	0.0	1 (1/0/0)	1.7
	p	10 (5/5/0)	7.3	0 (0/0/0)	0.0	1 (0/0/1)	1.7
	m	30 (7/10/13)	22.1	2 (0/1/1)	4.0	3 (1/1/1)	5.1
	d	8 (3/5/0)	5.9	4 (2/2/0)	8.0	2 (0/1/1)	3.4
	MNE	20	14.7	4	8.0	4	6.8
Tibia	c	8 (2/6/0)	5.9	2 (1/1/0)	4.0	2 (0/2/0)	3.4
	p	1 (0/1/0)	0.7	1 (0/1/0)	2.0	0 (0/0/0)	0.0
	m	2 (0/2/0)	1.5	0 (0/0/0)	0.0	2 (0/0/2)	3.4
	d	111 (70/41/0)	81.6	42 (29/13/0)	84.0	47 (21/26/0)	79.7
	MNE	119	87.5	44	88.0	49	83.0
Astragalus	MNE	90 (49/41/0)	66.2	50 (25/24/0)	100.0	48 (18/26/4)	81.4
Calcaneum	MNE	41 (18/23/0)	30.1	37 (13/22/2)	74.0	33 (15/17/1)	55.9
Metatarsal	c	72 (36/35/1)	52.9	2 (1/1/0)	4.0	29 (14/15/0)	49.1
	p	74 (30/34/10)	54.4	23 (9/13/1)	46.0	30 (15/15/0)	50.8
	m	26 (4/6/16)	19.1	6 (1/3/2)	12.0	7 (2/2/3)	11.9
	d	50 (19/31/0)	36.8	17 (1/9/7)	34.0	25 (3/9/13)	42.4
	MNE	136	100.0	24	48.0	59	100.0
Phalanges	1st	63 (2/5/56)	24.8	18 (5/0/13)	18.9	21 (0/0/21)	16.7
	2nd	41 (2/3/36)	16.1	10 (3/0/7)	10.5	17 (3/0/14)	13.5
	3rd	53 (1/1/51)	20.9	5 (0/1/4)	5.3	6 (0/1/5)	4.8
	MNE	157	20.6	33	11.6	44	11.6

Palmqvist and Arribas (2001) described specific bone-consuming sequences for several skeletal elements of horse *E. altidens* in Venta Micena. This study concluded that two factors determined the intensity of the bone-cracking behavior of hyenas: 1) the position of the bone in the equid skeleton, which relates to

the pattern of disarticulation of the horse carcass followed by the hyenas; and 2) the marrow content and mineral density of each skeletal element. According to the variations in both factors, three distinct types of bone-modifying activities by the hyenas were established:

- (i) In the first group are humerus, tibia, and calcaneum, which are consumed following a 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.
- (ii) 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 one or vice versa) and both epiphyses are finally lost.
- (iii) Third metacarpals and metatarsals: these bones are modified by crushing with a variable direction of activity and tend to be more abundantly preserved as complete elements than other major limb bones, which results from their higher mineral density and lower marrow yields.

The bone-consuming sequences described above are tested here statistically by a comparative analysis of the abundance of major long bones of the forelimb (humerus, radius and metacarpal) and hind limb (femur, tibia and metatarsal) preserved as complete elements, isolated epiphyses (proximal and distal) and diaphyses in ungulates. This generates a contingency table, which consists of a matrix with  $r$  rows and  $c$  columns for analysis of dependence of two characters that show several states. Let the first character (e.g., limb bones) be subdivided into  $r$  attributes and the second character (e.g., preservational states) into  $c$  attributes. There are  $r \cdot c$  cells or categories for this array. The  $ij$ -th cell contains the frequency ( $n_{ij}$ ) for the simultaneous presence of the  $i$ -th and  $j$ -th attributes. The statistic for testing independence is:

$$\chi^2 = \sum_{i=1}^r \sum_{j=1}^c \frac{(O_{ij} - E_{ij})^2}{E_{ij}},$$

where  $E_{ij}$  represents the expected frequency under the null hypothesis of independence and  $O_{ij}$  is the observed frequency that equals  $n_{ij}$ . When the null hypothesis holds,  $\chi^2$  is approximately distributed as a chi-square variable with  $(r - 1) \cdot (c - 1)$  degrees of freedom.

Let  $e_{ij} = (O_{ij} - E_{ij})/E_{ij}^{1/2}$ . This variable has mean 0 and its variance is  $v_{ij} = (1 - n_i/n) \cdot (1 - n_j/n)$ , where  $n_i$  and  $n_j$  are the total number of cases that show the  $i$ -th and  $j$ -th attributes, respectively (i.e., partial sums for rows and columns in the table). The adjusted residuals are  $d_{ij} = e_{ij}/v_{ij}^{1/2}$ , and they result from typifying  $e_{ij}$ . Adjusted residuals are approximately normally distributed  $[N(0,1)]$  when the characters generating the contingency table are independent (Everitt, 1979). Dependency of characters produces one or more adjusted residuals that are higher in absolute value than the standard normal deviates (e.g., 1.96 for  $p = 0.05$ ).

The ungulate species analyzed using this procedure are the six better represented in the Venta Micena assemblage, the perissodactyl *E. altidens* and five artiodactyl ruminants, bovids *Bison* sp., *Capra alba* and *Soergelia minor*, and cervids *P. verticornis* and *Metacervocerus rhenanus*. Of these species, only *E. altidens* provided high numbers of preserved specimens for all bones and bone portions, thus adequate for statistical analysis. In the case of ruminants, all of them showed less than five specimens in many cells of the contingency table, which precluded the use of the  $\chi^2$  test (although this stringent condition is discussed by Everitt, 1979). Given this limitation, the raw frequencies of all ungulate species were grouped in the contingency table.

Palmqvist and Arribas (2001) reported on similar patterns of bone preservation among these ungulate species. However, a preliminary comparison showed minor differences between perissodactyls and artiodactyls, on the one hand, and between bovids and cervids, on the other. For this reason, bovid and cervid

species were clustered for bone counts and MNE estimates in two separate groups (Table 1) and a comparative analysis of the distribution of major limb bones among preservational categories in equids, bovids and cervids was performed using correspondence analysis (CA). This multivariate methodology allows evaluating simultaneously the relationship between different categories. In brief, correspondence analysis extracts the eigenvalues and eigenvectors from a similarity matrix derived from a contingency table (Davis, 1986). The association between columns  $j$  and  $k$  (variables) in a contingency table with  $i$  rows (observations) is estimated as:

$$r_{jk} = \sum_{i=1}^n \left[ (O_{ij} - E_{ij})/E_{ij}^{1/2} \right] \cdot \left[ (O_{ik} - E_{ik})/E_{ik}^{1/2} \right],$$

which is a measure of their degree of correlation; as  $r_{jk}$  represents the product of two chi-square values, it is also called the  $\chi^2$  distance. Given that there is a direct relationship between the  $R$ - and  $Q$ -mode solutions in CA, an advantage of this methodology is that observations (i.e., limb bones) and variables (i.e., preservational categories) can be plotted onto the same axes, which facilitates the interpretation of the results.

As indicated before, MNE counts for major limb bones of each leg provided estimates of minimal numbers of fore- and hind-limbs. MNI counts based on teeth and legs allowed the estimation, for each ungulate group, of the percentage of bones preserved as complete elements or bone portions, respectively; these percentages can be related to structural properties of major limb bones such as mineral density and marrow content. Finally, the ratio of forelimbs to hind limbs was compared with the corresponding values for flesh and marrow contents, estimated from data for modern ungulates.

Size estimates for *P. brevirostris* were obtained using regression equations of body mass on craniodental and postcranial measurements adjusted with modern carnivores (Van Valkenburgh, 1990; Anyonge, 1993; Christiansen, 1999; Andersson, 2004). The predictions of these equations were tested in the living hyenas before applying them to the fossil specimens.

The search for skeletal adaptations of carnivores has emphasized in feeding behavior, hunting techniques and habitat preferences (see reviews in Van Valkenburgh, 1987; Anyonge, 1996; Biknevicius and Van Valkenburgh, 1996; Palmqvist et al., 2003). Several biomechanical approaches have been proposed for the study of carnivorous skull shape, including aspects of jaw geometry, bite strength and tooth blade sharpness (e.g., Radinsky, 1985; Van Valkenburgh and Ruff, 1987; Werdelin, 1989; Biknevicius, 1996; Biknevicius and Leigh, 1997; Binder, 1998).

With the exception of the aardwolf (*Proteles cristatus*), which feeds on insects and has extremely reduced cheek teeth (Koehler and Richardson, 1990), all extant hyaenids are adapted to bone-cracking activities and have well-developed premolar teeth. Striped and brown hyenas are strict scavengers (Rieger, 1981; Mills, 1982), while spotted hyenas behave more as active predators (Gasaway et al., 1991; Di Silvestre et al., 2000). Thus, it is worth analyzing if there are differences in the craniodental morphology of these extant hyenas that correlate with their feeding behavior and thus may provide clues to the paleobiology of *P. brevirostris*. For this reason, principal components analysis (PCA) was used in a comparative study of the mesiodistal and buccolingual dimensions of the lower teeth in the three living hyenas and in *P. brevirostris* (data from Torregrosa, 2008). The biomechanical advantage of the chewing muscles in *P. brevirostris* was studied, estimated from the input moment arm of masseter (MAM, measured as the distance from glenoid to angular process), the input moment arm of temporalis (MAT, measured as the distance from glenoid to apex of coronoid process) and the output moment arm of resistance for an object positioned at the lower canines (MAR, measured as the distance from

glenoid to lower canine). Jaw depth at the P<sub>4</sub>–M<sub>1</sub> joint estimates the resistance of the mandible against dorsoventral loads. The methodology and the comparative data set used are from Van Valkenburgh and Ruff (1987), including measurements for 34 extant species of carnivores, except for jaw depth in which 29 species were studied. In addition, the approach developed by Werdelin (1989) for estimating the muscle resultant for bite strength at the lower carnassial of *P. brevirostris* was followed.

Mandibular force profiles closely reflect the feeding behavior of extant carnivores (Therrien, 2005a, 2005b). For this reason, a biomechanical approach that models the mandibles of hyenas as beams was used to gain insights into the bone-cracking abilities of *P. brevirostris*. Given that the bite force applied at any point along the mandibular corpus must be proportional to the external jaw dimensions at this point, patterns of variation in these dimensions will reflect the jaw adaptations to specific loads that result in lateral and vertical bending stresses. A number of studies (e.g., Biknevicius and Ruff, 1992; Biknevicius and Van Valkenburgh, 1996; Therrien, 2005a,b; Therrien et al., 2005) have used the external dimensions of mandibles to model them as simplified solid, elliptical beams (i.e., cantilevers) that undergo bending loads during feeding.

The second moment of area (*I*), which measures the distribution of bone around a given axis of the ellipse that describes the section of the mandibular corpus, can be expressed as:

$$I_x = \pi ba^3/4, \text{ distribution of bone about the labiolingual axis,} \\ I_y = \pi ab^3/4, \text{ distribution of bone about the dorsoventral axis,}$$

where *a* and *b* are the dorsoventral and labiolingual radii of this ellipse, respectively (i.e., the distances from the neutral axis of the jaw cross section to the outer edges of the bone in the planes of bending).

