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Prey selection by terrestrial carnivores in a lower Pleistocene paleocommunity

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Abstract.—We report quantitative paleoecologic data on the large mammal assemblage preserved in lower Pleistocene deposits at Venta Micena (Orce, Granada, southeastern Spain). Taphonomic studies show that bones were collected mainly by hyaenids, which transported and deposited them near shallow dens. Differential fragmentation of major long bones was produced by hyaenas as a function of their density and marrow content. Strong selection of prey by carnivores—which preferentially killed juveniles, females, and individuals with diminished locomotor capabilities among ungulate prey species of larger body size—is indicated by (1) the abundance of remains of juvenile ungulates in relation to the average weight of adult individuals in each species, (2) attritional mortality profiles for ungulate species deduced from crown height measurements, (3) the presence of many metapodials with different osteopathologies in their epiphyses, such as arthrosis, and (4) a biased intersexual ratio of large bovids. Comparison of the frequencies with which modern African carnivores kill and scavenge ungulates from various size classes with the abundance of these size categories in the assemblage suggests that the Venta Micena hyaena (*Pachycrocuta brevirostris*) was a bone-cracking scavenger that fed largely on carcasses of ungulates preyed upon and partially consumed by fresh meat-eating carnivores such us saber-toothed felids (*Homotherium latidens* and *Megantereon whitei*) and wild dogs (*Canis falconeri*).

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Introduction and Background

The Venta Micena site (Orce, Granada, southeastern Spain) is located in the eastern sector of the Baza lacustrine basin (Fig. 1). The fossil assemblage was preserved in 90–98% pure micritic limestone, which precipitated in freshwater ponds emplaced on a caliche soil of diagenetic origin. This soil surrounded a lake that existed in the valley of Orce during the PlioPleistocene (Vera et al. 1985; Soria et al. 1987).

Biostratigraphic and systematic study of macromammals (Martínez-Navarro 1991, 1992a; Martínez-Navarro and Palmqvist 1995) places this site in the lower Pleistocene and reveals three faunal components: (1) Species evolved autochthonously in western Europe during the upper Pliocene (*Mammuthus meridionalis, Stephanorhinus etruscus, Homotherium latidens,* and *Ursus etruscus*); (2) immigrants from Asia (*Praeovibos* sp., Bovini cf. *Bubalus, Soergelia minor, Hemitragus alba,* "Cervidae" gen. et sp. indet., *Megaloceros* [*Megaceroides*] *solilhacus,* and *Canis etruscus*); and (3) species from Africa (*Megantereon whitei, Pachycrocuta brevirostris, Canis* [*Xenocyon*] *falconeri, Equus altidens, Hippopotamus antiquus,* and *Homo* sp.).

The presence of humans in the southern Iberian Peninsula during lower Pleistocene times has been demonstrated by comparative morphometric study of the scarce fossil remains (cranial fragment, humeral diaphysis, medial phalanx, and some humeral fragments; Gibert and Palmqvist 1995; Palmqvist et al. 1996). The human mandible and lithic industries in the lower Pleistocene (≥ 1.0 Ma) deposits from Dmanisi, East Georgia (Gabunia and Vekua 1995) are associated with *M. whitei,* the African machairodont also present in Venta Micena (Martínez-Navarro and Palmqvist 1995, 1996).

The accumulation of skeletal remains at Venta Micena (Fig. 2) is exclusively due to the biotic factors; geologic processes (e.g., fluvial transport) can be excluded, since the bones are randomly oriented and show no traces of abrasion from rolling or similar movements.

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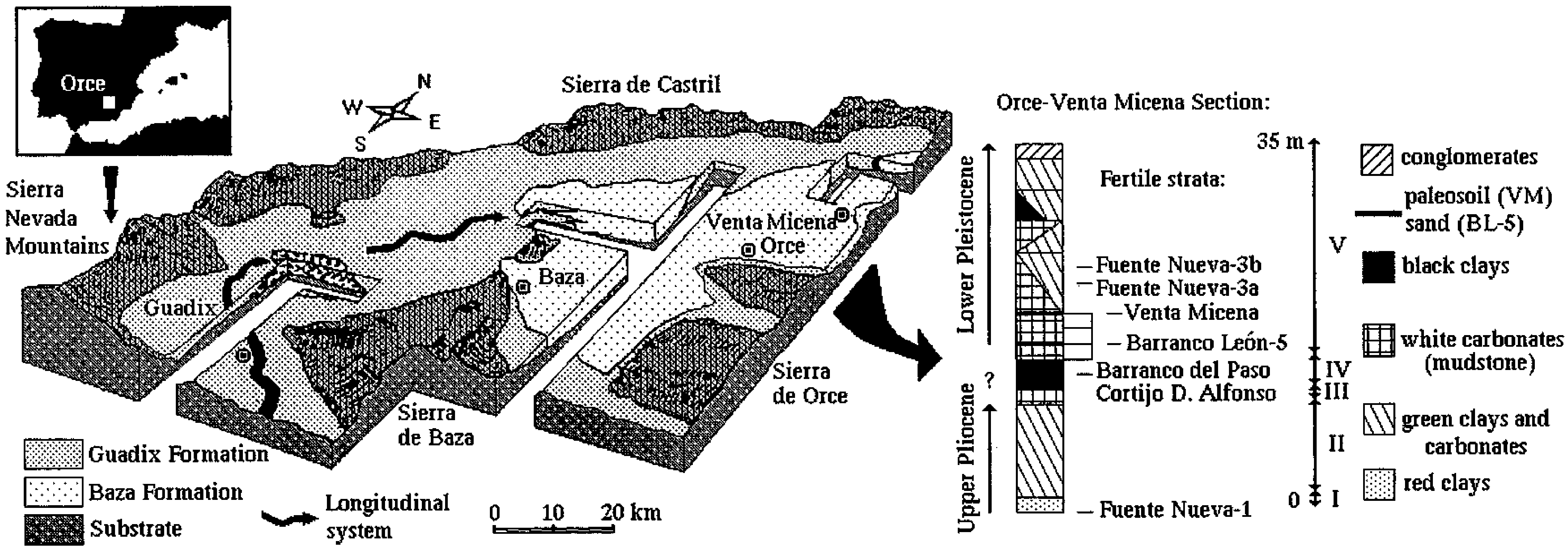

FIGURE 1. Geological location of Venta Micena and Orce in the intramountainous basin of Baza, and stratigraphic section of the Plio-Pleistocene deposits in the Orce-Venta Micena sector.

Furthermore, many bones were for quite some time exposed to the elements, and a very high percentage of specimens show marks of carnivore damage (with almost total dismembering of all elements, and bite marks and breakage in the most vulnerable places).

Preliminary analysis of size/abundance patterns for ungulate species at Venta Micena,

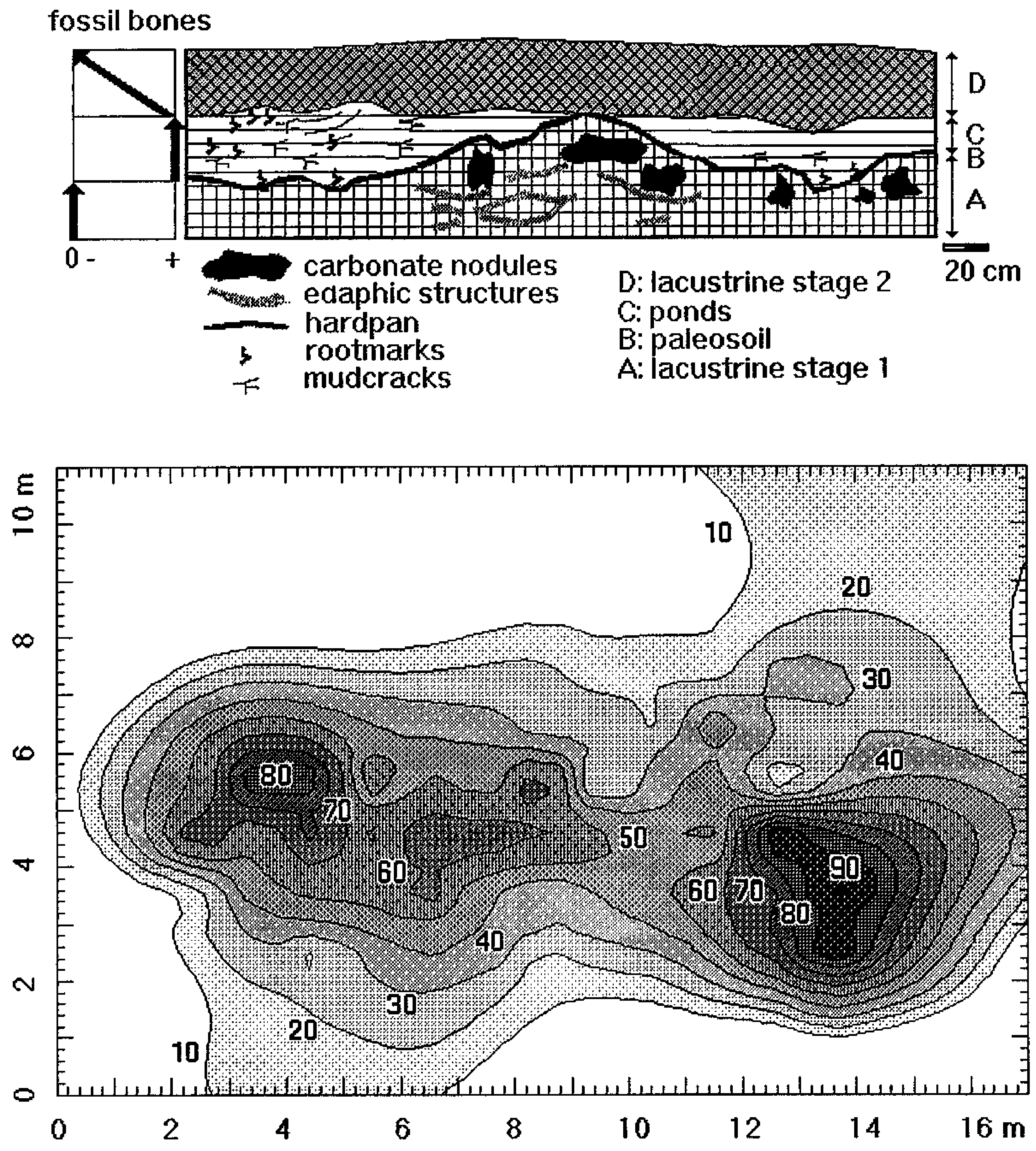

FIGURE 2. Idealized stratigraphic profile and abundance of skeletal remains (number of bones and teeth per square meter) in the Venta Micena excavation area (this graph was obtained using the *SYSTAT* program, Version 5.0).

using Damuth's (1982) model, indicated that the main preservational bias was a consequence of biological destruction by carnivores during the period when the bones were exposed at the surface, before their definitive burial, and that this loss of information affected predominantly species of smaller body size (Palmqvist et al. 1992). Comparison of relative abundances of skeletal elements in Venta Micena with assemblages from hyaena, leopard, and porcupine lairs, as well as carnivore open feeding grounds and bone accumulations made by man, suggests that this fossil assemblage was formed by the transport and accumulation by hyaenas of carcasses and bone remains close to the entries of shallow dens dug by these carnivores (Palmqvist et al. 1993; Mendoza et al. 1993). The finding of some coprolites, as well as the recovery of relatively high numbers of deciduous teeth of *Pachycrocuta brevirostris,* reinforces this hypothesis (as other carnivores are represented in the assemblage only by adult individuals), and also helps reject the possibility that bones were accumulated in open feeding places located at hunting sites distant from dens, since it can be presumed that juvenile individuals would not accompany adults on their hunts, but would stay near dens, as in modern spotted hyaenas (Kruuk 1972).

Paleoecological analyses (Martínez-Navarro 1991, 1992b; Mendoza et al. 1993), based on cenogram methodology (Valverde 1967; Legendre 1986) and multivariate comparisons among modern mammalian communities, suggest that the paleocommunity of Venta Micena was similar to communities from African savannas, with tall grass and spiny trees. The objective of the present study is to analyze some interspecific relationships that may have existed in the paleocommunity, such as those produced by the predatory activity of carnivores.

