



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



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### ABSTRACT

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 ( $\delta^{13}\text{C}/\delta^{18}\text{O}$ ) and radiocarbon dating ( $^{14}\text{C}$  with AMS). The results showed that *N. platensis* occurred between 12,125 and 19,594 cal yr BP and exhibited a grazer diet ( $\delta^{13}\text{C} = -1.1\text{‰} - 1.3\text{‰}$ ), while *E. laurillardi* lived between 11,084 and 27,690 cal yr BP, with a mixed feeder diet ( $\text{C}_3/\text{C}_4$  plants; values ratio  $\delta^{13}\text{C} = -7.7\text{‰}$  to  $-3.3\text{‰}$ ). The  $\delta^{18}\text{O}$  values of *N. platensis* ranged between 2.20‰ and 3.60‰, while the values of *E. laurillardi* ranged between  $-3.10\text{‰}$  and  $-1.10\text{‰}$ . 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 ( $\text{C}_4$  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.

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### 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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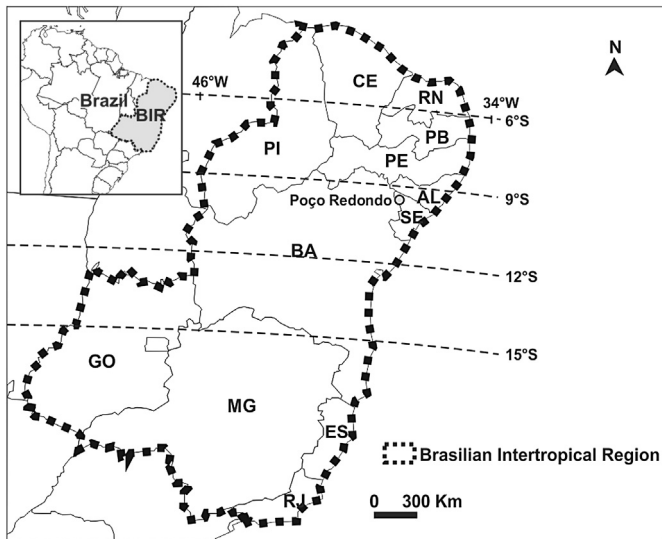


Fig. 1. Map Of the Brazilian Intertropical Region (sensu Cartelle, 1999).

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

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 ( $\text{C}_3$ ) photosynthetic cycle. These plants present average values of  $\delta^{13}\text{C}$ , of around  $-27\text{‰}$ . By contrast, the few terrestrial plants that use the Hatch-Slack ( $\text{C}_4$ ) 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  $\text{CO}_2$ . In general,  $\text{C}_4$  plants have higher  $\delta^{13}\text{C}$  values, averaging  $-13\text{‰}$  (MacFadden et al., 1999; MacFadden, 2005; Domingo et al., 2012). Although the majority of  $\text{C}_4$  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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  values between 12‰ and 14‰ (13‰ on average) in comparison with the values recorded for the vegetation ingested (Sánchez et al., 2004). Given this,  $\delta^{13}\text{C}$  values lower than  $-10\text{‰}$  are typical of animals with a diet consisting exclusively of  $\text{C}_3$  plants, while  $\delta^{13}\text{C}$  values higher than  $-1\text{‰}$  are consistent with a diet based on  $\text{C}_4$  plants. Intermediate  $\delta^{13}\text{C}$  values (between  $-10\text{‰}$  and  $-1\text{‰}$ ) indicate a mixed diet of  $\text{C}_3$  and  $\text{C}_4$  plants (MacFadden et al., 1999; MacFadden, 2005). However, this method does not differentiate between folivores or frugivorous consumers of  $\text{C}_3$  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  $\delta^{18}\text{O}$  as well. The proportion of  $^{18}\text{O}/^{16}\text{O}$  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  $^{18}\text{O}$  in local water bodies, thus, more enriched  $\delta^{18}\text{O}$  values (Dansgaard, 1964; Lopes et al., 2013). Thus, the oxygen isotopic composition in mammalian tooth is influenced by the atmospheric  $\text{O}_2$ , and water directly

**Table 1**  
Isotopic data compilation ( $\delta^{18}\text{O}/\delta^{13}\text{C}$ ) and datings ( $^{14}\text{C}$ , ESR, U-series) for *Eremotherium laurillardi* and *Notiomastodon platensis* in the Brazilian Intertropical Region (RIB).

