



Review of feeding ecology data of Late Pleistocene mammalian herbivores from South America and discussions on niche differentiation



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ABSTRACT

The present contribution provides a review of the feeding paleoecology studies based on carbon isotopic data available for 13 extinct megamammals that existed in South America during the Late Pleistocene. These ancient feed ecology data were grouped into four geographic ecoregions, supplying the basis for an analysis of the inter-specific interactions within a mammal assembly, based on the classification of taxa in three trophic guilds – grazers, browsers, and mixed-feeders.

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1. Introduction

Over the past few decades, several paleoecological studies of the herbivorous mammals from the South American Pleistocene have produced important insights about dietary adaptations. In addition to the characterization of feeding patterns, the results of these studies provide

valuable evidence on specific paleoenvironmental and paleoclimatic aspects of the habitats occupied by these species (e.g. MacFadden et al., 1994, 1999; Sánchez et al., 2004; Azevedo et al., 2012; Marcolino et al., 2012; Dantas et al., 2013a).

Traditionally, paleodietary studies have been based primarily on ecomorphological analyses, which evaluate potential analogies and homologies in the cranial, dental, and mandibular structural characteristics of the extinct taxa with those of modern species (MacFadden and Shockey, 1997). However, some innovative techniques have been

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developed and employed in the interpretation of South American fossil mammals, including analyses of isotopic composition from mineralized tissues, microwear patterns of tooth enamel, microfossils from teeth calculi and coprolites (e.g. MacFadden et al., 1994; Sánchez et al., 2004; Asevedo et al., 2012; Marcolino et al., 2012).

In the literature, the great contribution of isotopic studies to feeding pattern reconstructions is remarkable. This geochemical approach also permits the identification of environmental variables, such as temperature and humidity, as well as the type of vegetation found in the environment (Kohn and Law, 2006; Tapia and Adriano-Morán, 2012; Lopes et al., 2013). Thus, some isotopic paleodiet studies in South America (e.g. MacFadden et al., 1999; Sánchez et al., 2004; Dantas et al., 2013a; Lopes et al., 2013) have permitted inferences about the dynamics of plant communities in Late Pleistocene, through the diet information of the herbivorous megamammal specimens from a range of different latitudes represented by Quaternary fossiliferous sites.

The plant carbon isotope profiles ($\delta^{13}\text{C}$) depends primarily on the photosynthetic pathway (Koch, 2007). Most existing plants, ranging from trees and woody shrubs to grasses found on prairies and steppes at high altitudes or latitudes, are dependent on the Calvin–Benson (C_3) photosynthetic cycle. These plants present $\delta^{13}\text{C}_{\text{VPDB}}$ values of -22‰ to -30‰ , with a medium value of around -27‰ . By contrast, the few terrestrial plants that use the Hatch–Slack (C_4) photosynthetic route are primarily tropical and subtropical grasses. These species are typically found in open areas in warm regions subject to hydrological stress, and are able to tolerate low concentrations of CO_2 . In general, C_4 plants have $\delta^{13}\text{C}_{\text{VPDB}}$ values of -10‰ to -14‰ , averaging -12‰ . Plants that photosynthesize using Crassulacean Acid Metabolism (CAM), such as succulents, present intermediate $\delta^{13}\text{C}$ values (Ehleringer et al., 1991; Cerling, 1992; Quade et al., 1992; Ehleringer et al., 1997; MacFadden and Shockey, 1997; MacFadden et al., 1999; Sánchez et al., 2004; MacFadden, 2005; Domingo et al., 2012).

The diet of extinct mammals can be determined through $\delta^{13}\text{C}$ analysis from collagen and hydroxyapatite found in enamel, dentine or bone (Fricke, 2007; Bocherens and Drucker, 2013). A few decades ago the main source of this information was the enamel, because this tissue is less porous and, consequently, less susceptible to contamination by secondary carbonate, therefore this has contributed a large number of studies that used this component (e.g. MacFadden et al., 1999, and references there in). However, the use of hydroxyapatite extracted from fossil bone and dentine is extremely useful after specific treatments to remove the secondary carbonates.

The interpreted values of $\delta^{13}\text{C}$ in the different tissues represent fractionated values of the plant ingested. Studies of modern medium- to large-bodied herbivorous mammals have recorded fractionation values of $\delta^{13}\text{C}$ range of $14.1 \pm 0.5\text{‰}$ between diet and tissue (Cerling and Harris, 1999). Differences in diet-to-enamel $\delta^{13}\text{C}$ fractionation in mammals of different sizes (voles, rabbits, pigs and cattle) exposed to the same feed items were observed by Passey et al. (2005). These animals have differences in digestive physiology, including differences in methane production, which according to the authors, is the major determinant of enrichment of bioapatite-diet for an individual or species. For this reason, independent of the body mass of animals, our study only focuses on analysis of ruminants and monogastric South American herbivore megamammals, which potentially had the greatest similarities in digestive physiology and methane production.

