Revista Brasileira de Paleontologia, 23(2):138–152, Abril/Junho 2020
A Journal of the Brazilian Society of Paleontology

doi:10.4072/rbp.2020.2.05

ISOTOPIC PALEOECOLOGY (δ^{13}C, δ^{18}O) OF A LATE PLEISTOCENE VERTEBRATE COMMUNITY FROM THE BRAZILIAN INTERTROPICAL REGION

MÁRIO ANDRÉ TRINDADE DANTAS
Laboratório de Ecologia e Geociências, Instituto Multidisciplinar em Saúde, Universidade Federal da Bahia – *Campus* Anísio Teixeira, Vitória da Conquista, BA, Brazil.
matdantas@yahoo.com.br

ALEXANDER CHERKINSKY
Center for Applied Isotope Studies, University of Georgia, Athens, GA 30602, USA.
acherkin@uga.edu

CARLOS MICAEL BONFIM LESSA
Laboratório de Ecologia e Geociências, Instituto Multidisciplinar em Saúde, Universidade Federal da Bahia – *Campus* Anísio Teixeira, Vitória da Conquista, BA, Brazil.
biologolessa@gmail.com

LUCIANO VILABOIM SANTOS, MARIO ALBERTO COZZUOL
Programa de Pós-Graduação em Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil.
palaiosvilaboim@hotmail.com, *mario.cozzuol@gmail.com*

ÉRICA CAVALCANTE OMENA
Programa de Pós-Graduação em Geociências, Universidade Federal de Pernambuco, Recife, PE, Brazil.
erica.omena@gmail.com

JORGE LUIZ LOPES DA SILVA
Departamento de Paleontologia, Museu de História Natural, Universidade Federal de Alagoas, Maceió, AL, Brazil.
jluizlopess@gmail.com

ALCIDES NÓBREGA SIAL
NEG-LABISE, Departamento de Geologia, Centro de Tecnologia e Geociências,
Universidade Federal de Pernambuco, Recife, PE, Brazil.
sial@ufpe.br

HERVÉ BOCHERENS
Biogeology, Department of Geosciences and Senckenberg Center for Human Evolution and Palaeoenvironment (HEP), Universität Tübingen, Hölderlinstr. 12, 72074 Tübingen, Germany.
herve.bocherens@uni-tuebingen.de

ABSTRACT – Isotopes are one of the best tools to reconstruct the paleoecology of extinct taxa, allowing us to evaluate their diet (through carbon; C_3 and C_4 plants), their niche breadth (B_A) and the environment in which they lived. In the present work we go deeper in the use of isotopes, and explore a mathematical mixing model with the stable isotopic composition of one (carbon) and two elements (carbon and oxygen) to evaluate (i) the relative contributions of three types of food resources (leaves, fruits and C_4 grass) for meso- and megaherbivores (body mass > 100 kg) that lived during the late Pleistocene in Sergipe, Brasil, and (ii) which of these herbivores (together with some faunivorous taxa) could be potential preys for *Smilodon populator* and *Caiman latirostris*. Finally, we reconstructed the paleoenvironment in which the vertebrate community of Sergipe lived and concluded that the environment of Sergipe was a closer and drier landscape than African savannah nowadays, at least between 27 ka to 11 ka.

Keywords: Quaternary, mammals, paleoecology, South America, stable isotopes.

RESUMO – Isotópos são uma das melhores ferramentas para reconstruir a Paleoecologia de táxons extintos, permitindo sugerir dieta (por meio do carbono, plantas C_3 e C_4), o nicho ecológico (B_A) e ambiente em que viveram. No presente artigo nos aprofundamos no uso dos isotópos, e exploramos um modelo matemático misto com um isotópo (carbono) e dois isotópos (carbono e oxigênio) (i) para sugerir três recursos tipos de recursos alimentares (folhas, frutas e gramíneas C_4) para meso-megaherbívoros (massa corporal acima de 100 kg) que viveram no Pleistoceno final de Sergipe, Brasil, e (ii) qual desses herbívoros (juntamente com faunívoros) foram presas potenciais de *Smilodon populator* e *Caiman latirostris*. Por fim, reconstruímos o paleoambiente na qual a comunidade de vertebrados de Sergipe viveu, concluindo que era mais fechada e seca do que as savanas da Africa atualmente, pelo menos entre 27 mil a 11 mil anos atrás.

Palavras-chave: Quaternário, paleoecologia, América do Sul, isotópos estavéis.

INTRODUCTION

During the last three decades, stable isotopes have been used in paleoecology to infer the diet of extinct (and extant) taxa, based primarily on carbon isotopic data (*e.g.* Bocherens *et al.*, 1996; MacFadden, 2005; França *et al.*, 2014a). Besides, nitrogen isotopic data have been used to infer carnivory or omnivory in mammals as well (*e.g.* Bocherens *et al.*, 2016). Isotopic approaches represented a major advance in paleoecological studies, helping to infer two main food resources for herbivores (C_3 and C_4 plants) and the paleoenvironmental context in which herbivores and carnivores could live (forested or open environments; Kingston & Harrison, 2007; Dantas *et al.*, 2017).

However, stable isotopes can provide more ecological information than previously thought, such as an estimate of niche width and overlap, helping us to understand better the ecology of extinct taxa, the competition for resources and identify which species were keystone species in extinct communities (*e.g.* Dantas *et al.*, 2017). Two isotopic pairs in mathematical mixing models could be used to suggest more than two food resources for herbivores (for example seven resources; Phillips, 2012 and references therein).

Most researchers use carbon and nitrogen isotopic data, extracting these data from collagen. However, in tropical regions this protein is poorly preserved, leading to use only carbon and oxygen isotopic data extracted from hydroxyapatite. Indeed, hydroxyapatite usually survives much better than the organic fraction of bone, *i.e.* collagen (Cherkinsky, 2009), and therefore is the best option to recover diet information from extinct species in tropical regions.

The main aim of this paper was to use mathematical mixing models using only carbon, or carbon and oxygen isotopic data in combination (measured on hydroxyapatite) from fossil vertebrates from the late Pleistocene of Sergipe, Brazil, to: (i) infer three types of resources for herbivores (leaf, fruit and C_4 grass); (ii) suggest, among the vertebrate taxa, which ones contributed to the isotopic diet of predators such as *Smilodon populator* and *Caiman latirostris*, allowing to infer a trophic web structure for this community; and, finally, (iii) suggest a reconstruction of the paleoenvironment in which these taxa could have lived.

Knowing the paleoecology and structure of this community will help us to understand the role of environmental change in the extinction of the megafauna in the late Pleistocene/early Holocene.

MATERIAL AND METHODS

Dataset

Sixteen samples (Table S1) of adult individuals of *Eremotherium laurilardi* (Lund, 1842) (one exception is LPUFS 5693 assigned to a juvenile), *Catonyx cuvieri* (Lund, 1839), *Pachyarmatherium brasiliense* Porpino, Bergqvist & Fernicola, 2009, *Holmesina paulacoutoi* (Guerra & Marecha, 1984), *Glyptotherium* sp., *Panochthus* sp., *Toxodon platensis* Owen, 1837, *Palaeolama major* (Liais, 1872), *Equus* (*Amerhippus*) *neogeus* Lund, 1840 and *Smilodon populator* Lund 1842 from four localities in Sergipe (Fazenda Elefante, Gararu; Fazenda Charco and Fazenda São José, Poço Redondo; and Sítios Novos, Canhoba; Figure 1) were analyzed to retrieve the carbon and oxygen isotopic composition from structural carbonate of their bones, dentin and enamel.

The samples were collected in "tanks", which are natural depressions on Neo-Mesoproterozoic litotypes, characterized by numerous fractures resulting from physical and chemical erosion, that contain sediments transported by seasonal rains including the remains of animals and plants accumulated during the dry season (*e.g.* Oliveira & Hackspacher, 1989). The sediments in these depressions are estimated as being of late Pleistocene and Holocene ages.

The isotopic composition of hydroxyapatite can be preserved with minimal or no significant diagenetic alteration. Hydroxyapatite carbonate and phosphate in bone and dentin are more susceptible to diagenetic overprinting than enamel (Bocherens *et al.*, 1996, 2011; Lee-Thorp & Sponheimer, 2003). However, we noticed that in Sergipe localities diagenesis was no significant, because similar values for bone and dentine were found for *Eremotherium laurillardi* (UGAMS 9431 and 9432), and bone, dentine and enamel for *Notiomastodon platensis* (UGAMS 9437 and 9439) and *Toxodon platensis* (UGAMS 9446) (Table S1), which gives us confidence in isotopic results found in bone for *Catonyx cuvieri*, *Holmesina paulacoutoi*, *Glyptotherium* sp., *Panochthus* sp., *Palaeolama major*, and *Smilodon populator* (Table S1).

Substitutions are mainly in the phosphate position and are most likely in the hydroxyl position. The absorbed carbonates are more labile, but substituted ones are structural carbonates, and, thus, contribute to preserving the original isotopic composition (Cherkinsky, 2009).

The stable isotope analyzes were performed at NEG-LABISE in "Centro de Tecnologia e Geociências" of

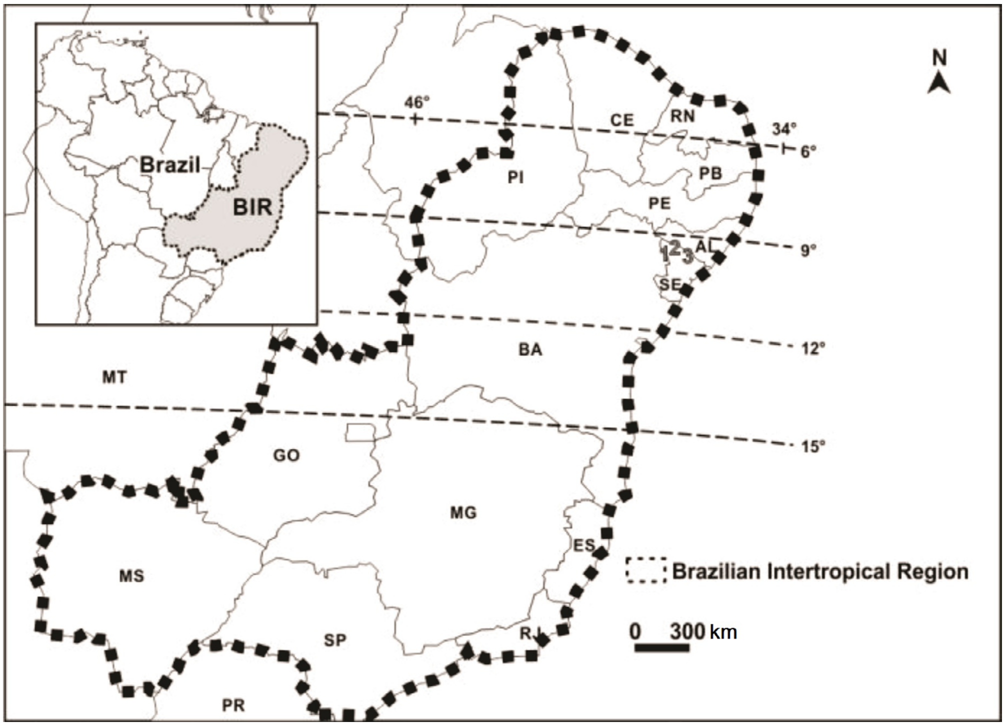

Figure 1. Brazilian Intertropical Region map (*sensu* Oliveira *et al.*, 2017) showing Gararu (**1**), Poço Redondo (**2**) and Canhoba (**3**) municipalities in Sergipe State, Brazil.