Species	Sample number	$\delta^{18}\text{O}$ (‰)	$\delta^{13}\text{C}$ (‰)	Lat (°S)	Localities	Ages (years)	Calibrated age (2 $\sigma$ range, cal yr BP)
<i>E. laurillardi</i>	UGAMS 9435 <sup>(1)</sup>	–	0.50 <sup>(d)</sup>	6	Currais Novos/RN	15,490 ± 40 <sup>(b,*)</sup>	18,580–18,850
<i>E. laurillardi</i>	UGAMS 9436 <sup>(1)</sup>	–	5.22 <sup>(d)</sup>	6	Barcelona/RN	–	–
<i>E. laurillardi</i>	SM-1 <sup>(2)</sup>	2.51 <sup>(d)</sup>	0.30 <sup>(d)</sup>	9	Maravilha/AL	–	–
<i>E. laurillardi</i>	MA-1 <sup>(3)</sup>	–	–12.00 <sup>(d)</sup>	9	Maravilha/AL	–	–
<i>E. laurillardi</i>	UGAMS 13,539 <sup>(4)</sup>	–1.10 <sup>(d)</sup>	–7.70 <sup>(d)</sup>	9	Poço Redondo/SE	10,990 ± 30 <sup>(d,*)</sup>	12,685–13,070
<i>E. laurillardi</i>	UGAMS 13,540 <sup>(4)</sup>	–2.00 <sup>(d)</sup>	–3.30 <sup>(d)</sup>	9	Poço Redondo/SE	11,010 ± 30 <sup>(d,*)</sup>	12,704–13,080
<i>E. laurillardi</i>	UGAMS 13,541 <sup>(4)</sup>	–1.20 <sup>(d)</sup>	–6.00 <sup>(d)</sup>	9	Poço Redondo/SE	9720 ± 30 <sup>(d,*)</sup>	11,084–11,233
<i>E. laurillardi</i>	UGAMS 13,542 <sup>(4)</sup>	–3.10 <sup>(d)</sup>	–3.30 <sup>(d)</sup>	9	Poço Redondo/SE	9730 ± 30 <sup>(d,*)</sup>	11,089–11,237
<i>E. laurillardi</i>	UGAMS 13,543 <sup>(4)</sup>	–1.20 <sup>(d)</sup>	–4.70 <sup>(d)</sup>	9	Poço Redondo/SE	11,580 ± 30 <sup>(d,*)</sup>	13,292–13,581
<i>E. laurillardi</i>	UGAMS 9431 <sup>(1)</sup>	–	–6.65 <sup>(d)</sup>	9	Poço Redondo/SE	–	–
<i>E. laurillardi</i>	UGAMS 9432 <sup>(1)</sup>	–	–3.85 <sup>(d)</sup>	9	Poço Redondo/SE	22,440 ± 50 <sup>(d,*)</sup>	26,690–27,690
<i>E. laurillardi</i>	UGAMS 9433 <sup>(1)</sup>	–	–2.45 <sup>(d)</sup>	9	Poço Redondo/SE	–	–
<i>E. laurillardi</i>	UGAMS 9434 <sup>(1)</sup>	–	–3.25 <sup>(d)</sup>	10	Gararu/SE	–	–
<i>E. laurillardi</i>	UGAMS 6136 <sup>(5)</sup>	–	–18.20 <sup>(b)</sup>	10	Quijingue/BA	15,770 ± 40 <sup>(b,*)</sup>	18,730–19,280
<i>E. laurillardi</i>	s/n <sup>(6)</sup>	–	–	10	Caatinga do Moura/BA	15,000 ± 500 <sup>(s,*)</sup>	–
<i>E. laurillardi</i>	s/n <sup>(6)</sup>	–	–	10	Caatinga do Moura/BA	16,100 ± 3,900 <sup>(s,*)</sup>	–
<i>E. laurillardi</i>	s/n <sup>(6)</sup>	–	–	10	Caatinga do Moura/BA	15,800 ± 2,000 <sup>(s,*)</sup>	–
<i>N. platensis</i>	UGAMS 9440 <sup>(11)</sup>	–	0.44 <sup>(e)</sup>	6	Barcelona/RN	16,150 ± 40 <sup>(e,*)</sup>	18,930–19,450
