BIOGEOCHEMICAL AND ECOMORPHOLOGICAL INFERENCES ON PREY SELECTION AND RESOURCE PARTITIONING AMONG MAMMALIAN CARNIVORES IN AN EARLY PLEISTOCENE COMMUNITY

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ABSTRACT

Biogeochemical ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ values) and ecomorphological analyses of the early Pleistocene fauna of Venta Micena (Orce, Guadix-Baza basin, SE Spain) provide interesting clues on the physiology, dietary regimes, habitat preferences, and ecological interactions of large mammals. Such inferences are useful in deciphering aspects of paleocommunity structure and predator-prey relationships. Specifically, the hypsodonty index combined with $\delta^{13}C$ values allows classifying the ungulates among grazers from open habitat (*Equus altidens*, *Bison* sp., *Praeovibos* sp., *Hemitragus albus*, *Hippopotamus antiquus*, and *Mammuthus meridionalis*), mixed feeders (*Soergelia minor* and *Pseudodama* sp.), and browsers from canopy areas (*Stephanorhinus* sp. and *Praemegaceros* cf. *verticornis*). Given that $\delta^{13}C$ values indicate that all these herbivores fed exclusively on C_3 plants, significant differences in isotopic values between perissodactyls (monogastric, hindgut fermenters) and ruminants (foregut fermenters) reflect differences in digestive efficiency. Values of $\delta^{18}O$ indicate the dietary water source of ungulates, revealing that *Pseudodama* sp., *Hemitragus albus*, and *Soergelia minor* obtained a significant fraction of their metabolic water from vegetation. Carnivores show higher $\delta^{15}N$ values than herbivores, which records the isotopic enrichment expected with an increase in trophic level. *Hippopotamus antiquus* and *Praeovibos* sp. have unexpectedly high $\delta^{15}N$ values, suggesting that they predominantly consumed aquatic plants and lichens, respectively. Inferences on predator-prey relationships, derived from the use of linear mixing models, indicate resource partitioning among sympatric predators; saber-tooth *Megantereon whitei* and jaguar *Panthera* cf. *gombaszoegensis* were ambushers in closed habitat while saber-tooth *Homotherium latidens* and wild dog *Lycaon lycaonoides* were coursing predators in open plains. The giant hyena *Pachycrocuta brevirostris* scavenged the prey of these hypercarnivores.

INTRODUCTION

Venta Micena (VM) lies in the eastern sector of the Guadix-Baza basin (Granada, SE Spain; Fig. 1). This basin was endorheic (i.e., characterized by interior drainage) from late Miocene to middle–Late Pleistocene times, which facilitated the preservation of large mammal assemblages in swampy and lacustrine environments. During the last decades, excavations in the VM quarry have provided a diverse and well-preserved assemblage of large mammals. The fossils are preserved in porous micrite limestone, and the assemblage is dated by biostratigraphy to the early part of the lower Pleistocene (Arribas and Palmqvist, 1999).

Taphonomic analyses have revealed that the huge bone assemblage of Venta Micena was accumulated by the giant, short-faced hyena *Pachycrocuta brevirostris* in the vicinity of a denning site (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). The bones show a low degree of bone weathering, which indicates that they were exposed at the surface for a very short time before burial, <1 year in most cases. The ratio of isolated teeth to vertebrae (0.94:1) is close to the value expected in the absence of hydrodynamic sorting, and the frequencies of bones grouped according to their potential for dispersal by water are similar to those in the mammalian skeleton. In addition, the surface of the fossils lacks any signs of abrasion or polish, and the longitudinal axes of long bones show no preferred orientation, indicating that they were not aligned by currents. Patterns of preservational completeness and analyses of mortality curves estimated for ungulate species have revealed (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001) (1) that most skeletal remains were scavenged by the hyenas from carcasses of animals hunted by the saber-toothed cats *Homotherium latidens* and *Megantereon whitei* and wild dogs *Lycaon lycaonoides*, (2) that the hyenas selectively transported ungulate carcasses and body parts to their maternity dens as a function of the mass of the ungulates scavenged, and (3) that the fracturing of major limb bones in the dens was also highly selective, correlating well with their marrow content and mineral density.

The VM assemblage has exceptional biomolecular preservation; previous biogeochemical and immunological studies have detected traces of fossil proteins such as albumin, collagen, and immunoglobin in several specimens (Torres et al., 2002). This has indicated the possibility of estimating the abundance of carbon and nitrogen isotopes from bone collagen (Palmqvist et al., 2003). Paleoecological analyses of the fauna, based on biogeochemistry and ecomorphology, have provided insights into the lifestyle and preferred habitat of the large mammal species, which in turn has allowed the synecological reconstruction of this ancient community (Mendoza et al., 2005).

In this article we use published $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ values of collagen and hydroxylapatite from 18 species of large mammals identified in the assemblage (Palmqvist et al., 2003; N = 65) and results obtained from new analyses of additional samples (N = 50) of juvenile individuals and of four species not sampled in previous studies (*Praeovibos* sp., *Hystrix major*, *Panthera* cf. *gombaszoegensis*, and *Ursus etruscus*; see Supplementary Data[1]). The new isotopic data, in conjunction with the results obtained in previous studies, provide deeper insights into the dietary niches and habitat preferences of these early Pleistocene species, utilizing a combined biogeochemical and ecomorphological approach. This creates the possibility of obtaining more detailed inferences of predator-prey relationships in the paleocommunity and also of niche partitioning among hypercarnivores, deduced from the use of linear mixing models.

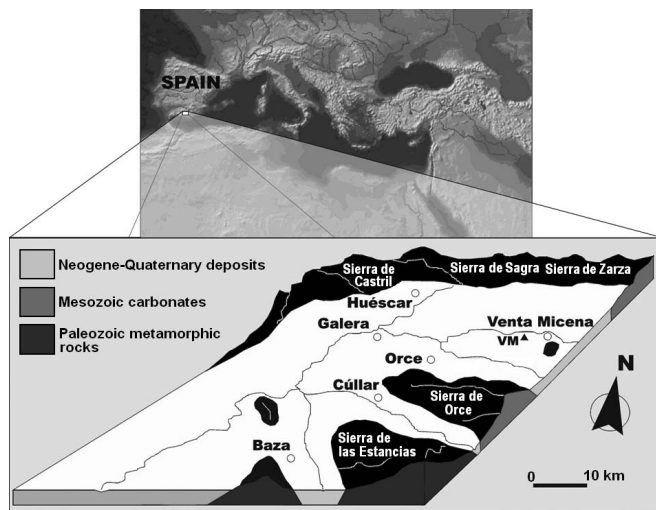* Corresponding author.

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FIGURE 1—Geographic location of the early Pleistocene deposits (VM) near Venta Micena in the eastern sector of the Guadix-Baza basin (Granada, southeastern Spain).

DIETARY AND ENVIRONMENTAL INFERENCES FROM STABLE ISOTOPES

Carbon and nitrogen isotopes of bone collagen are useful proxies for estimating the dietary niches and habitat preferences of extinct mammals (DeNiro and Epstein, 1978; Ambrose and DeNiro, 1986; Jones et al., 2001; Palmqvist et al., 2003; Coltrain et al., 2004; Bocherens et al., 2005; Phillips and Eldridge, 2006). According to their photosynthetic pathways (Edwards and Walker, 1983), terrestrial vegetation comprises C_3 plants (all trees and bushes, temperate shrubs, and grasses adapted to cool, moist climate or high altitude) and C_4 plants (tropical, arid-adapted grasses and some sedges). All plants are depleted in ^{13}C compared to atmospheric CO_2, but important differences in isotopic composition result from differences in their carboxylating enzymes (Smith and Epstein, 1971; O'Leary, 1988; Gannes et al., 1997; Koch, 1998; Fox and Fisher, 2001). Plants with C_3 photosynthesis have a mean $\delta^{13}C$ value of $-26‰$ while C_4 plants have a mean of $-12‰$. Herbivores incorporate the plant carbon into their bone collagen with a positive fractionation of $4‰–6‰$, and an additional enrichment of $1‰–2‰$ is recorded in the skeletal tissues of carnivores (Vogel et al., 1990; Koch, 1998; Bocherens and Mariotti, 2002; Bocherens and Drucker, 2003; Dalerum and Angerbjörn, 2005; Lee-Thorp and Sponheimer, 2006). Consequently, carbon isotope values measure the degree to which a herbivore consumed C_3 or C_4 resources and, similarly, may reveal if a carnivore preyed on C_3-browsing or C_4-grazing herbivores (DeNiro and Epstein, 1978; Klepinger and Mintel, 1986; Lee-Thorp et al., 1989; Koch, 1998; Phillips and Koch, 2002; Bocherens and Drucker, 2003; Sponheimer et al., 2007). Other sources of isotope variability include recycling of CO_2 within a forest (canopy effect), which causes a depletion of $2‰–5‰$ in plants from closed environments and thus a shift to more negative values in the collagen of forest herbivores and in carnivores preying on these herbivores (Van der Merwe and Medina, 1991; Stevens et al., 2006).

