Carbon stable isotope paleoecology of carnivorans from the Miocene localities of Batallones-1 and Batallones-3 (Madrid Basin, Spain)

Paleoecología de mamíferos carnívoros de los yacimientos miocenos de Batallones-1 y Batallones-3 (Cuenca de Madrid, España) a través de isótopos estables del carbono

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Palabras clave: isótopos estables del carbono, Cuenca de Madrid, Cerro de los Batallones, carnívoros, modelos de mezcla bayesianos

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

Sites dominated by carnivoran remains are rare in the fossil record because mammalian fossil assemblages normally reflect the herbivore:carnivoran proportion of living communities, which has been estimated as 10:1 (Eisenberg 1981). These sites are usually formed under exceptional taphonomic circumstances and constitute unique opportunities to study diverse aspects of past carnivoran guilds, from taxonomic diversity to ecomorphological traits to trophic interactions. Stable isotope analysis on dental enamel is a proven robust method to make inferences on the diet and resource and habitat use of extinct mammals.

In Cerro de los Batallones Miocene paleontological complex (Madrid Basin, Spain), two sites, Batallones-1 (BAT-1) and Batallones-3 (BAT-3), are primarily composed of carnivoran remains (> 97% of the large-mammal remains; Table 1) and are providing precious information about taxa that were previously unknown or poorly known in the fossil record of mammals. In the Late Miocene, these sites acted as natural traps for the fauna. The two sites are diverse in their carnivoran faunal composition with BAT-1 recording a total of 10 species and BAT-3 recording a total of 13 species. Although BAT-1 and BAT-3 are dated as Vallesian (ca. 10-9 Ma), it seems that BAT-3 is slightly younger than BAT-1 (based on small-mammal biochronology) and differences in their carnivoran compositions have been attributed to these temporal difference. An associated environmental shift has been proposed as a probable cause behind these taxonomic and abundance differences but it remains unclear.

In a previous study, we conducted carbon stable isotope analyses on three sympatric hypercarnivores from BAT-1: the sabertoothed cats *Promegantereon ogygia* and *Machairodus aphanistus,* and the amphicyonid *Magericyon anceps* (Domingo et al. 2013). In this paper, we expand the isotopic sampling to BAT-3 carnivorans (including *Promegantereon ogygia, Machairodus aphanistus* and *Magericyon anceps,* but also the ursid *Indarctos arctoides*, the giant mustelid *Eomellivora piveteaui* and the amphicyonid *Thaumastocyon* sp.) in order to compare the feeding ecology of BAT-1 and BAT-3 carnivore populations and to evaluate a possible environmental change between these two sites.

For mammals, the carbon stable isotope composition ($\delta^{13}C$) of tooth enamel tracks primarily the $\delta^{13}C$ values of their diet (Koch 2007). $\delta^{13}C$ values of herbivorous mammals reflect the values of ingested plants, which varies 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. $\delta^{13}C$ values of carnivore mammals reflect the values of ingested prey (Koch 2007). By extension, $\delta^{13}C$ values yielded by mammalian fossil enamel are a reliable tool for reconstructing the type(s) of habitats where the animals lived.

We sampled and analyzed the enamel of 63 carnivoran teeth. Twenty seven teeth belonged to BAT-1 carnivores. The remaining 36 teeth belonged to BAT-3 carnivores. The twenty six herbivore tooth samples analyzed in this study correspond to hipparionine horses (Family Equidae, *Hipparion* sp.), a pig (family Suidae, *Microstonyx* sp.), an antelope (Family Bovidae, *Austroportax* sp.) and another bovid that is under study (Bovidae indet.). Teeth analyzed in this work were all from adult individuals and are housed in the collections of the Museo Nacional de Ciencias Naturales-CSIC (Madrid, Spain). XRD