Universidade Federal de Pernambuco (Recife, Pernambuco, Brazil) and in Center for Applied Isotope Studies from University of Georgia (Georgia, USA). All samples were cleaned by ultrasonic bath with distilled water and then left to dry naturally. The samples were then crushed into smaller fragments to be treated with diluted 1N acetic acid to remove surface absorbed and secondary carbonates. Periodic evacuation ensured that evolved carbon dioxide was removed from the interior of the sample fragments, and that fresh acid was allowed to reach even the interior micro-surfaces.

The chemically cleaned samples were then reacted under vacuum with 100 % phosphoric acid to dissolve the bone/dentine/enamel mineral and release carbon dioxide from hydroxyapatite. The resulting carbon dioxide was cryogenically purified from other reaction products and catalytically converted to graphite (Cherkinsky, 2009).

All results are reported using delta notation, $\delta = [(R_{sample}/R_{standard} - 1)*1000]$ (Coplen, 1994). The reference for carbon isotope values ($R = {}^{13}C/{}^{12}C$) is V-PDB, and oxygen isotope values ($R = {}^{18}O/{}^{16}O$) is V-SMOW.

The studied samples were not dated. However, many ^{14}C Accelerator Mass Spectrometry (**AMS**) and Electron Spin Resonance (**ESR**) datings for *Eremotherium laurillardi* and *Notiomastodon platensis* are available (Table S1) for Fazenda São José, Poço Redondo, Sergipe, allowing us to suggest that this fossil accumulation had relatively limited time-averaging (~32 ky, considering both ^{14}C AMS and ESR datings techniques; Dantas *et al.*, 2011; 2017), similarly to another fossil assemblage in northeastern Brazil (~59 ky, based only on ESR datings; Baixa Grande, Bahia; *e.g.* Ribeiro *et al.*, 2014). In addition, França *et al.* (2014a) reported that isotopic diet ($\delta^{13}C$) of *Eremotherium laurillardi* and *Notiomastodon platensis* did not change between 12–19 ky, suggesting a stable environment.

Additional published data

In order to complement our results, and refine the determination of the isotopic diet of Sergipe taxa, we included previously published isotopic data ($\delta^{13}C$ and $\delta^{18}O$, of which most have ^{14}C AMS datings; Table S1) and ^{14}C AMS and ESR datings for *Eremotherium laurillardi*, *Notiomastodon platensis*, *Toxodon platensis* and *Caiman latirostris* (Dantas *et al.*, 2011; França *et al.*, 2014b; Dantas *et al.*, 2014; 2017, and references therein).

Furthermore, we refined and compared our results with isotopic diet data of some extant African mesoherbivores (body mass between 100 kg and 750 kg) and megaherbivores (body mass > 800 kg) from Kenya and Tanzania (Bocherens *et al.*, 1996; Kingston & Harrison, 2007; Cerling *et al.*, 2008), since they live in an open environment, corresponding to the modern environment most similar to the one where the extinct meso- and megaherbivores mammals from Brazilian Intertropical Region (**BIR**) probably lived: *Loxodonta africana* (Blumenbach, 1797), *Equus quagga* Boddaert, 1785 (= *E. burchelli*), *Dicerus bicornis* (Linnaeus, 1758), *Ceratotherium simum* (Burchell, 1817), *Connochaetes taurinus* (Burchell, 1823), *Syncerus caffer* Sparrman, 1779, *Kobus ellipsiprymnus* (Ogilby, 1833), *Oryx beisa* Rüppell, 1835, *Giraffa camelopardalis* (Linnaeus, 1758) and *Hippopotamus amphibius* Linnaeus, 1758 (Table 1).

Multivariate analyses

Carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopic data for meso-megaherbivores from Sergipe, Brazil and Africa was submited cluster analyses (Q-mode) using the weighted pair group method with simple arithmetic averages (UPGMA), with the Euclidean Similarity coefficient. A bootstrap test (N = 10000) was applied to evaluate the consistency of the clusterings. A Principal Component Analyses (**PCA**) was made as well. All analyses were performed in the PAST 2.17 (Hammer *et al.*, 2001).

Body mass estimation

To estimate carbon enrichment (subtopic 2.5) and to classify the studied mammals between mesoherbivores (body mass between 100 kg and 750 kg) and megaherbivores (body mass > 800 kg), we calculated the estimated body mass (**1**) for megafauna species that lived in Sergipe (Tables 1 and S2) using the following regression (Anderson *et al.*, 1985):

$$(\mathbf{1})\ bm = 0.078C_{(h+f)}^{2.73}$$

Where *bm* is the body mass (**g**), *C* is the minimum circumference of humerus and femur diaphysis (in mm). We calculated an average value of circumferences based on the information available in articles and gray literature (Cartelle & Abuhid, 1989; Porpino & Bergqvist, 2002; Castro & Langer, 2008; Porpino *et al.*, 2009; Molena, 2012; Oliveira *et al.*, 2017) and in some collections that were accessible (Laboratório de Paleontologia, Universidade Federal de Sergipe; Museu de Ciências Naturais, Pontifícia Universidade Católica de Minas Gerais). When the circumference information was not available, we estimated it using the minimum width of humerus and femur diaphysis as a diameter (***d***) measure (Table S2), through a circumference estimation: $C = d\pi$.

Xenarthrans have flat femur with a high circumference of diaphysis values, leading to an overestimation of body mass if using standard method. To avoid this problem, we multiplied their femur circumference by 0.4, trying to acquire a more realistic body mass estimation (**2**). The regression adaptation was calibrated using values for three extant taxa, one Cingulata (*Priodontes maximus* (Kerr, 1792)) and two Tardigrada (*Tamandua tetradactyla* (Linnaeus, 1758) and *Myrmecophaga tridactyla* Linnaeus, 1758) (Table S2). Exceptions were made for glyptodonts (*Panochthus* and *Glyptotherium*), whose body masses were estimated by original regression proposed by Anderson *et al.* (1985). For extant African megamammals we used maximum estimate body mass from Coe *et al.* (1976).

$$(\mathbf{2})\ bm = 0.078C_{(h+0.4f)}^{2.73}$$

Isotopic diet interpretation using $\delta^{13}C$ and $\delta^{18}O$ values

The interpretation of carbon isotopic values for meso- and megaherbivorous mammals is generally based on known average for C_3 plants ($\mu\delta^{13}C$ = -27±3 ‰), C_4 plants ($\mu\delta^{13}C$ = -13±2 ‰) and CAM plants (intermediate values between the $\delta^{13}C$ of C_3 and C_4 plants) (*e.g.* MacFadden, 2005; Dantas *et al.*, 2017). However, some authors (*e.g.* Diefendorf *et al.*, 2010; Kohn, 2010) showed that the fractionation of carbon isotopes in C_3 plants presents great variability in different environments through the globe, which could lead to an overestimation of the mean value of at least 2 ‰.

We tried to estimate the $\mu\delta^{13}C$ for C_3 plants in the late Pleistocene of Sergipe (altitude 186 m, latitude 10º), using the equation proposed by Kohn (2010). One problem that we faced was the absence of data about Mean Annual Precipitation (**MAP**) in late Pleistocene of Sergipe. Thus, we used present MAP data for Poço Redondo, Sergipe (MAP = 548 mm; Sergipe, 2011), and found a value of -26.80 ‰. As we do not have MAP for late Pleistocene of Sergipe, and the value found is similar to the know average for C_3 plants, we choose to use $\mu\delta^{13}C$ = -27 ‰. For Kenya (altitude 1140 m; latitude 20º; MAP 350 mm/year; Bocherens *et al.*, 1996) and Tanzania (altitude 1130 m; latitude 2º; MAP 550 mm/year; Magill, 2012) we found $\mu\delta^{13}C$ = -26.08 ‰ and $\mu\delta^{13}C$ = -26.48 ‰, respectively. Thus, for localities in Africa we used $\mu\delta^{13}C$ = -26 ‰.

Tejada-Lara *et al.* (2018) suggested that body mass influences physiological carbon enrichment ($\varepsilon^*_{\text{diet-bioapatite}}$) in mammals and provided equations to determine these values of enrichment. Carbon isotopic data presented here are from mammals (extinct and extant) with body mass varying from 38 to 6,300 kg (Tables 1 and S2), $\varepsilon^*_{\text{diet-bioapatite}}$ varied between 12.47 to 14.84 ‰, we used four values: +12 ‰ for taxa weighting less than 75 kg; +13 ‰ for taxa weighting between 75 kg to 600 kg; +14 ‰ for taxa weighting between 600 kg to 3,500 kg; and finally, +15 ‰ for taxa weighting more than 3,500 kg (Table S3).

Considering an enrichment of 12–15 ‰, in Upper Pleistocene of Sergipe, $\delta^{13}C$ values lower than -15 ‰ to -12 ‰ are typical of animals with a diet consisting exclusively of C_3 plants, while in Africa, $\delta^{13}C$ values lower than -14 ‰ to -11 ‰ are typical of animals with a diet consisting exclusively of C_3 plants. For both areas $\delta^{13}C$ values higher than -1 ‰ to +2 ‰ are consistent with a diet based on C_4 plants.

However, C_3 plants show different values of enrichment, for example, leaves in C_3 plants are depleted in ^{13}C about -1.0 ‰ than others non-photosynthetic tissues like fruits (in average 1.5±0.07 ‰) and roots (in average 1.1±0.09 ‰); in contrast, C_4 plants tend to show no enrichment of ^{13}C in tissues (*e.g.* fruits, roots) compared to leaves (*e.g.* Yoneyama & Ohtani, 1983; MacFadden, 2005; Badeck *et al.*, 2005; Cernuzak *et al.*, 2009). Thus, we can estimate different type of food resources using carbon isotopic values in a mathematical mixing model.

