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THE PALEOECOLOGY OF PLEISTOCENE GIANT MEGATHERIID SLOTHS: STABLE ISOTOPES (δ^{13}C, δ^{18}O) OF CO-OCCURRING *MEGATHERIUM* AND *EREMOTHERIUM* FROM SOUTHERN BRAZIL

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ABSTRACT – The Pampa in subtropical Brazil (State of Rio Grande do Sul) is the only area of South America known so far where fossils of the Pleistocene giant megatheriid sloths *Megatherium americanum*, characteristic of subtropical-temperate areas, and *Eremotherium laurillardi*, widespread in the tropical zone, were discovered in the same deposits (Pessegueiro Creek and Chuí Creek), but it is not clear whether this co-occurrence is a product of taphonomic mixture, or co-existence, which would imply niche partitioning. In order to understand their paleoecology and reconstruct the associated paleoenvironments, dentin samples of both megatheriids from the two sites were analyzed for their carbon (δ^{13}C) and oxygen (δ^{18}O) isotope ratios. The δ^{13}C values of *Megatherium* indicate mixed diet of C3-C4 plants with higher content of the latter in Pessegueiro Creek, whereas the δ^{13}C values of *Eremotherium* indicate C3-dominated diets, the more negative value in Pessegueiro Creek possibly related to the canopy effect. The δ^{18}O of *Eremotherium* points to ^{18}O-depleted water sources, possibly also influenced by the diet, whereas *Megatherium* ingested ^{18}O-enriched water. The results show that co-existence of both megatheriids would have been ecologically possible, and that the Pampa was occupied by open grasslands/woodlands, with closed forests in Pessegueiro Creek. The δ^{13}C of *Eremotherium* from intertropical Brazil indicate a more generalist habit than *Megatherium* from subtropical Brazil and Argentina, which probably facilitated its dispersion from the tropics up to subtropical areas along two different routes, one along the coastal plain, and the other along the Paraná River Basin across central South America, following the southward expansion of riparian forests during warmer stages. The reduction of those forests during intervening cold stages possibly led to its disappearance in southern Brazil.

Keywords: Quaternary, paleobiogeography, stable isotopes, Pampa, coastal plain, megafauna.

RESUMO – O Pampa, no Brasil subtropical (Estado do Rio Grande do Sul), é a única área da América do Sul conhecida, até o momento, onde fósseis das preguiças megaterídeas gigantes do Pleistoceno *Megatherium americanum*, característica de áreas temperadas subtropicais, e *Eremotherium laurillardi*, amplamente distribuída no zona tropical, foram descobertas nos mesmos sítios (Arroio Pessegueiro e Arroio Chuí), mas não está claro se esta coocorrência representa mistura tafonômica, ou coexistência, o que implicaria partição de nicho. A fim de entender a paleoecologia e reconstruir os paleoambientes associados a esses táxons, amostras de dentina de ambos megaterídeos dos dois sítios foram analisadas quanto às razões isotópicas de carbono (δ^{13}C) e oxigênio (δ^{18}O). Os valores de δ^{13}C de *Megatherium* indicam dieta mista de plantas C3-C4 com maior teor destas últimas no Arroio Pessegueiro, enquanto os valores de δ^{13}C de *Eremotherium* indicam dieta dominada por C3, sendo o valor mais negativo no Arroio Pessegueiro possivelmente relacionado ao efeito do dossel. O δ^{18}O de *Eremotherium* indica fontes de água empobrecidas em ^{18}O, possivelmente também influenciadas pela dieta, enquanto *Megatherium* ingeria água enriquecida em ^{18}O. Os resultados mostram que a coexistência de ambos os megaterídeos teria sido ecologicamente possível, e que o Pampa era ocupado por pastagens/matas abertas, com florestas fechadas no Arroio Pessegueiro. O δ^{13}C de *Eremotherium* do Brasil intertropical indica um hábito mais generalista do que *Megatherium* do Brasil subtropical e Argentina, o que pode ter facilitado sua dispersão desde os trópicos até áreas subtropicais ao longo de duas rotas diferentes, uma ao longo da planície costeira e outra ao longo do Rio Paraná na região central da América do Sul, seguindo a expansão para o sul das matas ciliares durante os estágios mais quentes. A redução dessas florestas durante os estágios frios subsequentes possivelmente levou ao desaparecimento de *Eremotherium* no sul do Brasil.

Palavras-chave: Quaternário, paleobiogeografia, isótopos estáveis, Pampa, planície costeira, megafauna.

INTRODUCTION

The Pleistocene terrestrial faunas of South America were remarkable for the presence of several large (body mass between 44 and 1,000 kg) and mega (body mass > 1,000 kg) mammals, collectively known as megafauna (Stuart, 1999; Cione *et al.*, 2009). Among the largest were the Middle–Late Pleistocene giant megatheriid sloths of the species *Megatherium americanum* Cuvier, 1796 and *Eremotherium laurillardi* (Lund, 1842) (Paula Couto, 1979; Vizcaíno *et al.*, 2012). Their large size was probably favored by climate-driven selective pressures, which allowed these taxa to survive the cold and dry Pleistocene environments by reducing heat loss and increasing digestive capacity, in conjunction with a better oral food processing (Naples & MacAfee, 2012).

Fossils of *Megatherium* have been discovered along the southwestern part of the continent (in Bolivia, Uruguay, Argentina and southern Brazil), whereas *Eremotherium* has been recorded from the northwestern continent (from Venezuela to Peru), and from northern to southern Brazil (Cartelle & De Iuliis, 1995; Rossetti *et al.*, 2004; Martinelli *et al.*, 2012). Although both species are recognized as herbivores based on tooth morphology (Cuvier, 1804; Owen, 1861; Cabrera, 1926; Spillmann, 1948), their allopatric distribution across South America has been considered as indicating preference for different plant types and habitats, with *Megatherium* inhabiting temperate and dry environments and *Eremotherium* preferring tropical environments (Paula Couto, 1953; 1975; 1979; Bargo, 2001; Bargo & Vizcaíno, 2008; Naples & McAffee, 2012).

The only area known so far where the distribution of these two species overlaps is the Pampa landscape in the lowlands across the State of Rio Grande do Sul, in southern Brazil. Fossils of both taxa were discovered in fluvial deposits of Pessegueiro Creek, in Caçapava do Sul county (Figure 1), in a locality that became known as '*Megatherium* Pass' (Toledo, 1986; Oliveira *et al.*, 2002). Fossils of megatheriids have been found in the coastal plain of Rio Grande do Sul (**CPRS**) along the shoreline and sediments exposed on the banks of Chuí Creek, but the poor preservation of most fossils led to the classification of all megatheriid remains as *Megatherium americanum* (Paula Couto & Souza Cunha, 1965; Paula Couto, 1975). Recent discoveries of better-preserved fossils have shown that in fact both species occur in the fossiliferous deposits of the CPRS (Pereira *et al.*, 2012; Lopes & Pereira, 2019).

The megatheriid remains found in the two sites are disarticulated and incomplete, but the restricted extension of the fluvial systems in which they were preserved indicates that the mixing of remains of allopatric individuals by long-distance fluvial transport is unlikely (Toledo, 1986; Oliveira *et al.*, 2002; Lopes & Ferigolo, 2015), therefore the individuals inhabited the same areas. Although preserved within the same stratigraphic settings, however, the fossils of the two taxa in each site were not in direct association, and there are no numerical ages associated, so it is unclear whether this co-occurrence represents sympatry, or allopatric individuals that lived at different times.

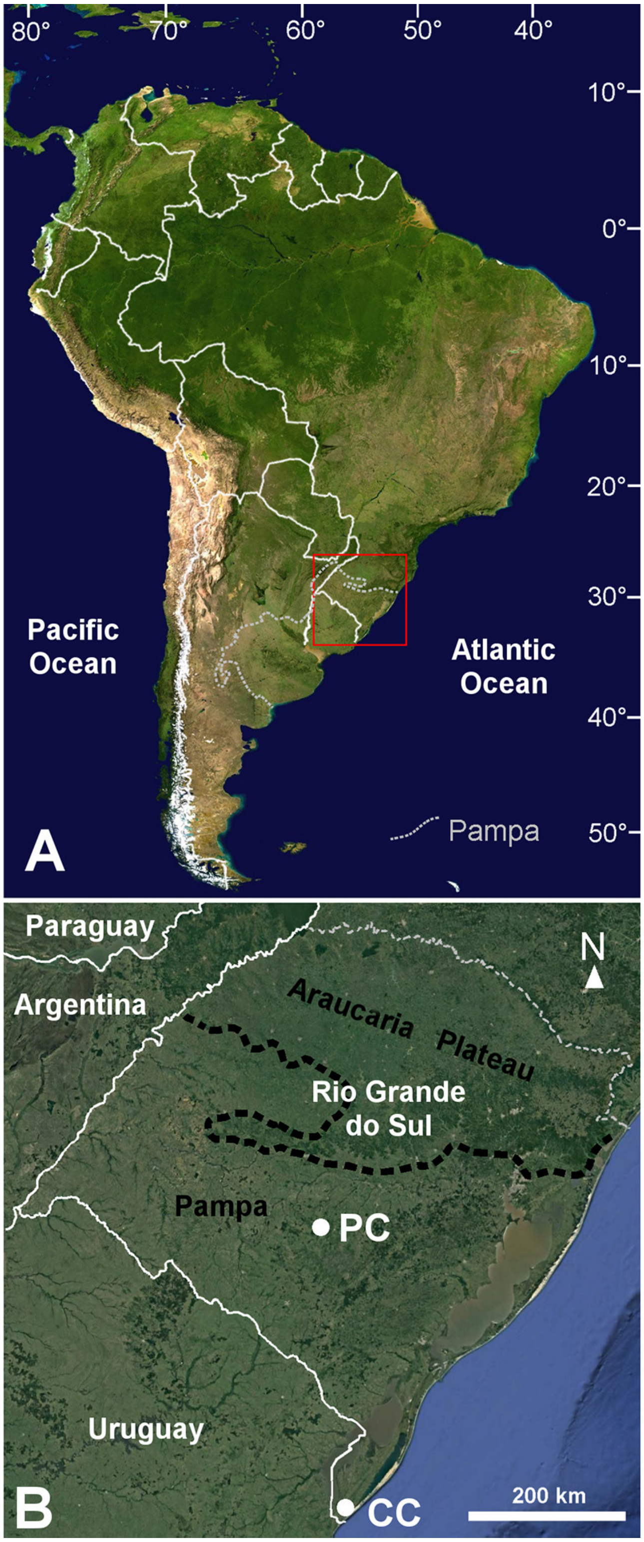

Figure 1. A, NASA Blue Marble image showing the location of Rio Grande do Sul in southern Brazil (indicated by the square), the dotted line shows the extension of the Pampa landscape. **B**, Google Earth image of Rio Grande do Sul showing the location of Chuí Creek (**CC**) and Pessegueiro Creek (**PC**) in the Pampa lowlands.

