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Chronology and ancient feeding ecology of two upper Pleistocene megamammals from the Brazilian Intertropical Region

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A B S T R A C T

In Brazilian Intertropical Region (BIR) fossil remains of the giant ground sloth *Eremotherium laurillardi* (Lund, 1842) and of the proboscidean *Notiomastodon platensis* (Ameghino, 1888) are the most abundant among megaherbivores. However, the paleoecology of both species needs to be better understood to enlighten why these species disappear in the end of the Pleistocene, an issue that is still debated. During the last decades, the carbon and oxygen stable isotopes have been increasingly being used to obtain paleoecological information about extinct animals, although this information is in most cases dissociated from chronological data. Thus, the main objective of this study is to contribute to the knowledge about feeding ecology and chronology of *E. laurillardi* and *N. platensis* within BIR. For each fossil sample we performed stable isotopes analyses ($\delta^{13}C/\delta^{18}O$) and radiocarbon dating (^{14}C with AMS). The results showed that *N. platensis* occurred between 12,125 and 19,594 cal yr BP and exhibited a grazer diet ($\delta^{13}C = -1.1‰–1.3‰$), while *E. laurillardi* lived between 11,084 and 27,690 cal yr BP, with a mixed feeder diet (C_3/C_4 plants; values ratio $\delta^{13}C = -7.7‰$ to $-3.3‰$). The $\delta^{18}O$ values of *N. platensis* ranged between 2.20‰ and 3.60‰, while the values of *E. laurillardi* ranged between $-3.10‰$ and $-1.10‰$. Neither species did exhibit differences in its diet through time, which suggests that the vegetational composition of this locality did not vary in the late Pleistocene. Both species were living in an open environment, rich in herbaceous plants (C_4 plants) and with tree and shrub with disjoint distribution, maybe similar to some parts of recent Caatinga, where they have partitioned the spatial and feeding niches.

1. Introduction

The giant sloth *Eremotherium laurillardi* (Lund, 1842) and the mastodont *Notiomastodon platensis* (Ameghino, 1888) are two of the most studied *taxa* of the South American Pleistocene fauna. Most of these studies deal with taxonomy and intraspecific variation of morphological characters (De Iullis and Cartelle, 1993; Cartelle and De Iullis, 1995, 2006; Mothé et al., 2012). Both species are megamammals (*see* Hansen and Galetti, 2009), with body mass above one ton. In the Brazilian Intertropical Region – BIR (*sensu* Cartelle, 1999, Fig. 1), the few chronological studies show that both species lived together during the end of Pleistocene (*e.g.* Dantas et al., 2013a), suggesting that they probably interacted, sharing or competing for resources.

Between 42 ka and 8.5 ka the Caatinga, a type of Seasonal Dry Tropical Forest – SDTF, was the predominant biome in BIR, similar to the actual environment (*see* Machado et al., 2012). Dantas et al. (2013b) suggested that the geographic distribution of *N. platensis* was linked to this kind of environment. The Caatinga, like the others SDTF, encompasses an ample range of habitat types, from denser vegetation in some humid locations to more open areas dominated by cacti and small shrubs (Behling et al., 2000; Pennington et al., 2000; Werneck et al., 2011).

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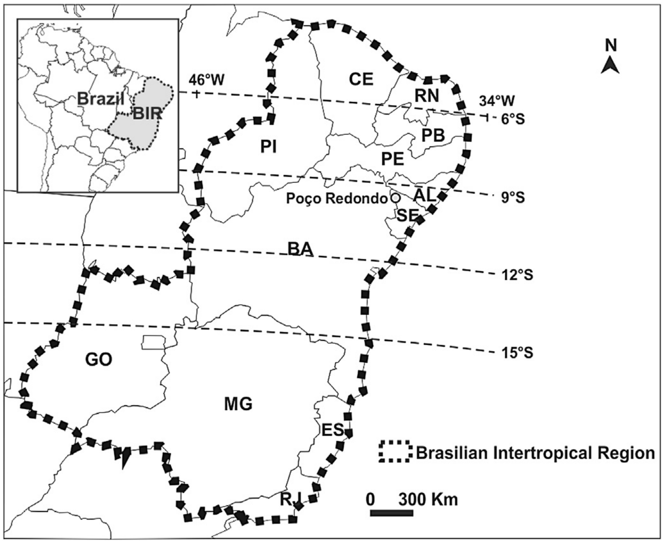

Fig. 1. Map Of the Brazilian Intertropical Region (*sensu* Cartelle, 1999).

Despite the information about their presence in BIR, the time scale wherein these species lived on this continent (a more complete chronological data), and the climate and paleoenvironment in which they lived are still poorly understood. Paleoecological analyses in fossils of both species are still scarce in BIR. There are some data for this region, as presented by Dantas et al. (2013a), which suggest different feeding strategies of these species in a wide area between the latitudes 6° S and 14° S during the late Pleistocene, between 11 ka and 28 ka.

Nevertheless, in the Pleistocene several climatic oscillations occurred, affecting the distribution of plant species and vegetation types, and consequently of the animal species that rely on them. Although there is some evidence about the diet of these species, the major part of the data is dissociated from chronological information, due to the lack of direct absolute dating, which prevents a good paleoenvironment reconstruction.