The section modulus (*Z*), a measure of the bending strength that the mandible is able to withstand, can be estimated from the following equations:

$$Z_x = I_x/a \text{ (dorsoventral plane),} \\ Z_y = I_y/b \text{ (labiolingual plane).}$$

Given that the properties of compact bone are relatively constant, the section modulus is equivalent to the product of the force (*F*) applied at any point of the mandible and the moment arm length (*L*), which is the distance between this point and the fulcrum of the cantilever (i.e., the articular jaw condyle):

$$Z = F \cdot L, F = Z/L$$

For animals with similarly developed jaw muscles (e.g., the carnivores), this force depends on their body mass (i.e., larger species will exert more powerful bites), but also reflects their jaw adaptations toward supporting specific loads. For this reason, a comparison of *Z/L* ratios for different species will reveal variations in the magnitude of the forces applied at different locations along the mandible (e.g., at interdental gaps), while the differences in *Zx/Zy* ratios will reflect variations in their overall mandibular shape (i.e., relative mandibular forces). For example, a deeper than wide mandibular corpus (*Zx/Zy* > 1) is well suited to resisting high dorsoventral loads (e.g., those resulting from bone fracturing), while a wider than deep jaw (*Zx/Zy* < 1) is better adapted to sustaining labiolingual loads (e.g., torsional stresses produced while biting a struggling prey) (Therrien, 2005a,b).

Average *Zx*, *Zy* and *L* values were calculated in a number of mandibles of spotted hyena (*N* = 17), brown hyena (*N* = 14), striped hyena (*N* = 14) and *P. brevirostris* (*N* = 5) for several points defined

at interdental gaps (behind the lower canine, at P<sub>2</sub>–P<sub>3</sub>, at P<sub>3</sub>–P<sub>4</sub>, at P<sub>4</sub>–M<sub>1</sub> and behind the lower carnassial).

Finally, a relative warp analysis (RWA) was performed for evaluating simultaneously the information on lower teeth size and jaw geometry. A series of 13 landmarks taken in the mandible were digitized on a number of high-resolution digital images of extant hyenas (*C. crocuta*, *N* = 22; *P. brunnea*, *N* = 9; *H. hyaena*, *N* = 14) and five specimens of *P. brevirostris* using the software TPSdig v.2.11 (Rohlf, 2008). Landmarks were not digitized on the ascending ramus because this anatomical region is rarely preserved in the fossils. The configuration of landmarks used in this study allows describing the depth of the mandibular corpus in relation to the development of the canine, the fourth premolar and the first molar, teeth which dimensions are associated with the feeding adaptations of carnivores (Biknevicius and Ruff, 1992; Biknevicius and Van Valkenburgh, 1996; Therrien, 2005a,b; Meloro et al., 2008).

Specimens were aligned using the Procrustes superimposition method (Dryden and Mardia, 1998). A multivariate regression analysis (Monteiro, 1999) of procrustes coordinates (shape) on centroid size was computed for exploring the effects of allometry. Statistical significance was tested permuting 10 000 times the null hypothesis of independence (Drake and Klingenberg, 2008). A PCA from the covariance matrix of the aligned coordinates was developed for obtaining the major dimensions of jaw shape variation around the mean shape. A canonical variates analysis (CVA) was also computed in order to search for the morphological traits that allow distinguishing among the four hyenid species. All the geometric morphometric procedures and statistical analyses were carried out with MORPHOJ software package (Klingenberg, 2008).

#### 4. Results

Table 1 shows the abundance of the main skeletal elements in equids (*E. altidens*), bovids (*Bison* sp., *C. alba* and *S. minor*) and cervids (*P. verticornis* and *M. rhenanus*). This table includes MNE estimates for these bone specimens and percentages of surviving bones and bone portions.

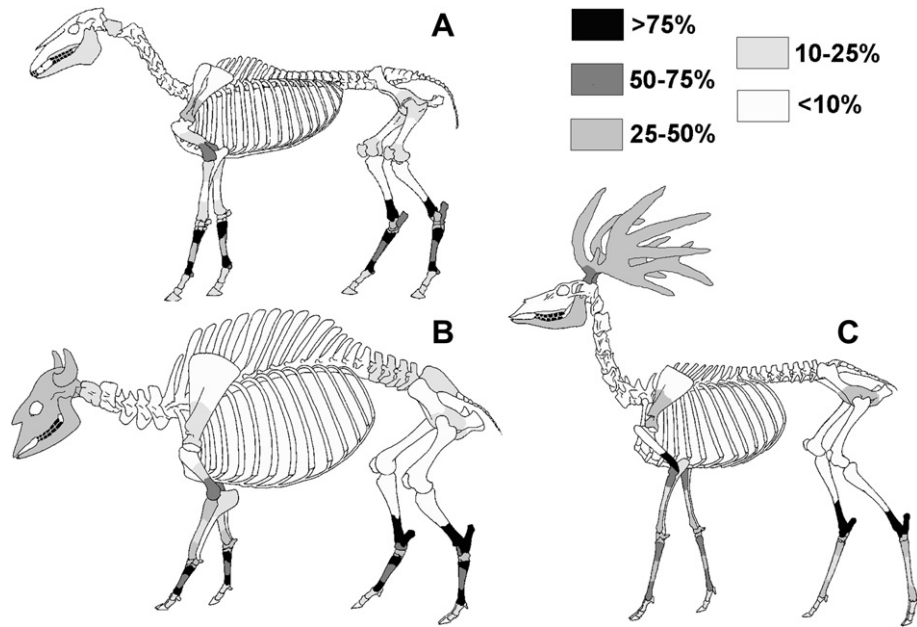
Table 2 shows MNI estimates for the three ungulate families, obtained from minimal number of heads (based on teeth counts and abundance of cranial elements) and estimates of minimal numbers of forelimbs and hind limbs (based from MNE counts, using the most abundant limb bone from each leg).

Fig. 2 depicts the skeletal completeness of these families, showing the overrepresentation of limb bones over the elements of the axial skeleton (vertebrae and ribs). Among the major limb bones, the frequencies of bone portions preserved agree well with the types of bone-modifying activities by the hyenas established by Palmqvist and Arribas (2001): a proximodistal pattern in the case of humerus and tibia, and a sequence of consumption of variable direction in the case of radius, metapodials and femur. The overall

**Table 2**

Minimum numbers of individuals (MNI) calculated from minimal number of heads (based on teeth counts and cranial elements; data from Palmqvist and Arribas, 2001) and minimal number (MN) of forelimbs and hind limbs (estimated from counts of minimal number of specimens, using the most abundant limb bone element for each leg; only specimens from adult individuals with fused epiphyses; data from Table 1) in the three ungulate families better represented in the early Pleistocene assemblage of Venta Micena.

Body part	Horse	Cervids	Bovids
MNI heads (juveniles/adults)	70 (32/38)	56 (18/38)	54 (21/33)
MN limbs (right/left)			
Forelimb	118 (59/59)	45 (18/27)	67 (33/34)
Hind limb	136 (66/69)	50 (25/24)	59 (29/30)



**Fig. 2.** Frequencies of preserved elements of the skeleton of (A) horse (*E. altidens*), (B) bovids (*Bison* sp., *C. alba* and *S. minor*) and (C) cervids (*P. verticornis* and *M. rhenanus*) in Venta Micena, estimated from minimal number of heads, forelimbs, and hind limbs (data from Table 1). The abundance of each anatomical region (i.e., proximal epiphysis, diaphysis and distal epiphysis) preserved for each major limb bone was calculated summing the raw frequency of complete elements and isolated bone parts.

patterns of skeletal representation for bovids and cervids are remarkably similar except in the case of cervid metapodials, less abundantly preserved in the assemblage given their slenderness and higher marrow contents (see below). Given the selective bone-cracking behavior of *P. brevirostris*, this reveals that the skeletal elements preserved in the assemblage are those that remained after the hyenas consumed the bone nutrients.

#### 4.1. Analysis of bone preservation

The cumulative value of the chi-square test obtained for the contingency table is statistically very significant ( $\chi^2 = 572.82$ ,  $p < 0.00001$ ; Table 3), which indicates a heterogeneous distribution of major limb bones among the preservational categories considered. Specifically, complete elements are underrepresented as humeri, femora and tibiae, while metapodials show higher frequencies than those expected from a random distribution. Proximal epiphyses are overrepresented as radii and metapodials, while proximal humeri and tibiae are less abundantly preserved than expected. Diaphyses are better represented in the case of femora, while radii and tibiae are preserved as isolated diaphyseal portions in lower proportions than expected. Finally, distal humeri and tibiae are clearly overrepresented in the assemblage, while all the other limb bones show lower frequencies of this epiphyseal region than expected.

Fig. 3 shows the results obtained in CA for the abundance of major limb bones distributed among preservational categories in horse, bovids and cervids. The projection of skeletal elements and bone portions on the plot defined by the first two axes of correspondences, which jointly account for 87% of the original variance, shows a similar pattern of bone consumption by *P. brevirostris* for horse, bovid and cervid limb elements: tibiae and humeri are better represented by distal epiphyses (which means that the hyenas destroy these elements starting at their proximal end), while radii and metapodials tend to be more frequently preserved as complete bones or proximal epiphyses (which indicates that their reduction by the hyenas starts at the distal end). Femur is the only element

that tends to be crushed at both ends and, consequently, it is mainly represented by isolated diaphyses, although such trend is only evident for the horse. In the case of bovids, diaphyses of tibia and humerus are comparatively more abundant, and the same applies for cervid metapodials and radii.

Fig. 4 shows the relationship between the percentage of major limb bones of bovids, cervids and horse preserved as complete elements (Y-axis) and the volume of their medullary cavities (X-axis). The frequencies of bones preserved complete were estimated dividing the raw abundances of complete bones for each element (Table 1) by the corresponding minimum numbers of limbs (Table 2). The medullary cavity volume provides an estimate of the marrow content of each limb bone (data for bovids from Emerson,

**Table 3**

Contingency table for the abundance of major limb bones of ungulates (equids, bovids and cervids) preserved as complete elements, isolated epiphyses and diaphyses in the fossil assemblage from Venta Micena (data from Table 1). Each cell shows the observed frequencies (OF) of skeletal elements, the bone frequencies expected from a random distribution (EF, between brackets), the adjusted residuals (normal deviates) and their level of statistical significance (two-tailed *t*-test; -:  $p > 0.05$ ; \*:  $p < 0.01$ ; \*\*:  $p < 0.001$ ; \*\*\*:  $p < 0.0001$ ). The table also includes the cumulative  $\chi^2$ -value [ $\sum_i \sum_j (OF - EF)^2 / EF$ ] with  $(r - 1) \cdot (c - 1)$  degrees of freedom.