The possibility of co-existence is relevant from a paleoecological standpoint because *Megatherium* and *Eremotherium* were herbivores with similar body size and mass (>1,000 kg), tooth morphologies, and masticatory apparatuses (Bargo, 2001; Bargo *et al.*, 2006a; Naples & McAfee, 2012), thus may have had similar dietary preferences and occupied similar ecological niches. This could have led to inter-specific competition for resources, thus precluding co-existence (Hardin, 1960; Feranec *et al.*, 2009). On the other hand, if the two species fed on distinct plant types then they could have been sympatric by occupying different niches, as shown by fossil and modern records of other large mammals (Klein & Bay, 1994; Perrin, 1994; MacFadden & Shockey, 1997; Feranec, 2007; Calandra *et al.*, 2008; Kaiser, 2011; Rivals & Lister, 2016).

One way of understanding the paleoecological significance of the co-occurrence of the two species is to assess their diet preferences by analyzing the stable carbon isotope ratios ($\delta^{13}C$) of the fossils. Because the carbon isotopes in tissues of herbivore mammals reflect the types of plants ingested, they represent the diet preferences of those animals (DeNiro & Epstein, 1978; Vogel, 1978). It is hypothesized that if both taxa exhibit similar $\delta^{13}C$, they probably consumed the same resources, therefore co-existence would have been less likely. If the $\delta^{13}C$ were different, however, this would indicate that their respective niches were distinct or only partially overlapped (*i.e.* shared some resources by consuming different parts of plants), indicating that both species may have co-existed due to niche partitioning.

Besides carbon, the ratios of stable oxygen isotopes ($\delta^{18}O$) also provide paleoecological and paleoenvironmental information. Although the $\delta^{18}O$ is influenced by several factors, the values obtained in different species from the same area can indicate whether they shared water from the same meteoric sources, or if the different types or parts of plants they fed on affected their isotopic compositions (Dunbar & Wilson, 1983; Yakir, 1992; Bocherens *et al.*, 1996; Kohn, 1996).

In order to understand the ecology of *Megatherium* and *Eremotherium* found in southern Brazil, stable isotope analyses were performed in teeth from the fossils collected in Pessegueiro Creek and Chuí Creek. The goal of the analysis was to obtain information about the feeding habits of the two species, which may help addressing aspects of their ecology and the possibility of co-existence. Moreover, the analysis also intended to characterize the paleoenvironments in which they lived and establish comparisons with the results of other isotopic studies in order to better understand the ecology of the two species across South America.

REGIONAL SETTING

The Pampa is the lowland area stretching between Argentina and the State of Rio Grande do Sul, in southern Brazil (Figure 1), where its northern limit is the escarpments of the Araucaria Plateau. Except for some low (<500 m) ridges and plateaus, the topography of the Brazilian Pampa is relatively smooth, dominated by broad hills (*coxilhas*) and is divided in three main geological provinces (Verdum *et al.*, 2019). Pessegueiro Creek is located some 17 km NW of the town of Caçapava do Sul, in the central state of Rio Grande do Sul (Figure 1B), in the domain of weakly folded and metamorphosed Proterozoic sedimentary rocks of the Sul-Rio-Grandense Plateau that form the Mantiqueira Province (Viero & Silva, 2010; Verdum *et al.*, 2019). The local terrain consists of up to ~100 m-high ridges and hills smoothed by erosive processes, intercalated with valleys. Local vegetation includes grasslands with herbaceous and shrubby formations, and trees are concentrated mostly along riverbanks and hillslopes (Overbeck *et al.*, 2007; Pillar *et al.*, 2009; Verdum *et al.*, 2019). The presence of relict elements of xerophytic woodlands indicates dry environments during glacial periods (Klein, 1975; Pillar & Quadros, 1997; Behling *et al.*, 2005).

Chuí Creek is located in the southernmost coastal plain some 340 km to the south of Pessegueiro Creek, close to the town of Santa Vitória do Palmar (Figure 1B). In this area the CPRS encompasses two Pleistocene and one Holocene barrier-lagoon depositional systems developed on the uppermost Pelotas Basin in response to glacioeustatic oscillations (Villwock & Tomazelli, 1995). The relief is smooth and low (<25 m), the highest altitudes corresponding to coastal barriers, intercalated with flat lowlands of the lagoon systems. Chuí Creek cuts across sedimentary deposits of the Lagoon System III, and the fossils are found in shallow (<1 m) fluvial channel deposits of the Santa Vitória Alloformation (Lopes *et al.*, 2021) exposed along the banks of the creek.

The plant cover of the coastal plain consists of a type of vegetation (*restinga*) dominated by graminoid and herbaceous plants adapted to nutrient-poor sandy soils and wetlands, with shrubs, xerophytic relicts and trees growing in soils developed on Pleistocene sediments (Klein, 1975).

MATERIAL AND METHODS

The mineral phase of the skeletal tissues (bone, dentin, and enamel) of vertebrates is bioapatite ($Ca_{10}[PO_4, CO_3]_6$ $[OH, CO_3]_2$), a form of hydroxyapatite (Koch, 1998). The $^{13}C/^{12}C$ ratios in skeletal tissues of herbivore mammals are directly controlled by the photosynthetic pathway of the vegetation they feed on (De Niro & Epstein, 1978; Vogel, 1978; Koch, 2007). Terrestrial plants that use the C3 pathway include trees, shrubs, herbs, and grasses that grow during the cold season, with $\delta^{13}C$ ranging from about -37‰ to -20‰ (mean of -28.5‰), whereas C4 plants include warm growing season grasses, some dicots, and sedges, with $\delta^{13}C$ ranging from -15 to -7‰ (mean of -14‰). A third group is formed of xerophytic plants that use the crassulacean acid metabolism (CAM) pathway, with $\delta^{13}C$ values between -10‰ and -20‰, similar to those of C4 plants in arid regions and intermediate between C3 and C4 in wetter environments (O'Leary, 1988; Koch, 2007; Marshall *et al.*, 2007). The large carbon isotope range of C3 plants allow correlating $\delta^{13}C$ values in mammalian herbivores to different habitats, the more negative values representing closed forests and more positive associated with open mesic woodlands and grasslands (MacFadden & Higgins, 2004; Kohn *et al.*, 2005; Feranec, 2007).

The ratios between the light (^{16}O) and heavy (^{18}O) oxygen isotopes in animal tissues reflect the isotopic composition of the ingested local surface (meteoric) water, which is controlled mainly by environmental processes such as climate, seasonality, atmospheric circulation, origin and amount of rainfall, distance from the shore (continentality), evaporation, composition of groundwater, latitude, and altitude (Dansgaard, 1964; Vogel, 1983; Rozansky *et al.*, 1993; Koch, 1998). Although these factors affect the $\delta^{18}O$ of the animals, in species that are obligatory drinkers, *i.e.* obtain most of the water directly from local sources rather than from food alone, the $\delta^{18}O$ in the tissues will reflect the isotopic composition of the meteoric water (Longinelli, 1984; D'Angela & Longinelli, 1990). If both species co-existed and ingested water from the same source they will likely exhibit similar $\delta^{18}O$ values. Nevertheless, the $\delta^{18}O$ in animal tissues may also be influenced by the diet (Bryant & Froelich, 1995; Bocherens *et al.*, 1996; Fricke & O'Neil, 1996; Kohn, 1996).

Different parts of plants exhibit distinct oxygen values because of evapotranspiration, with leaves more enriched than fruits, and these more enriched than stems (Dunbar & Wilson, 1983; Sternberg *et al.*, 1984; Silveira *et al.*, 1989). The leaves of C4 plants are usually more ^{18}O-enriched compared to C3 plants, especially under water stress in dry and hot environments (Koch, 1998; Helliker & Ehleringer, 2000; Marshall *et al.*, 2007; Hirl *et al.*, 2019), therefore sympatric species that drink from the same water sources may exhibit variations in $\delta^{18}O$ related to the types of ingested plants.

The teeth of xenarthrans are formed mostly of dentine, regarded as more prone to diagenetic modification compared to enamel because of its higher organic content, lower hardness, and smaller crystallites (MacFadden *et al.*, 2010), thus making enamel the preferred material for isotope analysis. Nevertheless, isotopic studies on teeth of extinct sloths have been performed, showing that such analysis is feasible on dentin as well (Kohn *et al.*, 2005; Ruez, 2005; Domingo *et al.*, 2012; França *et al.*, 2014; Silva, 2015; Dantas *et al.*, 2017; Larmon *et al.*, 2019; Pansani *et al.*, 2019; Oliveira *et al.*, 2020; Tomassini *et al.*, 2020). The teeth of megatheriid sloths are prismatic, hypsodont, with subrectangular to subtriangular transverse outline and bilobate occlusal surfaces formed by transversal sharp crests separated by a deep valley (Owen, 1861; Spillmann, 1948; Sicher, 1953; Cartelle & De Iuliis, 1995; Vizcaíno, 2009). The teeth of *Megatherium* and *Eremotherium* include an outermost layer of cementum, followed by an intermediate layer of orthodentine, a layer of orthovasodentine and the innermost modified orthodentine (Owen, 1845; Ferigolo, 1985).