The Venta Micena Assemblage

The Venta Micena collection is composed of 6429 identifiable skeletal remains of 19 macromammalian species ($\geq$ 5 kg) and more than 10,000 unidentifiable bone shafts. Table 1 summarizes the raw data on the abundance of species (NISP = total number of dental and non dental identifiable elements; MNI = minimal number of individuals; updated from Martínez-Navarro 1991, 1992). Also included are the estimated body weights (W, in kg) for adults of each species (mean and range), calculated from regression equations of weight on craniodental/postcranial variates in recent species (Janis 1990; Roth 1990; Scott 1990; Van Valkenburg 1990). For the species of largest body size in the assemblage, *Mammuthus meridionalis,* only two weight estimates were available for an adult specimen; these figures were obtained from the diaphyseal circumference of a humerus and a femur (9417 and 10,076 kg, respectively). These high values and the presence of a worn M_3 suggest that this individual was a large-bodied old male. To calculate a value most in keeping with the actual size of adult individuals of both sexes in this species, the mean weights of African elephants were used (Kingdon 1979): 5000 kg (range: 4000–6300 kg) for males and 2800 kg (range: 2400–3500 kg) for females. Simple interpolation was then used to calculate a mean weight of 6034 kg for adults of the fossil species, with a size interval ranging between 3713 (minimum for females) and 9747 kg (maximum for males).

Taphonomic Characteristics.—Descriptive taphonomic analysis of the Venta Micena assemblage was based on a well-restored sample of 1339 specimens housed at the Museum of Paleontology of Orce, which represents a random sample of the Venta Micena collection. Isolated teeth represent 12.5%, and 1.4% are fragments of deer antlers. In the sample of bone remains (*n* = 1152), limb bones dominate (64.7%), followed by vertebrae (15.5%), cranial elements (10.4%), phalanges (6.3%), and ribs (3.1 %). The most abundant limb bones are metapodials (34.6%), tibia (11.7%), humerus (10.5%), astragalus (6.8%), calcaneum (4.8%), radius (4.6%), femur (4.3%), and scapula (4.2%). The surfaces of the bones seem to have been exposed to the effects of subaerial weathering for a short time (0–3 years): 89.3% of the skeletal elements show weathering stage 0 (Behrensmeyer 1978), and only 10.7% of the bones present weathering stage 1, with few, shallow, and small split-line cracks due to insolation (1–8 in each bone), and without flaking of their outer surface (see Figure 3). These

TABLE 1. Abundance of the macromammal species (≥5 kg) identified in the Venta Micena assemblage (updated from Martínez-Navarro 1991, 1992a). NISP = number of identifiable elements (teeth/bones). MNI = minimum number of individuals (juveniles/adults). W = estimated body weight (in kg) for the adult individuals (mean and range).

Species	NISP (teeth/bones)	MNI (juven./adults)	% Juveniles	Wmean (range) (kg)
Homo sp.	4 (0/4)	2 (1/1)	50.0	50.0–70.0
Mammuthus meridionalis	48 (16/32)	5 (4/1)	80.0	6033.8 (3713.1–9746.9)
Hippopotamus antiquus	58 (19/39)	5 (3/2)	60.0	3131.4 (2408.7–3978.8)
Bovini cf. *Bubalus*	775 (382/393)	27 (16/11)	59.3	449.4 (371.4–745.0)
Soergelia minor	334 (215/129)	13 (3/10)	23.1	227.6 (127.6–324.0)
Praeovibos sp.	6 (3/3)	1 (0/1)	0.0	316.4 (195-2–388.8)
Hemitragus alba	305 (209/96)	14 (2/12)	14.3	75.2 (57.2–119.4)
Capridae gen. et sp. indet.	1 (0/1)	1 (0/1)	0.0	8.0–10.0
Megaloceros (*Megaceroides*) *solilhacus*	962 (557/405)	36 (15/21)	41.7	383.8 (269.0–567.8)
Cervidae gen. et sp. indet.	417 (213/186)	20 (3/17)	15.0	95.1 (63.5–170.6)
artiodactyla indet. size 2	12 (0/12)			
artiodactyla indet., size 2–3	9 (0/9)			
artiodactyla indet., size 3	91 (0/91)			
Stephanorhinus etruscus	90 (55/35)	6 (2/4)	33.3	1521.1 (1074.0–2176.0)
Equus altidens	2562 (1183/1379)	70 (32/38)	45.7	354.0 (243.8–486.7)
herbivore indet., size 2–3	11 (0/11)			
herbivore indet., size 3	357 (0/357)			
herbivore indet., size 3–4	20 (0/20)			
herbivore indet., size 4–5	15 (0/15)			
herbivore indet., size 5–6	6 (0/6)			
Vulpes praeglacialis	24 (19/5)	1 (0/1)	0.0	3.0–5.0
Canis (*Xenocyon*) *falconeri*	65 (40/25)	3 (0/3)	0.0	29.8 (24.7–34.7)
Canis etruscus	33 (20/13)	4 (0/4)	0.0	9.9 (9.3–11.5)
Lynx sp.	6 (2/4)	1 (0/1)	0.0	8.0–10.0
Megantereon whitei	16 (7/9)	3 (0/3)	0.0	52.9 (46.1–58.1)
Homotherium latidens	7 (6/1)	2 (0/2)	0.0	243.9 (183.5–338.0)
Felidae indet., size 2–3	24 (0/24)			
Pachycrocuta brevirostris	62 (34/28)	10 (4/6)	40.0	64.0 (57.8–70.7)
Ursus etruscus	27 (15/12)	3 (1/2)	33.3	374.9 (309.2–451.6)
carnivore indet., size 1	2 (0/2)			
carnivore indet., size 2–3	21 (0/21)			
mammal indet., size 1	4 (0/4)			
mammal indet., size 2	7 (0/7)			
mammal indet., size 2–3	73 (0/73)			

results indicate that subaerial weathering was relatively unimportant. The bones that were preserved completely lack sedimentary filling, even in those areas of the medullary cavity that are close to nutrient foramina, indicating that the bones were buried with the periosteum intact.

Horse (*Equus altidens*) remains (n = 457) are not very dispersed horizontally; groups of articulated elements represent nearly 20% of this sample, and the remaining 80% of non-articulated bones are found associated (i.e., crania and mandibles, metapodials and phalanges). Biostratinomic fractures are abundant (see Figure 3): only 29.1% (73/251) of major long bones are complete (most of them metapodials), and Type II spiral fractures (Shipman 1981; Lyman 1994) are predominant (100% of fragmented humeri, femuri, and radii, 74.4% of tibiae); other types are longitudinal fractures (25.6% of tibiae), undifferentiated fractures (ribs and vertebrae), and isolated maxillae with cheek tooth rows (33.3% of cranial elements). On the one hand, the outer surfaces of the bones are well preserved: none show signs of abrasion or polish, and only 0.9% are slightly dissolved. On the other hand, gnawing marks are very frequent: all cranial fragments, scapuli, humeri, radii, pelvis, femori, and tibiae show striations and biting marks produced by carnivores, the preserved epiphyses have furrows and punctures, and the diaphyses as well as the skull bones show scoring and pitting. These marks are also observed in all other taxa identified at Venta Micena.


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Abundance of Major Long Bones.—Two factors seem to have a substantial influence on the frequencies of skeletal parts in an untransported assemblage (Binford and Bertram 1977; Binford 1978, 1981; Lyman 1984, 1994; Blumenschine and Madrigal 1993): structural density of bones and within-bone nutrient utility. Overall meat/bone utility plus ease of disarticulation are also important factors affecting skeletal part representation in accumulations transported by carnivores (see Lyman 1994 and references therein). Several taphonomic processes, such as carnivore damage (Marean and Spencer 1991), are mediated by the structural density of bones (mechanical and chemical attrition have greater effects on bones with low bulk density), and by the extraction of nutrients within bones, particularly marrow. Many structural density estimates, obtained using photon absorptiometry, are available in the literature (see Lyman 1994), but the estimation of within-bone nutrients is rather problematic. Interspecific differences in the distribution of flesh between the hindlimb and forelimb of bovids seem to be related to locomotor type (Blumenschine and Caro 1986). In a similar way, absolute long bone marrow yields differ among species, and among individuals of different size within a species. Most published data (Binford 1978; Jones and Metcalfe 1988; Blumenschine 1991; Emerson 1990) are clearly inadequate for assessing this variability. Only Blumenschine and Madrigal (1993) have addressed this issue, using a broad sample of East African ungulates.

Figure 4 shows the abundance of long bone epiphyses of ruminants in the Venta Micena assemblage and their mean bone mineral density (estimated from values for modern bison and deer in Lyman 1994). The positive relationship observed between both variates is statistically significant, according with a least squares regression adjustment:

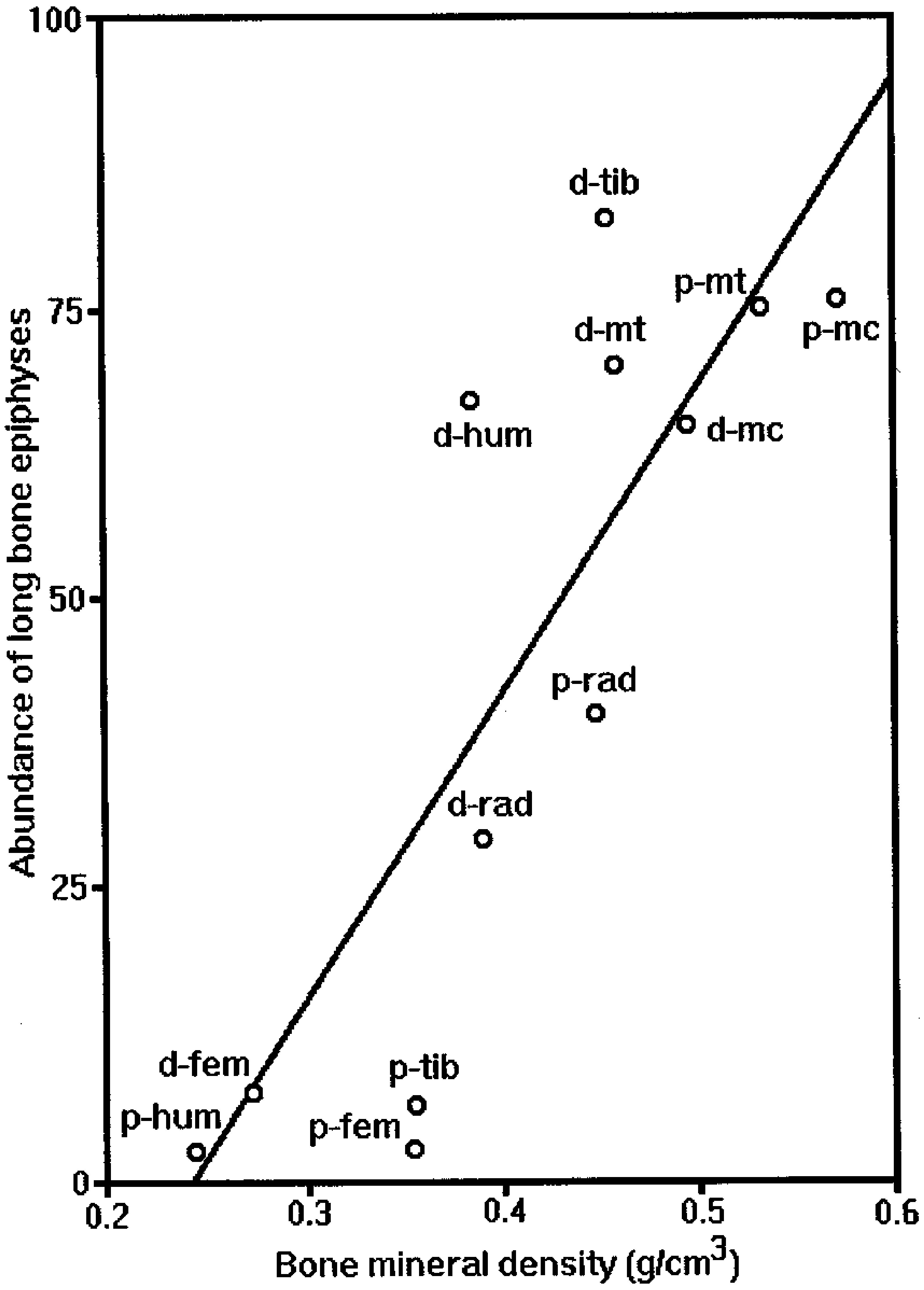

FIGURE 4. Number of epiphyses (d = distal, p = proximal) of long bones (hum = humerus, rad = radius, mc = metacarpal, fem = femur, tib = tibia, mt = metatarsal) of ruminant species in the Venta Micena assemblage (data from Martínez-Navarro 1991) and mean bone mineral density (average of bison and deer; values obtained from Lyman 1994: Table 7.6). The regression line was adjusted by minimum squares method.