Limb bone	Complete	Proximal epiphysis	Diaphysis	Distal epiphysis	$\Sigma_i N$
Humerus	7 (36.8) -5.92***	5 (45.5) -7.45***	28 (20.7) 1.83—	150 (87.0) 9.93 ***	190
Radius	24 (24.4) -0.10—	54 (30.2) 5.23***	4 (13.7) -2.93*	44 (57.7) -2.57*	126
Metacarpal	104 (68.2) 5.65 ***	115 (84.3) 4.48 ***	33 (38.4) -1.08—	100 (161.1) -7.64***	352
Femur	4 (12.4) -2.72*	11 (15.3) -1.30—	35 (7.0) 11.52 ***	14 (29.3) -3.93**	64
Tibia	12 (42.2) -5.67***	2 (52.2) -8.73***	4 (23.8) -4.71***	200 (99.8) 14.92 ***	218
Metatarsal	103 (69.9) 5.17 ***	127 (86.5) 5.87 ***	39 (39.4) -0.07—	92 (165.2) -9.09***	361
$\Sigma_j N$	254	314	143	600	$\Sigma_i \Sigma_j N = 1311$ , $\chi^2 = 572.82$ , d.f. = 15



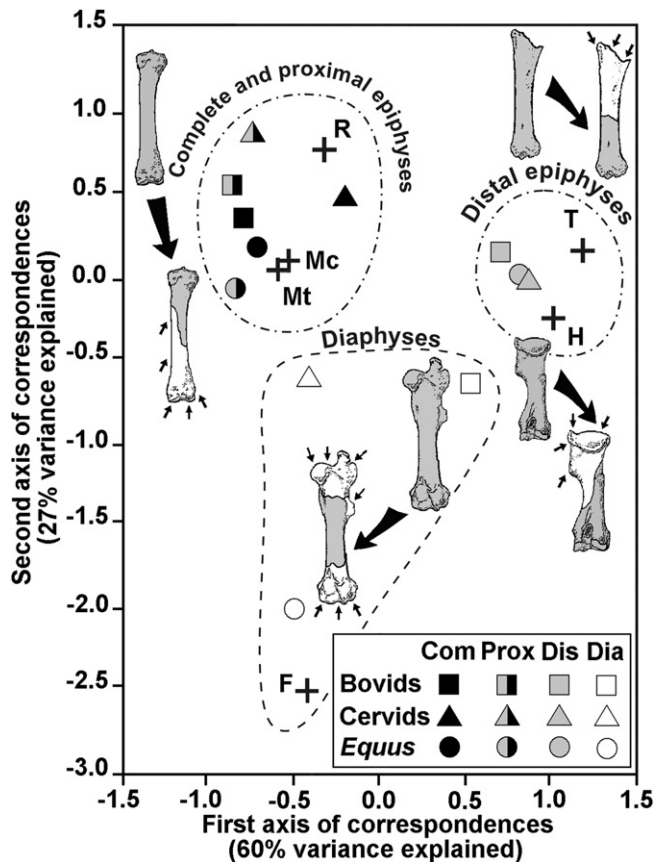


Fig. 3. Results of correspondence analysis of the abundance of major limb bones distributed among preservational categories: projection of complete elements and bone portions of the three ungulate groups analyzed (horse, bovids and cervids) on the bivariate plot defined by the first two correspondence axes. H: humerus, R: radius, Mc: metacarpal, F: femur, T: tibia, Mt: metatarsal. Com: complete bone, Prox: proximal epiphysis, Dis: distal epiphysis, Dia: diaphysis.

1990; data for cervids from Binford, 1978; data for horse from Outram and Rowley-Conwy, 1998). A least-squares regression revealed an inverse and statistically significant relationship between both variables, which unequivocally indicates that those limb bones with greater nutritional value (e.g., femur, humerus and tibia) were preferentially fractured by the hyenas (thus being preserved in the bone assemblage as bone portions), while those others that provided less marrow (e.g., metapodials) tend to be better represented as complete elements. It is worth noting that cervid metatarsals, which are comparatively less abundantly preserved as complete elements in the assemblage than those of bovids and horse, have a higher medullary volume.

The ratio of minimal number of horse forelimbs (118) to hind limbs (136) in the assemblage (Table 2) takes a value of 0.87. This ratio is clearly different from the proportion of flesh yields provided by both limbs, 0.30 (14/46, in kg), and closer to the ratio estimated for the cumulative marrow contents of major long bones in fore- and hind limbs, 0.67 (77/115, in g) (estimates of flesh and marrow contents from *Equus caballus*; Outram and Rowley-Conwy, 1998). In the case of ruminants, the ratio of fore- to hind-limbs is 1.03 (112/109), a value which is also different from that estimated for flesh contents, 0.30 (13/44, in kg), and similar to the ratio for marrow yields, 1.12 (628/562, in g) (data from *Bison bison*; Brink, 1997). This suggests the total marrow yields provided by the limb bones of each leg as the main factor determining the selectivity of hyenas in the transport of ungulate skeletal elements to their maternity dens, as suggested by Palmqvist and Arribas (2001).

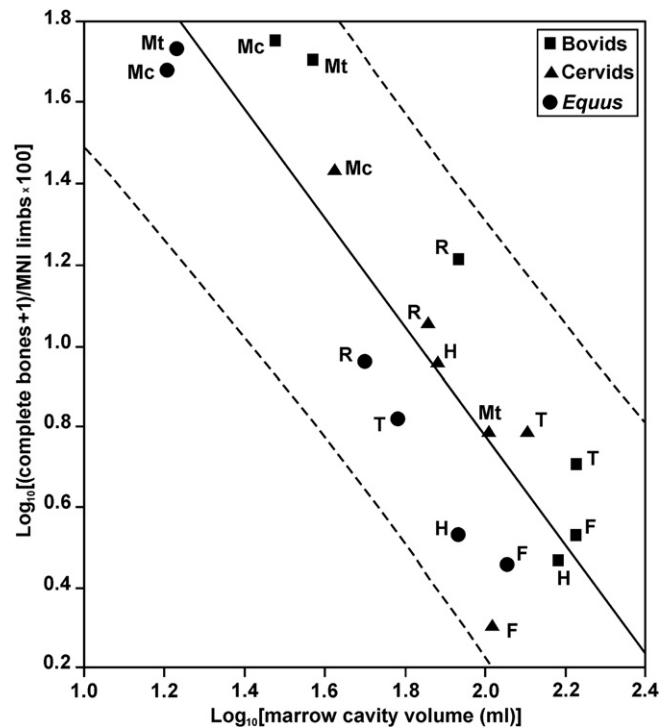


Fig. 4. Bilogarithmic least-squares regression of the percentage of bovid, cervid and equid bones preserved complete (estimated as the number of complete elements plus one, divided by the minimum number of fore- or hind limbs, respectively) on their estimated medullary cavity volume, in ml (data for bovids from Emerson, 1990; data for cervids from Binford, 1978; data for equids from Outram and Rowley-Conwy, 1998). H: humerus, R: radius, Mc: metacarpal, F: femur, T: tibia, Mt: metatarsal.  $\text{Log}_{10}(\% \text{ complete bones}) = 2.47 (\pm 0.35) - 1.35 (\pm 0.19) \text{Log}_{10}(\text{marrow volume})$ ,  $r = 0.87$ , s.e. = 0.24,  $F_{1,16} = 50.85$ ,  $p < 10^{-5}$ . Dashed lines represent the  $p = 0.05$  confidence interval for observations.

#### 4.2. Body size of *P. brevirostris*

Size estimates were obtained for *P. brevirostris* using published regression equations for body mass on postcranial measurements adjusted in modern carnivores (Anyonge, 1993; Christiansen, 1999; Andersson, 2004), as well as equations that provide mass estimates from craniodental variables (Van Valkenburgh, 1990) (Table 4). It must be emphasized, however, that these equations were developed with skeletal measurements of specimens collected in museums and graphing them against body masses of different sets of animals obtained from the literature, which introduces an additional source of error (see discussion in Turner and O'Regan, 2002). Due to this reason, their predictive power was tested with the living hyenas before obtaining mass estimates for *P. brevirostris*.

When a carnivore walks, the functions of supporting its body mass and of moving it forwards are unequally shared by the fore- and hind-limbs (Ewer, 1973): the hind limb does more than its share of propulsion, while the forelimb takes most of the weight. This means that the mass estimates derived from the forelimb bones tend to be more precise than those obtained from hind limb ones. Similarly, equations adjusted with the dimensions of the proximal limb segments (e.g., humerus and femur length) provide more accurate predictions of body mass for extinct mammals than those which use distal ones (e.g., radius and tibia length), because there is more variability in the size of the distal bones among locomotion types (e.g., cursors, ambushers and ambulators in carnivores; Gonyea, 1976; Van Valkenburgh, 1985, 1988; Damuth and MacFadden, 1990; Anyonge, 1996; Palmqvist et al., 2003).

The regression equations adjusted for body mass (BM) on humerus length (HL) and femur length (FL) provide estimates that



**Table 4**

Regression equations used for estimating the body mass of *Pachycrocuta brevirostris* and estimates of size obtained with them for the living hyenas. Deviations between estimated and actual masses for extant species [(mass estimate)/mass × 100] are shown between brackets.

References	Equation	N	<i>C. crocuta</i> (55 kg)	<i>P. brunnea</i> (42 kg)	<i>H. hyaena</i> (38 kg)	<i>P. brevirostris</i> (? kg)
Van Valkenburgh, 1990	$\log_{10}(\text{BM}) = 3.13\log_{10}(\text{SKL}) - 5.59$	72	63 (14.5%)	60 (42.9%)	44 (15.8%)	176
	$\log_{10}(\text{BM}) = 2.72\log_{10}(\text{LM}_1) - 2.03$		62 (12.7%)	57 (26.3%)	34 (–10.5%)	92
Anyonge, 1993	$\log_{10}(\text{BM}) = 2.93\log_{10}(\text{HL}) - 5.11$	28	54 (–1.9%)	55 (30.9%)	46 (21.1%)	115
	$\log_{10}(\text{BM}) = 2.92\log_{10}(\text{FL}) - 5.27$		52 (–5.5%)	40 (–4.8%)	35 (–7.9%)	86
Christiansen, 1999	$\log_{10}(\text{BM}) = 2.88\log_{10}(\text{HL}) - 5.05$	30	48 (–12.7%)	48 (14.3%)	42 (10.5%)	99
	$\log_{10}(\text{BM}) = 2.86\log_{10}(\text{FL}) - 5.15$		49 (–10.9%)	38 (–9.5%)	34 (–10.5%)	80
Andersson, 2004	$\log_{10}(\text{BM}) = 2.55\log_{10}(\text{TC}) - 0.60$	199	62 (12.7%)	41 (–2.4%)	38 (0.0%)	110
Average	All equations	–	56 (1.8%)	48 (14.3%)	39 (2.6%)	108

are generally close to the actual mass of the spotted hyena (Table 4). In the case of the brown hyena and the striped hyena, however, the estimates obtained from these equations tend to overestimate and underestimate their masses, respectively. The reason for such discrepancy is that hyenas show more developed forelimbs than other carnivores and comparatively shorter hind limbs, an anatomical design which facilitates the transport without dragging of carcasses. Interestingly, the saber-tooth cat *Homotherium serum*, in which the ability of transporting carcasses of juvenile elephants to a den site has been documented (Marean and Ehrhardt, 1995), also shows more developed forelimbs than hind limbs (Anyonge, 1996).

In a recent paper, Andersson (2004) provided a useful equation for estimating body mass on the perimeter of the trochlea of the distal humerus (TC), a weight-bearing joint whose surface scales similarly throughout the order Carnivora. This equation (Table 4) is highly correlated with body mass and was adjusted in a large sample of specimens from 93 species distributed over 57 genera and eight carnivore families. It provides size estimates for the tree living hyenas that are remarkably close to their actual masses (Table 4). In the case of *P. brevirostris*, the value obtained for the humerus from Inkaral (166.3 mm, estimated from Galobart et al., 2003: Pl. 2) is 116 kg, while the figure for the distal humerus from Dmanisi (159.2 mm, estimated from Vekua, 1995: Pl. 18) is 104 kg. This provides an average mass of 110 kg for the giant hyena.

