Paleoecological reconstruction of a lower Pleistocene large mammal community using biogeochemical (δ¹³C, δ¹⁵N, δ¹⁸O, Sr: Zn) and ecomorphological approaches

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Abstract.—Ecomorphological and biogeochemical (trace element, and carbon, nitrogen, and oxygen isotope ratios) analyses have been used for determining the dietary niches and habitat preferences of large mammals from lower Pleistocene deposits at Venta Micena (Guadix-Baza Basin, Spain). The combination of these two approaches takes advantage of the strengths and overcome the weakness of both approaches. The range of $\delta^{13}C_{collagen}$ values for ungulate species indicates that C₃ plants were dominant in the diet of these mammals. $\delta^{13}C_{collagen}$ values vary among ungulates: perissodactyls have the lowest values and bovids the highest ones, with cervids showing intermediate values. The hypsodonty index measured in lower molar teeth and the relative length of the lower premolar tooth row indicate that the horse, *Equus altidens*, was a grazing species, whereas the rhino, *Stephanorhinus etruscus*, was a mixed feeder in open habitats. The similar $\delta^{13}C_{collagen}$ values shown in both perissodactyls does not reflect differences in feeding behavior with other ungulates, but rather a lower isotope enrichment factor in these monogastric herbivores than in ruminants, owing to their lower metabolic efficiency. The cervids *Eucladoceros giulii* and *Dama* sp. show low hypsodonty values, indicating that they were mixed feeders or browsers from forested habitats, an ecomorphologically based conclusion corroborated in the former by its low $\delta^{15}N_{collagen}$ content (canopy effect). Bovid species (Bovini aff. *Leptobos*, *Soergelia minor*, and *Hemitragus albus*) presumably inhabited open environments, according to their comparatively high hypsodonty and $\delta^{15}N_{collagen}$ values. Carnivore species (*Homotherium latidens*, *Megantereon whitei*, *Pachycrocuta brevirostris*, *Canis falconeri*, and *Canis etruscus*) exhibit higher $\delta^{15}N_{collagen}$ values than ungulates. These results record the isotopic enrichment expected with an increase in trophic level and are also supported by low bone Sr:Zn ratios. The elevated $\delta^{15}N_{collagen}$ value for a sample of *Mammuthus meridionalis*, which came from an individual with unfused epiphyses, confirms that it was a suckling animal. The $\delta^{15}N_{collagen}$ value of the scimitar-cat *H. latidens* is well above that obtained for the young individual of *Mammuthus*, which indicates that juvenile elephants were an important part of its diet. The hippo, *Hippopotamus antiquus*, yielded unexpectedly high $\delta^{15}N_{collagen}$ values, which suggest feeding on aquatic, non-N₂-fixing plants. The high $\delta^{18}O_{hydroxyl}$ values of bovids *Hemitragus* and *Soergelia* and of cervid *Dama* indicate that these ungulates obtained most of their water requirements from the vegetation. The megaherbivores and *Eucladoceros* exhibit the lowest $\delta^{18}O_{hydroxyl}$ values, which suggest increased water dependence for them. Paleosynecological analysis was based on the relative abundance of species of large mammals from different ecological categories, determined by feeding behavior and locomotion types. The comparison of the frequencies of such categories in Venta Micena with those found in modern African communities indicates that the composition of the paleocommunity closely resembles those of savannas with tall grass and shrubs. The net above-ground primary productivity estimated for the on-crop biomass of the mammalian species preserved in the fossil assemblage also yields a figure congruent with that expected for an open environment.

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Introduction

Venta Micena (37°44′15″N, 2°24′9″W, elevation 974.5 m) lies near the village of Orce, in the eastern sector of the Guadix-Baza Basin (Betic Chains, southeastern Spain; Fig. 1). This site is dated by biostratigraphy to the early Pleistocene, with an estimated age of 1.3 ± 0.1 Ma (Arribas and Palmqvist 1999). The fossils were preserved in 98–99% pure micritic limestone, precipitated on a caliche paleosol that surrounded a shallow Pleistocene lake with swampy marginal zones (Arribas and Palm-
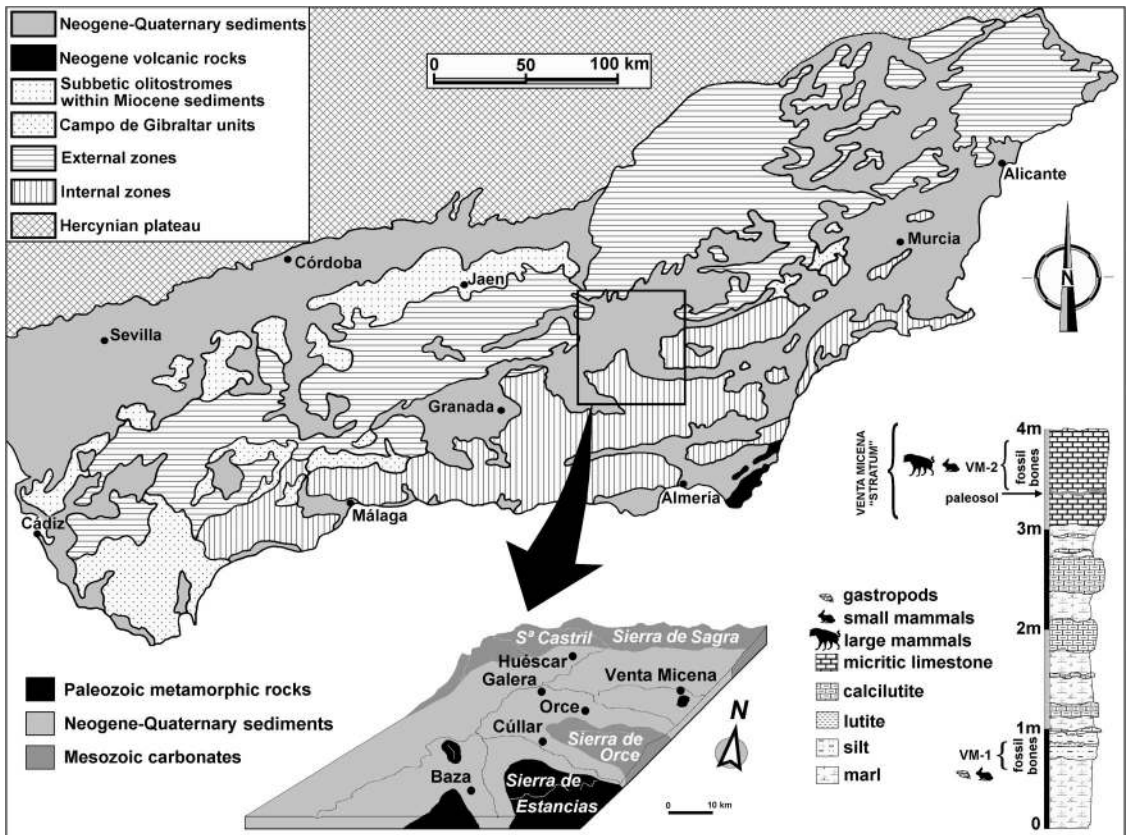
FIGURE 1. Geological map of the Betic Chains, showing the situation of the Guadix-Baza intramontane basin and the stratigraphic profile of the early Pleistocene locality at Venta Micena. This sedimentary basin was endorheic (i.e., characterized by interior drainage) until late Pleistocene times, thus facilitating an exceptional record of Plio-Quaternary taphocenoses of large mammals preserved in swampy and lacustrine sediments. The 80–120-cm-thick Venta Micena stratum (VM-2) is one of the various fossiliferous units in the sedimentary sequence of Orce, whose surface stands out topographically in the ravines of the region and can be followed along ~2.5 km. This stratum has the following vertical structure from bottom to top: (1) A basal unit that is one-third to one-half the total thickness, formed by homogeneous micrite with some carbonate nodules and small mud banks. The sediment preserves abundant shells of freshwater mollusks and is sterile in vertebrate fossils, thus attesting to a first generalized lacustrine stage in the region, in which the micrite was precipitated in water of variable depth. The absence of both pyrite and carbonate facies rich in organic matter is evidence that the lake was not eutrophic. (2) A 4–15-mm-thick calcrete paleosol (hardpan) developed on the surface of the micrite sediments. The calcrete forms an irregular surface, subparallel to the bedding plane, and is thicker at topographic highs. It defines a stratigraphic unconformity indicating a major drop of the Pleistocene lake level, and thus the emergence of an extensive plain around the lake. (3) An upper unit of micrite deposited in a subsequent rise of the lake level, which continues up to the top of the stratum, showing rootmarks, mudcracks, and a high density of fossil bones of large mammals resting on the paleosol.

qvist 1998). The macrovertebrate assemblage comprises ~5800 identifiable skeletal remains of 225 individuals, which belong to 20 species of large mammals (Table 1).

Taphonomic research on the composition of the Venta Micena assemblage has shown that the skeletal remains were scavenged by the giant, short-faced hyena *Pachycrocuta brevirostris* from carcasses of ungulates preyed upon by flesh-eating carnivores (Palmqvist et al. 1996;

Arribas and Palmqvist 1998). The selection by predators of specific ungulates was basically a function of differences in the body mass of juvenile and adult prey individuals, as well as in the sex of prey (Palmqvist et al. 1996). Major taphonomic biases in the preservation of the bone assemblage are related to the selective transport by hyenas of ungulate carcasses and body parts to their maternity dens, and to the preferential consumption of low-density, mar-

TABLE 1. Herbivores larger than 10 kg and carnivores larger than 5 kg found in the fauna of Venta Micena, their trophic habits, their number of identifiable specimens (NISP), their minimal number of individuals (MNI)(data from Palmqvist and Arribas 2001), their estimated mass (data from Palmqvist et al. 1996), their calculated on-crop biomass, and their mass-specific basal metabolic rate. Abbreviations: Br = browser, >75% leaves. Mf = mixed feeder, 25–75% grass. Gr = grazer, >75% grass. F = flesh eater, >70% vertebrate flesh in diet. Mi = meat and insect eater, 20–70% flesh. Mb = meat and bone eaters. O = omnivore, <20% flesh.

Species	Trophic habits	NISP (teeth/bones)	MNI (juv./adults)	Body mass (adults, in kg)	On-crop biomass (kg km^{-2})	Basal metabolic rate (J kg^{-1} s^{-1})
Mammuthus meridionalis	Mf	48 (16/32)	5 (4/1)	6000	840.5	0.47
Hippopotamus antiquus	Gr	58 (19/39)	5 (3/2)	3000	706.8	0.55
Bovini aff. *Leptobos*	Gr	775 (382/393)	27 (16/11)	450	439.8	0.89
Soergelia minor	Mf	334 (215/129)	13 (3/10)	225	369.9	1.06
Praeovibos sp.	Gr	6 (3/3)	1 (0/1)	320	403.9	0.97
Hemitragus albus	Gr	305 (209/96)	14 (2/12)	75	281.0	1.39
Caprini gen. et sp. indet.	Mf	1 (0/1)	1 (0/1)	10	169.8	2.31
Eucladoceros giulii	Br	962 (557/405)	36 (15/21)	385	423.0	0.93
Dama sp.	Mf	417 (231/186)	20 (3/17)	95	298.1	1.31
Stephanorhinus etruscus	Br	90 (55/35)	6 (2/4)	1500	594.3	0.66
Equus altidens	Gr	2562 (1183/1379)	70 (32/38)	350	413.1	0.95
Vulpes praeglacialis	Mi	24 (19/5)	1 (0/1)	5	3.6	2.93
Canis falconeri	F	65 (40/25)	3 (0/3)	30	6.9	1.80
Canis etruscus	Co	33 (20/13)	4 (0/4)	10	4.7	2.43
Lynx aff. *issiodorensis*	F	6 (2/4)	1 (0/1)	10	4.7	2.43
Megantereon whitei	F	16 (7/9)	3 (0/3)	100	10.7	1.30
Homotherium latidens	F	7 (6/1)	2 (0/2)	200	13.8	1.08
Pachycrocuta brevirostris	Mb	62 (34/28)	10 (4/6)	70	9.4	1.44
cf. *Meles* sp.	O	1 (1/0)	1 (0/1)	10	4.7	2.43
Ursus etruscus	O	27 (15/12)	3 (1/2)	375	17.2	0.91

row-rich skeletal parts (Palmqvist and Arribas 2001).

