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1 **Feeding ecology and habitat preferences of top predators from two**

2 **Miocene carnivore-rich assemblages**

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5 RRH: ISOTOPE ECOLOGY OF MIOCENE PREDATORS

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Abstract.— Carnivoran-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 in 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 may be rather 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.

Key words: carbon stable isotopes, Madrid Basin, Cerro de los Batallones, carnivores, Bayesian mixing-model

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65 **Introduction**

66 Top predators are key regulators of the food web, since their dynamics produce
67 cascading influences that directly affect herbivores and indirectly plants and that propagate
68 to other species such as meso-carnivores through intra-guild competition (Terborgh et al.
69 2010; Ripple et al. 2014). In certain ecosystems, carnivorans, particularly large carnivorans,

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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 bio-signal in bone, we are limited to working with the apatite bio-signal of dental enamel. An added challenge comes from the thin enamel of most predator 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.

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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 carnivorous remains greatly exceeds the number of herbivorous remains. In these sites, more than 97% of the large-mammal remains belong to carnivorous species (Table 1), resulting in an inverted herbivore:carnivore ratio compared to that of living populations and of most continental fossil assemblages. This abundance of carnivore specimens is the result of the 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). Carnivorous individuals actively entered these cavities in their search for prey and water but were unable to leave (Domingo et al. 2013a).

Comment [SD1]: Fig. 1 here

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 to 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 to 9.48 Ma) or J3 (9.34 to 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

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

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

Comment [SD2]: Fig. 2 here

128

129 **Background**

130 The Fossil Localities

131 In 1991, Batallones-1 (BAT-1) was the first fossil site discovered in Cerro de los
132 Batallones. It was found in the context of mining operations conducted in this area to extract
133 sepiolite, a clay mineral. Batallones-3 (BAT-3) was discovered in 2000, when fossils
134 became exposed on the surface as the result of slope erosion on the hillside of Cerro de los
135 Batallones (Fig. 1B).

136 These two fossil sites have diverse carnivore assemblages, with BAT-1 recording a
137 total of ten species and BAT-3 recording a total of 13 species (Table 1). At BAT-1, 13,954
138 carnivore specimens have been recovered, representing 97.0% of the large-mammal
139 assemblage. At BAT-3, 10,571 carnivore specimens have been unearthed, representing
140 99.5% of the large-mammal assemblage (Table 1). Although overall diversity of carnivores

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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 are 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.

Comment [SD3]: Table 1 here

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 it is the case at BAT-1, NISP is also a good measure of the taxon abundance at this site.

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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 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

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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).

Comment [SD4]: Table 2 here

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% non-vertebrate foods, Van Valkenburgh 2007); apart from meat, its diet included other elements such as plants (Abella 2011; Abella et al. 2011; Abella et al. 2015). Soibelzon (2012) recognized the difficulties of inferring the dietary preferences of bears, given the stability in the molar morphology of omnivore carnivores. Following the approach described by Soibelzon et al. (2014), we have used carbon stable 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 pivateaui.—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

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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).

Comment [SD5]: Table 3 here

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) as well as on 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 vs 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 $\delta^{13}\text{C}$

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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 of 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, i.e., resulting in 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 million years ago (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

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258 forested habitat may have occurred at BAT-3 than at BAT-1 (Abella et al. 2011; Monescillo
259 et al. 2014). *Prediction*: if the vegetation changed between the time of BAT-1 and BAT-3,
260 e.g., more open area vs more forested area, then the $\delta^{13}\text{C}$ values of mammal teeth should
261 reflect this change and, therefore, differ. If the $\delta^{13}\text{C}$ values of mammal teeth remain similar,
262 then there is no basis for inferring a change in vegetation cover from the viewpoint of carbon
263 stable isotopes.

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

277 *Question 2.*—Are there differences in the $\delta^{13}\text{C}$ values of *Promegantereon ogygia*
278 from BAT-1 and BAT-3 that imply that the BAT-3 population used a more open habitat than
279 the BAT-1 population? In a comparison of BAT-1 and BAT-3 populations of the
280 sabertoothed cat *Promegantereon ogygia*, Siliceo et al. (2014) considered them as a

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"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 to 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 to 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 to 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 carnivorans (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 carnivorans 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 carnivoran 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 carnivorans and are published here for the first time.

The exceptional proportion of carnivoran 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 Batallones-10 (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 dietary 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

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Aceratherium incisivum) (Supplementary Table 1). Megaherbivores were not used in the analyses of predator diets (see below), 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* ($H = 1.49, p = 0.47$), 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 pre-weaning teeth (first and second molars) vs post-weaning 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. Carnivoran tooth enamel is very thin compared to that of most herbivores and the teeth are delicate; in some instances, we could sample only 2 to 3 mg. Fortunately, in recent years, mass spectrometers have provided good results for apatite amounts as low as ~0.5 mg after chemical treatment.