Regression equations adjusted with craniodental variables such as skull length (SKL) and lower carnassial length (LM<sub>1</sub>; equation recalculated with data from Van Valkenburgh, 1990) were also used for estimating the body mass of *P. brevirostris* and the living hyenas. These equations were adjusted using a large data set that includes species from Canidae, Dasyuridae, Felidae, Hyaenidae, Mustelidae, Procyonidae, Ursidae, and Viverridae. However, the estimates obtained with SKL for the living hyenas are all in excess of their actual masses, which explains the high figure obtained for *P. brevirostris* (estimated with the very large skulls from Sainzelles and Zhoukoudian; Turner and Antón, 1996). In contrast, the regression for LM<sub>1</sub> provides values which are less biased.

The means of the mass estimates obtained with these equations for the living hyenids are close to their actual masses, especially in the case of spotted hyenas and striped hyenas, in which the

deviations represent less than 5% (Table 4). The mean mass predicted for the giant hyena is 108 kg, a value in agreement with the size estimate calculated with the equation based on TC.

#### 4.3. Functional morphology of *P. brevirostris*

As is to be expected from the results obtained in the taphonomic analysis of ungulate bones preserved at Venta Micena, the giant hyenas would have had mechanical advantages for bone fracturing of their robust premolar teeth, powerfully developed jaw-closing muscles and stoutly built mandibles that resisted dorsoventral bending under load.

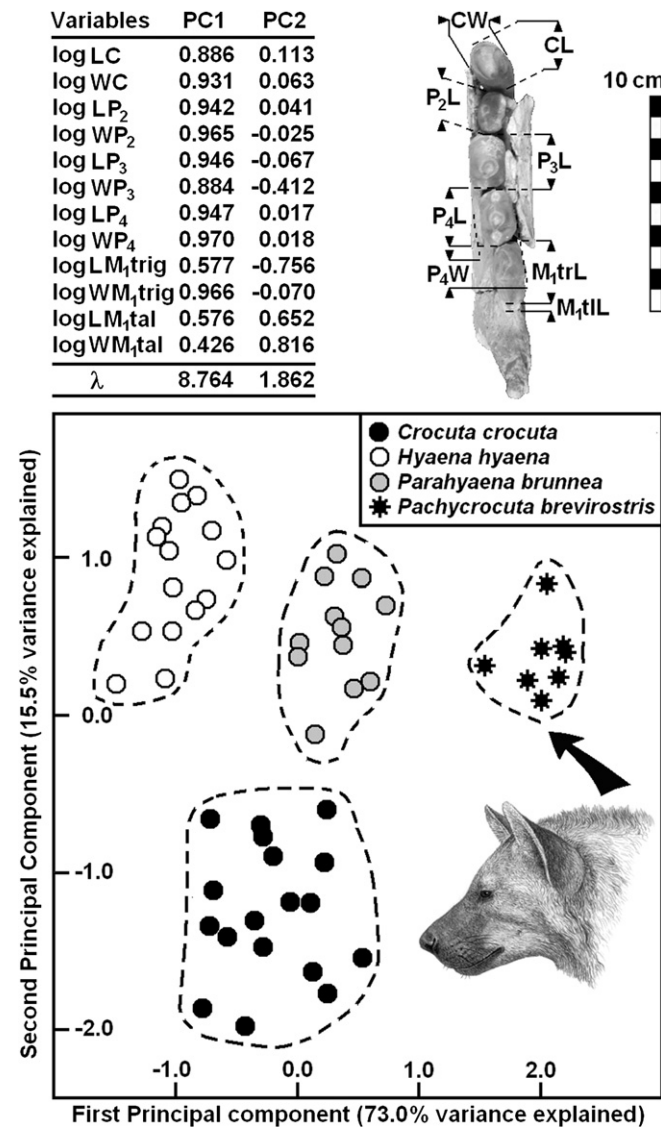
The bone-crushing adaptations of hyenas concern mainly their premolars, in which the anterior and posterior cusps are reduced but the central one is enlarged and widened, so that the tooth is converted from a blade-like structure (as in felids) to a heavy conical hammer (Ewer, 1973). In *P. brevirostris*, both the absolute and relative dimensions of the fourth premolar (and this holds also for the third one) indicate unequivocally the abilities of this hyena for fracturing large bones (Table 5). However, bone-crushing requires not only hammer-like teeth but also strong masticatory muscles. For this reason, the attachment of the temporalis muscle on the skull is enlarged in hyenas by a well-developed sagittal crest (Ewer, 1973).

Fig. 5 shows the results obtained in PCA of the mesiodistal length and buccolingual width of the lower teeth in the three living hyenas and in *P. brevirostris*. The plot for the two first components, which jointly account for more than 88% of the variance of the twelve original measurements, encompass a morphospace with separate regions for the two feeding styles of the extant hyenas, scavenging (brown and striped hyenas) vs. active predation (spotted hyenas). Given that the metric variables were logarithmically transformed prior to the analysis and that all them take positive factor loadings in the first component, this axis may be interpreted as a size vector (Reyment and Jöreskog, 1993), distributing the specimens according to their overall tooth dimensions. In contrast, a number of variables show positive values for the second component (e.g., LM<sub>1tal</sub> and WM<sub>1tal</sub>) while others are negative (e.g., WP<sub>3</sub> and LM<sub>1trig</sub>), which identifies this axis as a shape vector, arranging the specimens

**Table 5**

Values of brachial index, crural index and limb proportions in the three living hyenas, estimated using averages of mean length for radius, humerus, tibia and femur published by Turner and Antón (1996) and Walker (1984), and in the two extinct hyenas discussed in the text (values estimated from data in Turner and Antón, 1996). Several dental indexes are also provided (data for extant species from Van Valkenburgh, 1989, 1990; Van Valkenburgh et al., 2003; estimates for *Crocuta spelaea* teeth provided by L. Werdelin; data for *Pachycrocuta brevirostris* from Turner and Antón, 1996; Turner, 2001). Hum: humerus, rad: radius, fem: femur, tib: tibia, trig: trigonid, LM<sub>1</sub>: mesiodistal length of lower carnassial, LP<sub>4</sub>: length of lower fourth premolar, WP<sub>4</sub>: buccolingual width of lower fourth premolar.

Species	<i>H. hyaena</i>	<i>P. brunnea</i>	<i>C. crocuta</i>	<i>C. spelaea</i>	<i>P. brevirostris</i>
Brachial index (radius length/humerus length)	1.07 (220/205)	1.00 (217/218)	1.08 (235/217)	0.93 (218.0/235)	0.91 (254/280)
Crural index (tibia length/femur length)	0.88 (191/216)	0.82 (185/225)	0.82 (203/247)	0.75 (197/264)	0.74 (217/293)
Limb proportions (hum + rad)/(fem + tib)	1.04 (425/407)	1.06 (435/410)	1.00 (452/450)	0.98 (453/461)	1.06 (543/510)
Relative length of trigonid blade (L <sub>trig</sub> /LM <sub>1</sub> )	0.78 (15.9/20.4)	0.82 (20.2/24.6)	0.90 (22.9/25.4)	0.90 (29.5/32.6)	0.83 (24.3/29.4)
Relative length of fourth premolar (LP <sub>4</sub> /LM <sub>1</sub> )	0.95 (19.4/20.4)	0.85 (20.9/24.6)	0.78 (19.8/25.4)	0.75 (24.3/32.6)	0.89 (26.3/29.4)
Premolar shape (WP <sub>4</sub> /LP <sub>4</sub> )	0.58 (11.3/19.4)	0.70 (14.6/20.9)	0.68 (13.5/19.8)	0.62 (15.1/24.3)	0.62 (16.3/26.3)



**Fig. 5.** Results of principal components analysis of log-transformed measurements of the lower dentition, including mesiodistal length (L) and labiolingual width (W) at crown base of lower canine (C), second, third, and fourth premolars (P<sub>2</sub>, P<sub>3</sub>, P<sub>4</sub>), and trigonid (M<sub>1</sub>trig) blade and talonid (M<sub>1</sub>tal) basin of the lower carnassial (diagram, upper right), in the three extant bone-cracking hyenas and *P. brevirostris* (drawing by Mauricio Antón). The graph shows the scores of the specimens on the first two components, which jointly account for >88% of the original variance.

according to their tooth proportions. Specifically, the differences between the spotted hyenas, which show negative scores on the second component, and the brown and striped hyenas, which both score positively, is due to the relationship between the development of the trigonid blade and the talonid basin in the lower carnassial, the first more elongated in the hunting spotted hyenas and the second more robust in the scavenging brown and striped hyenas. The specimens of *P. brevirostris* are substantially larger than any of the living hyenas, and this is reflected in their high values for the first component. The relative proportions of the lower teeth are similar to those seen in the scavenging hyenas, however, as shown by positive scores on the second component, which indicates that the giant hyena had a masticatory apparatus well adapted for bone-cracking activities, with a comparatively large talonid basin in the lower carnassial. These results provide additional evidence of the scavenging habits of *P. brevirostris* and agree with those obtained in the taphonomic analysis of Venta Micena.

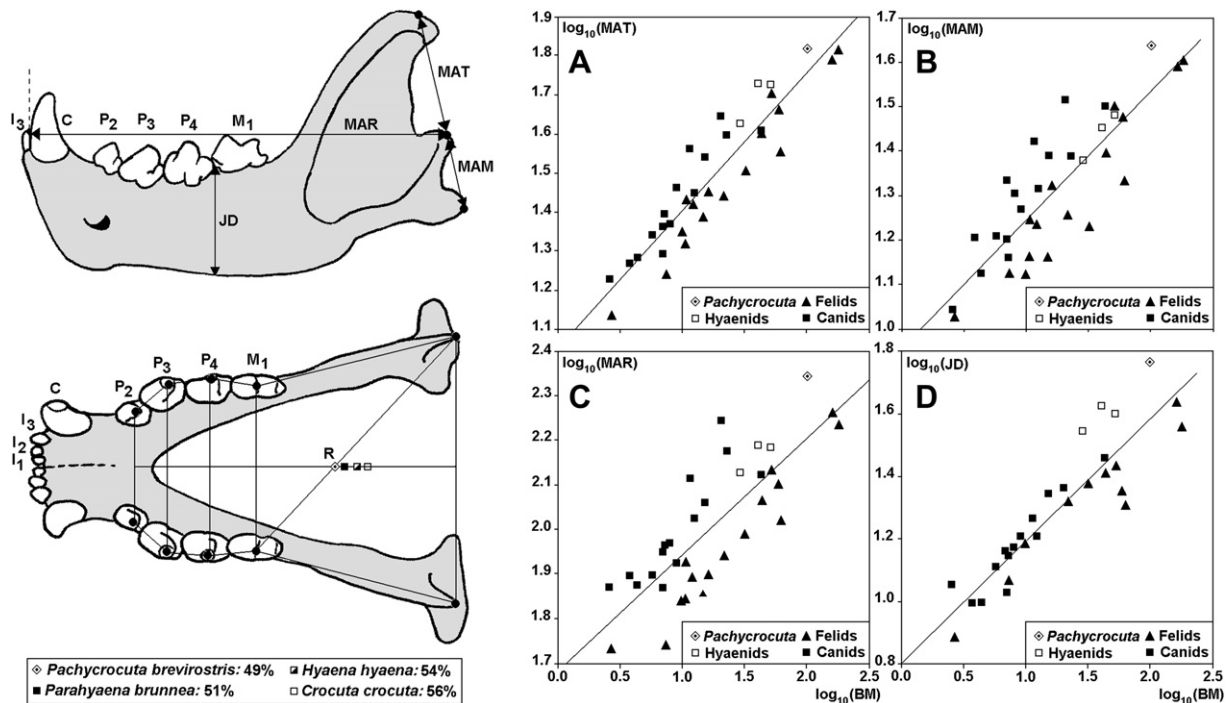
It could be argued, however, that this behavior was exclusive of the particular circumstances of the population of *P. brevirostris* that inhabited southeastern Spain during early Pleistocene times, as is the case of *C. crocuta* in Kruger National Park, where spotted hyenas hunt only 17% of the prey consumed (Henschel and Skinner, 1990). There are other Pleistocene localities, however, such as Untermassfeld (Kahlke and Gaudzinski, 2005) and Zhoukoudian (Boaz et al., 2000), that have been interpreted also as denning sites of *P. brevirostris* and which confirm the taphonomic interpretations made at Venta Micena. In addition, it is worth noting that the specimens of *P. brevirostris* included in the ecomorphological analysis performed here are from four Eurasian sites (Untermassfeld, Val d'Arno, Venta Micena and Zhoukoudian) and all show the same dietary specialization, reflected in their remarkably similar tooth morphology (Fig. 5).