The megatheriid specimens from Pessegueiro Creek are housed at the Museu de Ciências Naturais of Pontifícia Universidade Católica do Rio Grande do Sul (**PUC-RS**). The fossils of *Eremotherium* (collection number MCP-2364) consist of the cranium, jaw and postcranial elements (Toledo, 1986), whereas the fossils of *Megatherium* include a left dentary (MCP 3348) with the m3 preserved and one incomplete right femur (MCP 3348) (Oliveira *et al.*, 2002). The fossils from Chuí Creek are housed at the Museu Coronel Tancredo Fernandes de Mello, in the town of Santa Vitória do Palmar. The fossil of *Eremotherium* is one left dentary (EPM-PV0133) with most of the m1 missing and the m2–4 complete (Pereira *et al.*, 2012). Although the relatively small size indicates that this individual was a juvenile, the teeth exhibit well-developed transversal crests as the result of mastication (Cartelle & De Iuliis, 1995), thus indicating that it was already feeding on plants rather than suckling. The specimen of *Megatherium* is an incomplete adult skull (collection number MCTFM-PV0772) with the right M3-5 and left M5 preserved (Lopes & Pereira, 2019).

Most of the remains of megatheriids known from the coastal plain are incomplete, therefore cannot be assigned to either species. In order to increase the number of samples and assess the range of isotopic variation in this group, and to test whether isotopic values can be used to identify isolated specimens, two teeth of unidentified megatheriid (collection number JP125 and MCTFM-PV0438) collected in the Santa Vitória Alloformation were also analyzed. The specimens do not exhibit macroscopic signs of extensive *post-mortem* modification such as weathering or carbonate precipitation.

The specimens from Pessegueiro Creek were analyzed at the University of Georgia (U.S.A.), and those from Chuí Creek at Universidade de Pernambuco (Brazil), following similar protocols. From each specimen, about 0.3–0.5 g samples of dentine were extracted along the selected tooth using a micro drill. The samples were treated with 10% H_2O_2 to remove organic contaminants, then cleaned and washed using ultrasonic bath. After cleaning, the dried material was crushed to fine powder and treated with diluted 1N acetic acid to remove exogenous carbonates. Periodic evacuation ensured that evolved carbon dioxide was removed from the interior of the sample and that fresh acid was allowed to reach even the interior micro-surfaces. The chemically cleaned sample was then reacted under vacuum with 100% H_3PO_4 to dissolve the bioapatite and release carbon dioxide. The bioapatite samples from Pessegueiro Creek were analyzed for $\delta^{13}C$ and $\delta^{18}O$ using a gas bench device coupled with a Delta V mass spectrometer, whereas the samples from Chuí Creek were analyzed in a double inlet, triple collector mass spectrometer (VG Isotech SIRA II). The isotopic data are presented with reference to the standards PDB for $\delta^{13}C$, and SMOW for $\delta^{18}O$ calibrated according to the international standard NBS-19, and the precision was found to be better than 0.10‰ (2σ).

The amount of C4 plants in the in the diet can be calculated from the carbon values measured in the teeth ($\delta^{13}C_{apatite}$) according to the mathematical mixing model of Koch *et al.* (1998):

$$\delta^{13}C_{apatite} = (\delta^{13}C_{pure\ C4})*(x) + (\delta^{13}C_{pure\ C3})*(1-x),$$

where *x* is the percentage of C4 plants. This calculation, however, requires that the isotopic average values of pure C4 and C3 feeders are known, which in turn depends on the average isotopic composition of C3 and C4 plants. Because the levels (pCO_2) and isotopic composition ($\delta^{13}C_{CO2Atm}$) of atmospheric CO_2 have varied throughout the Cenozoic

(Marino *et al.*, 1992; Tipple *et al.*, 2010), the $\delta^{13}C$ of the plants also changed, but this variation is difficult to assess because most fossil records do not have associated numerical ages.

Despite the lack of numerical ages in the analyzed specimens, the fossil assemblage of Chuí Creek represents some 190 kyrs (~220–30 ka) between the Middle and Late Pleistocene (Lopes *et al.*, 2020; 2021), therefore this interval is considered here for reference. The $\delta^{13}C_{CO2Atm}$ during that interval exhibits marked variations (Figure 2), and although a mean value of -6.5‰ is in general considered for the last glacial period (112.5 to 11.7 ka), during warmer (interglacial and interstadial) phases the values were more positive, and during stadial (cold) phases were more negative, reaching an average of -7.1‰ (Marino *et al.*, 1992; Tipple *et al.*, 2010).

The isotopic range of terrestrial plants likely changed during the past in response to variations in the $\delta^{13}C_{CO2Atm}$, therefore affecting the isotopic values in herbivores that lived at different times. Today, an herbivore identified as a dominantly C3 feeder ($\delta^{13}C_{pureC3}$) exhibits values between -6‰ and -21‰ (average = -13.5‰), whereas a mainly C4 feeder ($\delta^{13}C_{pureC4}$) ranges from -1‰ to +7‰ (average = 1.5‰), and mixed C3/C4 feeders vary between -8‰ and -1‰ (Ehleringer *et al.*, 1997; Kohn, 2010), considering a current $\delta^{13}C_{CO2Atm}$ of about -8 ‰ due to fossil fuel burning (Marino *et al.*, 1992; Koch *et al.*, 2004; Tipple *et al.*, 2010). These differences were taken in account for comparisons with living mammals, and for estimating the percentage of C4 plants ingested by the sampled individuals, considering that they could have lived under cold (stadial) or warm (interglacial/interstadial) climates. For this calculation the average carbon values of plants ($\delta^{13}C_{C3}$ and $\delta^{13}C_{C4}$) and values of pure C3 feeders and pure C4 feeders (Koch *et al.*, 2004) relative to the average $\delta^{13}C_{CO2Atm}$ for both climate conditions were considered (Table 1).

As a way of reconstructing the paleoenvironments at the time the studied megatheriids lived, the $\delta^{13}C$ values were used for determining the type of plants the animals fed on, assuming the average ^{13}C enrichment factor (ε*) between the diet and apatite. Although this factor increases with increasing body masses (Tejada-Lara *et al.*, 2018), one major problem for determining the ε* is the large uncertainty of body mass estimates for extinct species without similar living relatives (such as giant sloths), as exemplified by the wide range of values estimated for *Megatherium* (Fariña *et al.*,1998). In the present work is adopted the average ε* of ~14.1‰ calculated from the isotopic composition of several large- and mega-herbivores (Cerling & Harris, 1999).

RESULTS

The measured $\delta^{13}C$ and $\delta^{18}O$ values exhibit notable differences regarding the diets and composition of ingested water of the two megatheriids (Table 2). As a result of variations in $\delta^{13}C_{CO2Atm}$, the estimated carbon isotope range values of C3 and C4 plants are 0.6‰ more positive during interglacials/interstadials compared to stadials. Consequently,

Table 1. Average carbon isotope values (in permil) of atmospheric CO_2, of C3 and C4 plants, and animals with pure C3 or C4 diets considered for Pleistocene climate conditions (from Koch *et al.*, 2004).

	Stadial	Interglacial/interstadial
$\delta^{13}C_{CO2}$	-7.1	-6.5
$\delta^{13}C_{C3}$	-26.6	-26.0
$\delta^{13}C_{C4}$	-11.6	-11.0
$\delta^{13}C_{pureC3}$	-12.6	-12.0
$\delta^{13}C_{pureC4}$	2.4	3.0

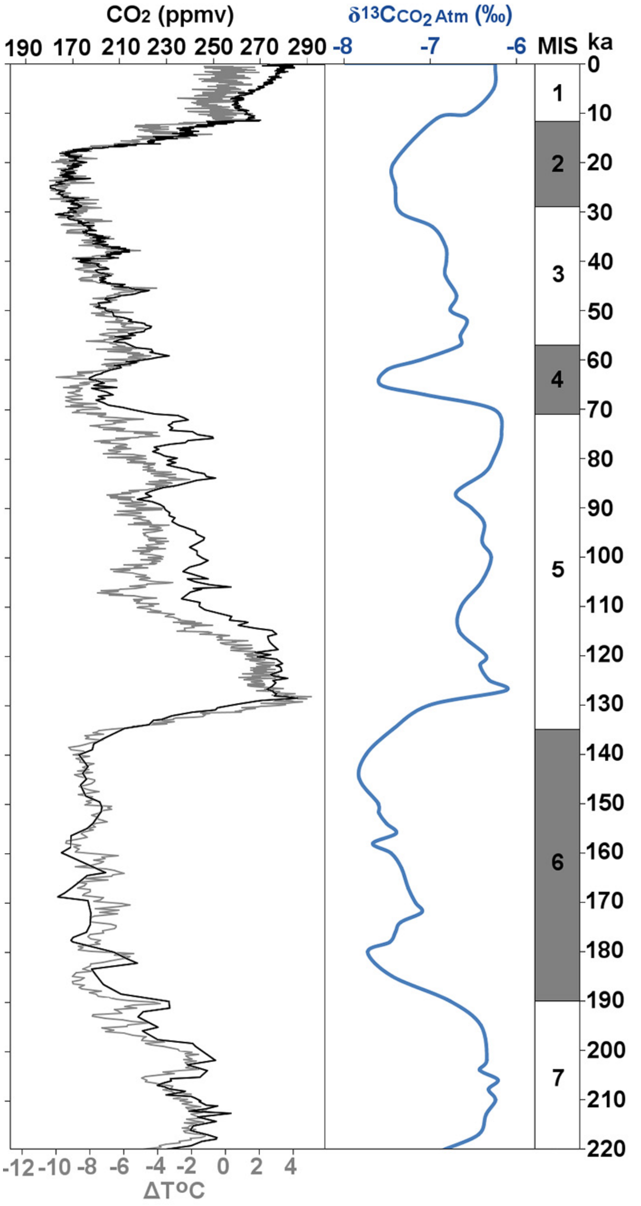

Figure 2. Concentration of atmospheric CO_2 and temperature anomaly from the EPICA Dome C ice core (Jouzel *et al.*, 2007), and variations of $\delta^{13}C_{CO2Atm}$ during cold (stadial, in grey) and warm (interglacial/interstadial) climatic stages for the last 220 kyrs (Tipple *et al.*, 2010).

a given δ^{13}C recorded in bioapatite will represent 4% less C4 plants in the diet during warm stages compared to cold stages (Table 2).