The main objective of this study was to determine the autecology of those species of large mammals represented at Venta Micena using biogeochemical and ecomorphological techniques, in order to (1) interpret niche and resource partitioning by the species from each trophic level; (2) infer ecological relationships such as those between predators and their prey; and (3) study the synecological properties of the paleocommunity. The use of this combined approach allows the researcher to take advantage of the strengths and overcome the weakness of both techniques.

Ecomorphological Analyses

Autecological inferences are presented for large mammals from Venta Micena, following an ecomorphological approach. Size estimates for these species (Table 1) range between 5 kg and 6000 kg and were obtained by Palmqvist et al. (1996) using ''taxon-free'' regression equations for body mass on craniodental and postcranial measurements in modern carni-

vore and ungulate species (e.g., Damuth and MacFadden 1990; Anyonge 1993).

Feeding preferences of extinct ungulates can be determined from their craniodental morphology, because several features of the skull and dentition are indicative of diet (see review in Janis 1995; see also Spencer 1995; Mendoza et al. 2002). In herbivores, the hypsodonty index (*HI*) or relative tooth crown height (defined here as unworn molar tooth crown height divided by molar width [Janis 1988]) is widely accepted as a useful indicator of diet (Fortelius 1985; Williams and Kay 2001): grazing ungulates from open habitats that feed upon abrasive grasses with high silicophytolith contents generally show higher hypsodonty values than browsers from forested environments that consume succulent leaves (in this article grazers are defined as species in which grass represents >75% of diet, browsers include ungulates consuming >75% of leaves, and those species taking between 25% and 75% of grass are considered as mixed feeders [Mendoza et al. 2002]). Muzzle shape is also a good indicator of the specific
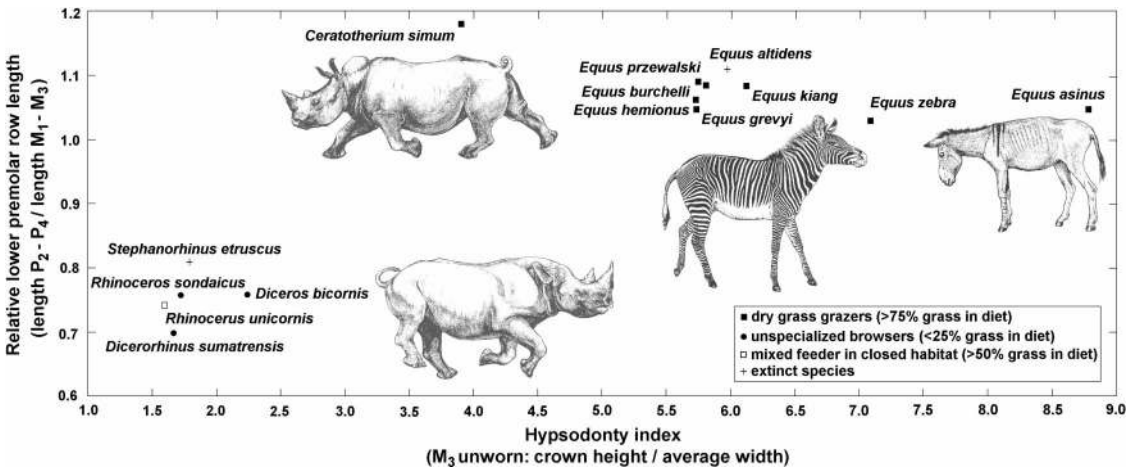
FIGURE 2.   Mean values of relative length of the lower premolar tooth row [(length P_2–P_4/length M_1–M_3) × 100] and hypsodonty index [(unworn M_3 crown height/average width) × 100] in modern perissodactyls (data from Mendoza et al. 2002) and extinct species (horse *E. altidens* and rhino *S. etruscus*) from Venta Micena.

adaptations related to the ''cropping mechanism,'' which includes the shape of the premaxilla and the corresponding mandibular symphyseal region, as well as the relative proportions of the incisor teeth (Gordon and Illius 1988; Solounias and Moelleken 1993; Pérez-Barbería and Gordon 2001): browsers usually show narrow muzzles (i.e., short premaxillary width), consisting of a rounded incisor arcade with the first incisor generally larger than the third, whereas grazers have broad muzzles with transversely straight incisor arcades, showing equal or subequal-sized teeth.

Although the hypsodonty index is probably the best single variable for predicting diet in both extant and ancient ungulates, in some cases molar crown height does not seem to be a good indicator of feeding habits (see review in Mendoza et al. 2002). For example, most grazing and mixed feeding ungulates have hypsodont teeth, but the hippo (*Hippopotamus amphibius*) and the rock hyrax (*Procavia capensis*) have brachyodont (i.e., short-crowned) teeth ($HI < 1.4$ and < 1.7, respectively). Both species have relatively low metabolic rates, consuming less food per day than would be expected for animals of their body size (Novak 1999), which means that the total amount of wear on the teeth would correspondingly be less.

Some second-order differences in cranio-dental morphology are related to phylogenetic constraints. For example, horses have relatively more narrow muzzles than grazing ruminants of similar body size (Janis and Ehrhardt 1988; MacFadden and Shockey 1997) and not all exclusively grass-eaters are similar in their degree of hypsodonty (Williams and Kay 2001). Furthermore, different ungulate groups have adopted different solutions when faced with the same ecological specializations (Mendoza et al. 2002). Grazers, for example, require a comparatively greater grinding area of cheek teeth than browsers and frugivores (Janis 1995). Perissodactyls have faced this problem by enlarging the size of the premolar tooth row, which in low-crowned, browsing and mixed feeding rhinos is comparatively shorter than the molar tooth row (Fig. 2). In these species, the mesiodistal length of the premolar row represents ~75% of the corresponding measurement for the molar row, but grazing perissodactyls have lower premolar and molar cheek teeth of nearly the same length, as can be seen in the white rhino (*Ceratotherium simum*), or even have a premolar row that is longer than the molar row, as in horses (Fig. 2). However, ruminants and camelids show an opposite trend in the size of the premolar tooth row; in these groups, grazers have comparatively shorter premolar tooth rows than browsers (premolars ~45% of the molar tooth row, vs. ~70%; Figs. 3, 4). This

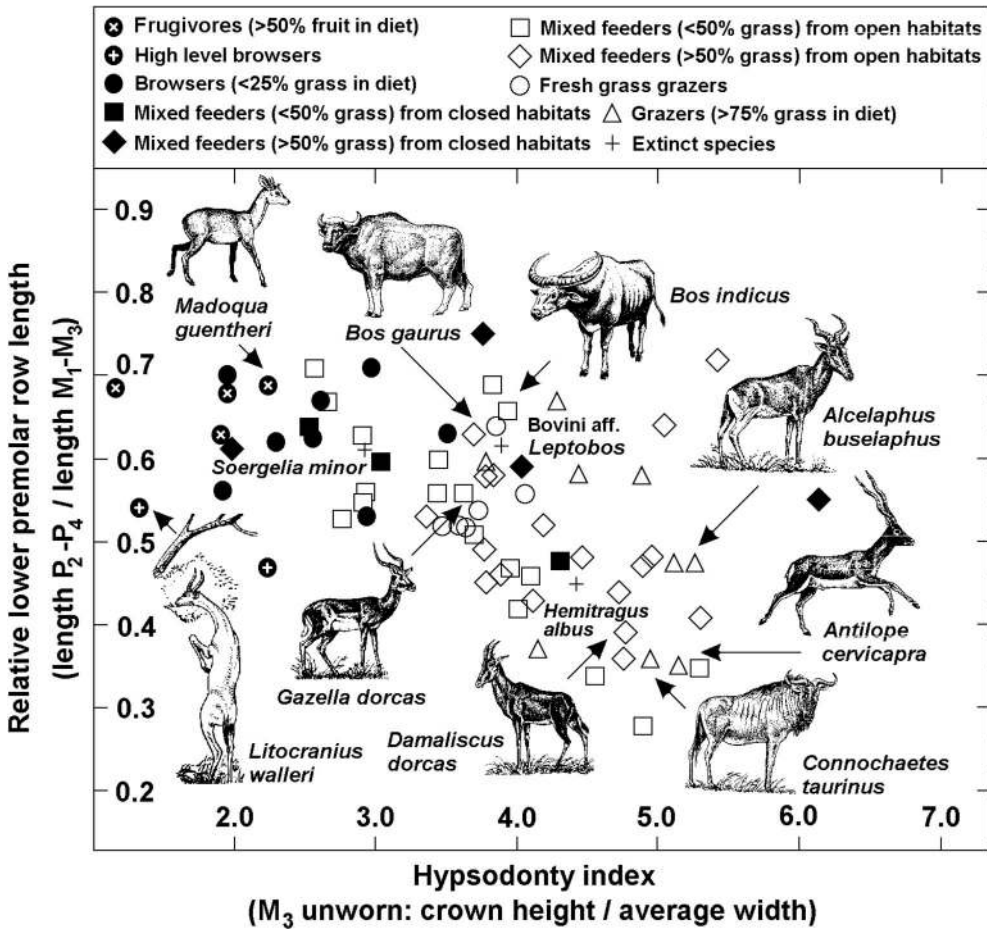FIGURE 3. Mean values of relative length of the lower premolar tooth row [(length P_2–P_4/length M_1–M_3) $\times$ 100] and hypsodonty index [(unworn M_3 crown height/average width) $\times$ 100] in modern bovids (data from Mendoza et al. 2002) and extinct species (Bovini aff. *Leptobos*, *S. minor*, and *H. albus*) from Venta Micena. The position in this diagram of nine extant species covering the whole range of values for hypsodonty and premolar tooth row length is shown, in order to facilitate the visual interpretation of the diagram. The feeding category ''high level browsers'' includes those browsing bovids that feed from trees and bushes at high levels above the ground (e.g., the long-necked gazelles of the genus *Litocranius*).

difference is probably due to differences in the way food is orally processed in foregut and hindgut fermenters (Mendoza et al. 2002).