According to Domingo et al. (2012), the $\delta^{13}\text{C}$ values expected for exclusively C_3 mammal consumers in different habitats are: -22‰ to -16‰ (closed canopy forests); -16‰ to -11‰ (mesic habitats or woodland); and -11‰ to -8‰ (wooded C_3 grassland to open arid C_3 grassland). These values are valid for regions at high latitudes ($35\text{--}40^\circ$) and high altitudes ($>3000\text{ m}$), no C_3 grasses are found in the tropics at low altitudes. In this case, $\delta^{13}\text{C}$ values lower than -10‰ should be interpreted as the product of an exclusive C_3 diet in closed habitats, i.e., trees and shrubs, which is typical of browsers (e.g. MacFadden

et al., 1999; Sánchez et al., 2003; Sánchez et al., 2004), while $\delta^{13}\text{C}$ values higher than -1‰ are consistent with a diet based on C_4 plants. Intermediate $\delta^{13}\text{C}$ values (between -10‰ and -1‰) indicate a mixed diet of C_3 and C_4 plants (MacFadden et al., 1999; MacFadden, 2005).

This study has two main objectives: (i) to review the data available on the feeding paleoecology of 13 herbivorous megamammals from the Late Pleistocene of South America, and (ii) to evaluate possible paleodietary patterns related to the geographic distribution of the taxa analyzed and identify potential interspecific interactions among the taxa, assigning them to ecological guilds based on three major feeding categories (grazers, browsers, and mixed-feeders).

2. Materials and methods

The present review analyzed data obtained from 15 published feeding paleoecology studies of 13 South American megamammal taxa that became extinct during the Late Pleistocene (Supplementary [Tables S1–S3]). Most of the articles reviewed used isotopic carbon analysis ($\delta^{13}\text{C}$) performed in hydroxyapatite (Table S1) and collagen (Table S2) in enamel, dentine or bone. The articles that used other analyses (Table S3) were compiled here for comparison. The taxa evaluated include: Proboscidea (Gomphotheriidae: *Notiomastodon*), Perissodactyla (Equidae: *Equus* and *Hippidion*), Artiodactyla (Camelidae: *Palaeolama*), Notoungulata (Toxodontidae: *Toxodon*), Liptoterna (Macrauchenidae: *Macrauchenia*), Pilosa (Megatheriidae: *Eremotherium*; Mylodontidae: *Scelidotherium*, *Scelidodon*, and *Valgipes*), and Cingulata (Glyptodontidae: *Sclerocalyptus*, *Glyptodon* and *Neosclerocalyptus*).

We follow the most current taxonomic arrangements proposed for the Gomphotheriidae taxa of South America. Thus the paleoecological data presented by Sánchez et al. (2004), Alberdi et al. (2008), and Lopes et al. (2013) for *Stegomastodon platensis* (Ameghino, 1888), *Stegomastodon waringi* (Holland, 1920), and *Stegomastodon* sp., respectively will be attributed to *Notiomastodon platensis* postulate by Mothé et al. (2012).

For monospecific taxa in our analysis – e.g. *Eremotherium* (*Eremotherium laurillardi*, Cartelle and De Juliis, 1995), *Notiomastodon* (*N. platensis*, Mothé et al., 2012) – only genus-level taxa are considered. This position is reinforced by the fact that some of the studies consulted consider only genera, e.g. *Equus* (MacFadden et al., 1999); *Toxodon* (MacFadden, 2005; Lopes et al., 2013); *Stegomastodon* (= *Notiomastodon sensu* Mothé et al., 2012) (Lopes et al., 2013).

In the articles reviewed the used $\delta^{13}\text{C}$ analysis from hydroxyapatite and collagen in bone or dentine (e.g. MacFadden et al., 1999; Drefahl, 2010; Dantas et al., 2013a; França et al., 2014) were chemically pretreated to eliminate the potential effects of diagenesis (secondary carbonate contamination), using the protocol described elsewhere. These, can be compared and analyzed together with other enamel analyses.

Although Dantas et al. (2013a) and Drefahl (2010) did not mention pretreatment of the samples in their texts, all analyses ($\delta^{13}\text{C}$ in CO_3 hydroxyapatite and collagen; AMS dating) were done with chemically pretreated samples (Dantas and Drefahl, personal communication).

All $\delta^{13}\text{C}$ data recovered were plotted on maps of vegetation reconstructed for South America during the Last Glacial Maximum – LGM (Pennington et al., 2000; Vivo & Carmignotto, 2004; Anhuf et al., 2006; Mayle, 2006; Fig. 1). We observed that the data are grouped into four ecoregions, mainly composed of Dry Forest vegetation, Savanna and grasslands (Fig. 1) in: (1) Ecuador and Peru; (2) Amazon basin; (3) northeastern Brazil, the Brazilian Intertropical Region (*sensu* Cartelle, 1999); and (4) a wide region, including southern Brazil, Uruguay and northern Argentina.

Geographic patterns and paleobotanical information for each area were used to corroborate the type of the habitat inferred by the carbon isotope data for these mammals, aiming to provide a more systematic evaluation of ecological patterns.

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