



Feeding ecology and habitat preferences of top predators from two Miocene carnivore-rich assemblages

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Abstract.—Carnivore-rich fossil sites are uncommon in the fossil record and, accordingly, provide valuable opportunities to study predators from vantages that are rarely applied to ancient faunas. Through stable isotopes of carbon and a Bayesian mixing model, we analyze time-successive (nearly contemporaneous), late Miocene carnivoran populations from two fossil sites (Batallones-1 and Batallones-3) from central Spain. Stable isotopes of carbon in tooth enamel provide a reliable and direct methodology to track ancient diets. These two carnivoran-dominated fossil sites display differences in the composition and abundance of the carnivoran species, with some species present at both sites and some present only at one site. This disparity has been interpreted as the consequence of habitat differences between Batallones-1, the older site, and Batallones-3, the younger site. However, carbon isotope values of carnivore and herbivore tooth enamel suggest a common habitat of C₃ woodland originally present at both sites. The differences in the carnivoran faunas rather may be the consequence of the dynamics of species entrance and exit from the Madrid Basin during the time elapsed between Batallones-1 and Batallones-3 and changes in population densities due to biotic factors. We infer higher levels of interspecific competition in Batallones-3 than in Batallones-1 because of the larger number of similar-sized, sympatric predators; the clear overlap in their $\delta^{13}\text{C}$ values (except for the amphicyonid *Magericyon anceps*); and similarity of their preferred prey: the hipparionine horses. Finally, carbon stable isotopic composition of *Indarctos arctoides* teeth implies that this ursid was a carnivorous omnivore rather than a herbivorous omnivore. This work demonstrates the insights that stable isotopes can provide in characterizing the feeding ecology and trophic interactions of ancient carnivoran taxa.

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Introduction

Top predators are key regulators of the food web, since their dynamics produce cascading influences that affect herbivores directly and plants indirectly and that propagate to other species such as mesocarnivores through intra-guild competition (Terborgh et al. 2010; Ripple et al. 2014). In certain ecosystems, carnivorans, particularly large carnivorans, may even enhance carbon storage by limiting the number

of herbivore prey and thereby allowing more plants to thrive (Ripple et al. 2014). As fundamental ecological processes, these interactions and their effects also pertain to ancient ecosystems; extinct carnivores must have played a crucial role in shaping past ecosystems. Nevertheless, our knowledge about the ecology of extinct carnivorans and past trophic interactions is limited, mainly as a consequence of the rarity of carnivore remains in the fossil record.

Fossil sites dominated by carnivoran remains are rare because mammalian fossil assemblages typically reflect the herbivore:carnivore proportion of extant communities, usually greater than 50:1 (Farlow 1993). Fossil sites rich in carnivoran remains form under exceptional taphonomic circumstances (Spencer et al. 2003; Domingo et al. 2013a) and represent unique opportunities to study ecological aspects of past carnivoran guilds, from taxonomic diversity to ecomorphological traits to trophic interactions.

Stable isotope analysis of dental enamel is a robust method to infer the diet and resource use of extinct mammals, as well as the habitat(s) where they lived. This method requires sampling of tooth enamel, so the technique is not always permitted when fossil remains are rare or delicate. In fossil sites too old for preservation of collagen or apatite biosignal in bone, we are limited to working with the apatite biosignal of dental enamel. An added challenge comes from the thin enamel of most predators' teeth and the small amount of sample that can be recovered from them. Fortunately, advances in mass spectrometry have led to a substantial decrease in the amount of sample required for analysis, so the damage caused to teeth during sampling

is now much reduced. Consequently, the number of studies of the feeding behavior of extinct predators through stable isotope analyses of fossil enamel is increasing, although most are restricted to Quaternary sites (e.g., Feranec 2004; Kohn et al. 2005; Lee-Thorp et al. 2007; Clementz et al. 2009; García García et al. 2009; Feranec et al. 2010; Kohn and McKay 2012; Domingo et al. 2013b; Feranec and DeSantis 2014).

The Cerro de los Batallones fossil complex (Madrid Basin, central Spain; Fig. 1) is known for abundant, well-preserved remains of diverse vertebrates, mainly mammals, of Vallesian age (late Miocene, MN10, ca. 10–9 Ma; Domingo et al. 2007; Gómez Cano et al. 2011; Fig. 2). Cerro de los Batallones stands out for two of its sites (Batallones-1 and Batallones-3), in which the number of carnivoran remains greatly exceeds the number of herbivore remains. In these sites, more than 97% of the large-mammal remains belong to carnivoran species (Table 1), resulting in an inverted herbivore:carnivore ratio compared with those of living populations and most continental fossil assemblages. This abundance of carnivore specimens is the result of the

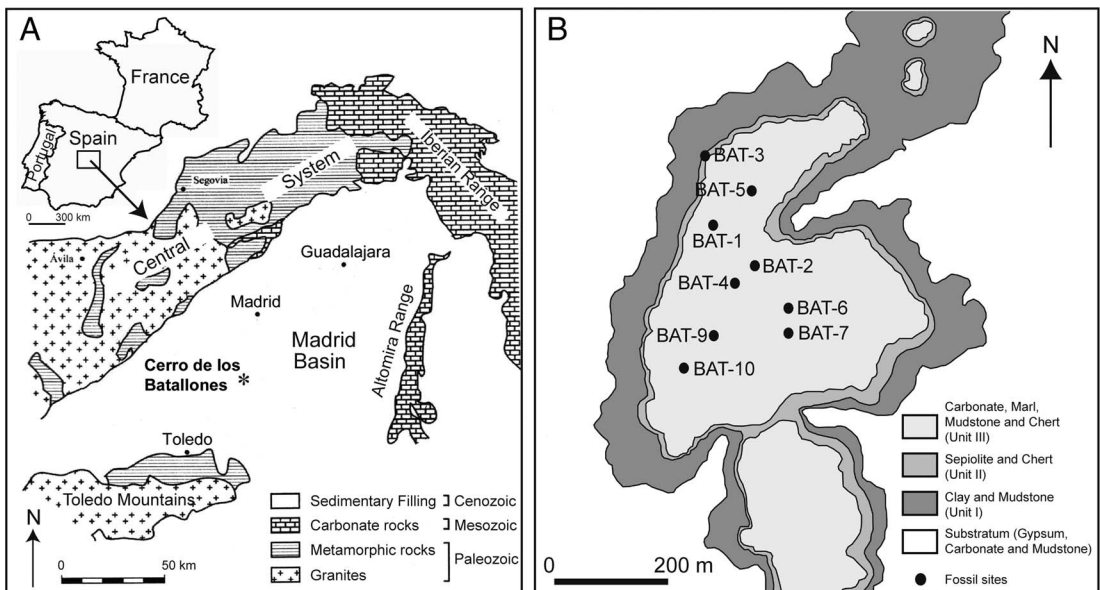


FIGURE 1. Location of Cerro de los Batallones fossil sites. A, Geological map of the Madrid Basin with Cerro de los Batallones (modified from Calvo et al. 1989). The location of the Madrid Basin in Spain is indicated in the upper left inset. B, Map of Cerro de los Batallones showing the location of the fossil sites (modified from Pozo et al. 2004). BAT-1, Batallones-1; BAT-2, Batallones-2; BAT-3, Batallones-3; and so on.

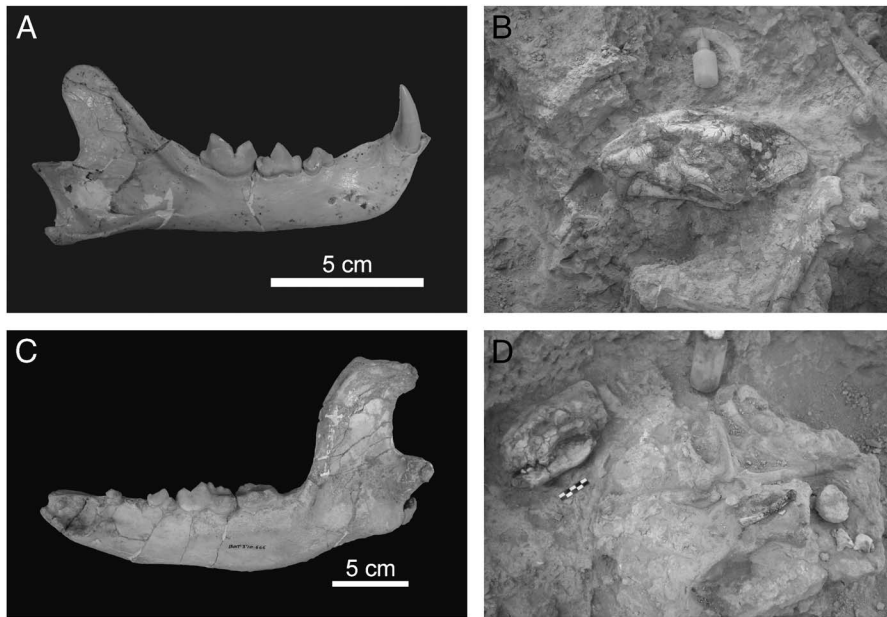


FIGURE 2. Carnivoran fossil specimens from Batallones-3. A, Right hemimandible BAT-3'13 1596 of *Promegantereon ogygia*. The p4 was sampled in this study. B, *Machairodus aphanistus* skull BAT-3'12 2448. Maximum length of the skull is 33 cm. C, Left hemimandible BAT-3'10 666 of *Indarctos arctoides*. The m1 was sampled in this study. D, Partial skeleton of *Eomellivora piveteaui*. Skull and mandible BAT-3'09 1000 are to the left. Scale, 5 cm. The P4 and p4 were sampled in this study.

taphonomic history of the sites: late Miocene pseudokarstic cavities present in this area acted as natural traps (Pozo et al. 2004; Morales et al. 2008; Calvo et al. 2013). Carnivoran individuals actively entered these cavities in their search for prey and water but were unable to leave (Domingo et al. 2013a).