<i>N. platensis</i>	s/n <sup>(7)</sup>	–	–	7	Puxinamã/PB	30,000 ± 5,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(7)</sup>	–	–	7	Puxinamã/PB	36,000 ± 7,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(7)</sup>	–	–	7	Puxinamã/PB	39,000 ± 7,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(8)</sup>	–	–	8	Brejo da Madre de Deus/PE	63,000 ± 8,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(8)</sup>	–	–	8	Brejo da Madre de Deus/PE	60,000 ± 9,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	SM-3 <sup>(2)</sup>	3.19 <sup>(d)</sup>	0.00 <sup>(d)</sup>	9	Maravilha/AL	–	–
<i>N. platensis</i>	MA-3 <sup>(3)</sup>	–	–9.27 <sup>(d)</sup>	9	Maravilha/AL	–	–
<i>N. platensis</i>	s/n <sup>(9)</sup>	–	–	9	Maravilha/AL	10,000 ± 500 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(9)</sup>	–	–	9	Maravilha/AL	39,800 ± 100 <sup>(e,#)</sup>	–
<i>N. platensis</i>	UGAMS 13,535 <sup>(4)</sup>	3.60 <sup>(e)</sup>	–0.40 <sup>(e)</sup>	9	Poço Redondo/SE	13,380 ± 35 <sup>(e,*)</sup>	16,022–16,840
<i>N. platensis</i>	UGAMS 13,536 <sup>(4)</sup>	2.40 <sup>(e)</sup>	–0.20 <sup>(e)</sup>	9	Poço Redondo/SE	16,370 ± 40 <sup>(e,*)</sup>	19,400–19,594
<i>N. platensis</i>	UGAMS 13,537 <sup>(4)</sup>	2.20 <sup>(e)</sup>	–1.10 <sup>(e)</sup>	9	Poço Redondo/SE	10,440 ± 30 <sup>(e,*)</sup>	12,125–12,533
<i>N. platensis</i>	UGAMS 13,538 <sup>(4)</sup>	2.50 <sup>(e)</sup>	1.30 <sup>(e)</sup>	9	Poço Redondo/SE	13,760 ± 35 <sup>(e,*)</sup>	16,718–17,048
<i>N. platensis</i>	UGAMS 9437 <sup>(1)</sup>	–	0.76 <sup>(e)</sup>	10	Poço Redondo/SE	–	–
<i>N. platensis</i>	s/n <sup>(10)</sup>	–	–	8	Poço Redondo/SE	28,000 ± 3,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(11)</sup>	–	–	8	Poço Redondo/SE	42,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(11)</sup>	–	–	10	Gararu/SE	50,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	UGAMS 9438 <sup>(1)</sup>	–	–1.04 <sup>(e)</sup>	10	Cel. JoãoSá/BA	13,980 ± 40 <sup>(e,*)</sup>	16,800–17,380
<i>N. platensis</i>	UGAMS 9439 <sup>(1)</sup>	–	–1.86 <sup>(e)</sup>	10	Canhoba/SE	17,910 ± 50 <sup>(e,*)</sup>	21,180–21,550
<i>N. platensis</i>	UGAMS 9441 <sup>(1)</sup>	–	–0.49 <sup>(e)</sup>	10	Cel. JoãoSá/BA	–	–
<i>N. platensis</i>	s/n <sup>(10)</sup>	–	–	8	Jaguarari/BA	114,000 ± 20,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(12)</sup>	–0.10 <sup>(e)</sup>	–8.20 <sup>(e)</sup>	10	Ourolândia/BA	–	–
<i>N. platensis</i>	s/n <sup>(12)</sup>	–1.90 <sup>(e)</sup>	–5.00 <sup>(e)</sup>	10	Ourolândia/BA	–	–
<i>N. platensis</i>	s/n <sup>(13)</sup>	–	–	11	Baixa Grande/BA	50,000 ± 10,000 <sup>(e,#)</sup>	–
<i>N. platensis</i>	s/n <sup>(10)</sup>	–	–	13	Matina/BA	100,000 ± 20,000 <sup>(e,#)</sup>	–