Nitrogen isotopes provide interesting clues on the position of ancient species in the food web because there is an enrichment in $\delta^{15}N$ values of $2‰–7‰$ per trophic level (Robinson, 2001; Bocherens and Mariotti, 2002; Phillips and Koch, 2002; Bocherens and Drucker, 2003; Vanderklift and Ponsard, 2003; Dalerum and Angerbjörn, 2005; Lee-Thorp and Sponheimer, 2006). Plants that fix atmospheric N_2 have $\delta^{15}N$ values close to $0‰$, while those that use soil NH_4^+ and NO_3^- show higher values (Koch, 1998; Robinson, 2001). Thus, animals consuming plants with symbiotic diazotrophs (i.e., microorganisms that fix atmospheric nitrogen) have lower $\delta^{15}N$ values than those feeding on non-N_2-fixing plants. Similarly, herbivores from closed environments show lower $\delta^{15}N$ values than those from grasslands, in this case because of soil acidity in dense forest (Sealy

et al., 1987; Rodière et al., 1996; Bocherens et al., 1996a; Gröcke et al., 1997). Plants near marine or salt-affected areas are enriched in $\delta^{15}N$ values, and deep-rooted plants are enriched over those with shallow roots (Virginia et al., 1989). Similarly, marine food sources show more positive $\delta^{15}N$ values than terrestrial ones (Schoeninger et al., 1983). The effects of nitrogen metabolism are also important. Animals living in arid regions concentrate urine and excrete concentrated urea, which causes elevated $\delta^{15}N$ values, and young, suckling animals have higher $\delta^{15}N$ levels than adults (Koch, 1998; Nelson et al., 1998; Jenkins et al., 2001). In addition, there are phylogenetic effects in nitrogen metabolism; for example, perissodactyls (monogastric, hindgut-fermenters) have higher $\delta^{15}N$ values than ruminants (Gröcke and Bocherens, 1996), due to the fact that ruminants have a distinct process of nitrogen cycling in which some waste urea is dumped into the rumen, and they are thus less water dependent than monogastric herbivores (Janis, 1976, 1989).

Fossil collagen may be degraded or contaminated during diagenesis, which would modify the original isotopic signal (Gröcke, 1997; Richards et al., 2000; Drucker et al., 2003). This is not the case in Venta Micena, where the average C:N ratio of the collagen material extracted (3.18) lies within the range of values for extant species (2.9–3.6) and the amino acid composition from four specimens is similar to that of living mammals (Palmqvist et al., 2003, fig. 6).

Oxygen isotopes of tooth and bone hydroxylapatite are useful paleoclimatic tracers (Koch et al., 1989; Ayliffe et al., 1992; Fox and Fisher, 2001) and, in a local fauna, may reveal the dietary water source of animals (Sponheimer and Lee-Thorp, 2001; Harris and Cerling, 2002). The $\delta^{18}O$ value of hydroxylapatite is a function of the isotopic composition of atmospheric O_2, liquid water, and oxygen in food. The isotopic composition of the latter two sources is highly variable and may explain the differences among sympatric taxa (Bryant and Froelich, 1995; Bryant et al., 1996; Kohn, 1996; Kohn et al., 1996). Given that leaf water is ^{18}O enriched owing to evapotranspiration, the $\delta^{18}O$ value in an ungulate that derives a significant fraction of its water requirements from the vegetation will be more positive than in another that relies more on drinking water (Sponheimer and Lee-Thorp, 2001; Harris and Cerling, 2002). Similarly, given that proteins are depleted in ^{18}O compared to carbohydrates, carnivores show lower ^{18}O contents than herbivores (Sponheimer and Lee-Thorp, 2001).

The feeding preferences of extinct mammals can be also addressed from comparative study of their craniodental morphology because several features of the skull, mandible, and dentition are indicative of diet (Janis and Ehrhardt, 1988; Palmqvist et al., 1999, 2003; Pérez-Barbería and Gordon, 2001). For example, the development of hypsodont, high-crowned cheek teeth represents an adaptation in ungulates against tooth wear. For this reason, the hypsodonty index, which is the ratio of unworn crown height to average width of the third molar (M_3), is a good indicator of dietary preferences and habitat selection (Williams and Kay, 2001; Mendoza et al., 2002). Those species that consume grasses with abundant silica phytoliths have more hypsodont teeth than those not specialized in grass consumption, such as browsers and omnivores. Similarly, those ungulates that feed at ground level in open habitats, where the vegetation accumulates airborne grit and dust, show higher values of hypsodonty than those that forage similar amounts of grass in closed environments. In fact, the degree of tree coverage seems to have been the main factor determining the evolution of hypsodonty, because the hypsodonty index discriminates primarily between ungulates from open and closed habitats, and only secondarily among dietary categories (Mendoza and Palmqvist, 2008).

METHODS

Isotopic analyses of the VM fauna were performed at the Stable-Isotope Biogeochemistry Laboratory at McMaster University, Hamilton, Ontario, Canada. Collagen was successfully extracted from 77 bone samples of 17 species (see Supplementary Data[1]). Carbon and nitrogen

isotopes were measured using a Thermo-Finnigan DeltaPlus XP coupled with a Costech elemental analyzer, normalized to the Vienna Pee Dee Belemnite and atmospheric N_2 standards, respectively. Oxygen isotopes were analyzed in 104 hydroxylapatite bone samples and 11 tooth-enamel samples of 18 species (see Supplementary Data[1]). These samples were reacted with 100% phosphoric acid at 90°C, using a Fison Optima isotope-ratio mass spectrometer and normalized to the standard mean composition of oceanic water. The precision for stable-isotope analysis was 0.1‰ for both carbon and oxygen, and 0.2‰ for nitrogen.

AUTECOLOGICAL INFERENCES ON THE VENTA MICENA FAUNA

The range of $\delta^{13}C$ values measured in the VM herbivores (−27‰ to −20‰; see Fig. 2) indicates that they fed exclusively on C_3 vegetation, which confirms that C_4 grasses were absent from southeast Spain during early Pleistocene times (Palmqvist et al., 2003). Similar results have been reported in other early–middle Pleistocene sites of North and South Africa, in which grazing ungulates show $\delta^{13}C$ values indicative of a diet of C_3 grasses (Bocherens et al., 1996b; Franz-Odendaal et al., 2002).

Carbon collagen data from herbivores provide an opportunity to make more detailed inferences on the vegetation cover of Venta Micena. Two assumptions are necessary before translating the $\delta^{13}C$ values of collagen into $\delta^{13}C$ values of vegetation, however. First, the enrichment factor between diet and collagen (roughly +5‰) must be subtracted; second, the −1.5‰ shift in the $\delta^{13}C$ value of atmospheric CO_2 caused by fossil fuel burning must be taken into account. This indicates that mean $\delta^{13}C$ values for C_3 and C_4 plants in the Pleistocene would be −24.5‰ and −10.5‰, respectively. Given these assumptions, the VM ungulates fall into two categories (Fig. 2). Megacerine deer (*Praemegaceros* cf. *verticornis*), horses (*Equus altidens*), and the rhino *Stephanorhinus* sp. show $\delta^{13}C$ values of <−25‰, which are unusually low for a C_3 environment and would reflect diets with compositions of <−30‰. The other species have $\delta^{13}C$ values between −24‰ and −20‰, which are typical to somewhat low for a C_3 environment and would reflect diets with compositions of −29‰ to −25‰. Given the reconstruction of Venta Micena as an open to semiwooded savanna with patches of forest (Mendoza et al., 2005), these data suggest that the environment of this region was not particularly arid during early Pleistocene times and that three out of ten ungulate species foraged in closed-canopy areas.

The main variations in carbon isotope values in the VM ungulates, however, do not arise exclusively from their ecological segregation among habitats or their dietary specializations; they also reflect physiological differences in digestive efficiency. For example, perissodactyls show the lowest $\delta^{13}C$ values among ungulates, while bovids have the highest ones. Although the isotopic difference between both groups is statistically significant (t = 19.25, p < 0.0001), it is unlikely that it reflects a dietary or habitat difference given their craniodental anatomy; rather, it results from the differing physiology of hindgut and foregut fermenters, which translates into different enrichment factors. In fact, the two perissodactyls of VM have similar $\delta^{13}C$ values, but the hypsodont teeth of *E. altidens* identify it as a grazer from open plains habitat, while the brachydont teeth of *Stephanorhinus* sp. indicate that it was a browser in a closed habitat (Table 1, Figs. 3A–B). Thus, their similarity in $\delta^{13}C$ values does not indicate similarity in diets or shared dietary differences with the ruminants. Instead, it reflects the lower digestive efficiency of hindgut fermenters compared to ruminants, which have higher rates of methane production in the forestomach, and the fact that the excreted methane is strongly fractionated (Crutzen et al., 1986; Metges et al., 1990; Vermorel et al., 1997; Schulze et al., 1998; Clauss et al., 2003). Dietary protein, however, is the main source of carbon for collagen, while the contribution of carbohydrates and lipids is only significant under situations of low dietary protein intake. For this reason, if the VM ungulates derived most collagen carbon from dietary protein, it would be unlikely that the differences in $\delta^{13}C$ values arose from differences in metabolic
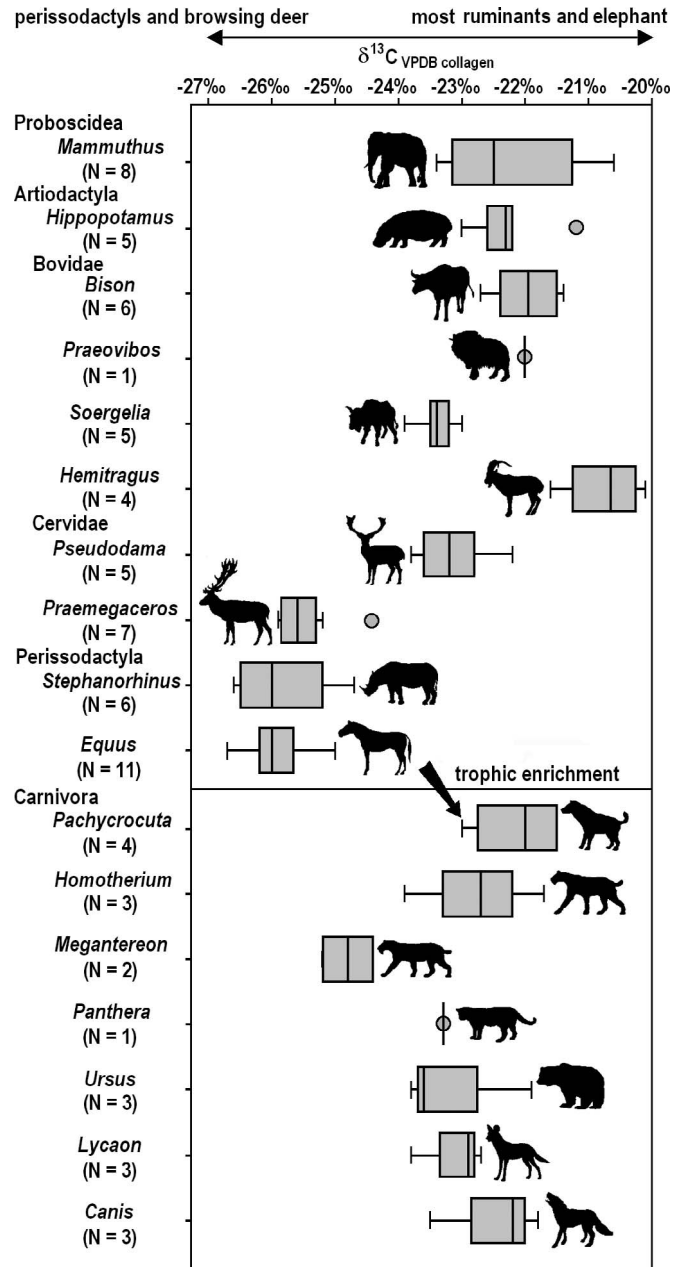