In carnivores, features of the dentition related to diet include the morphology of the upper canine (C^1), lower carnassial (M_1), and fourth premolar (P_4). Particularly indicative of feeding habits are the relative length of the trigonid blade and the morphology of cusps in the talonid basin of M_1, the shape of C^1 and P_4 (i.e., tooth length divided by tooth breadth), the total grinding area in the dentition, and the smaller masseter and temporalis moment arms (Van Valkenburgh 1988, 1989; Biknevicius and Van Valkenburgh 1996; Biknevicius et al. 1996). These variables provide discrimination between hypercarnivores, bone crackers, and omnivores. Relevant variables in the postcranial skeleton of carnivores include the brachial and crural indexes (i.e., radius length divided by humerus length and tibia length divided by femur length, respectively), the ungual phalanx shape and manus proportions, the ratio of phalanx length to metacarpal length, the biceps brachii leverage index, and cross-sectional geometric properties of long bones such as the midshaft femoral cross-sectional shape (Gonyea 1976; Van Valkenburgh 1985, 1987; Anyonge 1996; Lewis 1997). These variables allow the estimation of different as-
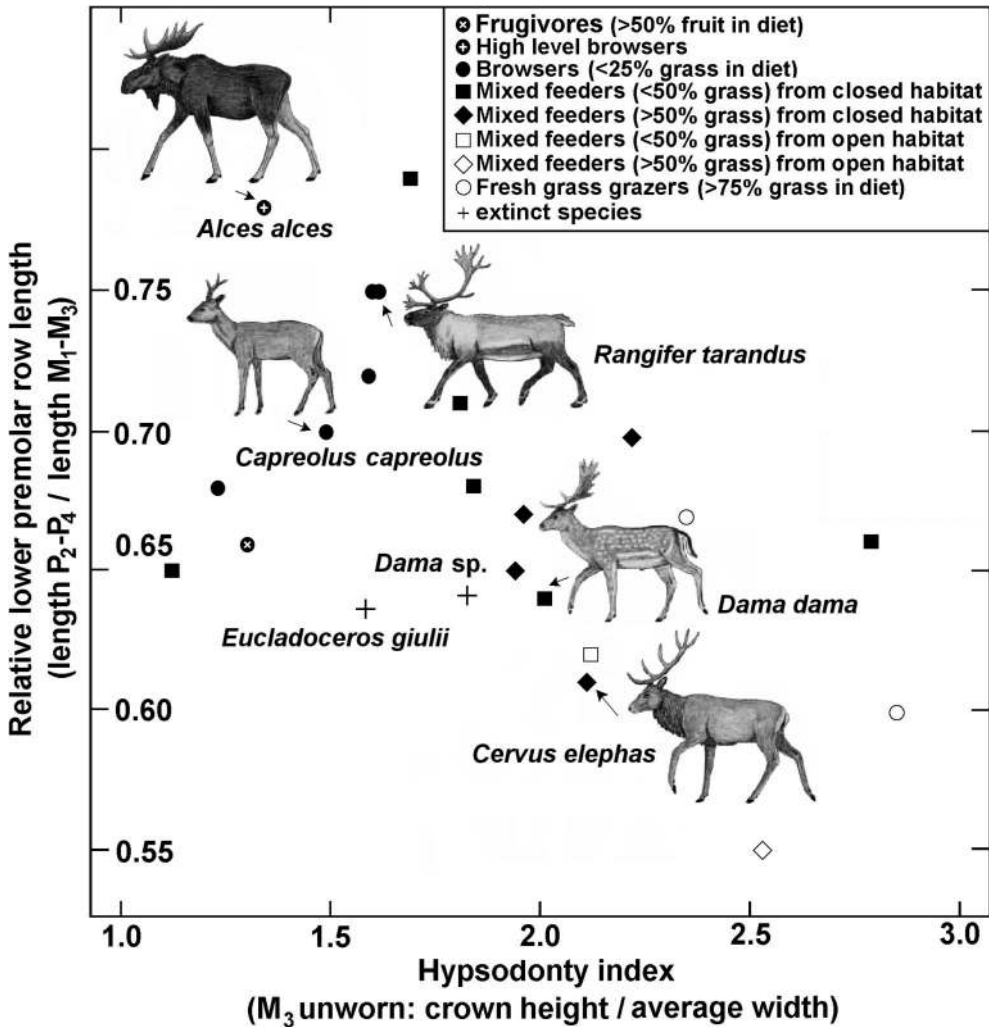
FIGURE 4. Mean values of relative length of the lower premolar tooth row [(length P_2–P_4/length M_1–M_3) × 100] and hypsodonty index [(unworn M_3 crown height/average width) × 100] in modern cervids (data from Mendoza et al. 2002) and extinct cerrid species (*E. giulii* and *Dama* sp.) from Venta Micena. The position in this diagram of five extant species is shown for illustrative purposes. The feeding category ''high level browsers'' includes the moose, *Alces alces*, which is the only cervid that is able to feed at a high level above the ground.

pects related to habitat preferences and hunting techniques: for example, the brachial and crural indexes (Fig. 5) are useful in felids to discriminate between predators that ambush and those that pursue their prey.

The species of large mammals preserved at Venta Micena can be classified in the following trophic groups, according to their craniodental and postcranial morphology:

Carnivores.—The order Carnivora is represented in the assemblage by nine species, including three felids (*Homotherium latidens*, *Megantereon whitei*, and *Lynx* aff. *issiodorensis*);

one hyenid (*P. brevirostris*); three canids (*Canis* [*Xenocyon*] *falconeri*, *Canis etruscus*, and *Vulpes praeglacialis*); one mustelid (cf. *Meles* sp.); and one ursid (*Ursus etruscus*). They can be classified in one of the following sub-categories:

1. Hypercarnivores (i.e., predators whose diet consists of >70% flesh): saber-tooths, *H. latidens* and *M. whitei*; the lynx, *L. issiodorensis*; and wild dog, *C. falconeri*.
2. Carnivores (i.e., those species in which flesh constitutes between 20% and 70% of the diet, with fruits and invertebrates mak-
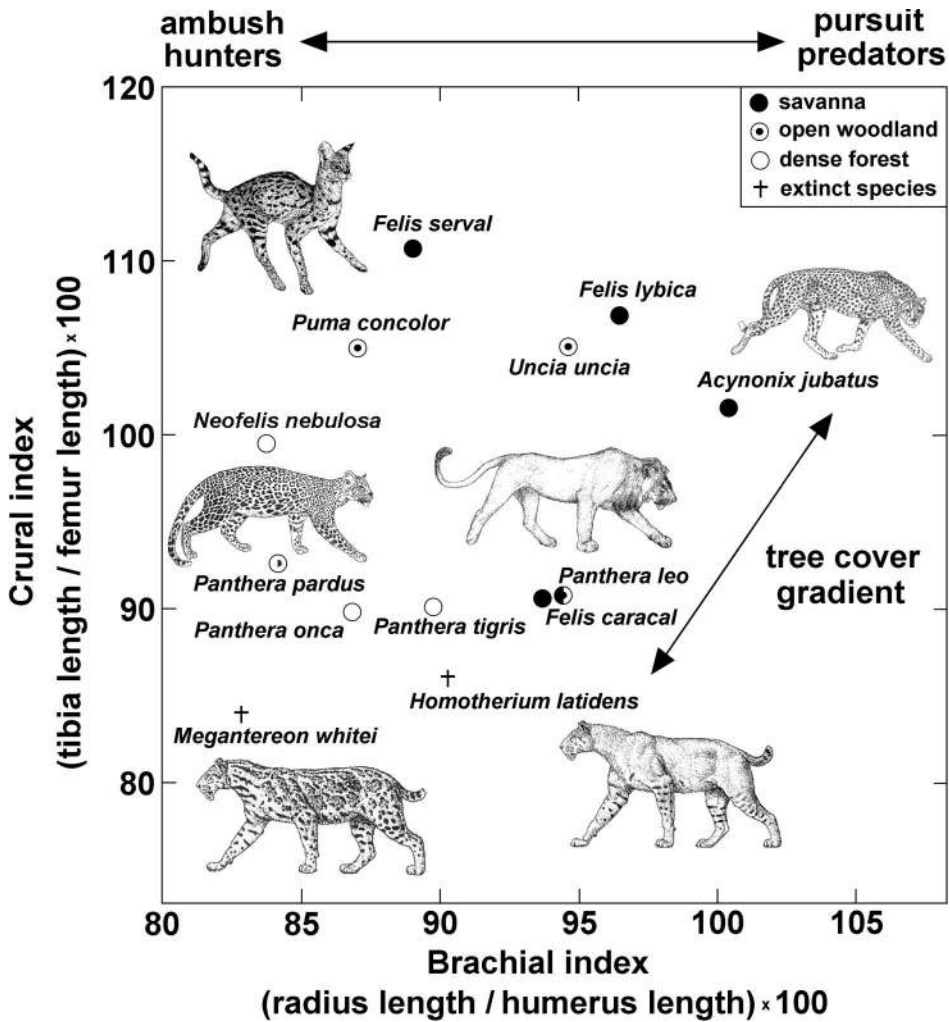
FIGURE 5. Mean values of brachial and crural indexes in several species of extant felids (data from Gonyea 1976 and Anyonge 1996) and in the saber-tooth species preserved in Venta Micena. The value for *H. latidens* is the mean obtained by averaging unpublished length measurements of major limb bones from the early Pleistocene site at Incarcal (kindly provided by A. Galobart) and those published for the North American species *H. serum* (Rawn-Schatzinger 1992). Given the absence of at least one complete radius and tibia of *M. whitei*, the means of the values estimated in *M. cultridens* (Lewis 1997) and in the closely related genus *Smilodon* (Gonyea 1976) were used. The brachial index is positively correlated in modern felids with their cursorial abilities, and the values obtained in both indexes are useful to describe the transition from closed environments, with dense tree cover, to open habitats.

ing up the balance): small-to-medium-sized canids, *C. etruscus* and *V. praeglacialis*.
3. Bone crackers (i.e., species that fracture bones for access to their marrow content): the hyena, *P. brevirostris*.
4. Omnivores (i.e., those species consuming <20% of vertebrate flesh): the ursid, *U. etruscus*, and the badger, cf. *Meles* sp.

M. whitei was a dirk-toothed machairodont with a strong body, similar in size to that of a jaguar, *Panthera onca* (Martínez-Navarro and

Palmqvist 1996). The low value estimated for the brachial index (~80%; Fig. 5) and the short metapodials indicate that it was an ambush predator, hunting in closed, forested habitats. The forelimbs are powerful, with large claws, and the upper canine teeth are extremely long, sharp, and laterally compressed (Arribas and Palmqvist 1999).

H. latidens was a scimitar-toothed cat similar in size to modern lions, *Panthera leo* (Anyonge 1993). It had small claws and elongated fore-

limbs (brachial index of ~90%; Fig. 5), which provided considerable leverage. These features suggest increased cursoriality in an open habitat (Martin et al. 2000), with less prey-grappling capability than other saber-tooths (Rawn-Schatzinger 1992). The upper canines were shorter and broader than in *Megantereon*, bearing coarse serrations in the enamel margins.

The results obtained in a comparative ecomorphological analysis of modern and Pleistocene canids (Palmqvist et al. 1999, 2002) indicate that *C. falconeri* was a hypercarnivore with a body mass of ~30 kg. The second metacarpal shows a reduced articular facet to the first metacarpal, which indicates that the latter bone was vestigial if not absent. Such condition is similar to that of the African painted dog, *Lycaon pictus*, and indicates increased cursoriality in open to intermediate forested country. *C. etruscus* was similar in size (~10 kg) and feeding habits to the modern coyote, *Canis latrans*. In this species, the trigonid blade represents <70% of the mesiodistal length of the lower carnassial, which suggests that scavenging probably represented an important fraction of its diet.

L. issiodorensis had a body mass comparable to extant *Lynx europaeus*. Given the small size of the prey hunted by modern lynxes, it is not likely that this extinct species was a predator of large mammals.

P. brevirostris was a hyena with a body and skull 10–20% larger than that of modern spotted hyenas, *Crocuta crocuta*, well-adapted for destroying carcasses and consuming bone (Palmqvist et al. 1996; Arribas and Palmqvist 1998). This giant hyena shows a relative shortening of the distal limb segments (Turner and Antón 1996), which suggests that it was less cursorial than other hyenas, although such shortening provided greater power and more stability to dismember and carry large pieces of carcasses. Several features of the dentition (e.g., the relative length of the trigonid blade in the lower carnassial) indicate that *Pachycrocuta* fed more heavily on carrion than spotted hyenas did.

The overall craniodental morphology of the etruscan bear, *U. etruscus*, is similar to that of modern brown bears, *Ursus arctos*, thus sug-

gesting that this extinct species was also omnivorous.

Herbivores.—Ungulates are represented by 11 taxa in Venta Micena, including one proboscidean (*Mammuthus meridionalis*); one hippopotamus (*Hippopotamus antiquus*); two perissodactyls (the horse, *Equus altidens*, and the rhino, *Stephanorhinus etruscus*); and seven artiodactyls (five bovids, Bovini aff. *Leptobos*, *Soergelia minor*, *Hemitragus albus*, *Praeovibos* sp., and Caprini indet.; two cervids, *Eucladoceros giulii* and *Dama* sp.). These taxa can be classified into feeding categories by using ecomorphological variables such as the hypsodonty index and the relative length of the lower premolar tooth row (Figs. 2–4).