$$\text{Abundance} = -68.522(\pm 23.997) + 270.841(\pm 56.458)\text{Density};$$

$$r = 0.835,\ \text{df} = 12;\ F = 23.01\ (p < 0.\ 001).$$

←

FIGURE 3. Selected fossils from Venta Micena showing the most significant taphonomic characteristics (marked by arrows). 1, Right humerus fragment of *Stephanorhinus etruscus* (VM-4510) with spiral fracture in the diaphysis and distal epiphysis gnawed by hyaenas (a, posterior side; b, anterior side). 2, Right humerus fragment of *Stephanorhinus etruscus* (VM-4519) with the same fractures as (1) and showing longitudinal split lines in the posterior side. 3, Femur diaphysis (VM-3106) of ruminant showing gnaw marks and chemical weathering of its distal end. 4, Right femur fragment of *Equus altidens* (VM-3599) with the cancellous tissue of the proximal epiphysis destroyed and tooth marks (premolars of hyaenids) in the distal end of the diaphysis. 5, Left humerus of *Homotherium latidens* (VM-4516) with an important fossildiagenetic fracture located between the diaphysis and the distal epiphysis. 6, Left femur fragment of *Megaloceros (Megaceroides) solilhacus* (VM-3568) showing breakage by premolar pressure in the diaphysis, rootmarks, and destruction of the distal epiphysis by gnawing. 7, Vertebrae of equid in anatomical connection (VM-4129), showing a micritic crust in the intervertebral space and the apophyses destroyed by gnawing.

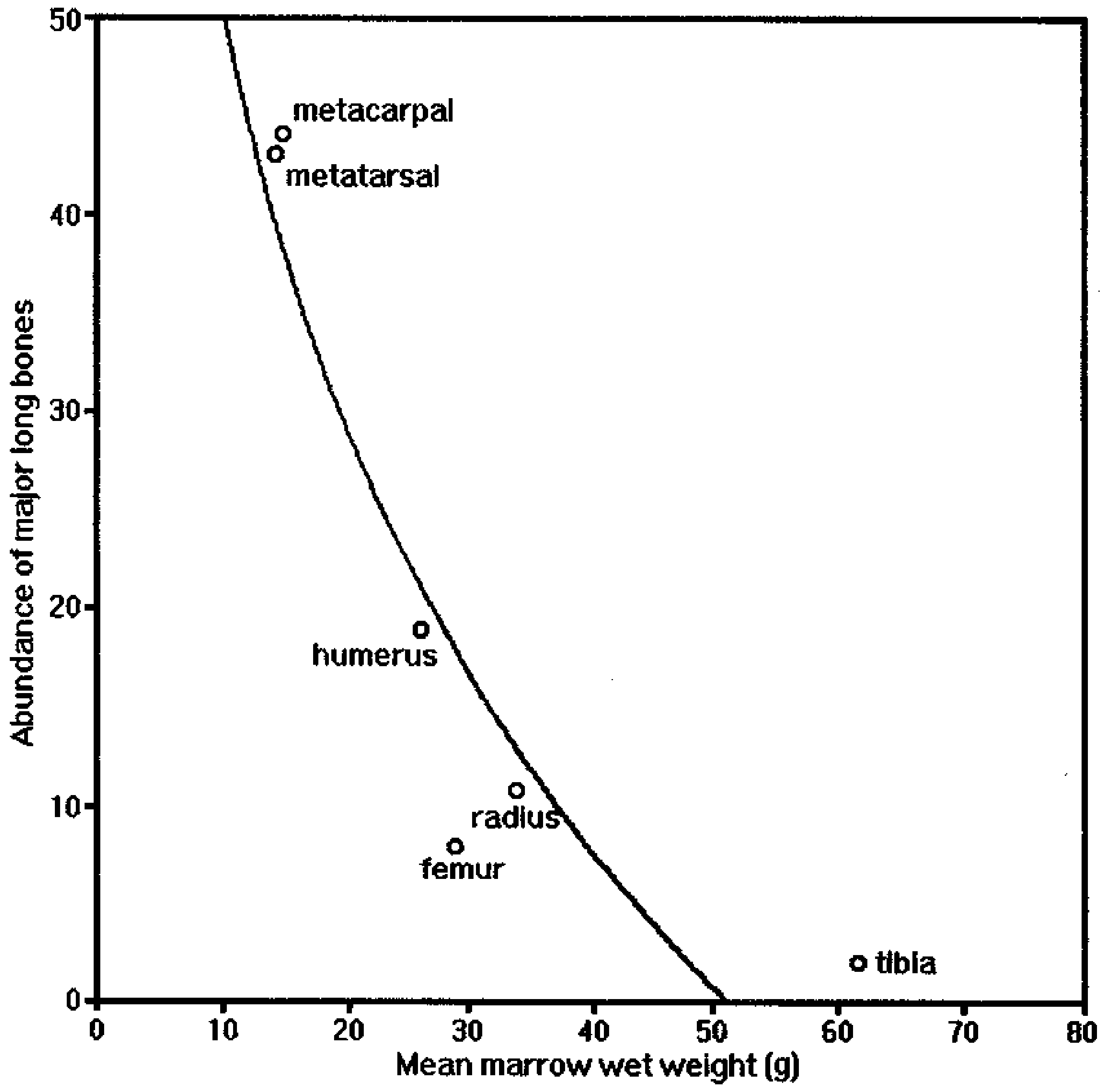

FIGURE 5. Number of major long bones (complete limb bones and long bone cylinders, lacking one or both epiphyses) of ruminant species in the Venta Micena assemblage (data from Martínez-Navarro 1991), and mean wet weights (in g) of marrow content (estimated from values for modern wildebeest in Blumenschine and Madrigal 1993: Table 2). The curve was adjusted by minimum squares regression.

The abundance of major long bones of ruminants in Venta Micena (complete limb bones and long bone cylinders, lacking one or both epiphyses) and their mean wet weights of marrow content (estimated from values for modern wildebeest in Blumenschine and Madrigal 1993) is shown in Figure 5. There is an inverse relationship between the abundance of each long bone and its marrow content, which is linearized by means of logarithmic transformation as:

$$\text{Log(Abundance)} = 9.249(\pm 0.819)$$
$$- 2.033(\pm 0.248)\cdot\text{Log(Marrow content)};$$
$$r = 0.972,\ \text{df} = 5;\ F = 67.29\ (p < 0.001).$$

These results indicate the preferential consumption by hyaenas of low-density skeletal parts, and differential fragmentation leading to less dense bone parts being crushed into unidentifiable fragments in contrast to denser bone parts simply being broken into small but recognizable pieces during the extraction of marrow (Lyman 1994). Preferential breakage by hyaenas of the richer marrow bones (Fig. 5) was thus a major factor biasing the composition of the Venta Micena assemblage.

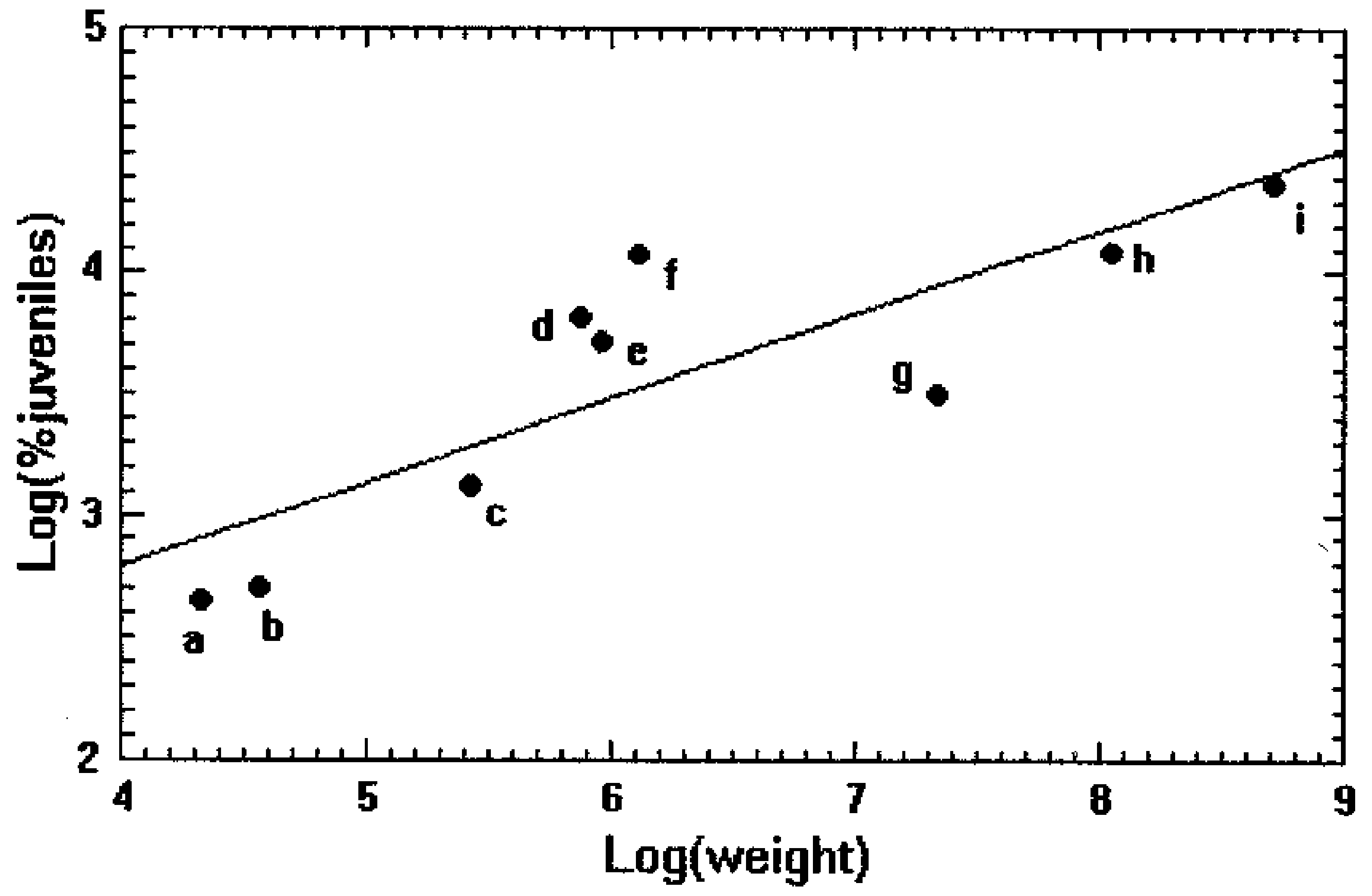

FIGURE 6. Regression analysis (minimum squares method) of the proportion of juvenile individuals (% juveniles) on estimated adult body weight (in kg) for ungulate species ($n = 9$) of the Venta Micena assemblage (data from Table 1): Log(% juveniles) = 1.401(±0.540) + 0.346(±0.084) Log(weight); $r = 0.841$, $F = 16.95$ ($p < 0.004$). a = *Hemitragus alba*, b = Cervidae, gen. et sp. indet., c = *Soergelia minor*, d = *Megaloceros (Megaceroides) solilhacus*, e = *Equus altidens*, f = Bovini, cf. *Bubalus*, g = *Stephanorhinus etruscus*, h = *Hippopotamus antiquus*, i = *Mammuthus meridionalis*.