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

359 After treatment, isotopic analyses were performed on Thermo MAT253 dual-inlet
360 isotope-ratio mass spectrometers coupled to a Kiel IV Carbonate Device at the Stable
361 Isotope Laboratory of the Department of Earth and Environmental Sciences of the
362 University of Michigan and at the Stable Isotope Laboratory of the University of California
363 Santa Cruz. Duplicate analyses were carried out for ~ 90% of the samples.

364 Carbon stable isotope results are reported in δ -notation, $\delta^H X_{\text{sample}} = [(R_{\text{sample}} - R_{\text{standard}}) /$
365 $R_{\text{standard}}] \times 1000$, where X is the element, H is the mass of the rarer, heavy isotope, and
366 $R = {}^{13}\text{C} / {}^{12}\text{C}$. The isotopic reference standard for carbon is Vienna Pee Dee Belemnite (VPDB).
367 The standards used were Carrara Marble (CM; $\delta^{13}\text{C} = 2.05\text{‰}$), NBS-18 ($\delta^{13}\text{C} = -5.03\text{‰}$)
368 and NBS-19 ($\delta^{13}\text{C} = 1.95\text{‰}$). The standard deviations for repeated measurements of CM (n
369 = 15), NBS-18 (n = 10), and NBS-19 (n = 8) were 0.09‰, 0.04‰, and 0.08‰, respectively.

370 To compare the Miocene $\delta^{13}\text{C}$ values to those documented for modern vegetation, it
371 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
372 geohistorical changes in $\delta^{13}\text{C}$ of CO_2 since the late Miocene and the increase in light carbon
373 released by the burning of fossil fuels in the last 200 years (Friedli et al. 1986; Marino and

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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 $\sim -6\text{‰}$, a difference of $\sim 2\text{‰}$ relative to modern $\delta^{13}\text{C}_{\text{atmCO}_2}$ ($\sim -8\text{‰}$). 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. L (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. Cut-off values given here for closed-canopy forest and woodland-mesic C_3 grassland, wooded grassland-xeric C_3 grassland and mixed C_3 - C_4 grassland, and mixed C_3 - C_4 grassland and pure C_4 grassland were obtained from widely accepted values in the literature, e.g., MacFadden and Cerling (1996), Feranec (2003), Kohn et al. (2005), Tütken et al. (2013). The cut-off $\delta^{13}\text{C}$ value between woodland-mesic C_3 grassland and wooded grassland-xeric C_3 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 cut-off $\delta^{13}\text{C}$ values for wooded grassland-xeric C_3 grassland correspond well with $\delta^{13}\text{C}$ values for C_3 trees, shrubs and grasses found mainly in Mediterranean forest, woodland and scrub, tropical and subtropical dry broadleaf forest, and desert and xeric shrubland.

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397 According to the UNESCO classification of African vegetation (White 1983), (1)
398 closed forest is a continuous stand of trees at least 10 m tall with interlocking crowns, (2)
399 woodland has trees with canopy heights of 8 to 20 m, with their crowns covering at least
400 40% of the land surface but not overlapping extensively, (3) wooded grassland has a cover
401 of grasses and other herbs, with woody plants covering between 10% to 40% of the ground,
402 and (4) grassland is covered with grasses and other herbs, with woody cover less than 10%.
403 Habitat inferences are based on the $\delta^{13}\text{C}$ values of herbivores since they feed directly from
404 the surrounding vegetation. Based on their dental adaptations, the herbivores in our study
405 cover a dietary spectrum from browsers (rhinoceroses, Bovidae indet.) to mixed feeders
406 (*Hipparion* spp.) to mixed feeder-grazers (*Austroportax* sp.). The multi-taxic approach used
407 here guarantees that habitat inference is supported by several taxa of different dietary habits.
408 To infer dietary preferences from the $\delta^{13}\text{C}$ values of carnivorans and further delineate
409 the habitat present in the study area, it is necessary to account for the trophic discrimination
410 between predator and prey, usually herbivores. This $\delta^{13}\text{C}$ offset results in slightly lower $\delta^{13}\text{C}$
411 values in carnivoran enamel bioapatite compared to that of the herbivores (Fox-Dobbs et al.
412 2006; Clementz et al. 2009). To account for this trophic discrimination, we adjusted
413 carnivoran $\delta^{13}\text{C}$ values by + 1.3‰, following Fox-Dobbs et al. (2006) and Clementz et al.
414 (2009).
415 As previously indicated, we have also used carbon stable isotope analyses in this
416 study to provide further information about the diet of the bear *Indarctos arctoides* from
417 BAT-3. Different approaches are reported in the literature to study the diet of these
418 omnivore carnivores such as dental microwear texture analysis, dental paleopathology
419 analysis, biomechanical and anatomical analyses or stable isotope analyses (e.g., Donohue et
420 al. 2013; Soibelzon et al. 2014, and references therein). Here, we use the approach described