Therefore, in this paper, we suggest a refinement of proportion of food items that medium- to large-bodied herbivorous mammals (extant summing +2 ‰ to compare to extinct animals due to Suess effect - Keeling, 1979 - in carbon isotopic data) could intake using $\delta^{13}C$ values in a single element mathematical mixing model (Phillips, 2012), suggesting as food types: leaves, fruits and C_4 grass. Trying to distinguish food resources, we suggest carbon (using a difference of 2.5 ‰ between leaves and fruits in C_3 plants) (Table S4) to be applied in equations (**3**) in Excel (Microsoft Corporation, Redmond, Washington) through Solver supplement (presuming non-negative values):

$$\text{(3)} \quad \begin{gathered} \delta^{13}C_{mix} = \delta^{13}C_1 f_1 + \delta^{13}C_2 f_2 + \delta^{13}C_3 f_3 \\ 1 = f_1 + f_2 + f_3 \end{gathered}$$

To compare environmental conditions between Africa and Sergipe, we considered $\delta^{18}O_{CO3}$ values of proboscideans as a "thermometer", since these animals are considered evaporation-insensitive taxa, as their oxygen isotopes values come mostly from drinking water (from lakes, rivers, pools), presenting no correlation between carbon and oxygen (Figure 2; Levin *et al.*, 2006) and water in plant tissues (except leaves) carries the same ^{18}O isotopic signal as source water of environment (Marshall *et al.*, 2007).

Thus, we used the mean values of $\delta^{18}O_{CO3}$ found in *Loxodonta africana* (Proboscidea; $\mu\delta^{18}O_{CO3}$ = 30.03±1.05 ‰; Figure 2A; Table 1) in comparison with $\delta^{18}O_{CO3}$ values of *Notiomastodon platensis* (Proboscidea; $\mu\delta^{18}O_{CO3}$ = 32.57±1.95 ‰; Figure 2B; Table 1) as a proxy to establish the enrichment (+2.5 ‰) of ^{18}O Sergipe environment in comparison to Africa environment.

For carnivores (*Smilodon populator* and *Caiman latirostris*) we used a mathematical mixing model with two isotopes (**4**). In general, nitrogen is used together with carbon to estimate food resources in a mathematical mixing model with two isotopes (*e.g.* Phillips, 2012, and examples therein), however, analyses in hydroxyapatite are unable to generate nitrogen isotopic data, thus, the only option available is to use oxygen isotopic data instead.

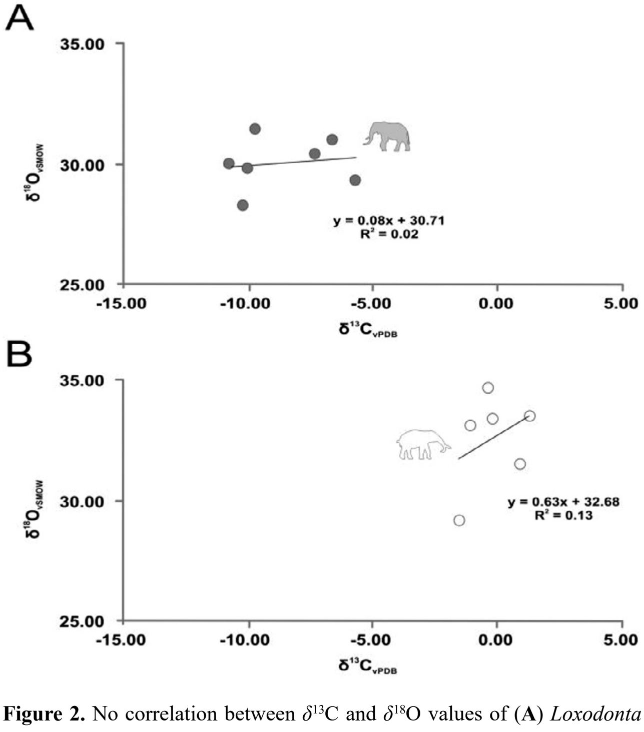

Figure 2. No correlation between $\delta^{13}C$ and $\delta^{18}O$ values of (**A**) *Loxodonta africana* and (**B**) *Notiomastodon platensis* allowing to suggest that their oxygen isotopes values come mostly from drinking water.

Herbivores and carnivores acquire oxygen isotopic through respiration, drunk water and food (Bocherens & Drucker, 2013), thus, for the carnivores we could use carbon and oxygen isotopic data to establish the proportion of their potential prey as they contribute with these isotopic values. We used the isotopic data of the African lion *Panthera leo* ($\mu\delta^{13}C$ = -5.40 ‰, $\delta^{18}O$ = 31.64 ‰, Cerling *et al.*, 2008) to test the use of carbon and oxygen to suggest the isotopic diet of carnivores such as *Smilodon populator* and *Caiman latirostris*.

In these regressions we used as potential prey all the taxa present in Sergipe, Brazil (carnivores and herbivores; Tables S1 and 3), summing -1 ‰ due to trophic level (Bocherens & Drucker, 2013) in carbon data.

$$\text{(4)} \quad \begin{gathered} \delta^{13}C_{mix} = \delta^{13}C_1 f_1 + \delta^{13}C_2 f_2 + \delta^{13}C_3 f_3 + \delta^{13}C_4 f_4 + \ldots + \delta^{13}C_{11} f_{11} \\ \delta^{18}O_{mix} = \delta^{18}O_1 f_1 + \delta^{18}O_2 f_2 + \delta^{18}O_3 f_3 + \delta^{18}O_4 f_4 + \ldots + \delta^{18}O_{11} f_{11} \\ 1 = f_1 + f_2 + f_3 + f_4 + \ldots + f_{11} \end{gathered}$$

Ecological measurements

To estimate ecological measurements, we calculated isotope niche breadth (*B)* using Levins' (1968) measure (**5**), where p_i is the relative proportion of individuals in isotope bin *i*. This measure was then standardized (B_A) from 0 to 1 following equation (**6**), where *n* is total number of isotope bins available. Values lower or equal to 0.5 suggests a specialist, and above 0.5, a generalist.

$$\textbf{(5)}\ B = \frac{1}{\Sigma p_i^2} \qquad \textbf{(6)}\ B_A = \frac{B-1}{N-1}$$

Finally, to estimate the mean (y_{mean}) and maximum (y_{max}) potential prey size for *Smilodon populator* (*x* - body mass of *S. populator*), we used regressions (7–8) proposed for Radloff & Du Toit (2004) by carnivores from Africa:

$$\textbf{(7)}\ \mathrm{Log}_{10} y_{mean} = 1.39 \mathrm{Log}_{10} x - 0.74$$

$$\textbf{(8)}\ \mathrm{Log}_{10} y_{max} = 1.46\ \mathrm{Log}_{10} x - 0.17$$

RESULTS

Body mass estimation

For the Brazilian Intertropical Region (including Sergipe), there are no body mass estimations for Pleistocene mammals. Thus, following the first attempt proposed by Dantas *et al.* (2017), we continued the efforts to infer the body mass of mammals that lived there, which could help us to better reconstruct their ecology.

For localities in Sergipe, we were able to suggest body mass estimates (Tables 1 and S2) only for *Eremotherium laurillardi* (*bm* = ~3,416 kg) and *Toxodon platensis* (*bm* = ~1,770 kg). For other taxa there are no fossils available to estimate their body masses. Therefore, we estimated body masses based on fossils from other geographical regions through Brazilian Intertropical Region (Table S2). We estimated and used the following body masses: *Catonyx cuvieri* (*bm* = ~777 kg), *Pachyarmatherium brasiliense* (*bm* = ~38 kg), *Panochthus* sp. (*bm* = ~785 kg), *Glyptotherium* sp. (*bm* = ~710 kg), *Holmesina paulacoutoi* (*bm* = ~120 kg), *Palaeolama major* (*bm* = ~285 kg), *Equus* (*Amerhippus*) *neogeus* (*bm* = ~420 kg) and *Smilodon populator* (*bm* = ~315 kg). The body mass estimations for *E. laurillardi*, *C. cuvieri*, *T. platensis* and *S. populator* are similar to those proposed for similar taxa from Argentina and Uruguay (Fariña *et al.*, 1998; Christiansen & Harris, 2005). For *P. brasiliense*, *H. paulacoutoi* and *P. major* there is no body mass estimation for comparison. We hypothetize that the lower body mass estimation for *Panochthus* and *Glyptotherium* in BIR is due the avaibility of few bones (humerus and femur; Table S2) for both taxa and the lower circunference of the diaphysis in comparison to specimens found in United States and Argentina.

Finally, in Sergipe, we had a fauna composed by one megacarnivore (*Smilodon populator*), one omnivore (*Pachyarmatherium brasiliense*), six mesoherbivores (*Holmesina paulacoutoi*, *Catonyx cuvieri*, *Glyptotherium* sp., *Panochthus* sp., *Palaeolama major* and *Equus* (*A.*) *neogeus*) and three megaherbivores (*Eremotherium laurillardi*, *Toxodon platensis* and *Notiomastodon platensis*).

Isotopic diet (δ^{13}C, δ^{18}O)

The use of carbon in an one element isotopic mixing model to suggest three resources allows us to refine the type of C_3 plants consumed by herbivores in leaves and fruits. The proportion of C_3 (summing proportions of leaves and fruits) and C_4 plants in this model presents similar values if we compare the proportions found in one element isotopic mixing model suggesting only C_3 and C_4 plants (Tables 1 and S5).

For Sergipe, we generated new isotopic data for *Eremotherium laurillardi* and *Toxodon platensis*, completed with unpublished isotopic data for *Catonyx cuvieri*, *Holmesina paulacoutoi*, *Glyptotherium* sp., *Panochthus* sp., *Palaeolama major* and *Equus* (*Amerhippus*) *neogeus*, and include published isotopic data for *Eremotherium laurillardi*, *Toxodon platensis* and *Notiomastodon platensis* (França *et al.*, 2014a; Dantas *et al.*, 2017, and references therein; Table S1; Figures

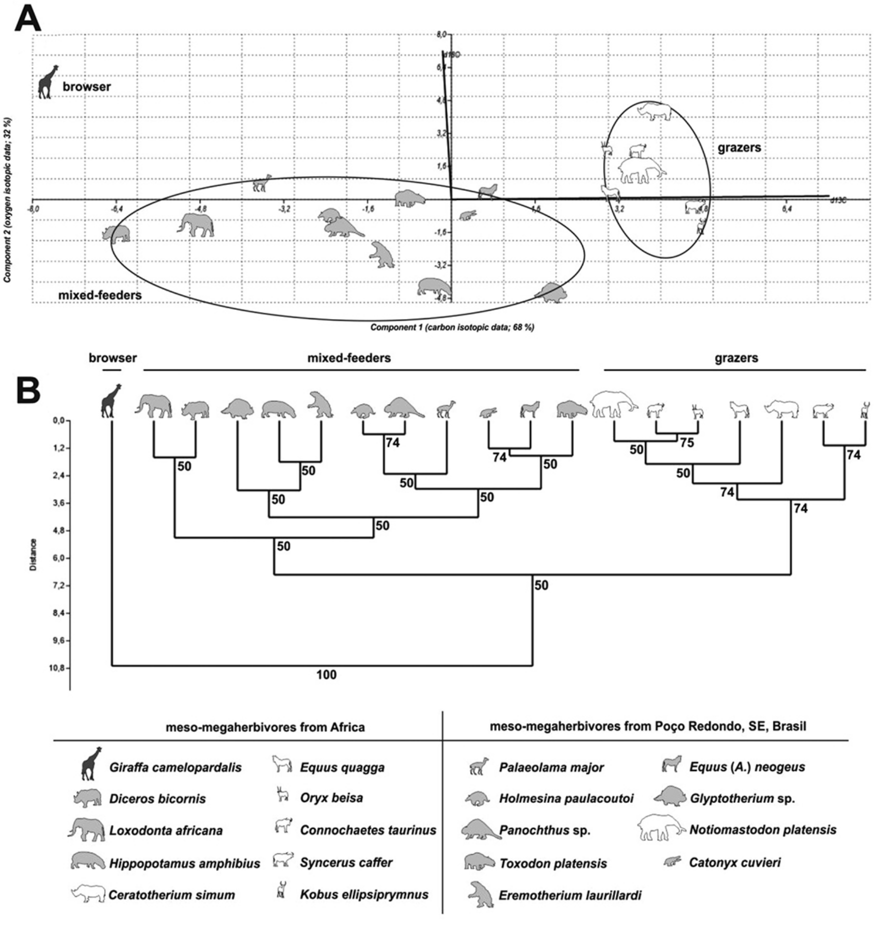

Figure 3. A, Principal Component Analyses (**PCA**) using δ^{13}C and δ^{18}O values for meso-megaherbivores from Africa and Sergipe, Brazil; **B**, Dendogram with clustering of taxa according to their ecological guilds (bootstrap test, N = 10.000).