Both, Batallones-1 (BAT-1) and Batallones-3 (BAT-3) are Vallesian (ca. 10–9 Ma), but López-Antoñanzas et al. (2010) suggested that BAT-3 is slightly younger than BAT-1, based on the more derived dental characters of the cricetid *Hispanomys moralesi* at BAT-3 compared with BAT-1. Based on the small-mammal association, López-Antoñanzas et al. (2010) concluded that Cerro de los Batallones localities were probably correlated to local subzone J2 (dated at 9.71–9.48 Ma) or J3 (9.34–9.05 Ma) of the Teruel Basin (van Dam et al. 2001, 2006). On this basis, we suggest an age difference among Cerro de los Batallones sites on the order of 0.30 Myr. The Cerro de los Batallones research team is currently refining the chronology of the fossil sites through new analyses on the small-mammal assemblages and magnetostratigraphic surveys. Differences

in taxonomic composition and proportional abundance of carnivore remains between BAT-1 and BAT-3 (Table 1) have been attributed to this temporal difference, but an associated environmental difference remains unclear.

In a previous study, we reported on stable isotopes of carbon for three sympatric hypercarnivores from BAT-1: the sabertoothed cats *Promegantereon ogygia* and *Machairodus aphanistus* and the amphicyonid *Magericyon anceps* (Domingo et al. 2013b). Here, we expand the isotopic sampling to BAT-3 carnivores (including *Promegantereon ogygia*, *Machairodus aphanistus*, and *Magericyon anceps*, and the ursid *Indarctos arctoides*, the mustelid *Eomellivora piveteaui*, and the amphicyonid *Thaumastocyon* sp.) to assess the feeding ecology of BAT-1 and BAT-3 carnivore populations and the environmental (vegetation) context of these sites.

Background

The Fossil Localities

In 1991, BAT-1 was the first fossil site discovered in Cerro de los Batallones. It was

TABLE 1. Abundances and proportions of large mammals from Batallones-1 and Batallones-3. In this table, we do not account for undetermined remains. Taxa analyzed in this study are marked with an asterisk. NISP, number of identified specimens.

Taxon	Family/order	BAT-1 ¹		BAT-3	
		NISP	%	NISP	%
<i>Promegantereon ogygia</i> *	Felidae/Carnivora	7125	49.53	3116	29.33
<i>Machairodus aphanistus</i> *	Felidae/Carnivora	3226	22.43	3869	36.42
Amphicyonidae* ²	Amphicyonidae/Carnivora	858	5.96	525	4.94
<i>Indarctos arctoides</i> *	Ursidae/Carnivora	ABSENT		1984	18.68
<i>Eomellivora piveteaui</i> *	Mustelidae/Carnivora	ABSENT		251	2.36
<i>Protictitherium crassum</i>	Hyaenidae/Carnivora	1339	9.31	418	3.93
<i>Simocyon batalleri</i>	Ailuridae/Carnivora	178	1.24	ABSENT	
Felinae ³	Felidae/Carnivora	775	5.39	142	1.34
Mustelidae/Mephitidae ³	Mustelidae-Mephitidae/Carnivora	453	3.15	266	2.50
<i>Hipparion</i> spp.* ⁴	Equidae/Perissodactyla	30	0.21	18	0.17
Rhinocerotidae*	Rhinocerotidae/Perissodactyla	273	1.90	6	0.06
Moschidae	Moschidae/Artiodactyla	56	0.39	5	0.05
<i>Microstonyx</i> sp.*	Suidae/Artiodactyla	67	0.47	5	0.05
Bovidae*	Bovidae/Artiodactyla	5	0.03	18	0.17
	Total Carnivora	13954	97.00	10571	99.51
	Total Perissodactyla	303	2.11	24	0.23
	Total Artiodactyla	128	0.89	28	0.26

¹It refers to BAT-1 lower-level assemblage, which is the carnivoran-dominated assemblage (see Domingo et al. 2013a for further information)

²In BAT-1, Amphicyonidae is exclusively represented by *Magericyon anceps*. In BAT-3, Amphicyonidae is represented by *Magericyon anceps* and *Thaumastocyon* sp.

³Several species are included within Felinae and Mustelidae/Mephitidae, but except for the feline *Styriofelis vallesiensis* (which is present both in BAT-1 and BAT-3; Salesa et al. 2012), the rest of the species are under study.

⁴Hipparionine horses from Cerro de los Batallones are under study but more than one species is included in *Hipparion* spp.

found in the context of mining operations conducted in this area to extract sepiolite, a clay mineral. BAT-3 was discovered in 2000, when fossils became exposed on the surface as the result of slope erosion on the hillside of Cerro de los Batallones (Fig. 1B).

These two fossil sites have diverse carnivore assemblages, with BAT-1 recording a total of 10 species and BAT-3 recording a total of 13 species (Table 1). At BAT-1, 13,954 carnivore specimens have been recovered, representing 97.0% of the large-mammal assemblage. At BAT-3, 10,571 carnivore specimens have been unearthed, representing 99.5% of the large-mammal assemblage (Table 1). Although overall diversity of carnivores from BAT-1 and BAT-3 is comparable, there are notable differences in the composition and abundance of species. For example, the ailurid *Simocyon batalleri* is present in BAT-1, whereas no remains of this species have been found in BAT-3 (Table 1). In turn, the amphicyonid *Thaumastocyon* sp., the mustelid *Eomellivora piveteaui*, and the ursid *Indarctos arctoides* are present in BAT-3 but absent from BAT-1. The sabertoothed cats *Promegantereon ogygia* and *Machairodus aphanistus*, the feline *Styriofelis*

vallesiensis, the amphicyonid *Magericyon anceps*, and the hyaenid *Protictitherium crassum* occur in both sites.

These species also differ in proportional abundance at the two sites. In terms of the number of identified specimens (NISP), in BAT-1, the most abundant species among all large mammals is the sabertoothed cat *Promegantereon ogygia* (49.5%), followed by *Machairodus aphanistus* (22.4%) (Table 1). The remaining BAT-1 carnivoran species are represented by less than 10% of the NISP for large mammals. In BAT-3, the two sabertoothed cats are also the most abundant species, but *Machairodus aphanistus* (36.4%) is more abundant than *Promegantereon ogygia* (29.3%). The ursid *Indarctos arctoides* is also represented by a high frequency of remains (18.7%). In Table 1, we reported NISP instead of MNI (minimum number of individuals), because this last index has not been yet estimated for the BAT-3 assemblage. This could be a concern in fossil sites where remains are very fragmented, because NISP can lead to a distorted estimation of the real abundance of individuals. Fragmentation of remains at BAT-1 and BAT-3 is very low and, specifically at BAT-1, NISP and MNI

are strongly correlated (Pearson's $r=0.97$; $p<0.01$; Domingo et al. 2013a). Fossils from BAT-3 are well preserved and show little fragmentation, so we consider that, as in the case of BAT-1, NISP is also a good measure of the taxon abundance at this site.

Less can be said about the herbivore faunas due to the scarcity of their remains at BAT-1 and especially at BAT-3. Four hundred and thirty-one herbivore remains have been unearthed at BAT-1, representing 3% of the total large-mammal assemblage (Table 1). At BAT-3, herbivore representation is even lower, with only 52 herbivore specimens found, which comprises only 0.5% of the total large-mammal assemblage (Table 1). Although some of the herbivore taxa present at BAT-1 also occur at BAT-3 (e.g., *Hipparion* sp.), more material would be necessary to assess the degree of similarity of the herbivore faunas at these two sites.