Obs. Oxygen isotope and carbon isotope data in VPDB.

Legends. <sup>(b)</sup>Bone; <sup>(d)</sup>Dentine; <sup>(e)</sup>Enamel; <sup>(s)</sup>Speleothem; <sup>(\*)</sup> $^{14}\text{C}$  dating; <sup>(#)</sup>ESR dating; <sup>(S)</sup>U-series dating; RN: Rio Grande do Norte; AL: Alagoas; SE: Sergipe; BA: Bahia.

Cited articles. <sup>(1)</sup>Dantas et al. (2013a); <sup>(2)</sup>Viana et al. (2011); <sup>(3)</sup>Silva (2008); <sup>(4)</sup>Our data; <sup>(5)</sup>Drefahl (2010); <sup>(6)</sup>Auler et al. (2006); <sup>(7)</sup>Kinoshita et al. (2005); <sup>(8)</sup>Kinoshita et al. (2008); <sup>(9)</sup>Oliveira et al. (2010); <sup>(10)</sup>Dantas et al. (2013b); <sup>(11)</sup>Dantas et al. (2011); <sup>(12)</sup>Sánchez et al. (2004); <sup>(13)</sup>Ribeiro et al. (2013).

drunken from natural water bodies or present in their food, but only the latter two are highly variable and capable to explain the differences among taxa (Sponheimer and Lee–Thorp, 2001).

Grazers (consumers of  $C_4$  plants) are more likely to show higher values of  $\delta^{18}\text{O}$  than browsers and mixed-feeders, because  $C_4$  plants have  $^{18}\text{O}$ -enriched in comparison to  $C_3$  plants. So, grazers have higher  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values (Kohn et al., 1996; Helliker and Ehleringer, 2000). Nevertheless, some studies show that the  $\delta^{18}\text{O}$  values of tooth apatite is a reflection of the isotopic composition of the meteoric and environmental water which megamammals were drinking, because large mammals (those with an obligatory drinking behavior) obtain most of the water by drinking rather than from their diets (Bryant and Froelich, 1995; Gehler et al., 2012). In the late Pleistocene of Southern Brazil, Lopes et al. (2013) found a poor correlation between the  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values for fossils of *N. platensis* and *Toxodon platensis*, suggesting that these animals obtained most of its water contents from drinking rather than from food. So, the correlation of both isotopic ratios could indicate if the oxygen isotopic content of the body water is dependent or not of the diet.

Furthermore, the interpretation of  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  data together helps in the refine the ecological niche for those animals that lived in forest canopy, or in your borders, feeding on  $C_3$  plants, suggesting what type of different plant parts they fed on. It is expected that fruits have lower values of  $\delta^{18}\text{O}$  than leaves, because of the transpiration promoted by leaves, and high moisture content present in fruits. Following the interpretations made by Nelson (2013) for primates, we interpret that animals that have  $C_3$  plants in their diet, could be differentiated by  $\delta^{18}\text{O}$  values in three categories: values more negative than  $-1.3\text{‰}$ , suggests a diet on forest floor plants, values near  $0.6\text{‰}$  suggests frugivore diet, and, finally, values greater than  $2.1\text{‰}$  suggest a folivore diet.