3A and 4) to refine isotopic diet of all taxa that lived in Sergipe during the late Pleistocene.

For the giant ground sloth *Eremotherium laurillardi* we present five new carbon and oxygen isotopic data, which shows δ^{13}C values ranging from -6.0 ‰ to -3.9 ‰ ($\mu\delta^{13}$C = -4.9±0.9) and a δ^{18}O of 23.4 to 29.4 ($\mu\delta^{18}$O = 27.4±2.3). Including published isotopic data (França *et al.*, 2014a; Dantas *et al.*, 2014; 2017) this interval increases, for carbon to -9.2 ‰ to -2.0 ‰ ($\mu\delta^{13}$C = -5.0±1.8), and for oxygen to 23.4 to 30.3 ‰ ($\mu\delta^{18}$O = 28.4±1.6) (Tables 1 and S1). Using all available data for Sergipe in one isotopic mixing model, we suggest a diet composed of leaves (p_i = 18 %), fruits (p_i = 27 %) and, mainly, in C$_4$ grasses (p_i = 55 %) (Table 1).

It is worth noting that LPUFS 5693 was an unworn molariform from a juvenile (perhaps from a suckling individual), and we noticed that the carbon isotopic data (δ^{13}C = -6.0 ‰) was not different from the adults of the same locality (Fazenda São José, Poço Redondo; $\mu\delta^{13}$C = -5.4±2.3), being equivalent to mother diet, because carbon isotopic values of mother milk and offspring would not have significant differences (*e.g.* trophic level; Jenkins *et al.*, 2001).

Catonyx cuvieri (δ^{13}C = -3.4 ‰; δ^{18}O = 30.2 ‰) was another giant ground sloth analyzed, showing diet based mainly in C$_4$ grass (p_i = 67 %), but in fruits (p_i = 23 %) and leaves (p_i = 10 %), as well (Tables 1 and S1).

We generated isotopic data for three Cingulata. The pampathere *Holmesina paulacoutoi* presents a δ^{13}C of -6.0 ‰ and δ^{18}O of 30.3 ‰, its diet was composed of 16 % of leaves, 29 % of fruits and 55 % of grasses (Tables 1 and S1). For *Glyptotherium* sp. was found a carbon isotopic value of -1.8 ‰ and oxygen isotopic value of 26.4 ‰, this taxon fed in 77 % of C$_4$ grasses, and little in fruits (p_i = 20 %) and leaves (p_i = 3 %) (Tables 1 and S1). *Panochthus* sp. presents δ^{13}C of -5.9 ‰ and oxygen isotopic value of 29.7 ‰, showing a diet based on leaves (p_i = 22 %), fruits (p_i = 29 %) and C$_4$ grass (p_i = 49 %) (Tables 1 and S1).

For the Notoungulata *Toxodon platensis* four unpublished isotopic data were generated, which present a δ^{13}C variation of -9.8 ‰ to -3.3 ‰ ($\mu\delta^{13}$C = -5.0±3.2), and oxygen isotopic values between 27.4 ‰ to 34.2 ‰ ($\mu\delta^{18}$O = 31.0±2.9) (Table S1). Including the isotopic data presented by Dantas *et al.* (2017), carbon isotopic interval increases for -9.8 ‰ to -2.8 ‰ ($\mu\delta^{13}$C = -4.5±2.9), the oxygen isotopic range remains the same, but presents as mean values 31.2±2.5 ‰. This taxon presented a high consumption of C$_4$ grass (p_i = 58 %), followed

Figure 4. A, Pleistocene meso- megamammals from Sergipe, Brazil; **B**, two *Smilodon populator* stalking a *Palaeolama major* group, while two *Caiman latirostris* are scavenging a *Notiomastodon platensis* corpse (Images: Julio Lacerda, 2020).

by consumption of fruits (p_i = 26 %), and low consumption of leaves (p_i = 16 %) (Table 1).

The diet of *Palaeolama major* ($\delta^{13}C$ = -7.3 ‰; $\delta^{18}O$ = 31.9 ‰) was composed mainly of C_4 grass (p_i = 45 %) but fed also on fruits (p_i = 32 %) and leaves (p_i = 23 %) (Tables 1 and S1).

For the horse *Equus* (*Amerhippus*) *neogeus* fossil we found a carbon isotopic value of -3.0 ‰, and a $\delta^{18}O$ of 31.3 ‰, indicating a diet composed mainly of grasses (p_i = 70 %), while feeding on fruits (p_i = 22 %) and leaves (p_i = 8 %) was limited (Tables 1 and S1).

The proboscidean *Notiomastodon platensis* ($\mu\delta^{13}C$ = -0.1±1.1 ‰; $\mu\delta^{18}O$ = 32.5±1.9 ‰; Table S1) presented a diet based mainly in C_4 grass (p_i = 83 %), 12 % in fruits, and low proportions of leaves (p_i = 5 %) (Table 1).

In addition to the isotopic data of meso-megaherbivores from Poço Redondo, Sergipe, we generated isotopic data of carbon and oxygen for *Pachyarmatherium brasiliense* and *Smilodon populator*, and included published isotopic data for *Caiman latirostris* (França *et al.*, 2014b), to suggest a trophic web in this assemblage (Figure 5). Besides, isotopic data were used to estimate the possible habitat in which the terrestrial predators hunted.

Downing & White (1995) suggested, based on an edentulous jaw tentatively assigned to *Pachyarmatherium leiseyi*, a diet composed mainly of termites and ants. Unfortunately, as we do not have nitrogen isotopic data for *P. brasiliense*, we could not test this hypothesis. However, following Downing & White (1995), our results in mathematical mixing model ($\delta^{13}C$ = -6.6 ‰; δ18O = 28.7 ‰; Table S1) would not reflect a diet based on plants, but on Blattodea taxa which lived in close (p_i = 48 %), as well as in open areas (p_i = 52 %).

Smilodon populator ($\delta^{13}C$ = -6.0 ‰; $\delta^{18}O$ = 30.5 ‰; Table S1) hunted similarly in closed (p_i = 52 %) and in open areas (p_i = 48 %), and had as main preys ($p_i \geq 10$ %; Table 3; Figure 5), *Palaeolama major* (p_i = 14 %), *Holmesina paulacoutoi* (pi = 12 %), *Toxodon platensis* (p_i = 12 %), *Pachyarmatherium brasiliense* (p_i = 11 %), *Panochthus* sp. (p_i = 12 %), *Catonyx cuvieri* (p_i = 10 %), *Equus* (*Amerhippus*) *neogeus* (p_i = 10 %) and *Caiman latirostris* (p_i = 10 %) (Table 3).

Another carnivore found in Sergipe was *Caiman latirostris* ($\delta^{13}C$ = -3.0 ‰, $\delta^{18}O$ = 31.4 ‰; França *et al.*, 2014b; Table S1), our analyses allow us to suggest that it could feed on a variety of taxa, mainly on taxa that lived in open areas (pi = 82 %), as *Notiomastodon platensis* (p_i = 44 %), as well

Table 1. Weight (**t**), mean values of proportional contributions (**p_i**) of food sources (leaf, fruit, C_4 grass), carbon isotopes (**$\delta^{13}C$**), standardized isotopic niche breadth (**B_A**), oxygen isotopes (**$\delta^{18}O$**) and niche overlap (***O***) for extant meso-megamammals from Africa and Pleistocene of Sergipe. **References:** (1) Coe *et al.* (1976); (2) Our data. **Abreviations:** mammals from Sergipe, Brazil. ***El***, *Eremotherium laurillardi*; ***Cc***, *Catonyx cuvieri*; ***Hp***, *Holmesina paulacoutoi*; ***G***, *Glyptotherium* sp.; ***P***, *Panochthus* sp.; ***Tp***, *Toxodon platensis*; ***Np***, *Notiomastodon platensis*; ***Pm***, *Palaeolama major*; ***En***, *Equus* (*Amerhippus*) *neogeus*. Mammals from Africa. ***La***, *Loxodonta africana*; ***Eq***, *Equus quagga*; ***Db***, *Diceros bicornis*; ***Cs***, *Ceratotherium simum*; ***Ct***, *Connochaetes taurinus*; ***Sc***, *Syncerus caffer*; ***Ke***, *Kobus ellipsiprymnus*; ***Ob***, *Oryx beisa*; ***Gc***, *Giraffa camelopardalis*; ***Ha***, *Hippopotamus amphibius*.