Felids and hyaenids have relatively stronger bites than canids, which is reflected in their jaw structure and in the length of the jaw-closing muscles: cats and hyenas have a more developed temporalis muscle than canids of similar mandible length (Van Valkenburgh and Ruff, 1987). Mandible length, and thus snout length, varies greatly among carnivores: mustelids and felids have shorter snouts than canids and hyaenids. Short snouts are associated with increased force when biting with the anterior dentition because, all other things being equal, the resistance moment arm to these teeth is shorter than that found in longer snouts (Radinsky, 1981a,b, 1982). The ability to produce a large bite force at a wide gape is important to carnivores and this forces a compromise: the carnassials must be positioned far enough forward in the jaw to allow complete separation between the upper and lower blades at full gape, but they must also be positioned rearward enough to produce substantial bite forces (Werdelin, 1989; Biknevicius and Van Valkenburgh, 1996). The dental configuration of the spotted hyena, in which the lower carnassial tooth (M<sub>1</sub>) is positioned closer to the temporomandibular joint than in most other carnivores, represents an exception to this compromise for a midpoint-positioned carnassial. The functional consequence of the concomitant caudal shifting of the bone-cracking premolars (P<sub>3</sub> and P<sub>4</sub>) is that they are effectively placed within or near the region of maximum bite force while still maintaining a substantial gape (Biknevicius and Van Valkenburgh, 1996).

In a study on the adaptation and constraint of the bone-cracking canid *Osteoborus*, Werdelin (1989) developed a biomechanical approach for comparing the jaw geometry of canids and hyaenids. The point R is defined as that resulting from the intersection between a line separating both hemimandibles and a line joining the mandibular condyle of one side with the lower carnassial of the opposite side (Fig. 6). The relative position of this point measures the distance between the condyle and M<sub>1</sub>, which is directly related to the bite strength at the carnassial. The value of R is very similar in *P. brevirostris* and *P. brunnea*, which indicates that the bone-cracking premolars are close to the zone of maximal muscle force in the mandible. Thus, the posteriorly positioned carnassial and premolars relative to the jaw joint allowed the giant hyenas to accommodate bones of large diameter while accomplishing a strong bite force.

Fig. 6A shows the least-squares bilogarithmic regression of moment arm of temporalis (MAT), which measures the extent of the attachment area of the temporalis muscle, on BM in extant felids, hyaenids and canids (data from Van Valkenburgh and Ruff, 1987), and in *P. brevirostris*:  $\text{Log}_{10}(\text{MAT}) = 0.353 (\pm 0.026) \text{Log}_{10}(\text{BM}) + 1.050 (\pm 0.034)$ ,  $r^2 = 0.848$ ,  $F_{1,34} = 191.36$  ( $p < 0.001$ ).

The scatter plot around the regression line for the species analyzed reveals significant differences in bite strength for a given body mass among extant carnivores, because canids and hyaenids show higher MAT values than felids of similar size. The MAT



**Fig. 6.** Landmarks in the jaw of *P. brevirostris* that allow estimation of jaw depth (JD), moment arm of temporalis muscle (MAT), moment arm of masseter muscle (MAM) and moment arm of resistance for an object positioned at canines (MAR) (based in Van Valkenburgh and Ruff, 1987). A: least-squares regression of MAT (in mm) on body mass (BM, in kg) for the living felids, hyaenids and canids (variables log-transformed). B: regression of MAM (in mm) on BM. C: regression of MAR (in mm) on BM. D: regression of JD (in mm) on BM. The muscle resultant for bite at the lower carnassial ( $M_1$ ) is also shown (values for modern hyenas from Werdelin, 1989).

estimate for *P. brevirostris* is in agreement with that expected for a hyena this large, representing approximately the same value of the tiger (*Panthera tigris*), a species 60% heavier than the giant hyena.

Fig. 6B shows the log–log regression of the superficial masseter moment arm (MAM), a rough estimator of masseter and pterygoid muscle size (Radinsky, 1985), on BM (data for modern carnivores from Van Valkenburgh and Ruff, 1987):  $\text{Log}_{10}(\text{MAM}) = 0.290 (\pm 0.031) \text{Log}_{10}(\text{BM}) + 0.957 (\pm 0.041)$ ,  $r^2 = 0.715$ ,  $F_{1,34} = 86.19$  ( $p < 0.001$ ).

As in the case of the temporalis muscle, canids and hyaenids also tend to scatter above the regression line, while most felids have lower MAM values than other carnivores of similar mass. Interestingly, the MAM measurement for *P. brevirostris* is higher than the one expected for a hyena this large, as indicated by the greater distance in the plot between *P. brevirostris* and the regression line compared to the living hyenas. This suggests that the masseter and pterygoid muscles were disproportionally large in this extinct species.

In carnivores, the large canine teeth pose a mechanical problem (Ewer, 1973): to use them effectively a powerful bite must be delivered with the jaws widely open, whereas the carnassials are in operation with the jaws almost closed. The masseter muscle is so arranged that it acts with maximal efficiency in the latter situation (e.g., when a bone is positioned between the bone-cracking premolars) but its line of action is brought progressively nearer the condyle the wider the jaws are opened and its mechanical advantage consequently decreases (Ewer, 1973). In the case of the temporalis, however, downward rotation of the coronoid as the jaw opens actually brings the line of action of the main muscle fibers into a position where their action is more effective as a jaw closer. Due to this reason, the high value of MAM in *P. brevirostris* indicates a substantial strength for bone-cracking activities.

Fig. 6C shows the log–log regression for the moment arm of resistance for an object positioned at canines (MAR) on BM (data

from Van Valkenburgh and Ruff, 1987):  $\text{Log}_{10}(\text{MAR}) = 0.262 (\pm 0.034) \text{Log}_{10}(\text{BM}) + 1.682 (\pm 0.045)$ ,  $r^2 = 0.632$ ,  $F_{1,34} = 59.42$  ( $p < 0.001$ ).

Inspection of the scatters of each family shows that felids and hyaenids have relatively stronger bites than canids of similar size (or, in other words, that canids have on average longer mandibles for a given body mass). However, compared with the values of MAR in the modern hyenas, the estimate obtained for *P. brevirostris* is higher than the one expected for a hyenaid this large. On the one hand, this indicates a loss of bite strength at the canines and thus less predatory abilities for the giant hyena compared to the living hyenas and felids; this is in agreement with the scavenging niche deduced for the giant hyena in the taphonomic analysis of Venta Micena. On the other hand, the comparatively high value of MAR (which measures mandible length) indicates that *P. brevirostris* was not a truly short-faced hyena, as suggests its specific name (the Latin word “brevirostris” means “short face”).

Finally, Fig. 6D shows the scaling of jaw depth measured at the  $P_4$ – $M_1$  interdental joint (JD) on BM (data from various sources and unpublished measurements taken by V. Torregrosa):  $\text{Log}_{10}(\text{JD}) = 0.392 (\pm 0.035) \text{Log}_{10}(\text{BM}) + 0.801 (\pm 0.047)$ ,  $r^2 = 0.821$ ,  $F_{1,29} = 128.43$  ( $p < 0.001$ ).

The scatter plot around the regression line reveals significant differences in jaw strength among the members of the three carnivorous families analyzed. For a given body mass, hyaenids show an increased height of the mandible corpus compared to canids and felids. This produces a mandible more resistant to vertical bending in the region of maximum stress (i.e., behind the premolars), which reflects their adaptation for consuming bones. On the one hand, the high estimate obtained for jaw depth in *P. brevirostris* is in agreement with the one expected for a hyena this large, revealing a substantial resistance of the mandible against dorsoventral loads during bone-cracking activities. On the other hand, jaw depth is proportionally more developed in *P. brevirostris*



than in the spotted hyena judging from the distance to the regression line for both species; leaving aside scaling effects, however, the mandible of the giant hyena is similarly proportioned to those of brown and striped hyenas, whose diet includes more bones, which constitutes additional evidence on the scavenging habits of *P. brevirostris*.

Fig. 7 shows the mandibular force profiles obtained for the extant bone-cracking hyenas and *P. brevirostris*. The values depicted in these diagrams were transformed logarithmically for avoiding bias resulting from allometric scaling (Smith, 1984, 1993). The profile along the dorsoventral axis of the jaw (Fig. 7A) is very similar in the three living hyenas and shows a decrease in the resistance to bending stresses toward the anterior dentition, a trend more accentuated in the spotted hyena, although this species shows a slight increase at the level of the lower canine. This shape profile helps in dissipating the stress generated with the anterior premolar teeth when fracturing the bones, which is the typical behavior of the living hyenas (Rensberger, 1995; Van Valkenburgh, 1996). It is worth noting that the brown hyena is the species with a jaw more developed dorsoventrally, except behind the lower carnassial. The profile obtained for *P. brevirostris* parallels the one of *P. brunnea*, but with values for  $Zx/L$  that are between twice and three times more elevated, which indicates that the jaw of this extinct hyena was able of exerting a substantially greater bite force during bone fracturing. This is particularly evident at the level of the canine, because the mandibular symphysis of *P. brevirostris* is extremely buttressed dorsoventrally, which suggests that the jaw of the giant hyena was better suited for fracturing bones than those of the living hyenas.

The force profiles along the labiolingual axis (Fig. 7B) show that the mandibles of all hyenas are more resistant to lateral bending at the level of the canine than at any other point, which probably reflects the elevated torsional loads that must be dissipated with the mandibular symphysis during bone-cracking (Therrien, 2005a). The profile of *P. brevirostris* is again more similar to the one of *P. brunnea*, although the values obtained are between twice and two and a half greater.

Finally, relative force profiles (Fig. 7C), which allow estimating differences in the shape of the section along the mandibular corpus, are similar in all hyenas and show that their jaws are better adapted for exerting dorsoventral loads than for resisting sagittal stresses ( $Zx/Zy > 1$ ). However, the  $Zx/Zy$  ratio approaches one toward the anterior dentition, which reflects that the mandibular ramus adopts here a more rounded section and, thus, is reinforced for resisting the torsional forces generated when biting a moving prey. This is particularly evident in *C. crocuta*, the only living hyena that behaves more as a hunter than as a scavenger, in which the  $Zx/Zy$  ratio takes a value slightly lower than one at the level of the canine. In addition, the spotted hyena shows the highest  $Zx/Zy$  value at the level of the carnassial, which indicates that its jaw is better suited for resisting the dorsoventral loads produced when this tooth is used for slicing the skin and defleshing a carcass.