FIGURE 2—Box plots of $\delta^{13}C$ values of collagen from bone samples of large mammal species preserved at Venta Micena. Vertical line inside each box is the median. Box length is interquartile range (IQR) and shows the difference between 75th and 25th percentiles. Horizontal bars enclose values of 5%–95% (the smallest and largest values that are not outliers). Circles are the outliers (i.e., those values which lie more than 1.5 lower than the first quartile or 1.5 higher than the third quartile). VPDB = Vienna Pee Dee Belemnite.

physiology (Ambrose and Norr, 1993). Of interest to this study, Burchell's zebras are depleted in $\delta^{13}C$ values for tooth enamel compared to sympatric grazing ruminants (Lee-Thorp and Van der Merwe, 1987; Cerling and Harris, 1999). Similarly, recent studies of bone collagen isotopes of the European fauna over the last glacial cycle and the Holocene have consistently shown 1‰–2‰ depleted $\delta^{13}C$ values in horses compared to ruminants (Bocherens and Drucker, 2003; Richards and Hedges, 2003). In Venta Micena, it is worth noting that the difference in $\delta^{13}C$ values between ruminants and perissodactyls is greater than those reported at other sites, which suggests that some dietary or habitat differences could be also involved.

TABLE 1—Mean relative abundances of carbon and nitrogen isotopes of bone collagen ($\delta^{13}C$, $\delta^{15}N$), hypsodonty index (HI) measured in the lower third molar, and estimated dietary and habitat preferences of the Venta Micena ungulates.

| Species	HI	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Autecology
Mammuthus meridionalis	–	−22.2	+3.8	grazer, open habitat
Hippopotamus antiquus	–	−22.3	+6.8	grazer, aquatic
Bison sp.	3.9	−22.0	+3.8	grazer, open habitat
Praeovibos sp.	–	−22.0	+6.7	grazer, high mountain
Soergelia minor	2.9	−23.4	+3.4	mixed feeder, plain-forest mosaic
Hemitragus albus	4.4	−20.7	+3.7	grazer, open habitat
Pseudodama sp.	1.7	−23.1	+2.4	mixed feeder, plain-forest mosaic
Praemegaceros cf. *verticornis*	1.6	−25.5	+1.7	browser, closed habitat
Stephanorhinus sp.	1.8	−25.8	+3.2	browser, plain-forest mosaic
Equus altidens	6.1	−25.9	+2.8	grazer, open habitat
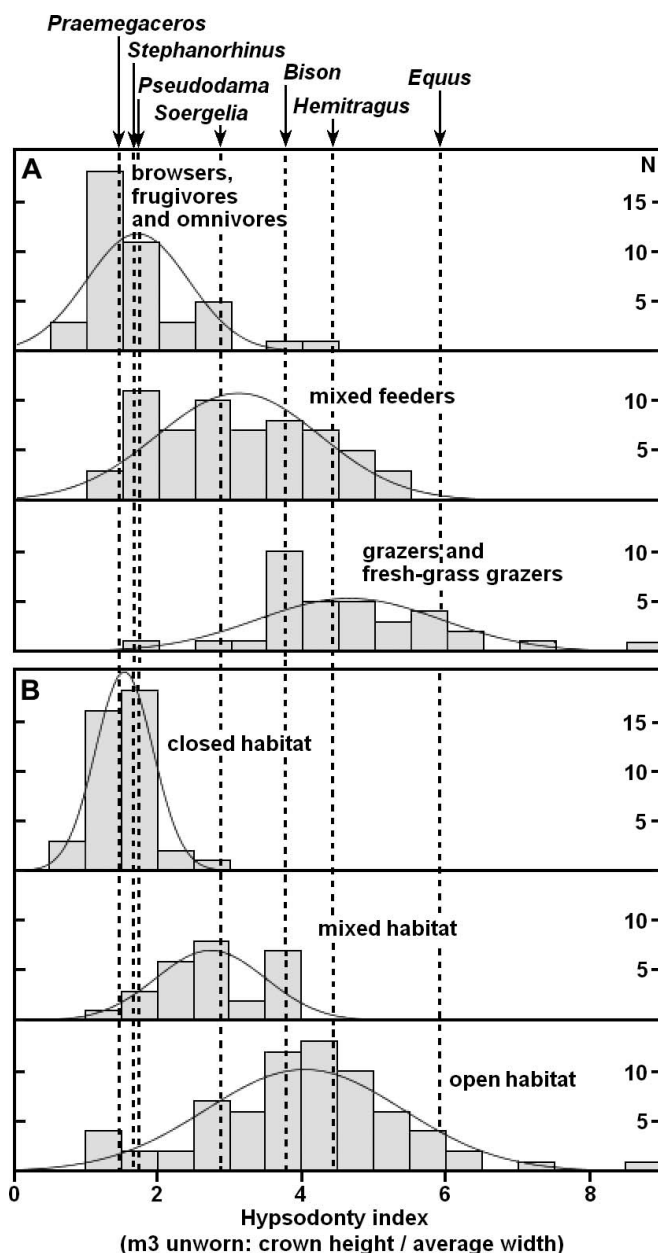
FIGURE 3—Values of the hypsodonty index in a set of extant artiodactyl and perissodactyl species ($N = 134$; data from Mendoza and Palmqvist, 2008) distributed among feeding categories (A) and habitat types (B). Arrows mark the hypsodonty values measured in the Venta Micena ungulates.

Among bovids, *Bison* sp. and *Hemitragus albus* have moderately hypsodont teeth and, in the latter, very high $\delta^{13}C$ values, indicative of a diet composed mainly of grass in open habitat. In contrast, *Soergelia minor* has mesodont teeth and lower $\delta^{13}C$ values, suggestive of a mixed diet of grasses and leaves in habitats with sparse trees (Table 1, Figs. 3A–B). Among ruminants, the different isotopic signature of bovids and cervids may be interpreted in terms of dietary regimes and habitat preferences. Cervids *Praemegaceros verticornis* and *Pseudodama* sp. show lower $\delta^{13}C$ values than bovids (t = 5.15, p < 0.001). Both species have brachydont teeth, which indicates that they were mixed feeders or browsers (Table 1, Figs. 3A–B), as are most species of this family today. In fact, *Praemegaceros verticornis* has the lowest $\delta^{13}C$ values among ruminants, which suggests a hyperbrowsing behavior in closed canopy areas. In contrast, no bovid shows a craniodental anatomy indicative of a diet based exclusively on leaves, and, consequently, they have higher $\delta^{13}C$ values than cervids (Table 1).

Mammuthus meridionalis and *Hippopotamus antiquus* show high $\delta^{13}C$ values, similar to those of bovids (Table 1, Fig. 2). Both megaherbivores are represented in the assemblage by few specimens, and unworn teeth were not available for obtaining estimates of hypsodonty. Based on $\delta^{13}C$ values of tooth enamel in fossil *Mammuthus* from Africa and North America, *M. meridionalis* was a mixed feeder like modern African elephants, although grass was probably a more significant component of its diet (Koch et al., 1998; Cerling et al., 1999). Reconstruction of Venta Micena as a wooded savanna (Mendoza et al., 2005) opens the possibility that the elephant was foraging in the drier part of the ecosystem. Additionally, Vogel et al. (1990) have reported a carbon enrichment factor for bone collagen of +5.5‰ in elephants, which is relatively high compared to other ungulates and may explain the high $\delta^{13}C$ values of *M. meridionalis*. In the case of *H. antiquus*, modern hippos are grazers with brachydont teeth, as in the specimens from VM. The reason for this tooth morphology is that hippos have a low metabolic rate and consume less food per day than would be expected for animals of their size (Schwarm et al., 2006), and thus the amount of wear on the teeth is correspondingly less (Mendoza et al., 2002). In addition, a study of the isotopic composition of tooth enamel in several hippo populations has shown that this animal has a more varied diet than usually thought, including significant amounts of C_3 plants in closed to moderately open environments (Boisserie et al., 2005).

