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Paleoenvironment and paleoecology associated with the early phases of the Great American Biotic Interchange based on stable isotope analysis of fossil mammals and new U–Pb ages from the Pampas of Argentina

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ABSTRACT

The analysis of stable isotopes in fossil mammals is useful for reconstructing paleoenvironmental and paleoecological conditions, but has been rarely applied to the Neogene of South America. In this study, we perform an integrative analysis (including U–Pb zircon dates and mammalian stable isotopes data) for the Late Miocene–Early Pliocene of central Argentina. We provide radioisotopic ages for some classic fossiliferous localities in this region, including an age of 9.7 ± 0.3 Ma for Arroyo Chasicó and 4.5 ± 0.2 Ma for Farola Monte Hermoso, and address the interval covering the Chasicoan (Late Miocene), Huayquerian (Late Miocene–Early Pliocene), and Montehermosan (Early Pliocene) stages/ages. In the Chasicoan Stage/Age, taxa with mixed C_3–C_4 diets are recorded, suggesting the existence of favorable conditions for the C_4 photosynthetic pathway before its full expansion. However, taxa represented across most of the Huayquerian Stage/Age show a preference for C_3–based diets, which changes in the latest Huayquerian–Montehermosan stages/ages when an increase in the percentage of C_4 plants in the diet of notoungulates, rodents, and xenarthrans is recorded, coinciding with the global expansion of C_4 plants. For the first time, the dietary behavior of two South American endemic sparassodont metatherians (*Lycopsis* and *Thylacosmilus*) has been evaluated from using stable isotope; analysis of these hypercarnivores show differences in δ^{13}C values, suggesting prey partitioning, partly due to the difference in body size. The fossiliferous sites studied, and the new isotopic and chronological information obtained, provide more detailed paleoecological and paleoenvironmental contexts for the Argentine Pampas during the last stages of the isolation of South America and the first pulses of the Great Biotic American Interchange. In addition, the new ages allow to better adjust the arrival of the first Holarctic immigrants in the region.

1. Introduction

The evolutionary history of South American mammals was notably influenced by the isolation of the continent during most part of the Cenozoic (Simpson, 1980; Cione et al., 2015). The South American Neogene land mammals record constitutes an exclusive natural laboratory for testing the effects of some of the most important abiotic and biotic events occurred in the late Cenozoic in America, such as the formation of the Panama Isthmus, the consequent Great American Biotic Interchange (GABI), and the expansion of C_4 grasses.

The GABI was a complex event of faunal interchange that took place between North and South America (Marshall et al., 1982; Vrba, 1992;

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Webb, 2006; Cione et al., 2015; Pelegrin et al., 2018), provoking long–lasting consequences in the configuration of modern Neotropical faunas (Croft, 2001; Moreno Bofarull et al., 2008; Carrillo et al., 2020; Catena and Croft, 2020). The GABI occurred in several phases during more than nine million years (Montes et al., 2015; Cione et al., 2007, 2015). Although the formation of the Panama Isthmus as a permanent dry land since ~3.1–2.7 Ma ago (Webb, 2006; Leigh et al., 2014; O'Dea et al., 2016) favored the most intense faunal interchange between these two continents (Marshall et al., 1982; Webb, 2006, Woodburne, 2010; Leigh et al., 2014; Defler, 2019), the first pulses, called ProtoGABI (sensu Cione et al., 2015), occurred during the Late Miocene–Pliocene and represent intermittent connections of land masses related to glacial events and low sea levels (Cione et al., 2007, 2015; Woodburne, 2010). Some of the oldest Holarctic representatives reported from Late Miocene–Early Pliocene deposits (Huayquerian Age) of Argentine Pampas were procyonids (Telén, Quehué, and Salinas Grandes de Hidalgo sites; Montalvo et al., 1998 Moreno Bofarull et al., 2008; Vizcaíno and Farina, 1999) and cricetids (Caleufú site; Verzi and Montalvo, 2008), which represent the also called "New Island Hoppers" (Simpson, 1950) or "Heralds" (Webb, 1985).

The expansion of C_4 grasslands coincided with this time interval, leading to changes in the diet of some herbivore mammals (e.g., MacFadden et al., 1996; Prado et al., 2011; Domingo et al., 2020). At a global level, towards the end of the Miocene, environments shifted in large regions from tropical/subtropical forested areas to more open woodlands and grasslands in response to the global development of arid and semiarid climates with increased hydric seasonality (Kohn and Cerling, 2002; Edwards et al., 2010; Strömberg, 2011; Saarinen et al., 2020).

In southern South America, the period spanned between the Late Miocene–Late Pliocene (~12–3 Ma; Chasicoan–Chapadmalalan stages/ages) is known as the "Edad de las Planicies Australes" (Age of the Southern Plains) (Pascual and Bondesio, 1982), since a large part of the landmass was a semiarid grassland (Ortiz Jaureguizar, 1998). Studies of the fossil record and paleosols carbonates from Argentina reveal they became dominant in South America around ~7 Ma (Kleinert and Strecker, 2001), although C_4 grasses were present since the Eocene, around 44 Ma (Bellosi et al., 2021), and were relatively abundant at 16.5 Ma (Strömberg, 2011; and references therein). The carbon isotope composition ($\delta^{13}C$) from the tooth enamel of herbivorous mammals points to a significant percentage of C_4 resources in their diets around 7.3–6.7 Ma (MacFadden et al., 1996; Cerling et al., 1997; Latorre et al., 1997; Domingo et al., 2020). In the Argentine Pampas, Domingo et al. (2020) recorded herbivorous mammal diets with significant percentages of C_4 plants during the latest Miocene/earliest Pliocene (late Huayquerian/Montehermosan stages/ages).

The Late Miocene–Early Pliocene mammalian fossil record from Argentine Pampas is profuse and diverse, and includes both endemic and immigrant mammalian lineages. Although numerous works evaluate these faunas from taxonomic and biostratigraphic standpoints, few studies have focused on the paleoenvironment, paleoclimate, and paleoecological context by means of stable isotope analysis (MacFadden et al., 1996; Latorre et al., 1997; Hynek et al., 2012; Domingo et al., 2020; and references therein). In this regard, the paper of Domingo et al. (2020) is the only isotopic study for the late Cenozoic that analyzes the paleoenvironmental and paleoecological changes over a protracted time interval (~9.5 Ma to ~12 ky) using a multi–taxonomic approach. The scarcity of integrative analyses for the Neogene of this region is, in part, due to the limited number of numerical ages for key localities, which prevents the establishment of a precise chronological framework to pinpoint the occurrence of the paleoenvironmental events.

Therefore, our study aims at significantly enhancing the isotopic approach by putting together a large dataset with mammalian stable isotope information at a genus level from eight fossiliferous localities of the Argentine Pampas (Buenos Aires and La Pampa provinces) over a wide time interval (~5 Ma) within the Late Miocene–Early Pliocene. In addition, we provide radioisotopic ages of some of these localities. The importance of this study lies in presenting a paleoecological and paleoenvironmental analysis of fossil mammal at genus level, several of which have not been studied from an isotopic approach until now, in the context of new locality dating. This work substantially refines the previous interpretations proposed in the work of Domingo et al. (2020), in which the specimens were evaluated at the order level. Consequently, the goals of this work are: i) to establish a paleoenvironmental and paleoecological context for the Late Miocene–Early Pliocene of the Argentine Pampas through the isotopic analysis of a high diversity of mammals; ii) to shed some light on trophic interactions by studying, for the first time, the dietary behavior of two genera of South American endemic hypercarnivorous Sparassodonta (Metatheria); and iii) to refine the chronology of some localities, adjusting the current biostratigraphic schemes, in order to assess more accurately the climatic, environmental, and faunal episodes.

2. Geographical and geological setting

The mammalian fossils analyzed in this work were recovered from eight fossiliferous localities from the Argentine Pampas. Fossil bearing levels correspond to the Cerro Azul Formation for Arroyo Chasicó (Buenos Aires Province), Cerro La Bota, Telén, Quehué, Salinas Grandes de Hidalgo, Bajo Giuliani and Caleufú (La Pampa Province) sites, and Monte Hermoso Formation for Farola Monte Hermoso site (Buenos Aires Province) (Fig. 1).

2.1. The Cerro Azul Formation

The Cerro Azul Formation corresponds to a continental, nearly flat–lying sedimentary unit composed of massive siltstones and fine–grained sandstones with interbedded poorly pedogenically modified beds (Linares et al., 1980), i.e. paleosols mostly characterized by frequent carbonate nodules and structures (Visconti, 2007; Folguera and Zárate, 2009). Primary, dominant aeolian deposits (loess deposits) were recognized, which in some cases were reworked by aqueous agents (loess–like deposits) (Folguera and Zárate, 2009). At the beginning, this formation was described for the center and east of La Pampa Province. Other units were later correlated to this formation, enlarging its geographical extension to southwestern Buenos Aires Province and southeastern Mendoza Province. Deposits outcropping at Arroyo Chasicó (firstly assigned to the Arroyo Chasicó Formation, see Zárate et al., 2007; Folguera and Zárate, 2009) are particularly interesting because this site represents the type locality of the Chasicoan Stage/Age. More geological information about this formation in the different studied localities is provided in Supplementary Material 1.

2.2. The Monte Hermoso Formation

The Monte Hermoso Formation is mainly composed of muddy siltstones, although sandy siltstones, silty sandstones, and clast–supported breccias (i.e. embedded silty and sandy intraclasts) are also present (Zavala, 1993). These deposits were accumulated in a dynamic fluvial environment of high–sinuosity rivers, which are represented by channel, lateral accretion, and overbank deposits (Zavala and Navarro, 1993). The Monte Hermoso Formation crops out at Farola Monte Hermoso locality, particularly in the abrasion platform and the lower part of a marine cliff in the Atlantic coast. This site is of great interest due to: i) the abundance and diversity of vertebrate fossils, some of them key in the assembling and development of Darwin's ideas on the transmutation of species during his round-the-world voyage aboard the Beagle (Farinati et al., 2010), ii) because it represents the type locality of the Montehermosan Stage/Age (Tomassini and Montalvo, 2013). More geological information about this formation is provided in Supplementary Material 1.