The results (Figure 3) are shown in comparison with the δ^{13}C and δ^{18}O obtained in fossils of two other megamammals (*Notiomastodon* and *Toxodon*) collected in Chuí Creek (Lopes *et al.*, 2013). The carbon values plotted against the estimated isotopic ranges of plants found in different habitats (Kohn *et al.*, 2005; Domingo *et al.*, 2012) allow distinguishing herbivore guilds based on the proportion of ingested C4 plants, consisting of browsers (≤25% C4), grazers (≥75% C4) or mixed feeders (du Toit, 2003; Cerling *et al.*, 2015).

With increasing altitude, the δ^{18}O of meteoric water becomes more negative by a factor of about 0.28‰/100 m (Dansgaard, 1964; Poage & Chamberlain, 2001). This effect is negligible in the deposits along Chuí Creek, located at an altitude of only 10–11 m, whereas in Pessegueiro Creek, at an altitude of ~140 m, it results in δ^{18}O values more negative by 0.39‰ compared to the former. This depletion is indicated as the corrected values in Table 2.

Carbon and oxygen isotope ratios of *Megatherium americanum*

The δ^{13}C of the two individuals of *Megatherium* are more positive than the specimens of *Eremotherium*, thus indicating a higher proportion of C4 plants in their diets (Table 2; Figure 3). Both individuals are classified as mixed feeders under cold and warm climates, but the enrichment of 4.84‰

Table 2. Isotopic composition (**δ^{13}**C and **δ^{18}**O, in permil) of megatheriid specimens from Pessegueiro Creek (**PC**) and Chuí Creek (**CC**), the **δ^{18}**O values in parentheses are the correction for the altitude of PC. Also shown are the **δ^{13}**C of the respective diets, considering the isotopic enrichment of 14.1‰ (Cerling & Harris, 1999), and estimated percentages of C4 plants in the diets for stadial (%C4$_{\text{Sta}}$) and interglacial/interstadial (%C4$_{\text{Int}}$) conditions.

Taxon	Specimen	$\delta^{13}C_{PDB}$	$\delta^{18}O_{SMOW}$	$\delta^{13}C_{diet}$	%C4$_{\text{Sta}}$	%C4$_{\text{Int}}$
Megatherium PC	MCP3348	-2.05	28.45 (28.84)	-16.15	70	66
Megatherium CC	MCTFM-PV0722	-6.89	28.65	-20.99	38	34
Eremotherium PC	MCP2364	-14.74	25.32 (25.71)	-28.84	-14	-18
Eremotherium CC	MCTFM-PV1033	-10.18	27.66	-24.28	16	12
Megatheriidae CC	JP125	-6.87	30.39	-20.97	38	34
Megatheriidae CC	EPM-PV0438	-8.97	28.99	-23.07	24	20

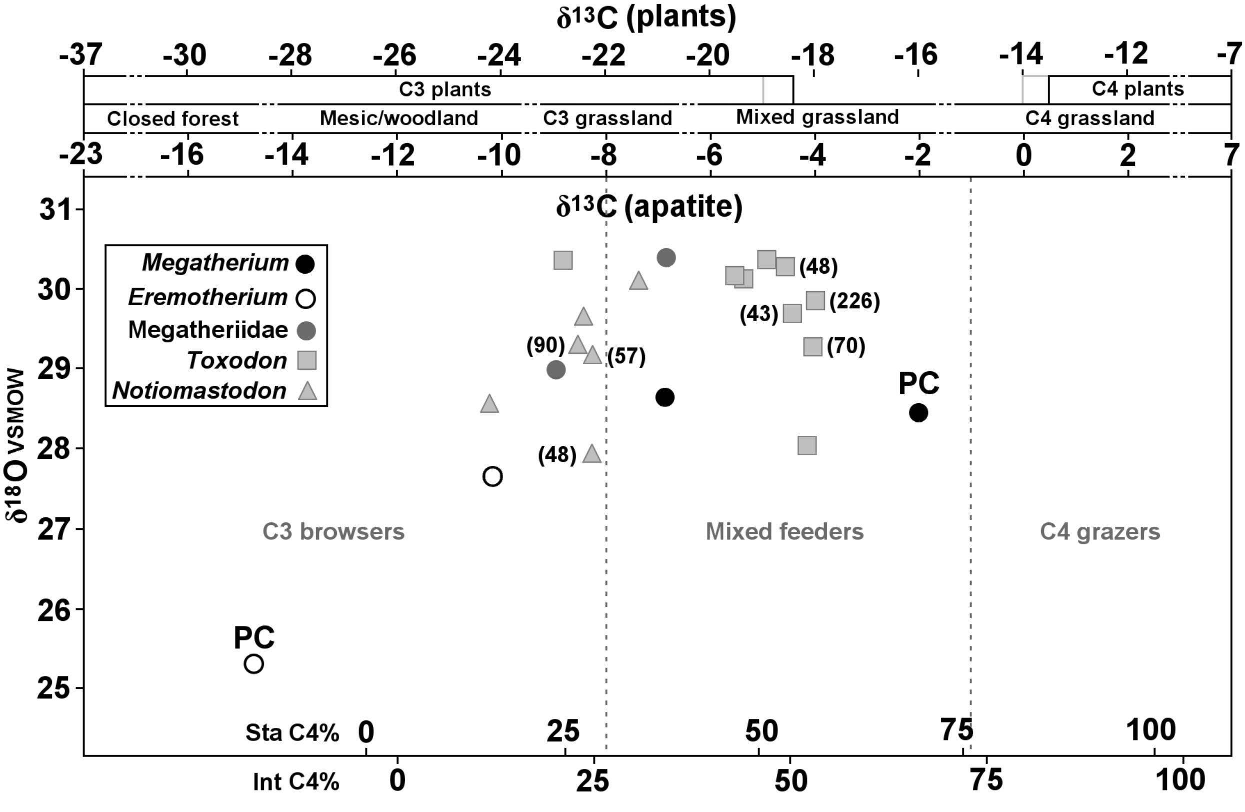

Figure 3. Carbon and oxygen isotopic values of the analyzed fossils from Pessegueiro Creek (PC) and Chuí Creek, including data of *Toxodon* and *Notiomastodon* from the latter (Lopes *et al.*, 2013), the numbers in parentheses next to some specimens indicate electron *spin* resonance ages (ESR, combined uptake model) in ka (Lopes *et al.*, 2010; 2014). The isotopic range of C3 and C4 plants (grey vertical bars indicate the range during stadials) and the percentage of C4 plants in the diets are considered for both stadial (Sta) and interglacial/interstadial (Int) conditions, considering the variations of $\delta^{13}C_{CO2Atm}$.

in the specimen from Pessegueiro Creek compared to the specimen from Chuí Creek represents almost twice of C4 plants in its diet. It also consumed more C4 plants compared to the other analyzed mammals from Chuí Creek, whereas the individual from this site exhibits intermediate proportions (Figure 3).

The $\delta^{18}O$ values are similar in the two individuals of *Megatherium*, but the specimen from Pessegueiro Creek is 0.2‰ more positive. Both are ^{18}O-enriched compared to *Eremotherium*, but more depleted than most of the other analyzed fossils from Chuí Creek (Figure 3).

Carbon and oxygen isotope ratios of *Eremotherium laurillardi*

The two *Eremotherium* exhibit more negative $\delta^{13}C$ values than *Megatherium*, thus are classified as browsers that fed predominantly on C3 plants (Table 2; Figure 3). Considering stadial and interglacial/interstadial conditions, the specimen from Chuí Creek would have ingested low (<15%) proportions of C4 plants, lower than most of the other mammals from this site (Figure 3). In the individual from Pessegueiro Creek, however, the estimated percentage of C4 plants resulted in negative values for either paleoclimatic conditions (Table 2), indicating a pure C3 diet, with a significant proportion of plants with more negative $\delta^{13}C$ than plants of open woodlands, possibly due to the 'canopy effect' (Koch *et al.*, 1998).

Although the $\delta^{18}O$ of the individual from Pessegueiro Creek is more negative than the specimen from Chuí Creek, both are ^{18}O-depleted compared to the specimens of *Megatherium* and the other mammals from Chuí Creek (Figure 3).

Isotope ratios of unidentified megatheriids from Chuí Creek

The $\delta^{13}C$ of these two specimens differ from each other by 2.1‰ and exhibit values similar to both *Megatherium* and *Eremotherium*. The $\delta^{13}C$ of JP125 is virtually identical to the *Megatherium* from Chuí Creek, but it is more ^{18}O-enriched than all the other megatheriids (Table 2), although comparable to the other analyzed fossils (Figure 3). The specimen MCTFM-PV0438 is classified as a predominantly C3 feeder, with $\delta^{13}C$ value 2.08‰ more negative than the specimen of *Megatherium* but only 1.21‰ more positive than the specimen of *Eremotherium*. Its $\delta^{18}O$ value, however, is 1.33‰ more positive compared to the latter, but more similar (only 0.34‰ more positive) to the specimen of *Megatherium*.

DISCUSSION

Fossils unequivocally assigned to either megatheriid species are scarce in Chuí Creek and the two individuals from Pessegueiro Creek are so far the only known fossils from that area. Despite the low number of samples available, the results presented here nevertheless provide a first approximation to aspects of the ecology of those animals in southern Brazil and provide information about the environmental conditions at the time they were living.

Dentin is regarded as less suitable than enamel for isotopic studies because it is potentially more prone to diagenetic alteration (MacFadden *et al.*, 2010), but it may retain unaltered isotopic signals for at least the Plio-Pleistocene time range (Ayliffe *et al.*, 1992; Kohn & Cerling, 2002; Bocherens *et al.*, 2017; Domingo *et al.*, 2020). The carbon isotopic composition of the specimens from Chuí Creek is within the range of variation obtained in enamel from mammals from this assemblage (Figure 3, Lopes *et al.*, 2013), thus indicating that the isotopic composition of the dentin does reflect the local vegetation, and diagenetic alteration (if happened) was minimal. No other fossils have been found in Pessegueiro Creek that could be used for comparison, so it must be stressed that the possibility of diagenetic effects on these specimens is not discarded. The discussion of the results is made on the assumption that these specimens also retained the original isotopic signals.