Figure 4 shows a plot of nitrogen isotope values measured in large mammals from Venta Micena. With the exception of *H. antiquus* and *Praeovibos* sp., all ungulates record relatively low $\delta^{15}N$ values, suggesting that they consumed a minor but significant fraction of plants with N_2-fixing symbiotic prokaryotes. Modern hippos consume terrestrial grasses, showing similar $\delta^{15}N$ values to those of other grazing ungulates (Sealy et al., 1987). The very high $\delta^{15}N$ values of *H. antiquus*, more elevated than those of carnivores, suggest that it fed predominantly on aquatic plants in the Pleistocene lake of Orce, which had relatively saline waters (Anadón et al., 1994). Such an unexpected diet probably relates
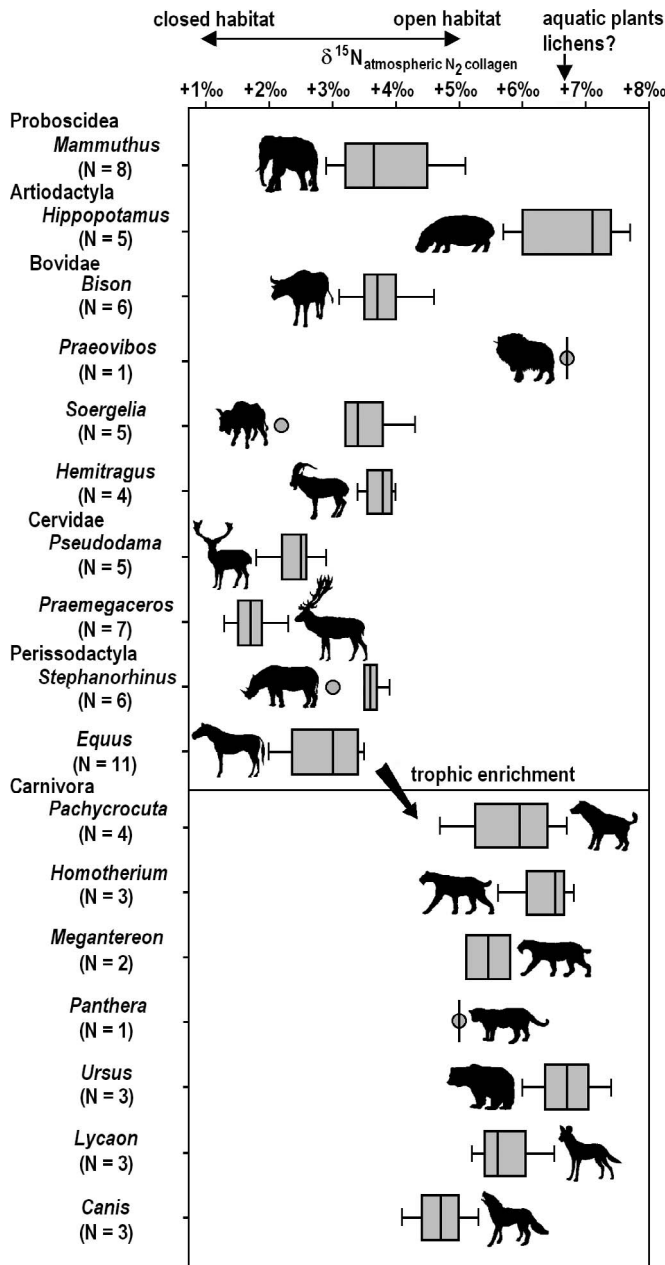
FIGURE 4—Box plots of $\delta^{15}N$ values of collagen material extracted from bone samples of large mammal species from Venta Micena. See Figure 2 for explanation of box plots.

to the huge size of this extinct hippo. Preliminary estimates based on the diaphyseal diameter of major limb bones provide a figure of ~3200 kg average body mass for *H. antiquus*, compared with 1500 kg for modern *H. amphibious* (Novak, 1999). In addition, the Pleistocene hippo shows a number of anatomical features that evidence a more advanced degree of specialization for the aquatic way of life compared to the living species, including a more elongated muzzle, a shortened and high neurocranium with more inclined parietals and highly positioned ocular orbits (Petronio, 1995), and shortened distal limb segments (Kalhke, 2001). Overall, *H. amphibious* does not appear to be particularly well designed for dwelling on land, and the enormous size and short metapodials of *H. antiquus* must have posed even more severe limitations for terrestrial locomotion.

Praeovibos sp., an ungulate represented in the assemblage by only a

few remains of a single individual, was clearly allochthonous to the paleocommunity (Arribas and Palmqvist, 1998). This extinct musk ox presumably lived in the mountainous areas that surrounded the Pleistocene lake (Fig. 1), which include the highest summit in the Iberian Peninsula (Mount Mulhacén, 3481 m), and was spatially segregated from other ungulates. Modern musk oxen (*Ovibos moschatus*) inhabit highly seasonal environments, consuming willow, forbs, and sedge-dominated vegetation (Klein and Bay, 1994). During winter, however, musk oxen subsist primarily on lichens and some senescent browse. Lichens, although potentially high in digestible energy, contain less protein than required for metabolic maintenance (Barboza and Reynolds, 2004; Parker et al., 2005). Today, lichens mostly cover the upper slope sectors of the mountain environments that surround the Guadix-Baza basin (Cantón et al., 2003). Thus, the elevated $\delta^{15}N$ ratio estimated in the single specimen of *Praeovibos* sp. can be tentatively interpreted as indicating increased recycling of nitrogen from body protein owing to a poor quality diet.

Perissodactyls and bovids show more positive $\delta^{15}N$ values than cervids (t = 7.36, p < 0.05), which confirms that the cervids preferably fed in closed habitats, where their low ^{15}N contents would result from soil acidity (Rodière et al., 1996; Gröcke, 1997). Among the perissodactyls, the comparatively high $\delta^{15}N$ values of *Stephanorhinus* sp. suggest that this browsing rhino inhabited plain-forest mosaics, in a similar fashion to modern black rhinos, while those of *Equus altidens* are congruent with a hindgut fermenter of medium size living in a plains habitat. Values of $\delta^{15}N$ for the elephant *Mammuthus meridionalis* are similar to those expected for a large, monogastric herbivore (Gröcke and Bocherens, 1996).

The mean fractionation values for carbon and nitrogen isotopes between carnivores and herbivores ($\Delta^{13}C$: +0.8‰; $\Delta^{15}N$: +2.8‰) are in accordance with the enrichment values expected from increasing one trophic level (Koch, 1998; Bocherens and Mariotti, 2002; Phillips and Koch, 2002; Bocherens and Drucker, 2003; Dalerum and Angerbjörn, 2005), which confirms that the collagen extracted from the fossils did not undergo diagenetic alteration.

The wide range of carbon and nitrogen isotope values in the VM carnivores (Figs. 2, 4) reflects resource partitioning among sympatric predators, as suggested by Palmqvist et al. (2003). For example, *Homotherium latidens* has the highest $\delta^{13}C$ and $\delta^{15}N$ values among felids, while *Megantereon whitei* and *Panthera* cf. *gombaszoegensis* show the lowest levels. This suggests that *Homotherium* was the top predator in the paleocommunity, pursuing juveniles of megafauna and adult ungulates of medium-to-large size in open plains, while *Megantereon* and *Panthera* ambushed medium-sized ungulates in closed habitat (see below). Such inferences are congruent with the postcranial anatomy of these predators, which suggests that they specialized on different prey types (Anyonge, 1996; Arribas and Palmqvist, 1999; Palmqvist et al., 2003). *Megantereon* had a robust body, similar in mass to extant jaguars (~90 kg). Based on the low value (~80%) estimated for the brachial index (i.e., radius length divided by humerus length) and the short metapodials, it was an ambushing predator in the forest. In such habitat, browsing ungulates with depleted $\delta^{13}C$ values would be an important fraction of its diet (Palmqvist et al., 2007). In the case of *P. gombaszoegensis*, the European jaguar, it is worth noting that the extant jaguar is an opportunistic predator that inhabits tropical or subtropical, evergreen moist forest, consuming prey relative to its availability (Weckel et al., 2006). *Homotherium* was a scimitar-toothed cat with comparatively long and slender limbs and a body mass similar to that of modern lions (~140 kg). The forelimb (brachial index of ~100%) was more elongated than the hind limb, which suggests adaptations to carry away large prey, as in the tiger. The claws were small, with the exception of a well-developed dewclaw in the first digit of the forefoot. These features suggest increased cursoriality in open plains and less prey-grappling capability than other felids (Arribas and Palmqvist, 1999; Palmqvist et al., 2003).

Canids *Lycaon lycaonoides* and *Canis mosbachensis* have intermediate isotopic signatures, while the hyaenid *Pachycrocuta brevirostris* shows high $\delta^{13}C$ and $\delta^{15}N$ values, and the bear *Ursus etruscus* has the highest

$\delta^{15}N$ values among carnivores (Figs. 2, 4). The comparative ecomorphology of modern and Pleistocene canids (Palmqvist et al., 1999, 2002) indicates that *L. lycaonoides* was a medium-sized ($\sim$35 kg), pack-hunting species ($>$70% vertebrate flesh in diet) with a tetradactyl forelimb that indicates increased cursoriality in open country. In contrast, the body mass ($\sim$15 kg) and the craniodental anatomy of *C. mosbachensis* are both similar to those of modern jackals, with a well-developed talonid basin in the lower carnassial that provides evidence for a more omnivorous behavior. This is consistent with the low $\delta^{15}N$ values obtained for *C. mosbachensis* (Fig. 4).