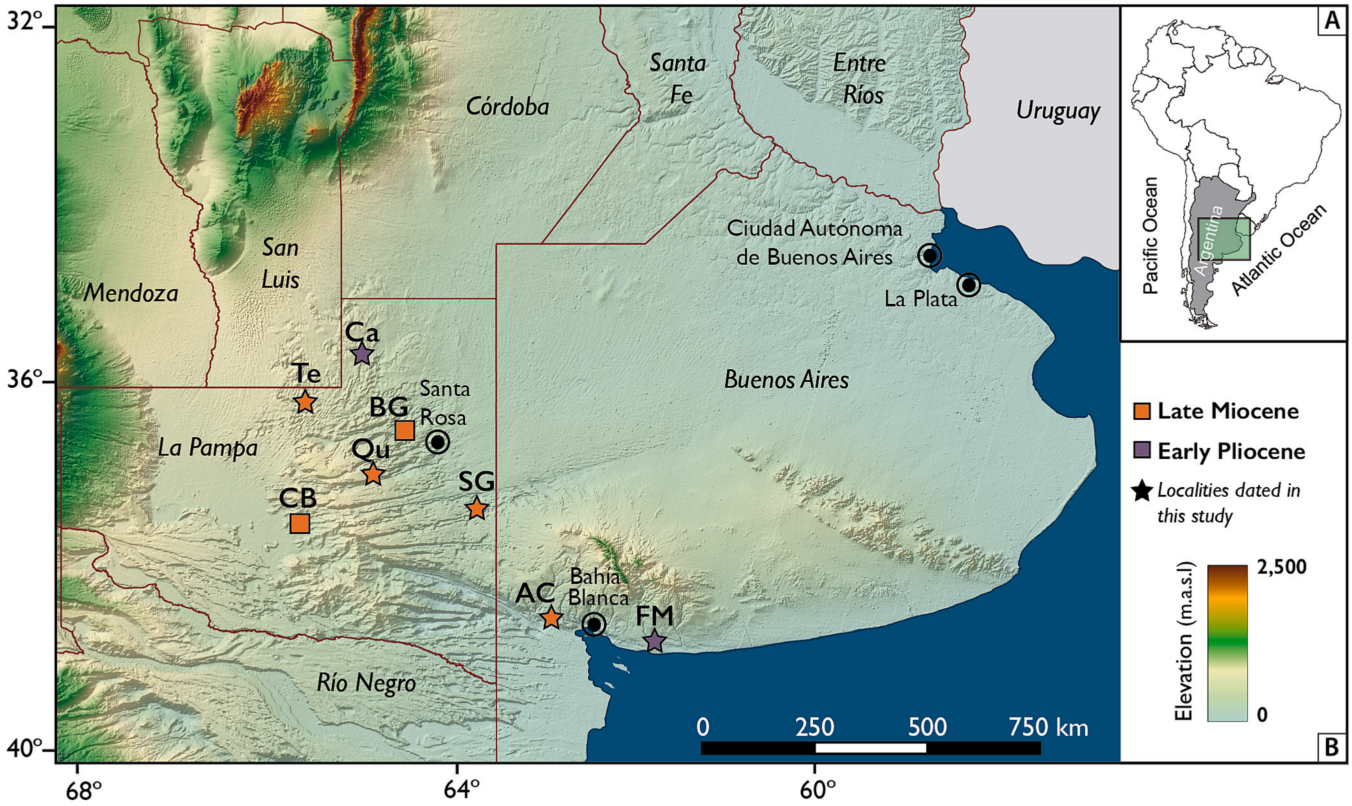

Fig. 1. Geographical location of the paleontological sites. A) General map of South America. B) Map of the Late Miocene and Early Pliocene localities of the Buenos Aires and La Pampa provinces (AC: Arroyo Chasicó, BG: Bajo Giuliani, Ca: Caleufú, CB: Cerro La Bota, FM: Farola Monte Hermoso, Qu: Quehué, SG: Salinas Grandes de Hidalgo, Te: Telén). The stars represent the localities that have been dated in this work.

2.3. Background of numerical dating for the Late Miocene-Early Pliocene of Argentine Pampas

The scarcity of numerical dating for the Late Miocene–Early Pliocene interval of the studied area in the Argentine Pampas (most of them obtained in levels of the Cerro Azul Formation) hinders the accurate temporal assignment of the vertebrate assemblages. Based on a ^{40}Ar/^{39}Ar age of 9.23 ± 0.09 Ma, obtained from impact glasses ("escoria") and high–resolution magnetostratigraphic profiles, it was proposed the deposits of the Cerro Azul Formation outcropping at Arroyo Chasicó were accumulated between 9.4 and 8.7 Ma (Late Miocene, Chasicoan Stage/Age; Zárate et al., 2007), in accordance with the age obtained herein (see Table 2). The analysis of an "escoria" from Cantera Vialidad, a locality near Bahía Blanca city (Buenos Aires Province) with Cerro Azul Formation deposits, yielded an age ^{40}Ar/^{39}Ar of 5.28 ± 0.04 Ma (Late Miocene, Huayquerian Stage/Age; Schultz et al., 2006). A detrital zircon age, achieved by the U–Pb SHRIMP method, from the basal deposits of the Cerro Azul Formation outcropping at Cerro Patagua (La Pampa Province) provided a youngest zircon age of 12.3 ± 1.8 Ma (late Middle Miocene, Chasicoan Stage/Age; Montalvo et al., 2023). Also, a paleosol sample, no litho–stratigraphically contextualized, from the General Acha city (La Pampa Province) yield an age of 8.47 ± 0.39 Ma for the younger detrital zircon analyzed (Bruner et al., 2022); this age is reported in a study of provenance of the Pleistocene to Holocene loessic and aeolian dune deposits at the Argentine Pampas. Analysis of younger detrital zircon from Cerro Azul Formation levels at different localities of center and western La Pampa Province were recently published (Stubbins et al., 2023); this work includes an age of 6.2 ± 0.9 Ma for Telén, which is concordant with the value obtained herein (see Table 2). Other ^{40}Ar/^{39}Ar ages from "escorias" include an average value of 7.09 Ma for Telén (Romano et al., 2023) and values of 5.17 ± 0.08 Ma (Early Pliocene, Huayquerian Stage/Age) and 4.33 ± 0.06 Ma (Early Pliocene, Montehermosan Stage/Age) for different levels of the "Irene" Formation at Quequén Salado River (Buenos Aires Province) (Prevosti et al., 2021); difference between our value (see Table 2) and the average suggested by Romano et al. (2023) for Telén may be due to methodological issues ("escorias" vs zircons).

Based on several of these numerical ages and the study of the evolutionary patterns of octodontoid rodent fauna present in the Cerro Azul and Monte Hermoso formations, different biostratigraphic schemes were proposed for the temporal interval represented in the localities here studied (Tomassini et al., 2013; Deschamps and Tomassini, 2016; Piñero et al., 2021; and references therein): i) Arroyo Chasicó and Cerro La Bota correspond to the Late Miocene, Chasicoan Stage/Age; ii) Telén, Quehué, Salinas Grandes de Hidalgo, and Bajo Giuliani correspond to the Late Miocene, Huayquerian Stage/Age; iii) Caleufú corresponds to the Early Pliocene, latest Huayquerian Stage/Age; and iv) Farola Monte Hermoso corresponds to the Early Pliocene, Montehermosan Stage/Age. Considering these values and the new dating obtained herein (see below), the interval covered in this work is ca. 5 Ma., ranging from the Late Miocene (ca. 9.4 Ma) to the Early Pliocene (ca. 4.5 Ma).

3. Methodology

3.1. U–Pb geochronology

We report new numerical radiometric U–Pb ages on detrital zircons from continental deposits of the Cerro Azul Formation, exposed at Arroyo Chasicó, Telén, Quehué, Salinas Grandes de Hidalgo, and Caleufú localities and the Monte Hermoso Formation exposed at Farola Monte Hermoso locality (SM2). Zircon grains were analyzed at the LA.TE.Andes laboratory (Salta Province, Argentina). Zircons were separated from the silt/sandy silt sediments by conventional density and magnetic techniques, hand–picked with the help of a binocular microscope (15X), embedded in resin epoxy and mounted in a 25 mm diameter cylinder. Subsequently, they were mirror polished by roughing and polishing with diamond pastes. Zircons age determination was conducted by laser ablation inductively coupled plasma mass spectrometry (LA–ICP–MS) with in situ double dating capacity 8900 Triple Quadrupole ICP–MS made by Agilent Technologies and the Resolution–SE 193 nm excimer laser ablation system made by Applied Spectra.

Point isotope analysis on individual grains of zircon was conducted, avoiding grains with inclusions or fractures. Measurements included one spot per analyzed zircon. However, if the morphology allowed it, two or more spots were taken to corroborate consistency in the calculated ages from the same grain. The spot diameters selected were 20, 24 or 30 μm according to the size and homogeneity of the zircon grains. The larger the spot diameter, the lower the fluence value selected (Mukherjee et al., 2019). In general, a lower frequency was selected based on the lowest relative standard dispersion (RSD) achieved during ICP–MS tuning in LA–ICPMS mode.

Elemental concentrations were obtained considering NIST 610 glass as primary reference material (RM) and NIST 612 as secondary (Jochum et al., 2011). U/Pb ages were calculated from isotopic ratios using zircon 91,500 as RM (Wiedenbeck et al., 2004) and repeated measurements on Plesovice zircon (TIMS reference age 337.13 ± 0.37 Ma; Sláma et al., 2008). The analytical sequence consisted of 106–119 grains per sample; and three measurements of NIST 610 and NIST 612 glass, three of zircon 91,500 and two of Plesovice at the beginning and end of each sample process; with a Plesovice and a 91,500 analyses point after every 20–30 analyses. The accuracy of the results was confirmed by obtaining the weighted average $^{206}Pb/^{238}U$ age of the control (Plesovice). The following masses were monitored by ICP–MS: 89 (Y), 91 (Zr), 111 (Cd), 131 (La), 206 (Pb), 207 (Pb), 208 (Pb), 232 (Th), 235 (U) and 238 (U). Data reduction was done with the LADR 1.1.0.7 Software (Norris and Danyushevsky, 2018), and post–processing was done with Isoplot 4.15 (Ludwing Moreno Bofarull et al., 2008) and IsoplotR (Vermeesch, 2018, 2021).