Diet patterns of *Megatherium* and *Eremotherium*

The lack of numerical ages precludes establishing whether the two megatheriid species were sympatric in the Brazilian Pampa; nevertheless, the isotopic results indicate that in terms of diet preferences this could have been ecologically possible. The $\delta^{13}C$ values indicate a substantial proportion of C4 plants in the diet of *Megatherium*, classified as a mixed feeder. The higher $\delta^{13}C$ in the individual from Pessegueiro Creek (Table 2) is comparable to values of modern African grazers such as zebras and wildebeest (Bocherens *et al.*, 1996), and fossil equids from North and South America (MacFadden *et al.*, 1999; Prado *et al.*, 2011), thus indicating that it foraged predominantly on C4 grasses. The lower proportion of C3 plants could be related to seasonal dietary shifts or opportunistic feeding on other plant types.

The *Megatherium* from Chuí Creek fed on C3 and C4 plants with a smaller proportion (<40%) of the latter (Table 2), a diet similar to that of modern African elephants from Kenya (Bocherens *et al.*, 1996), fossil camelids (*Hemiauchenia*) from Florida (Feranec & MacFadden, 2000) and *Megatherium* from Argentina (Praderio *et al.*, 2012; Bocherens *et al.*, 2017; Domingo *et al.*, 2020; Tomassini *et al.*, 2020). Compared to the other mammals from Chuí Creek, the proportion of C4 plants in the diet of this individual was intermediate between *Toxodon* and *Notiomastodon* (Figure 3). The virtually identical value of the unidentified specimen JP125 indicates that this could be a *Megatherium*, although the possibility that it was an *Eremotherium* that consumed more C4 plants cannot be discarded. The carbon values in these fossils thus indicate a predominantly C3 diet that shifted seasonally to include C4 plants during warm rainy seasons.

The specimens of *Eremotherium* are isotopically distinct from *Megatherium*. The individual from Pessegueiro Creek exhibits the more negative $\delta^{13}C$ of all the analyzed specimens (Figure 3), indicating only C3 plants in its diet. It is too low, however, for an animal that fed mainly on plants of mesic woodlands or arid/wooded grasslands, which exhibit more positive $\delta^{13}C$ (Farquhar *et al.*, 1989; Tieszen, 1991; Nunez *et al.*, 2010), thus it indicates foraging in areas not subject to significant droughts. The $\delta^{13}C$ of forest trees and undergrowth are 2–5‰ more negative than free-standing trees or shorter plants from open areas (Heaton, 1999), and although the equivalent carbon value of its diet (-28.84 ‰) is consistent with browsing in closed canopy forests (Kohn *et al.*, 2005; Cerling *et al.*, 2015), it is not as low as to indicate feeding on plants growing on the understory, which exhibit $\delta^{13}C$ values ≤30 ‰ (van der Merwe & Medina, 1991; Cerling *et al.*, 2004; Zin-Maung-Maung-Thein *et al.*, 2011).

The $\delta^{13}C$ value of this individual is similar to specimens from the Amazon and central-western Brazil (Pansani *et al.*, 2019; Oliveira *et al.*, 2020; Asevedo *et al.*, 2021), and intermediate between closed canopy forest and forest gaps/open woodland (Secord *et al.*, 2008), thus it suggests foraging in riparian forests and neighboring open woodlands and grasslands, similar to the habit inferred for *Megalonyx* sloths from New Mexico (McDonald & Morgan, 2011). According to Oliveira *et al.* (2002), riparian forests were present along Pessegueiro Creek based on the type of vegetal remains (tree trunks and leaves) associated with the sloth fossils found in the channel deposits.

Spillmann (1948) suggested a partially xilophagous diet for *Eremotherium* based on the presence of stems with tooth cutmarks in coprolites of this animal from Ecuador, so it is possible that the individual from Pessegueiro Creek also ingested this material. It could have ingested fruits, but these were probably a minor component of the diet, because although the $\delta^{13}C$ of frugivorous mammals from the upper canopy is similar (Cerling *et al.*, 2004) these are small-bodied taxa, whereas large species tend to rely more on leaves (Secord *et al.*, 2008). Giraffes are hyper-browsers that feed predominantly on leaves of the upper canopy, with ≤7% of herbaceous plants in their diets (Owen-Smith, 1988) and have average values (-13‰) more positive compared to the *Eremotherium* from Pessegueiro Creek (Cerling & Harris, 1999). On the other hand, living sloths feed solely on leaves and fruits, and exhibit values more negative than -15.6‰ (Tejada *et al.*, 2020), although these probably cannot be directly compared to the giant ground sloths due to their unique physiologies (Gilmore *et al.*, 2008).

Compared to the specimen from Pessegueiro Creek, the $\delta^{13}C$ of *Eremotherium* from Chuí Creek is 4.56 ‰ more positive, indicating a diet of C3 plants from open woodlands that also included 12% to 16% of C4 plants (Table 2), similar to the lowest value obtained in the specimens of *Notiomastodon* from this site (Figure 3; Lopes *et al.*, 2013) and also in teeth of modern black rhinoceroses and African elephants from semi-arid woodlands and grasslands in Kenya (Bocherens *et al.*, 1996; Cerling *et al.*, 2018). Comparable values in Pleistocene equids from lowlands at latitudes higher than 23°S in Argentina are interpreted as grazing mostly on C3 grasses (MacFadden *et al.*, 1999; Sánchez *et al.*, 2006; Prado *et al.*, 2011).

The unidentified megatheriid PV0438 exhibits $\delta^{13}C$ intermediate between the *Eremotherium* and *Megatherium* (and also the unidentified JP125) from Chuí Creek (Table 2), being more similar to the specimens of *Notiomastodon* (Figure 3). This individual was a mixed feeder that ingested a larger proportion of C3 plants and could have been an *Eremotherium* that included more C4 plants (20–24%) in its diet than the two other individuals of this species.

Oxygen isotopes in *Megatherium* and *Eremotherium*

The ^{18}O in mammals follows a linear relationship with the ingested water (Longinelli, 1984; D'Angela & Longinelli, 1990; Sponheimer & Lee-Thorp, 1999), therefore variations in the fossils can indicate ^{18}O-enrichment or depletion of the water sources. Differences of $\delta^{18}O$ among mammals inhabiting the same area may indicate the influence of physiological factors (panting *vs.* sweating, drought tolerance, excretion), dietary differences (C3 *vs.* C4 plants), or drinking from distinct sources (rivers or lakes) (Kohn *et al.*, 1996). Assuming that *Megatherium* and *Eremotherium* did not differ much physiologically, it can be hypothesized that the observed $\delta^{18}O$ differences are related to the water sources and/or diet.

C4 Grazers are regarded as better trackers of the isotopic composition of meteoric water because tend to drink more, sweat, and consume more stems than co-occurring mixed feeders and C3 browsers that are water-independent, pant, and feed preferentially on leaves that may provide substantial amount of water (Bocherens *et al.*, 1996; Kohn *et al.*, 1996; Sponheimer & Lee-Thorp, 1999).

Wild herbivores obtain 35–50% of their oxygen from plants, and the isotopic effects of environmental conditions on plants influence the ^{18}O, which is the transferred to herbivores through diet (Kohn *et al.*, 1996). The ^{18}O content in different plants is controlled by the isotopic enrichment of leaf water due to evapotranspiration and the maintenance of photosynthesis under drought conditions (Sternberg, 1989; Kohn, 2007). The isotopic composition of stem water is the same as the soil water, but leaves are isotopically enriched due to evapotranspiration (Marshall *et al.*, 2007). C4 plants exhibit higher $\delta^{18}O$ than C3 plants, and the observed isotopic enrichment is C3 dicots < C3 grasses < C4 grasses (Sternberg *et al.*, 1984; Helliker & Ehleringer, 2000; 2002; Koch, 2007). Moreover, C4 plants continue to photosynthesize under conditions of decreased relative humidity such as seasonal droughts or in the later part of the day when leaf water becomes enriched in ^{18}O, whereas C3 plants cease to photosynthesize under such conditions (Sternberg, 1989).

The ^{18}O-enrichment of C4 plants apparently is not recorded in the *Megatherium* from Pessegueiro Creek, which does not exhibit the highest $\delta^{18}O$ despite ingesting more C4 plants than all other specimens (Figure 3), thus suggesting that its ^{18}O was influenced mostly by the isotopic composition of the ingested water rather than the diet. This could also explain the ^{18}O-enrichment of the specimen JP125 compared to the *Megatherium* from Chuí Creek, despite the similar $\delta^{13}C$ values.

The $\delta^{13}C$ and $\delta^{18}O$ in the specimens of *Toxodon* and *Notiomastodon* from Chuí Creek exhibit very weak correlations (Lopes *et al.*, 2013). Moreover, the range of $\delta^{18}O$ variation in those taxa is wider than the range of $\delta^{13}C$

(Figure 3), which suggests that surface water rather than diet was the main control on their oxygen isotopic composition. The inter-specific differences of $\delta^{18}O$ probably reflect the effects of physiology and diet, but the intra-specific variations in each taxon can be related to the time-averaging of the Chuí Creek fossil assemblage (~190 kyrs). The available numerical ages (Figure 3; Lopes *et al.*, 2010; 2014) indicate that those sampled individuals lived at different times, and likely reflect meteoric waters with distinct isotopic compositions.

The primary control on the isotopic composition of meteoric water is the $\delta^{18}O$ of rainfall, and differences between fossil specimens from time-averaged assemblages could reflect changes in rainfall regimes through time. The amount and isotopic composition of rainwater in Rio Grande do Sul today (Figure 4) varies seasonally according to its different sources. The ^{18}O-enriched winter-spring rainfall is higher and of subtropical origin, whereas the summer-autumn rainfall of tropical origin is lower and ^{18}O-depleted as the result of transport from the Amazon Basin (Nimer, 1989; Cruz *et al.*, 2006). Similar isotopic variations recorded in speleothems show that the composition of rainfall also have varied in orbital timescales at least for the last 120 kyrs, controlled by precession-driven insolation cycles of ~21 kyrs, with high (low) $\delta^{18}O$ recorded during periods of low (high) insolation (Cruz *et al.*, 2006).