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by Soibelzon et al. (2014) to shed light on the diet of this ursid, specifically on its degree of carnivory. Soibelzon et al. (2014) approach is based in 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, i.e., 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 diet source for the ursid, i.e., the ursid would be a herbivorous omnivore.

Statistical Analysis and Diet Characterization

We checked for normality in all of the data sets used in this study with Shapiro-Wilk tests. 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, analysis of variance (ANOVA), and post-hoc Tukey tests. Non-parametric 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).

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445 Prey species included in the mixing model were selected on the basis of their body
446 size. We selected herbivores with a medium body size for ungulates (i.e., hipparionine
447 horses, suid and bovids; Table 2) as the most probable prey for the predators considered here.
448 In the analysis of the dietary preferences of the predators, we did not include megaherbivore
449 species present in Cerro de los Batallones sites (rhinoceroses, giraffids and proboscideans),
450 as we consider that the carnivorans would have consumed these species only under
451 exceptional circumstances (i.e., young, diseased, or old megaherbivore individuals, or as
452 carrion) and not on a regular basis (see Domingo et al. 2013b).

453 The combination of some sources to reduce their total number in the Bayesian
454 analysis is recommended so as to achieve a more constrained solution (Phillips et al. 2005,
455 2014). Combining sources must have a logical basis, e.g., combination within the same
456 higher taxon or combination of taxa from well-differentiated habitats such as marine vs
457 terrestrial. Following this recommendation and their statistically non-different $\delta^{13}\text{C}$ values
458 (see above), we grouped together the hipparionine horses from BAT-1, BAT-3, and BAT-
459 10.

460 The more different that food sources are from each other in terms of their isotopic
461 composition, the more constrained is the result obtained from the mixing model, i.e., the
462 estimates indicative of the contribution of each source to the diet of the consumer (Phillips et
463 al. 2005, 2014). For Cerro de los Batallones, $\delta^{13}\text{C}$ values of the herbivore prey species show
464 considerable overlap (Fig. 3, Supplementary Table 2), so we anticipate that the mixing
465 model will provide less source discrimination than in a scenario with highly distinctive
466 sources. Still, MixSIAR can provide useful information for characterizing trophic
467 relationships in this ancient food web.

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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 C_3 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).

Comment [SD6]: Fig. 3 here

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 ($t = 1.99$, $p = 0.06$), nor when the variances of these two groups were compared ($F = 1.52$, $p = 0.81$).

We also compared $\delta^{13}\text{C}$ values of carnivorous 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

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492 *Promegantereon* samples ($F = 1.07, p = 0.93$) did not differ significantly. No significant
493 differences in the $\delta^{13}\text{C}$ means were observed for the other sabertoothed cat, *Machairodus*
494 *aphanistus* ($t = -1.48, p = 0.16$), and similarly, no significant differences were detected in
495 their variances ($F = 1.57, p = 0.49$). For *Magericyon anceps*, we could not perform statistical
496 comparison between the two sites, since we sampled only one tooth from BAT-3 (Table 4).

Comment [SD7]: Table 4 here

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

503 To assess the degree of carnivory of *Indarctos arctoides* from BAT-3, we have
504 determined the difference between the $\delta^{13}\text{C}$ values of the ursid of interest and potential
505 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
506 trophic discrimination between predator and prey (Fox-Dobbs et al. 2006; Clementz et al.
507 2009). From the viewpoint of carbon stable isotope analyses, *Indarctos arctoides* would be
508 considered an ursid with a omnivorous diet that incorporated a large proportion of meat.
509 Then, this ursid is analyzed in this paper as a potential competitor for the rest of the
510 predators. To maintain the comparability with the rest of the predators, we used the 1.3‰
511 adjustment for *Indarctos arctoides* (Table 4, Fig. 3).

512 As expected, the contributions of different prey species to predator diets had median
513 values that generally were close to one another (Table 6). MixSIAR median results indicated
514 that the four prey taxa analyzed could have contributed quite similarly to most of the
515 predator diets. Taking this into account, it is possible to extract further inferences. At BAT-1,

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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 might be considered with caution. Future discoveries 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 to analyze 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 million

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years ago. 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.