The $^{238}U/^{206}Pb$ ages were used with a 100 ± 10% concordance cut–off based on the $^{238}U/^{206}Pb$ vs. $^{235}U/^{207}Pb$. The maximum depositional age reported for the silt/sandy silt sediments samples from Arroyo Chasicó, Telén, and Monte Hermoso localities was the determined by the Minimum Age Model referred by Vermeesch (2021) as the Maximun Likehood Age (MLA). In the cases of Quehué, Salinas Grandes de Hidalgo, and Caleufú localities, the maximum depositional age was determined on the base of younger single grain datum (YSG; Coutts et al., 2019), since the Minimun Age Model provided a not suitable maximun depositational age (i.e, Cretaceous for Quehué and Caleufú). Respect to Salinas Grandes de Hidalgo both the biostratigraphic schemes and composition of faunal assemblage suggest a most modern age (see Verzi and Montalvo, 2008; Sostillo et al., 2021; Piñero et al., 2021).

3.2. Stable isotope data and analysis

In Domingo et al. (2020), a first approach to the paleoenvironmental and paleontological context from the Late Miocene to the Pleistocene of Argentina was performed by studying mammals at the order level. In this new study, we have made an additional effort to reach a finer taxonomic control of the Late Miocene to the Early Pliocene samples and analyze the data at genus level. We compiled 270 bioapatite samples on the carbonate fraction ($\delta^{13}C_{CO3}$ and $\delta^{18}O_{CO3}$) data from a previous work (Domingo et al., 2020) for eight fossiliferous localities spanning the Late Miocene–Early Pliocene (Table 1, SM3). Data on the phosphate fraction ($\delta^{18}O_{PO4}$) of these samples, also taken from Domingo et al. (2020), are included in Supplementary Material 3. Carbon and oxygen isotope compositions were measured from the tooth enamel of litopterns, notoungulates, rodents, and sparassodonts, whereas orthodentine was the osseous tissue analyzed in the case of pilosans and dasypodids, chlamiphorids, and glyptodonts cingulates (xenathrans) molariforms. The carbon and oxygen isotope results are reported in δ–notation, $\delta^{H}X_{sample} = [(R_{sample} - R_{standard}) / R_{standard}]x1000$, where X is the element, H is the mass of the rare, heavy isotope and $R = {}^{13}C/{}^{12}C$ or $^{18}O/^{16}O$. Vienna Pee Dee Belemnite (VPDB) is the standard for $\delta^{13}C$ values and Vienna Standard Mean Ocean Water (VSMOW) is the standard for $\delta^{18}O$. The chemical treatment of the samples was described in Domingo et al. (2013), while diagenetic alteration of bioapatite was surveyed by comparing the oxygen isotope composition of the carbonate and phosphate fraction of bioapatite samples (see supplementary material in Domingo et al., 2020).

Fossil bioapatite $\delta^{13}C$ values provide information on paleoecological and paleoenvironmental parameters, allowing the characterization of paleodiets and the reconstruction of ancient habitats. For herbivorous mammals, tooth enamel $\delta^{13}C$ value is directly related to the ingested vegetation, successively conditioned by the photosynthetic pathway followed by plants (C_3, C_4, CAM), as well as by environmental and ecological factors (e.g., aridity, canopy density) (Farquhar et al., 1989; Koch, 1998, 2007; Hayes, 2001). To evaluate the type of vegetation consumed by herbivorous mammals (C_3–dominated, mixed C_3–C_4 and dominated C_4), we must consider the $\delta^{13}C$ values of the atmospheric CO_2 ($\delta^{13}C_{CO2atm}$), source of plant carbon, at the period of study. For the Late Miocene, the $\delta^{13}C_{CO2atm}$ value was −6.2‰, according to Tipple et al. (2010). The past values of $\delta^{13}C$ for C_3 and C_4 were estimated by adding the difference between modern $\delta^{13}C_{atmCO2}$ (−8‰) and past $\delta^{13}C_{atmCO2}$ (−6.2‰) to modern $\delta^{13}C$ plant values following Koch et al. (2004). For the vegetation end member of C_3 and C_4 the $\delta^{13}C$ are −25.7‰ and −10.7‰, respectively. In addition, it is necessary to consider the dietary-bioapatite $\delta^{13}C$ enrichment ($\varepsilon^*_{diet–bioapatite}$) associated with carbonate equilibria and metabolic processes (Cerling and Harris, 1999; Passey et al., 2005). In this work, we used the following $\varepsilon^*_{diet–bioapatite}$ values to estimate the vegetation $\delta^{13}C$ cut–off ranges:

- Notoungulates and litopterns: $\varepsilon^*_{diet–enamel} = +14.1$‰ (Cerling and Harris, 1999).
- Rodents: $\varepsilon^*_{diet–enamel} = +12.8$‰ (Passey et al., 2005).
- Xenarthrans: $\varepsilon^*_{diet–bioapatite} = +15.6$‰ (Tejada–Lara et al., 2018)

Domingo et al. (2020) considered $\varepsilon^*_{diet–bioapatite}$ dietary enamel may not be applicable to all xenarthrans due to their different masses. For example, $\varepsilon^*_{diet–bioapatite}$ for fossil cingulates taxa have not been estimated yet. Hence, it is not possible to draw definitive conclusions about their vegetation $\delta^{13}C$ cut–off values.

In the case of carnivorous sparassodonts, their $\delta^{13}C$ values record the isotopic values of ingested prey. Carnivore tooth enamel $\delta^{13}C$ values are ^{13}C–depleted ~1.3‰ with respect to prey tooth enamel $\delta^{13}C$ values (Fox–Dobbs et al., 2006; Clementz et al., 2009). This correction must be addressed before conducting trophic models that provide information about predator–prey interactions. Since, to the best of our knowledge, there are no studies concerning the $\delta^{13}C$ dietary isotopic discrimination of metatherian carnivorous taxa, we made use of the established value for the order Carnivora.

Mammalian bioapatite $\delta^{18}O_{CO3}$ and $\delta^{18}O_{PO4}$ values record the $\delta^{18}O$ value of body water, constituting a combination of oxygen entering and exiting the body. Obligate drinkers, who cover most of their water needs by drinking (usually grazers), reflect changes in $\delta^{18}O$ values of meteoric water controlled, in turn, by shifts in temperature and evaporation rate. Non–obligate drinkers (usually browsers) obtain their water from plant and metabolic water and their values better reflect evaporation processes suffered by the vegetation (Levin et al., 2006; Koch, 2007; Domingo et al., 2012). The $\delta^{18}O$ values of water bodies and plants are positively correlated with mean annual temperature (MAT) and aridity rate; an increase in MAT and/or aridity rate is reflected in ^{18}O–enriched water (Luz et al., 1990).

Table 1

Summary of stable isotope values of mammals from all the Pampean localities analyzed in this study. Locality, Stage/Age, taxa, number of carbonate samples (#C), mean and standard deviation (SD) $\delta^{13}C$ (‰VPDB), $\delta^{18}O_{CO3}$ (‰ VSMOW), number of phosphate samples (#P), mean and standard deviation (SD) $\delta^{18}O_{PO4}$ (‰ VSMOW). * Mean $\delta^{13}C$ values of sparassodont have been corrected for a trophic discrimination of +1.3 ‰ (Fox–Dobbs et al., 2006; Clementz et al., 2009).