The relative ^{18}O enrichment in *Megatherium* and the other species from Chuí Creek that ingested variable proportions of C3/C4 plants (Figure 3) could indicate that they lived during periods of increased subtropical rainfall, or that they drank mostly from water sources enriched due to evaporation under warm or dry conditions (Luz & Kolodny, 1989; Ayliffe *et al.*, 1992). The shallow, rain-fed fluvial systems of the Santa Vitória Alloformation (Lopes *et al.*, 2021) had their isotopic composition controlled by rainfall, but stagnant water sources such as ponds or small lakes were likely subject to evaporative enrichment. The *Megatherium* from Pessegueiro Creek also may have obtained most of its water from sources fed by ^{18}O-enriched rainfall, or from evaporatively enriched ponds or lakes associated with the grasslands where it foraged.

The $\delta^{18}O$ of the *Eremotherium* from Chuí Creek is lower compared to the other fossils from this site, indicating that it drank from ^{18}O-depleted water sources. The *Eremotherium* from Pessegueiro Creek also has the lowest $\delta^{18}O$ of all specimens, and although higher $\delta^{18}O$ would be expected due to the predominance of C3 plants in its diet (Kohn *et al.*, 1996), its oxygen composition indicates that it ingested mostly ^{18}O-depleted water. This could have been obtained from the rivers associated with the riparian forests where it presumably foraged, whose water is ^{18}O-depleted, especially close to springs (Lambs, 2004). If this was the case, then the $\delta^{18}O$ difference compared to the *Megatherium* from this site would be explained by habitat and niche partitioning if the two species co-existed.

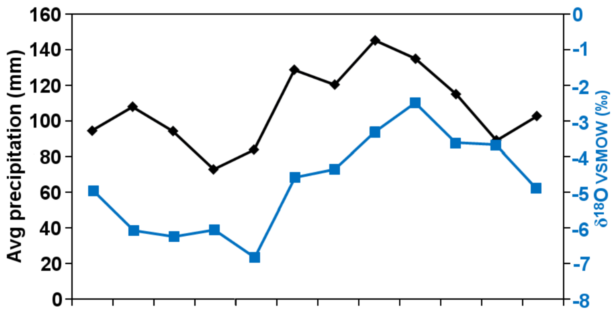

Figure 4. Relationship between the average oxygen isotopic composition of rainwater ($\delta^{18}Ow$) and amount of precipitation in the city of Porto Alegre (n = 27 years), from the IAEA-GNIP database (https://www.iaea.org/services/networks/gnip).

On the other hand, if the $\delta^{18}O$ of the two specimens of *Eremotherium* reflects the isotopic composition of precipitation, this could imply that these individuals lived at times dominated by ^{18}O-depleted rainfall of tropical origin, and therefore may not have co-existed with *Megatherium*. In southern Brazil, periods of high summer insolation, especially associated with warmer stages such as interglacials/interstadials or the millennial-scale warm pulses recorded during the Late Pleistocene (Cruz *et al.*, 2006; Lopes *et al.*, 2020), and periods with enhanced influence of the South America summer monsoon (SASM) (Novello *et al.*, 2017), were characterized by increased summer precipitation of tropical origin.

The scarce number of samples precludes any definite conclusion, but the low relative $\delta^{18}O$ in *Eremotherium* could be at least in part related to the high amount of C3 plants in the diet, although specimens of *Eremotherium* from northeastern Brazil (9°S) exhibit an opposing pattern, with ^{13}C-depleted individuals also exhibiting more positive $\delta^{18}O$ (França *et al.*, 2014). Although C4 plants are more ^{18}O-enriched than C3 plants, in closed forests there is a progressive ^{18}O-enrichment from the roots and stems up to the leaves and finally the fruits, driven by evaporation and decreased humidity and respired CO_2 between the forest floor and the upper canopy, so in closed forests there is an upward increase of 3–4‰ in leaf $\delta^{18}O$ (Dunbar & Wilson, 1983; Silveira *et al.*, 1989; van der Merwe & Medina, 1991; Yakir, 1992; Heaton, 1999), and these differences are reflected in the isotopic composition of forest herbivores (Cerling *et al.*, 2004; Zin-Maung-Maung-Thein *et al.*, 2011). On the other hand, trees in riparian forests apparently obtain their water not only from the surface but also from ^{18}O-depleted groundwater (Ehleringer & Dawson, 1992), therefore may exhibit low $\delta^{18}O$.

The $\delta^{13}C$ in the *Eremotherium* from Pessegueiro Creek does not indicate feeding on plants of the understory, thus its low $\delta^{18}O$ could indicate foraging preferentially on less ^{18}O-enriched leaves in the lower parts of trees, or a mixture of different parts of trees on its diet, such as a combination of ^{18}O-enriched leaves and ^{18}O-depleted stems (especially if these trees absorbed groundwater), which would be consistent with the partially xylophagous diet inferred for this taxon (Spillmann, 1948).

Paleoenvironmental and paleoecological inferences

The fossil mastofauna of the Pampa landscape of southern Brazil indicates predominance of open environments such as grasslands and woodlands developed under drier climate during the Pleistocene (Oliveira, 1999). In fact, the modern flora contains plant relicts of drier environments, but palynomorphs show that this flora has changed through time in response to variations in moisture, temperature, and CO_{2Atm} driven by glacial-interglacial cycles (Klein, 1975; Behling *et al.*, 2005; Pillar *et al.*, 2009).

The distinct $\delta^{13}C$ in the specimens of *Eremotherium* and *Megatherium* indicate feeding on different types of plants. If both species were sympatric in the area of Pessegueiro Creek, the landscape could be characterized as open, C4-dominated grasslands with closed riparian forests along riverbanks and hillslopes, similar to the modern landscape (Figure 5; Klein, 1975; Pillar *et al.*, 2009), and apparently not subject to large seasonal variations in composition of plant assemblages, although the ~30% of C3 plants in the diet of *Megatherium* could indicate seasonal shifts. Pollen data show that during the last glacial period the central-western Rio Grande do Sul and northern Uruguay were dominated by grasslands (*campos*) with scarce arboreal vegetation, which expanded as riparian forests during the Early Holocene interglacial as the climate became warmer and wetter (Behling *et al.*, 2005; Iriarte, 2006; Mourelle *et al.*, 2018; 2020).

If this pattern repeated during the Pleistocene, the carbon isotopes of *Eremotherium* and *Megatherium* from Pessegueiro Creek could indicate that both lived during a warm (interglacial or interstadial) stage. Although higher pCO_2 and precipitation during such stages also favor the expansion of C3 plants, the higher temperatures and summer rainfall favor C4 plants (Vogel, 1983; Cerling *et al.*, 1997; Epstein *et al.*, 1997; Connin *et al.*, 1998; Ehleringer *et al.*, 2002). Such conditions, together with the variable topography (Figure 5) that influences the diversity and abundance of C3 and C4 plants (Barnes *et al.*, 1983), would have produced habitat heterogeneities that could have allowed their co-existence by occupying the browser and mixed feeder guilds (du Toit, 2003).

It can be hypothesized that the reduction of arboreal vegetation during the cold/dry stadials led to the extinction of *Eremotherium* in central Rio Grande do Sul, whereas *Megatherium* could have survived on plants adapted to dry conditions. The progressively drier climate between the Miocene and Pleistocene in the Argentinean Pampas led to a reduction in forests and expansion of grasslands, contributing for the extinction of arboreal sloths in that area (Ortiz-Jaureguizar & Cladera, 2006). The disappearance of *Eremotherium* from the Atlantic and Gulf coastal plain of the United States is regarded as a result of environmental changes driven by the overall cooling from the last interglacial (MIS 5) to the stadial MIS 4 (McDonald & Lundelius Jr., 2009), a scenario similar to what is suggested for southern Brazil.

The isotopic values of the studied fossils of megatheriids point to distinct plant communities between the two areas, which could be the result of differences of latitude, topography, soil types, continentality, and also of climate regimes, considering that the individuals from Pessegueiro Creek and Chuí Creek may have lived at distinct times. Closed forest habitats seem to have been absent in the landscape around Chuí Creek, which is consistent with the absence of forest adapted mammals in the fossil assemblage of the Santa Vitória Alloformation (Lopes *et al.*, 2020). The sandy substrate with only incipient soils limits the types of plants capable of settling in the coastal plain, although C4 plants are favored over C3 in such substrates (Epstein *et al.*, 1997). Plants with $\delta^{13}C$ between -25.5‰ and -22‰ indicate conditions of hydric stress (Kohn, 2010), which would have affected at least the megatheriid PV0438 and the *Eremotherium* (Figure 3).

The $\delta^{13}C$ of *Megatherium* and JP125 indicate the presence of C3 to mixed C3-C4 grasslands in the coastal plain but seems too high to have included plants of open woodlands (Figure 3). On the other hand, the values in *Eremotherium* and PV0438 indicate woodland vegetation and C3 grasslands. These differences could reflect the niche partitioning between the two species, which would have allowed co-existence, but

Figure 5. The modern landscape in the surroundings of Pessegueiro Creek (Caçapava do Sul County).

could also indicate that the two species inhabited the area at different times under distinct environmental conditions.

This overall pattern and smaller range of $\delta^{13}C$ variation between megatheriids from Chuí Creek suggest a landscape with lower diversity of plants and higher seasonality compared to Pessegueiro Creek. Because C3 grasses have physiological advantage over C4 grasses under cooler temperatures (Cerling *et al.*, 1997), the presence of both types in the mammals from that site seems consistent with seasonal climate, with C3 plants growing during winter-spring and C4 growing during summer (Teeri & Stowe, 1976; Ehleringer *et al.*, 1997).

The higher $\delta^{13}C$ of *Toxodon* from Chuí Creek indicates feeding on both C3 and C4 grasses (Figure 3), whereas the lower values of *Megatherium* and the specimen JP125 indicate that these ingested more C3 plants, suggesting absence of competition between these taxa and also with *Eremotherium* and the megatheriid PV0438. On the other hand, the $\delta^{13}C$ of *Eremotherium* and PV0438 indicate feeding on C3 woodlands and grasslands, and are similar to the specimens of *Notiomastodon*, which suggests that competition between the two species may have occurred. This could imply that *Eremotherium* and *Notiomastodon* may not have been sympatric and lived at different times in the CPRS. Nevertheless, large herbivores can co-exist in the same area by segregating spatially, or by consuming different plants or distinct parts of the same plants (du Toit & Owen-Smith, 1989; Perrin, 1994; Feranec & MacFadden, 2000).