Concerning the perissodactyls, *E. altidens* was a grazer, showing high values of both the hypsodonty index ($HI = 6.1$) and the relative lower premolar row length (~110%), similar to those of living equids (Fig. 2). This species had elongate, slender metapodials and phalanges, very similar to those of modern Grevy's zebra, *Equus grevyi*, which indicates that it was adapted to open and dry habitats (Guerrero-Alba and Palmqvist 1997). *S. etruscus* was a browser or mixed feeder with brachyodont teeth ($HI = 1.8$) and a short premolar tooth row (~82%), similar to those of modern rhinos in which grass represents <50% of the diet (Fig. 2). It was clearly not a grazer, because the white rhino, *C. simum*, the only living hypergrazing rhino, shows a hypsodonty value ($HI = 3.9$) 2.5 times greater than both *Stephanorhinus* and modern mixed feeding rhinos, and a longer premolar tooth row (~118%). The Etruscan rhino presumably inhabited open to mid-covered habitats, as suggested by its slender metapodials.

Within the artiodactyls, the goat *H. albus* ($HI = 4.4$) and the bison Bovini aff. *Leptobos* ($HI = 3.9$) were presumably grazers or mixed feeders dwelling in unforested habitats, as deduced from their comparatively high hypsodonty values (Fig. 3), which are similar to those of modern grazing ($HI = 3.8–6.1$) and mixed feeding ruminants ($HI = 2.5–5.3$) from open habitats (range of values for extant bovids estimated from data in Mendoza et al. 2002). *S. minor* shows intermediate values in both the hypsodonty index ($HI = 2.9$) and the

lower premolar row length, indicative of mixed feeding habits (Fig. 3). The dentition of the giant deer, *E. giulii*, shows a very low value of hypsodonty ($HI = 1.6$). A comparison with hypsodonty data in modern deer (Fig. 4) suggests that it was a mixed feeder from closed habitats ($HI = 1.1$–2.8) or more probably a browser ($HI = 1.2$–1.6 [values from Mendoza et al. 2002]). The fallow deer, *Dama* sp., was a mixed feeder, judging from its moderately hypsodont teeth ($HI = 1.7$) and diet of its closest living relative, *Dama dama*. Of relevance to *H. antiquus*, modern hippos are basically fresh-grass grazers, although Bocherens et al. (1996) reported carbon isotope values unusual for a diet on terrestrial C_4 grasses in Pleistocene hippos from localities in North and East Africa, which suggests that they fed predominantly on aquatic vegetation.

The proboscidean, *M. meridionalis*, was a browser or mixed feeder like modern African elephants, *Loxodonta africana*, which consume on average 20% grass and 80% leaves, although grass was probably a more significant component of diet in *Mammuthus* according to carbon isotopes of tooth enamel (Cerling et al. 1999).

Biogeochemical Analyses: Stable-Isotope Ratios

Biogeochemical techniques have proved extremely useful in determining the dietary niche of fossil mammalian species, and in providing detailed environmental reconstructions (see reviews and references in Bocherens et al. 1996; Gröcke 1997a; Koch 1998; and MacFadden 2000). We analyzed carbon, nitrogen, and oxygen isotope content of collagen material and hydroxylapatite from bone and tooth enamel of large mammals preserved in Venta Micena to determine dietary niches and trophic relationships, following the methodology described by Gröcke (1997a).

Stable isotopes are useful as paleobiological and paleoclimatological tracers because, as a result of mass differences, different isotope ratios of an element (e.g., ^{12}C vs. ^{13}C, ^{14}N vs. ^{15}N, ^{16}O vs. ^{18}O) have different thermodynamic and kinetic properties. For elements with an atomic mass of <40, these differences can lead to measurable isotopic partitioning between substances during physical and chemical processes that labels the substances with distinct isotopic ratios. Natural fractionations are small, so isotopic ratios are reported as parts per thousand (‰) deviation in isotope ratio from a standard, using the δ notation, where $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, with $X = C$, N, or O, and $R = {}^{13}C/{}^{12}C$, $^{15}N/{}^{14}N$, or $^{18}O/{}^{16}O$. R_{sample} and $R_{standard}$ are the high-mass to low-mass isotope ratios of the sample and the standard, respectively: commonly used standards for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{18}O$ are Peedee belemnite (PDB), atmospheric N_2, and standard mean ocean water (SMOW), respectively. Positive δ values indicate enrichment in the high-mass isotope relative to the standard, whereas negative values indicate depletion.

Terrestrial plants can be divided into three main groups on the basis of their photosynthetic pathway (Edwards and Walker 1983): (1) C_3 plants, which follow the Calvin-Benson cycle, fixing atmospheric CO_2 directly through the reductive pentose phosphate pathway; (2) C_4 plants, which use the Hatch-Slack cycle (C_4-dicarboxylic acid pathway); and (3) CAM (crassulacean acid metabolism) plants. C_3 plants are all trees, temperate shrubs, and grasses of cool/moist climates and high altitudes. Most C_4 plants are herbaceous, tropical, arid-adapted grasses and warm/dry herbs. Succulent or CAM plants use an intermediate C_3/C_4 photosynthetic pathway, which is modified in response to environmental changes.

All plants take up $^{12}CO_2$ in preference to $^{13}CO_2$, but there are important differences in their isotopic composition related to their carboxylating enzymes. C_3 plants use the ribulose 1,5-biphosphate carboxylase, which discriminates effectively against $^{13}CO_2$, producing a depletion of -19.5‰. Given that the mean $\delta^{13}C$ value of atmospheric CO_2 is -6.5‰ (Koch 1998), C_3 plants show an average $\delta^{13}C$ value of -26 ± 2‰, with a range from -34‰ in dense forests to -21‰ in open areas exposed to water stress. C_4 plants use the phosphoenolpyruvate carboxylase, which is less effective at discriminating against $^{13}CO_2$, and produces a depletion of only -5.5‰. As a consequence, C_4 plants have an average $\delta^{13}C$ value of -12 ± 1‰, with a more restricted isotopic range from -15‰ to -7‰. CAM

plants are capable of fixing carbon with either photosynthetic pathway and therefore display $\delta^{13}C_{plant}$ values covering the range for C_3 and C_4 plants (see reviews and references in Smith and Epstein 1971; Bocherens et al. 1996; Gröcke 1997a,b; 1998; Ehleringer et al. 1997; Collatz et al. 1998; Zazzo et al. 2000; Freeman and Colarusso 2001; and Franz-Odendaal et al. 2002).

When a plant is consumed by a herbivore, the plant's carbon is incorporated into the animal's skeletal tissues with some additional fractionation. The difference between the $\delta^{13}C$ value of the animal's diet and that subsequently incorporated into collagen translates into an increase in $\delta^{13}C_{collagen}$ per trophic level from +3‰ to +5‰. This implies that a mammal consuming C_3 vegetation (i.e., fruits, leaves, and roots of trees and bushes) will record an average $\delta^{13}C_{collagen}$ value of −22‰ (range: −30‰ to −17‰), whereas a herbivore feeding on C_4 plants (i.e., tropical grass blades, seeds and roots) will exhibit a value around −8‰ (range: −11‰ to −3‰). The $\delta^{13}C_{collagen}$ enrichment is similar for carnivores: a predator consuming C_3-browsing ungulates will record an average $\delta^{13}C_{collagen}$ value of −18‰, whereas a carnivore that consumes C_4-grazers will show a value close to −4‰ (DeNiro and Epstein 1978; Van der Merwe 1982; Klepinger and Mintel 1986; Gröcke 1997a,b; Koch 1998). Isotope variability among mammals is not solely a result of diet, however: for example, recycling of CO_2 in closed forests (i.e., canopy effect) causes a shift to more negative $\delta^{13}C_{plant}$ values and, thus, in the collagen and hydroxylapatite of those browsing herbivores consuming such plants.

The $\delta^{13}C$ value of herbivore hydroxylapatite is also enriched with respect to that of the animal's diet. $\delta^{13}C_{hydroxyl}$ ranges from +9‰ to +14‰ for wild ungulates, but the precise enrichment value probably varies among species because of differences in digestive physiology (Cerling and Sharp 1996; Koch 1998). For medium- to large-bodied mammals, the enrichment is ∼+14‰ (Cerling and Harris 1999; Feranec and MacFadden 2000; Zazzo et al. 2000). Therefore, a continuous range of $\delta^{13}C_{hydroxyl}$ values is observed for mammalian herbivores, ranging from −16‰ for C_3 brows-

ers in humid, closed-canopy conditions to as high as +3‰ for hypergrazers. Intermediate $\delta^{13}C_{hydroxyl}$ values are observed for mixed C_3/C_4 feeders. A cut-off $\delta^{13}C_{hydroxyl}$ value of −8‰ has been proposed to identify pure C_3 feeders. $\delta^{13}C_{hydroxyl}$ values for a pure C_4 diet are located between −2‰ and +3‰ (Lee-Thorp et al. 1989; MacFadden and Cerling 1996; Cerling et al. 1997a,b, 1999; Cerling and Harris 1999).

The $\delta^{15}N$ composition of collagen in mammals records their position within the energetic pyramid, because each trophic level above herbivore is indicated by an increase in $\delta^{15}N_{collagen}$ between +1‰ and +6‰ (average ∼3.4‰ [Robinson 2001]). For herbivores, the primary factors that affect the $\delta^{15}N$ value expressed in collagen are (1) soil synthesis of nitrogen, (2) the diet of the animal (i.e., if it consumes N_2-fixing or non-N_2-fixing plants), and (3) nitrogen metabolism in that animal (Koch 1998). Herbivores from forests generally exhibit lower $\delta^{15}N_{collagen}$ values than herbivores from grassland environments as a consequence of soil acidity in densely forested habitats (Rodière et al. 1996; Gröcke et al. 1997). Plants that fix nitrogen have $\delta^{15}N$ values that cluster close to the atmospheric N_2 value of 0‰, whereas those that do not fix nitrogen and use other sources (e.g., soil NH_4^+ and NO_3^-) usually show a wider range of $\delta^{15}N_{plant}$ values (Robinson 2001). As a result, animals consuming N_2-fixing plants exhibit $\delta^{15}N_{collagen}$ values between 0‰ and +4‰, whereas herbivores feeding on non-N_2-fixing plants record $\delta^{15}N_{collagen}$ values between +2‰ and +8‰. The $\delta^{15}N$ value of plants near marine and/or salt-affected areas is also enriched, reflecting the higher ^{15}N content of soil nitrate and ammonium in saline environments (Sealy et al. 1987; Matheus 1995; Koch 1998).

The effect of nitrogen metabolism in animals is also very important. The higher $\delta^{15}N_{collagen}$ values observed in animals inhabiting arid regions result from differences in nitrogen recycling and/or urea loss associated with adaptations for drought tolerance (Ambrose and DeNiro 1986a,b; Gröcke 1997a; Gröcke et al. 1997; Koch 1998; Schwarcz et al. 1999): in arid regions, the diets of herbivores are low in protein content and the animals are more dependent on recycling their urea to

conserve nitrogen; in such conditions, herbivores concentrate urine and excrete concentrated urea depleted in ^{15}N relative to diet, subsequently causing elevated $\delta^{15}N$ values. Similarly, the isotopic signature in cave bears has been related to the physiology of dormancy: higher $\delta^{15}N_{collagen}$ values are recorded in those sites corresponding to colder periods, owing to the reuse of urea in synthesizing amino acids during prolonged periods of dormancy (Nelson et al. 1998; Fernández-Mosquera et al. 2001). In general, $\delta^{15}N_{collagen}$ values are higher in large monogastric herbivores than in ruminants (Gröcke and Bocherens 1996). Elevated nitrogen isotope levels, however, may also indicate either advanced age or young suckling animals. Such an elevation, caused by excretion of concentrated urea or by ingestion of nutrient-enriched milk, respectively, can cause an apparent increase in that animal's trophic level by one (Minagawa and Wada 1984; Nelson et al. 1998; Witt and Ayliffe 2001).