The family Ursidae is represented today by eight species that are distributed worldwide, except in Africa, Antarctica, and Australia. Despite their low diversity, the feeding ecology of bears varies markedly (Sacco and Van Valkenburgh, 2004; Christiansen, 2007), from exclusively herbivorous (giant panda), through omnivorous (black, brown, spectacled, and sun bears) and largely insectivorous (sloth bear) to carnivorous (polar bear). The high $\delta^{15}N$ values measured in *U. etruscus* are intriguing, as they could tentatively suggest a carnivorous or insectivorous diet for this extinct bear, which is considered the ancestor of the cave bear (*U. spelaeus*), a species thought to have been primarily herbivorous (Nelson et al., 1999). For this reason, and because *U. etruscus* is well represented by jaw fragments in several late Pliocene and early Pleistocene localities of Europe (e.g., Dmanisi, Saint Vallier, Venta Micena, and Untermassfeld), the feeding ecology of *U. etruscus* was investigated through a comparative study of the lower dentition in extant ursids (Fig. 5). Canonical discriminant analysis was used for choosing the best variables for discriminating among feeding categories, following a stepwise procedure with cross validations. This allowed identifying the ratios of tooth measurements that provide more correct assignments in the discrimination of herbivorous, omnivorous, and carnivorous bears (Fig. 5). Results obtained indicate that *U. etruscus* was a generalized omnivore, as are most living bears, instead of a hypercarnivore, as suggested by its high $\delta^{15}N$ values. Perhaps the Etruscan bear regularly consumed fish, in contrast to the other members of the carnivore guild, or its high $\delta^{15}N$ values may have resulted from a prolonged hibernation and the reuse of urea in synthesizing amino acids, as reported by Fernández-Mosquera et al. (2001) in populations of cave bears that lived during cold periods.

Pachycrocuta brevirostris was a giant ($\sim$110 kg), short-faced hyena with a craniodental anatomy that was adapted for destroying carcasses and consuming bones (Arribas and Palmqvist, 1999). Its massive and shortened distal limb segments evidence a less cursorial life style than in other hyenas, although such shortening provided greater power and more stability for dismembering and carrying large pieces of ungulate carcasses to the denning sites (Turner and Antón, 1996). Taphonomic evidence unequivocally indicates that *P. brevirostris* was specialized in scavenging the prey of hypercarnivores (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). It has been argued, however, that this giant hyena may have behaved more like an active hunter and less like a pure scavenger (Turner and Antón, 1996). The main argument is that a heavier and more powerful animal could have used its weight and strength to subdue larger prey animals. In addition, individual strength would be important in any contest with competitors (e.g., in defense of a kill, in attempts to appropriate kills made by others, and for avoiding intraguild predation) and this advantage would be best employed within a group. Taphonomic data from Venta Micena, however, reveals that the giant hyenas transported selected anatomical parts from the carcasses of large ungulate species to the denning site, suggesting that each hyena foraged alone in search of carcasses to scavenge. If they had foraged in groups, the members of the clan would have transported all parts of each scavenged carcass to the maternity den (Palmqvist and Arribas, 2001).

The question of whether an extinct carnivore habitually killed its own prey or scavenged the prey of others is a difficult one to address, as admitted by Turner and Antón (1996), but it is always possible to draw inferences about past behavior by looking at the ecomorphological correlates of modern species. With the exception of the aardwolf (*Proteles*
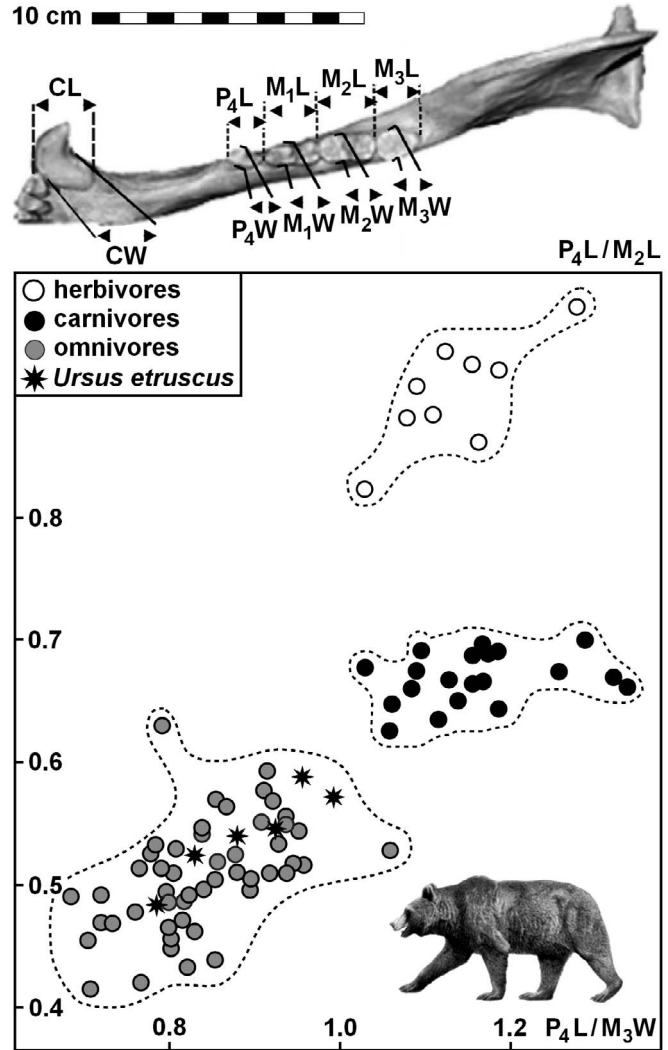

FIGURE 5—Bivariate plot of two ratios of tooth measurements of the lower dentition, including mesiodistal length (L) and labiolingual width (W) at crown base of lower canine (C), fourth premolar (P_4), and first, second, and third molars (M_1, M_2, M_3), which help in discriminating among feeding categories in extant bears. Drawing by Mauricio Antón.

cristatus), which feeds on insects and has extremely reduced cheek teeth (Koehler and Richardson, 1990), all extant hyaenids are adapted to bone-cracking activities. Striped (*Hyaena hyaena*) and brown (*Parahyaena brunnea*) hyenas are strict scavengers (Rieger, 1981; Mills, 1982), while spotted hyenas (*Crocuta crocuta*) behave more as active predators (Gasaway et al., 1991; Di Silvestre et al., 2000). Thus, it is worth analyzing any differences in the craniodental design of these extant hyenas that correlate with their feeding behavior and thus may provide clues to the paleobiology of *P. brevirostris*.

A principal components analysis of the mesiodistal and buccolingual dimensions of the lower teeth in the three living hyenas and in *Pachycrocuta* (Fig. 6) reveals that the two first components, which jointly account for $>$88% of the variance of the 12 original measurements, encompass a morphospace with separate regions for the two feeding styles of hyenas, scavenging versus active predation. Given that the metric variables were logarithmically transformed prior to the analysis and that all have positive factor loadings in the first component, this axis may be interpreted as a size vector (Reyment and Jöreskog, 1993), distributing the specimens according to their overall tooth dimensions. In contrast, some variables show positive values for the second component while others are negative, which identifies this axis as a shape vector, arranging
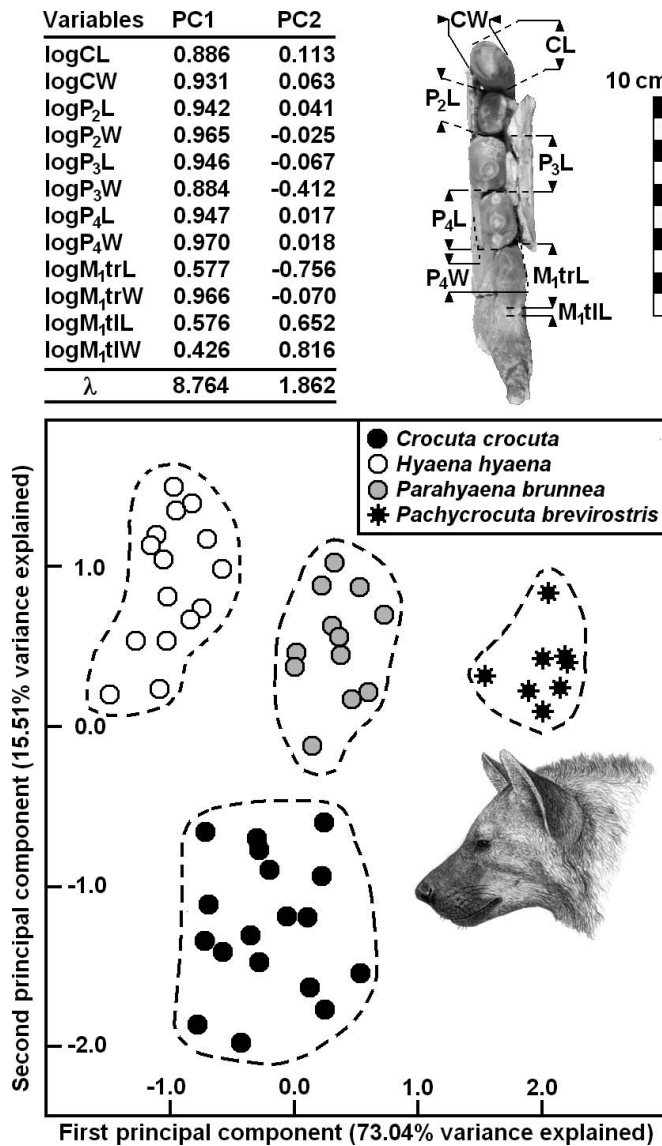
Variables	PC1	PC2
logCL	0.886	0.113
logCW	0.931	0.063
logP$_2$L	0.942	0.041
logP$_2$W	0.965	-0.025
logP$_3$L	0.946	-0.067
logP$_3$W	0.884	-0.412
logP$_4$L	0.947	0.017
logP$_4$W	0.970	0.018
logM$_1$trL	0.577	-0.756
logM$_1$trW	0.966	-0.070
logM$_1$tlL	0.576	0.652
logM$_1$tlW	0.426	0.816
λ	8.764	1.862

FIGURE 6—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$_2$, P$_3$, P$_4$), and trigonid (M$_1$tr) and talonid (M$_1$tl) basin of the lower carnassial (diagram, upper right), in three extant hyenas and *Pachycrocuta brevirostris*. The graph shows the scores of the specimens on the first two components, which jointly account for >88% of the original variance. Drawing by Mauricio Antón.

the specimens 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 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. *Pachycrocuta brevirostris* has a masticatory apparatus well adapted for bone-cracking activities, with a comparatively large talonid basin in the lower carnassial (Fig. 6). These results provide additional evidence of the scavenging habits of *P. brevirostris* and agree with those obtained in the taphonomic analysis of Venta Micena (Palmqvist et al., 1996; Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001).