An Analysis of Prey Selection

Four types of evidence strongly support a model of prey selection by carnivores: (1) Interspecific analysis of the relative abundance of remains of juvenile individuals among ungulates, in relation to the average weight estimated for adults in each species, shows a direct and statistically significant relationship between both variates; (2) mortality curves deduced for those ungulate species with greater abundance in the assemblage suggest characteristic U-shaped attritional profiles; (3) many metapodials display osteopathologies such as arthrosis; and (4) the sex ratio deduced from the metacarpals of large bovids is biased in favor of females.

Juvenile/Adult Ratios.—Minimal numbers of individuals (MNI) estimated for each species in the Venta Micena assemblage are shown in Table 1. MNI of juveniles with deciduous teeth and of adults with fully erupted permanent dentition are given. The percentage of juvenile individuals for each ungulate species, in relation to the mean weight estimated for adults, is shown in Figure 6. Larger species are represented in the fossil assemblage by a greater MNI for juveniles than that of smaller species.

The ratio of juvenile/adult individuals in a population depends on two factors: the annual birth rate or reproduction rate, and the duration of infancy. The reproduction rate scales approximately to the −0.3 power of adult body weight of a given species (the slope for births/year ranges from −0.26 [Eisenberg 1981] to −0.33 [Western 1979, 1980; Peters 1983]). The duration of infancy is interspecifically related to body mass by a power close to 0.3 (0.29 for the time needed to reach reproductive maturity [Calder 1982, 1984] and 0.28 for the rate of incremental growth [Case 1978]). The proportion of juvenile individuals for a given species is thus the product of annual birthrate (B_r) and duration of infancy (D_i):

$$\begin{aligned}\%\text{ juvenile individuals} &= K_1W^{-0.3}K_2W^{0.3}\\ &= K_3W^0.\end{aligned}$$

This percentage will be approximately constant and independent of species body size.

However, in the ungulate species from the Venta Micena assemblage we noted a positive relationship between the two variates, which is highly significant statistically:

$$\text{Log}(\%\text{ juveniles}) = 1.401(\pm0.540) + 0.346\cdot(\pm0.084)\text{Log}(W\text{ adults});$$

$$r = 0.841,\ \text{df} = 8;\ F = 16.95\ (p < 0.004).$$

This result suggests strong selection by carnivores, according to the age and size of their ungulate prey, since predation of comparatively larger species such as elephant and hippo is focused on juvenile and more vulnerable individuals, whereas in smaller species young and adult individuals are captured at similar frequencies. This interpretation agrees well with available data on prey selection by Recent carnivores as a function of size and age of the ungulate prey (Corbertt 1892; Deane 1962; Bourlière 1963; Mitchell et al. 1965; Bere 1966; Estes and Goddard 1967; Goddard 1967; Kruuk and Turner 1967; Pimlott 1967; Schaller 1967, 1972; Cullen 1969; Hirst 1969; Eaton 1970; Kolenoski 1972; Kruuk 1972; Sinclair 1974; Malcom and Van Lawick 1975; Seidensticker 1976; Floyd et al. 1978; Mills 1984; Potvin et al. 1988; FitzGibbon and Fanshawe 1989; Cooper 1990; Fuller and Kat 1990, 1993; Ruggiero 1991; Johnsingh 1992; Mills and Shenk 1992; Fanshawe and FitzGibbon 1993; Mills and Biggs 1993). In the discussion that follows, average percentages of predated juvenile individuals were obtained by pooling all data sets for each predator and each prey species; calculations of frequencies of juvenile individuals hunted were made using data on deciduous teeth when such were available.

The wild dog, *Lycaon pictus*, a small-to-medium-sized African predator (average weight for adult specimens, 25 kg), hunts a mean proportion of around 30% (82/272) juvenile individuals of Thomson's gazelle (*Gazella thomsoni*, 23 kg), the most appropriate prey relative to its body size. This percentage is similar to the proportion of juvenile gazelles found in wild populations. However, in the case of the Grant's gazelle (*Gazella granti*, 55 kg) the mean percentage of juveniles captured rises to 44% (4/9), in the impala (*Aepyceros melampus*, 51 kg) juveniles constitute 61% (29/48), in the reedbuck (*Redunca redunca*, 45 kg) 65% (11/17), in the hartebeest (*Acelaphus buselaphus*, 150 kg) 64% (9/14), in the blue wildebeest (*Connochaetes taurinus*, 170 kg) 83% (144/173), and in the greater kudu (*Tragelaphus strepsiceros*, 210 kg) 70% (7/10). These data clearly suggest that as the size of the hunted species increases, the wild dog selects more juvenile individuals, which are comparatively easier to hunt and capture. The exception to this trend is zebra (*Equus burchelli*, 230 kg), in which the mean percentage of hunted juveniles approaches 29% (12/42). This may be because a mother zebra can effectively protect her foal from attack by wild dogs, and predation is therefore more focussed on old and sick individuals. The dhole (*Cuon priscus*, 17 kg), a smaller Asiatic canid equivalent to the wild dog, shows similar behavior, capturing 43% (100/232) young chitals (*Axis axis*, 35 kg), a proportion similar to that found in the composition of wild populations, and 82% (45/56) of juvenile sambar (*Cervus unicolor*, 175 kg). Of the prey hunted by the American wolf (*Canis lupus*, 40 kg) 38% (44/116) are fawns and immature individuals of white-tailed deer (*Odocoileus virginianus*, 65 kg), while the mean percentage of juvenile moose (*Alces alces*, 430 kg) hunted is 59% (10/17), due to the larger size of this species.

With respect to solitary medium-sized predators, the cheetah (*Acinonyx jubatus,* 50 kg) captures a mean proportion of juveniles around 38% (120/317) for Thomson's gazelle, 22% (43/199) for springbok (*Antidorcas marsupialis,* 31 kg), 34% (15/44) for impala, 38% (3/8) for Grant's gazelle, and 33% (4/12) for puku (*Kobus vardoni,* 72 kg). These percentages are similar to those in which juveniles of these species are represented in their respective wild populations. On the contrary, of the prey species of greater size available to this predator, the proportion of young individuals is 80% (8/10) for hartebeest, 93% (14/15) for wildebeest, and 100% (5/5) for topi (*Damaliscus lunatus,* 112 kg), gemsbok (6/6) (*Oryx gazella,* 150 kg), waterbuck (4/4) (*Kobus ellipsiprymnus,* 210 kg), and zebra (5/5). Hunting behavior by the leopard (*Panthera pardus,* 50 kg) is similar: this predator captures 21% (18/88) juveniles of Thomson's gazelle, 21% (11/52) of springbok, 23% (186/809) of impala, 29% (11/38) of chital, 33% (4/12) of puku, and 38% (8/21) of Grant's gazelle, all species of appropriate size for this carnivore. Larger prey species are represented predominantly by young individuals: 60% (6/10) of the captures of reedbuck, 67% (4/6) of sambar, 72% (13/18) of hartebeest, 89% (16/18) of warthog (*Phacochoerus aethiopicus,* 75 kg), 90% (18/20) of wildebeest, and 100% of gemsbok (6/6) and zebra (4/4).

The largest predators also tend to select juvenile individuals of larger prey species. The lion (*Panthera leo,* 160 kg) captures mean proportions of juvenile individuals of those species of appropriate size (≤900 kg) (Schaller 1972) that are near to proportions in which they are represented in wild populations: 27% (13/48) of springbok, 28% (5/18) of waterbuck, 39% (80/204) of Thomson's gazelle, 42% (16/38) of impala, 27% (275/1017) of wildebeest, 37% (206/557) of zebra, 32% (33/103) of hartebeest, 22% (2/9) of reedbuck, 46% (19/41) of warthog, 35% (42/120) of gemsbok, 16% (5/31) of eland (*Taurotragus oryx,* 560 kg), and 23% (111/481) of buffalo (*Syncerus caffer,* 600 kg). However, in larger prey species, the percentage of young individuals increases proportionately to body weight (although captures are quite rare for extremely large prey): 71% (10/14) in giraffe (*Giraffa camelopardalis,* 1100 kg), 80% (8/10) in black rhino (*Diceros bicornis,* 1200 kg), 89% (8/9) in hippo (*Hippopotamus amphibius,* 2000 kg) and 100% (3/3) in white rhino (*Ceratotherium simum,* 2500 kg) and elephant (11/11) (*Loxodonta africana,* 3800 kg). The Asiatic felid equivalent of the lion, the tiger (*Panthera tigris,* 170 kg) shows similar hunting behavior, capturing 21% (22/103) juvenile individuals of chital, 18% (13/73) of sambar, and 28% (11/39) of barasinga (*Cervus duvauceli,* 210 kg), proportions similar to their abundance. In contrast, when it sometimes hunts larger species, the tiger clearly selects juvenile individuals: 57% (8/14) of the captures of gaur (*Bos gaurus,* 780 kg), and 100% (2/2) of Indian one-horned rhino (*Rhinoceros unicornis,* 2500 kg) and Indian elephant (3/3) (*Elephas maximus,* 3900 kg). The other African superpredator, the spotted hyaena (*Crocuta crocuta,* 60 kg), shows selective behavior similar to that of the two species just mentioned, since its smaller body size is compensated for by the formation of hunting packs of large size. This ensures that young individuals of the species of appropriate size for this social predator are captured at a mean proportion close to the proportion in which they are represented in their respective populations: 43% (27/62) for Thomson's gazelle, 40% (4/10) for springbook, 33% (3/9) for hartebeest, 38% (54/143) for wildebeest, and 41% (24/58) for zebra. These percentages increase in prey species of greater size, reaching 60% (3/5) in eland, 87% (13/15) in giraffe, 90% (9/10) in black rhino, and 100% in hippo (8/8) and elephant (3/3).

The mean percentages of juvenile individuals of each African ungulate species hunted, obtained by averaging the proportions of young killed by the five main predators (wild dog, cheetah, leopard, spotted hyaena, and lion) are shown in Figure 7. Percentages were calculated only for prey species for which there were available data on the predation of juveniles by at least three species of carnivores, except for ungulate species of larger size (≥1000 kg) which are seldom hunted by lions and spotted hyaenas. These pooled per-