Carnivoran Species

We briefly summarize below some aspects of the biology of the carnivores analyzed in this study, as well as their temporal range in relation to Cerro de los Batallones localities.

Promegantereon ogygia.—This sabertoothed cat was the size of a leopard (Table 2, Fig. 2A). It was a hypercarnivore with a diet mainly consisting of meat (Morales et al. 2008). It is present both in BAT-1 and BAT-3. The first

appearance of this species in Spain is at Cerro de los Batallones, specifically in Batallones-10 (BAT-10), a locality slightly older than BAT-1 and BAT-3 (Table 3).

Machairodus aphanistus.—This sabertoothed cat was the size of a tiger (Table 2, Fig. 2B) and also was a hypercarnivore. It is present both in BAT-1 and BAT-3. This species occurs in Spanish fossil sites older and younger than those at Cerro de los Batallones (Table 3).

Magericyon anceps.—This amphicyonid was the size of a tiger (Table 2). Its dentition exhibits hypercarnivorous traits that imply less scavenging and more active hunting than other members of this family (Peigné et al. 2008). This amphicyonid is exclusively known from BAT-1 and BAT-3 (Table 3). Remains of this predator are rare in BAT-3, so we sampled only one tooth.

Thaumastocyon sp.—This amphicyonid had body proportions similar to those of a brown bear and a diet that mainly consisted of meat. This species is only known from BAT-3 (Table 3).

Indarctos arctoides.—This ailuropodine ursid (Abella 2011; Abella et al. 2014) was the size of a European brown bear (Table 2, Fig. 2C). Based on its dental and skeletal traits, this animal was a hypocarnivore (diet >70% nonvertebrate foods; Van Valkenburgh 2007); apart from meat, its diet included other elements such as plants (Abella 2011; Abella et al. 2011, 2015). Soibelzon (2012) recognized the difficulties of

TABLE 2. Body mass of the carnivores and herbivores included in the predator-diet analysis in this study. Body mass for *Promegantereon ogygia*, *Machairodus aphanistus*, and *Magericyon anceps* was obtained from BAT-1 specimens. Siliceo et al. (2014) indicated that body mass for BAT-1 and BAT-3 *Promegantereon ogygia* was similar. Based on dental measurements, Monescillo et al. (2014) indicated that *Machairodus aphanistus* from BAT-3 remained towards BAT-1 lower body mass values. Min., minimum body mass; max., maximum body mass. For *Microstonyx* sp. and Bovidae indet., only the median value is provided.

Taxon	Body mass in kg (min.-max.)	Reference
Carnivores		
<i>Promegantereon ogygia</i>	28–97	Domingo et al. 2013b
<i>Machairodus aphanistus</i>	117–285	Domingo et al. 2013b
<i>Magericyon anceps</i>	175–195	Domingo et al. 2013b
<i>Thaumastocyon</i> sp.	170–321	A. Valenciano (unpublished data)
<i>Eomellivora piveteaui</i>	30–40	A. Valenciano (unpublished data)
<i>Indarctos arctoides</i>	137–266	Abella et al. 2013
Herbivores		
<i>Hipparion</i> spp.	92–294	Domingo et al. 2013b
<i>Microstonyx</i> sp.	330	Liu 2003
<i>Austroportax</i> sp.	47–280	Moyà-Solà 1983; Domingo et al. 2013b
Bovidae indet.	60	J. Morales (unpublished data)

TABLE 3. Temporal ranges of Cerro de los Batallones carnivoran species in Spain. 1, taxon is present; 0, taxon is absent. Of the nine Cerro de los Batallones localities, BAT-10, BAT-1 and BAT-3 have been included here because their temporal relationships are known: BAT-10 is older than BAT-1, and BAT-1 is older than BAT-3 (López-Antoñanzas et al. 2010). Estimated temporal difference among these three sites is not longer than 0.3 Myr (see text). Taxa analyzed in this study are marked with an asterisk. Note that the presence/absence data as well as the temporal duration reported here refers only to the fossil record of this taxa in Spain. Species only found at Cerro de los Batallones sites were given a duration of 0.3 Myr if they are present in more than one site (see text). *Indarctos arctoides* has been found at BAT-3 and BAT-5, and this is why we give a duration of 0.3 Myr to this taxon. *Thaumastocyon* sp. has only been found in one site, BAT-3, and, because the total time elapsed in the formation of the site is unknown, we just indicated that its temporal range in Spain coincides with the duration of formation of the site. Data were obtained from Domingo et al. (2014), references therein, and unpublished data.

Taxon	Family/order	Before					After	Temporal duration of the species (Myr)
		BAT-10	BAT-10	BAT-1	BAT-3	BAT-3		
<i>Promegantereon ogygia</i> *	Felidae/Carnivora	0	1	1	1	1	1.6	
<i>Machairodus aphanistus</i> *	Felidae/Carnivora	1	1	1	1	1	3.0	
<i>Styriofelis vallesiensis</i>	Felidae/Carnivora	0	0	1	1	0	0.3	
<i>Magericyon anceps</i> *	Amphicyonidae/Carnivora	0	0	1	1	0	0.3	
<i>Thaumastocyon</i> sp.*	Amphicyonidae/Carnivora	0	0	0	1	0	Duration of BAT-3	
<i>Protictitherium crassum</i>	Hyaenidae/Carnivora	1	1	1	1	0	3.7 to 5.3	
<i>Simocyon batalleri</i>	Ailuridae/Carnivora	1	0	1	0	0	0.5	
<i>Indarctos arctoides</i> *	Ursidae/Carnivora	0	0	0	1	0	0.3	
<i>Eomellivora piveteaui</i> *	Mustelidae/Carnivora	1	1	0	1	0	0.5	

inferring the dietary preferences of bears, given the stability in the molar morphology of omnivorous carnivores. Following the approach described by Soibelzon et al. (2014), we have used stable carbon isotope analyses in this study to test the dietary preferences of *Indarctos arctoides* from Cerro de los Batallones that, for the time being, are exclusively based on anatomical traits. This species is known only at Cerro de los Batallones sites, specifically BAT-3 and BAT-5 (Table 3).

Eomellivora piveteaui.—This giant mustelid had a body mass comparable to that of a brown hyaena (Table 2, Fig. 2D). Its diet mainly consisted of meat but also incorporated some bone (Valenciano et al. 2015). It is present at BAT-3 and BAT-10 but absent from BAT-1. This mustelid was present in Spanish fossil sites older than Cerro de los Batallones localities; its last appearance in the Spanish fossil record occurred at BAT-3 (Table 3).

Other carnivoran species also found at BAT-1 and BAT-3 include the ailurid *Simocyon batalleri*, the primitive hyaenid *Protictitherium crassum*, and the feline *Styriofelis vallesiensis* (Table 1). They were not included in this study due to rarity of their remains or the small size of their teeth. Their patterns of appearance and disappearance, along with the species described above, highlight the important role

of the Cerro de los Batallones fossil complex in our current knowledge of late Miocene carnivores from Spain. *Simocyon batalleri* and *Protictitherium crassum* were present in fossil sites older than Cerro de los Batallones, but their last appearance in Spain is recorded in BAT-1 and BAT-3, respectively (Table 3). The feline *Styriofelis vallesiensis* is known in Spain only from the remains excavated at BAT-1 and BAT-3 (Table 3).

Previous Isotopic Analyses in Cerro de los Batallones

For mammals, the carbon stable isotope composition ($\delta^{13}\text{C}$) of tooth enamel tracks primarily the $\delta^{13}\text{C}$ values of their diet (Koch 2007; Clementz 2012, and references therein). The $\delta^{13}\text{C}$ values of herbivorous mammals reflect the values of ingested plants, which vary depending on plant photosynthetic pathways (C_3 , C_4 , CAM) and ecological factors (e.g., aridity, canopy density) that affect fractionation during photosynthesis (Kohn and Cerling 2002). The $\delta^{13}\text{C}$ values of carnivorous mammals reflect the values of ingested prey (Koch 2007). Multitaxic studies with species showing different resource and landscape use (e.g., more forested versus more open areas) constitute a reliable tool for

reconstructing the type(s) of habitats where the animals lived.