It could be argued, however, that this behavior was exclusive to 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 in southern Africa, where spotted hyenas hunt only 17% of the prey consumed (Henschel and Skinner, 1990). There are other Pleistocene localities, however, such as Untermassfeld in Germany (Kahlke and Gaudzinski, 2005) and Zhoukoudian in China (Boaz et al., 2000), that have been interpreted also as denning sites of *P. brevirostris* and that 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 in Italy, Venta Micena, and Zhoukoudian) and all show the same dietary specialization, reflected by remarkably similar tooth morphology (Fig. 6). Within this context, the high δ^{13}C and δ^{15}N values in the specimens of *P. brevirostris* (Figs. 2, 4) may be interpreted as evidence that the giant hyenas mostly scavenged ungulate carcasses in open environments, as do living hyenas.

Figure 7 shows a plot of oxygen isotope values measured in large mammals from Venta Micena. It is worth noting that no differences were detected between δ^{18}O values estimated in samples of bone and tooth enamel (see Supplementary Data[1]); given the greater susceptibility of bone hydroxylapatite to oxygen isotope alteration, these results suggest that the original composition of fossils did not undergo diagenetic changes. The high δ^{18}O values of *Pseudodama* sp., *H. albus*, *S. minor*, and *U. etruscus* suggest that these species obtained a significant fraction of their water requirements from the vegetation. In contrast, *M. meridionalis*, *H. antiquus*, *Praeovibos* sp., and *Stephanorhinus* sp. exhibit the lowest δ^{18}O values, indicating greater water dependence for these species. *Bison* sp., *P. verticornis*, and *E. altidens* show intermediate δ^{18}O values, suggesting moderate water dependence for them. These results agree with expectations from the closest living relatives of these Pleistocene species (see reviews in Bocherens et al., 1996b; Sponheimer and Lee-Thorp, 2001; Harris and Cerling, 2002; Palmqvist et al., 2003).

PREDATOR-PREY RELATIONSHIPS AT VENTA MICENA

Carbon and nitrogen isotopic compositions of collagen provide a proxy for reconstructing ancient trophic webs and also for deciphering relationships between predators and their potential prey, inferences that may be correlated with ecomorphology (Bocherens and Drucker, 2003; Palmqvist et al., 2003; Coltrain et al., 2004). As outlined in the previous section, there are interesting differences in δ^{13}C and δ^{15}N values among hypercarnivores (Figs. 2, 4). These suggest the presence of specific predator-prey pairs in the community (Palmqvist et al., 1996, 2003) and indicate the possibility of quantifying resource partitioning among the early Pleistocene carnivores.

Taphonomic studies of the Venta Micena fauna have revealed a high degree of preservational completeness in the bone assemblage collected by the hyenas (Arribas and Palmqvist, 1998; Palmqvist and Arribas, 2001). For this reason, it seems reasonable to assume that all hypercarnivores living in the original community and all of their potential ungulate prey were preserved in the taphocoenosis. The issue here is to assign the preferred prey to each predator and to quantify their relative contributions to the predator's diet.

Given that the only sources of carbon and nitrogen for a carnivore come from its diet, the composition of its tissues will be a function of what the animal ate. Using the isotopic enrichment from prey to predator and the principle of mass balance, the dual linear mixing model (Phillips, 2001) provides a quantitative estimate of the proportional contribution of different ungulate prey taxa to the diet of a carnivore. For two isotopes and three prey sources, their relative abundances in the diet of a predator consuming them may be estimated from the following equations:

$$\delta^{13}C_{predator} = f_A \delta^{13}C'_{prey\ A} + f_B \delta^{13}C'_{prey\ B} + f_C \delta^{13}C'_{prey\ C},$$

$$\delta^{15}N_{predator} = f_A \delta^{15}N'_{prey\ A} + f_B \delta^{15}N'_{prey\ B} + f_C \delta^{15}N'_{prey\ C},$$

$$1 = f_A + f_B + f_C,$$

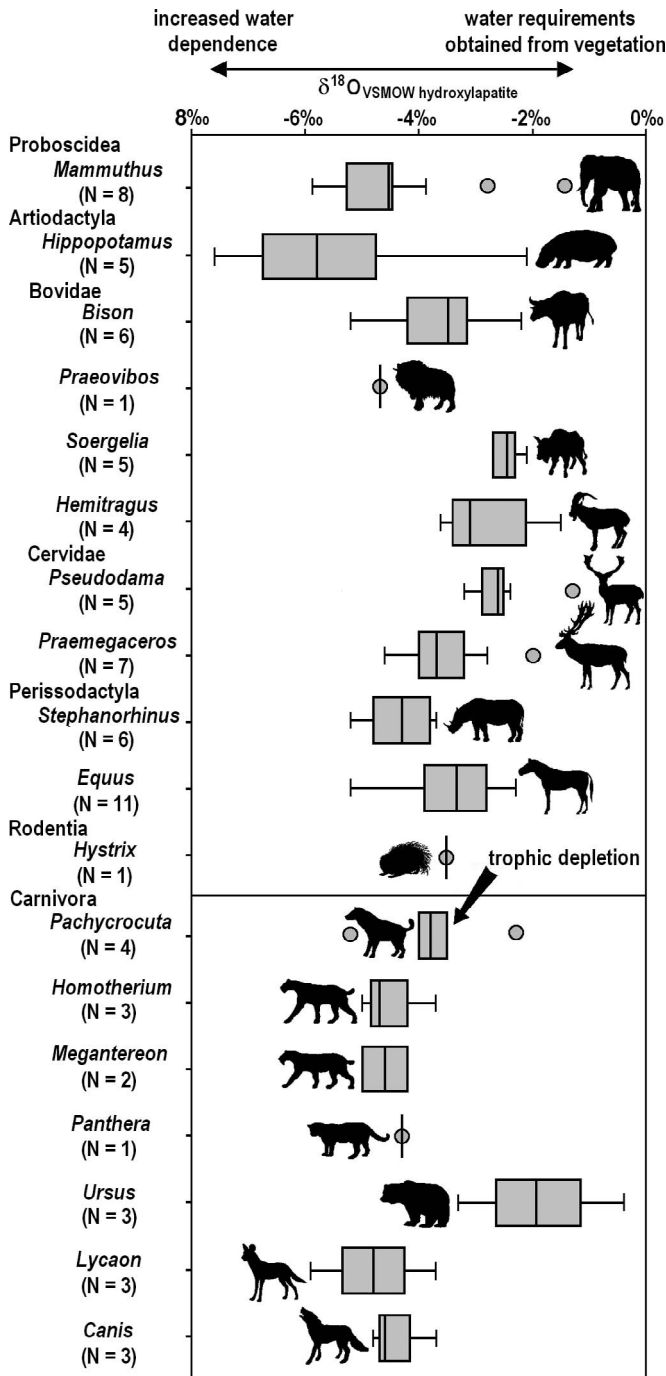**FIGURE 7**—Box plots of $\delta^{18}O$ values of bioapatite from bone samples and tooth enamel of large mammal species preserved at Venta Micena. See Figure 2 for explanation of box plots. VSMOW = standard mean composition of oceanic water.

where $\delta^{13}C'_{prey}$ and $\delta^{15}N'_{prey}$ are the carbon and nitrogen isotope values of prey after correction for trophic fractionation, and f represents the relative contributions of preys A, B, and C to the diet of predator, respectively. If an apparently unreasonable solution is obtained for the contribution of a given prey species (i.e., if $f < 0$ or >1), this can mean either that an important food source was not included in the analysis or that trophic correction factors were not estimated appropriately.

This approach, called the dual-isotope, three-source linear mixing model (Phillips, 2001), has been improved in order to address those cases in which the proportional contribution of a source to a mixture is not the same for both elements (Phillips and Koch, 2002) and also to quantify

the variability of the estimates of source proportions (Phillips and Gregg, 2003). The model does not generate unique solutions for the relative contributions of several dietary sources, however, if the number of potential prey is higher than the number of analyzed isotopes plus one. If stable isotopes from bone collagen ($\delta^{13}C$, $\delta^{15}N$) are used, this implies that accurate estimates on the dietary preferences of an extinct predator will be obtained only if a maximum of three prey accounted for the bulk of the predator's diet. There are two ways of avoiding this limitation: (1) by analyzing all combinations of prey species that match the predator's isotopic signature within some small tolerance and summarizing the range of dietary percentages for each prey (Phillips and Gregg, 2003), and (2) by lumping together some related dietary sources with isotopic signatures that are not significantly different (Phillips et al., 2005).