Oxygen isotope ratios reflect prevailing climatic conditions (e.g., paleotemperature), but for a local fauna they also can be used to interpret the dietary water source (Ayliffe et al. 1992; Kohn et al. 1996; Sponheimer and Lee-Thorp 2001; Harris and Cerling 2002). $\delta^{18}O_{hydroxyl}$ parallels the $\delta^{18}O$ of body water, whose composition is related to three major oxygen sources: air oxygen, drinking water, and food. Although the oxygen isotope composition of air is the same worldwide and local water compositions show limited variability, diet and physiology differ among animals. The $\delta^{18}O$ is more positive in plants than in their source water, which is derived from local rain. Thus, among sympatric herbivorous mammals a more positive result would indicate that the species is obtaining most of its water requirements from the vegetation that it eats rather than from drinking. This depends on the digestive physiology of ungulates and on the water content of their food, which represents only 5% of dry grass but may reach up to 70% of succulent forage.

Use of stable isotopes to reconstruct animal diets was first demonstrated with collagen (DeNiro and Epstein 1978). More recently, it was shown that tooth enamel is a faithful re-

corder of diets in the geological record (see reviews in Cerling and Harris 1999 and in Sponheimer and Lee-Thorp 1999a,b). Carbon and nitrogen isotope ratios in bone collagen are indicative of overall diet during the last few years of an animal's life. The information obtained from enamel isotopes is more limited, as it only records the dietary preference of the animal during the time the teeth were formed (in large mammals, around 1.5 years from birth). Moreover, retrieval of environmental information from isotopic ratios in collagen, bone carbonate, and enamel is further complicated by potential diagenetic overprinting. Tooth enamel is much less porous than bone and dentine, and it has greater inorganic content, density, and crystallinity. For these reasons, enamel is less susceptible to diagenetic change, reflecting more closely the original abundance of trace elements and stable isotopes. Similarly, cortical bone is less prone to diagenetic contamination than porous, cancellous bone tissue. Because the mineral in bones and teeth, carbonate hydroxylapatite, survives much longer than protein, most isotope analyses have been performed in enamel and bone hydroxylapatite (see review in Sponheimer et al. 1999).

Several methods are available to identify alteration of collagen, including analysis of C:N ratios and amino acid composition (DeNiro and Epstein 1978; Gröcke 1997a; Richards et al. 2000). The acceptable values for the C:N ratio are between 2.9 and 3.6. This C:N ratio criterion allows for the identification and exclusion of collagen that is heavily degraded and/or contaminated. There are no equivalent criteria for integrity of stable isotope measurements of bioapatite in bone mineral and enamel, and appropriate monitors of its isotopic integrity are yet to be developed.

Biogeochemical Analyses: Trace Element Ratios

In both fresh and fossil bones the hydroxylapatite is far from being chemically pure; rather it is substituted with small amounts of carbonate, citrate, and a host of minor and trace elements. Interest in them stems from the fact that their concentration in bone reflects dietary intakes. Among the different elements,

TABLE 2. Relative abundance of carbon, oxygen, and nitrogen isotope ratios ($\delta^{13}C$, $\delta^{18}O$, and $\delta^{15}N$, expressed in ‰) in carbonate hydroxylapatite and collagen material extracted from bone (b) and tooth (t) samples collected in large mammals species from Venta Micena. The relative abundance of strontium vs. zinc is shown. Asterisk indicates skeletal remains from juvenile individuals (i.e, limb bone with unfused epiphyses or milk tooth). Means for species (± one standard deviation for those in which at least three estimates were available) are also provided.

Species	Sample	$\delta^{13}C_{hydroxyl}$	$\delta^{18}O_{hydroxyl}$	$\delta^{13}C_{collagen}$	$\delta^{15}N_{collagen}$	C:N$_{collagen}$	Sr:Zn
Mammuthus meridionalis	VM-4439 (b)*	−7.1	−4.5	−21.4	+4.7	3.1	27.8
Mammuthus meridionalis	VM-OX1 (t)*	−7.0	−3.9	—	—	—	—
Mammuthus meridionalis	VM-3581 (b)	−6.2	−2.8	−20.6	+2.9	3.3	70.1
Mean for *Mammuthus*		−6.77 (±0.49)	−3.73 (±0.86)	−21.0	+3.8	3.2	48.95
Hippopotamus antiquus	VM-4123 (b)	−6.4	−2.1	−22.3	+7.7	3.5	—
Hippopotamus antiquus	VM-OX6 (t)	−7.8	−5.8	—	—	—	—
Hippopotamus antiquus	VM-4299 (b)	−6.9	−3.7	−22.6	+7.4	3.4	55.6
Mean for *Hippopotamus*		−7.03 (±0.24)	−3.87 (±0.62)	−22.45	+7.55	3.45	55.6
Bovini aff. *Leptobos*	VM-3473 (b)	−7.3	−2.2	−22.1	+3.8	3.1	64.4
Bovini aff. *Leptobos*	VM-3503 (b)	−6.4	−4.1	−21.5	+3.6	3.3	61.2
Bovini aff. *Leptobos*	VM-4185 (b)	−7.0	−2.8	—	—	—	66.6
Bovini aff. *Leptobos*	VM-4444 (b)	−8.7	−3.1	—	—	—	62.9
Bovini aff. *Leptobos*	VM-OX7 (t)	−7.7	−5.2	—	—	—	—
Bovini aff. *Leptobos*	VM-3583 (b)	−7.6	−3.7	—	—	—	65.3
Bovini aff. *Leptobos*	VM-3473 (b)	−6.9	−3.2	−21.4	+3.5	3.3	62.8
Bovini aff. *Leptobos*	VM-544 (b)	−8.2	−4.3	−21.8	+4.0	3.4	63.6
Bovini aff. *Leptobos*	VM-4164 (b)	−7.7	−3.3	—	—	—	64.1
Mean for Bovini aff. *Leptobos*		−7.50 (±0.70)	−3.54 (±0.89)	−21.70 (±0.32)	+3.73 (±0.22)	3.28 (±0.13)	63.86 (±1.65)
Soergelia minor	VM-3448 (b)	−8.2	−2.7	—	—	—	62.8
Soergelia minor	VM-3867a (b)	−8.3	−2.1	−23.2	+3.2	3.4	64.2
Soergelia minor	VM-3867b (b)	−8.5	−2.3	−23.5	+3.4	3.5	65.6
Soergelia minor	VM-OX10 (t)	−8.1	−2.6	—	—	—	—
Soergelia minor	VM-3982 (b)	−8.7	−2.7	−23.0	+3.8	3.3	63.3
Mean for *Soergelia*		−8.36 (±0.24)	−2.48 (±0.27)	−23.23 (±0.25)	+3.47 (±0.31)	3.40 (±0.10)	63.98 (±1.23)
Hemitragus albus	VM-3802 (b)	−5.9	−3.4	−20.9	+4.0	3.3	53.9
Hemitragus albus	VM-3922 (b)	−7.3	−1.5	−20.1	+3.9	3.4	58.0
Hemitragus albus	VM-OX11 (t)	−5.9	−3.3	—	—	—	—
Hemitragus albus	VM-3157 (b)	−6.8	−2.1	—	—	—	55.5
Hemitragus albus	VM-3449 (b)	−6.3	−2.9	−20.4	+3.7	3.5	56.4
Mean for *Hemitragus*		−6.44 (±0.61)	−2.64 (±0.82)	−20.47 (±0.40)	+3.87 (±0.15)	3.40 (±0.10)	55.95 (±1.71)
Eucladoceros giulii	VM-3297 (b)	−7.4	−3.3	−25.9	+1.6	3.2	96.9
Eucladoceros giulii	VM-4155 (b)	−7.1	−2.8	—	—	—	89.9
Eucladoceros giulii	VM-3111 (b)	−6.7	−4.0	—	—	—	—
Eucladoceros giulii	VM-3556 (b)	−6.3	−4.2	−25.6	+1.3	3.6	—
Eucladoceros giulii	VM-OX8 (t)	−8.3	−4.6	—	—	—	—
Eucladoceros giulii	VM-4181 (b)	−7.0	−3.7	−25.4	+1.8	3.4	91.2
Eucladoceros giulii	VM-3111 (b)	−6.2	−3.9	—	—	—	93.2

TABLE 2. Continued.

Species	Sample	δ¹³C$_{hydroxyl}$	δ¹⁸O$_{hydroxyl}$	δ¹³C$_{collagen}$	δ¹⁵N$_{collagen}$	C:N$_{collagen}$	Sr:Zn
Eucladoceros giulii	VM-3124 (b)	−7.5	−3.1	−25.8	+1.4	3.5	—
Eucladoceros giulii	VM-3780 (b)	−6.7	−4.0	—	—	94.1	—
Mean for *Eucladoceros*		−7.02 (±0.65)	−3.73 (±0.57)	−25.68 (+0.22)	+1.53 (±0.22)	3.43 (±0.17)	93.06 (±2.71)
Dama sp.	VM-3055 (b)	−6.6	−3.2	—	—	—	68.1
Dama sp.	VM-3482 (b)	−6.9	−2.6	−23.6	+2.5	3.5	67.2
Dama sp.	VM-4330 (b)	−7.9	−2.4	—	—	—	65.7
Dama sp.	VM-OX9 (t)	−7.0	−2.6	—	—	—	—
Dama sp.	VM-4410 (b)	−7.5	−2.9	—	—	—	64.9
Dama sp.	VM-3047 (b)	−7.1	−3.0	−23.8	+2.9	3.3	67.8
Dama sp.	VM-3060 (b)	−7.8	−2.5	−23.2	+2.6	3.4	66.2
Mean for *Dama*		−7.26 (±0.49)	−2.74 (±0.29)	−23.53 (±0.31)	+2.67 (±0.21)	3.40 (±0.10)	67.0 (±0.7)
Equus altidens	VM-3028 (b)	−7.0	−2.5	−26.1	+2.0	3.2	78.2
Equus altidens	VM-3119 (b)	−8.6	−2.8	−26.7	+3.5	3.6	78.2
Equus altidens	VM-3162 (b)	−7.3	−3.0	−26.0	+3.0	3.5	82.4
Equus altidens	VM-3258 (b)	−8.1	−2.9	—	—	—	70.7
Equus altidens	VM-3430 (b)	−6.8	−2.3	—	—	—	78.2
Equus altidens	VM-3529 (b)	−6.9	−3.3	−26.0	+3.3	3.4	89.9
Equus altidens	VM-4189 (b)	−8.2	−2.3	−25.5	+3.5	3.5	73.1
Equus altidens	VM-4421 (b)	−8.7	−3.8	−25.0	+2.1	3.4	73.5
Equus altidens	VM-OX2 (t)	−7.2	−3.4	—	—	—	—
Equus altidens	VM-OX3 (t)	−7.5	−5.2	—	—	—	—
Equus altidens	VM-3089 (b)	−7.7	−3.5	—	—	—	72.6
Equus altidens	VM-4421 (b)	−7.1	−3.9	−25.8	+2.8	3.4	78.4
Equus altidens	VM-3279 (b)	−8.2	−4.3	−26.6	+3.1	3.5	82.5
Equus altidens	VM-3428 (b)	−7.6	−2.8	—	—	—	80.1
Mean for *Equus*		−7.64 (±0.63)	−3.29 (±0.82)	−25.96 (±0.55)	+2.91 (±0.58)	3.44 (±0.12)	78.15 (±5.59)
Stephanorhinus etruscus	VM-3578 (b)	−6.9	−4.6	—	—	—	86.9
Stephanorhinus etruscus	VM-4487 (b)	−7.6	−3.7	−26.5	+3.9	3.5	91.9
Stephanorhinus etruscus	VM-4510 (b)	−7.5	−3.7	−26.6	+3.7	3.3	89.3
Stephanorhinus etruscus	VM-OX4 (t)	−9.4	−3.7	—	—	—	—
Stephanorhinus etruscus	VM-OX5 (t)	−8.0	−5.1	—	—	—	—
Stephanorhinus etruscus	VM-3610 (b)	−7.8	−4.2	−26.2	+3.5	3.3	87.3
Stephanorhinus etruscus	VM-3578 (b)	−7.5	−4.8	—	—	—	90.8
Mean for *Stephanorhinus*		−7.81 (±0.78)	−4.26 (±0.59)	−26.43 (±0.21)	+3.70 (±0.20)	3.37 (±0.12)	89.24 (±2.17)
Homotherium latidens	VM-4340 (b)	−8.3	−3.7	−21.7	+6.8	3.4	41.3
Megantereon whitei	VM-3301 (b)	−8.1	−4.2	−25.2	+5.8	3.5	45.8
Pachycrocuta brevirostris	VM-2226 (b)	−6.8	−4.0	−22.5	+6.1	3.4	45.5
Canis falconeri	VM-2261 (b)	−7.6	−4.8	−22.7	+6.5	3.5	48.2
Canis etruscus	VM-2254 (b)	−7.2	−4.8	−23.5	+5.3	3.6	51.9
Ursus etruscus	VM-1172 (b)	−4.9	−3.3	—	—	—	—

strontium and zinc have proven particularly useful as indicators of paleodietary niches (Toots and Voorhies 1965; Wyckoff and Doberenz 1967; Sillen and Kavanagh 1982; Klepinger 1984; Nedin 1991). We analyzed the abundance of strontium and zinc in the bone tissue of large mammals from Venta Micena with inductively coupled plasma atomic emission spectrometry at Royal Holloway University of London. This was done on the resultant supernatant from collagen extraction, evaporated to incipient dryness and re-dissolved in 40 mL of 3M HCl. Triplicate analyses resulted in an internal error of <10%.