Comment [SD8]: Table 5 here

(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 to 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 the 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 to 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, later they entered the region during the time when BAT-3 was active as a trap. The

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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 carnivorous 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 that the absence of some of the carnivorous in these localities might be a matter of chance, i.e., 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 carnivorous guild of the Madrid Basin not associated with a shift in vegetation and emphasizes the potential role of interactions among the carnivorous 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 to *Promegantereon* from BAT-3, BAT-1 *Promegantereon*

Comment [SD9]: Table 6 here

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588 incorporated into its diet a higher proportion of Bovidae indet., a dweller of rather closed
589 woodland habitat (Table 6). This bovid was found at BAT-3 and not at BAT-1; but notably,
590 previous studies hypothesized that *Promegantereon ogygia* from BAT-1 was incorporating a
591 prey source, not represented among the BAT-1 fossil remains, with $\delta^{13}\text{C}$ values indicative of
592 a closed woodland (Domingo et al. 2013b).
593 The lack of significant differences in the $\delta^{13}\text{C}$ values does not point to an increase in the
594 cursorial abilities (i.e., use of more open portion of the habitat) of the BAT-3
595 *Promegantereon* population compared to the BAT-1 population from the viewpoint of
596 carbon stable isotopes.

597 (3) *Is there significant overlap in the predators' $\delta^{13}\text{C}$ values that could be indicative*
598 *of high levels of competition among them?*.—When BAT-1 and BAT-3 *Machairodus*
599 *aphanistus* samples were compared, we obtained similar results to those for
600 *Promegantereon ogygia*; that is, $\delta^{13}\text{C}$ values did not differ significantly, but the BAT-3
601 sample displayed slightly higher values (Table 4, Fig. 3). The mixing model suggests that
602 Bovidae indet. was the preferred prey species for BAT-1 *Machairodus aphanistus* and that,
603 by the time when BAT-3 was forming, this sabertoothed cat had changed its preferred prey
604 species to herbivores from slightly more open woodland, e.g., *Hipparion* spp. (Table 6).

605 The $\delta^{13}\text{C}$ values of the carnivorans from BAT-3 show considerable overlap (Fig. 3).
606 The ANOVA and Kruskal-Wallis tests demonstrated no significant differences among the
607 carbon isotope signatures of BAT-3 carnivores (Table 5; Supplementary Table 3), and the
608 MixSIAR analysis revealed that all BAT-3 predators evaluated had a common preferred diet
609 source: the hipparionine horses (Table 6). In any event, the predators could have also
610 strongly competed for the rest of the prey in view of the very similar contribution values.

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611 These results are consistent with high levels of interspecific competition among BAT-3
612 predators, with similar-sized species competing for the same prey. Yet, further information
613 on the partitioning of resources among these large predators can be added. First, at BAT-1,
614 *Magericyon anceps* showed $\delta^{13}\text{C}$ values that were significantly more positive than those of
615 *Promegantereon ogygia* and *Machairodus aphanistus* (Domingo et al. 2013b). *Magericyon*
616 *anceps* was not included in the statistical analysis of BAT-3 predators because we could
617 only sample one tooth from BAT-3 (Table 4). Results obtained by Domingo et al. (2013b)
618 were similar to those from MixSIAR for *Magericyon anceps*: its preferred prey species was
619 the antelope *Austroportax* sp., a dweller of the open part of the woodland-mesic C₃
620 grassland habitat inferred for Cerro de los Batallones (Table 6). In BAT-3, as in BAT-1, the
621 sampled tooth of *Magericyon anceps* had a higher $\delta^{13}\text{C}$ value than those of the sabertoothed
622 cats (and the rest of BAT-3 carnivores) and fell close to the threshold between woodland-
623 mesic C₃ grassland and wooded grassland-xeric C₃ grassland (Table 4, Fig. 3). Then, it is
624 plausible to infer resource use coincident with that inferred from BAT-1 specimens: the
625 coexistence of *Magericyon anceps* with the other predators (especially those larger than 100
626 kg) was facilitated because this amphicyonid hunted prey from a more open portion of the
627 habitat (Domingo et al. 2013b).

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

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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 carnivorans 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 carnivoran guilds, other strategies that permit the coexistence of predators include separation of hunting-activity times (diurnal vs nocturnal carnivores) (Karanth and Sunquist 2000; Owen Smith and Mills 2008). These strategies could also have occurred in the BAT-3 carnivoran guild but they cannot be directly inferred from the fossil record.