The multivariate regression of shape on centroid size values was highly significant ( $p < 0.0001$ ) and the total amount of shape variation accounted for size differences was 13.1%. Therefore, allometry is a significant causal factor for shaping the mandibular corpus shape in hyenas.

Fig. 8A shows the morphospace depicted from the first two PCs, which jointly account for more than 75% percent of mandible shape variation. The first PC separates the spotted hyena, with negative scores, from the other two living hyenas plus *P. brevirostris*, which score positively. This shows that the mandible of *C. crocuta* is characterized by the presence of a well-developed carnassial, a curved mandibular corpus and a shallow mandibular body below the premolars and the canine tooth (Fig. 7B). In contrast, the jaws of

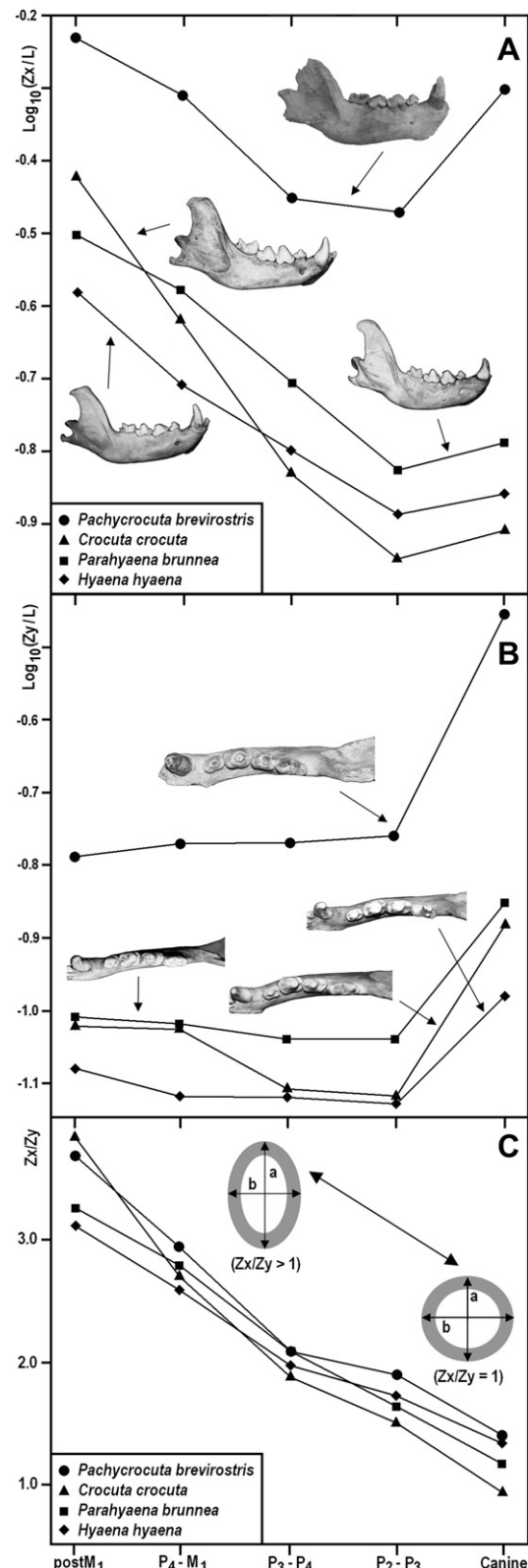
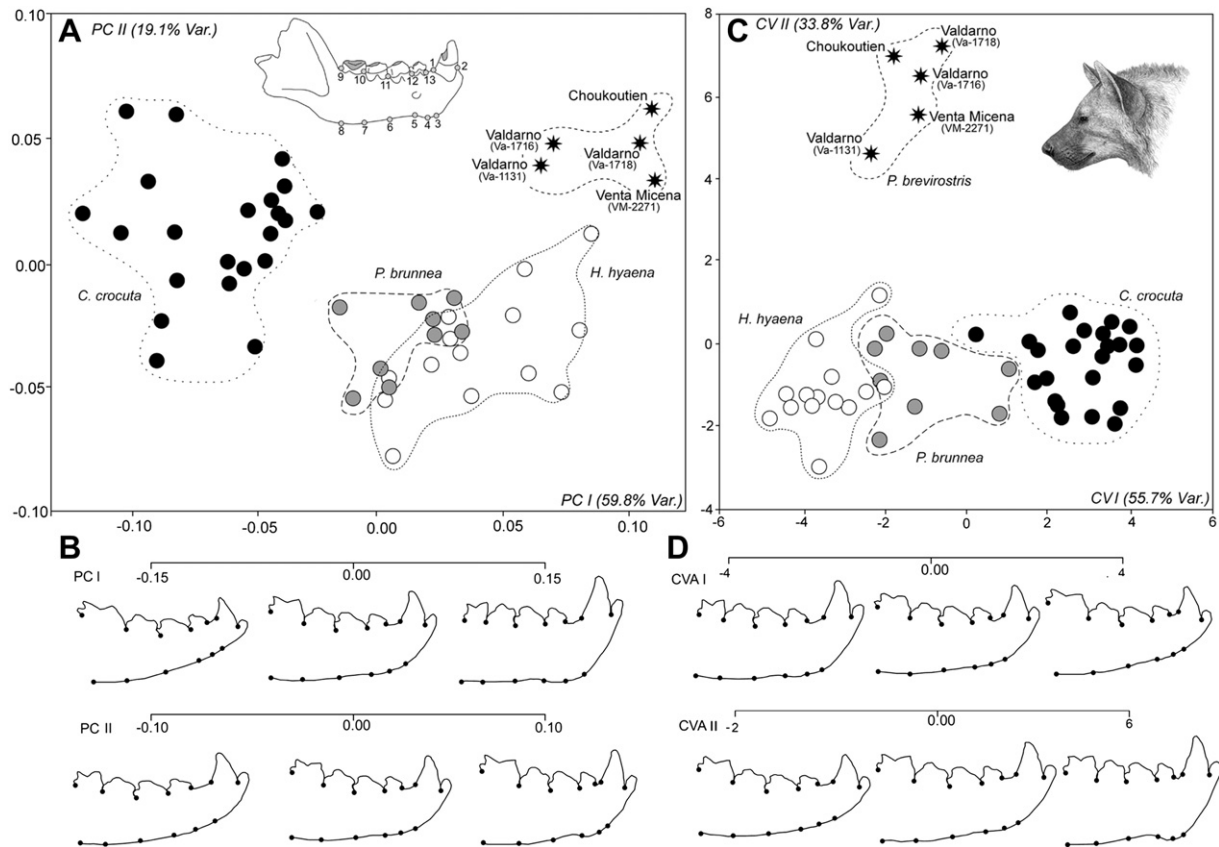


Fig. 7. Mandibular force profiles calculated for the living hyenas and *P. brevirostris*. A, dorsoventral plane. B, labiolingual plane. C, relative force profiles.

*H. hyaena*, *P. brunnea* and *P. brevirostris* are more straight, deeper below the premolars and canine, and have a shorter carnassial tooth (Fig. 8B). This suggests that *P. brevirostris* has a jaw shape more similar to the living brown and striped hyenas, which are



**Fig. 8.** Morphometric analysis of mandible shape in the living hyenas and *P. brevirostris*. A, pairwise plot of the first two PCs derived from PCA of mandible shape. B, jaw shape variation accounted for by PC I and PC II. C, pairwise plot of the first two CVs derived from CVA of mandible shape. D, jaw shape variation accounted for by CVA I and CVA II.

both specialized bone-cracking scavengers (Rieger, 1981; Mills, 1982), rather with the spotted hyena which behaves more as an active, pack-hunting predator (Gasaway et al., 1991; Di Silvestre et al., 2000). The second PC separates *P. brevirostris* from *H. hyaena* and *P. brunnea*, revealing that the extinct giant hyena has a comparatively larger carnassial and a deeper mandibular body at the level of the canine (Fig. 7B).

Fig. 8C shows the morphospace depicted from the first two CVs, which jointly explain nearly 90% of jaw shape variation. Again, the first CV separates *C. crocuta*, which takes positive scores, from *H. hyaena*, *P. brunnea* and *P. brevirostris*, species which score negatively. The jaw of the spotted hyena is curved and shallow below the canine and premolars, has a large carnassial and shows a short distance between the canine and the first premolar (Fig. 8D). All these traits are typical of flesh-eating carnivores. For example, a well-developed and sharp carnassial blade is well suited for processing meat (Biknevicius and Van Valkenburgh, 1996) and is usually associated to a curved mandibular corpus (Melo et al., 2008). In contrast, the jaws of *H. hyaena*, *P. brunnea* and *P. brevirostris* share a set of traits that could be interpreted as adaptations to bone-cracking. For example, their deep anterior body is well suited for dissipating the high torsional forces generated in the parasagittal plane as a result of chewing bones with the enlarged premolar teeth (Biknevicius and Ruff, 1992; Therrien, 2005a,b). The second CV mainly describes those aspects of jaw shape that separate the extinct giant hyena from the living hyenids, showing that the mandibular corpus of *P. brevirostris* is deeper and has a more developed symphysis (Fig. 8D). These features evidence the more extreme adaptations for bone-cracking of *P. brevirostris* compared to *P. brunnea* and *H. hyaena*.

## 5. Discussion

What does the craniodental and postcranial anatomy of the giant hyena indicate? Apart from its large size, *P. brevirostris* differed from other hyenids in the relative shortening of its distal limb segments (Table 5), with a brachial index (radius length to humerus length) of 0.91 (range for modern hyenas: 1.00–1.08) and a crural index (tibia length to femur length) of only 0.74 (range: 0.82–0.88). Although such shortening may be explained in part as a consequence of the enormous size of this extinct hyena, given the inverse relationship in modern carnivores of brachial and crural indexes with body mass (Anyonge, 1996), the tibia of *P. brevirostris* seems to have been particularly short in relation to the femur (Table 5). Such reduction has been envisioned in hyenas as an adaptation to carry large pieces of carcasses without dragging (Sporer, 1985). Modern hyenas show a comparatively long radius, which raises the forequarters and therefore the head of the animal. Although the radius is also shortened in *P. brevirostris* compared to other hyenas (Table 5), the ratio between the fore- and hind limb lengths (1.06) falls close to the values of brown hyenas (1.06) and striped hyenas (1.04). This is achieved by the more extreme shortening of the tibia in the giant hyena, which indicates a similar emphasis on the forequarters to that seen in brown and striped hyenas. All these features of the postcranial anatomy suggest a less cursorial life style for *P. brevirostris* than in the spotted hyena, although the shortening of the limbs provided greater power and more stability to dismember and carry large pieces of ungulate carcasses (Turner and Antón, 1996; Palmqvist and Arribas, 2001). The permanent dentition of *P. brevirostris* (Table 5, Figs. 5 and 8) reflects also its adaptations for scavenging, with a trigonid blade in the lower carnassial

relatively short and a robust and well-developed fourth premolar, as in brown and striped hyenas. Spotted hyenas are efficient predators thanks to their strong social organization, hunting their prey in ~60% of cases and scavenging ungulate carcasses in the remaining 40% (mostly from the prey of lions, *Panthera leo*, and painted dogs, *Lycaon pictus*; see review in Palmqvist and Arribas, 2001). On the contrary, brown and striped hyenas are mainly carrion eaters due to their smaller size and solitary habits (Mills, 1984; Kerbis-Peterhans and Horwitz, 1992). As an adaptation for their higher consumption of flesh, spotted hyenas show a larger trigonid blade in the carnassial, more efficient for meat slicing than the one of brown and striped hyenas, and premolars of smaller size relative to the carnassial tooth, less adapted for bone-cracking (Turner and Antón, 1996). Some of the adaptations of *P. brevirostris* were developed convergently in the late Pleistocene by the European cave hyena, *Crocota spelaea*, which indicates its scavenging habits (Table 5).