## 2.2. Statistical analyses

First, the carbon and oxygen isotopes data of the two species were submitted to a normality test (Shapiro–Wilk test). Then, to test whether the diet of these species had significant differences a  $t$ -test was made on values of  $\delta^{18}\text{O}$  ( $p = 0.18$ ) and  $\delta^{13}\text{C}$  ( $p = 0.82$ ), through the PAST software, version 2.17c, using a significance level

of 5%. A correlation test between the values of  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  was made in the PAST software as well, to determine whether the  $\delta^{18}\text{O}_{\text{water}}$  values significantly correlate with the isotopic composition of the tooth tissues, using the same significance level.

### 3. Results

#### 3.1. Radiocarbon dating

The results show that the *E. laurillardii* included in this study lived between 11,084 cal yr BP and 13,581 cal yr BP ( $9720 \pm 30$ – $11,580 \pm 30$  years BP), while the *N. platensis* were dated between 12,125 cal yr BP and 19,594 cal yr BP ( $10,440 \pm 30$  to  $16,370 \pm 40$  years BP) (Table 1). We observed that some samples of *E. laurillardii* (UGAMS 13,541 and 13,542; UGAMS 13,539 and 13,540) presented similar dating results, which could mean that they represent samples from the same individual. However we interpret these as two different individuals based on the carbon and oxygen isotopic signatures, as we will present in the next section.

#### 3.2. Carbon and oxygen isotopic analyses

The statistical analyses showed different  $\delta^{13}\text{C}$  ( $p < 0.01$ ;  $t = -4.99$ ) and  $\delta^{18}\text{O}$  ( $p < 0.01$ ;  $t = -8.60$ ) values for *E. laurillardii* and *N. platensis*, indicating different diets for these species. For *E. laurillardii*  $\delta^{13}\text{C}$  values ranged from  $-7.7\text{‰}$  to  $-3.3\text{‰}$  (mean values of  $-5.0\text{‰}$ ), suggesting a diet based on  $\text{C}_3$  and  $\text{C}_4$  plants, and possibly CAM plants. The  $\delta^{18}\text{O}$  data refine the diet based on  $\text{C}_3$  plants (ranged from  $-3.10\text{‰}$  to  $-1.10\text{‰}$ , mean =  $-1.72\text{‰}$ ), suggesting a border forest habitat, with a diet on forest floor  $\text{C}_3$  plants (Fig. 2A). For *N. platensis*,  $\delta^{13}\text{C}$  values between  $-1.1\text{‰}$  and  $1.3\text{‰}$  (mean values of  $-0.1\text{‰}$ ) were found, indicating a grazer diet ( $\text{C}_4$  plants),  $\delta^{18}\text{O}$  data (between  $2.20\text{‰}$  and  $3.60\text{‰}$ , mean =  $2.68\text{‰}$ ) confirm this information, since high values of  $\delta^{18}\text{O}$  reflect an enrichment of  $^{18}\text{O}$  found in  $\text{C}_4$  grass (Fig. 2B).

The correlations between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values are different for these species. In *E. laurillardii* there is a negative correlation (Fig. 2A), while in *N. platensis* no correlation was observed (Fig. 2B).

### 4. Discussion

#### 4.1. Chronological distribution

The data presented here (Table 1) expand the temporal distribution of these species, mainly in the BIR. The short temporal range observed could be explained by taphonomic process, as observed in other tanks in the BIR (Araújo Junior et al., 2011). The revision of the

available dates (direct dates on bone and teeth), document the occurrence of *E. laurillardii* in BIR between 11,084 cal yr BP to 27,690 cal yr BP (based mainly in  $^{14}\text{C}$ , Table 1), while *N. platensis* occurred between  $10,000 \pm 500$  yr BP to  $114,000 \pm 20,000$  yr BP ( $^{14}\text{C}$ , Electron Spin Resonance – ESR, Table 1).

The dating results show that *N. platensis* have a wider temporal occurrence than *E. laurillardii*, however, this does not mean that these species did not live at the same time. This difference in temporal occurrence is most likely based on a limitation of the techniques that could date fossils of *E. laurillardii*. The available dates were made mainly by  $^{14}\text{C}$  (AMS), which has a temporal limitation up to 58 ka (Bird et al., 2004). The absence of enamel in the giant sloth does not allow the use of ESR (Baffa et al., 2000) dating technique, as used for *N. platensis*. Techniques with wide temporal range could reveal older dates for this species, as showed by an indirect date (U-series; Beltrão and Locks, 1989), which suggests the occurrence of *E. laurillardii* in the BIR at 295 ka.