Paleobiology of the giant megatheriids

The isotopic data available for both *Eremotherium* and *Megatherium* found across South America (Figures 6A–B) indicate that these species occupied a wide range of habitats, due to their ability of to feed on different types of plants, including less digestible parts, which results from a combination of their large body sizes and masticatory apparatuses. Despite some anatomical differences in skull and jaw bones, both species share morphological features of browsers (narrow muzzle) and grazers (hypsodont teeth,

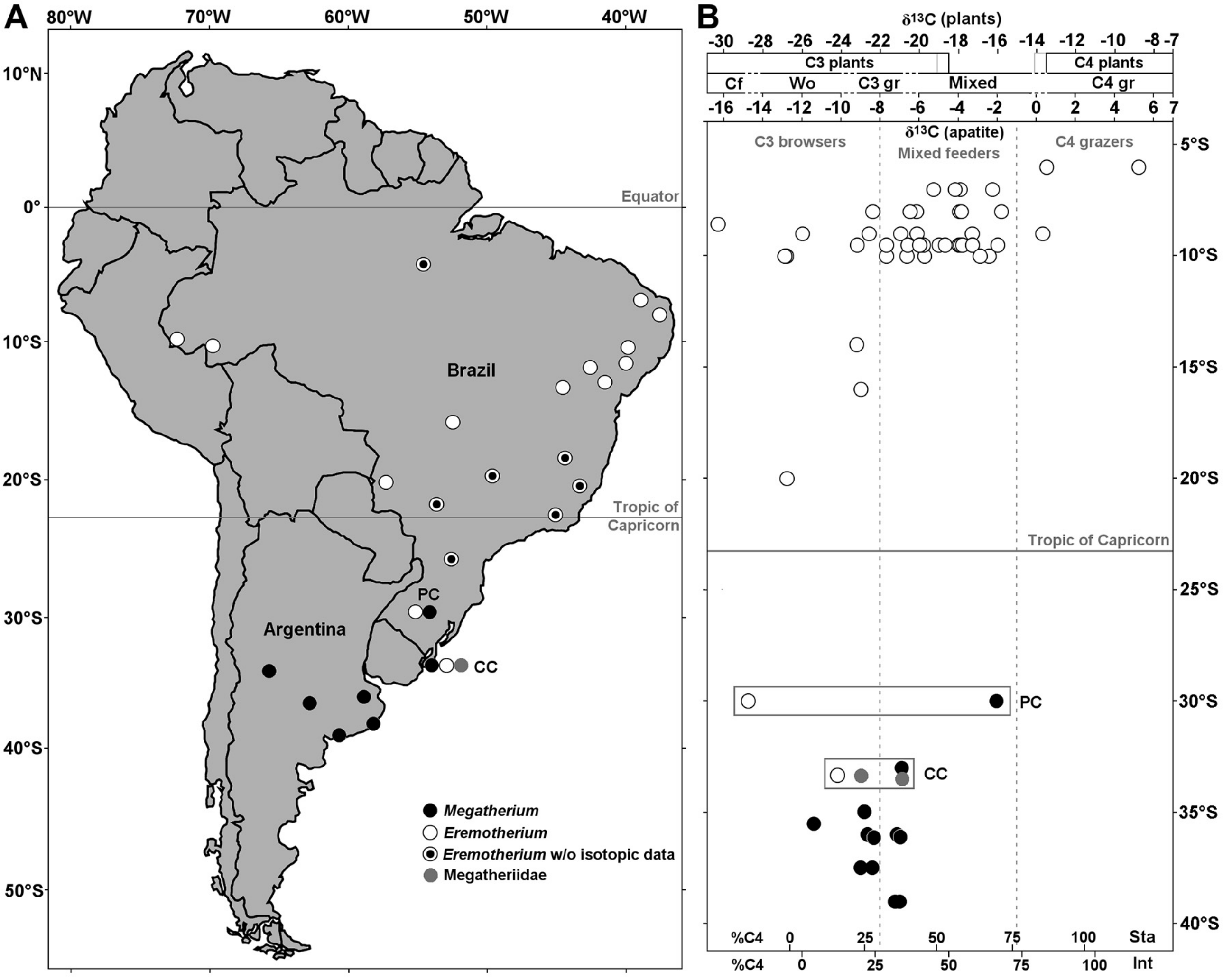

Figure 6. A, distribution of fossils of *Megatherium americanum* and *Eremotherium laurillardi* with associated isotopic data found across South America; records of *Eremotherium* without isotopic data are also shown (from Paula Couto, 1979; Cartelle & De Iuliis, 1995; Rossetti *et al.*, 2004; Praderio *et al.*, 2005; Martinelli *et al.*, 2012; Bocherens *et al.*, 2017; Lopes & Pereira, 2019; Pansani *et al.*, 2019; Domingo *et al.*, 2020; Oliveira *et al.*, 2020; Tomassini *et al.*, 2020; Asevedo *et al.*, 2021). **B**, Comparative $\delta^{13}C$ data of both megatheriids across the continent. **Abbreviations: PC**, Pessegueiro Creek; **CC**, Chuí Creek; **Cf**, closed forest; **Wo**, woodlands; **Gr**, grasslands.

large attachment for the masseteric muscles, posteriorly located orbits) (Saarinen, 2019). The large gut volumes associated with large body sizes imply in longer time for the enzymes to digest plant material thus enabling these animals to feed on fibrous and less digestible parts of plants (Geist, 1974; Demment & Van Soest, 1985; Owen-Smith, 1988). The fossil record of Argentina shows that increasingly larger body sizes allowed sloths to progressively incorporate more C4 plants in their diets, which increased in abundance in the South American Pampas from the Miocene to the Pleistocene as the atmospheric $p\mathrm{CO}_2$ lowered and forests retracted and grasslands expanded (Cerling *et al.*, 1997; 1998; Ortiz-Jaureguizar & Cladera, 2006; Vizcaíno *et al.*, 2012; Domingo *et al.*, 2020).

Megatherium americanum was considered a specialized, mixed, or selective feeder with preference for certain types of plants (shrubs) or specific parts such as leaves, stems, and fruits, based on its oral and dental morphology (McDonald, 2005; Bargo *et al.*, 2006a; 2008; Bocherens *et al.*, 2017). Its masticatory apparatus was appropriate for strong, vertical bite, with mostly ortal jaw movements, and the double-crested molariform teeth were ideal for cutting rather than grinding, thus inappropriate for processing hard, fibrous plants (Bargo, 2001). *Megatherium* was more hypsodont than *Eremotherium*, with taller maxillae and dentaries (De Iuliis, 1996; Bargo *et al.*, 2006b; Cartelle & DeIuliis, 2006), although the large occlusal surface of the teeth of both species provided high capacity for oral processing, possibly related to higher metabolic needs, or compensating for relatively low fermentation capacity (Vizcaíno, 2009). The apparatus of *Eremotherium* was somewhat different, with masticatory movements restricted to the mediolateral axis due to the shape and position of the glenoid fossa and mandibular condyle. Apparently, it had a more anteriorly extended cheek and reduced size of the oral opening (Naples & MacAfee, 2012). The premaxillae of *Eremotherium* were shorter and subtriangular-shaped, less derived compared to *Megatherium*, thus considered as an indicator of a more generalized diet than the latter (McDonald, 2005).

Although *Megatherium* has been usually reconstructed with a long prehensile tongue used for pulling leaves off branches (Figure 7), analysis of its hyoid apparatus showed that it had relatively low capacity for tongue protrusion (Pérez *et al.*, 2010). Moreover, the isotopic results show that, as *Eremotherium*, it was capable of ingesting morphologically similar (graminoid) plants, possibly aided by fleshy prehensile

Figure 7. Reconstruction of *Megatherium americanum* with long prehensile tongue by J. Smit, from Hutchinson (1910).

upper lips (Bargo *et al.*, 2006b; Bargo & Vizcaíno, 2008; Naples & MacAfee, 2012). Muscular reconstructions suggest that *Megatherium* had a pointed upper lip of capable of selecting leaves in branches (Bargo & Vizcaíno, 2008), similar to the browsing black rhinoceros *Diceros bicornis* (Hillmann-Smith & Groves, 1994). Although sharing similar skeletal muzzle anatomy and lacking incisor teeth as the latter, the white rhinoceros *Ceratotherium simum* has broad-shaped lips used for grazing (Groves, 1972). The pointed lip of *Diceros*, however, allows it to include up to ~20% of C4 grasses and CAM plants in its diet (Cerling *et al.*, 2018), so a similar morphology in *Megatherium* (and possibly also in *Eremotherium*) would allow for the varied diet inferred from isotopes. Based on their overall generalist feeding habits, both megatheriids could have had less specialized lip morphology compared to the two rhinos. Microwear features in teeth of *Megatherium* from Argentina are distinct from those in folivore sloths and interpreted as greater oral processing and ingestion of substantial amounts of grit with the food (Green & Kalthoff, 2015). Those features could indicate the ingestion of plant roots as suggested by Cuvier (1804), which are carbohydrate reserves of plants exploited by elephants during dry seasons (Owen-Smith, 1988), but the isotopic data indicate that they may also result from feeding on abrasive grasses as well.

Isotopic analyses of *Megatherium* found in different sites in Argentina (Figure 6A, Praderio *et al.*, 2012; Bocherens *et al.*, 2017; Domingo *et al.*, 2020) show carbon values similar to the megatheriids and *Notiomastodon* from Chuí Creek, consistent with C3 browsing to mixed-feeding in open woodlands and grasslands. The higher proportion of C4 plants in *Megatherium* from Pessegueiro Creek compared to Argentina (Figure 6B) was probably an adaptation to the increasing abundance in this type of plants towards lower latitudes, which resulted in a diet pattern similar to that of some *Eremotherium* from northeastern Brazil (Figure 6B). It is noteworthy that this individual apparently did not incorporate arboreal elements in its diet, if it was sympatric with *Eremotherium*. The absence of closed forests as indicated by the isotopic values in Pleistocene *Megatherium* from Argentina (Figure 6B) is consistent with the replacement of forests by steppes and grasslands from the Miocene onwards (Ortiz-Jaureguizar & Cladera, 2006), therefore it can be hypothesized that Middle-Late Pleistocene megatheriids from the Argentinean Pampas were not behaviorally adapted to feed on arboreal vegetation.