This could contribute to explain the cause of the extinction of megamammals in South America in the Pleistocene–Holocene transition, which is a matter with constant debates. The two main explanations for this extinction are direct human impacts and nutritional stress due to changes in climatic conditions (*e.g.* Sánchez et al., 2004). This issue might be better understood with paleodietary and chronological data associated, which could demonstrate if the diet of these mammals suffered or not some kind of impact related to climatic oscillations during the final Pleistocene (*e.g.* Asevedo et al., 2012).

Considering the well-known climatic variations along the late Pleistocene, the diet of the megamammals was likely to change, due to possible changes in the vegetation. Thus, the main objectives of this paper are: i) to present chronological data associated with ratio carbon and oxygen isotopes analyses for fossils of the species *E. laurillardi* and *N. platensis* found in the Brazilian Intertropical Region (BIR); and ii) to observe if the diet, and the environment in which they lived, varied through time.

In the last 20 years, at least, carbon and oxygen isotopic analyses of bioapatite from bone, dentine or enamel (Bocherens and Drucker, 2013) have contributed to the understanding of the feeding paleoecology of extinct species, and also the environment in which they lived (*e.g.* Domingo et al., 2012; Dantas et al., 2013a). This approach will be used in the present work to decipher paleoecology of these two extinct megafauna species.

2. Materials and methods

2.1. ^{14}C Dating and isotopic analyses ($\delta^{13}C$ and $\delta^{18}O$)

Five tooth samples of *E. laurillardi* and four tooth samples of *N. platensis* were dated through accelerator mass spectrometry (AMS) at the Center for Applied Isotope Studies of the University of Georgia/USA, calibrated using IntCal98 (Reimer et al., 2009), and measured to obtain the ratio isotope values of oxygen and carbon. The samples were collected in a tank (coordinates 09°55′37″S, 37°45′13″W) located at the São José farm, Poço Redondo municipality, Sergipe state, northeastern Brazil (Fig. 1; França et al., 2011). No permits were required for this study, which complied with all relevant regulation. The specimen numbers used in this study are listed in Table 1.

All analyses were made on bioapatite because in tropical regions such as BIR collagen is lost easily through diagenetic processes. These results are reliable, and are consistent with those found in collagen (*e.g.* Sánchez et al., 2004; Cherkinsky, 2009). In *N. platensis* bioapatite was extracted from enamel. In *E. laurillardi* it was extracted from dentine, since this species lacks tooth enamel like all members of the order Xenarthra (Paula Couto, 1979). Nowadays, there are some doubts about the effects of diagenesis in sloth dentine, but, for now, we consider that these data are reliable.

The interpretation of the diet was based on the fact that most existing plants, ranging from trees and woody shrubs to grasses found on prairies and steppes at high altitudes or latitudes, utilize the Calvin–Benson (C_3) photosynthetic cycle. These plants present average values of $\delta^{13}C$, of around −27‰. By contrast, the few terrestrial plants that use the Hatch-Slack (C_4) photosynthetic route are primarily tropical and subtropical grasses (Ehleringer et al., 1991; Cerling, 1992). 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 higher $\delta^{13}C$ values, averaging −13‰ (MacFadden et al., 1999; MacFadden, 2005; Domingo et al., 2012). Although the majority of C_4 plants are grasses (family Poaceae), other botanical families utilizing this photosynthetic route include Cyperaceae, Asteraceae and Amaranthaceae (Sage, 2004). Plants that photosynthesize using Crassulacean Acid Metabolism (CAM), such as the succulents, present intermediate $\delta^{13}C$ values (MacFadden et al., 1999; MacFadden, 2005; Domingo et al., 2012).

Studies of modern medium- to large-bodied herbivorous mammals have recorded an enrichment in $\delta^{13}C$ values between 12‰ and 14‰ (13‰ on average) in comparison with the values recorded for the vegetation ingested (Sánchez et al., 2004). Given this, $\delta^{13}C$ values lower than −10‰ are typical of animals with a diet consisting exclusively of C_3 plants, while $\delta^{13}C$ values higher than −1‰ are consistent with a diet based on C_4 plants. Intermediate $\delta^{13}C$ values (between −10‰ and −1‰) indicate a mixed diet of C_3 and C_4 plants (MacFadden et al., 1999; MacFadden, 2005). However, this method does not differentiate between folivores or frugivorous consumers of C_3 plants (Sponheimer and Lee–Thorp, 1999).

The paleodietary data of these species helped us in the reconstruction of the paleoenvironment in which they lived. However, to make better reconstructions, we measured the values of $\delta^{18}O$ as well. The proportion of $^{18}O/^{16}O$ in an animal's body is influenced by external factors, such as temperature and water precipitation in local water bodies (MacFadden et al., 1999; Sánchez et al., 2004; Lopes et al., 2013). Environments with high evaporation and low precipitation have a higher proportion of ^{18}O in local water bodies, thus, more enriched $\delta^{18}O$ values (Dansgaard, 1964; Lopes et al., 2013). Thus, the oxygen isotopic composition in mammalian tooth is influenced by the atmospheric O_2, and water directly