#### 4.2. Ancient feeding ecology and paleoenvironment

The  $\delta^{13}\text{C}$  results for both species are similar to those published for the same locality (Table 1, Dantas et al., 2013a), revealing that, at least from 11,084 cal yr BP to 27,690 cal yr BP, these species maintained their diets (*E. laurillardii*  $\delta^{13}\text{C} = -7.7\text{‰}$  to  $-2.45\text{‰}$ , mean value of  $-4.7\text{‰}$ ; *N. platensis*  $\delta^{13}\text{C} = -1.1\text{‰}$ – $1.3\text{‰}$ , mean value of  $0.07\text{‰}$ ), thus, suggesting environmental stability (Table 1). This scenario may have occurred in nearby regions, also the results for these species found in Poço Redondo, Sergipe are similar to those found in fossils of *E. laurillardii* and *N. platensis* in Maravilha, Alagoas (latitude  $9^\circ$  S; Silva, 2008; Viana et al., 2011) and Coronel João Sá, Bahia (latitude  $10^\circ$  S; Dantas et al., 2013a).

In addition to the stability of diet and environment through time, our results confirm the interpretation made by Dantas et al. (2013a) about the diet of these species in BIR between latitudes  $6^\circ$  S and  $10^\circ$  S. Between these latitudes *N. platensis* maintained a  $\text{C}_4$  grazer diet, while *E. laurillardii* at latitude  $6^\circ$  S was a  $\text{C}_4$  grazer, changing its diet to a mixed-feeder, at latitude  $9^\circ$  S and  $10^\circ$  S.

Dantas et al. (2013a) also suggested that in the BIR, at latitudes  $9^\circ$  S and  $10^\circ$  S, the megafauna species may have lived in a more forested environment, in a mosaic of Rain Forest and Seasonal Dry Forest (SDF hereafter). However, recently, Dantas et al. (2013b) made a potential distribution map for *N. platensis* in South America at 21 ka, which included the paleodiet data. The created map and the biogeography of SDF in the late Pleistocene allowed to draw a new conclusion, that this species may have lived only in the habitats of SDF.

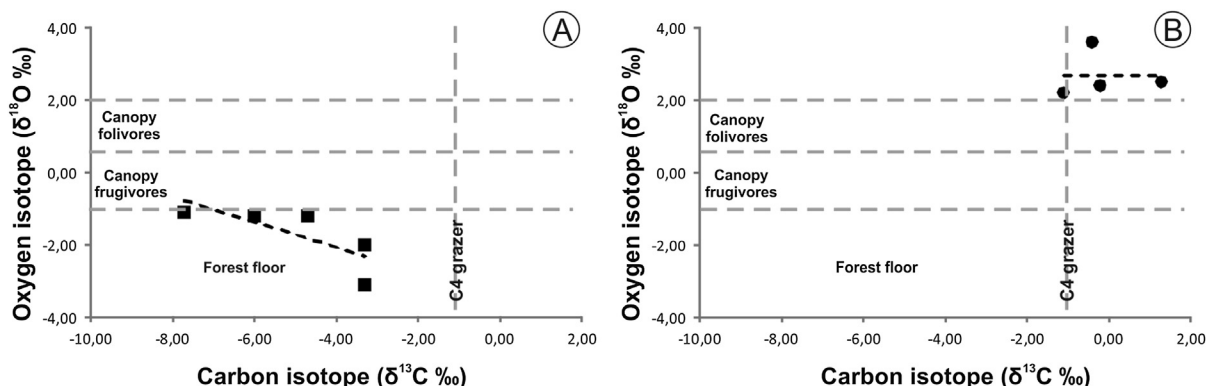


Fig. 2.  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  correlation of (A) *Eremotherium laurillardii* and (B) *Notiomastodon platensis*.