	W (t)	$\delta^{13}C$	p_i			B_A	$\delta^{18}O$
			leaves	fruits	C_4 grass		
Sergipe							
El	3.42	-5.0±1.8	0.18	0.27	0.55	0.68	28.4±1.6
Cc	0.78	-3.4	0.10	0.23	0.67	0.49	30.2
Hp	0.12	-6.0	0.16	0.29	0.55	0.72	30.3
G	0.71	-1.8	0.03	0.20	0.77	0.28	26.4
P	0.78	-5.9	0.22	0.29	0.49	0.84	29.7
Tp	1.77	-4.7±2.8	0.16	0.26	0.58	0.57	31.2±2.5
Np	6.27	-0.2±1.1	0.05	0.12	0.83	0.22	32.5±1.9
En	0.42	-3.0	0.08	0.22	0.70	0.43	31.3
Pm	0.28	-7.3	0.23	0.32	0.45	0.89	31.9
Africa							
La	5.00	-8.6±2.0	0.34	0.33	0.33	0,88	30.0±1.0
Eq	0.29	-0.6±1.1	-	0.01	0.99	0.01	31.2±1.8
Db	1.00	-10.1±1.8	0.35	0.36	0.29	0.89	29.5±1.3
Cs	2.00	0.3±0.2	-	-	1.00	0.00	35.2
Ct	0.22	-0.1±1.3	-	0.01	0.99	0.01	33.3±0.9
Sc	0.66	0.9±1.3	-	-	1.00	0.00	30.6±1.4
Ke	0.20	1.0	-	-	1.00	0.00	29.5
Ob	0.16	-0.7	-	-	1.00	0.00	33.4
Gc	1.20	-11.3±1.9	0.42	0.39	0.19	0.80	37.0±1.5
Ha	1.40	-4.1±1.5	0.06	0.21	0.73	0.38	26.9±1.5

as *Equus (A.) neogeus* (p_i = 18 %), *Toxodon platensis* (p_i = 16 %), *Catonyx cuvieri* (p_i = 12 %) and *Glyptotherium* sp. (p_i = 10 %; Table 3).

Niche breadth

We estimated the niche breadth for all vertebrates found in Sergipe, Brazil (Table 1), suggesting as specialists (B_A < 0.50), in crescent order: *Notiomastodon platensis* (B_A = 0.22±0.13), *Glyptotherium* sp. (B_A = 0.28), *Equus* (*A.*) *neogeus* (B_A = 0.43) and *Catonyx cuvieri* (B_A = 0.49). *Toxodon platensis* (B_A = 0.57±0.19), *Eremotherium laurillardi* (B_A = 0.68±0.21), *Holmesina paulacoutoi* (B_A = 0.72), *Panochthus* sp. (B_A = 0.84) and *Palaeolama major* (B_A = 0.89) were generalists. The faunivorous *Pachyarmatherium brasiliense* (B_A = 0.78) and *Smilodon populator* (B_A = 0.85) were generalists, presenting similar values of niche breadth, and *Caiman latirostris* was a specialist with the lowest niche breadth (B_A = 0.29) (Table 1).

DISCUSSION

Isotopic paleoecology (δ^{13}C, δ^{18}O): feeding habit

Through the one element isotopic mixing model we could refine the suggestion of diet for several taxa from Sergipe, in all studied specimens we noted a diet composed mainly of abrasive resources, such as C_4 grass.

Eremotherium laurillardi presented a consumption of 45 % of C_3 plants (fruits and leaves) and mainly a C_4 grass diet (p_i = 55 %; Table 1). Bargo *et al.* (2006a) suggested that *E. laurillardi* and *Megatherium americanum* had masticatory apparatus with similar biomechanical functions, presenting robust cranial muscles which allows them to had a strong bite, and a thick cone-shaped and prehensile upper lip which could select part of plants. To support the discussion of our isotopic results for *E. laurillardi* we followed Vizcaíno *et al.* (2006) and Bargo *et al.* (2006b), and estimated the occlusal surface area (OSA) and the Hypsodonty index (HI) for a dentary of *E. laurillardi* (LPUFS 4755) from Poço Redondo, Sergipe (Table 2).

The estimated OSA from LPUFS 4755 was 10,650.83 mm^2, which is equivalent to the OSA found for *Megatherium americanum* (Table 2), suggesting that it could process a large amount of turgid to soft food items, such as C_4 grass and fruits.

The HI of *Eremotherium laurillardi* LPUFS 4755 was higher (HI = 0.96; Table 2) than those found for northeastern Brazilian species (MCL and MNRJ samples; HI = 0.76±0.02; Table 2), and closer to the HI found for *Megatherium americanum* (HI = 1.02±0.07; Table 2). This is unexpected, but it could suggest that in Sergipe a population adapted to a diet with a higher consumption of dust and grid ingested together with their food items (such as C_4 grass), which reinforces our interpretation based on the mathematical mixing model of carbon isotopes.

Another evidence came from L. Asevedo (pers.comm.), which analyzed the feeding ecology of *Eremotherium laurillardi* from Gararu and Poço Redondo (both in Sergipe, Brazil) through stereomicrowear analysis, and noted high values of scratch (fine and coarse), as well hypercoarse scratches, gouges, cross-scratches and pits, which suggests a mixed feeder diet based mainly in grasses, but feeding in fruits and leaves as well, consistent with our interpretation based on stable isotopes.

The diet of the other Pilosa, *Catonyx cuvieri,* was partially in contrast to the expectation for a Scelidotherinae, as a selective feeder habit was expected, feeding more in fruits, leaves, buds and roots (Bargo *et al.*, 2006a,b). The analyzed sample (UGAMS 35324; Table S1) belonged to an adult individual (Dantas & Zucon, 2007), which presented a diet lower in fruits and leaves (p_i = 33 %) and a major consumption of C_4 grass (p_i = 67 %) (Table 1). Maybe competition or environmental conditions induced a change in its feeding habits, leading to a consumption of the most available resources that were C_4 grasses.

Some authors (Vizcaíno *et al.*, 1998; 2011) suggested that *Glyptotherium*, *Panochthus* and *Holmesina* could be mainly grazers, based in biomechanics of the masticatory apparatus and hypsodonty index. However, these observations could be effects of natural selection, based on the environments in which these taxa evolved, and did not reflect an exclusive diet on grass, thus, our isotopic results (Table 1) from Sergipe are not odd, as presented a good consumption of C_4 grasses (p_i > 49 %), plus fruits and leaves of C_3 plants.

In Sergipe *Toxodon platensis* presented a diet composed mainly of C_4 grass (p_i = 57 %; Table 1). Compared to the data presented by Dantas *et al.* (2017) for all BIR, we noted a contrast, as it fed more on C_3 plants (p_i = 60 %) than on C_4 plants (p_i = 40 %), suggesting a drier environment in Sergipe than in other regions of BIR. For *Palaeolama major* our analyses yielded a fair consumption of C_4 grass (p_i = 46 %). Compared to the data based on the analysis of coprolites (Marcolino *et al.*, 2013), we found a partial correspondence, as it suggested a diet based exclusively on C_3 plants and our results suggest the consumption of, at least, 54 % of C_3 plant

Table 2. Oclusal Surface Area (**OSA**) and Hypsodonty index (**HI**) of *Megatherium americanum* and *Eremotherium laurillardi*. **Abbreviations: LTR**, length of the tooth row; **DM**, depth of the mandible; **HI**, Hypsodonty Index. Data from Bargo *et al.* (2006b) and Vizcaíno *et al.* (2006).

	M. americanum	*E. laurillardi* (LPUFS 4755)	*E. laurillardi* (MCL & MNRJ)
OSA (mm²)	10,818.36±464.23	10,650.83	-
LTR	213.00±17.91	172.94	188.44±7.13
DM	215.64±18.14	166.06	143.56±8.50
HI	1.02±0.07	0.96	0.76±0.02

tissues (fruits and leaves). *Equus* (*Amerhippus*) *neogeus* presented in Sergipe a diet composed mainly on C_4 plants (p_i = 69 %), which is in accordance with the isotopic results presented for Bahia (p_i = 84 %; Dantas *et al.*, 2017). Finally, *Notiomastodon platensis* exhibited a diet composed of 83 % of C_4 plants, presenting a similar consumption of C_4 plants in comparison with the mean value of the diet in BIR (p_i = 70 %; Dantas *et al.*, 2017). Silva (2015), through stereomicrowear analysis, noticed that *N. platensis* individuals from Canhoba were mixed feeders, but with a diet composed mainly of grasses.

Isotopic paleoecology (δ^{13}C, δ^{18}O): guilds

Using carbon and oxygen isotopic data in PCA we noticed that the contribution of carbon (p_i = 68 %) is higher than that of oxygen (p_i = 32 %) and together with the Cluster analyses showed three well defined groups/guilds: browsers, mixed-feeders and grazers (Figure 3).

To better understand isotopic paleoecology of Sergipe Pleistocene mammalian taxa, we compared their isotopic data with those available for 11 extant mammals from Africa (Table 1 and Figure 3), and we analyzed the isotopic diet patterns found using mathematical mixing model using carbon isotopes.

In Africa savannahs there were, at least, 20 species of grazers, 13 of browsers, 10 of mixed-feeders and one of omnivore (Owen-Smith, 1982). The grazer guild was composed of the megaherbivore *Ceratotherium simum*, a specialist grazer (B_A = 0.00), and for the specialists mesoherbivores *Equus quagga* (B_A = 0.01±0.02), *Connochaetes taurinus* (B_A = 0.01±0.02), *Syncerus caffer* (B_A = 0.00), *Kobus ellipsiprymnus* (B_A = 0.00) and *Oryx beisa* (B_A = 0.00), which have a diet composed mainly of C_4 grass (varying from 99 % to 100 %; Table 1; Figure 3), consumption of leaves and fruits were virtually inexistent.

In the browser guild we have data only for *Giraffa camelopardalis* (B_A = 0.80±0.18) feeding in 42% of leaves and 39 % of fruits (Table 1; Figure 3), and, in the mixed-feeder guild are *Loxodonta africana* (B_A = 0.88±0.07) and *Diceros bicornis* (B_A = 0.89±0.16), which fed similarly on C_4 grass (p_i = 29–33 %), fruits (p_i = 33–36 %) and leaves (p_i = 34–35 %; Table 1; Figure 3). *Hippopotamus amphibius* (B_A = 0.38±0.23) fed more on C_4 grass (p_i = 73 %), while in its case, values attributed to fruits and leaves (p_i = 27 %) could be C_3 aquatic plants (Table 1).

Based on PCA and Cluster Analyses of the Sergipe extinct mammals (Figure 3), we noticed that only *Notiomastodon platensis* was included in the grazer guild, feeding on more than 83 % of C_4 grass, as observed in herbivores mammals from Africa. The remaining studied taxa were included in the mixed-feeder guild (Figure 3), being subdivided in four subgroups, which presented mainly variations in their consumption of C_4 plants.

The taxa *Toxodon platensis*, *Equus* (*A.*) *neogeus* and *Catonyx cuvieri* showed an important consumption of C_4 grass (p_i = 43–57 %) but fed significantly on fruits (p_i = 22–26 %) and leaves (p_i = 8–16 %). In the other subgroup we have *Palaeolama major*, *Panochthus* sp. and *Holmesina paulacoutoi*, these taxa exhibited a moderate consumption of C_4 grass (p_i = 45–55 %), fruits (p_i = 29–32 %) and leaves (p_i = 16–23 %).

Finally, *Eremotherium laurillardi* and *Glyptotherium* sp. were grouped with *Hippopotamus amphibius*, mainly because of their lower oxygen isotopic values. For *Glyptotherium* sp. we have only one sample, its lower value of oxygen is odd, as it had a great consumption of C_4 grass (p_i = 77 %). Gillette & Ray (1981) suggested that *Glyptotherium* could have had a semi-aquatic habit, like *H. amphibius*. However, as we have only one sample, we cannot discard or confirm this hypothesis.