In this study, we performed new analyses of the carnivoran-rich BAT-3 assemblage and have rejected the hypothesis that differences between the carnivoran 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 Neogene carnivores only on limited occasions.

Conclusions

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Cerro de los Batallones, and specifically the localities of Batallones-1 and Batallones-3, stand out in the Miocene record of mammals for preserving an unusual concentration of carnivoran remains that represent diverse predator guilds. These time-successive sites display notable differences in the composition and abundance of carnivoran species. A habitat change was proposed as a possible hypothesis to explain the differences in the carnivoran 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 C₃ grassland habitat. The carnivoran guild from the Madrid Basin experienced a rapid change in its component species without a significant change in habitat. The faunal differences could reflect changes in the original carnivoran population densities and the sequence of appearances and disappearances of carnivoran species from the Madrid Basin driven by competitive interactions rather than by vegetation change. The alternative hypothesis that differences in the carnivoran 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 carnivorous omnivore.

A Bayesian mixing model allowed us to characterize the contribution of selected prey to carnivoran 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

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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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Figure captions

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 hemi-mandible 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 hemi-mandible 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 is 5 cm long. The P4 and p4 were sampled in this study.

FIGURE 3. Stable carbon isotope values (mean $\pm$ 1 SD) for Batallones-1 (BAT-1) and Batallones-3 (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.

Fig. 1. Two-column.

82x45mm (300 x 300 DPI)

Figure 2. Two-column

110x83mm (300 x 300 DPI)

Figure 3. Two-column

123x103mm (300 x 300 DPI)

Table 1. Abundances and proportions of large mammals from Batallones-1 and Batallones-3. NISP = Number of Identified Specimens. In this table, we do not account for undetermined remains. Taxa analyzed in this study are marked with an asterisk.

TAXON	FAMILY/ORDER	BATALLONES-1 ^a		BATALLONES-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* ^b	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 ^c	Felidae/Carnivora	775	5.39	142	1.34
Mustelidae/Mephitidae ^c	Mustelidae-Mephitidae/Carnivora	453	3.15	266	2.50
<i>Hipparion</i> spp.* ^d	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

^aIt refers to Batallones-1 Lower Level Assemblage, which is the carnivoran-dominated assemblage (see Domingo et al. 2013a for further information)

^bIn Batallones-1, Amphicyonidae is exclusively represented by *Magericyon anceps*. In Batallones-3, Amphicyonidae is represented by *Magericyon anceps* and *Thaumastocyon* sp.

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

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

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Table 2. Body mass of the carnivores and herbivores included in the predators' 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, only Batallones-10 (BAT-10), Batallones-1 (BAT-1) and Batallones-3 (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. 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 BAT-10	BAT-10	BAT-1	BAT-3	After BAT-3	Temporal duration of the species (Myr)
<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

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	Procedence	N	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					
	BAT-1, BAT-3,				
<i>Hipparion</i> spp.	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

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.

	<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
$F = 0.094, p = 0.984$				
Levene's test = 0.376, $p = 0.824$				

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' diet are marked in bold.

Predators	Procedence	<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</i> sp.	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)

Supplementary Table 1. $\delta^{13}\text{C}$ values of carnivores (A) and herbivores (B) from Cerro de los Batallones (Madrid Basin, Spain). The + 1.3‰ adjustment is provided for the carnivore taxa (Fox-Dobbs et al. 2006; Clementz et al. 2009). Lower premolars (p) and molars (m) are expressed in lower case. Upper premolars (P) and molars (M) are expressed in upper case. R = Right, L = Left. BAT-1 = Batallones-1; BAT-3 = Batallones-3; BAT-10 = Batallones-10.