This interpretation of the paleobiology of *P. brevirostris*, however, is questioned by Turner and Antón (1996), Galobart et al. (2003) and Dennell et al. (2008) on the basis of the enormous size of this species, which they consider that may have represented an adaptation for subduing large-sized ungulates under concerted action within a pack.

Modern hyenas, as well as many other carnivores, show marked differences in predatory behavior (i.e., hunting vs. scavenging, optimal prey size and hunting techniques) among localities depending on resource availability, type of habitat (which determines killing success and foraging efficiency) and interactions with other predators (Kruuk, 1972; Schaller, 1972; Höner et al., 2002). For this reason, the feeding preferences of a living carnivore cannot be

unequivocally assessed from the study of a single population. As an example, Fig. 9 shows the relative abundance of ungulates distributed among size classes in the diet of four African populations of spotted hyenas. Although medium-sized (100–200 kg) species are in all cases the best represented in the carcasses consumed by the hyenas, the frequencies of prey killed and scavenged show clear differences between localities as well as among size classes. Specifically, the proportion of kills varies between only 17% in Kruger (data from Henschel and Skinner, 1990) and up to 99% in Masai Mara (data from Cooper et al., 1999). In the Ngorongoro crater, where spotted hyenas hunt in 76% of cases and scavenge the prey of lions in the remaining 24% (data from Kruuk, 1972; Höner et al., 2002), there is a significant difference between the percentage of scavenged carcasses for ungulates <100 kg and >100 kg, 14% (18/125) and 29% (85/296), respectively ( $t = 5.49$ ,  $p < 0.0001$ , one-tailed). In Serengeti, however, kills and scavenging are more equally represented in the diet of hyenas, 43% and 57%, respectively (data from Kruuk, 1972), and hyenas scavenge similar proportions of ungulates <100 kg and >100 kg, 55% (125/229) and 60% (164/274), respectively ( $t = 1.02$ ,  $p > 0.1$ ). In Ngorongoro, spotted hyenas must hunt more than in Serengeti because, given the size of the crater, lions can watch the movements of hyenas and kleptoparasitize most of their kills (Kruuk, 1972). Obviously, the craniodental anatomy of these lions does not reflect their scavenging habits.

The most conclusive evidence favoring a strict scavenging behavior for *P. brevirostris* arises from the taphonomic study of the bone assemblage preserved at Venta Micena, although it is worth noting here that the study of a single (paleo)population introduces a cautionary note. Previous research on this early Pleistocene locality has shown that the skeletal remains were scavenged by the giant hyenas from carcasses of ungulates preyed upon by flesh-eating carnivores (Palmqvist et al., 1996). Major taphonomic biases introduced in the assemblage by the hyenas result from the selective transport of ungulate carcasses and body parts to their maternity dens (Palmqvist and Arribas, 2001) and from the preferential consumption of low-density, marrow-rich skeletal parts (Arribas and Palmqvist, 1998).

Results obtained here in the analysis of contingency tables for the distribution of major limb bones of ungulates among preservational categories show a well defined proximodistal sequence of consumption by hyenas for humerus and tibia, as described by Palmqvist and Arribas (2001), an inverse sequence of bone modification for metapodials and a less clearly defined pattern of consumption in the case of radius and femur. The better preservation of metapodials as complete elements relate to their higher mineral density and lower nutritional value (Arribas and Palmqvist, 1998). The lower frequencies of distal epiphyses for these bones suggest that they were preferentially fractured by the hyenas at their distal end, which probably reflects a selective behavior for accessing the fat content of phalanges, given that the latter bones are poorly preserved in the assemblage (Table 1). The low frequencies of humeri and tibiae preserved complete and the abundance of femoral diaphyses also relates to the grease contents of these bones, as in both modern horse and bison the marrow yields of humerus (41 and 409 g, respectively), femur (72 and 371 g), tibia (33 and 145 g) and radius (24 and 185 g) are greater than those of metacarpal (11 and 34 g) and metatarsal (9 and 46 g) [estimates for modern *E. caballus* from Outram and Rowley-Conwy (1998) and for *B. bison* from Brink (1997)]. These results indicate the selective bone-crushing behavior of *P. brevirostris*, with significant differences in the patterns of consumption of limb bones related to their position within the ungulate skeleton and their nutritional value.

Recent bone accumulations made by striped hyenas show a preservational completeness for ungulate taxa similar to that of

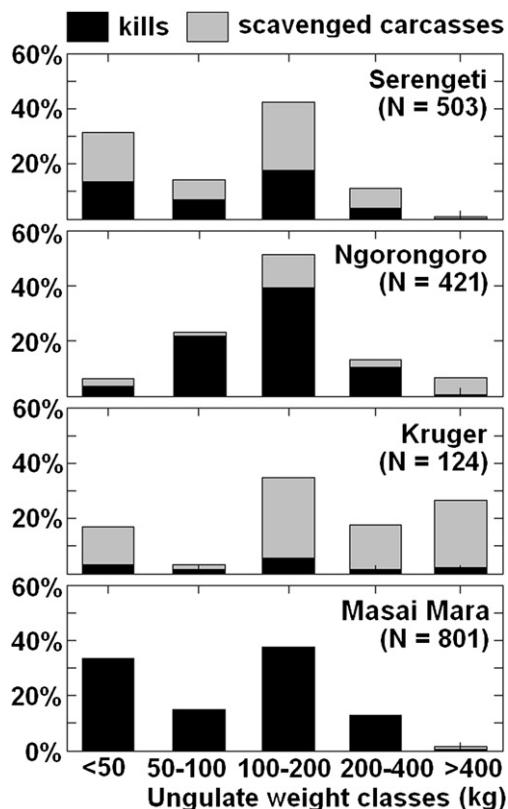


Fig. 9. Abundance of ungulates grouped by weight classes in the diet (kills and scavenged carcasses) of spotted hyenas in four African National Parks: Serengeti (data from Kruuk, 1972), Ngorongoro (data from Kruuk, 1972; Höner et al., 2002), Kruger (data from Henschel and Skinner, 1990) and Masai Mara (data from Cooper et al., 1999).



Venta Micena: tibia and humerus tend to be preserved as distal epiphyses while radius and metapodials are the less fractured limb bones (Skinner et al., 1980; Kerbis-Peterhans and Horwitz, 1992; Leakey et al., 1999). Sutcliffe (1970) found the same basic pattern of skeletal representation in the bone assemblages collected by spotted hyenas, although the larger size of this species translates in a greater ability for destroying bones than in the case of brown and striped hyenas, as deduced from the percentage of unidentifiable bone shafts and fragments in the maternity dens: 20–72% for spotted hyenas (Skinner et al., 1986; Hill, 1989; Lam, 1992), 21–30% for brown hyenas (Skinner and van Aarde, 1991) and <18% for striped hyenas (Skinner et al., 1986; Kerbis-Peterhans and Horwitz, 1992; Leakey et al., 1999). The percentage of bone shafts in Venta Micena is 65%, thus close to the upper limit of spotted hyena dens. However, this fossil assemblage includes comparatively more skeletal remains of large mammals with a body mass above 1000 kg than those collected by spotted hyenas and larger bones are more resistant to destruction due to their lower outer surface to inner volume ratio (Behrensmeyer, 1991).

Given that bone survival against hyena damage depends on the structural resistance of skeletal elements (i.e., mineral density and degree of epiphyseal closure) as well as on their nutritional contents (Brain, 1981; Arribas and Palmqvist, 1998), the consistent pattern of bone consumption shown by both living and extinct hyenas indicates an optimization of the ratio of benefit to cost in these carnivores, with independence of their intrinsic capabilities of bone destruction. This confirms that the skeletal elements and bone portions preserved in Venta Micena are basically those that remained around the maternity dens once all their within-bone nutrients were consumed by the giant hyenas (Palmqvist and Arribas, 2001).

The results obtained here in the biomechanical analyses indicate that *P. brevirostris* had a powerfully built body with massive and relatively short limbs, a mass nearly twice that of a spotted hyena, strong and posteriorly positioned bone-cracking premolars, temporalis and masseter jaw-adductor muscles well developed, a deep mandibular corpus well designed for resisting high dorsoventral strains and a comparatively lower bite strength at the canines than in the spotted hyena. All these features provide an emerging picture of a very robust carnivore, well adapted for scavenging ungulate carcasses, transporting them to the maternity den and fracturing the bones for accessing their medullary cavities, as documented at Venta Micena (Palmqvist and Arribas, 2001). Thus, the giant hyenas may have been similar in habits to the brown and striped hyenas, which subsist primarily on carrion complemented by small vertebrates, fruits, and insects, but they likely emphasized carrion even more and included a larger percentage of bone in its diet, as evidenced by the huge accumulation of bones preserved at Venta Micena.

However, although *P. brevirostris* exhibits a unique combination of body size and craniodental features among the modern hyenas that suggests a unique mode of life, more based on scavenging than in spotted hyenas, this interpretation is not free of problems. First, scavengers must be able to find carcasses without traveling long distances and no living mammal lives entirely by scavenging due to time constraints (Van Valkenburgh, 1985). Today, only vultures are pure scavengers because soaring at high altitude is an energetically efficient mode of locomotion that allows them to cover huge distances and discover carcasses by sight or watching the movements of other neighboring birds (Palmqvist and Vizcaíno, 2003). Second, among the living terrestrial carnivores, only striped and brown hyenas rely heavily on carrion, and their postcranial skeleton is more lightly built than that of spotted hyenas, which are efficient hunters, reflecting their need of covering longer distances in the search of scavengeable carcasses. The short-leggedness of *P. brevirostris*, which may reflect in part the effects of allometric

scaling given the enormous size of this hyena, would represent a clear disadvantage for this mode of life. Third, given the relationship between body mass and diet among living carnivores (Carbone et al., 1999), which shows that almost all species larger than ~21 kg take prey as large or larger than themselves, it is unlikely that an animal as big as *P. brevirostris* would have relied more on scavenging than on hunting (although it must be remembered that brown and striped hyenas, with body masses in excess of this value, are predominantly scavengers).

According to the reasons discussed above, the massive body and short limbs of the giant hyenas could argue against the interpretation of this extinct carnivore as a strict scavenger, because carrion eaters must range over large areas in search of food, a task for which the stocky and robust nature of the body of *P. brevirostris* was not well designed, and the taphonomic evidence of scavenging habits collected at Venta Micena could then merely reflect their behavior in a given locality, as evidenced by modern spotted hyenas at Kruger National Park (see above). However, there is compelling evidence from other Pleistocene localities, which may be also interpreted as *Pachycrocuta* dens (e.g., Dmanisi, Untermassfeld and Zhoukoudian), that support this interpretation. A possible explanation for the evolution of a hyena this large, with such a highly specialized morphology and scavenging behavior but showing less cursorial habits than the extant hyaenids, is that *P. brevirostris* did not prospect at random long distances searching for scavengeable carcasses, but pursued other predators such as saber-tooth cats and exploited their kills acting as a kleptoparasite (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). High carcass predictability as in Venta Micena, where an open habitat prevailed (Palmqvist et al., 2003, 2008a,b; Mendoza et al., 2005) and scavenging birds would have improved carcass finding by the giant hyenas, would then be a prerequisite for this trophic specialization.