Locality	Stage/Age	Taxa	# C	Mean $\delta^{13}C$ (‰ VPDB)	SD $\delta^{13}C$ (‰ VPDB)	Mean $\delta^{18}O_{CO3}$ (‰ VSMOW)	SD $\delta^{18}O_{CO3}$ (‰, VSMOW)	# P	Mean $\delta^{18}O_{PO4}$ (‰ VSMOW)	SD $\delta^{18}O_{PO4}$ (‰ VSMOW)
Farola Monte Hermoso	Huayquerian	*Caviodon*	1	−5.7		29.3		0		
		Eoauchenia	2	−9.6	0.4	30.3	1.1	0		
		Epitherium	2	−10.7	0.9	27.7	1.2	2	18.4	0.7
		Lagostomus	4	−8.8	3.0	27.3	2.3	2	20.5	0.9
		Paedotherium	6	−8.0	1.2	28.3	1.2	0		
		Phugatherium	8	−7.6	3.1	26.1	2.1	6	17.6	2.2
		Pilosa indet.	1	−5.0		27.0		1	17.9	
		Promacrauchenia	4	−10.1	0.7	29.0	1.3	3	19.2	1.8
		Proscelidodon	2	−7.3	1.0	28.2	1.0	2	18.8	0.9
		Pseudotypotherium	8	−8.1	1.2	31.3	1.0	6	22.0	1.2
		Xotodon	3	−5.9	2.2	30.7	1.1	3	21.3	0.6
Caleufú	latest Huayquerian	Caviidae indet.	5	−7.1	2.5	27.5	2.0	5	18.6	1.9
		Lagostomus	1	−7.9		27.6		1	18.5	
		Paedotherium	6	−7.5	1.0	28.4	1.0	6	19.4	0.8
		Pseudotypotherium	2	−7.7	0.8	30.1	0.6	2	20.7	0.4
		Pseudotypotherium/ Typotheriopsis	4	−8.5	1.2	30.0	0.8	4	20.9	0.7
		Scelidotheriinae indet.	3	−7.2	0.3	28.4	0.3	3	19.3	0.3
		Tetrastylus	4	−7.8	1.2	28.5	1.0	4	19.7	1.2
		Caviidae indet.	1	−9.5		28.0		1	18.8	
		Dinomyidae indet.	1	−8.3		29.6		1	20.7	
		Lagostomus	6	−10.2	0.6	28.4	1.0	6	19.6	0.8
Bajo Giuliani	Huayquerian	*Pseudotypotherium/ Typotheriopsis*	2	−9.4	0.1	29.9	0.3	2	20.8	0.3
		Brachytherium	1	−10.2		31.6		0		
		Cardiomys	1	−10.2		25.4		0		
		Dasypodidae indet.	1	−8.6		28.4		0		
		Dinomyidae indet.	4	−8.8	1.3	31.8	1.7	4	23.8	1.4
		Diplasiotherium	2	−10.6	1.2	30.5	0.5	2	21.2	0.3
		Glyptodontidae	2	−9.2	0.3	28.0	0.1	1	18.8	
		Hemihegetotherium	3	−10.1	0.5	29.6	0.8	3	20.6	0.8
		Lagostomus	6	−10.9	1.2	28.7	1.2	2	20.2	1.6
		Macraucheniidae indet.	2	−11.2	3.1	29.6	2.0	1	23.0	
		Macroeuphractus	1	−10.4		28.0		0		
		Paedotherium	7	−9.3	1.0	28.6	1.4	3	19.3	0.8
		Prodolichotis	2	−9.3	1.1	32.1	1.1	1	22.9	
		Promacrauchenia	2	−11.4	0.5	28.4	0.4	1	20.7	
		Proscelidodon	4	−10.8	0.3	28.0	0.8	3	19.4	1.0
		Pseudotypotherium/ Typotheriopsis	7	−10.0	1.1	30.3	1.1	5	22.0	1.1
		Scalabrinitherium	1	−10.3		30.2		0		
		Stenotephanos	3	−10.2	0.3	31.6	0.3	2	21.7	0.3
		Tetrastylus	1	−10.7		28.2		1	20.9	
		*Thylacosmilus**	3	−9.6	0.1	28.6	0.3	0		
Salinas Grandes de Hidalgo	Huayquerian	Toxodontidae indet.	3	−10.3	0.2	29.1	0.9	3	20.2	1.2
		Caviidae indet.	2	−9.2	0.4	29.6	0.3	2	20.7	0.1
		Dinomyidae indet.	1	−9.4		30.0		1	21.0	
		Glyptodontidae indet.	4	−9.0	0.3	27.9	0.4	4	19.0	0.4
		Hemihegetotherium	1	−9.3		28.7		1	20.0	
		Lagostomus	5	−9.2	1.3	28.7	1.1	5	19.6	0.7
		Litopterna indet.	1	−10.0		29.4		1	20.2	
		Macraucheniinae indet.	1	−10.1		29.1		1	20.3	
		Pseudotypotherium	2	−9.3	0.7	28.6	1.8	2	19.6	1.5
Telén	Huayquerian	*Pseudotypotherium/ Typotheriopsis*	6	−9.0	0.4	29.1	0.7	6	20.0	0.7
		Caviidae indet.	3	−10.2	0.5	29.9	1.7	0		
		Glyptodontidae indet.	2	−8.4	0.0	27.1	0.3	2	17.7	0.3
		Lagostomus	6	−9.7	1.0	29.2	2.0	2	20.5	3.0
		Paedotherium	3	−10.3	0.6	28.9	0.8	0		
		Pseudotypotherium/ Typotheriopsis	5	−9.3	0.6	28.9	2.3	5	19.8	1.9
Quehué	Huayquerian	*Thylacosmilus**	4	−10.0	0.3	27.6	0.8	0		
		Cardiatherium	5	−12.7	0.6	24.7	1.2	5	16.0	1.2
		Caviodon	2	−9.0	1.4	30.8	1.7	2	21.7	1.8
		Chasicotherium	5	−10.5	1.7	31.7	1.6	5	22.9	1.6
		Cullinia	6	−10.1	1.4	29.9	1.3	6	21.4	1.3
		Hemihegetotherium	6	−8.8	1.2	30.8	2.5	6	21.8	2.5
		Hemixotodon	5	−7.7	1.6	30.0	1.2	5	21.2	1.2
Arroyo Chasicó	Chasicoan	*Lagostomus*	2	−11.1	0.6	26.7	1.7	2	17.9	1.4

(*continued on next page*)

Table 1 (*continued*)

Locality	Stage/Age	Taxa	# C	Mean δ^{13}C (‰ VPDB)	SD δ^{13}C (‰ VPDB)	Mean $\delta^{18}O_{CO3}$ (‰ VSMOW)	SD $\delta^{18}O_{CO3}$ (‰, VSMOW)	# P	Mean $\delta^{18}O_{PO4}$ (‰ VSMOW)	SD $\delta^{18}O_{PO4}$ (‰ VSMOW)
		*Lycopsis**	2	−10.0	0.2	26.2	0.5	2	17.4	0.7
		Macraucheniidae indet.	1	−9.5		32.8		1	23.8	
		Nothrotheriidae indet.	2	−9.7	1.6	27.6	0.6	2	18.6	0.6
		Paedotherium	5	−8.6	0.5	29.1	0.8	5	20.2	0.9
		Pampatheriidae indet.	1	−10.3		27.6		1	18.5	
		Paratrigodon	4	−10.2	0.3	27.2	1.0	4	18.1	1.1
		Pisanodon	3	−9.3	0.7	28.8	1.7	3	19.7	1.6
		Pseudohegetotherium	2	−8.4	0.6	30.0	1.0	2	21.1	0.6
		Tetrastylus	5	−10.1	1.9	26.5	1.9	5	17.7	1.9
		Theosodon	3	−10.9	2.9	31.1	1.5	3	22.3	1.4
		Typotheriopsis	6	−8.7	0.8	30.7	2.6	6	21.8	2.5
		Caviidae indet.	1	−8.7		29.9		1	20.4	
		Dinomyidae indet.	3	−9.2	1.6	27.2	0.7	3	17.8	1.0
		Hemihegetotherium	4	−8.7	1.1	29.5	2.3	4	20.7	1.8
		Hemixotodon	7	−8.7	1.3	28.5	1.1	7	19.5	1.0
		Lagostomus	2	−10.0	0.3	28.6	0.1	2	19.6	0.0
		Paedotherium	4	−9.0	1.0	29.0	0.6	4	20.1	0.4
	Chasicoan	*Tetrastylus*	1	−8.7		28.6		1	19.4	
Cerro La Bota		*Typotheriopsis*	5	−8.5	1.0	29.0	1.1	5	19.8	1.1

3.3. *Data analyses*

Statistical analyses and niche and trophic modeling were performed with the R software version 4.0.3 (R Core Team, 2019). Prior to statistical analyses, we tested the normal distribution of isotopic data with a Shapiro–Wilk test and two localities do not show a normal distribution (Farola Monte Hermoso and Quehué). For this reason, we used non–parametric analyses (Kruskal-Wallis) for detection of significant differences in mean isotopic values between localities and taxa through time. However, since Holm adjustment does not seem to be indicated if the degree freedom is equal to or more than five and we have several groups with df ≥ 5 (Kim, 2015), we had to use the Kruskal–Wallis and Tukey-Kramer Honest Significant Difference post–hoc analysis. In order to observe temporal changes of δ^{13}C and $\delta^{18}O_{CO3}$, we grouped our localities by stages/ages (Chasicoan, Huayquerian, latest Huayquerian, and Montehermosan) and performed non–parametric analyses (Kruskal–Wallis and post-hoc analysis with the Holm correction, since the degree freedom is equal to 3). We have also used statistical analysis to look for significant differences in δ^{13}C and $\delta^{18}O_{CO3}$ values grouped by orders: Litopterna, Notoungulata and Rodentia. For this, we performed non–parametric analyses (Kruskal–Wallis and Tukey-Kramer Honest Significant Difference post–hoc analysis). The significance level was set at $p = 0.05$ in all cases.

Bayesian stable isotope ellipses in R (SIBER, Jackson et al., 2011) were used to estimate the isotopic niches of the analyzed taxa. An isotopic niche is an area or volume (δ–space), whose coordinates are isotope values (δ–values), so it is necessary to use at least two isotopic systems to delimitate a 2D δ–space (δ^{13}C and δ^{18}O, in this study). We calculated the isotopic niches for each taxon based on an ellipse of 1 SD centered on the mean, containing roughly 40% of the data in those localities with three or more taxa where each taxon has a good sampling record ($n \geq 3$). These analyses allowed us to evaluate the superposition and trophic relationships between taxa in the same locality.

In order to assess resource preferences for the sampled sparassodonts, we performed parametric analyses (t-Student test) to test for differences in the mean of δ^{13}C values corrected for trophic discrimination among carnivorous - potential prey pairs, since Shapiro-Wilk tests revealed normal distributions. Evaluating the degree of δ^{13}C overlap, it is possible to detect most feasible prey (resource) options (Feranec et al., 2010). We do not include in this work an evaluation of predator-prey relationships with the R package MixSIAR (Stock and Semmens, 2016) due to a combination of three factors: i) we have only one isotopic system, ii) the number of prey is greater than three, and iii) it is not possible to group prey a priori into statistically different δ^{13}C groups.

4. Results and discussion

4.1. *U–Pb dating*

At Arroyo Chasicó (119 detrital zircons analyzed), Telén (116 detrital zircons analyzed), and Monte Hermoso (115 detrital zircons analyzed) localities, the Minimun Likehood Age (MLA) model provided maximum depositional ages for the analyzed siltstones/sandy siltstones samples of 9.7 ± 0.3 Ma, 6.3 ± 0.2 Ma, and 4.5 ± 0.2 Ma, respectively (Table 2). In regard to Quehué (114 detrital zircon analyzed) and Caleufú (100 detrital zircons analyzed) localities, the MLA calculated age was discarded for being too old (67.0 ± 1.1 Ma and 67.5 ± 1.1 Ma, respectively). At Salinas Grandes de Hidalgo (106 detrital zircons analyzed), the MLA calculate age was 8.2 ± 0.5 Ma, considered old based on the characteristics of the recovered faunistic assemblage (Verzi and Montalvo, 2008; Sostillo et al., 2021; Piñero et al., 2021. At Quehué a single zircon crystal was dated at 7.1 ± 0.6 Ma [with a concordance of a 96% on the relationship (^{206}Pb/^{238}U) / (^{207}Pb/^{235}U)], at Salinas Grandes de Hidalgo was 5.9 ± 0.4 [84% (^{206}Pb/^{238}U) / (^{207}Pb/^{235}U)], and at Caleufú was of 4.7 ± 0.5 Ma [86% (^{206}Pb/^{238}U) / (^{207}Pb/^{235}U)] (Table 2). These three younger single grain ages (YSG) fit the well–established biostratigraphic data of these localities (Verzi and Montalvo, 2008; Sostillo et al., 2021; Piñero et al., 2021). Accordingly, they could be considered as the maximum deposition ages for the Cerro Azul Formation in these three localities. The scarcity of young Neogene detrital zircons measured (SM2) could be related to i) low input from younger rock sources; ii) low uranium content of younger detrital zircons; and/or iii) low concentration of lead due to a short time for uranium radioactive decaying.