In previous studies, we investigated the diet and resource partitioning of three apex predators from BAT-1 by comparing their carbon isotope values and those of potential prey (Domingo et al. 2013b). To evaluate the relative contribution of different herbivore species to carnivore diets, we used the mixing model IsoSource (Phillips and Gregg 2003). The two sabertoothed cats, *Promegantereon ogygia* and *Machairodus aphanistus*, displayed $\delta^{13}\text{C}$ values that were statistically indistinguishable (Tukey post hoc test, $p = 0.845$). This result suggested that they were feeding on prey from a similar habitat (not necessarily on the same species, given the different body sizes of these two predators). IsoSource failed to resolve the diet of some sabertoothed cat individuals because their $\delta^{13}\text{C}$ values lay off the mixing line formed by the $\delta^{13}\text{C}$ values of the prey species evaluated. Specifically, their $\delta^{13}\text{C}$ values were lower than the lowest herbivore $\delta^{13}\text{C}$ value. We concluded that these unresolved individuals may have included in their diets one or more prey sources that were not measured in the analysis and that occupied a dense woodland, thus producing lower $\delta^{13}\text{C}$ values (Domingo et al. 2013b). The $\delta^{13}\text{C}$ values of the amphicyonid *Magericyon anceps* were significantly higher than those of the sabertoothed cats (Tukey post hoc tests, *Promegantereon*–*Magericyon*: $p = 0.004$; *Machairodus*–*Magericyon*: $p = 0.01$), implying resource partitioning with the use of prey from more open woodland (Domingo et al. 2013b). The $\delta^{13}\text{C}$ values of both carnivores and herbivores indicated that a C_3 woodland with patches of C_3 wooded grassland prevailed when BAT-1 formed 9 Ma (Domingo et al. 2013b).

Research Questions

Based on the carbon stable isotope biogeochemistry of fossil tooth enamel of taxa from Cerro de los Batallones, we evaluate three questions about the habitat present in this area 9 million years ago and the ecology of carnivorans from BAT-1 and BAT-3.

Question 1: Is the Difference in Carnivoran Composition and Abundance Observed in BAT-1 and

BAT-3 the Consequence of an Environmental Difference Between the Two Sites?

The presence of hypocarnivore individuals of large size, such as the ursid *Indarctos arctoides*, at BAT-3 and their absence from BAT-1, led some authors to suggest that a more forested habitat may have occurred at BAT-3 than at BAT-1 (Abella et al. 2011; Monescillo et al. 2014). *Prediction*: if the vegetation changed between the time of BAT-1 and BAT-3, for example, more open area versus more forested area, then the $\delta^{13}\text{C}$ values of mammal teeth should reflect this change and therefore differ. If the $\delta^{13}\text{C}$ values of mammal teeth remain similar, then there is no basis for inferring a change in vegetation cover from the viewpoint of carbon stable isotopes.

Vegetation structure is most usually assessed from $\delta^{13}\text{C}$ values of herbivores because herbivore dental enamel directly reflects the type vegetation on which they are feeding. Nevertheless, authors such as Bump et al. (2007) have turned our attention to the importance of the isotopic values of predators as proxies to detect environmental change. These authors consider that environmental patterns are better represented when increasing the trophic level up to the predator level, as predators act as ecological integrators. Therefore, we consider that $\delta^{13}\text{C}$ values of carnivores can provide clues about vegetation landscape, since they are indicative of the habitat those carnivores preferentially exploited. $\delta^{13}\text{C}$ values of carnivores are a good complement to further corroborate environmental shifts obtained from the $\delta^{13}\text{C}$ values of herbivores in terms of habitat present at a given area; this is especially true if the same predator species are present in the time periods environmentally compared. This is the case in our study, because *Promegantereon ogygia*, *Machairodus aphanistus*, and *Magericyon anceps* are present at BAT-1 and BAT-3.

Question 2: Are There Differences in the $\delta^{13}\text{C}$ Values of *Promegantereon ogygia* from BAT-1 and BAT-3 That Imply That the BAT-3 Population Used a More Open Habitat than the BAT-1 Population?

In a comparison of BAT-1 and BAT-3 populations of the sabertoothed cat *Promegantereon*

ogygia, Siliceo et al. (2014) considered them a “chronopopulation,” with BAT-3 individuals showing more derived dental and postcranial traits than BAT-1 individuals. Based on differences in the postcranial skeleton related to a reduction of the hind limb weight in BAT-3, these authors suggested that *Promegantereon* from BAT-3 could have increased its cursorial abilities compared with the BAT-1 population (Siliceo et al. 2014). *Prediction*: increased cursorial abilities should be linked to use of a more open habitat, implying higher $\delta^{13}\text{C}$ values for BAT-3 *Promegantereon ogygia* specimens compared with those from BAT-1.

Question 3: Do the $\delta^{13}\text{C}$ Values of Predators at BAT-3 Signify High Levels of Interspecific Competition?

In a comparison of BAT-1 and BAT-3 populations of the sabertoothed cat *Machairodus aphanistus*, Monesillo et al. (2014) indicated that the population from BAT-3 displays more derived dental traits than the BAT-1 population. The derived dental traits were interpreted as improved efficiency in feeding. Monesillo et al. (2014) indicated that, for example, the buccolingually narrower p4 and m1 of BAT-3 individuals, compared with BAT-1 individuals, imply a more efficient carnassial blade and, therefore, faster meat consumption. The derived dental characters in BAT-3 *Machairodus* individuals would have constituted an advantage that might reflect a higher degree of interspecific competition among BAT-3 carnivores (Monesillo et al. 2014). High levels of competition at BAT-3 are supported by the presence of several large predators: while at BAT-1 only two predators larger than 100 kg have been recovered (*Machairodus aphanistus* and *Magericyon anceps*), at BAT-3 there are four carnivores with an estimated adult body size of more than 100 kg (*Machairodus aphanistus*, *Magericyon anceps*, *Thaumastocyon sp.*, and *Indarctos arctoides*) (Table 2). These carnivores would potentially compete for similar prey. *Prediction*: an overlap of predators' $\delta^{13}\text{C}$ values would be consistent with high levels of interference competition, as they would be potentially feeding from same prey within the same habitat.

Materials and Methods

Fossil Teeth

We sampled the enamel of 63 carnivore teeth (Supplementary Table 1). Twenty-seven teeth belong to BAT-1 carnivores and were published by Domingo et al. (2013b). The remaining 36 teeth belong to BAT-3 carnivores and are published here for the first time.

The exceptional proportion of carnivore fossils found in BAT-1 and BAT-3 assemblages is not without its drawbacks: herbivore remains are very rare at both sites (Table 1). Therefore, for the predator-diet analysis, we included herbivore tooth samples not only from these two localities but also from the nearby herbivore-rich site of BAT-10. These fossil sites differ slightly in age (by 0.30 Myr at most), and herbivore species present at the three sites, the hipparionine horses, do not differ significantly in their $\delta^{13}\text{C}$ values ($F=0.7$, $p=0.51$). We acknowledge that it is ideal to draw trophic inferences from contemporaneous predator and prey remains; nevertheless, we consider that the small age difference between the sites makes it feasible to perform a valid predator-diet analysis. BAT-1 has now been exhaustively excavated, but continued excavation at BAT-3 and BAT-10 may provide additional herbivore samples.

The 32 herbivore teeth analyzed for this study are from hipparionine horses (Family Equidae, *Hipparion* spp.), a pig (Family Suidae, *Microstonyx* sp.), an antelope (Family Bovidae, *Austroportax* sp.), another bovid (Bovidae indet.) that is under study (but it is not *Austroportax* sp.), and two rhinoceroses (Family Rhinocerotidae, Rhinocerotinae indet. and *Aceratherium incisivum*) (Supplementary Table 1). Megaherbivores were not used in the analyses of predator diets (see “Results” section), but we included the teeth from two rhinoceros species recovered at BAT-1 (Supplementary Table 1) for a more complete assessment of the vegetation present at this site. The teeth sampled were all from adult individuals and are archived in the vertebrate paleontology collection of the Museo Nacional de Ciencias Naturales–CSIC (Madrid, Spain).

It was not possible to sample the same tooth position for all the taxa analyzed. Mann-Whitney (U) and Kruskal-Wallis (H) tests showed that there were not significant differences in tooth position for taxa with large enough sample sizes for comparison: BAT-1 *Promegantereon* ($H=1.78$, $p=0.41$), BAT-1 *Machairodus* ($H=1.81$, $p=0.40$), BAT-3 *Promegantereon* ($U=1$, $p=0.11$), BAT-3 *Machairodus* ($H=1.49$, $p=0.47$), and BAT-3 *Indarctos* ($U=8$, $p=0.90$). In the case of *Hipparion* sp. from BAT-1 and Rhinocerotinae indet. from BAT-1, there were too few teeth for comparison by tooth position, but we were able to compare preweaning teeth (first and second molars) versus postweaning teeth (second, third, and fourth premolars and third molar) (Higgins and MacFadden 2004). No significant differences were found for BAT-1 *Hipparion* sp. ($U=2$, $p=0.49$) or BAT-1 Rhinocerotinae indet. ($U=0$, $p=0.24$).

Isotopic Methods

Generally, 4 to 5 mg of dental enamel powder was sampled from each tooth. Carnivorous tooth enamel is very thin compared with that of most herbivores, and the teeth are delicate; in some instances, we could sample only 2–3 mg. Fortunately, in recent years, mass spectrometers have provided good results for apatite amounts as low as ~0.5 mg after chemical treatment.