The following paragraphs attempt to decipher the ecological circumstances that favored the evolution of such a specialized behavior in *P. brevirostris*.

The marked seasonality that characterized temperate Europe for most of the Pleistocene, with cooler and drier conditions than those of tropical Africa, made the availability of large ungulate carcasses for scavenging a key resource for both hyenas and hominids (Turner, 1990, 1992; Turner and Antón, 1998; Arribas and Palmqvist, 1999). The European carnivore guild included two species of saber-toothed cats (*H. latidens* and *M. whitei*) during the early Pleistocene; these predators presumably maximized the amount of flesh that remained on their kills, given their highly specialized teeth, thus opening broad opportunities of scavenging for other species (Martínez-Navarro and Palmqvist, 1996; Palmqvist et al., 2007).

The Middle-Upper Villafranchian transition in southwestern Europe was marked by an important turnover in the composition of the mammalian assemblages. This faunal replacement was originally named by the Italian palaeontologist Augusto Azzaroli as the “Wolf event” (Azzaroli, 1983; Azzaroli et al., 1988) because it seemed to be coincident with the first record of the genus *Canis* (Senèze, France; Costa San Giacomo, Italy; ~2.1 Ma) (Rook and Torre, 1996). However, it is worth noting that the biochronological value of the Azzaroli’s “Wolf Event” has been discussed (e.g., Sardella and Palombo, 2007) and that an earlier occurrence of *Canis* was recorded recently in the early Villafranchian local fauna of Viallette, France (Lacombat et al., 2008). Because of this, Martínez-Navarro (2010) has proposed to name this event as the “*Pachycrocuta brevirostris* event”, because it would be related to the arrival of this giant hyena into Eurasia and would reflect the important record and impact of this hyena on most fossil assemblages during the Upper Villafranchian (Rook and Martínez-Navarro, 2010). In any case, this Early Pleistocene replacement seems to have been rather gradual, as

recorded in Italy within the Olivola and Tasso Villafranchian faunal units.

The comparative systematic study of macrovertebrate assemblages from several northern circum mediterranean localities (e.g., Apollonia, Dmanisi and Venta Micena) shows the presence of typical early Pleistocene species, as the small-sized ovibovine *Soergelia*, and it is characterized by the arrival in Europe of both African and Asian species (Martínez-Navarro, 1991; Martínez-Navarro and Palmqvist, 1995, 1996; Arribas and Palmqvist, 1999). Immigrants originating in Asia are basically ruminant species, the giant hyena *P. brevirostris* and canids *C. etruscus* (recorded in Dmanisi), *C. mosbachensis* and *L. lycaonoides* (recorded in Apollonia-1 and Venta Micena; Martínez-Navarro and Rook, 2003). African immigrants include a megaherbivore (the hippo, *Hippopotamus antiquus*), the jaguar-sized saber-tooth *M. whitei* (Martínez-Navarro and Palmqvist, 1995, 1996) and the first members of the genus *Homo* recorded in Eurasia, which according to Lordkipanidze et al. (2007: p. 309) would be comparable to the earliest *Homo* (cf. *Homo habilis*). Finally, the late Pliocene horse *Equus stenonis* is replaced by *E. altidens*, a species whose postcranial anatomy is similar to that of modern grevy's zebras (Guerrero-Alba and Palmqvist, 1997). Later, during late Early Pleistocene times, a large terrestrial cercopithecoid, the giant gelada *Theropithecus oswaldi*, is also found out of Africa (Cueva Victoria, Spain; Pirro Nord, Italy; Ubeidiya, Israel; Mirzpur, India) (Delson, 1993; Gibert et al., 1995; Belmaker, 2002; Rook et al., 2004).

Saber-tooth cats show an extremely specialized craniodental anatomy, sharing among others the following derived characters (see reviews in Arribas and Palmqvist, 1999; Palmqvist et al., 2007): (i) elongated and laterally compressed upper canines, enlarged and procumbent upper incisors, and reduced, incisor-shaped lower canines; (ii) upper carnassials with a reduced or absent protocone, constituting a long and thin blade that allowed saber-tooths to deflesh their prey rapidly; (iii) a lowered glenoid fossa, a reduced height of the coronoid process, a laterally shifted angular process, and a shortened zygomatic arch (features that allowed a wide gape in saber-tooths, but imply that their temporalis muscle was weaker than in modern felids); and (iv) an enlarged, lowered and ventrally extended mastoid process, which indicates that the neck muscles must have been correspondingly large (thus suggesting that a head-depressing motion was involved in the penetration of the canines). These morphological features indicate that saber-tooths were able to hunt large ungulate prey relative to their own size and that they left on the carcasses variable amounts of flesh and all bone nutrients, resources that could subsequently be scavenged by the giant hyenas and the hominids (Marean, 1989; Arribas and Palmqvist, 1999).

Saber-tooths became extinct in East Africa ~1.5 Ma, which coincides with the emergence of the Acheulean (Mode 2) Industrial Complex associated to *H. ergaster*, but inhabited Eurasia until ~0.5 Ma (Turner, 1990, 1992; Turner and Antón, 1998). Their persistence may explain the success of the Oldowan (Mode 1) tools in Eurasia, where the Oldowan/Acheulean technological transition took place approximately one million years later than in Africa, following the disappearance of saber-tooths in this continent (Arribas and Palmqvist, 1999). The reason is that the sharp flakes characteristic of Oldowan assemblages were fully appropriate for scavenging on partially defleshed carcasses abandoned by the saber-tooths and the cores were useful to break the bones for accessing their marrow content.

The masticatory apparatus of the early members of the genus *Homo* was not well configured for supporting the stresses generated during the mastication of hard foods. Two evolutionary trends took place in the genus *Homo*: brain enlargement and tooth reduction (Wood and Collard, 1999; McHenry and Coffing, 2000).

Given that brain tissue is metabolically expensive, the increase in the degree of encephalization resulted in greater energetic costs, which could be contributed by improvements in dietary quality and/or changes in body composition (Aiello and Wheeler, 1995; Leonard et al., 1996). In fact, carnivores have shorter guts than herbivores, and the gastrointestinal tract is also a metabolically expensive tissue. This opens the possibility that the high metabolic demands of the enlarged brain of *Homo* were offset by a corresponding reduction of the gut linked to a greater consumption of high-quality, easy-to-digest foods such as meat and bone marrow (Aiello and Wheeler, 1995; Leonard et al., 1996). It is worth noting that these anatomical and physiological changes were linked to an aridification trend in Africa that resulted in a decrease of nutrient-rich foliage (de Menocal, 1995). In this context, the progressive incorporation of animal foods would be the best option for satisfying the increased dietary requirements of *Homo* (Milton, 1999) and competition between hominids and other carrion feeders for accessing animal resources arise as a possibility. However, if *P. brevirostris* had primary access to the ungulate carcasses left by saber-tooths, the remains available for the hominids would be scarce. For this reason, a thought-provoking hypothesis of "kleptoparasitic behavior" has been proposed for the hominids. The accumulation of manuports in a reduced surface of the Dmanisi excavation quarry as well as the anatomical configuration of the arm–shoulder complex in the Dmanisi hominids have both a behavioral implication: hominids could have intimidated other carnivores before accessing the carcasses by throwing them a large amount of stones (Jashashvili, 2005). If *M. whitei* and *P. brevirostris* were solitary predators and scavengers, respectively (Palmqvist and Arribas, 2001), it would be relatively easy for a group of hominids to scare them. However, further research is necessary for assessing manuport functionality and also for investigating if such evidence is found in other archaeological sites.

The emergence of human sociability during Early Pleistocene times is another intriguing issue that arises from the Dmanisi record. Specifically, the presence of a toothless skull showing an advanced degree of alveolar resorption – which implies the survival of this individual for a lengthy period without consuming foods that required heavy chewing – together with the finding of cut-marks and percussion-marks on large mammal bones indicative of carcass processing and meat-eating allowed Lordkipanidze et al. (2005) to suggest that it was fed with animal soft tissues – e.g., brain and marrow – by other members of the group. Such behavioral approach opens the possibility of further exploring the changes in social structure, life history and subsistence strategies that allowed the success of *Homo* out of Africa in highly seasonal environments.

Modern pantherine cats such as lions and leopards arrived in Europe during the Middle Pleistocene and this was followed by the extinction of saber-tooths and other large felids such as the European jaguar (*Panthera gombaszoegensis*) and the giant cheetah (*Acinonyx pardinensis*). Presumably, these new predators exploited their kills more in depth than saber-tooths (Turner et al., 2008), which resulted in the loss of a regular source of scavengeable carcasses for the giant hyenas and the hominids. Under these new ecological circumstances, the trophic niche that they exploited vanished.

In addition, the hominids that may be included within *H. erectus* s.l. had a larger body size and a higher degree of encephalization than those grouped in *H. habilis* s.l. (Ruff et al., 1997), which translated in higher energetic demands compared to the earliest members of *Homo*. The consequence was probably an increase in the consumption of high-quality foods from ungulate carcasses obtained from regular scavenging. This opened a new ecological scenario in which the competence with other carnivores was also increased. In sociocultural terms, a larger brain allowed to develop more complex behaviors, which would have been reflected in the

expansion of the cognitive repertoire of these hominins [e.g., use and control of fire (Goren-Inbar et al., 2004; Alpersen-Afil, 2008), spatial organization and more in-depth exploitation of their home range areas, consumption of aquatic resources (Alpersen-Afil et al., 2009) and, ultimately, technological innovations that resulted in cooperative hunting (Stiner et al., 2009)].

Arribas and Palmqvist (1999) suggested that the change in the composition of the carnivore guild with the replacement of saber-tooths by pantherine cats forced the hominins toward behavioral and technological improvements that resulted in the development of the more effective Acheulean tools of *H. erectus* s.l., which replaced the technologically less elaborated Oldowan flakes of earlier populations. However, such replacement was not abrupt, as evidenced at Isernia La Pineta (Italy), a locality that shows the coexistence during middle Pleistocene times of an Oldowan assemblage with pantherine cats (Peretto, 2006; Arzarello and Peretto, 2010). Such co-occurrence has been explained as a special case on the basis of both the features of the raw material (poor quality flint with tectonic fractures) and the activities made in this site (mainly carcass processing). In this context, the flakes were configured for obtaining a functional cutting edge in an easy and fast way (Arzarello and Peretto, 2010).

An alternative hypothesis can be added to this ecological scenario: the arrival of new human contingents with the Acheulean complex that replaced the descendants of the first populations of *H. habilis* s.l. that initially dispersed out of Africa (Jiménez-Arenas et al., 2007; Lordkipanidze et al., 2007) and survived in Europe during the Early Pleistocene and the early Middle Pleistocene. The possibility of this second dispersal event is favored by Templeton (2002), who traced from gene sequence data of the hemoglobin  $\beta$ -chain locus, the melanocortin 1 receptor and a hypervariable minisatellite region on chromosome 16 a more recent out of Africa expansion between 0.84 and 0.42 Ma.

Being constrained by its enormous size and by a highly specialized anatomy derived from its strict scavenging behavior, the inevitable destiny of the giant hyena *P. brevirostris* during this period of change was extinction.

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