These new ages allow us to test previous biostratigraphic schemes based on rodents and other mammals present in each assemblage (Verzi et al., 2008; Tomassini et al., 2013; Sostillo et al., 2021; Piñero et al., 2021). The value obtained for Arroyo Chasicó supports the assignment of their assemblage to the Late Miocene, as Chasicoan Stage/Age. The fossil assemblages of the youngest localities, Caleufú and Farola Monte Hermoso, were previously assigned to the Early Pliocene, as latest Huayquerian and Montehermosan stages/ages respectively (Tomassini et al., 2013; Piñero et al., 2021), which agrees with the ages obtained herein. The other ages correspond to the Late Miocene, Huayquerian Stage/Age, and suggest the following temporal sequence, from the oldest to the youngest locality: Quehué, Telén, and Salinas Grandes de

Table 2
Maximum depositional U–Pb ages from detrital zircons obtained from Cerro Azul (Late Miocene/Early Pliocene) and Monte Hermoso (Early Pliocene) formations. The age we consider valid at each locality is marked in bold.

Sample number (LA.TE.Andes Laboratory)	C846	C710	C711	C585	C731	C744
Locality name	Arroyo Chasicó	Quehué	**Telén**	Salinas Grandes de Hidalgo	Caleufú	Farola Monte Hermoso
Maximun Likehood Age (MLA) model *	**9.7 ± 0.3 Ma**	66.96 ± 2.0 Ma**	**6.3 ± 0.2 Ma**	8.2 ± 0.5 Ma***	67.52 ± 2.0 Ma**	**4.5 ± 0.2 Ma**
Younger Single Grain *	–	**7.1 ± 0.6 Ma**	6.4 ± 0.5 Ma	**5.9 ± 0.4 Ma**	**4.7 ± 0.5 Ma**	–
	10.1–9.4 Ma	7.7–6.5 Ma	6.5–6.1 M	6.3–5.5 Ma	5.2–4.2 Ma	4.7–4–3 Ma
Time interval	Late Miocene	Late Miocene	Late Miocene	Late Miocene	Early Pliocene	Early Pliocene
	Tortonian	Messinian	Messinian	Messinian	Zanclean	Zanclean
Stage/Age	Chasicoan	Huayquerian	Huayquerian	Huayquerian	Huayquerian	Montehermosan

[*] A 100 ± 10% cut–off based on ^{206}Pb /^{238}U vs ^{207}Pb /^{235}U.
[**] MLA calculated age discarded for being too old.
[***] MLA calculated age is old in relation with the biochronological and faunistic assemblage from Salinas Grandes de Hidalgo.

Hidalgo. This sequence inverts, therefore, the relative order proposed in previous biostratigraphic schemes for Telén and Quehué (see Sostillo et al., 2014; Piñero et al., 2021); however, this situation does not cause controversy since both locations share the same species of the rodents *Reigechimys* (*R. plesiodon*), *Metacaremys* (*M. calfulcalel*), and *Neophanomys* (*N. pristinus*), showing a clear temporal correlation. On the other hand, although both localities share with Salinas Grandes de Hidalgo the species of *Metacaremys* (*M. calfucalel*), the assemblage of the latter locality includes a species of *Reigechimys* (*R. octodontiformis*) with more advanced characters than the one found in Quehué and Telén

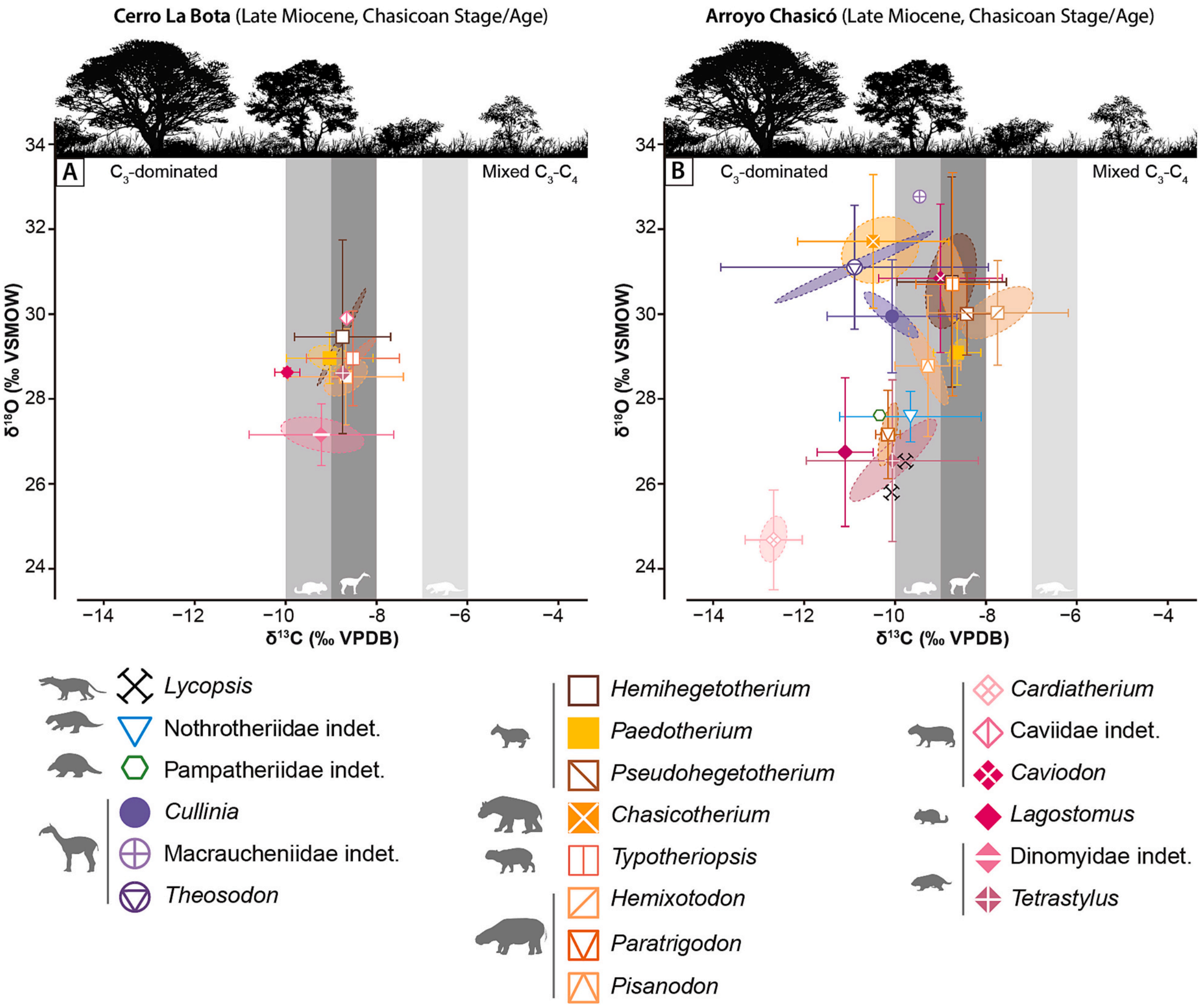

Fig. 2. Mean ± 1 standard deviation δ^{18}O (‰ VSMOW) and δ^{13}C (‰ VPDB) values for different mammals from localities with assemblages assigned to the Chasicoan Stage/Age. A) Cerro La Bota and B) Arroyo Chasicó. The gray bars represent the vegetation δ^{13}C cut–off values between a C_3–dominated diet and an intermediate C_3–C_4 diet. The darkest gray denotes a δ^{13}C bioapatite–diet enrichment of +14.1‰ for notoungulates and litopterns (Cerling and Harris, 1999), the intermediate one indicates an enrichment of +12.8‰ for rodents (Passey et al., 2005), and the lightest gray corresponds to an enrichment of +15.6‰ for xenarthrans (Tejada–Lara et al., 2018). Sparassodonta δ^{13}C values have been corrected for the trophic offset, adding 1.3‰ to the raw values (Fox–Dobbs et al., 2006; Clementz et al., 2009). The number of samples of each taxon is shown in Table 1.

(*R. plesiodon*) (see Sostillo et al., 2014), which agrees with the temporal ordering interpreted from the new dating.

Finally, Cerro La Bota and Bajo Giuliani localities, also included in the present study but without numerical dating, have Late Miocene faunal assemblages. Cerro La Bota assemblage was assigned to the Chasicoan Stage/Age (Montalvo et al., 2019), possibly rather older than Arroyo Chasicó (see Piñero et al., 2021), while Bajo Giuliani assemblage was assigned to the Huayquerian Stage/Age, possibly located between Salinas Grandes de Hidalgo and Caleufú (see Piñero et al., 2021).

4.2. Paleoecological inferences through the GABI

In the entire sample evaluated in this study, $\delta^{13}C_{CO3}$ values of the herbivores show a wide range from −14.2 to −3.5‰, indicating the taxa consumed food items from different environments, from woodland to mixed C_3–C_4 grassland. Oxygen values ($\delta^{18}O_{CO3}$) of the whole dataset also show a wide variation of 23.6 to 35.4‰, reflecting differences in the $\delta^{18}O$ values of meteoric and plant water among the different taxa and time periods studied.