We sampled each tooth from the occlusal surface to the cervix, so the samples represent the time span of tooth formation. Sampling was performed using a dental rotary drill with a diamond-tipped burr. We followed the protocol of Koch et al. (1997) for enamel pretreatment. The enamel powder was first treated with 2% NaOCl for 24 hours to remove organic matter. After the samples were rinsed five times with ultrapure water, enamel powder was soaked in a 1 M acetic acid–1 M calcium acetate buffer solution for 24 hours to eliminate diagenetic carbonates. After the supernatant was removed, the samples were again rinsed five times with ultrapure water and were freeze-dried overnight.

After the samples were treated, isotopic analyses were performed on Thermo MAT253

dual-inlet isotope-ratio mass spectrometers coupled to a Kiel IV carbonate device at the Stable Isotope Laboratory of the Department of Earth and Environmental Sciences of the University of Michigan and at the Stable Isotope Laboratory of the University of California–Santa Cruz. Duplicate analyses were carried out for ~90% of the samples.

Carbon stable isotope results are reported in δ -notation, $\delta^H X_{\text{sample}} = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] \times 1000$, where X is the element; H is the mass of the rarer, heavy isotope; and $R = {}^{13}\text{C}/{}^{12}\text{C}$. The isotopic reference standard for carbon is Vienna Pee Dee Belemnite (VPDB). The standards used were Carrara marble (CM; $\delta^{13}\text{C} = 2.05\text{‰}$), NBS-18 ($\delta^{13}\text{C} = -5.03\text{‰}$), and NBS-19 ($\delta^{13}\text{C} = 1.95\text{‰}$). The standard deviations for repeated measurements of CM ($n=15$), NBS-18 ($n=10$), and NBS-19 ($n=8$) were 0.09‰, 0.04‰, and 0.08‰, respectively.

To compare the Miocene $\delta^{13}\text{C}$ values to those documented for modern vegetation, it was necessary to adjust for changes in the $\delta^{13}\text{C}$ of the atmosphere ($\delta^{13}\text{C}_{\text{atmCO}_2}$) due to both geohistorical changes in $\delta^{13}\text{C}$ of CO_2 since the late Miocene and the increase in light carbon released by the burning of fossil fuels in the last 200 years (Friedli et al. 1986; Marino and McElroy 1991). For the late Miocene age of the Cerro de los Batallones fossil sites, based on the work of Tipple et al. (2010), the $\delta^{13}\text{C}_{\text{atmCO}_2}$ value was ~-6‰, a difference of ~2‰ relative to modern $\delta^{13}\text{C}_{\text{atmCO}_2}$ (~-8‰). Taking this adjustment into account, the ranges of $\delta^{13}\text{C}$ used to infer different kinds of vegetation and canopy cover from fossil teeth from Cerro de los Batallones are similar to those proposed by Domingo et al. (2012, 2013): (1) closed-canopy forest, $\delta^{13}\text{C}$ values less than -14.2‰, (2) woodland–mesic C_3 grassland, values from -14.2‰ to -9.2‰, (3) wooded grassland–xeric C_3 grassland, from -9.2‰ to -6.2‰, (4) mixed C_3 – C_4 grassland, from -6.2‰ to -1.2‰, and (5) pure C_4 grassland, greater than -1.2‰. No data are available for the $\delta^{13}\text{C}$ values of modern vegetation from the Iberian Peninsula for directly extracting the $\delta^{13}\text{C}$ threshold values between these types of vegetation. Cutoff values given here for closed-canopy forest and woodland–mesic C_3 grassland, wooded grassland–xeric C_3 grassland and

mixed C₃–C₄ grassland, and mixed C₃–C₄ grassland and pure C₄ grassland were obtained from widely accepted values in the literature, for example, MacFadden and Cerling (1996), Feranec (2003), Kohn et al. (2005), and Tütken et al. (2013). The cutoff $\delta^{13}\text{C}$ value between woodland–mesic C₃ grassland and wooded grassland–xeric C₃ grassland is more difficult to determine, but our selected value is in agreement with previous work. For example, Kohn et al. (2005) suggested a threshold value of -9‰ between woodland and more open conditions when investigating a North American Pleistocene fossil site. Matson et al. (2012) compiled plant $\delta^{13}\text{C}$ values from different types of modern ecosystems, and our cutoff $\delta^{13}\text{C}$ values for wooded grassland–xeric C₃ grassland correspond well with $\delta^{13}\text{C}$ values for C₃ trees, shrubs, and grasses found mainly in Mediterranean forest, woodland, and scrub; tropical and subtropical dry broadleaf forest; and desert and xeric shrubland.

According to the UNESCO classification of African vegetation (White 1983), (1) closed forest is a continuous stand of trees at least 10 m tall with interlocking crowns, (2) woodland has trees with canopy heights of 8–20 m, with their crowns covering at least 40% of the land surface but not overlapping extensively, (3) wooded grassland has a cover of grasses and other herbs, with woody plants covering between 10% to 40% of the ground, and (4) grassland is covered with grasses and other herbs, with woody cover less than 10%. Habitat inferences are based on the $\delta^{13}\text{C}$ values of herbivores, since they feed directly from the surrounding vegetation. Based on their dental adaptations, the herbivores in our study cover a dietary spectrum from browsers (rhinoceroses, Bovidae indet.) to mixed feeders (*Hipparion* spp.) to mixed feeder–grazers (*Austroportax* sp.). The multitaxic approach used here guarantees that habitat inference is supported by several taxa of different dietary habits. To infer dietary preferences from the $\delta^{13}\text{C}$ values of carnivorans and further delineate the habitat present in the study area, it is necessary to account for the trophic discrimination between predator and prey, usually herbivores. This $\delta^{13}\text{C}$ offset results in slightly lower $\delta^{13}\text{C}$ values in carnivoran enamel

bioapatite compared with those of the herbivores (Fox-Dobbs et al. 2006; Clementz et al. 2009). To account for this trophic discrimination, we adjusted carnivoran $\delta^{13}\text{C}$ values by $+1.3\text{‰}$, following Fox-Dobbs et al. (2006) and Clementz et al. (2009).

As previously indicated, we have also used carbon stable isotope analyses in this study to provide further information about the diet of the bear *Indarctos arctoides* from BAT-3. Different approaches for studying the diet of these omnivorous carnivores, such as dental micro-wear texture analysis, dental paleopathology analysis, biomechanical and anatomical analyses, or stable isotope analyses, are reported in the literature (e.g., Donohue et al. 2013; Soibelzon et al. 2014, and references therein). Here, we use the approach described by Soibelzon et al. (2014) to shed light on the diet of this ursid, specifically on its degree of carnivory. The Soibelzon et al. (2014) approach is based on quantifying the difference in the $\delta^{13}\text{C}$ values of the ursid of interest and coeval herbivores ($\Delta\delta^{13}\text{C}_{\text{bear-herb}}$). If the value is close to the previously mentioned $\delta^{13}\text{C}$ offset between carnivores (other than bears) and herbivores, then a significant contribution of meat to the diet of the ursid can be accepted, that is, the ursid would be a carnivorous omnivore. If $\Delta\delta^{13}\text{C}_{\text{bear-herb}}$ is far from the $\delta^{13}\text{C}$ difference between carnivores and herbivores, then meat is not considered an important dietary source for the ursid, that is, the ursid would be a herbivorous omnivore.

Statistical Analysis and Diet Characterization

We used Shapiro-Wilk tests to check for normality in all of the data sets used in this study. Because we found that all data sets are normally distributed, we contrasted $\delta^{13}\text{C}$ values of BAT-1 and BAT-3 using Student's *t*-tests, ANOVA, and post hoc Tukey tests. Nonparametric tests (i.e., Mann-Whitney test, Kruskal-Wallis test) are also reported when any of the data sets had a small sample size ($n \leq 3$). The significance level used was $p = 0.05$.

We used MixSIAR (Stock and Semmens 2013), a Bayesian mixing model, to estimate the proportion of prey contributions to the diet of each predator. In contrast to other mixing

models, Bayesian mixing models are able to incorporate variability in isotopic values of both source (prey) and consumer (predator) and in the trophic enrichment factor, analyze multiple sources, and incorporate prior information. MixSIAR resulted from a collaboration between the developers of SIAR (Stable Isotope Analysis in R; Parnell et al. 2010) and MixSIR (SIR = sampling-importance-resampling; Moore and Semmens 2008) and is written in open-source code in R and JAGS (Plummer 2003; R Development Core Team 2015).