Isotopic paleoecology (δ^{13}C, δ^{18}O): trophic web

To show the efficiency of the use of carbon and oxygen (mainly this last one) isotopes values in a mathematical mixing model to suggest the proportional contribution of herbivores in the diet of carnivores, we estimated the proportional contribution of African herbivores (Table 1) to the diet of the lion *Panthera leo*.

Our results suggest that *Panthera leo* has a diet based on *Giraffa camelopardalis* (p_i = 20 %), *Diceros bicornis* (p_i = 15 %), *Loxodonta africana* (p_i = 14 %), *Hippopotamus amphibius*

Table 3. Prey isotopic (δ^{13}C, δ^{18}O) contribution (%) to isotopic diet of two vertebrate carnivores from the Late Pleistocene of Sergipe, Brazil.

Potential preys (weight in kg)	*Smilodon populator*	*Caiman latirostris*
Smilodon populator (315)	-	-
Caiman latirostris (60)	0.10	-
Eremotherium laurillardi (3,416)	0.06	-
Catonyx cuvieri (777)	0.10	0.12
Pachyarmatherium brasiliense (38)	0.11	-
Holmesina paulacoutoi (120)	0.12	-
Glyptotherium sp. (710)	0.02	0.10
Panochthus sp. (785)	0.12	-
Toxodon platensis (1,770)	0.12	0.16
Notiomastodon platensis (6,300)	0.01	0.44
Palaeolama major (285)	0.14	-
Equus (*Amerhippus*) *neogeus* (420)	0.10	0.18

(p_i = 12 %), *Equus quagga* (p_i = 9 %), *Connochaetes taurinus* (p_i = 8 %), *Syncerus caffer* (p_i = 8 %), *Kobus ellipsiprymnus* (p_i = 8 %) and *Oryx beisa* (p_i = 8 %). These results are in agreement with the literature (*e.g.* Hayward & Kerley, 2005; Loveridge *et al.*, 2006) which shows a prey preference of *P. leo* on *G. camelopardalis*, *L. africana* (calves, probably the same for *D. bicornis* and *H. amphibius*), *E. quagga*, *C. taurinus*, *S. caffer* and *O. beisa*, in other words, 67 % of what was estimated by the mathematical mixing model using oxygen and carbon isotopes.

For Sergipe isotopic data are available for three faunivorous taxa (*Smilodon populator*, *Caiman latirostris* and *Pachyarmatherium brasiliense*), allowing us to suggest a trophic web structure for this late Pleistocene vertebrate community (Figure 5) using the mathematical mixing model using oxygen and carbon isotopes.

Smilodon populator hunted more or less equally in closed landscapes (p_i = 52 %) and open environments (p_i = 48 %). Using regressions proposed by Radloff & Du Toit (2004) we estimated that the mean and maximum prey size for *S. populator* could had ranged between 540–3,000 kg, suggesting that only 36 % of its diet was composed of taxa belonging to his optimal interval (Table 3). Above this limit there is a low percentage (p_i = 7 %), including the megaherbivores *Eremotherium laurillardi* and *Notiomastodon platensis*. However, the majority of its diet (p_i = 56 %) was based on mammals weighting lower than 540 kg (Table 3).

It is possible that *Smilodon populator* hunted actively *Equus* (*A.*) *neogeus* (p_i = 10 %) and *Palaeolama major* (p_i = 14 %), as their body mass is not so distant from their mean prey size. The predation on *Caiman latirostris* is suggested (p_i = 10 %) based mainly on observations of predation nowadays by the extant Felidae *Panthera onca* on this crocodilian taxon (*e.g.* Azevedo & Verdade, 2011). Isotopic contribution of *Pachyarmatherium brasiliense* (p_i = 11 %) and *Holmesina paulacoutoi* (p_i = 12 %) for *S. populator* diet could represent a scavenging habit for this carnivore (Table 3; Figure 5). In Sergipe *S. populator* could not have a specialization on a prey type, which could suggest a pack-hunting behavior, as individuals of this pack could feed on a variety of prey samples proportionally.

In southern Chile, Prevosti & Martin (2013), based on carbon and nitrogen isotopes, suggested as possible prey for *Smilodon*: *Hippidion,* indeterminated Camelidae and *Lama guanicoe* (Camelidae). This is similar to the results of the present study, where the dominant prey also belonged to Camelidae taxa. However, the isotopic approach depends on the herbivore isotopic data available, and Bocherens *et al.* (2016) suggested as main prey for *Smilodon, Macrauchenia* (Macraucheniidae), followed by *Megatherium* (Megatheriidae) and *Lestodon* (Mylodontidae), which is different from the results of the present study, mainly because we do not have isotopic data for Macraucheniidae and Mylodontinae taxa in Sergipe. These results could reflect a regional difference in prey types for *S. populator*, or, as stated previously, it could be a consequence of the absence of isotopic data for more herbivores in our analyses.

The crocodylian *Caiman latirostris* could not actively hunt mammals' taxa found in Sergipe, as they body mass were more than 420 kg (Table 3). However, we suggest that

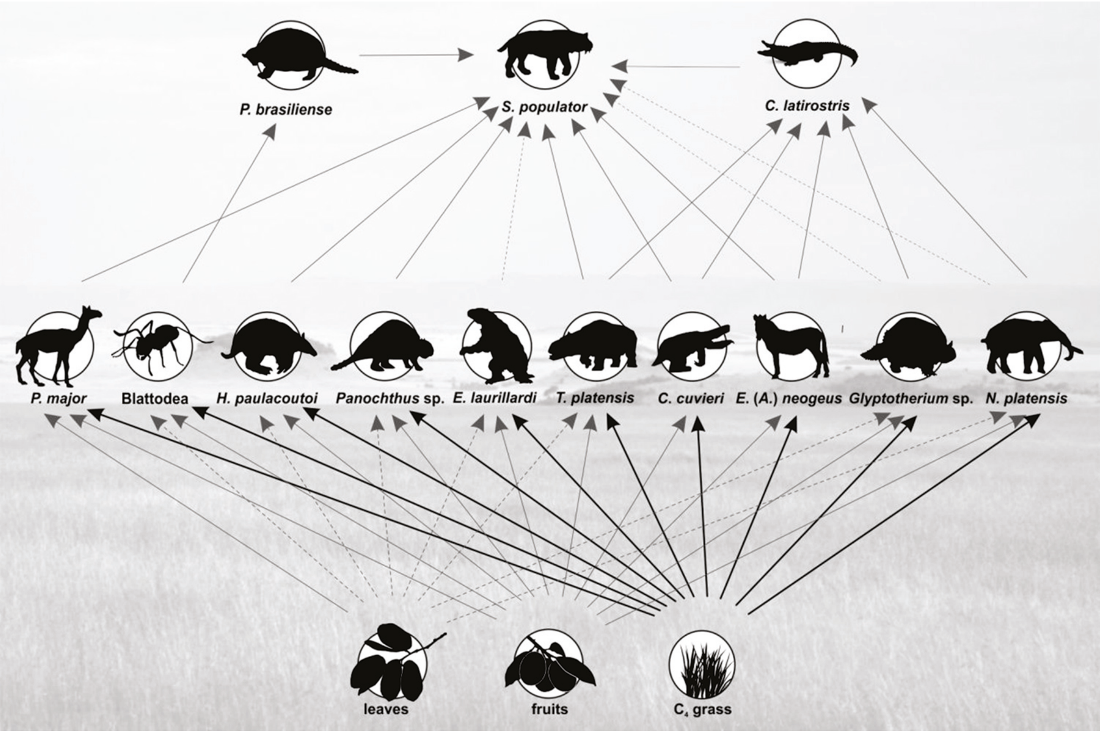

Figure 5. Isotopic (δ^{13}C and δ^{18}O) trophic web from pleistocenic meso-megamammals from Sergipe, Brazil. **Labels:** bold arrows, food resources that contributed more than 50% in isotopic signature of consumer; gray thin arrow, food resources that contributed more than 10% in isotopic signature of consumer; gray thin cracked arrow, food resources that contributed less than 10% in isotopic signature of consumer.

it could feed on carcasses, acting as a scavenger, like other crocodiles, since this would facilitate the dismembering of large prey corpses (*e.g.* Dixon, 1989; Perez-Higareda *et al.*, 1989; Figures 4B and 5).

Paleoenvironmental reconstruction

The available isotopic data from extant megamammals from Kenya and Tanzania (Table 1; Figure 3) yield a good illustration of the meso-megaherbivore fauna from Africa, with a predominance of grazer species with high consumption of C_4 plants (p_i = 99–100 %; Table 1), and where even mixed-feeder and browser species had a significant consumption of grass (p_i = 19–33 %).

In the late Pleistocene of Sergipe, the available data of meso-megaherbivores fauna showed a mammal assemblage composed of mixed-feeders and grazing species (Table 1; Figure 3). They fed less on C_4 grass (p_i = 45–83 %) than extant fauna from Africa, which could indicate that they lived in a more closed environment in comparison, with more C_3 plants, as herbs and shrubs.

Looking at the oxygen isotopic values of the evaporation-insensitive taxa *Loxodonta africana* (extant, Africa) and *Notiomastodon platensis* (extinct, late Pleistocene of Sergipe Brazil) (Figure 2) we noticed that Sergipe presented, in comparison, a drier environment than Africa nowadays, with a difference of almost +2.5 ‰.

França *et al.* (2014) noticed that, at least between 27 ka and 11 ka, the diet of *Eremotherium laurillardi* and *Notiomastodon platensis* did not change, suggesting an environmental stability in Poço Redondo, Sergipe, including dated carbon isotopic data from *Toxodon platensis* for Poço Redondo, *N. platensis* from Canhoba and *E. laurillardi* from Gararu, we tentatively expand this interpretation to Sergipe.