4.2.1. Late Miocene – Chasicoan Stage/Age

In Arroyo Chasicó, type locality of Chasicoan Stage/Age, the rodents *Cardiatherium* (Hydrochoerinae) and *Lagostomus* (Chinchillidae), the notoungulates *Paratrigodon* (Toxodontidae) and *Chasicotherium* (Homalodotheriidae), the cingulate pampatherids, and the litopterns macrauchenid *Cullinia*, *Theosodon*, and Macraucheniidae indet. Show $\delta^{13}C$ values indicative of the consumption of plants from woodland and wooded C_3 grassland, while the $\delta^{13}C$ values of the rest of notoungulates (including different representatives of Toxodontidae, Mesotheriidae, and Hegetotheriidae) and the rodent caviid *Caviodon* suggest a diet based on more xeric C_3 environments (Fig. 2, Table 1, SM3).

The statistical analysis shows significant differences ($\chi^2 = 26.350$, $p = 0.003$, SM4) between the extinct capybara *Cardiatherium* and the notoungulates *Hemihegetotherium* and *Paedotherium* (Hegetotheriidae), *Typotheriopsis* (Mesotheriidae), and *Hemixotodon* (Toxodontidae), with the latter having diets from more open environments. Corriale and Loponte (2015) observed in Northeastern Argentina a high variability in bone isotopic values in extant capybaras (*Hydrochoerus hydrochaeris*), between diets based on C_3 and C_4 plants. Despite the high isotopic variability, the data show a trend towards higher consumption of C_3 versus C_4 plants regardless of resource availability. The authors relate this preference to the better nutritional value of C_3 plants (higher carbohydrate and protein content and lower fiber and silica content; Corriale and Loponte, 2015 and references therein). This result may explain the low $\delta^{13}C$ values of the *Cardiatherium* observed at Arroyo Chasicó. These low values may also be related to the consumption of aquatic plants, having isotopic values similar to C_3 plants. *Cardiatherium* may have had a semi–aquatic habit, inhabiting areas with water bodies, and may have included aquatic plants in their diet, as it occurs with extant capybaras (Barreto and Quintana, 2013; Felix et al., 2014).

Arroyo Chasicó's $\delta^{18}O_{CO3}$ values show two groups (Fig. 2) and the difference between the taxa in this locality is also statistically significant ($\chi^2 = 34.088$, $p < 0.001$, SM4), pointing to ingestion of water subject to different hydrological conditions. The first group, with higher values, includes all the litopterns, almost all the notoungulates (except the toxodontids *Paratrigodon* and *Pisanodon*) and the rodent *Caviodon* (this taxon, as well as Macraucheniidae indet., could not be included in the statistical analyses as it had less than 3 samples).

The second group includes the rest of the rodents caviid, chinchillid, and dinomyid (*Cardiatherium*, *Lagostomus*, and *Tetrastylus* respectively), toxodontid *Paratrigodon*, pilosan Nothotheriidae indet., and cingulate pampatheriids (Fig. 2). In the case of *Cardiatherium*, its $\delta^{13}C$ values could suggest it had a semi-aquatic habit, and observing its $\delta^{18}O$ values we observe it has less variability than the rest of the taxa. According to Clementz and Koch (2001), the variability of mammalian oxygen values is much higher in terrestrial than in aquatic environments, supporting the hypothesis of a semi-aquatic habit for this rodent. The values of the toxodontid *Pisanodon*, intermediate between both groups, do not show significant differences with any taxon. Trayler et al. (2020) show large notoungulates would need to drink water daily to cover their physiological needs, like many other large mammals (e.g., perissodactyls). Since it has been proposed litopterns are related to extant perissodactyls (Buckley, 2015; Welker et al., 2015), we assume here their representatives would also be obligate drinkers and they obtained most of their water through drinking. Following Lopes et al. (2013) and Dantas et al. (2020) we tested the relationship between $\delta^{13}C$ and $\delta^{18}O$ in the families of both orders (Litopterna and Notoungulata) to determine if the plants they consume control the isotopic composition of their body water (non-obligate drinkers). There is no statistically significant relationship between $\delta^{13}C$ and $\delta^{18}O$ values (SM5). This lack of significant differences would suggest these taxa were obligate drinkers, and therefore their tooth enamel $\delta^{18}O$ values would be mainly influenced by the oxygen isotope composition of drinking water.

In contrast, rodents probably obtained most of the water they needed through eating and did not need to ingest free water. The uptake of water through food items coincides with the behavior observed in modern species [i.e., mara (*Dolichotis patagonum*), capybara (*Hydrochoeris hydrochaeris*), plains vizcacha (*Lagostomus maximus*); Borges et al., 1996; Cortés et al., 2003; Hagen et al., 2015; Clauss et al., 2019]. Litopterns and notoungulates would drink water from sources with similar evaporation rates, except *Paratrigodon* (Toxodontidae), showing lower $\delta^{18}O$ values as also observed in the xenarthrans Pampatheriidae indet. and Notrotheriidae indet. These three latter taxa would have obtained water from sources that suffered less evaporation.

In any case, more precise interpretations cannot be made since most of the taxa analyzed in this interval and the subsequent ones (see below) do not have current representatives to compare. As far as rodents are concerned, the isotopic values suggest the caviid *Caviodon* fed on plants that underwent more evaporation than the vegetation consumed by the other rodents (Fig. 2). Rasia (2016) indicates all the fossil species of the plains vizcacha *Lagostomus* would have had a diet based on grasses and low vegetation as they share similar dental characteristics with the living species (*Lagostomus maximus*).

In Cerro la Bota, the $\delta^{13}C$ – $\delta^{18}O$ ellipses show an intense overlap (Fig. 2) and statistical analysis reported no significant differences (SM4). This result indicates similar diets and water sources subject to similar evaporation conditions, which would suggest a homogeneous environment. The herbivores from this locality show $\delta^{13}C$ values of diets based on vegetation from open C_3 woodland/xeric C_3 grassland environments. As the taxa analyzed at this locality are the same as in Arroyo Chasicó, the same ecological behavior of the taxa is inferred from non-isotopic studies (see references above).

The notoungulates (both the hegetotherids *Paedotherium* and *Hemihegetotherium*, and the mesotherid *Typotheriospsis*) also fed on leaves of low–growing plants in open habitats (Croft, 2006). The species present in Chasicoan assemblages, *Paedotherium minor*, has dental characteristics that suggest a more abrasive diet, compared to other species of *Paedotherium*, due to feeding in open grasslands more widely in this region (Reguero et al., 2015). *Paedotherium* isotopic values (−9.0 ± 1.0‰) are indicative of open grassland-based diets and the values of the toxodontid *Hemixotodon* (−8.7 ± 1.3‰) also suggest feeding on low vegetation, like the rest of rodents (e.g., Caviidae indet., Dinomyidae indet. and *Tetrastylus,* and the Chinchillidae *Lagostomus*), being congruent with non-isotopic studies. No statistical differences are observed between the taxa from Arroyo Chasicó and Cerro la Bota (Table 1 and Fig. 2), and similar diets are inferred for the taxa from both localities. Regarding $\delta^{18}O$ values, notoungulates and rodents would obtain water from water sources (drinking or feeding) subject to similar evaporation rates.

4.2.2. Late Miocene/Early Pliocene – Huayquerian Stage/Age

This is the best–represented time period of the dataset, including five localities: Quehué, Telén, Salinas Grandes de Hidalgo, Bajo Giuliani (Late Miocene), and Caleufú (Early Pliocene) (Table 2). The range of average bioapatite $\delta^{13}C$ values oscillates between C_3–dominated diets in the Late Miocene and an increase of species with more mixed C_3–C_4 diet in the Early Pliocene (Fig. 3, Table 1).

In Quehué, Telén, and Bajo Giuliani the $\delta^{13}C$ values of the mammals analyzed point to an overall C_3–dominated diet (Fig. 3, Table 1). The chinchillid *Lagostomus*, in the three localities, shows a wide dietary range from open woodland to some samples that point to a preference for mixed C_3–C_4 grassland vegetation. Nevertheless, the rest of the rodents (caviids and dinomyids), representatives of the notoungulates Hegetotheriidae (*Paedotherium* and *Hemihegetotherium*) and Mesotheriidae (*Pseudotypotherium* and *Pseudotypotherium/Typotheriopsis*), glyptodontids, Litopterna indet. and Macraucheniidae indet. show a preference for diets based on vegetation of open C_3 grassland (Fig. 3). No statistical differences were found in any of the localities (SM4): Quehué ($\chi^2 = 5.1156$, $p = 0.276$) and Telén ($\chi^2 = 0.384$, $p = 0.826$). Statistical analyses could not be performed in the case of Bajo Giuliani since more than three samples are only available for *Lagostomus*. All these localities show a narrow range of variation of $\delta^{18}O_{CO3}$ values (Fig. 3). In addition, there are no statistical differences among the taxa from each locality (SM4): Quehué ($\chi^2 = 4.5455$, $p = 0.337$) and Telén ($\chi^2 = 5.336$, $p = 0.069$). The results suggest the water ingested by the taxa (either, obligate and non-obligate drinkers) may have had similar $\delta^{18}O$ values.

Salinas Grandes de Hidalgo's $\delta^{13}C$ values are indicative of C_3–dominated diets, but some samples of the rodents Dinomyidae indet. and *Prodolichotis* (Caviidae) and notoungulate mesotherid *Pseudotypotherium/Typotheriopsis* surpass the vegetation $\delta^{13}C$ threshold value between a C_3–dominated diet and a mixed C_3–C_4 diet. The pilosan mylodontid *Proscelidodon*, the cingulate chlamyphorid *Macroeuphractus*, litopterns *Brachytherium* and *Diplasiotherium* (Proterotheriidae), and *Promacrauchenia*, *Scalabrinitherium*, and Macraucheniidae indet. (Macraucheniidae), and the rodent chinchillid *Lagostomus* suggest a preference for C_3 plants from an open woodland.