Strontium shares many chemical properties with calcium, including partial replacement of calcium in the metabolic processes of plants and animals. Strontium levels in bone are a consequence of strontium levels in the soil and of biological factors (Toots and Voorhies 1965). Plants incorporate strontium in place of calcium but the amount is determined by the relative abundance of these elements in the soil. However, different kinds and even different parts of plants vary in strontium content: tree and bush leaves as well as the exposed parts of succulent herbaceous vegetation are usually enriched, whereas grass leaves and roots of trees, bushes and grasses appear to be depleted (Bowen and Dymond 1955). Animals incorporate elements differentially; they discriminate against strontium, and as a result the proportion of Sr:Ca in the tissues and organs of herbivores is 50–80% less than the levels in the plants that are ingested (Kshirasagar et al. 1966; Schoeninger 1979). Uptake in carnivores also discriminates against the strontium content of the flesh consumed. The proportion of Sr:Ca is thus useful for discriminating between plant-eating, primary consumers and flesh-eating, secondary consumers, because this proportion is a function of the initial intake (Richards et al. 2000; Balter et al. 2001). Similarly, strontium levels discriminate between browsing, leaf-eating herbivores and grazing herbivores, with the former showing higher contents in their bones. Strontium levels also allow identification of specific predator-prey pairs; the Sr:Ca ratio of the carnivore is 50–80% less than that of its prey (Toots and

Voorhies 1965; Sillen 1986, 1992; Grupe and Krüger 1990; Sillen and Lee-Thorp 1994).

Strontium values can be used to determine paleodiet provided the following conditions are met: (1) only bones from the same locality are compared, because trace element abundance depends heavily on the geochemistry of the soil, which varies greatly between localities; (2) only adult bones are used, because juveniles show markedly reduced bone strontium levels owing to the very small amounts of strontium in mammalian milk; (3) teeth and ribs are discarded from the analysis, because strontium levels in teeth do not change during growth and ribs, which are more metabolically active than other bones, are prone to short-term resetting, especially in lactating females; (4) more than one species should be used for comparison; and (5) there is no evidence of diagenetic alteration (Toots and Voorhies 1965; Nedin 1991; Sillen 1992; Sillen and Lee-Thorp 1994).

Relative levels of zinc and strontium in bone have also been used as a tool for predicting paleodietary niches (Nedin 1991). However, in contrast to strontium, zinc levels increase through the food chain; carnivores have higher concentrations than herbivores because zinc levels in blood and flesh are higher than in plants (Elias et al. 1982).

Paleodietary Inferences

Table 2 shows $\delta^{13}C_{hydroxyl}$, $\delta^{18}O_{hydroxyl}$, and Sr:Zn values measured in bone and enamel obtained from fossil mammals preserved at Venta Micena ($n = 68$). Collagen, preserved in only 37 out of 57 bone samples analyzed, provided $\delta^{13}C_{collagen}$ and $\delta^{15}N_{collagen}$ values. The precision for stable-isotope analysis was <0.1‰ for both carbon and oxygen, and <0.2‰ for nitrogen. C:N ratios of the collagen material extracted averaged 3.4, and the amino acid composition from four specimens is similar to that of bone collagen in modern mammals, indicating good preservation (Fig. 6).

The recovery of collagen in fossils older than one million years is not rare, and high amino acid concentrations have been found in fossils from Cretaceous–Pleistocene samples (Wyckoff 1972; Ostrom et al. 1994), although
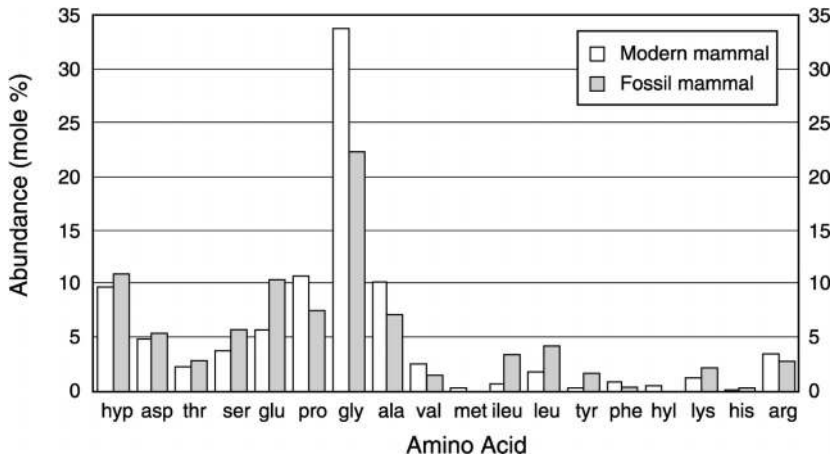
FIGURE 6. Amino acid spectra of the modern Tammar Wallaby (*Macropus eugenii*) (Gröcke 1997a) and the average amino acid abundance (hyp = hydroxyproline; asp = aspartic acid; thr = threonine; ser = serine; glu = glutamic acid; pro = proline; gly = glycine; ala = alanine; val = valine; met = methionine; ileu = isoleucine; leu = leucine; tyr = tyrosine; phe = phenylalanine; hyl = hydroxylysine; lys = lysine; his = histidine; arg = arginine) of four herbivore specimens from Venta Micena (VM-3473, VM-3867b, VM-3297, VM-3047). The similarity in composition of extant and extinct specimens indicates that the bone collagen preserved in the fossils was not altered during diagenesis.

as noted above a number of specimens analyzed here yielded no collagen. Other fossil proteins (e.g., albumin and immunoglobulin) have been detected in fossil samples from Venta Micena with immunological techniques (Torres et al. 2002). We have some reservations concerning the isotopic signature recorded in the bone apatite samples, however, because a previous geochemical study (Arribas and Palmqvist 1998) showed that in several fossils a fraction of the original hydroxylapatite was replaced during diagenesis by other mineral phases. Therefore, the following discussion of carbon isotopes focuses on the analysis of collagen.

Carbon Isotope Ratios.—Figure 7 shows a range of $\delta^{13}C_{collagen}$ values from $-20‰$ to $-27‰$ for large mammal species preserved at Venta Micena, which agrees well with that of modern mammals eating C_3 plants. This indicates that C_4 grasses were not a major constituent of the plant ecosystem in southern Spain during early Pleistocene times. In fact, C_4 plants are poorly represented today in the vegetation of this semi-desert Mediterranean region, constituting only ~5% of grass species (Sagredo 1987) and representing <1% of total plant biomass; their growth (from April to September) reflects a marked seasonality (J. M. Nieto personal communication 2002). Sim-

ilar results were reported by Bocherens et al. (1996) and Franz-Odendaal et al. (2002) in the isotopic analyses of terrestrial mammals from the early–middle Pleistocene site at Tighenif, Algeria, and from the early Pliocene site at Langebaanweg, South Africa, respectively. In both localities all ungulate species showed $\delta^{13}C_{enamel}$ values exclusive of a diet of C_3 plants.

The inferences that can be drawn from $\delta^{13}C_{collagen}$ values are complicated by physiological factors. According to the hypsodonty index, the Venta Micena perissodactyls include one grazing species with high-crowned molars, the horse *E. altidens*, and another that was clearly a mixed feeder or browser given its low hypsodonty, the Etruscan rhino, *S. etruscus*. Thus, the similarity in the $\delta^{13}C_{collagen}$ values shown by both monogastric herbivores (Fig. 7) does not indicate either a similarity in their feeding requirements or differences with those of other ungulates that show higher $^{13}C/^{12}C$ ratios. A *t*-test indicates that the difference between the mean $\delta^{13}C_{collagen}$ values for perissodactyls ($-26.09‰ \pm 0.52‰$, $n = 11$) and artiodactyls ($-22.95‰ \pm 1.78‰$, $n = 19$) is statistically significant (one-tailed test, adjusted for small sample size: $t = 6.23$, $p < 0.001$). This difference may owe to the fact that perissodactyls, being hindgut fermenters, are less metabolically efficient for the extraction of nu-
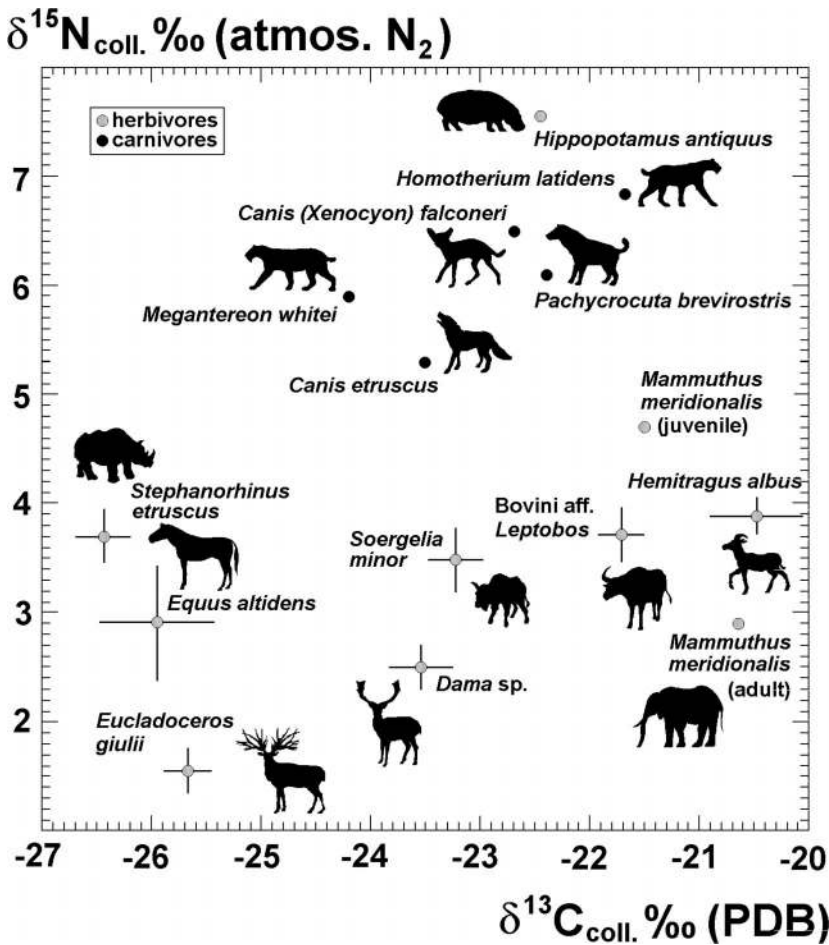
FIGURE 7.   δ¹³C and δ¹⁵N values of collagen material extracted from bone samples of those species of large mammals preserved in the lower Pleistocene site at Venta Micena. The lines represent one standard deviation around the mean for those species in which three or more measurements of stable isotopes were available (data from Table 2).

trients from plant foods (~70% on average) than ruminants, which are foregut fermenters (Janis 1976; Janis et al. 1994). Of interest to this study, Cerling and Harris (1999) found that Burchell's zebras, whose diet is composed of 100% grass, are consistently 1–2‰ depleted in δ¹³C values for tooth enamel as compared with sympatric ruminant hypergrazers such as alcelaphine bovids (e.g., buffalo, wildebeest, hartebeest, and topi) from Kenya, thus implying a lower isotope enrichment factor for zebras. A similar difference was detected by Lee-Thorp and Van der Merwe (1987) in bone hydroxylapatite between zebra and wildebeest. The higher isotope enrichment of ruminants is probably related to their higher rates of methane production (six times, on average) than those of non-ruminant ungulates (Crutzen et al. 1986), because ruminant methane has very negative δ¹³C values (Metges et al. 1990).