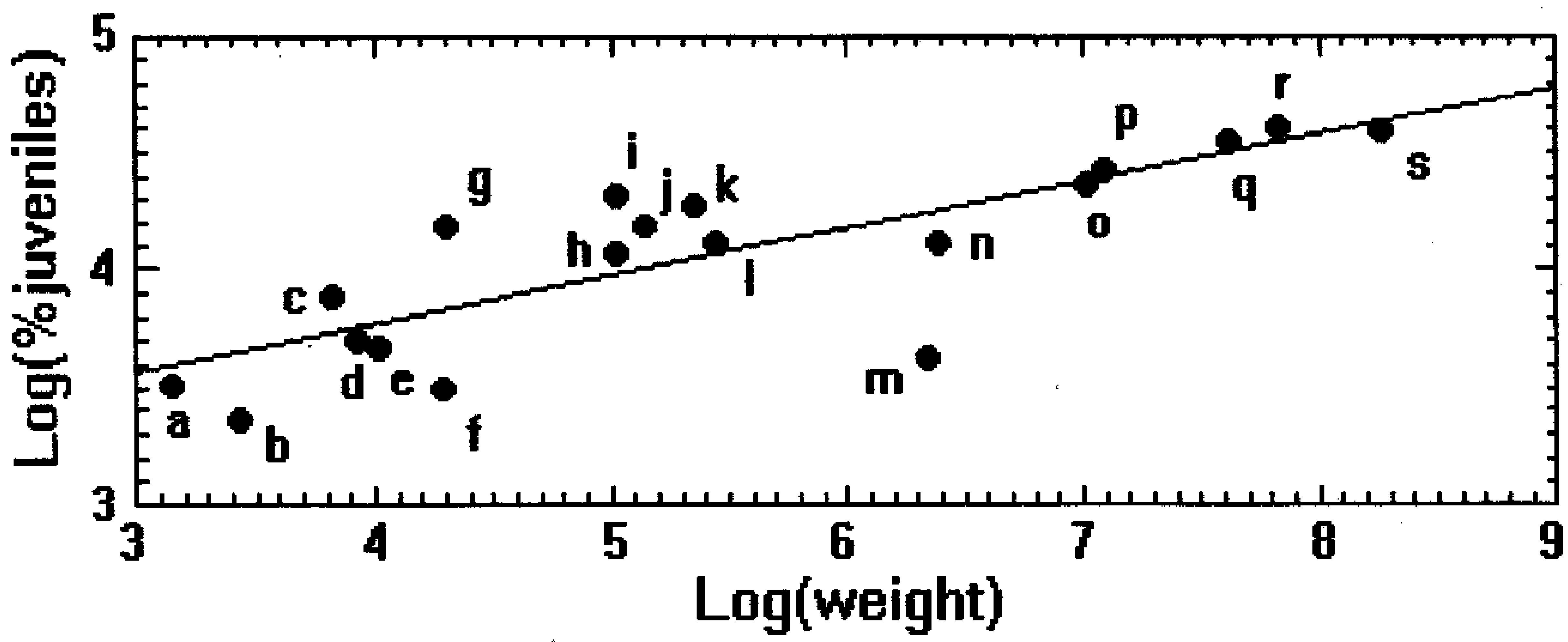

FIGURE 7. Regression analysis by minimum squares method of the mean percentage of juvenile individuals (% juveniles) of some African ungulate species ($n = 19$) hunted by the five large African predators (*Lycaon pictus, Acinonyx jubatus, Panthera pardus, Crocuta crocuta,* and *Panthera leo*) on mean adult body weight (in kg): Log(% juveniles) = 2.966(±0.201) + 0.203(±0.036) Log(weight); $r = 0.805$, $F = 31.38$ ($p < 0.0001$). a = *Gazella thomsoni*, b = *Antidorcas marsupialis*, c = *Redunca redunca*, d = *Aepyceros melampus*, e = *Gazella granti*, f = *Kobus vardoni*, g = *Phacochoerus aethiopicus*, h = *Alcelaphus buselaphus*, i = *Oryx gazella*, j = *Connochaetes taurinus*, k = *Kobus ellipsiprymnus*, 1 = *Equus burchelli*, m = *Taurotragus oryx*, n = *Syncerus caffer*, o = *Giraffa camelopardalis*, p = *Diceros bicornis*, q = *Hippopotamus amphibius*, r = *Ceratotherium simum*, s = *Loxodonta africana*.

centages would give the figures expected in an assemblage originating exclusively from the accumulation of bones of hunted animals. A highly significant direct relationship exists between the percentages of juvenile individuals and the body weights of the ungulate species:

$$\text{Log(\% juveniles)} = 2.966(\pm 0.201) + 0.203 \cdot (\pm 0.036)\text{Log(W adults)};$$

$$r = 0.805,\ \text{df} = 18;\ F = 31.38\ (p < 0.\ 0001).$$

The value for the slope in this fit (0.203) is within the 95% confidence interval of the slope that relates the percentages of juvenile individuals and the estimated weights for the ungulate species of Venta Micena (Fig. 6: slope = 0.346, standard error of slope = 0.084, confidence limits, with $p < 0.05$ = 0.156, 0.536) and reveals that the two parameters do not differ in a statistically significant way.

Therefore the proportions of juvenile individuals representing the ungulate species in theVenta Micena assemblage reflect prey selection by the carnivores as a function of body size of the prey hunted. The increase in infant/adult ratios in relation to estimated weight of the ungulate species allows us to rule out the hypothesis that the ungulate carcasses amassed by hyaenas in the fossil assemblage were generated by catastrophic mortality events that would accompany recurrent droughts; in this case the percentage of juvenile individuals of the different species would be approximately constant and size-independent. We consequently conclude that the skeletal remains transported and accumulated by hyaenas in Venta Micena came from attritional mortality in ungulate populations, caused by selective choice of carnivores.

This scenario of juvenile selection by predators is also applicable to other fossil accumulations such as that of Swartkrans Member 1, which was presumably collected by leopards (Brain 1981). In this bone assemblage, primate species are represented by proportions of immature individuals that show a clear relationship to body size of the species: 25% (2/8) of *Parapapio jonesi* (estimated mean weight for adults of 14.5 kg), 23.7% (9/38) of *Papio robinsoni* (26 kg), 35.3% (6/17) of *Theropithecus danieli* (36 kg), 38.5% (10/26) of *Dinopithecus ingens* (36 kg), and 48.3% (42/87) of *Australopithecus africanus* (52 kg). This relationship is again statistically significant:

$$\text{Log(\% juveniles)} = 1.589(\pm 0.515) + 0.570 \cdot (\pm 0.151)\text{Log(W adults)};$$

$$r = 0.909,\ \text{df} = 4;\ F = 14.26\ (p = 0.033).$$

On the other hand, the equation that relates the percentage of juvenile individuals of each species in the Venta Micena fossil assemblage to mean weight estimated for adults (% juveniles = 4.059 W adults$^{0.346}$) makes it possible to deduce how the efficiency of carnivore predation varied as a function of the size of the prey species. A species weighing 100 kg would be represented in the assemblage by 20% juvenile individuals and 80% adults, while for a species weighing 1000 kg these percentages would be 44.3% and 55.7%, respectively. Since the proportion of young individuals in modern wild populations of ungulate especies is constant and independent of body size, these variations must have been caused by differences in hunting success of the Venta Micena predators depending on the size of their prey. Specifically, the ratio of the frequencies of juvenile to adult individuals [(44.3/55.7)/(20/80) = 3.2] indicates that an increase of an order of magnitude in body size of the prey species would have led to an increase in the efficiency in predation on juveniles as compared to adults (ratio of hunting success of the predator on juveniles/hunting success on adults) of approximately 3.2-fold.

This ratio could be overestimated, given the important role of differential bone preservation in the composition of the fossil assemblage, as indicated before. Several studies (Behrensmeyer et al. 1979; Shipman 1981; Damuth 1982) have shown that body size is a factor that has great influence on the preservation of vertebrate remains, since the bones of the largest species resist more the effects of physicochemical weathering processes and biological destruction, as a function of their small outer surface to inner volume ratio. Similarly, the skeletal remains of juvenile individuals have lower fossilization potential than those of adult individuals, due to bone properties such as their low structural density. However, we have no reasons to expect in Venta Micena higher differences of fossilization potential between the juveniles and adults of species of small body size and those of large body size.

Mortality Profiles.—Interspecific analysis of juvenile/adult ratios for ungulates in Venta Micena indicates a different age of death depending on the size of the prey, as a consequence of selection by predators, which would increase the proportion of young and more vulnerable individuals hunted of those ungulate prey species of larger body size. However, the juveniles/adults ratio has poor resolution with respect to habitual prey age selection by carnivore species. Given this limitation, mortality profile patterns were deduced for those ungulate species that show greater relative abundance in the assemblage, the horse *E. altidens* (MNI = 70, 37.4% of the total MNI of ungulates in the assemblage) and the large deer *M. solilhacus* (36, 19.3% of the ungulates). Age at death was calculated from dP_4 and P_4 crown height measurements (after Klein and Cruz-Uribe 1983).

The mortality curve deduced for *E. altidens* (Fig. 8A) indicates a clear U-shaped age profile, which suggests that death occurred mainly as a result of predation, and that predation was focussed both on very young individuals (most of them showing unworn dP_4) and past prime adults (with medium-to-heavily worn P_4). This pattern of mortality is similar to those observed for modern ungulate prey species hunted in a selective way by different carnivores ranging in size from the wild dog (*Lycaon pictus*) to the lion (*Panthera leo*) (Figs. 9, 10).

The attritional profile of *M. solilhacus* (Fig. 8B) shows a very pronounced peak corresponding to death in the first 10% of potential lifespan. This difference from the mortality curve deduced for the horse may be due to the somewhat greater size estimated for *M. solilhacus* (269–568 kg, in contrast with a range of weights for *E. altidens* of 244–487 kg). The shape of the curve for *M. solilhacus* is similar to that found for Cape buffalo (*Syncerus caffer*) from the Middle Stone Age layers of Klasies River Mouth Cave 1, South Africa (Klein and Cruz-Uribe 1983), which approximates an idealized attritional profile.

Osteopathologies.—Detailed analysis of the long bones from the Venta Micena assemblage revealed many osteopathologies (Fig. 11A,B). The most frequent is arthrosis, found in the distal epiphyses of a metacarpal of a large deer (*M. solilhacus*) and in two third metatarsals of equid (*E. altidens*); these cases were manifested as considerable osseous overgrowths. Another type of abnormality is present in the diaphyses of a goat metacarpal (*H. alba*) and of an equid metatarsal, both of which present a wrinkled surface with osseous accretions. A third type of osteopathology was found in the proximal epiphyses of several

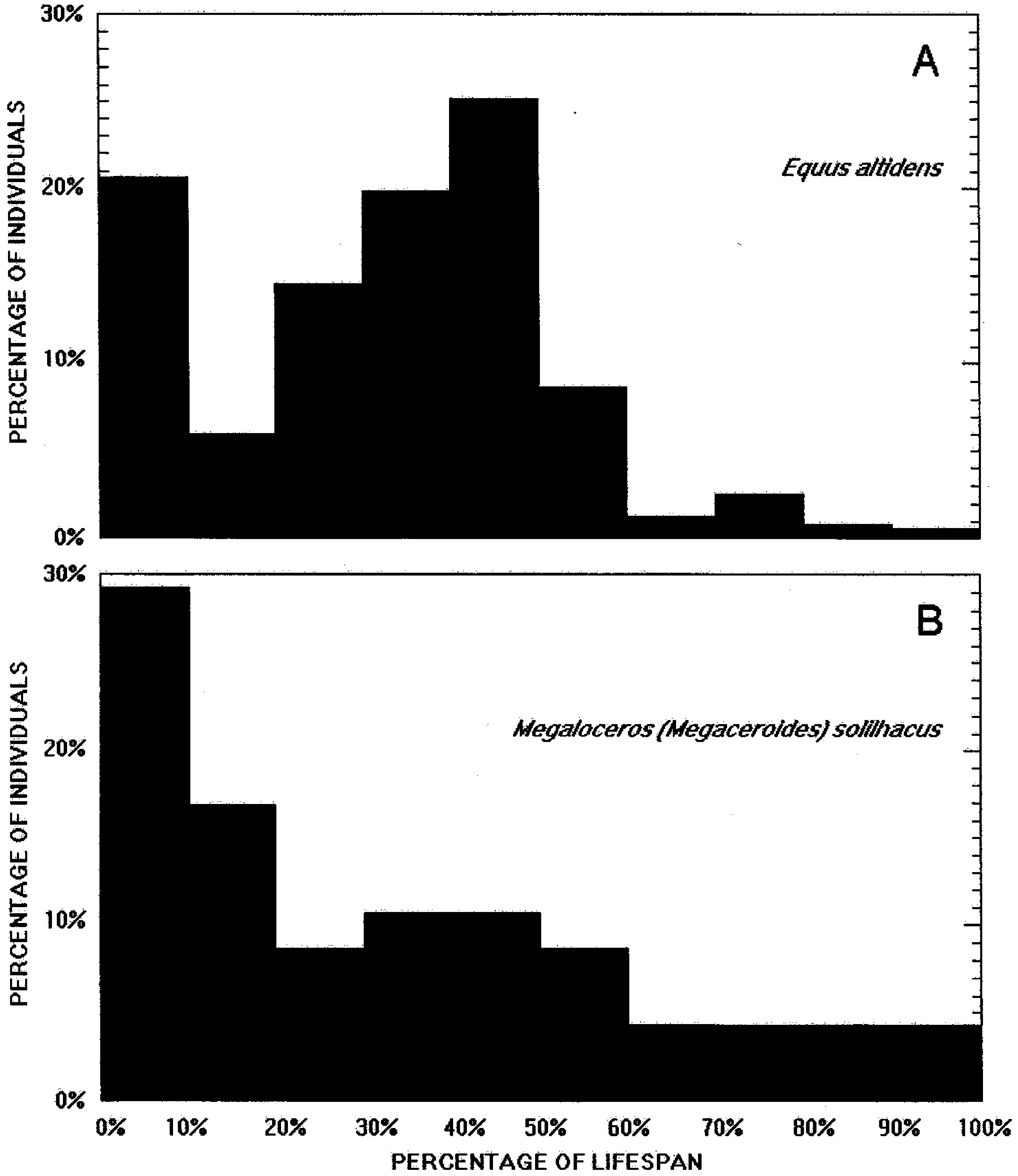

FIGURE 8. Mortality profiles of *Equus altidens* (A) and *Megaloceros* (*Megaceroides*) *solilhacus* (B) in Venta Micena, calculated from dP_4 and P_4 crown height measurements (values for *E. altidens* kindly provided by V. Eisenmann, unpublished data, $n = 81$; values for *M. solilhacus* obtained from Menéndez 1987: Fig. 15, $n = 48$). The proportion of death individuals in each 10% of potencial lifespan interval was calculated using the software developed by Klein and Cruz-Uribe (1983).

horse and buffalo (Bovini, cf. *Bubalus*) metacarpals and metatarsals, affecting the articular facets of the metapodials, which are absent or showed abnormal growth. These pathologies must have limited the ability of these animals to run, thus reducing their chances of escaping from predators.