The dual-isotope, multiple-source mixing model (IsoSource, 2006) provides an alternative to lumping prey sources and allows for discrimination of dietary contributions from more than three prey sources that are consistent with isotopic mass balance (Phillips and Gregg, 2003; Phillips et al., 2005). In order to do this, the model examines all possible combinations of each prey-source contribution (0%–100%) in small increments. Those that sum to the predator's observed mixture isotopic signature within a small tolerance ($\pm 0.1‰$) are considered feasible solutions, from which the frequency and range of potential source contributions can be determined. A major limitation of this procedure is that it provides non-unique solutions, which is reflected in the often broad ranges of feasible contributions for each individual source (Phillips and Gregg, 2001, 2003; Phillips et al., 2005). It is possible *a posteriori*, however, to sum the contributions from functionally related groups of dietary sources, which results in a considerably narrower range of solutions for the aggregate source (Phillips et al., 2005). In the case of Venta Micena, all ungulate species preserved in the assemblage cannot be considered to be potential prey of each hypercarnivore, as this would lead to some unrealistic solutions (e.g., that wild dogs hunted megafauna or that saber-toothed cats pursued small ungulates; see discussion in Palmqvist et al., 1996), which would in turn distort the estimates obtained for the more probable prey sources.

In a recent study of the dietary preferences of extant predators based on scat analyses, Pérez-Claros and Palmqvist (2008) found that three prey species account for an important fraction of the diet (85%–95%) of pack-hunting canids, lynxes (*Lynx*), and cheetah (*Acinonyx jubatus*). In contrast, between five and seven prey species on average are required to account for these percentages in most stalking felids, which relates to the diversity of small-sized prey accessible to these predators in dense forest, and this is also the case in those omnivorous canids that are not pack hunters. Thus linear mixing models will only provide well-defined solutions using two isotopic ratios in the dietary reconstruction of extinct hypercarnivorous canids and probably also in felids with cursorial adaptations or that lived in temperate habitats (Pérez-Claros and Palmqvist, 2008). Linear mixing models have been satisfactorily used to quantify the contribution of different prey sources when isotopic composition can be individually analyzed and related to the diet of living carnivores, as well as to provide clues for the diet of extinct species, including Neanderthals and anatomically modern humans (Bocherens et al., 1999, 2001, 2005; Phillips, 2001; Drucker and Bocherens, 2004; Newsome et al., 2004; Drucker and Henry-Gambier, 2005; Phillips et al., 2005).

This methodological approach was applied to the four hypercarnivores identified at Venta Micena: *H. latidens*, *M. whitei*, *P. gombaszoegensis*, and *L. lycaonoides*. The hyena *P. brevirostris* was excluded from the analysis, given its extremely specialized scavenging behavior. Among ungulates, *Praeovibos* sp. was discarded as potential prey because this species, poorly represented in the assemblage, presumably lived in high mountain areas, as modern musk oxen do, and was thus less accessible to the carnivores. The elephant *Mammuthus meridionalis* was analyzed (even though its enormous size makes it difficult to imagine a predator specializing on it) because isotopic data were available for several young individuals (see Supplementary Data[1]), the only age stage that would be

TABLE 2—Relative contributions (mean percentages of consumption and their standard deviations) of each of the nine ungulate prey species that are well represented in the Venta Micena assemblage to the diet of each of the four hypercarnivores, calculated in 5% increments with the software IsoSource (Phillips and Gregg, 2003; IsoSource, 2006).

Prey-predator	Homotherium latidens	Megantereon whitei	Panthera cf. gombaszoegensis	Lycaon lycaonoides
Mammuthus meridionalis	12.9 ± 12.3	0.7 ± 1.8	1.8 ± 3.0	8.5 ± 8.9
Hippopotamus antiquus	7.9 ± 5.9	0.5 ± 1.5	0.0 ± 0.0	2.6 ± 3.6
Bison sp.	11.8 ± 11.3	0.6 ± 1.7	2.4 ± 3.6	8.7 ± 8.9
Soergelia minor	14.1 ± 14.1	2.1 ± 3.3	2.3 ± 3.5	12.0 ± 12.2
Hemitragus albus	9.1 ± 8.7	0.5 ± 1.5	5.1 ± 5.9	7.4 ± 7.4
Pseudodama sp.	9.8 ± 9.9	2.3 ± 3.5	39.6 ± 11.9	16.6 ± 13.1
Praemegaceros cf. verticornis	9.8 ± 9.5	33.5 ± 10.5	46.6 ± 8.3	22.8 ± 12.4
Stephanorhinus sp.	12.5 ± 9.8	21.2 ± 14.4	0.5 ± 1.6	8.3 ± 7.6
Equus altidens	12.1 ± 10.2	38.6 ± 22.6	1.8 ± 3.0	13.1 ± 10.8

susceptible to predation (see the review in Palmqvist et al., 1996). Commonly quoted enrichment values of bone collagen for carnivores of +1‰ for carbon and +3‰ for nitrogen were used for trophic fractionation between herbivores and carnivores (Phillips and Koch, 2002; Bocherens and Drucker 2003; Phillips and Gregg, 2003).

Table 2 shows the mean percentages of consumption of each ungulate species by particular hypercarnivores, calculated using the dual-isotope, multiple-source mixing model. Although there is a high degree of uncertainty in these estimates, as evidenced by their high standard deviations, some general conclusions on the dietary preferences of each predator can be drawn. For example, *Panthera gombaszoegensis* (European jaguar) focused on the two browsing deer, *Pseudodama* sp. and *P. verticornis*, and these contributed >85% of its diet. This inference of prey choice is in agreement with the expectations for a stalking predator of dense forest, one that mostly consumed ungulates living in a closed habitat. In contrast, it is worth noting that Pérez-Claros and Palmqvist (2008) found a mean percentage of <55% for the two prey most consumed by extant American jaguars. These data suggest that the extinct European jaguar had a more specialized diet than its living relative. The data also suggest that *M. whitei*, the other ambushing predator of the paleocommunity, specialized in three ungulate prey, *E. altidens*, *P. verticornis*, and *Stephanorhinus* sp., which jointly accounted for >90% of the biomass ingested by this saber-tooth cat. In contrast, *H. latidens* and *L. lycaonoides*, the two predators with cursorial adaptations, had a more varied diet that included a significant contribution of ungulates from open habitat. More specifically, five prey species provide a dietary contribution >10% for *H. latidens* and four for *L. lycaonoides*. In the case of *L. lycaonoides*, a species that hunted in packs (Palmqvist et al., 1999), these results are in disagreement with those observed in the living hypercarnivorous canids (Pérez-Claros and Palmqvist, 2008), which concentrate on only three prey. Concerning the megaherbivores, the results shown in Table 2 reveal that very large prey, such as *Mammuthus meridionalis* and *Hippopotamus antiquus*, were relatively minor components of the diet of all hypercarnivores except *H. latidens*, for which juvenile elephants may have represented a significant proportion of its diet. The likelihood of such specialized hunting behavior is evident in the case of the related North American species *Homotherium serum*, known in high numbers from the Late Pleistocene Friesenhahn cave site in Texas, United States, a locality interpreted as a saber-tooth's den and associated with numerous skeletal remains of adult bison and juvenile mammoths (Marean and Ehrhardt, 1995). In contrast to the megaherbivores, the two ungulates that are well represented in the assemblage, *E. altidens* (horse) and *P. verticornis* (megacerine deer), were consumed in significant amounts by three out of four predators.

The results provided by the multiple-source mixing model, combined with the inferences on the predatory behavior and prey-size preferences of the Venta Micena hypercarnivores (Palmqvist et al., 1996, 1999, 2003), help in identifying the three prey species more frequently consumed by each predator. This opens the possibility of using the three-source mixing model for more accurately estimating their dietary contributions, depicted

in the δ¹³C–δ¹⁵N plots in Figure 8. For *H. latidens*, a cursorial predator of open habitat, the estimates obtained with IsoSource (2006; Table 2) suggest that its preferred prey would be medium-to-large size, grazing herbivores from open habitat, such as *Bison* sp., *E. altidens*, and *M. meridionalis*. In the case of *M. whitei*, its diet would include *E. altidens*, *P. verticornis*, and *Stephanorhinus* sp. (Table 2). Of these prey, *E. altidens* is the most abundant ungulate in Venta Micena, reinforcing the hypothesis that horses were the main prey of this ambushing saber tooth. Although the estimates of IsoSource indicate that rhinos should have been captured by *M. whitei* at relatively high frequencies (>20%), the skeletal remains of this ungulate represent only a minor fraction of the bone assemblage (Palmqvist and Arribas, 2001). In addition, it seems improbable that a medium-sized predator such as *M. whitei* could have specialized on prey with an average body mass of ~1500 kg (Palmqvist et al., 1996). For these reasons, it is more reasonable to consider *S. minor* as the third prey of *M. whitei*. In the case of *P. gombaszoegensis*, cervids *P. verticornis* and *Pseudodama* sp. must have constituted the bulk of its diet according to the estimates provided by IsoSource (2006; Table 2). As in the case of *M. whitei*, the third prey consumed more often by this stalking felid was probably *S. minor*, the only ungulate, apart from cervids and rhinos, that foraged in mixed habitats (Fig. 8).

Finally, there are several possibilities for estimating the diet of *L. lycaonoides* (Table 2), a pack-hunting species with an elaborated social behavior that was likely the most versatile predator of this early Pleistocene community (Palmqvist et al., 1999). Given the predatory habits of modern African wild dogs (Malcolm and Van Lawick, 1975; Krüger et al., 1999), the most reasonable solution is that this hypercarnivorous canid focused on small-to-medium-sized ungulates such as horse, goat, and fallow deer. It is worth noting that the percentages of prey consumption estimated for *L. lycaonoides* and *P. gombaszoegensis* (Fig. 8) agree with the expectations for a pack-hunting canid and a solitary stalking felid, respectively, according to the dietary contribution (in biomass) of the first three prey sources consumed by living hypercarnivores (Pérez-Claros and Palmqvist, 2008, table 1). In contrast, the estimates obtained for the two saber-tooth cats, *H. latidens* and *M. whitei* (Fig. 8), are closer to those expected for a pack-hunting canid. This may result from the highly specialized craniodental anatomy of saber-tooth predators compared to pantherine felids, which probably resulted in a greater degree of ecological and ethological specialization (Arribas and Palmqvist, 1999; Palmqvist et al., 2007).