Finally, the $\delta^{13}C$ values of the notoungulates (including different representatives of Hegetotheriidae, Mesotheriidae, and Toxodontidae), the rodent caviid *Cardiomys*, and the rest of cingulates (Dasypodidae indet. and Glyptodontidae indet.) indicate these taxa fed on C_3 plants from more open environments. Macraucheniidae indet. showed a wide isotopic range, from more wooded to open areas, probably due to the inclusion of samples from different macraucheniid genera. Significant differences were observed in this locality ($\chi^2 = 15.479$, $p = 0.050$, SM4) between the rodents *Lagostomus* (with lower $\delta^{13}C$ values) and Dinomyidae indet. (with higher $\delta^{13}C$ values) (SM4), supporting a difference in the diet of these rodents (Fig. 3).

The notoungulate toxodontid *Sthenophanus*, rodent caviid *Prodolichotis,* Dinomyidae indet., and litoptern proterotherid *Brachytherium* showed higher $\delta^{18}O_{CO3}$ values than the rest of the mammals evaluated, which may point to ingestion of water sources subject to a higher evaporation rate. This hypothesis is supported by the statistical analysis ($\chi^2 = 23.401$, $p = 0.003$, SM4) since significant differences were observed between the notoungulates *Sthenophanus* (Toxodontidae), and *Paedotherium* (Hegetoteriidae), the rodents Dinomyidae indet. and *Lagostomus*, and the pilosan mylodontid *Proscelidodon*. The caviid *Cardiomys* shows the lowest $\delta^{18}O_{CO3}$ values in the assemblage (Table 1), but could not be included in the statistical analysis due to lack of samples.

The $\delta^{13}C$ values of the Caleufú herbivores (Table 1) point to a preference for intermediate C_3–C_4 diets, and the statistical analysis did not show significant differences among them ($\chi^2 = 1.3511$, $p = 0.853$, SM4). The $\delta^{13}C$ range of the rodents Caviidae indet. and Dinomyidae *Tetrastylus* was wider than in the older Huayquerian localities. Hynek et al. (2012) reported rodent tooth enamel carbon values that point to C_4 plant consumption for the Early Pliocene of Northwestern Argentina, supporting the results of this work. In the case of the rodent Caviidae indet. its wide isotopic range (Fig. 3) could be due to the fact that it might include representatives of different genera. Regarding the notoungulates, including representatives of Hegetotheriidae (*Paedotherium*) and Mesotheriidae (*Pseudotypotherium* and *Pseudotypotherium/Typotheriopsis*), they also show a wider $\delta^{13}C$ range than older localities including C_3–dominated and C_3–C_4 diets (Fig. 3). Statistical analyses report significant differences when comparing the assemblage of Caleufú assigned to the latest Huayquerian Stage/Age with the other ancient assemblages assigned to the Huayquerian Stage/Age (Table 3). Isotopic and statistical results suggest a change in the diets and resource preference for the assemblage corresponding to the latest Huayquerian Stage/Age, when C_4 plants expanded in South America (Strömberg, 2011).

As far as Caleufú's $\delta^{18}O_{CO3}$ values are concerned, significant differences were observed between the notoungulate mesotherid *Pseudotypotherium/Typotheriopsis* and the rodent Caviidae indet. (SM4). However, it is not clear whether these notoungulates were obligate drinkers or not. As mentioned above, large notoungulates, such as toxodontids, most likely needed to drink to supply their physiological needs (Trayler et al., 2020), but small–medium notoungulates may have been non–obligate drinkers. The lack of extant representatives does not allow further interpretations.

In Caleufú, mesotherids showed the highest $\delta^{18}O_{CO3}$ values, for this reason, we can infer they obtained water from sources subject to higher evaporation (water bodies or by the consumption of leaves). Regarding Caviidae indet., these rodents show adaptations to avoid dependence on free water supplies for their needs. The wide $\delta^{18}O$ range of this taxon and of the dinomyid *Tetrastylus* could suggest access to a wide variety of water sources (e.g. vegetation and surface water). It should be noted the mesotherid *Pseudotypotherium* and the chinchillid *Lagostomus* could not be included in the statistical analysis due to lack of samples. The two taxa of mesotheriids (*Pseudotypotherium/Typotheriopsis* and *Pseudotypotherium*) showed higher $\delta^{18}O_{CO3}$ values than rodents (Fig. 3, Table 1), supporting the hypothesis the notungulate water source (probably free water) at Caleufú was subject to greater evaporation than the rodent source (vegetation and surface water).

The assemblages from all these localities, assigned to the Huayquerian Stage/Age, share some taxa with the assemblages assigned to the Chasicoan Stage/Age [i.e. rodents *Lagostomus* (Chinchillidae) and *Tetrastylus* (Dinomyidae), and notoungulates *Hemihegetotherium* and *Paedotherium* (Hegetotheriidae)]. This point allows extrapolating the paleoecological interpretations proposed in the previous subsection to these more modern records. During most part of the Huayquerian Stage/Age the rodents showed diets of open C_3 environments, with some representatives with mixed C_3–C_4 diet values, while the notoungulates only showed a preference for vegetation of open C_3 environments (Figs. 2 and 3). However, a shift to diets based on vegetation mixed C_3–C_4 grasslands vegetation was detected in the latest Huayquerian Stage/Age (Early Pliocene, Caleufú locality). Hence, during ca. 3 Ma (between ~7.7 to 4.7 Ma), no major changes in the diet of these taxa are observed and 4.7 ± 0.5 Ma ago an increase of C_4 plants in their diets is recorded, possibly related to the global expansion of C_4 plants (Cerling et al., 1997; Strömberg, 2011; Domingo et al., 2020). Rodents were more variable regarding the oxygen isotope composition than for carbon values, probably due to the fact they were not obligate drinkers. No major differences were observed in the notoungulate $\delta^{18}O_{CO3}$ values between the Chasicoan and Huayquerian stages/ages pointing to stable conditions in the hydrological cycle, at least as far as $\delta^{18}O$ values of water sources are concerned (Table 1, Fig. 2–3).

4.2.3. *Early Pliocene – Montehermosan Stage/Age*

In this section we analyzed the data from Farola Monte Hermoso locality, the type locality of Montehermosan Stage/Age. The average $\delta^{13}C$ value was −8.1 ± 2.2‰, with a minimum value of −12.5‰ for a sample of the rodent chinchillid *Lagostomus* and a maximum of −3.5‰ for a sample of notoungulate toxodontid *Xotodon* (SM3). Fig. 4 shows only litopterns (*Eoachenia*, *Epitherium*, and *Promacrauchenia*) tooth enamel $\delta^{13}C$ values point to a preference for C_3–dominated diets. The

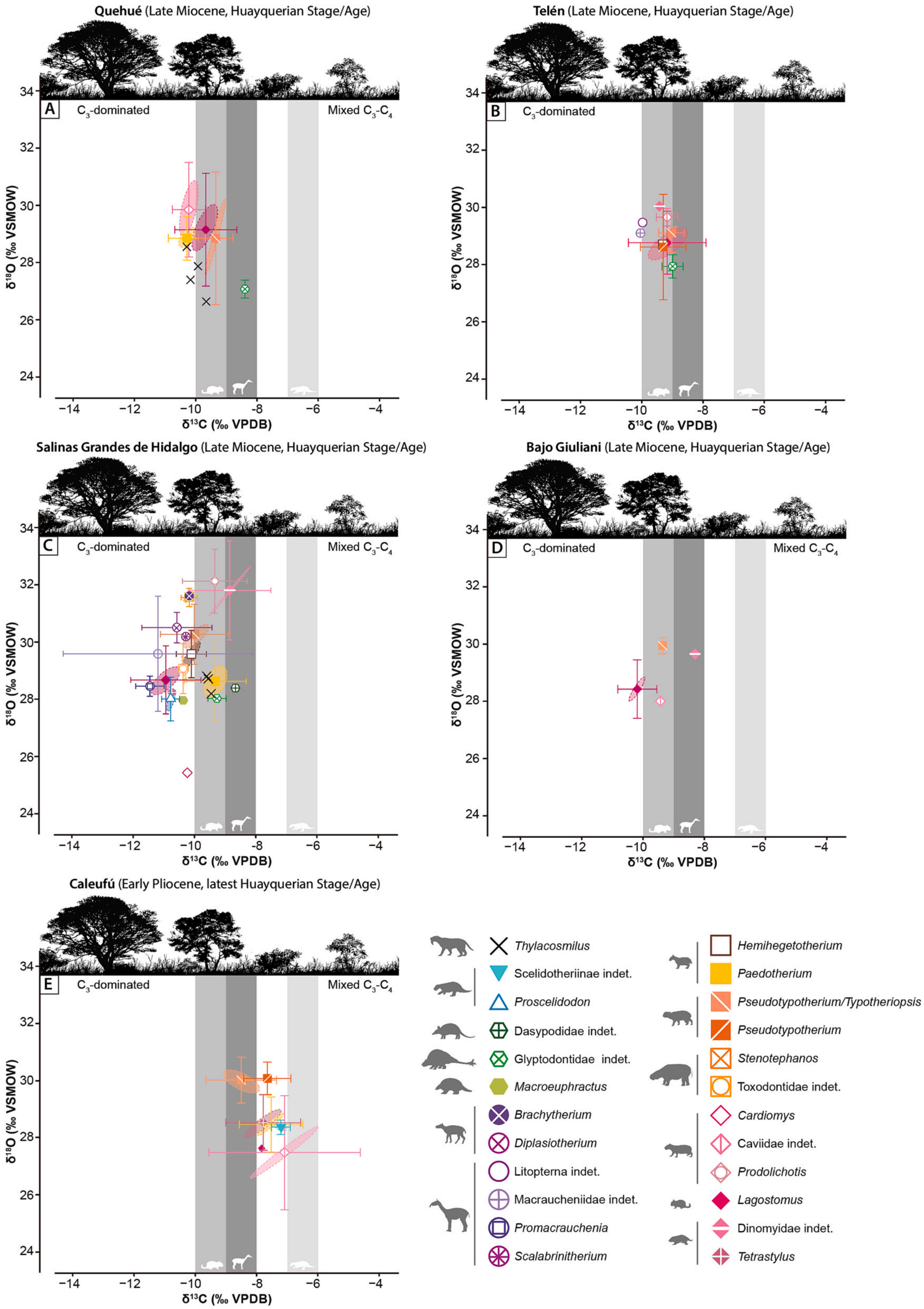

Fig. 3. Mean ± 1 standard deviation $\delta^{18}O$ (‰ VSMOW) and $\delta^{13}C$ (‰ VPDB) values for different mammals from the localities with assemblages assigned to the Huayquerian Stage/Age. A) Quehué, B) Telén, C) Salinas Gandes de Hidalgo, D) Bajo Giuliani, E) Caleufú. The gray bars represent the vegetation $\delta^{13}C$ cut–off values between a C_3–dominated diet and an intermediate C_3–C_4 diet. The darkest gray denotes a $\delta^{13}C$ bioapatite–diet enrichment of +14.1‰ for notoungulates and litopterns (Cerling and Harris, 1999), the intermediate one indicates an enrichment of +12.8‰ for rodents (Passey et al., 2005), and the lightest gray corresponds to an enrichment of +15.6‰ for xenarthrans (Tejada–Lara et al., 2018). Sparassodonta $\delta^{13}C$ values have been corrected for the trophic offset, adding 1.3‰ to the raw values (Fox–Dobbs et al., 2006; Clementz et al., 2009). The number of samples of each taxon is shown in Table 1.