The isotopic analyses in teeth of *Eremotherium* from several localities across northeastern to central-western Brazil (Figure 6A–B), have shown a wide diet range, from pure C4 to C3-dominated, but mostly mixed feeding (Dantas *et al.*, 2013; 2017; França *et al.*, 2014; 2015; Silva, 2015). Despite few analyzed specimens from central-western Brazil, these seem to indicate predominance of C3 plants in the diet towards higher latitudes (Pansani *et al.*, 2019; Oliveira *et al.*, 2020). Being a species of tropical origin, possibly from southeastern-southern North America (Cartelle & De Iuliis, 2006), *Eremotherium* may have originally fed on arboreal vegetation but was also capable of incorporating significant amounts of C4 plants and C3 grasses in drier environments, thus seems to have been more generalist than *Megatherium*. Similar patterns of latitudinal changes in the proportions of C3 and C4 in the diets of the megafauna are recorded in fossil proboscideans and equids across South America, reflecting latitudinal changes of vegetation (MacFadden *et al.*, 1999; Prado *et al.*, 2005; 2011; Lopes *et al.*, 2013; França *et al.*, 2015).

Paleobiogeography of *Eremotherium*

One relevant question is the migration route of *Eremotherium* from the tropics up to subtropical southern Brazil. The steep escarpments of the Araucaria Plateau, the northern limit of the Pampa in Rio Grande do Sul, would have been a barrier for the migration of the megafauna from the Brazilian Intertropical Region (BIR, *sensu* Cartelle, 1999) across the highlands of southeastern Brazil, especially during warm periods when the escarpments were covered by the dense Atlantic Forest (Figure 8A), therefore *Eremotherium* probably reached up to southern Brazil along other routes. The distribution of the scarce known fossils of megatheriids across southeastern Brazil (Figure 8B, Paula Couto, 1979; Sedor, 2014), found in floodplain deposits of large perennial fluvial systems of the Paraná River Basin, suggests that migration would have been facilitated by its ability to browse on riparian forests developed along rivers flowing from the BIR to subtropical South America.

The biogeographic corridor developed along the fluvial systems of the Paraná-Paraguay basins (Oakley *et al.*, 2005) served for the migration of tropical taxa to subtropical areas and vice-versa, as exemplified by the presence of Brazilian (tropical) fauna in the Mesopotamian region of northeastern Argentina (Scillato-Yané *et al.*, 2005; Francia *et al.*, 2015). The giant sloth *Lestodon armatus* found in the western state of São Paulo (Figure 8B) (Paula Couto, 1973) probably followed this route to migrate from the Pampas to the north, possibly originating the species *Ocnotherium giganteum* found in the State of Minas Gerais (Cartelle, 2012).

The *Eremotherium* found in Pessegueiro Creek could have reached Rio Grande do Sul along the Paraná River corridor (Figure 8B), accompanying the southwards and eastwards expansion of broadleaf and gallery forests along its distributaries and southern border of the Araucaria Plateau during a warm stage (Klein, 1975). This migration route could also have been used by tropical Nothrotheriinae sloths that reached northern Uruguay (Perea, 2007) and northern Argentina (Brandoni & Vezzosi, 2019; Vezzosi *et al.*, 2019), found in fluvial and palustrine sediments deposited during the last interglacial (MIS 5). Considering the faunal similarities between fossil assemblages of western Rio Grande do Sul and the Argentinean Mesopotamia (Carlini *et al.*, 2004) it is hypothesized that fossils of *Eremotherium* may eventually be found in the latter as well.

The mixture of Pampean and Brazilian taxa in the Chuí Creek local fauna indicates an ecotone area between tropical and temperate zones, whose limits shifted latitudinally in

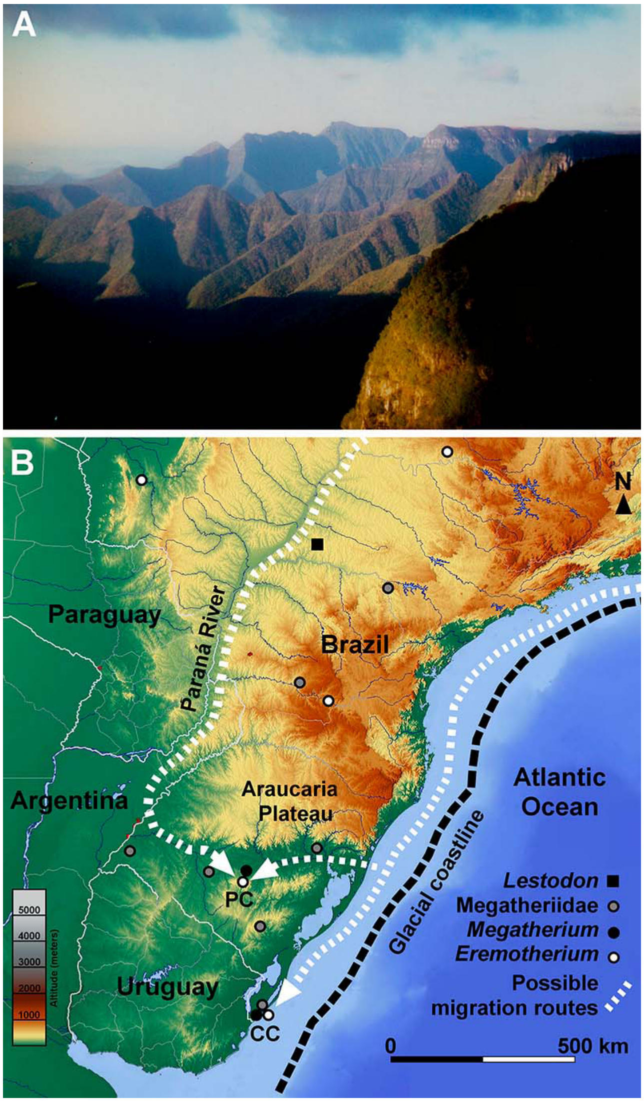

Figure 8. A, escarpments bordering the Araucaria Plateau in Rio Grande do Sul, covered by the Atlantic forest. **B**, digital elevation map with the location of fossil sites with remains of megatheriids in southeastern-southern Brazil, showing the hypothetical migration routes of *Eremotherium*.

response to Pleistocene climate changes (Lopes, 2013; Lopes *et al.*, 2020). *Eremotherium* may have reached the area of Chuí Creek during a warm stage following an eastern route along the coastal plain. Although interglacial sea-levels were equal or higher than the present, during the relatively warm interstadials within a glacial cycle, such as the MIS 3 (57–29 ka ago), sea-level remained below the present (Dillenburg *et al.*, 2020), thus would provide a wider Atlantic corridor that facilitated the southward migration of tropical species.

Some of species of the Atlantic forest that currently occupy inner areas of the northern coastal plain and escarpments of the Araucaria Plateau (Figure 8A) expanded westward and southward in Rio Grande do Sul (Klein, 1975; Behling *et al.*, 2005; Pillar *et al.*, 2009), and *Eremotherium* could have followed this expansion up to Chuí Creek. Palynomorphs obtained in tooth calculi of mastodonts from the southern CPRS indicate the presence of plant species of the Atlantic forest (Asevedo *et al.*, 2020). Some *Eremotehrium* migrating southward along the Atlantic corridor could have taken an alternative route along the lowlands across the central state (Figure 8B) up to the area of Pessegueiro Creek following the westward expansion of the Atlantic forest (Klein, 1975; Behling *et al.*, 2005), as suggested by the presence of a few fossils of unidentified megatheriids in this area.

Considering the co-occurrence of Brazilian and Pampean fossils in the Chuí Creek local fauna (Lopes *et al.*, 2021), this Atlantic corridor allowed other elements of the intertropical megafauna such as the canid *Protocyon troglodytes* (Oliveira *et al.*, 2005) and the glyptodont *Panochthus greslebini* (Ferreira *et al.*, 2015) to reach the CPRS, following southward expansion of tropical environments during warm (interglacial/interstadial) stages. On the other hand, some Pampean taxa found in the CPRS such as *Megatherium* and the glyptodont *Doedicurus clavicaudatus* (Pereira *et al.*, 2012), which is absent in northeastern Argentina (Francia *et al.*, 2015), may have also migrated northward along this route, possibly during glacial epochs, when sea-levels lower than the present one exposed most of the continental shelf, as indicated by the abundance of mammalian fossils on the inner shelf off Rio Grande do Sul (Lopes & Buchmann, 2010; Aires & Lopes, 2012; Lopes & Pereira, 2019). The *Megatherium* found in Pessegueiro Creek probably migrated across the Pampa plains from Argentina or Uruguay.

CONCLUSIONS

The results presented here contribute for a better understanding of the biology and ecology of the two largest known sloth species, *Megatherium americanum* and *Eremotherium laurillardi*, and provide inferences about the past vegetation of the Brazilian Pampa, which could help understand how the environments are modified through time in response to climate changes. Although limited by the number of samples available, the results are in general in agreement with those obtained for both species in Brazil and Argentina, but exhibit some differences related to specific habitat preferences.

In ecological terms, the results show that both species could have co-existed by occupying different niches. The isotopic values in *Eremotherium* and *Megatherium* from Pessegueiro Creek and Chuí Creek indicate that the former was a mainly a C3 browser, whereas the latter was a mixed feeder that ingested more C4 plants. Compared to the fossil records from northeastern Brazil and the Argentinean Pampas, both species exhibit latitudinal changes in their feeding habits, suggesting opportunistic incorporation of the locally available plant types in their diets. The wider diet preference of *Eremotherium* would have allowed it to expand from the tropics to the subtropics, following the southward expansion of forests during warm stages, whereas *Megatherium* apparently preferred to forage on subtropical-temperate landscapes.

The isotopic data presented here indicate that mammalian fossils can help understand the effects of glacial-interglacial, and possibly smaller-scale (millennial), climate changes on the vegetation and environments of the Pampa, thus may contribute for preservation and management efforts under scenarios of present and future climate change.

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