Results of a preliminary quantitative study of part of the Venta Micena assemblage indicate that these bone abnormalities are rather common: 13 of 184 metapodials analyzed of *M. solilhacus*, Bovini cf. *Bubalus* and *E. altidens* show signs of disease. Given that each ungulate has four metapodials, the pooled percentage of crippled animals of all three species is approximately 28% (31% of equid, 19% of deer, and 26% of buffalo); this proportion is higher than expected in wild populations, and thus suggestive that such individuals in less than optimum condition were actively selected by predators.

In a study of prey condition, assessed from

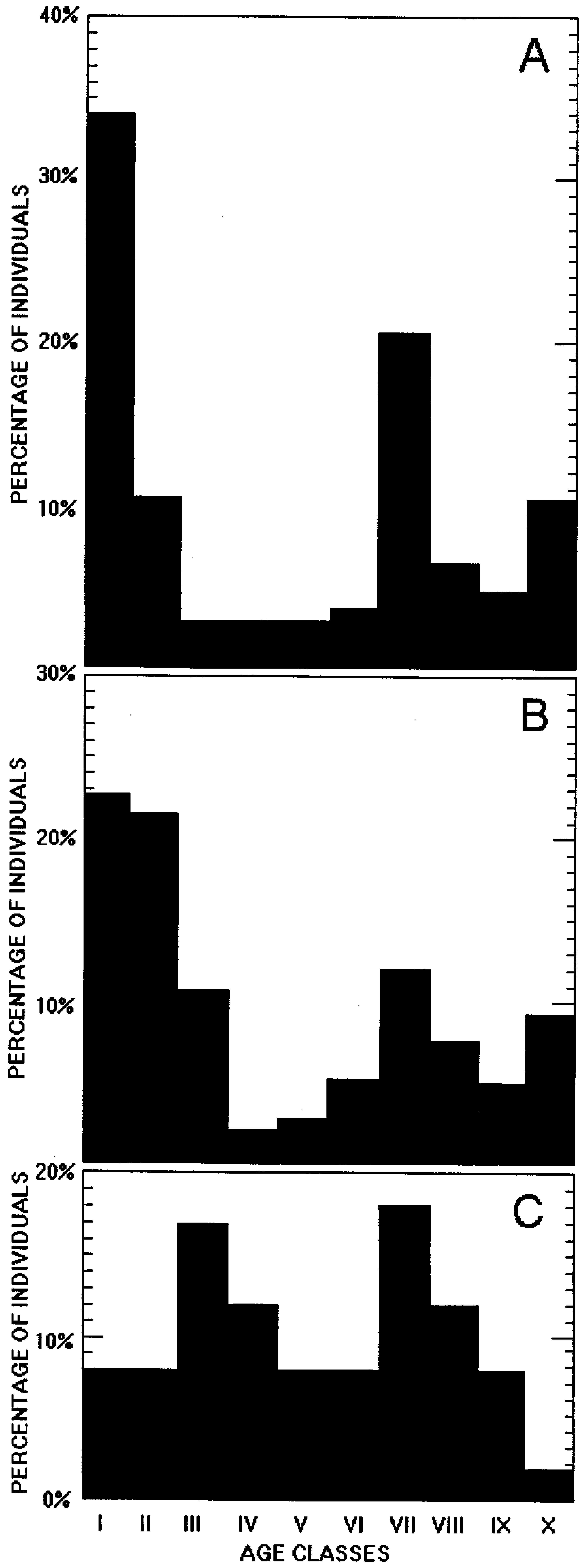

FIGURE 9. Age classes, as determined from tooth wear, of Thomson's gazelles killed by cheetahs (A), Thomson's gazelles hunted by wild dogs (B), and buffalo killed by lions (C) (data from Schaller 1972; FitzGibbon and Fanschawe 1989).

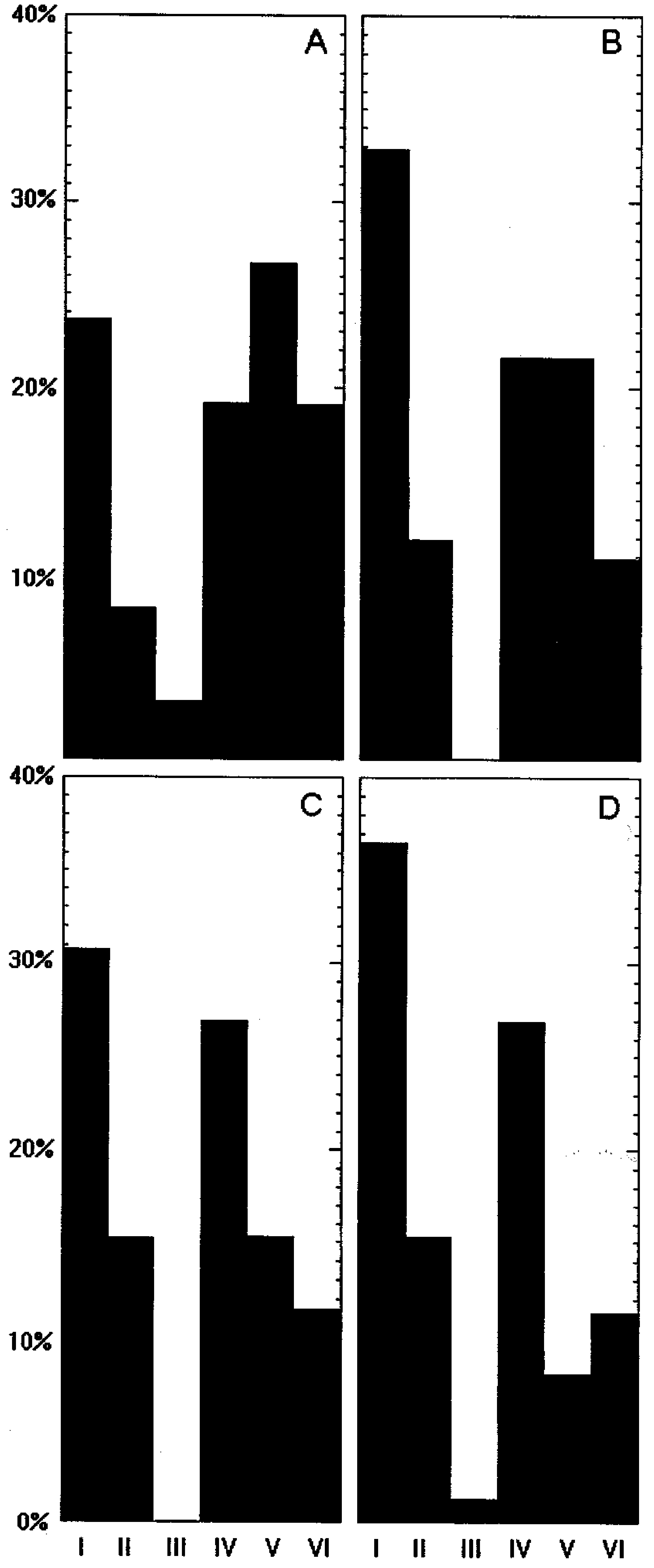

FIGURE 10. Percentages of ungulate prey of different age groups hunted by large carnivores. A, *Panthera leo*, $n = 410$ kills. B, *Panthera pardus*, $n = 96$. C, *Acinonyx jubatus*, $n = 33$. D, *Lycaon pictus*, $n = 96$) in the Kafue National Park, Zambia (data for 20 ungulate prey species, Mitchell et al. 1965). I: calves, lambs, foals, or piglets, less than 12 months old; II: yearlings; III: two-year-old animals; IV: young prime adults, with full permanent dentition but teeth having only light wear; V: prime adults, showing dentition with medium wear; VI: past prime adults (i.e., old animals with teeth showing heavy wear).

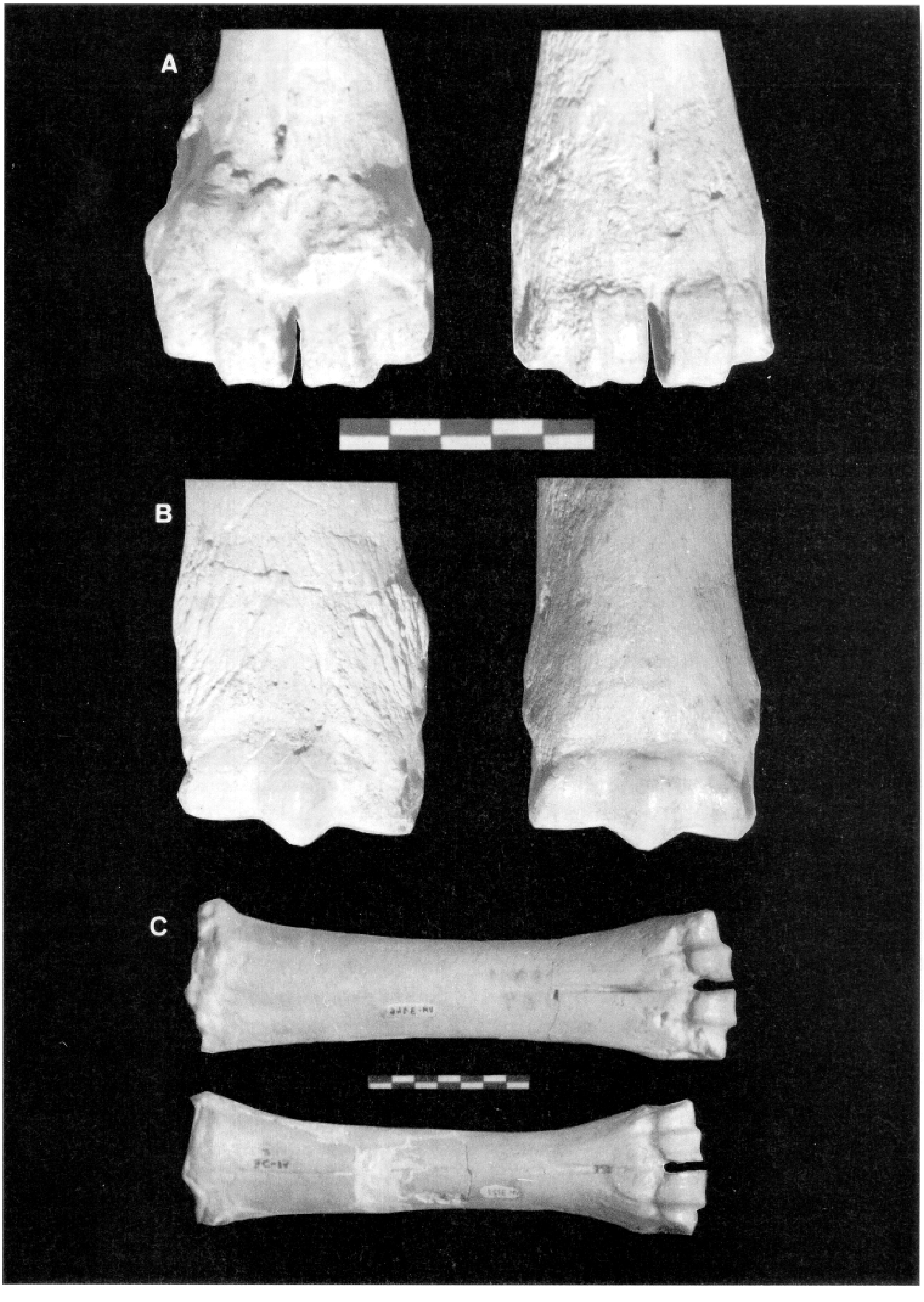

FIGURE 11. Osteopathologies in the epiphyses of metapodials. A, Arthrosis in a deer metacarpal [*Megaloceros* (*Megaceroides*) *solilhacus*] (left: pathologic bone, right: healthy bone). B, Arthrosis in an equid metatarsal (*Equus altidens*) (left: pathologic bone, right: healthy bone). C, Size dimorphism in buffalo metacarpals (Bovini, cf. *Bubalus*) (above: male, below: female).