Prey species included in the mixing model were selected on the basis of their body size. We selected herbivores with a medium body size for ungulates (i.e., hipparionine horses, suids, and bovids; Table 2) as the most probable prey for the predators considered here. In the analysis of the dietary preferences of the predators, we did not include megaherbivore species present in Cerro de los Batallones sites (rhinoceroses, giraffids, and proboscideans), as we consider that the carnivorans would have consumed these species only under exceptional circumstances

(i.e., young, diseased, or old megaherbivore individuals or as carrion) and not on a regular basis (see Domingo et al. 2013b).

The combination of some sources to reduce their total number in the Bayesian analysis is recommended to achieve a more constrained solution (Phillips et al. 2005, 2014). Combining sources must have a logical basis, for example, combination within the same higher taxon or combination of taxa from well-differentiated habitats such as marine versus terrestrial. Following this recommendation and their statistically non-different $\delta^{13}\text{C}$ values (see above), we grouped together the hipparionine horses from BAT-1, BAT-3, and BAT-10.

The more food sources vary from each other in terms of their isotopic composition, the more constrained is the result obtained from the mixing model, that is, the estimates indicative of the contribution of each source to the diet of the consumer (Phillips et al. 2005, 2014). For Cerro de los Batallones, $\delta^{13}\text{C}$ values of the herbivore prey species show considerable overlap (Fig. 3, Supplementary Table 2), so

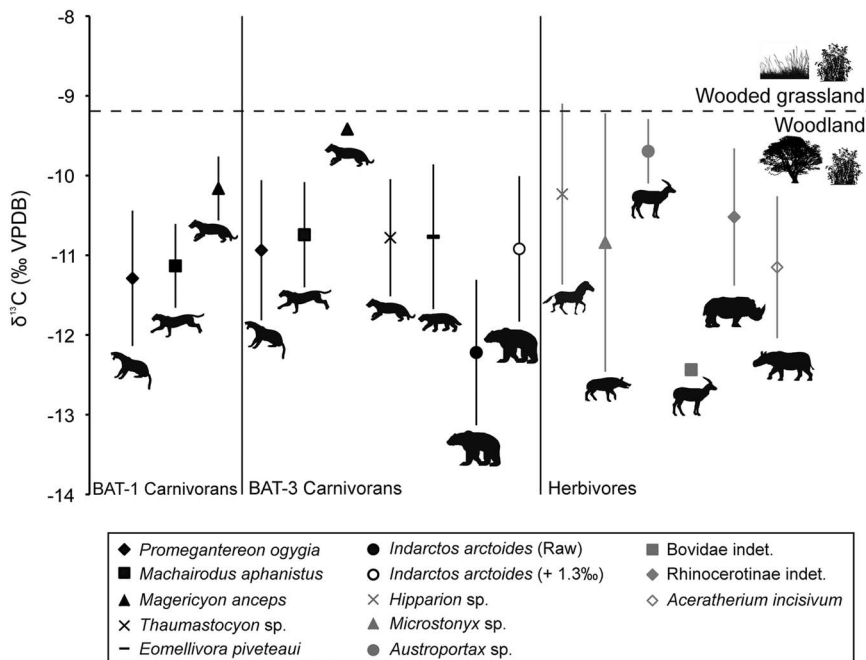


FIGURE 3. Stable carbon isotope values (mean \pm 1 SD) for BAT-1 and BAT-3 carnivore and herbivore species. Carnivore values were adjusted by +1.3‰ to account for trophic discrimination (Fox-Dobbs et al. 2006; Clementz et al. 2009). *Indarctos arctoides* $\delta^{13}\text{C}$ values are shown with adjustment and without adjustment given the omnivorous nature of this taxon. The dashed horizontal line marks the carbon isotopic threshold between woodland and wooded grassland. Profiles of the animals are not to scale.

TABLE 4. Mean and 1 standard deviation (SD) $\delta^{13}\text{C}$ values for the taxa analyzed in this study. Carnivore $\delta^{13}\text{C}$ values are adjusted by +1.3‰ to account for trophic discrimination (Fox-Dobbs et al. 2006; Clementz et al. 2009). Hipparionine horses from Cerro de los Batallones are under study, so note that *Hipparion* spp. from BAT-1, BAT-3, and BAT-10 might be different species. In the case of *Indarctos arctoides*, we provide raw and adjusted data. The last column represents the difference between the $\delta^{13}\text{C}$ mean value of *Indarctos arctoides* (raw value) and the $\delta^{13}\text{C}$ mean value of herbivores that could be potential prey. *n*, number of teeth sampled.

Taxon	Origin	<i>n</i>	Mean $\delta^{13}\text{C}$ (‰ VPDB)	SD	$\Delta\delta^{13}\text{C}_{\text{bear-herb}}$
Carnivores					
<i>Promegantereon ogygia</i>	BAT-1	9	-11.29	0.85	
<i>Machairodus aphanistus</i>	BAT-1	11	-11.13	0.52	
<i>Magericyon anceps</i>	BAT-1	7	-10.16	0.40	
<i>Promegantereon ogygia</i>	BAT-3	8	-10.94	0.88	
<i>Machairodus aphanistus</i>	BAT-3	9	-10.74	0.66	
<i>Magericyon anceps</i>	BAT-3	1	-9.42	-	
<i>Thaumastocyon</i> sp.	BAT-3	3	-10.78	0.73	
<i>Eomellivora piveteaui</i>	BAT-3	6	-10.77	0.91	
<i>Indarctos arctoides</i> (raw)	BAT-3	9	-12.22	0.91	
<i>Indarctos arctoides</i>	BAT-3	9	-10.92	0.91	
Herbivores					
<i>Hipparion</i> spp.	BAT-1, BAT-3, BAT-10	19	-10.23	1.13	-1.99
<i>Microstonyx</i> sp.	BAT-10	4	-10.84	1.62	-1.38
<i>Austroportax</i> sp.	BAT-1	2	-9.70	0.40	-2.52
Bovidae indet.	BAT-3	1	-12.44	-	0.22
Rhinocerotinae indet.	BAT-1	4	-10.52	0.86	
<i>Aceratherium incisivum</i>	BAT-1	2	-11.15	0.89	
				Mean $\Delta\delta^{13}\text{C}_{\text{bear-herb}}$	-1.42
				SD $\Delta\delta^{13}\text{C}_{\text{bear-herb}}$	1.19

we anticipate that the mixing model will provide less source discrimination than in a scenario with highly distinctive sources. Still, MixSIAR can provide useful information for characterizing trophic relationships in this ancient food web.

MixSIAR results (posterior probabilities of dietary proportions) are reported as the median and 95% Bayesian credible intervals of the likely contribution of each prey taxon to the tissue composition of the predators. MixSIAR uses a Markov chain Monte Carlo (MCMC) model-fitting algorithm. We considered model results as satisfactory when they converged in probability space, as indicated by trace plots and Gelman-Rubin and Geweke tests provided in MixSIAR (Stock and Semmens 2013).

Results

The $\delta^{13}\text{C}$ values of BAT-3 herbivore and carnivore teeth (after adjustment for trophic discrimination) imply the prevalence of a C₃ woodland habitat in the Cerro de los Batallones area (Table 4, Fig. 3). This result

agrees with habitat inferences established for BAT-1 (Domingo et al. 2013b).

Among herbivores, no significant differences were detected when the $\delta^{13}\text{C}$ values of BAT-3 *Hipparion* sp. were compared with the $\delta^{13}\text{C}$ values of BAT-1 *Hipparion* sp. (Student's *t*-test: $t = 1.35$, $p = 0.21$; Mann-Whitney tests: $U = 4$, $p = 0.17$). The same was true for comparison of variances ($F = 2.66$, $p = 0.14$). The $\delta^{13}\text{C}$ values for BAT-1 herbivores range from -11.78‰ to -8.31‰ whereas the $\delta^{13}\text{C}$ values for BAT-3 herbivores extend from -12.44‰ to -10.67‰ (Supplementary Table 1). There was no significant difference when means of all herbivores from BAT-1 and all herbivores from BAT-3 were compared ($t = 1.99$, $p = 0.06$) or when the variances of these two groups were compared ($F = 1.52$, $p = 0.81$).

We also compared $\delta^{13}\text{C}$ values of carnivoran species present at both sites. BAT-1 and BAT-3 *Promegantereon ogygia* samples did not differ significantly in their $\delta^{13}\text{C}$ values ($t = -0.84$, $p = 0.41$). Likewise, the variance in $\delta^{13}\text{C}$ values of BAT-1 and BAT-3 *Promegantereon* samples ($F = 1.07$, $p = 0.93$) did not differ significantly. No significant differences in the $\delta^{13}\text{C}$ means were observed for the other sabertoothed cat,

TABLE 5. Results of the ANOVA and Tukey post hoc tests for $\delta^{13}\text{C}$ values of BAT-3 carnivores. $p > 0.05$, no significant difference; $p < 0.05$, significant difference. $F = 0.094$, $p = 0.984$. Levene's test = 0.376, $p = 0.824$.