The oxygen isotopic data of *Eremotherium laurillardi* and *Toxodon platensis* allowed us to suggest that these taxa acquired their oxygen content through the drinking water, as well as *Notiomastodon platensis* (Figure 6A). Oxygen isotopic data for dated *T. platensis* are similar to those from *N. platensis*, but this is an isolated observation and does not allow us to discuss this point further. The $\boldsymbol{\delta}^{18}$O values of dated *N. platensis* did not show variations trough time,

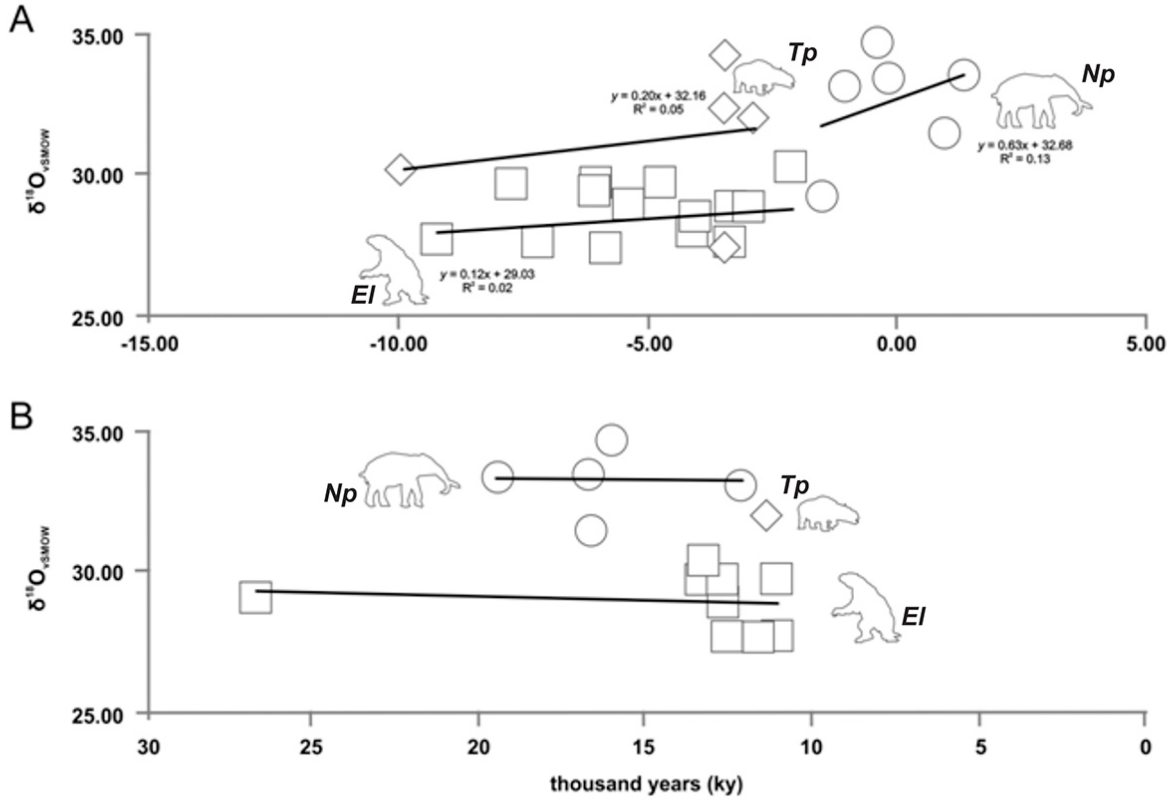

Figure 6. A, δ^{18}O values through time: No correlation between δ^{13}C and δ^{18}O values for *Eremotherium laurillardi* (*El*; $y = 0.12x + 29.03$, $R^2 = 0.02$), *Toxodon platensis* (*Tp*; $y = 0.20x + 32.16$, $R^2 = 0.05$) and *Notiomastodon platensis* (*Np*; $y = 0.63x + 32.68$, $R^2 = 0.13$) allowing to suggests that their oxygen isotopes values reflect mostly their drinking water. **B**, δ^{13}C values through time: Environmental stability through the late Pleistocene of Sergipe, between 27 ka to 11 ka.

while oxygen isotopic values of dated *E. laurillardi* showed a slight variation, which could indicate an increase of humidity through time, but virtually, it is similar to the oxygen data from *N. platensis* (Figure 6B).

FINAL REMARKS

The herbivore fauna had a high consumption of C_4 grass, belonging to two guilds: grazers ($p_i C_4$ grass > 83%; *N. platensis*) and Mixed Feeders (*Glyptotherium* sp; *Equus neogeus*; *Toxodon platensis*; *Holmesina paulacoutoi*; *Panochthus* sp.; *Catonyx cuvieri*; *Eremotherium laurillardi*; and *Palaeolama major*).

Smilodon populator could feed on meso-megaherbivores weighting between 285 kg to 6,300 kg (p_i = 67 %), eventually they could have hunted *Caiman latirostris* (p_i = 10 %), and we suggest that *S. populator* acted as scavengers feeding on the carcasses of *Pachyarmatherium brasiliense* (p_i = 11 %) and *Holmesina paulacoutoi* (p_i = 12 %). Besides this, we suggest that *C. latirostris* could have behaved as a scavenger, feeding on carcasses of these meso-megamammals, especially *Notiomastodon platensis* (p_i = 44 %).

Finally, we suggest that the meso-megamammals from the late Pleistocene of Poço Redondo, Sergipe, lived in a more closed (presence of C_3 plants, like herbs and shrubs) and drier environment than that found nowadays in Africa savannah, and that this environment occurred in Sergipe between 27 ky to 11 ky at least.

ACKNOWLEDGEMENTS

To CNPq by financial support through Universal project (process 404684/2016-5) and research fellowship to MATD (PQ/CNPq 311003/2019-2); To A. Liparini (Laboratório de Paleontologia/UFS) and C. Cartelle (PUC/MG) for allow measurements in fossils collection that they are responsible for; To biologist V. Gomes and L. Alves for help in Solver (Excel) analysis; To H. Araujo Jr., L. Asevedo and reviewers for critical evaluation of manuscript.

REFERENCES

Anderson, J.F.; Hall-Martin, A. & Russel, D.A. 1985. Long-bone circumference and weight in mammals, birds and dinosaurs. *Journal of Zoology*, **207**:53–61. *doi:10.1111/j.1469-7998.1985.tb04915.x*

Azevedo, F.C.C. & Verdade, L.M. 2011. Predator–prey interactions: jaguar predation on caiman in a floodplain forest. *Journal of Zoology*, **286**:200–207. *doi:10.1111/j.1469-7998.2011.00867.x*

Badeck, F.W.; Tcherkez, G.; Nogues, S.; Piel, C. & Ghashghaie, J. 2005. Post-photosynthetic fractionation of stable carbon isotopes between plant organs - a widespread phenomenon. *Rapid Communications in Mass Spectrometry*, **19**:1381–1391. *doi:10.1002/rcm.1912*

Bargo, M.S.; De Iuliis, G. & Vizcaíno, S.F. 2006a. Hypsodonty in Pleistocene ground sloths. *Acta Palaeontologica Polonica*, **51**:53–61.

Bargo, M.S.; Toledo, N. & Vizcaíno, S.F. 2006b. Muzzle of South American Pleistocene ground sloths (Xenarthra, Tardigrada). *Journal of Morphology*, **267**:248–263. *doi:10.1002/jmor.10399*

Bocherens, H.; Cotte, M.; Bonini, R.; Scian, D.; Straccia, P.; Soibelzon, L. & Prevosti, F.J. 2016. Paleobiology of sabretooth cat *Smilodon populator* in the Pampean Region (Buenos Aires Province, Argentina) around the Last Glacial Maximum: insights from carbon and nitrogen stable isotopes in bone collagen. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **449**:463–474. *doi:10.1016/j.palaeo.2016.02.017*

Bocherens, H. & Drucker, D.G. 2013. Terrestrial teeth and bones. *In*: S.A. Elias (ed.) *The Encyclopedia of Quaternary Science*, Elsevierp. 304–314. *doi:10.1016/B0-44-452747-8/00353-7*

Bocherens, H.; Koch, P.L.; Mariotti, A.; Geraards, D. & Jaeger, J.J. 1996. Isotopic biogeochemistry (^{13}C, ^{18}O) of mammalian enamel from African Pleistocene hominid sites. *Palaios*, **11**:306–318. *doi:10.2307/3515241*

Bocherens, H.; Sandrock, O.; Kullmer, O. & Schrenk, F. 2011. Hominin palaeoecology in Late Pliocene Malawi: Insights from isotopes (^{13}C, ^{18}O) in mammal teeth. *South African Journal of Science*, **107**:95–100. *doi:10.4102/sajs.v107i3/4.331*

Cartelle, C. & Abuhid, V.S. 1989. Novos espécimes brasileiros de *Smilodon populator* Lund, 1842 (Carnivora, Machairodontinae): morfologia e conclusões taxonômicas. *In*: CONGRESSO BRASILEIRO DE PALEONTOLOGIA, 11, 1989. *Anais*, Curitiba, p. 607–620.

Castro, M.C. & Langer, M.C. 2008. New postcranial remains of *Smilodon populator* Lund, 1842 from south-central Brazil. *Revista Brasileira de Paleontologia*, **11**:199–206. *doi:10.4072/rbp.2008.3.06*

Cerling, T.E; Harris, J.M.; Hart, J.A.; Kaleme, P.; Klingel, H.; Leakey, M.G.; Levin, N.E.; Lewison, R.L. & Passey, B.H. 2008. Stable isotope ecology of the common hippopotamus. *Journal of Zoology*, **276**:204–212. *doi:10.1111/j.1469-7998.2008.00450.x*

Cernusak, L.A. *et al.* 2009. Why are non-photosynthetic tissues generally ^{13}C enriched compared with leaves in C_3 plants? Review and synthesis of current hypotheses. *Functional Plant Biology*, **36**:199–213. *doi:10.1071/FP08216*

Cherkinsky, A. 2009. Can we get a good radiocarbon age from "bad bone"? Determining the reliability of radiocarbon age from bioapatite. *Radiocarbon*, **51**:647–655. *doi:10.1017/S0033822200055995*

Christiansen, P. & Harris, J.M. 2005. Body size of *Smilodon* (Mammalia: Felidae). *Journal of Morphology*, **266**:369–384. *doi:10.1002/jmor.10384*

Coe, M.J.; Cumming D.H. & Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, **22**:341–354. *doi:10.1007/BF00345312*

Coplen, T.B. 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure and Applied Chemistry*, **66**:273–276. *doi:10.1016/0375-6505(95)00024-0*

Dantas, M.A.T.; Cherkinsky, A.; Bocherens, H.; Drefahl, M.; Bernardes, C. & França, L.M. 2017. Isotopic paleoecology of the Pleistocene megamammals from the Brazilian Intertropical Region: Feeding ecology (δ^{13}C), niche breadth and overlap. *Quaternary Science Reviews*, **170**:152–163. *doi:10.1016/j.quascirev.2017.06.030*

Dantas, M.A.T.; Porpino, K.O.; Bauermann, S.G.; Prata, A.P.N.; Cozzuol, M.A.; Kinoshita, A.; Barbosa, J.H.O. & Baffa, O. 2011. Megafauna do Pleistoceno superior de Sergipe, Brasil:

registros taxonômicos e cronológicos. *Revista Brasileira de Paleontologia*, **14**:311–320. *doi:10.4072/rbp.2011.3.10*

Dantas, M.A.T.; Santos, D.B.; Liparini, A.; Queiroz, A.N.; Carvalho, O.A.; Castro, É.S.V. & Cherkinsky, A. 2014. A dated evidence of the interaction between humans and megafauna in the late Pleistocene of Sergipe state, northeastern Brazil. *Quaternary International*, **352**:197–199. *doi:10.1016/j.quaint.2014.09.040*

Dantas, M.A.T. & Zucon, M.H. 2007. Occurrence of *Catonyx cuvieri* (Lund, 1839) (Tardigrada, Scelidotheriinae) in Late Pleistocene-Holocene of Brazil. *Revista Brasileira de Paleontologia*, **10**:129–132.