The Venta Micena bovids show the highest δ¹³C_collagen levels among ruminants. The three species show hypsodonty values that are comparatively high, similar to those of modern grazing and mixed feeding ruminants from open habitats. Thus, the more positive δ¹³C_collagen values of bovids relative to those of perissodactyls (Fig. 7) probably indicate that the former predominantly fed on grass, having a greater metabolic efficiency for the assimilation of carbon. As mentioned above, the comparison of the hypsodonty values of cervids with those of modern deer suggests that

the cervids were mixed feeders or browsers from closed habitats. The difference between the mean $\delta^{13}C_{collagen}$ values for cervids ($-24.76‰ \pm 1.17‰$, $n = 7$) and bovids ($-21.79‰ \pm 1.17‰$, $n = 10$) is statistically significant according to a t-test ($t = 5.15$, $p < 0.001$). Such a difference, especially in the case of *E. giulii*, could indicate the influence of a hyperbrowsing behavior in a forested habitat and the recycling of CO_2 (i.e., the canopy effect). Alternatively, cervids may exhibit a lower metabolic efficiency to assimilate carbon (and then a lower isotope enrichment factor) than bovids, which are more advanced ruminants with a better compartmentalized stomach.

Nitrogen Isotope Ratios.—Figure 7 also shows $\delta^{15}N_{collagen}$ values for large mammals from Venta Micena. It is interesting to mention that the values recorded by all herbivore species except the hippo agree with those expected in animals consuming N_2-fixing plants. Carnivores *H. latidens*, *M. whitei*, *P. brevirostris*, *C. falconeri*, and *C. etruscus* show higher values than ungulates except in the case of *H. antiquus* and one sample of *M. meridionalis*. The isotope enrichment in carnivores (mean $\delta^{15}N_{collagen}$ for all taxa: $+6.10‰$) relative to herbivores (mean $\delta^{15}N_{collagen}$ for all taxa, excluding the hippo: $+2.94‰$) is in good accordance with the enrichment value expected from increasing one trophic level ($\sim3.4‰$), thus suggesting that the collagen extracted from the fossils did not undergo diagenetic alteration. The very high $\delta^{15}N_{collagen}$ record of *H. antiquus* probably implies that this species fed predominantly on aquatic, non-N_2-fixing plants, instead of on C_4 grasses as in the case of modern *H. amphibius*. Such a difference was also suggested by Bocherens et al. (1996) for Pleistocene hippopotami from several African localities. The elephant sample that shows a high $\delta^{15}N_{collagen}$ value was obtained from a bone specimen with unfused epiphyses, which belonged to a young individual that may still have been suckling; the other sample came from an adult individual and records a $\delta^{15}N_{collagen}$ value similar to those of other herbivores.

Interesting differences in $\delta^{15}N_{collagen}$ values among the carnivore species are probably related to specific predator-prey relationships in this paleocommunity (Palmqvist et al. 1996). The large saber-tooth, *H. latidens*, shows the highest $\delta^{15}N_{collagen}$ value and this would indicate that it was the top predator in the paleocommunity. Interestingly, the single $\delta^{15}N_{collagen}$ value available for this species (Table 2, Fig. 7) is well above that obtained for the young individual of *Mammuthus*, suggesting that juvenile elephants were an important part of the diet of this scimitar cat. The likelihood of such specialized hunting behavior is evident in the case of the related American species *H. serum*, known in high numbers from the late Pleistocene site of Friesenhahn cave, Texas. This locality is interpreted as a saber-tooth den and is associated with numerous skeletal remains of juvenile mammoths (Rawn-Schatzinger 1992; Marean and Ehrhardt 1995). *C. falconeri*, a cursorial canid that presumably hunted in an open environment, shows the second highest $\delta^{15}N_{collagen}$ value among the hypercarnivores. *M. whitei*, an ambush predator that probably inhabited forests, records the lowest $\delta^{15}N_{collagen}$ value. Such differences may indicate that these carnivores preyed upon different ungulate species, with *Megantereon* hunting browsing and mixed feeding cervids in a closed habitat, and the wild dogs focusing on grazing bovids and horses from open environments. Interestingly, the large hyena *P. brevirostris*, a species that scavenged the prey of these hypercarnivores (Arribas and Palmqvist 1998), shows an intermediate $\delta^{15}N_{collagen}$ value. Finally, the medium-sized canid *C. etruscus*, whose teeth indicate clearly a more omnivorous behavior than that of *C. falconeri*, records the lowest $\delta^{15}N_{collagen}$ value of all the carnivores.

In the case of the ungulates, the ecomorphological analyses indicated that all perissodactyl and bovid species presumably inhabited an open environment, without tree cover, a finding corroborated by differences in nitrogen isotope ratios. These species show more positive $\delta^{15}N_{collagen}$ values (mean for all samples: $+3.40‰ \pm 0.55‰$, $n = 21$) than cervids ($+2.01‰ \pm 0.64‰$, $n = 7$). Such a difference is statistically significant ($t = 4.37$; $p < 0.001$) and indicates that the latter species tended to feed in a closed habitat. The lower $\delta^{15}N_{collagen}$ values in the diet of cervids would have re-

sulted from greater soil acidity in the forest (Rodière et al. 1996; Gröcke 1997a). This is particularly the case for the megacerine deer *E. giulii*, which exhibits the lowest $\delta^{15}N_{collagen}$ values in the fauna. The high $\delta^{15}N_{collagen}$ value of *S. etruscus*, a mixed feeding or browsing rhino of open habitats, is congruent with that expected from a large monogastric herbivore (Gröcke and Bocherens 1996).

Oxygen Isotope Ratios.—Bovids *H. albus* and *S. minor* and cervid *Dama* sp. show the highest $\delta^{18}O_{hydroxyl}$ values among herbivores (Table 2). Given that the $\delta^{18}O$ value in plants is more positive than in their source water (Sponheimer and Lee-Thorp 2001; Harris and Cerling 2002), the high $\delta^{18}O_{hydroxyl}$ values of these ungulates suggest that they obtained most of their water requirements from the vegetation rather than from drinking. On the contrary, the three megaherbivores represented in the assemblage (i.e., those species with a body mass above 1000 kg), *M. meridionalis*, *H. antiquus*, and *S. etruscus*, as well as the megacerine deer *E. giulii*, exhibit the most negative $\delta^{18}O_{hydroxyl}$ values, which indicate an increased water dependence for these species. $\delta^{18}O_{hydroxyl}$ values of the equid *E. altidens* and the bison Bovini aff. *Leptobos* are intermediate but closer to those of megaherbivores and large deer, suggesting that both species had moderate water dependence. These results agree well with expectations from their living closest relatives. For example, goats are particularly well adapted for arid conditions, obtaining most of their water requirements from the vegetation eaten (Novak 1999), and this also seems to have been the case for the caprine *Hemitragus* and the ovibovine *Soergelia*, according to their high mean values of $\delta^{18}O_{hydroxyl}$. Similarly, the modern fallow deer, *D. dama*, tolerates more arid climates than the red deer, *Cervus elaphus*, showing a lower water intake rate per kg of body mass (Braza and Alvarez 1987). On the contrary, large monogastric mammals such as rhinos, hippos and elephants are obligate drinkers, with greater water requirements (Novak 1999), a characteristic that agrees well with the comparatively low $\delta^{18}O_{hydroxyl}$ values measured for fossil *Stephanorhinus*, *Hippopotamus*, and *Mammuthus*.

Trace Element Ratios.—Strontium and zinc levels also provide additional information on the diet of large mammals from Venta Micena (Table 2, Fig. 8). As expected from their higher position within the food chain, carnivores show lower Sr:Zn ratios (range = 41.3–51.9) than herbivores (53.9–96.9, excluding the juvenile elephant). This suggests that the original abundances of both trace elements in the fossil bones were not altered during the diagenesis.

Homotherium records the lowest Sr:Zn value (41.3), as expected from its hypercarnivorous diet. *Megantereon* shows a slightly higher ratio (45.8), which suggests a different habitat from that of *Homotherium* and, hence, leaf-browsing ungulates (which show higher Sr levels) as the main prey. This interpretation agrees well with the results obtained in the ecomorphological analysis, which indicate that *Homotherium* was a pursuit predator whereas *Megantereon* was an ambusher. The giant hyena *Pachycrocuta*, a bone crusher that presumably inhabited open habitats, also shows a higher Sr:Zn ratio (45.5) than *Homotherium*, as expected from its diet, which included large amounts of bone material (Palmqvist and Arribas 2001). The wild dog, *C. falconeri*, has a dentition extremely specialized for meat-slicing and records a lower Sr:Zn value (48.2) than the more omnivorous species *C. etruscus* (51.9), which shows a well-developed talonid in the lower carnassial (Palmqvist et al. 1999). Such difference indicates that in the latter species bone material, as well as fruits and insects, probably composed a greater part of the diet.

Concerning the herbivores, Sr:Zn ratios are higher in Bovini aff. *Leptobos* (mean = 63.9, range = 61.2–66.9, $n = 8$), *S. minor* (mean = 64.0, range = 62.8–65.6, $n = 4$), and *H. albus* (mean = 56.0, range = 53.9–58.0, $n = 4$) than in the carnivores. These data agree well with the ecomorphologically based paleodietary inference of a grazing niche in an open habitat for all these bovids, although it is worthy to mention that the goat, *H. albus*, records somewhat low ratios. The medium-sized cervid, *Dama* sp., shows a relatively low Sr:Zn ratio (mean = 67.0, range = 64.9–68.1, $n = 6$), but the large deer, *E. giulii*, records the highest ratio among ungulates (mean = 93.1, range = 89.9–96.9, $n = 5$), as expected from its very
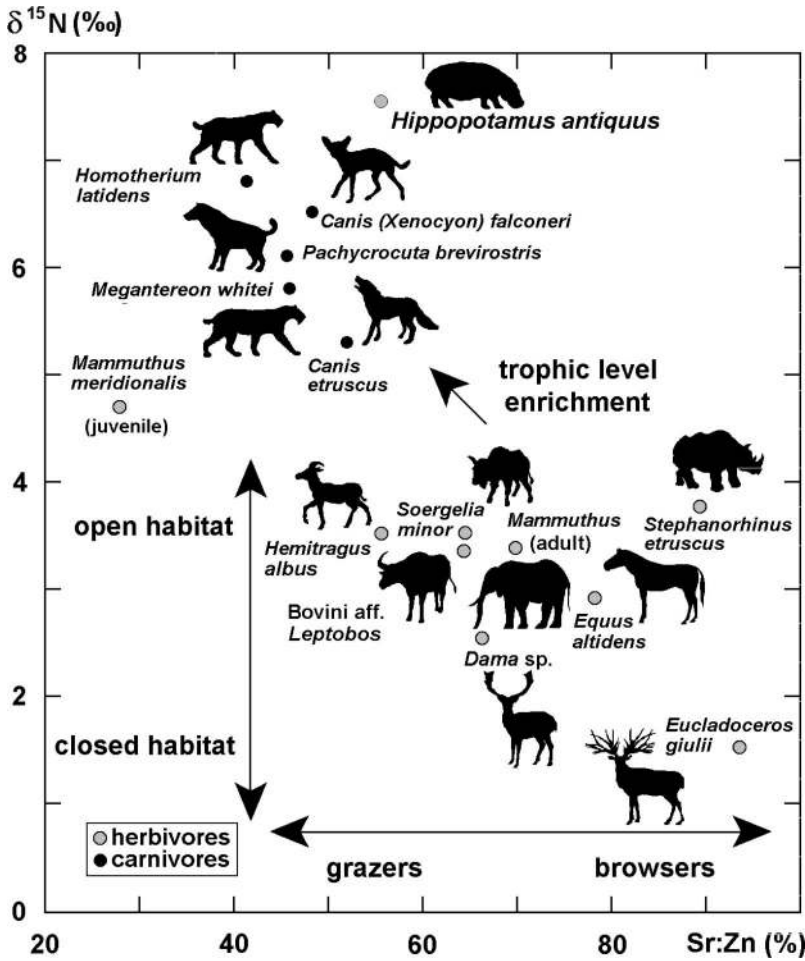
FIGURE 8. Sr:Zn abundance (%) and $\delta^{15}N$ collagen values (‰) of bone samples of large mammals preserved in Venta Micena (data from Table 2).