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Taxon	Family/Order	Batallones-1		Batallones-3	
		NISP	%	NISP	%
*Promegantereon ogygia**	Felidae/Carnivora	7125	49.53	3116	29.33
*Machairodus aphanistus**	Felidae/Carnivora	3226	22.43	3869	36.42
Amphicyonidae*	Amphicyonidae/Carnivora	858	5.96	525	4.94
*Indarctos arctoides**	Ursidae/Carnivora	-		1984	18.68
*Eomellivora piveteaui**	Mustelidae/Carnivora	-		251	2.36
Protictitherium crassum	Hyaenidae/Carnivora	1339	9.31	418	
Simocyon batalleri	Ailuridae/Carnivora	178	1.24	-	
Felinae	Felidae/Carnivora	775	5.39	142	1.34
Mustelidae/Mephitidae	Mustelidae-Mephitidae/ Carnivora	453	3.15	266	2.50
Hipparion sp.*	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
Suidae*	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	

Table 1. Abundances and proportions of large-mammals from Batallones-1 and Batallones-3. NISP = Number of Identified Specimens. Undetermined remains are excluded from this table. Taxa analyzed in this study are marked with an asterisk. In Batallones-1, Amphicyonidae is exclusively represented by *Magericyon anceps*. In Batallones-3, Amphicyonidae is represented by *Magericyon anceps* and *Thaumastocyon* sp. Several species are included within Felinae, Mustelidae/Mephitidae, Rhinocerotidae, Moschidae and Bovidae.

was performed on a subset of Cerro de los Batallones teeth to control for diagenetic changes. All the teeth analyzed yielded a hydroxyapatite mineralogy, demonstrating that they preserved the original mineral composition.

We followed the protocol of Koch et al. (1997) for enamel pretreatment. Carbon stable isotope results are reported in δ-notation, $\delta^{H}X_{sample}=[(R_{sample}–R_{standard})/\ R_{standard}]\times1000$, where X is the element, H is the mass of the rare, heavy isotope, and $R={}^{13}C/{}^{12}C$. The isotopic reference standard for carbon is Vienna Pee Dee Belemnite (VPDB).

We contrasted $\delta^{13}C$ values of BAT-1 and BAT-3 using Student's *t*-tests, analysis of the variance (ANOVA) and post-hoc Tukey tests. We used MixSIAR (Stock and Semmens 2013), a Bayesian mixing model, to estimate the proportions of prey contributions to the diet of each predator based on their $\delta^{13}C$ values.

All the statistical comparisons carried out on the $\delta^{13}C$ values, i.e., BAT-1 *vs* BAT-3 entire carnivore faunas, BAT-1 *vs* BAT-3 *Promegantereon ogygia*, BAT-1 *vs* BAT-3 *Machairodus aphanistus*, and BAT-1 *vs* BAT-3 *Hipparion* sp., demonstrate that the habitat remained stable (i.e., there are no statistical differences in the $\delta^{13}C$ values) in the time elapsed between BAT-1 and BAT-3 with the predominance of a woodland-mesic C_3 grassland habitat. Then, changes observed in the carnivoran composition and proportions of remains do not seem to be the consequence of a shift in the environmental conditions occurred over the time between the formation of BAT-1 and BAT-3. Rather, the differences in the taxonomic composition and remain abundances (Table 1) between BAT-1 and BAT-3 could be a reflection of the real carnivoran population densities and of the pattern of entrance and exit of carnivoran species from the Madrid Basin that would be driven by carnivore interactions (e.g., competitive displacement) rather than by a shift in the habitat.

The Bayesian mixing model allowed us to characterize the contribution of selected prey to the carnivoran diet. In the case of the two sabertoothed cats, we have detected subtle changes in their prey preferences, with BAT-1 populations preferring to take the undetermined Bovidae and BAT-3 populations preferring the hipparionine horses.

The considerable amount of medium to large predator species in BAT-3 with hypercarnivore diets along with the high overlap in their $\delta^{13}C$ values and similar $\delta^{13}C$ variances implying the occupation and use of a similar portion of the habitat are indicative of a strong interspecific competition among them (stronger than in BAT-1). The Bayesian mixing model also points to high levels of rivalry among BAT-3 predators as it resulted into a common preferred prey for BAT-3 carnivores: *Hipparion* sp. Both in BAT-1 and BAT-3, the exception seems to be the amphicyonid *Magericyon anceps,* whose $\delta^{13}C$ values imply resource partitioning with the use of prey from a more open portion of the woodland-mesic C_3 grassland habitat compared to the rest of carnivorans.

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