Diefendorf, A.F.; Mueller, K.E.; Wing, S.L.; Koch, P.L. & Freeman, K.H. 2010. Global patterns in leaf ^{13}C discrimination and implications for studies of past and future cimate. *Proceedings of the National Academy of Science of the Unites States of America*, **107**:5738–5743. *doi:10.1073/pnas.0910513107*

Dixon, D.M. 1989. A note on some scavengers of ancient Egypt. *World Archaeology*, **21**:193–197. *doi:10.1080/00438243.1989.9980101*

Downing, K.F. & White, R.S. 1995. The cingulates (Xenarthra) of the Leisey Shell Pit local fauna (Irvingtonian), Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History*, **37**:375–396.

Fariña, R.A.; Vizcaíno, S.F. & Bargo, M.S. 1998. Body mass estimations in Lujanian (late Pleistocene-early Holocene of South America) mammal megafauna. *Mastozoología Neotropical*, **5**:87–108.

França, L.M.; Dantas, M.A.T.; Bocchiglieri, A.; Cherkinsky, A.; Ribeiro, A.S. & Bocherens, H. 2014a. Chronology and ancient feeding ecology of two upper Pleistocene megamammals from the Brazilian Intertropical Region. *Quaternary Science Reviews*, **99**:78–83. *doi:10.1016/j.quascirev.2014.04.028*

França, L.M.; Fortier, D.C.; Bocchiglieri, A.; Dantas, M.A.T.; Liparini, A.; Cherkinsky, A. & Ribeiro, A.S. 2014b. Radiocarbon dating and stable isotopes analyses of *Caiman latirostris* (Daudin, 1801) (Crocodylia, Alligatoridae) from the late Pleistocene of Northeastern Brazil, with comments on spatial distribution of the species. *Quaternary International*, **352**:159–163. *doi:10.1016/j.quaint.2014.06.046*

Gillette, D.D. & Ray, C.E. 1981. Glyptodonts of North America. *Smithsonian Contributions to Paleobiology*, **40**:1–255.

Hammer, Ø.; Harper, D.A.T. & Ryan, P.D. 2001. PAST: Paleontologial Statistics Software Package for Education and Data Analysis. *Palaeontology Electronica*, **4**:1–9.

Hayward, M.W. & Kerley, G.I.H. 2005. Prey preferences on the lion (*Panthera leo*). *Journal of Zoology*, **267**:309–322. *doi:10.1017/S0952836905007508*

Jenkins, S.G.; Partridge, S.T.; Stephenson, T.R.; Farley, S.D. & Robbins, C.T. 2001. Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. *Oecologia,* **129**:336–341. *doi:10.1007/s004420100755*

Keeling, C.D. 1979. The Suess effect: ^{13}Carbon-^{14}Carbon interrelations. *Environment International*, **2**:229–300. *doi:10.1016/0160-4120(79)90005-9*

Kigston, J.D. & Harrison, T. 2007. Isotopic dietary reconstructions of Pliocene herbivores at Laetoli: Implications for early hominin paleoecology. *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **243**:272–306. *doi:10.1016/j.palaeo.2006.08.002*

Kohn, M.J. 2010. Carbon isotopic compositions of terrestrial C3 plants as indicator of (paleo)ecology and (paleo)climate. *Proceedings of the National Academy of Science of the Unites States of America*, **107**:19691–19695. *doi:10.1073/pnas.1004933107*

Lee-Thorp, J.A. & Sponheimer, M. 2003. Three case studies used to reassess the reliability of fossil bone and enamel isotope signals for paleodietary studies. *Journal Anthropology Archaeology*, **22**:208–216. *doi:10.1016/S0278-4165(03)00035-7*

Levin, N.E.; Cerling, T.E.; Passey, B.H.; Harris, J.M. & Ehleringer, J.R. 2006. A stable isotope aridity index for terrestrial environments. *Proceedings of the National Academy of Science of the Unites States of America*, **103**:11201–11205. *doi:10.1073/pnas.0604719103*

Levins, R. 1968. *Evolution in changing environments*. New Jersey, Princeton University Press, 120 p.

Loveridge, A.J.; Hunt, J.E.; Murindagomo, F. & MacDonald, D.W. 2006. Influence of drought on predation of elephant (*Loxodonta africana*) calves by lions (*Panthera leo*) in an African wooded savannah. *Journal of Zoology*, **270**:523–530. *doi:10.1111/j.1469-7998.2006.00181.x*

MacFadden, B.J. 2005. Diet and habitat of toxodont megaherbivores (Mammalia, Notoungulata) from the late Quaternary of South and Central America. *Quaternary Research*, **64**:113–124. *doi:10.1016/j.yqres.2005.05.003*

Marcolino, C.P.; Isaias, R.M.S.; Cozzuol, M.A.; Cartelle, C. & Dantas, M.A.T. 2012. Diet of *Palaeolama major* (Camelidae) of Bahia, Brazil, inferred from coprolites. *Quaternary International*, **278**:81–86. *doi:10.1016/j.quaint.2012.04.002*

Marshall, J.D.; Brooks, J.R. & Lajtha, K. 2007. Sources of variation in the stable isotopic composition of plants. *In*: K. Michemer (ed.) *Stable isotopes in ecology and environmental ccience*, Blackwell Publishing, p. 22–60.

Molena, F.P. 2012. *Variação individual no esqueleto apendicular de mastodontes (Proboscidea: Gomphotheriidae) provenientes de São Bento do Una, Pernambuco, Brasil*. Universidade de São Paulo, Dissertação de Mestrado, 185 p. *doi:10.11606/D.41.2012.tde-01052013-093838*

Oliveira, A.M.; Becker-Kerber, B.; Cordeiro, L.M.; Borghezan, R.; Avilla, L.S.; Pacheco, M.L.A.F. & Santos, C.M.D. 2017. Quaternary mammals from Central Brazil (Serra da Bodoquena, Mato Grosso do Sul) and comments on Paleobiogeography and Paleoenvironments. *Revista Brasileira de Paleontologia*, **20**:31–44. *doi:10.4072/rbp.2017.1.03*

Oliveira, L.D.D. & Hackspacher, P.C. 1989. Gênese e provável idade dos tanques fossilíferos de São Rafael-RN. *In*: CONGRESSO BRASILEIRO DE PALEONTOLOGIA. *Anais*, Curitiba, UFPR, p. 30–34.

Owen-Smith, N. 1982. Factors influencing the consumption of plant products by large herbivores. *In*: B.J. Huntley & B.H. Walker (eds.) *The ecology of tropical savannas*, Springer-Verlag, p. 359–404.

Pérez-Higareda, G.; Rangel-Rangel, A.; Smith, H.M. & Chiszar, D. 1989. Comments on the food and feeding Hhabits of Morelet's Crocodile. *Copeia*, **4**:1039–1041. *doi:10.2307/1445994*

Phillips, D.L. 2012. Converting isotope values to diet composition: the use of mixing models. *Journal of Mammalogy*, **93**:342–352. *doi:10.1644/11-MAMM-S-158.1*

Porpino, K.O. & Bergqvist, L.P. 2002. Novos achados de *Panochthus* (Mammalia, Cingulata, Glyptodontidae) no nordeste do Brasil. *Revista Brasileira de Paleontologia*, **4**:51–62.

Porpino, K. O.; Fernicola, J.C. & Bergqvist, L.P. 2009. A new Cingulate (Mammalia: Xenarthra) *Pachyarmatherium brasiliense* sp. nov. from the late Pleistocene of northeastern Brazil. *Journal of Vertebrate Paleontology*, **29**:881–893. *doi:10.1671/039.029.0305*

Prevosti, F.J. & Martin, F.M. 2013. Paleoecology of the mammalian predator guild of Southern Patagonia during the latest Pleistocene: ecomorphology, stable isotopes, and taphonomy. *Quaternary International*, **304**:74–84. *doi:10.1016/j.quaint.2012.12.039*

Radloff, F.G.T. & Du Toit, J.T. 2004. Large predators and their prey in a southern African savanna: a predator's size determines its prey size range. *Journal of Animal Ecology*, **73**:410–423. *doi:10.1111/j.0021-8790.2004.00817.x*

Ribeiro, R.C.; Araújo-Júnior, H.I.; Kinoshita, A.; Figueiredo, A.M.G.; Baffa, O. & Carvalho, I.S. 2014. How much time is represented in the fossil record of tank deposits? *In*: SIMPÓSIO BRASILEIRO DE PALEONTOLOGIA DE VERTEBRADOS, 9, 2014. *Boletim de resumos*, Vitória, SBP, p. 115.

Secretaria de Estado do Planejamento, da Ciência e da Tecnologia. 2011. *Atlas digital sobre recursos hídricos Sergipe*. Sergipe, SEPLANTEC/SRH. CD-ROM.

Silva, L.A. 2015. *Paleoecologia alimentar dos gonfotérios (proboscidea: mammalia) pleistocênicos da América do Sul.* Universidade Federal do Estado do Rio de Janeiro, Dissertação de Mestrado, 139 p.

Tejada-Lara, J.V.; MacFadden, B.J.; Bermudez, L.; Rojas, G.; Salas-Gismondi, R. & Flynn, J.J. 2018. Body mass predicts isotope enrichment in herbivorous mammals. *Proceedings of the Royal Society Biological Sciences B*, **285**:20181020. *doi:10.1098/rspb.2018.1020*

Vizcaino, S.F.; Bargo, M.S. & Cassini, G.H. 2006. Dental occlusal surface area in relation to body mass, food habits and other biological features in fossil xenarthrans. *Ameghiniana*, **43**:11–26.

Vizcaíno, S.F.; Cassini, G.H.; Fernicola, J.C. & Bargo, M.S. 2011. Evaluating habitats and feeding habits through ecomorphological features in glyptodonts (Mammalia, Xenarthra). *Ameghiniana*, **48**:305–319. *doi:10.5710/AMGH.v48i3(364)*

Vizcaíno, S.F.; De Iullis, G. & Bargo, M.S. 2008. Skull shape, masticatory apparatus, and diet of Vassalia and Holmesina (Mammalia: Xenarthra: Pampatheriidae): when anatomy constrains destiny. *Journal of Mammalian Evolution*, **5**:291–322. *doi:10.1023/A:1020500127041*

Yoneyama, T. & Ohtani, T. 1983. Variations of natural ^{13}C abundances in leguminous plants. *Plant & Cell Physiology*, **24**:971–977. *doi:10.1093/oxfordjournals.pcp.a076627*

Received in 24 September, 2019; accepted in 30 March, 2020.