The SDF (like the Brazilian Caatinga) could present a high diversity of phytophysiognomy, varying from forested environment to open environments, richer in herbs and cacti (Pennington et al., 2000). Palynological studies suggest that the Caatinga existed in the BIR since 42 ka. Some authors found a higher percentage (60–75%) of herb pollens of Poaceae, Cyperaceae, *Borreria*, Asteraceae, and a lower percentage (15–25%) of shrubs and tree pollens of Palmae, Myrtaceae, Melastomataceae/Combretaceae, Arecaceae, Malpighiaceae, Moraceae/Urticaceae, which may indicate the occurrence of semiarid conditions in the late Pleistocene (Behling et al., 2000; Mayle, 2006). Therefore, the interpretation of Dantas et al. (2013b) could be correct, and needs to be tested.

Grazers ( $C_4$  plant consumers) tend to have higher values of  $\delta^{18}O$  than browsers and mixed-feeders (Kohn et al., 1996; Helliker and Ehleringer, 2000). This was observed in the fossils of *N. platensis* (grazer). For *E. laurillardi* the statistical tests shows a negative correlation between  $\delta^{13}C$  and  $\delta^{18}O$  values, namely more  $C_3$  forest floor species in the food consumed the less  $\delta^{18}O$  values (Fig. 2A). There are possible explanations for this result, but they only can be tested in future studies. First of all, the giant sloth metabolism could have affected the isotopic content in their body tissues, but all the giant sloths are extinct and their unusual form makes comparisons with recent large mammals very complicated (Naish, 2005). Second, the oscillations in climatic conditions could affect the  $\delta^{18}O$  ratios in the precipitation and, consequently, in the local water bodies, reflecting in the mammalian tooth. Unfortunately, until now this kind of information is not available in the locality studied here. Therefore these considerations, plus the mixed-feeder dietary behavior ( $C_3$  and  $C_4$  plants, and possibly CAM plants) could influence in the oxygen isotopic content of *E. laurillardi* tooth, resulting in the negative correlation found here.

The absence of correlation in the statistical tests found for *N. platensis* (Fig. 2B) suggests that this animal obtained most of its water from natural water sources rather than from the  $C_4$  plants diet. Despite the fact that the population inhabiting Southern Brazil was mixed-feeder, a poor correlation between  $\delta^{13}C$  and  $\delta^{18}O$  values was found there, and it is also the case for modern African elephants, as discussed by Lopes et al. (2013). Therefore, the large amount of drinking water is most likely responsible for the  $^{18}O$ -enriched in *N. platensis* tooth.

## 5. Conclusions

The data presented here, together with those previously published, allow us to expand the temporal distribution of *E. laurillardi* and *N. platensis* throughout the late Pleistocene inside the BIR. During this time range, we observed the stability in the diets of the two species in Sao Jose farm locality (Poço Redondo, Sergipe; latitude  $9^\circ S$ ), even during climatic oscillations characteristic of this geological epoch. The two *taxa* were associated with the area of Caatinga, an STDF, with different types of vegetation, low rainfall and high temperatures. This information has been preserved indirectly, as values of  $\delta^{18}O$  and  $\delta^{13}C$ .

The data presented by Dantas et al. (2013a) suggested that these species possessed an ecological flexibility, which allowed them to feed on different kind of resources, in different environments. Since the present study suggests that in the Sao Jose farm locality these species did not change their diet through time, this indicates either a stability of the environment in which those species lived, or the same diet in an environment that was changing because of the climatic oscillations during the late Pleistocene. This could indicate that this species could not change their diets in a short period of time. In this scenario, both species might become locally extinct or started to emigrate to other areas. Considering a stability of the environment during the late Pleistocene in the studied locality,

other questioning may be done in the future to explain why this species became extinct.

Our research is ongoing, and we will continue to improve our vision of the chronologies and diets of the species that lived in the BIR, generating new data to help us better understand the behavior of these species through the climate changes that occurred during the late Pleistocene, trying to explain possible causes for their extinction.

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