the state of the femoral marrow, Mitchell et al. (1965) found that 27% of ungulates killed by lions, leopards, cheetahs, and wild dogs were in fair or poor condition. Given that the marrow test operates only at the lower end of the condition scale, the proportion of unhealthy individuals is probably underestimated. The selection of prey in poor condition is higher for those ungulate species of larger body size: 68.4% of buffalo killed by lions, in contrast with only 9.1 % of hartebeest, 8.5% of wildebeest, and 23.5% of zebra (Mitchell et al. 1965; Schaller 1972). Similarly, Crisler (1956) found that the caribou the wolf catches is usually the one that slows down: at least 50% of the kills involve crippled or sick individuals, whose incidence is 1.8% or even lower in the caribou herds.

Sex Ratio in Large Bovids.—A fourth line of evidence on prey selection is provided by analysis of the sex ratio for the buffalo (Bovini, cf. *Bubalus*), the largest ruminant of the Venta Micena assemblage (MNI = 27, 13.8% of the total MNI of ungulates in the assemblage). This large bovid shows marked sexual dimorphism in the size of metacarpals (Fig. 11C), allowing estimation of the ratio of males and females in the fossil assemblage: 26% (5/19) and 74% (14/19), respectively (i.e., approximately 1:3). These percentages are significantly different ($t = 9.36$, $p < 0.001$), which suggests that predators selected females given their smaller body size and absence of horns. However, we cannot discard the possibility that the sex ratio found in the fossil assemblage reflects the original proportion of males and females in the biocoenoses. In the case of the African buffalo (*Syncerus caffer*), their closest living analog, lions kill more males than females (Schaller 1972; Sinclair 1974), although females are more abundant in the populations, because bulls show solitary habits.

The Hunters and the Hunted

The high proportion of juveniles of larger species (elephant and hippo) in the assemblage indicates that the hunting behavior of the saber-toothed felid *Homotherium latidens*, presumably the only such carnivore at Venta Micena able to attack ungulates this large, was similar to that of the modern African lion. The proboscidean *M. meridionalis* is represented in the fossil assemblage by five individuals, four of which are juveniles. The worn molars of the remaining individual suggest that it was old and probably died of starvation and was subsequently scavenged by hyaenas and hominids. Similarly, a study by Rawn-Schatzinger (1992) of the Friesenhahn Cave assemblage, which was accumulated by the great scimitar cat, *Homotherium serum,* has revealed a very high selection (almost 100%) of juveniles among the two proboscidean species identified in this site (*Mammuthus americanus* and *Mammuthus* cf. *columbi*). In contrast, other ungulate species of smaller body size such as *Mylohyus nasutus, Odocoileus virginianus,* and *Bison* sp. are represented in this assemblage by much lower percentages of young individuals (40%, 33%, and 50%, respectively). As noted above, lions are only able to hunt very young elephants, because the large size of protective adult individuals makes them virtually invulnerable to predation. The high selection of juveniles of large ungulate prey species in Venta Micena suggests then that the hunting behavior of large machairodonts would be similar to that of recent large felids, which first subdue prey with their claws while biting the neck, as opposed to specialization in the capture of large proboscideans by stabbing them with their elongated canines and waiting for the prey to bleed to death, as suggested in some classic studies. Otherwise, the proportion of adult individuals of large species in the assemblage would have been much higher. In this connection we agree with Gonyea (1976), who reached the same conclusions starting from a comparative functional analysis of claw retraction and the relative proportions of postcranial bones in saber-toothed felids.

It is at present difficult to determine the role played by different carnivores in the Venta Micena paleocommunity. Evidence that supports the model of prey selection proposed here (i.e., the results of the interspecific analysis of juvenile/adult ratios in ungulate species, the attritional U-shaped mortality profiles, the presence of many bone diseases, and a biased intersexual ratio of large bovids) clearly indicates that most of the skeletal remains preserved in the assemblage come from

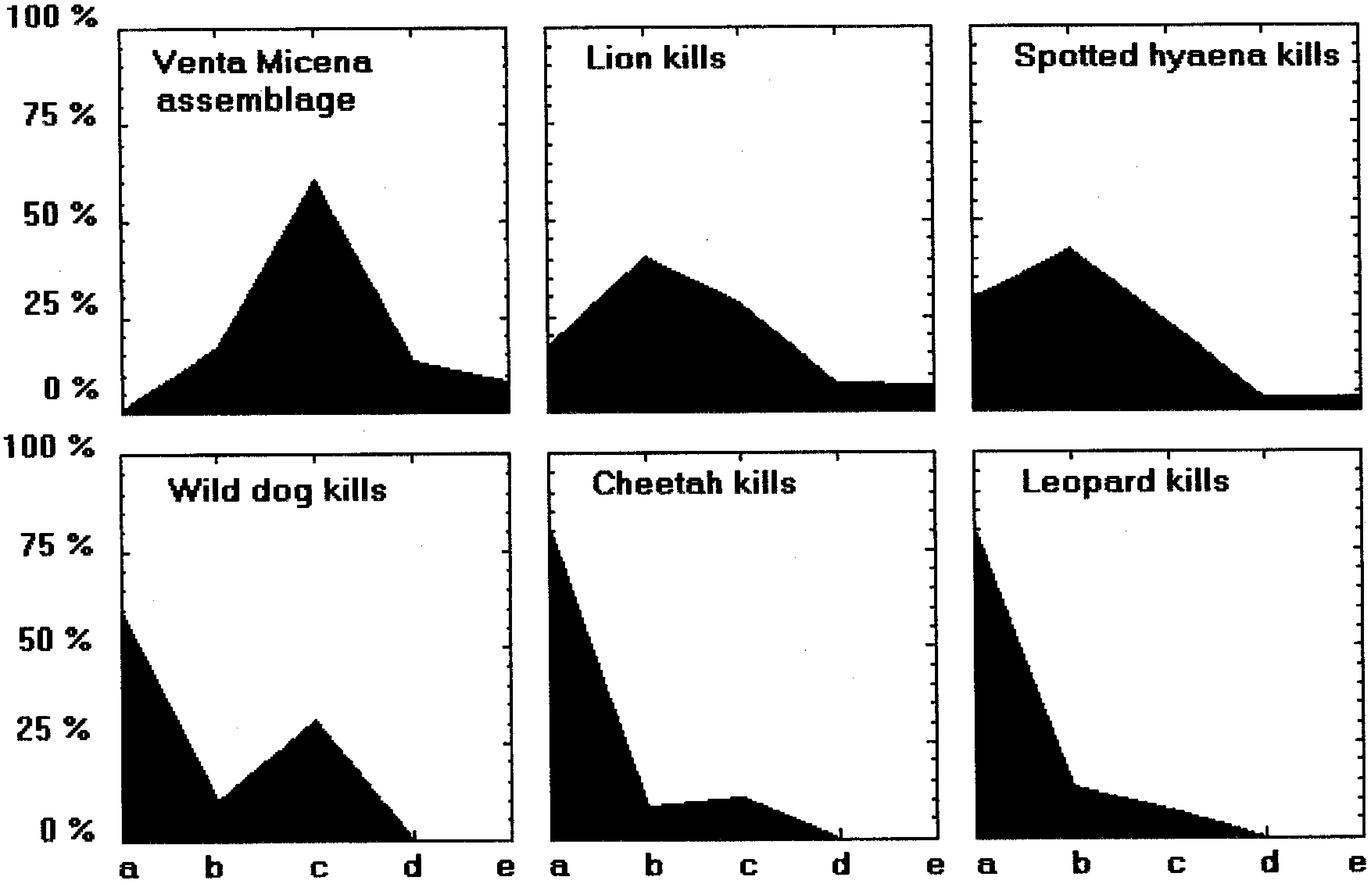

FIGURE 12. Mean percentages of different ungulate size classes (a: <50 kg, b: 50–150 kg, c: 150–400 kg, d: 400–800 kg, e: >800 kg) killed by the five main African predators (lion, spotted hyaena, cheetah, leopard, and wild dog; see references in text) and abundance of these size classes in the Venta Micena assemblage.

hunted individuals. But, who were the hunters?

Four large carnivore species have been preserved in the assemblage: the great machairodont *H. latidens,* the medium-sized sabertoothed felid *M. whitei,* the large hyaena *P. brevirostris,* and the hypercarnivorous wild dog *C. falconeri.* A possible way to deduce the respective ecological roles of these fossil carnivores in the Venta Micena paleocommunity may be to compare them with their modern analogs. Figure 12 shows the mean percentages of ungulates of different size classes (<50 kg, 50–150 kg, 150–400 kg, 400–800 kg, and >800 kg) that are killed by the five main African predators (lion, spotted hyaena, cheetah, leopard, and wild dog) (proportions obtained and averaged from original data in Wright 1960; Bourliere 1963; Mitchell et al. 1965; Estes and Goddard 1967; Foster and Kearney 1967; Kruuk and Turner 1967; de Pienaar 1969; Eaton 1970; Kruuk 1972; Schaller 1972; Malcom and Van Lawick 1975; Elliot and Cowan 1978; Mills 1984; Van Orsdol 1984; Cooper 1990; Fuller and Kat 1990, 1993; Henschell and Skinner 1990; Ruggiero 1991; Johnsingh 1992; Mills and Shenk 1992; Skinner et al. 1992; Mills and Biggs 1993). The abundance of the five size classes in the Venta Micena assemblage is also included in this figure to facilitate comparisons. As can be appreciated, lions and spotted hyaenas show similar prey preferences according to body size: most kills involve animals that weigh between 50 and 150 kg. However, lions capture more ungulates of 150–400 kg, and especially >400 kg, and hyaenas prey more often on smaller species (<50 kg). Cheetahs and leopards show similar hunting behaviors, killing mostly ungulates of <50 kg. Wild dogs show two peaks: ungulates of <50 kg, and animals weighing between 150 and 400 kg, like the wildebeest, which they are able to capture thanks to their cooperative hunting techniques.

When these graphs are compared with that for the Venta Micena assemblage, some interesting similarities emerge: the maximum for Venta Micena is in the intermediate size category (150–400 kg), similar to prey sizes of the lion and the wild dog, and there are two minima for the highest and lowest weight classes. The abundance in the fossil assemblage of large ungulates (>400 kg) is similar to the proportion of such prey species in lion kills. The relative scarcity of ungulates weighing less than 150 kg, in comparison with the abundance of skeletal remains from species of 150–400 kg, resembles the proportion of captures by wild dogs. These results suggest that two carnivores—the saber-toothed felid *H. latidens* and the canid *C. falconeri*—played important ecological roles at Venta Micena.