	<i>Machairodus aphanistus</i>	<i>Eomellivora piveteaui</i>	<i>Thaumastocyon sp.</i>	<i>Indarctos arctoides</i>
<i>Promegantereon ogygia</i>	0.989	0.996	0.999	1.000
<i>Machairodus aphanistus</i>		1.000	1.000	0.991
<i>Eomellivora piveteaui</i>			1.000	0.997
<i>Thaumastocyon sp.</i>				0.999

TABLE 6. Predicted diet proportions of predators from BAT-1 and BAT-3 derived from MixSIAR mixing model. Median estimates and 95% posterior intervals (CI) are provided. Largest prey contributions to predators' diets are marked in bold.

Predators	Origin	<i>Hipparion</i> spp. median (CI)	<i>Microstonyx</i> sp. median (CI)	<i>Austroportax</i> sp. median (CI)	Bovidae indet. median (CI)
<i>Promegantereon ogygia</i>	BAT-1	0.207 (0.008–0.662)	0.253 (0.010–0.692)	0.151 (0.007–0.557)	0.284 (0.019–0.639)
<i>Machairodus aphanistus</i>	BAT-1	0.226 (0.012–0.573)	0.173 (0.008–0.553)	0.188 (0.008–0.525)	0.360 (0.069–0.616)
<i>Magericyon anceps</i>	BAT-1	0.228 (0.010–0.673)	0.135 (0.007–0.511)	0.473 (0.054–0.809)	0.099 (0.004–0.354)
<i>Promegantereon ogygia</i>	BAT-3	0.261 (0.012–0.720)	0.233 (0.009–0.672)	0.186 (0.010–0.604)	0.208 (0.015–0.568)
<i>Machairodus aphanistus</i>	BAT-3	0.285 (0.013–0.701)	0.205 (0.008–0.630)	0.225 (0.014–0.637)	0.193 (0.010–0.501)
<i>Thaumastocyon sp.</i>	BAT-3	0.265 (0.013–0.729)	0.211 (0.007–0.645)	0.219 (0.011–0.651)	0.186 (0.009–0.571)
<i>Eomellivora piveteaui</i>	BAT-3	0.288 (0.015–0.739)	0.233 (0.010–0.676)	0.197 (0.010–0.637)	0.165 (0.008–0.534)
<i>Indarctos arctoides</i>	BAT-3	0.272 (0.014–0.730)	0.235 (0.010–0.696)	0.175 (0.008–0.600)	0.197 (0.009–0.564)

Machairodus aphanistus ($t = -1.48$, $p = 0.16$), and similarly, no significant differences were detected in their variances ($F = 1.57$, $p = 0.49$). For *Magericyon anceps*, we could not perform statistical comparison between the two sites, since we sampled only one tooth from BAT-3 (Table 4).

We compared $\delta^{13}\text{C}$ values among five carnivores from BAT-3 and did not find significant differences among them (ANOVA F -test) or between any pair of species (Tukey post hoc test) (Table 5). Again, *Magericyon anceps* was not included in the analysis because it is represented by only one sample from BAT-3. Levene's test revealed equal variances in all comparisons (Table 5). The same results were obtained for the Kruskal-Wallis test (Supplementary Table 3).

To assess the degree of carnivory of *Indarctos arctoides* from BAT-3, we determined the difference between the $\delta^{13}\text{C}$ values of the ursid of interest and potential herbivore prey ($\Delta\delta^{13}\text{C}_{\text{bear-herb}}$; Table 4). The $\Delta\delta^{13}\text{C}_{\text{bear-herb}}$ is -1.42‰ , very close to the trophic discrimination between predator and prey (Fox-Dobbs et al. 2006; Clementz et al. 2009). From the viewpoint of carbon stable isotope analyses, *Indarctos arctoides* would be considered an

ursid with a omnivorous diet that incorporated a large proportion of meat. Therefore, this ursid is analyzed in this paper as a potential competitor for the rest of the predators. To maintain the comparability with the rest of the predators, we used the 1.3‰ adjustment for *Indarctos arctoides* (Table 4, Fig. 3).

As expected, the contributions of different prey species to predator diets had median values that generally were close to one another (Table 6). MixSIAR median results indicated that the four prey taxa analyzed could have contributed quite similarly to most of the predator diets. Taking this into account, it is possible to extract further inferences. At BAT-1, the undetermined bovid (Bovidae indet.) seemed to be the most feasible prey for the two sabertoothed cats, while the antelope *Austroportax* sp. had the lowest contribution to their diets. We observe the opposite pattern in the diet of BAT-1 *Magericyon anceps*: *Austroportax* sp. constituted the most important diet source for this amphicyonid, whereas the median contribution of the undetermined bovid was quite low. The undetermined bovid is represented by only one tooth, so results concerning this taxon must be considered with caution. Future analyses will allow us to

confirm or discard dietary inferences of Cerro de los Batallones predators relative to this herbivore. In any event, the extreme negative $\delta^{13}\text{C}$ value of this bovid can act as a good representative of taxa from closer environments at Cerro de los Batallones and for analysis of the relations of predators with dwellers from a closer habitat. At BAT-3, the prey contributing most importantly to the diet of all the predators were the hipparionine horses, and less feasible prey species varied among the carnivorans (Table 6).

Discussion

Exceptional taphonomic histories resulted in the predominance of carnivoran remains in the Miocene fossil assemblages of BAT-1 and BAT-3 (Domingo et al. 2013a). The discovery of these sites was significant for Neogene vertebrate paleontology of the Iberian Peninsula, since the faunal remains significantly increased the carnivoran diversity known for the late Vallesian period. Almost 30% of the carnivoran species known for the MN10 (Mammalian Neogene) biochronological unit in Spain occur exclusively at Cerro de los Batallones sites.

The $\delta^{13}\text{C}$ values of herbivorous and carnivorous mammals from BAT-3 suggest that C_3 plants dominated the vegetation surrounding Cerro de los Batallones 9 to 10 Ma. The $\delta^{13}\text{C}$ ranges of mammals from BAT-3 fall within the values assigned to woodland–mesic C_3 grassland (Table 4, Fig. 3). These inferences largely agree with the carbon isotope analyses performed on fossils from BAT-1 (Domingo et al. 2013b). Statistical analyses of the $\delta^{13}\text{C}$ values of carnivorans and herbivores together with the mixing model dietary inferences allow us to address the research questions posed earlier.

(1) Does the Difference in Carnivoran Composition and Abundance Observed in BAT-1 and BAT-3 Result from an Environmental Difference between the Two Sites?

The $\delta^{13}\text{C}$ values of carnivorous and herbivorous taxa present at both sites, *Promegantereon*, *Machairodus*, and *Hipparion* spp., did not differ significantly. Although the $\delta^{13}\text{C}$ range for herbivores from BAT-1 was greater than the range obtained at BAT-3, the means and the

variances of the two data sets showed no statistical differences. A greater $\delta^{13}\text{C}$ range for herbivores at BAT-1 probably reflects the fact that more herbivorous species and teeth have been sampled at this fossil site (15 teeth sampled) compared with BAT-3 (4 teeth sampled). The $\delta^{13}\text{C}$ values of predators from BAT-1 and BAT-3 indicated that they were hunting and feeding on herbivores within a woodland–mesic C_3 grassland habitat. Thus, changes observed in carnivoran composition and proportional abundance cannot be attributed to a significant shift in the environmental conditions between the times of formation of BAT-1 and BAT-3. The $\delta^{13}\text{C}$ values do not support the view that the Cerro de los Batallones area was more forested during the lifetimes of the mammals preserved at BAT-3 compared with those preserved at BAT-1. The absence of *Eomellivora piveteaui*, *Thaumastocyon* sp., and *Indarctos arctoides* at BAT-1 and their presence at BAT-3 was, therefore, not likely the consequence of a major habitat change in the area. Rather, their absence could indicate that these taxa were absent from the area at the time when BAT-1 was working as a trap, and they later entered the region during the time when BAT-3 was active as a trap. The disappearance of *Simocyon batalleri* (present in BAT-1 but absent in BAT-3) could have been the consequence of its competitive displacement by the new arrivals at BAT-3. BAT-3 still lacks a comprehensive taphonomic study, but if we assume a taphonomic history similar to the one inferred for BAT-1, based on the predominance of carnivores and similar geological context, then the differences in the abundance of carnivoran species could reflect different original population densities in the area through the time period represented between BAT-1 and BAT-3. Alternatively, we cannot discard the possibility that the absence of some of the carnivorans in these localities might be a matter of chance, that is, taxa were present in the area but did not become trapped in the cavities. Nevertheless, we consider that differences in the taxonomic composition of BAT-1 and BAT-3 are very pronounced (e.g., complete absence in one site of taxa that are abundant in the other site, such as *Indarctos arctoides*) as to consider them caused by pure chance.