A. CARNIVORES

Fossil site	Signature1	Signature2	Family	Taxon	Tooth	$\delta^{13}\text{C}$ (‰ VPDB)	$\delta^{13}\text{C}$ (‰ VPDB) +1.3‰
BAT-1	B-1006 (3)	S1	Felidae	<i>Promegantereon ogygia</i>	Rp4	-12.39	-11.09
BAT-1	B-3153	S2	Felidae	<i>Promegantereon ogygia</i>	Lp4	-13.04	-11.74
BAT-1	B-2179	S3	Felidae	<i>Promegantereon ogygia</i>	lower canine	-12.28	-10.98
BAT-1	B-1676(8)	S5	Felidae	<i>Promegantereon ogygia</i>	Rp3	-11.97	-10.67
BAT-1	SS	S18	Felidae	<i>Promegantereon ogygia</i>	upper canine	-13.09	-11.79
BAT-1	SS	S19	Felidae	<i>Promegantereon ogygia</i>	upper canine	-12.08	-10.78
BAT-1	SS	S20	Felidae	<i>Promegantereon ogygia</i>	upper canine	-14.38	-13.08
BAT-1	BAT-1'02 D3-19	S36	Felidae	<i>Promegantereon ogygia</i>	lower canine	-11.44	-10.14
BAT-1	B-757	S37	Felidae	<i>Promegantereon ogygia</i>	upper canine	-12.62	-11.32
BAT-1	B-4962	S6	Felidae	<i>Machairodus aphanistus</i>	Rp4	-11.74	-10.44
BAT-1	B-5279	S7	Felidae	<i>Machairodus aphanistus</i>	Lp3	-11.94	-10.64
BAT-1	B-855(2)	S8	Felidae	<i>Machairodus aphanistus</i>	LP3	-12.26	-10.96
BAT-1	B-1018	S9	Felidae	<i>Machairodus aphanistus</i>	LP3	-12.75	-11.45
BAT-1	B-1183(2)bis	S10	Felidae	<i>Machairodus aphanistus</i>	RP3	-13.19	-11.89
BAT-1	SS	S12	Felidae	<i>Machairodus aphanistus</i>	upper canine	-12.98	-11.68
BAT-1	SS	S13	Felidae	<i>Machairodus aphanistus</i>	upper canine	-12.46	-11.16
BAT-1	SS	S14	Felidae	<i>Machairodus aphanistus</i>	upper canine	-13.09	-11.79
BAT-1	SS	S15	Felidae	<i>Machairodus aphanistus</i>	lower canine	-11.99	-10.69
BAT-1	SS	S16	Felidae	<i>Machairodus aphanistus</i>	lower canine	-12.56	-11.26

BAT-1	SS	S17	Felidae	<i>Machairodus aphanistus</i>	m1	-11.81	-10.51
BAT-1	B-3365	S11	Amphicyonidae	<i>Magericyon anceps</i>	Lp3	-11.2	-9.9
BAT-1	B-5441	S28	Amphicyonidae	<i>Magericyon anceps</i>	m2	-11.56	-10.26
BAT-1	B-5439 (2)	S29	Amphicyonidae	<i>Magericyon anceps</i>	RM1	-12.12	-10.82
BAT-1	B-5439 (2) bis	S38	Amphicyonidae	<i>Magericyon anceps</i>	RM2	-11.10	-9.80
BAT-1	B-396	S39	Amphicyonidae	<i>Magericyon anceps</i>	incisor	-11.70	-10.40
BAT-1	B-1337	S40	Amphicyonidae	<i>Magericyon anceps</i>	incisor	-11.59	-10.29
BAT-1	B-475	S41	Amphicyonidae	<i>Magericyon anceps</i>	lower canine	-10.97	-9.67
BAT-3	BAT-3'11 132	S100	Felidae	<i>Promegantereon ogygia</i>	Rm1	-12.50	-11.20
BAT-3	BAT-3'11 1467	S101	Felidae	<i>Promegantereon ogygia</i>	Rm1	-11.16	-9.86
BAT-3	BAT-3'10 1773	S104	Felidae	<i>Promegantereon ogygia</i>	Rm1	-11.58	-10.28
BAT-3	S-683A	S105	Felidae	<i>Promegantereon ogygia</i>	Lm1	-11.82	-10.52
BAT-3	BAT-3'01 60A	S106	Felidae	<i>Promegantereon ogygia</i>	LP4	-11.47	-10.17
BAT-3	BAT-3'13 2070	S108	Felidae	<i>Promegantereon ogygia</i>	Rp4	-13.32	-12.02
BAT-3	BAT-3'13 1596	S119	Felidae	<i>Promegantereon ogygia</i>	Rp4	-13.55	-12.25
BAT-3	BAT-3'13 2057	S120	Felidae	<i>Promegantereon ogygia</i>	Lp4	-12.49	-11.19
BAT-3	BAT-3'11 2495	S93	Felidae	<i>Machairodus aphanistus</i>	LP4	-13.28	-11.98
BAT-3	BAT-3'09 1622	S94	Felidae	<i>Machairodus aphanistus</i>	RP4	-11.19	-9.89
BAT-3	BAT-3'10 2044	S95	Felidae	<i>Machairodus aphanistus</i>	RP4	-12.67	-11.37
BAT-3	BAT-3'12 2448	S96	Felidae	<i>Machairodus aphanistus</i>	LP4	-11.88	-10.58
BAT-3	BAT-3'10 235	S97	Felidae	<i>Machairodus aphanistus</i>	Lm1	-11.70	-10.40
BAT-3	BAT-3'08 92	S98	Felidae	<i>Machairodus aphanistus</i>	Lp4	-12.53	-11.23
BAT-3	BAT-3'10 149	S99	Felidae	<i>Machairodus aphanistus</i>	Rp4	-11.67	-10.37
BAT-3	BAT-3'09 786b	S102	Felidae	<i>Machairodus aphanistus</i>	Lm1	-11.51	-10.21
BAT-3	BAT-3'09 786b	S107	Felidae	<i>Machairodus aphanistus</i>	LP4	-11.95	-10.65
BAT-3	BAT-3'07 582	S125	Amphicyonidae	<i>Magericyon anceps</i>	Lm3	-10.72	-9.42
BAT-3	BAT-3'08 604	S110	Amphicyonidae	<i>Thaumastocyon</i> sp.	L lower canine	-12.70	-11.40
BAT-3	BAT-3'10 347	S111	Amphicyonidae	<i>Thaumastocyon</i> sp.	incisor	-11.27	-9.97