However, one question remains: What was the role of the large hyaenid *P. brevirostris* in this paleocommunity? Modern spotted hyaenas both kill and scavenge ungulates, depending on factors such as their interaction with lions and other predators (see Kruuk 1972). It is therefore difficult to ascertain their role at Venta Micena. Figure 13 nonetheless sheds some light on the problem. This figure illustrates the mean percentages of ungulates of the five size classes that are scavenged by modern spotted hyaenas (data from Kruuk 1972; Henschell and Skinner 1990) and the abundance of these size categories in the Venta Micena assemblage. The similarity between the two graphs indicates that Venta Micena hyaenas fed largely on ungulates preyed upon by other predators. The only difference that emerges is in the abundance of small ungulates (<50 kg), which are practically absent from Venta Micena. This may be explained if we consider that these carcasses were almost entirely consumed on the spot where the large extinct hyaenas found them, rather than being carried back to their dens. A similar selective behavior has been reported among modern spotted hyaenas (Kruuk 1972; Brain 1981).

If hyaenas failed to transport the carcasses of individuals of small species to their dens, this preservational bias could then explain the scarcity of ungulate prey of very small size, which are represented in the fossil assemblage by only one distal epiphysis of a metacarpal of Caprini indet. (8–10 kg). Such selective behavior in the transport to dens of carcasses by hyaenas could then lead to poorer preservation of the young of small species in the assemblage than the juveniles of large species, thus affecting the interpretation of differential size effects on hunting success proposed here. However, this bias is only important for species of <50 kg, since those ungulate species weighing 50–150 kg (*Hemitragus alba* and Cervidae, gen. et sp. indet.) are well represented in the Venta Micena collection (MNI = 14 and 20, respectively), in a proportion similar to that found among ungulates scavenged by spotted hyaenas (Fig. 13). Consequently, the increasing values of the juvenile/adult ratio as a function of body size for ungulate species weighing >50 kg (Fig. 6) is not an artefact of

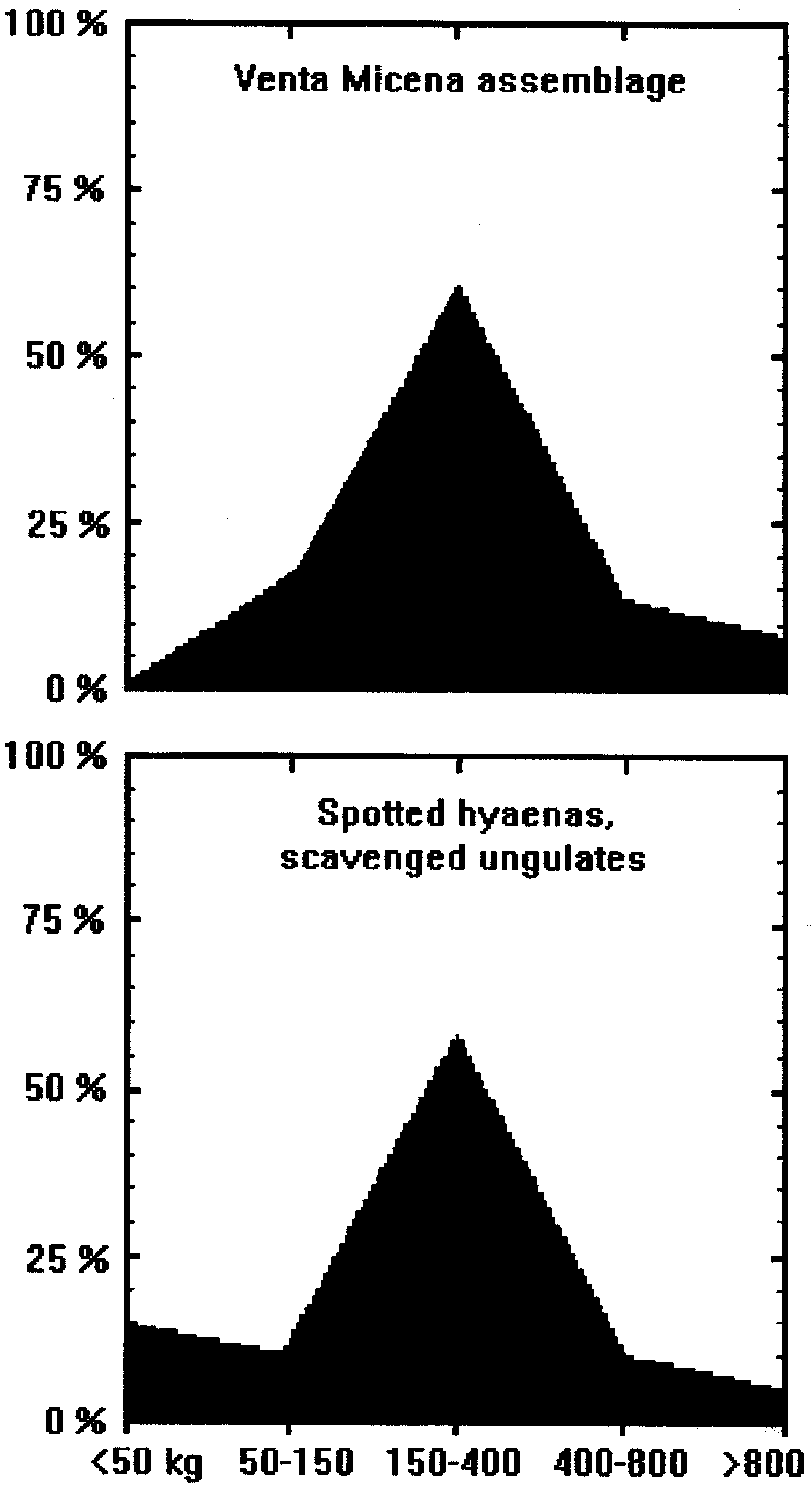

FIGURE 13. Mean percentages of different ungulate size classes scavenged by spotted hyaenas (data from Kruuk 1972; Henschell and Skinner 1990) and abundance of these size classes in the Venta Micena assemblage.

differential size effects on bone transport by hyaenas.

The obtained results suggest that *P. brevirostris* was a bone-cracking scavenger in the Venta Micena paleocommunity. It fed mainly on carcasses of animals killed and partially consumed by other fresh-meat-eating carnivores, in contrast with the behavior of modern spotted hyaenas, which are both hunters and scavengers. With respect to large ungulate prey species (>1000 kg), *H. latidens* was probably the only species capable of hunting them, since only modern lions and spotted hyaenas can hunt juveniles or critically ill individuals of such large species. So far as other ungulates are concerned, one of the most suitable candidates for predation seems to be the canid *C. falconeri*, as suggested by the high frequency of osteopathologies. These canids must have pursued their prey over long distances, like modern African wild dogs, thus leading to intense selection of individuals unable to withstand prolonged running. This hypothesis is supported by the finding of numerous juveniles of intermediate ungulate species (46% horse, 42% large deer, and 60% water buffalo), since lions and spotted hyaenas do not select young individuals among modern ungulate species of comparable sizes as strongly as they are represented in the Venta Micena assemblage.

With regard to the possible ecological role of *Megantereon* in this paleocommunity, we can offer some morphofunctional considerations. Saber-toothed cats all fall into one of two groups, depending on the shape of their upper canines (Martin 1989): *H. latidens* (tribe Homotherine) was a "scimitar-toothed" felid with relatively short, broad canines bearing coarse crenulations, and *M. whitei* (tribe Smilodontini) was a "dirk-toothed" cat with long, narrow upper canines without crenulations. The postcranial skeletons of scimitar-toothed and dirk-toothed predators are quite different. *H. latidens* was relatively long-legged (some closely related forms as *H. sainzelli* had cheetah-like skeletal proportions) and was probably a pursuit predator, with a comparatively large brain and an enlargement of the optic center in the brain. Smilodontini cats were relatively short limbed and developed bearlike, plantigrade hind feet (that perhaps allowed them to adopt a similar vertical posture when surveying the countryside). Their forelimbs were powerfully developed, and a killing bite in the throat may have been coupled with the immobilization of the prey by the front limbs. Their brains are comparatively small and the olfactory lobes are well developed. Anatomically, dirk-toothed cats must have been ambush predators and were most likely solitary hunters (Martin 1989).

Preliminary results of a study currently in progress of the skeletal remains of *M. whitei* from Venta Micena and Dmanisi (East Georgia, Caucasus) suggest that the dimensions of this machairodont differ markedly depending on whether they are estimated from the teeth or from the postcranial skeleton. When body size is calculated with minimum squares regression analysis (Van Valkenburg 1990) of lower carnassial tooth (M_1) length on body weight in modern species of felids, the value obtained is of 55 kg (see Table 1). This suggests that this African species was leopard-sized (Martínez-Navarro and Palmqvist 1995). On the other hand, surface area of the diaphyseal cross section of the humerus in this species (532 mm^2) is approximately half of that in *Homotherium* (1052 mm^2), suggesting a weight of at least 100 kg for *M. whitei*. However, the width of the distal epiphysis of the humerus, which articulates with the radius, is greater in *M. whitei* (47.5 mm) than in the leopard (38.5 mm) or even in the lion (46 mm), which suggests that the animal was larger than this latter species (around 200 kg). These three independent estimates differ widely, although the most reliable estimate is probably that obtained from the diaphysis of the humerus, given that the section of this long bone bears the weight of the forepart of the body. If we consider this estimate correct, we are then dealing with a predator of about 100 kg, whose muscular strength used in immobilizing prey (estimated from the width of the distal epiphysis of the humerus) while it used its elongated canines to kill was fourfold greater than would be suggested by its food requirements or the speed at which it could eat (deduced from its markedly reduced carnassials).

We therefore have a hypercarnivorous felid that would presumably generate large amounts of carrion, since it would exploit the carcasses of its prey to a small degree, leaving enough meat for the hyaenas (which behaved in Venta Micena as strict scavengers; see Fig. 13 and discussion above), as well as for hominids. In the light of this likely situation, the recent discoveries of *Homo* both in southern Spain (Gibert and Palmqvist 1995; Palmqvist et al. 1996) and at Dmanisi (Gabunia and Vekua 1995) associated with African *M. whitei* (Martínez-Navarro and Palmqvist 1995, 1996) are not surprising, since this latter species would have made the first dispersal of hominids to Eurasia in the lower Pleistocene possible, due to the greater scavenging opportunities it provided.

Conclusions

Interspecific analysis of the proportion of juvenile individuals among ungulates in relation to the estimated adult body weights indicates a strong selection of prey by carnivores, and makes it possible to infer that an increase of an order of magnitude in the body size of the hunted species would lead to a 3.2-fold increase in the ratio of hunting success on juveniles/hunting success on adults. Mortality profiles show a selection of prey by carnivores, since hunting is focused on both very young and past-prime individuals. Selection of ungulate prey is corroborated by the finding of many bones with different osteopathologies such as arthrosis, which limited the locomotive capabilities of the animals and therefore their ability to escape predation. The highly biased sex ratio of large bovids (1:3 males/females ratio) also points to this hypothesis of prey selection, as females are more vulnerable to predation given their smaller body size. These results thus fully confirm that the Venta Micena assemblage was formed by attritional mortality produced by carnivores preying on the ungulate populations, and allows us to rule out that the assemblage originated from catastrophic mortality events.

Comparisons of the relative frequencies at which ungulates of different sizes are killed and scavenged by the main African predators, and the proportions in which different-sized ungulates are found in the Venta Micena assemblage, suggest that hyaenas there fed largely on carcasses of animals hunted by the large machairodont *H. latidens* and the hypercarnivorous canid *C. falconeri*. Morphofunctional analysis of the medium-sized machairodont *M. whitei* shows that it may have also played a significant role in this paleocommunity as a source of fresh meat for both hyaenas and hominids.

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