If the observed pattern of presence and absence in Cerro de los Batallones is real and not the consequence of chance, then our results suggest that a rapid change occurred in the carnivoran guild of the Madrid Basin not associated with a shift in vegetation and emphasizes the potential role of interactions among the carnivorans in shaping guild composition.

(2) Did *Promegantereon ogygia* from BAT-3 Occupy a More Open Portion of the Habitat Than BAT-1 Individuals?

The BAT-3 *Promegantereon* sample showed $\delta^{13}\text{C}$ values slightly higher than those at BAT-1 (the same is true for *Machairodus* and *Magericyon*; Table 4, Fig. 3), but the difference was small and not statistically significant. The two *Promegantereon* populations used a similar habitat. Still, the MixSIAR results show some differences in the contribution of prey species to the diet of the two *Promegantereon* populations (Table 6). Compared with *Promegantereon* from BAT-3, BAT-1 *Promegantereon* incorporated into its diet a higher proportion of Bovidae indet., a dweller of rather closed woodland habitat (Table 6). This bovid was found at BAT-3 and not at BAT-1; but notably, previous studies hypothesized that *Promegantereon ogygia* from BAT-1 was incorporating a prey source not represented among the BAT-1 fossil remains, with $\delta^{13}\text{C}$ values indicative of a closed woodland (Domingo et al. 2013b).

The lack of significant differences in the $\delta^{13}\text{C}$ values does not point to an increase in the cursorial abilities (i.e., use of more open portion of the habitat) of the BAT-3 *Promegantereon* population compared with the BAT-1 population from the viewpoint of stable carbon isotopes.

(3) Is There Significant Overlap in the Predators' $\delta^{13}\text{C}$ Values That Could Be Indicative of High Levels of Competition among Them?

When BAT-1 and BAT-3 *Machairodus aphanistus* samples were compared, we obtained similar results to those for *Promegantereon ogygia*; that is, $\delta^{13}\text{C}$ values did not differ significantly, but the BAT-3 sample displayed slightly higher values (Table 4, Fig. 3). The mixing model suggests that Bovidae indet. was

the preferred prey species for BAT-1 *Machairodus aphanistus* and that, by the time when BAT-3 was forming, this sabertoothed cat had changed its preferred prey species to herbivores from slightly more open woodland, for example, *Hipparion* spp. (Table 6).

The $\delta^{13}\text{C}$ values of the carnivorans from BAT-3 show considerable overlap (Fig. 3). The ANOVA and Kruskal-Wallis tests demonstrated no significant differences among the carbon isotope signatures of BAT-3 carnivores (Table 5, Supplementary Table 3), and the MixSIAR analysis revealed that all BAT-3 predators evaluated had a common preferred diet source: the hipparionine horses (Table 6). In any event, the predators could have also strongly competed for the rest of the prey in view of the very similar contribution values. These results are consistent with high levels of interspecific competition among BAT-3 predators, with similar-sized species competing for the same prey. Yet, further information on the partitioning of resources among these large predators can be added. First, at BAT-1, *Magericyon anceps* showed $\delta^{13}\text{C}$ values that were significantly more positive than those of *Promegantereon ogygia* and *Machairodus aphanistus* (Domingo et al. 2013b). *Magericyon anceps* was not included in the statistical analysis of BAT-3 predators because we could only sample one tooth from BAT-3 for this predator (Table 4). Results obtained by Domingo et al. (2013b) were similar to those from MixSIAR for *Magericyon anceps*: its preferred prey species was the antelope *Austroportax* sp., a dweller of the open part of the woodland–mesic C_3 grassland habitat inferred for Cerro de los Batallones (Table 6). In BAT-3, as in BAT-1, the sampled tooth of *Magericyon anceps* had a higher $\delta^{13}\text{C}$ value than those of the sabertoothed cats (and the rest of BAT-3 carnivores) and fell close to the threshold between woodland–mesic C_3 grassland and wooded grassland–xeric C_3 grassland (Table 4, Fig. 3). It is plausible, then, to infer resource use coincident with that inferred from BAT-1 specimens: the coexistence of *Magericyon anceps* with the other predators (especially those larger than 100 kg) was facilitated because this amphicyonid hunted prey from a more open portion of the habitat (Domingo et al. 2013b).

Following the approach of Soibelzon et al. (2014), we find that the $\delta^{13}\text{C}$ values of the ursid *Indarctos arctoides* are consistent with the consumption of meat by this taxon (Table 4). Accordingly, this ursid could have been a potential competitor for the rest of predator species at BAT-3 (Table 5, Fig. 3, Supplementary Table 3). In any event, most ursids, and *Indarctos arctoides* is not an exception, are omnivores species, so coexistence would be facilitated by this taxon consuming substantial amounts of vegetation.

Coexistence of the large predators (*Machairodus aphanistus*, *Magericyon anceps*, *Thaumastocyon* sp., *Indarctos arctoides*) and the medium-sized predators (*Promegantereon ogygia*, *Eomellivora piveteaui*) in BAT-3 could have been further facilitated by elusive behavior of the latter relative to the former. By analogy with the behavior of modern sympatric felids, Salesa et al. (2006) suggested that coexistence of the two sabertoothed cats was possible because the smaller species, *Promegantereon ogygia*, would have used tree cover (plausible with our inferred presence of woodland habitat) to hide from encounters with the larger species, *Machairodus aphanistus*. Coexistence between the two medium-sized carnivores analyzed from BAT-3, *Promegantereon ogygia* and *Eomellivora piveteaui*, could have been facilitated by *Eomellivora* being not only an active hunter but also a scavenger and bone-crusher (Valenciano et al. 2015). In modern carnivore guilds, other strategies that permit the coexistence of predators include separation of hunting-activity times (diurnal versus nocturnal carnivores; Karanth and Sunquist 2000; Owen-Smith and Mills 2008). These strategies could also have occurred in the BAT-3 carnivore guild, but they cannot be directly inferred from the fossil record.

In this study, we performed new analyses of the carnivore-rich BAT-3 assemblage and have rejected the hypothesis that differences between the carnivore guilds of BAT-1 and BAT-3 were a consequence of significant habitat changes during the time elapsed between the formation of the two sites. We have expanded our knowledge of the feeding ecology and habitat preferences of these ancient predators with stable isotopic analysis of tooth enamel, a powerful tool that has been

applied to the study of Neogene carnivores only on limited occasions.

Conclusions

Cerro de los Batallones, and specifically the localities of BAT-1 and BAT-3, stand out in the Miocene record of mammals for preserving an unusual concentration of carnivore remains that represent diverse predator guilds. These time-successive sites display notable differences in the composition and abundance of carnivore species. A habitat change was proposed as a possible hypothesis to explain the differences in the carnivore guild composition.

Our carbon isotope analyses and comparison of the herbivore and carnivore faunas, as well as of individual species present at both sites, demonstrate that the vegetation remained stable during the time between the formation of BAT-1 and BAT-3, with the predominance of a woodland to mesic C_3 grassland habitat. The carnivore guild from the Madrid Basin experienced a rapid change in its component species without a significant change in habitat. The faunal differences could reflect (1) the original carnivore population densities and (2) the sequence of appearances and disappearances. These were driven by competitive interactions rather than by vegetation change. The alternative hypothesis, that differences in the carnivore taxonomic composition between BAT-1 and BAT-3 were caused by chance, cannot, however, be rejected at this point.

Evidence from carbon stable isotopic composition of *Indarctos arctoides* teeth are consistent with a diet including meat, so this ursid can be considered a carnivore omnivore.

A Bayesian mixing model allowed us to characterize the contribution of selected prey to carnivore diets. For the two sabertoothed cats, we detected subtle changes in their prey preferences, with BAT-1 populations preferring the unidentified bovid species and BAT-3 populations preferring the hipparionine horses. The considerable number of medium to large predator species with hypercarnivore diets in BAT-3, along with the high overlap in their $\delta^{13}\text{C}$ values, imply the occupation and use of a similar portion of the habitat (with the

possible exception of *Magericyon anceps*). This amount of overlap for several species suggests that strong interspecific competition occurred among them (stronger than at BAT-1). The mixing model also points to high levels of rivalry among BAT-3 predators, as it identified a common preferred prey for BAT-3 carnivores: the equids *Hipparion* spp.

Advances in stable isotope sampling techniques along with smaller sample sizes needed by modern laboratories make it possible to minimize damage inflicted to fossils. Therefore, at those fossil sites where remains are abundant enough to support statistically sound analyses, it is highly advisable to perform stable isotope analyses, since the insights gained about the ecology and trophic interactions of extinct mammals are invaluable and sometimes impossible to obtain with other techniques.

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