BAT-3	BAT-3'10 1689	S115	Amphicyonidae	<i>Thaumastocyon</i> sp.	R upper canine	-12.27	-10.97
BAT-3	BAT-3'13 185	S112	Mustelidae	<i>Eomellivora piveteaui</i>	LP4	-11.18	-9.88
BAT-3	BAT-3'09 1000	S113	Mustelidae	<i>Eomellivora piveteaui</i>	LP4	-13.47	-12.17
BAT-3	BAT-3'09 1000	S114	Mustelidae	<i>Eomellivora piveteaui</i>	Rp4	-11.49	-10.19
BAT-3	BAT-3'09 250	S116	Mustelidae	<i>Eomellivora piveteaui</i>	RP3	-11.63	-10.33
BAT-3	BAT-3'09 688	S117	Mustelidae	<i>Eomellivora piveteaui</i>	R incisor	-11.74	-10.44
BAT-3	BAT-3'08 526	S118	Mustelidae	<i>Eomellivora piveteaui</i>	R lower canine	-12.91	-11.61
BAT-3	BAT-3'06 563	S84	Ursidae	<i>Indarctos arctoides</i>	Rm1	-14.24	-12.94
BAT-3	BAT-3'11 1130	S85	Ursidae	<i>Indarctos arctoides</i>	Lm1	-12.06	-10.76
BAT-3	BAT-3'10 666	S86	Ursidae	<i>Indarctos arctoides</i>	Lm1	-11.95	-10.65
BAT-3	BAT-3'10 400	S87	Ursidae	<i>Indarctos arctoides</i>	Lm1	-12.59	-11.29
BAT-3	BAT-3'08 358	S88	Ursidae	<i>Indarctos arctoides</i>	Rm1	-12.22	-10.92
BAT-3	BAT-3'09 791	S89	Ursidae	<i>Indarctos arctoides</i>	Lm1	-10.74	-9.44
BAT-3	BAT-3'09 31	S90	Ursidae	<i>Indarctos arctoides</i>	Rm2	-11.84	-10.54
BAT-3	BAT-3'05 254	S91	Ursidae	<i>Indarctos arctoides</i>	Rm2	-12.23	-10.93
BAT-3	BAT-3'05 255	S92	Ursidae	<i>Indarctos arctoides</i>	Lm2	-12.11	-10.81

B. HERBIVORES

Fossil site	Signature1	Signature2	Family	Taxon	Tooth	$\delta^{13}\text{C}$ (‰ VPDB)
BAT-1	B/S695	S31	Equidae	<i>Hipparion</i> sp.	RP3/P4	-9.80
BAT-1	B-4496	S32	Equidae	<i>Hipparion</i> sp.	Lm3	-11.66
BAT-1	B/S708	S33	Equidae	<i>Hipparion</i> sp.	Rm1	-9.79
BAT-1	B/S696	S35	Equidae	<i>Hipparion</i> sp.	RM1/M2	-8.31
BAT-1	B/S709a	S45	Equidae	<i>Hipparion</i> sp.	Rm2	-10.64
BAT-1	B/S709b	S46	Equidae	<i>Hipparion</i> sp.	Rm1	-10.77
BAT-1	B-3050	S47	Equidae	<i>Hipparion</i> sp.	incisor	-9.69