low hypsodonty value, similar to that of modern hyperbrowsers. Such a difference could indicate an ecological segregation between *Dama* sp. and *E. giulii*, with the former inhabiting more open habitats and feeding more grass. The high Sr:Zn ratio obtained in the case of *S. etruscus* (mean = 89.2, range = 86.9–91.9, *n* = 5) clearly indicates its browsing or mixed feeding diet, a conclusion previously inferred from the low values of the hypsodonty index and the length of the premolar tooth row. However, in the case of *E. altidens* the moderately high Sr:Zn ratio (mean = 78.2, range = 70.7–89.9, *n* = 11) could suggest that it was a mixed feeder, a conclusion that would be in clear disagreement with the grazing niche deduced from the very high hypsodonty index in this species. This discrep-

ancy could be due, perhaps, to the fact that this species had a migratory behavior, as modern zebras do, and thus moved between localities. Finally, the strikingly low Sr:Zn ratio estimated in one sample from *M. meridionalis* (27.8) may represent a young, suckling individual; the other sample analyzed, obtained from an adult elephant, records a value (70.1) in agreement with the mixed feeding diet inferred for this species (Cerling et al. 1999).

Taxon-Free Characterization of the Paleocommunity

Distribution by habitat type of large mammal species in modern African communities is shown in Figure 9. Community types were established by Reed (1998) according to the vegetation cover, and species were assigned to
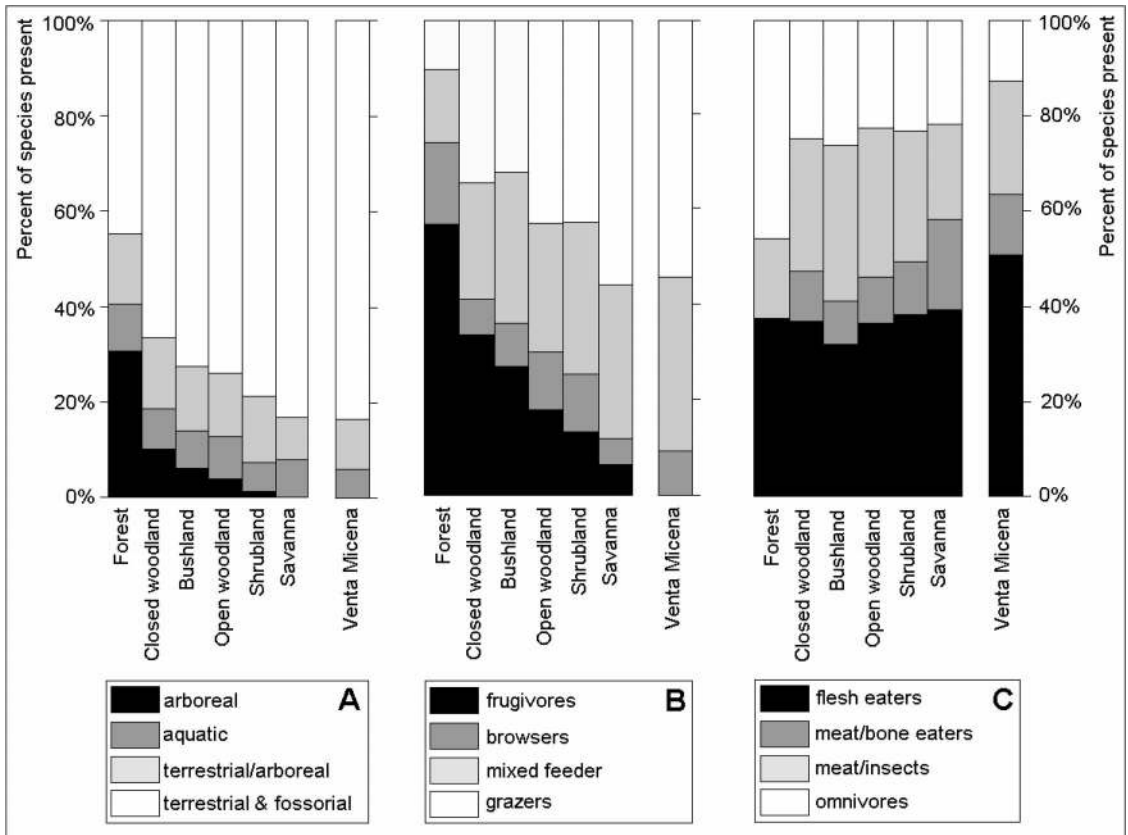
FIGURE 9. Average proportion of species of different locomotor types (A) and trophic groups (B = herbivores, C = carnivores) in several modern African communities of large mammals, established according to major vegetation types (frequencies of species estimated from data in Reed 1998). The corresponding values for the lower Pleistocene site at Venta Micena are also included (data from Table 1). Categories of vegetative habitats are broadly characterized and cluster forests (lowland rain, tropical temperate, and montane forests), closed woodlands (including woodland-bushland transition), bushlands (including medium density woodland and bushland areas), open woodlands, shrublands (including scrub woodlands), and savanna (including grasslands and plains). These habitats provide an ecological gradient from areas that are well watered throughout the year (forests) to those that are extremely dry or quite seasonal (shrublands and savannas). Deserts were not included in the analysis because Reed's sample size of this habitat type was too small. Locomotor types include species adapted to arboreal locomotion (mostly primates), aquatic habitats (e.g., the hippo), mixed terrestrial and arboreal locomotion (e.g., the saber-tooth *Megantereon*), and exclusively terrestrial (e.g., the ungulates except the hippo and most carnivores) and/or fossorial species (e.g., the badger). Feeding categories as follows: frugivores, diet >50% of fruit; browsers, >75% leaves; mixed feeders; 25–75% grass; grazers: >75% grass; flesh eaters, >70% vertebrate meat; meat/bone eaters, hyenas; meat/insects, 20–70% meat; omnivores, <20% meat.

several ecological categories by feeding behavior and locomotion, following the approach proposed by Andrews et al. (1979). The frequencies of such ecological categories in Venta Micena are also shown.

When species are grouped by type of locomotion (Fig. 9A), the relative abundance of species adapted to arboreal locomotion is positively correlated with the proportion of the habitat covered by trees and bushes. Conversely, the proportion of terrestrial species

increases as grass cover increases. The proportions of locomotor types estimated for Venta Micena, in which terrestrial species are dominant, are very similar to those in African savannas. The average frequencies of different types of primary consumers (Fig. 9B) also show a gradient from closed to open habitats. In forested environments the dominant species are frugivores (largely represented by primates) and browsing ungulates. In open habitats the most abundant species are mixed

feeders and grazers. The proportions of such trophic categories in Venta Micena are again very close to those in modern savannas, although frugivores are absent from Venta Micena. Further, the frequencies of different types of secondary consumers in Venta Micena (Fig. 9C) are similar to those shown by such ecological categories in modern savannas and shrublands. The main difference is the proportion of omnivorous species, which are represented exclusively by the bear because suids are absent from Europe during the early Pleistocene.

These results indicate that the region that surrounded the Pleistocene lake of Orce at Venta Micena was very similar to that represented in modern African savannas with tall grass and low bush/tree cover, suggesting that the countryside in the Guadix-Baza basin was relatively unforested during early Pleistocene times, as happens today.

Such reconstruction can be assessed also through an analysis of another aspect of the trophic relationships of this fauna, following the general ecological relationships between population density and body size (Damuth 1987) and between basal metabolic rate and body size (Kleiber 1932; McNab 1980). This type of approach has previously been applied to both South and North American faunas at Luján and Rancho La Brea (Fariña 1996).

All of the herbivore species found at Venta Micena were classified according to their probable diet (those species whose masses were estimated at <10 kg were not considered), and their population densities and basal metabolic rates were estimated (Table 1) according to the appropriate equations of Damuth (1987) and Peters (1983). The energy requirements for each species were obtained by multiplying its on-crop biomass by its basal metabolic rate. A typical assimilation efficiency of 50% (of the edible material) was assumed, and average actual maintenance metabolism was taken to be 2.5 times the basal rate, an average of the values given for modern species (2 to 3, according to Peters 1983). Adding up the requirements of all the herbivore species considered, and converting the units, it follows that they must have needed some 683 kJ m^{-2} year^{-1}, or 12.5 g C m^{-2} year^{-1}, in habitat primary productivity. The three megaherbivores alone account for the consumption of almost 186 kJ m^{-2} year^{-1}, or 3.4 g C m^{-2} year^{-1}.

Table 1 lists also the carnivores at Venta Micena, which range in mass from 5 kg to 375 kg. The on-crop biomass for each species was obtained by multiplying the calculated population density by its body mass. The total on-crop biomass for these carnivores was 71.1 kg km^{-2}, or 497 J m^{-2}. Adding up the requirements of all the large carnivore species, and converting the units, it follows that they must have needed about 6.6 kJ m^{-2} year^{-1} as habitat secondary productivity to sustain their basal metabolism if an assimilation efficiency of 50% was assumed (see Peters 1983). It was also assumed that the actual maintenance metabolism was 2.5 times as high as the basal rate. Therefore, the energy required to carry their maintenance metabolism was about 16.5 kJ m^{-2} year^{-1}. For an on-crop biomass such as that estimated here, the net above ground primary productivity predicted by the equation of McNaughton et al. (1989) is 14.5 MJ m^{-2} year^{-1}, a figure congruent with that expected for an open environment such as that proposed above. A savanna has a productivity of 130 g C m^{-2} year^{-1}, or 7.3 MJ m^{-2} year^{-1} (Margalef 1980). This savanna possibly had small wooded areas, as deduced from the presence of the hyperbrowsing deer *Eucladoceros*; in this case its productivity would have doubled, and the estimate of productivity would therefore be congruent. It should be further taken into account that some of the herbivore species are poorly represented (e.g., *Praeovibos* sp. and the small caprine), which suggests that they may have been transient species and therefore should not be completely included in the requirements of the herbivores. Moreover, according to nitrogen isotopes, the hippo must have fed at least partially on aquatic vegetation, which may have reduced even more the overall herbivores requirements.

As stated earlier, the metabolic requirements of the large carnivores would have been fulfilled with 16.5 kJ m^{-2} year^{-1}. The secondary productivity predicted by the appropriate equations of McNaughton et al. (1989) for an ecosystem able to support the herbivore bio-

mass inferred above is 20 kJ m^{-2} year $^{-1}$, or a bit lower according to the primary productivity estimated after Margalef (1980). Further, if a growth efficiency of 0.025 is assumed (Peters 1983), the secondary productivity must have reached 17.1 kJ m^{-2} year $^{-1}$. Both figures are very close to that obtained for the requirements of the carnivores, suggesting that all large carnivore species living in the original paleocommunity were finally represented in the bone assemblage collected by the hyenas. This is congruent with the results obtained by Arribas and Palmqvist (1998) in the comparison of the taxonomic composition of the faunal assemblage preserved at Venta Micena with those from other Plio-Pleistocene localities of the Guadix-Baza Basin.

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