The distribution of prey species described above, based on isotopic signatures, reflects resource partitioning among sympatric predators in Venta Micena. According to these results, pursuit carnivores *H. latidens* and *L. lycaonoides* hunted ungulate prey of large and low-to-medium size, respectively, in open habitat, while *M. whitei* and *P. gombaszoegensis* ambushed their prey in the margins between forest and savannah. This is congruent with the palaeoenvironmental reconstruction of Venta Micena, which is interpreted as a wooded savannah (Mendoza et al.,
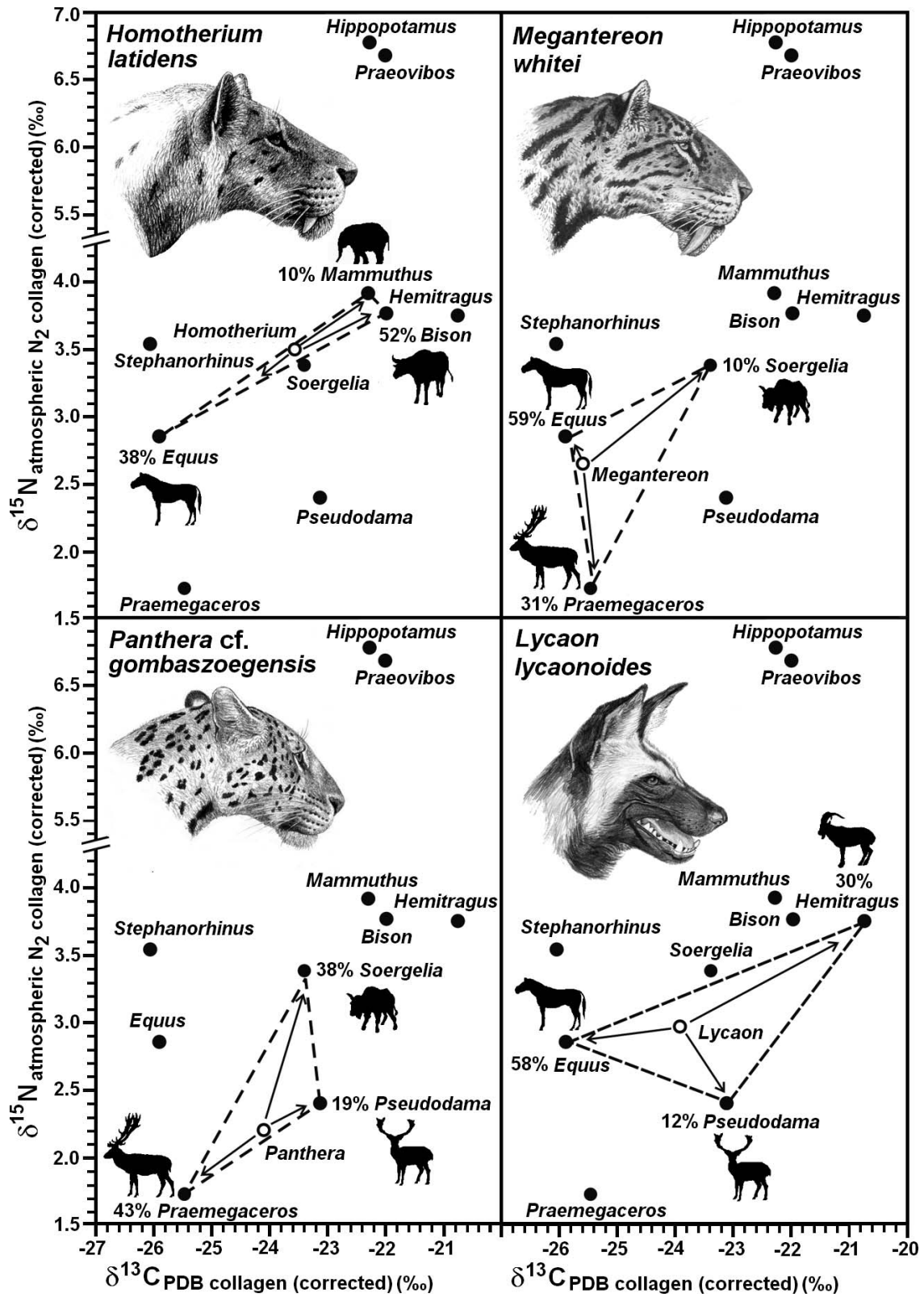
FIGURE 8—Plot of δ^{13}C and δ^{15}N values for the four Venta Micena hypercarnivores and their ungulate prey, corrected for trophic fractionation. Each predator lies within the triangle defined by its three most probable prey species. According to the linear mixing model, the contribution to carnivore diet of each prey defining a vertex in the triangle is defined as the distance from this vertex to the opposite side in relation to its distance to the predator (both measured on the line connecting prey and predator). PDB = Pee Dee Belemnite. Drawings by Mauricio Antón.
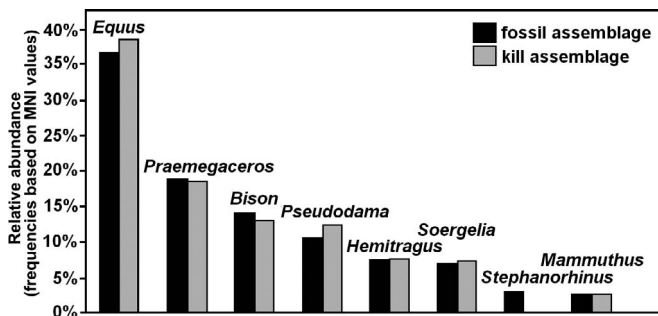
FIGURE 9—Comparison between the relative abundance of ungulate species in the bone assemblage, corrected for taphonomic bias, and the relative frequencies in which these species were hunted by the hypercarnivores, deduced from the application of the linear mixing model and assuming that each predator contributed similarly to the kill assemblage collected by the hyenas. MNI = minimal number of individuals.

2005). It is interesting to note that the bone-cracking hyena *P. brevirostris*, a species that, according to taphonomic analyses, specialized in scavenging the prey of hypercarnivores (Palmqvist et al., 1996; Palmqvist and Arribas, 2001), shows a range of $\delta^{15}N$ values (Fig. 4) that matches that expected for a carnivore that consumed all of the ungulates preserved in the faunal assemblage.

Finally, the average frequencies of ungulate species estimated for a hypothetical death assemblage based on the expectations of the dual-isotope, three-source linear mixing model are shown in Figure 9. Such frequencies were calculated assuming that (1) each carnivore exploited the carcasses of its prey to the same degree, and (2) each predator contributed similar proportions of kills to the death assemblage collected by the hyenas. This theoretical assemblage was compared with the relative frequencies of herbivores in Venta Micena, based on the number of identified specimens counted, after correction for preservational bias related to body size (Arribas and Palmqvist, 1998). Figure 9 shows that there are only relatively minor differences between the expected and observed abundance for most ungulate species. This suggests that the hyenas scavenged the ungulate carcasses in the proportions in which they were available and confirms the accuracy of the estimates obtained with the linear mixing model for the diet of the Venta Micena predators.

CONCLUSIONS

Patterns of abundance of stable isotopes of bone collagen ($\delta^{13}C$, $\delta^{15}N$) and hydroxylapatite ($\delta^{18}O$) are a useful proxy for reconstructing the ecology of the early Pleistocene large-mammal community of Venta Micena and also help in deciphering predator-prey relationships. Carbon-isotope values reveal physiologic differences between hindgut- and foregut-fermenting ungulates related to their digestive systems and the differential assimilation of cellulose, with perissodactyls showing a lower isotopic enrichment than elephants and artiodactyls from open habitat. The low $\delta^{13}C$ values seen in deer suggest that they were mixed feeders or browsers in closed habitat. Nitrogen isotope values of carnivores and herbivores reflect the isotopic enrichment expected from a higher trophic level, indicating that the collagen preserved was not diagenetically altered. All ungulate species except hippo and musk oxen record isotopic values that agree with a diet that included a minor but significant fraction of plants with N_2-fixing symbiotic microorganisms. Cervids show depleted $\delta^{15}N$ values resulting from higher soil acidity in a forest habitat, which confirms a browsing diet in closed habitat. The high $\delta^{15}N$ values of hippo specimens suggest that it consumed aquatic vegetation. In the case of the musk ox *Praeovibos* sp., this mountainous species probably fed on lichens. Oxygen isotopes of enamel and bone apatite reveal that *Pseudodama* sp. (fallow deer) and bovids *H. albus* and *S. minor* derived a significant fraction of their water requirements from the vegetation. The low $\delta^{18}O$ values of megaherbivores *Stephanorhinus* sp., *H. antiquus*, and *M.*

meridionalis suggest a greater degree of water dependence for these species.

Carbon and nitrogen isotope values in hypercarnivores reflect differences in prey choice, providing interesting clues on predator-prey relationships within the paleocommunity. The application of linear mixing models allows a quantitative estimate of the contribution of several prey species to the diet of each hypercarnivore. Specifically, *H. latidens* focused on large herbivores from open habitat, *M. whitei* and *P. gombaszoegensis* preyed on medium-to-large-sized browsing herbivores from the forest, and *L. lycaonoides* cooperatively hunted small-to-medium-sized ungulates from open habitat. Finally, the isotopic signature of *P. brevirostris* corresponds to one expected for a hyena that scavenged all of the ungulates preserved in the faunal assemblage.

ACKNOWLEDGMENTS

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