BAT-10	BAT-10'09 F5-13	S48	Equidae	<i>Hipparion</i> sp.	incisor	-11.89
BAT-10	BAT-10'09 G4-41	S49	Equidae	<i>Hipparion</i> sp.	incisor	-9.07
BAT-10	BAT-10'09 G2-138	S50	Equidae	<i>Hipparion</i> sp.	incisor	-12.04
BAT-10	BAT-10'09 G2-141	S51	Equidae	<i>Hipparion</i> sp.	incisor	-8.17
BAT-10	BAT-10'11 G1-1	S75	Equidae	<i>Hipparion</i> sp.	RM1/M2	-10.81
BAT-10	BAT-10'11 G5-10	S76	Equidae	<i>Hipparion</i> sp.	incisor	-9.28
BAT-10	BAT-10'11 C6-25a	S77	Equidae	<i>Hipparion</i> sp.	incisor	-9.66
BAT-10	BAT-10'11 D6-21	S78	Equidae	<i>Hipparion</i> sp.	incisor	-10.8
BAT-10	BAT-10'11 F3-6	S79	Equidae	<i>Hipparion</i> sp.	Rp3/p4	-9.18
BAT-3	BAT-3'13 1866	S121	Equidae	<i>Hipparion</i> sp.	Upper molar	-11.12
BAT-3	BAT-3'13 1168	S122	Equidae	<i>Hipparion</i> sp.	m3	-11.08
BAT-3	BAT-3'10 1454	S124	Equidae	<i>Hipparion</i> sp.	molar	-10.67
BAT-10	BAT-10'09 F4-24	S65	Suidae	<i>Microstonyx</i> sp.	incisor	-9.03
BAT-10	BAT-10'11 G2-43	S80	Suidae	<i>Microstonyx</i> sp.	incisor	-10.02
BAT-10	BAT-10'11 F2-16	S81	Suidae	<i>Microstonyx</i> sp.	incisor	-12.62
BAT-10	BAT-10'11 F2-14	S82	Suidae	<i>Microstonyx</i> sp.	incisor	-11.68
BAT-1	BAT-1'03 D4-323	S74	Bovidae	<i>Austroportax</i> sp.	LM2	-9.98
BAT-1	BAT-1'05 D4-78	S83	Bovidae	<i>Austroportax</i> sp.	LM2	-9.41
BAT-3	BAT-3'08 699	S123	Bovidae	Bovidae indet.	p2	-12.44
BAT-1	B-461	S27	Rhinocerotidae	Rhinocerotinae indet.	p2	-9.42
BAT-1	SS BLOQUE1	S43	Rhinocerotidae	Rhinocerotinae indet.	Lp3	-10.3
BAT-1	BAT-1'05 E3-150	S69	Rhinocerotidae	Rhinocerotinae indet.	LM1	-11.41
BAT-1	BAT-1'07 F4-22	S72	Rhinocerotidae	Rhinocerotinae indet.	Lm1	-10.96
BAT-1	BAT-1'04 F5-157	S70	Rhinocerotidae	<i>Aceratherium incisivum</i>	RM1	-10.52
BAT-1	B-2788	S71	Rhinocerotidae	<i>Aceratherium incisivum</i>	Lm1	-11.78

Supplementary Table 2. A, Results of the ANOVA and Tukey post-hoc tests for $\delta^{13}\text{C}$ values of the selected prey. B, Results of the Kruskal-Wallis test for $\delta^{13}\text{C}$ values of the selected prey. Bovidae indet. could not be included in the analysis because only 1 tooth was sampled. $p > 0.05$ = no significant difference, $p < 0.05$ = significant difference.

A. ANOVA test

	<i>Microstonyx</i> sp.	<i>Austroportax</i> sp.
<i>Hipparion</i> spp.	0.632	0.817
<i>Microstonyx</i> sp.		0.519
$F = 0.695, p = 0.510$		
Levene's test = 2.381, $p = 0.116$		

B. KRUSKAL-WALLIS test

	<i>Microstonyx</i> sp.	<i>Austroportax</i> sp.
<i>Hipparion</i> spp.	0.490	0.590
<i>Microstonyx</i> sp.		0.488
$H = 1.026, p = 0.599$		

Supplementary Table 3. Results of the Kruskal-Wallis test for $\delta^{13}\text{C}$ values of BAT-3 carnivores. $p > 0.05$ = no significant difference, $p < 0.05$ = significant difference.

	<i>Machairodus aphanistus</i>	<i>Eomellivora piveteaui</i>	<i>Thaumastocyon sp.</i>	<i>Indarctos arctoides</i>
<i>Promegantereon ogygia</i>	0.962	0.847	0.912	0.885
<i>Machairodus aphanistus</i>		0.768	0.853	0.453
<i>Eomellivora piveteaui</i>			0.897	0.444
<i>Thaumastocyon sp.</i>				0.712
$H = 0.593, p = 0.964$				