Table 3
Mann–Whitney post–hoc analysis with the Holm correction comparing the δ^{13}C values (‰ VPDB) among the different studied Stages/Ages. Pairs with significant differences ($p < 0.05$) are shown in bold.

δ^{13}Cvalues ($\chi^2 = 51.768$, df = 3, $p < 0.001$)	Huayquerian	latest Huayquerian	Montehermosan
Chasicoan	**0.030**	**<0.001**	**0.009**
Huayquerian		**<0.001**	**<0.001**
latest Huayquerian			0.178

δ^{13}C range of the rest of the analyzed taxa are indicative of the incorporation of C_4 resources, placing them between a C_3–dominated diet and a mixed C_3–C_4 diet, except the toxodontid *Xotodon*, caviid *Caviodon*, and xenarthran Pilosa indet., which adopted an exclusive intermediate C_3–C_4 diet (Fig. 4, Table 1).

In the case of the extinct capybara *Phugatherium*, and the extinct genus *Cardiatherium* from the Chasicoan Stage/Age (see above), they may have had a similar habit to the extant *Hydrochoerus hydrochaeris*. Both taxa might use plant resources from water bodies (Felix et al., 2014) and feed in semiaquatic freshwater grasses, having isotopic values similar to terrestrial C_3 plants (Tütken, 2011). This semiaquatic habit partly agrees with the wide range of δ^{13}C values obtained at Farola Montehermoso (Fig. 4), reflecting a diet based on aquatic plants, but also on C_3–C_4 grassland vegetation. Significant differences were, however, not found when comparing δ^{13}C values among taxa from Farola Monte Hermoso ($\chi^2 = 9.095$, $p = 0.105$, SM4). This result may be due to: i) the low number of samples ($n < 3$) of the taxa with diets at the extremes of the vegetation spectrum (pure C_3 and mixed C_3–C_4 diets: *Epitherium*, *Eoauchenia*, and Pilosa indet., Fig. 4), and/or ii) chinchillid *Lagostomus*, hydrochoerine *Phugatherium*, and toxodontid *Xotodon* having a very wide isotopic range.

As in the case of the assemblages assigned to the Chasicoan and Huayquerian stages/ages, we assume large litopterns and large notoungulates would need to drink water to cover their physiological needs, while rodents probably obtained most of their water from food. Small–medium notoungulates' water requirement could be closely covered by their diet. Regarding the oxygen isotope composition, a minimum δ^{18}O value of 24‰ was recorded by the extinct capybara *Phugatherium* sample (non–obligated drinker), whereas a maximum δ^{18}O value of 32.8‰ corresponded to a sample of the mesotherid *Pseudotypotherium* (probably an obligated drinker) (SM3). Statistical analyses showed significant differences between these taxa ($\chi^2 = 22.766$, $p < 0.001$, SM4). The low values of *Phugatherium* in comparison with the other rodents could be explained by a semi–aquatic habit (see references in Vucetich et al., 2013). According to Clementz et al. (2008), semi-aquatic animals have generally lower δ^{18}O average values in contrast to terrestrial mammals. However, it is important to remark the wide range of δ^{18}O (also δ^{13}C) in the rodents *Lagostomus* and *Phugatherium*, which may point to a consumption of a large variety of resources. The toxodontid *Xotodon* and the mesotherid *Pseudotypotherium* δ^{18}O values overlap, pointing to ingestion of water subjected to similar evaporation conditions. Nevertheless, the hegetotheriid *Paedotherium* showed lower δ^{18}O values, similar to those of the pilosan mylodontid *Proscelidodon*, and possibly related to water sources subject to less evaporation. Fig. 4 shows some differences between the litoptern δ^{18}O values, possibly indicating a certain distribution of water resources, since *Epitherium* and *Promacrauchenia* would ingest water subject to conditions more like those of the hegetoteriid *Paedotherium* and the mylodontid *Proscelidodon*.

There were no significant differences in the δ^{13}C values of the fauna from Farola Monte Hermoso assigned to the Montehermoso Stage/Age (4.5 ± 0.2 Ma) when compared to that of the latest Huayquerian Stage/Age (4.7 ± 0.5 Ma) from Caleufú (Table 3). However, when comparing with older assemblages assigned to the Huayquerian Stage/Age, statistical analyses showed significant differences in δ^{13}C values with the assemblages assigned to the Montehermosan (Table 3) and, as mentioned before, latest Huayquerian (Table 3) stages/ages. A higher consumption of C_4 plants can be observed in the two Early Pliocene localities (Caleufú and Farola Monte Hermoso) by those taxa also

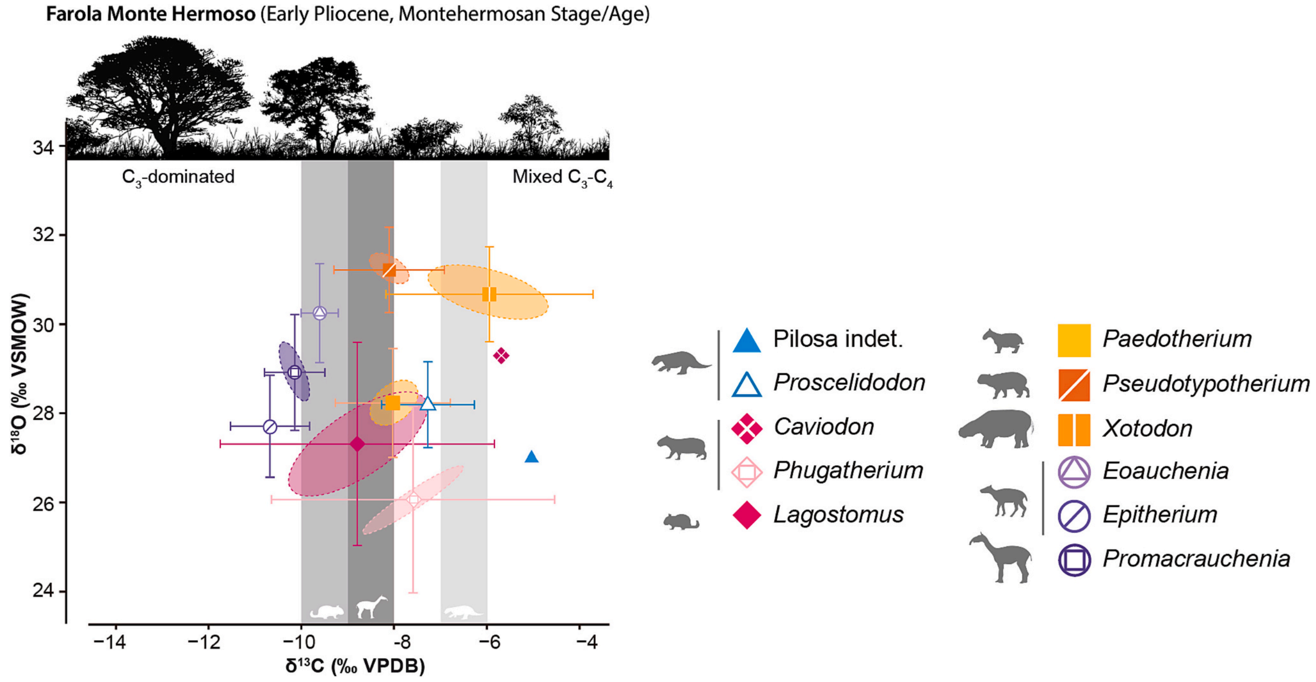

Fig. 4. Mean ± 1 standard deviation δ^{18}O (‰ VSMOW) and δ^{13}C (‰ VPDB) values for different mammals from the locality of Farola Monte Hermoso, which has an assemblage assigned to the Montehermosan Stage/Age. The gray bars represent the vegetation δ^{13}C cut–off values between a C_3–dominated diet and an intermediate C_3–C_4 diet. The darkest gray denotes a δ^{13}C bioapatite–diet enrichment of +14.1‰ for notoungulates and litopterns (Cerling and Harris, 1999), the intermediate one indicates an enrichment of +12.8‰ for rodents (Passey et al., 2005), and the lightest gray corresponds to an enrichment of +15.6‰ for xenarthrans (Tejada–Lara et al., 2018). The number of samples of each taxon is shown in Table 1.

recorded in many of the older localities, such as the hegetotheriid *Paedotherium* and the chinchillid *Lagostomus*. Tooth enamel δ^{13}C values of the litoptern *Promacrauchenia*, also recorded at Salinas Grandes de Hidalgo (5.9 ± 0.4 Ma), point to a preference for C_3–dominated in both localities but records higher δ^{13}C values at Farola Monte Hermoso, indicative of vegetation from more open environments. Therefore, throughout the analyzed temporal sequence spanning between the Late Miocene and the Early Pliocene, there is a trend towards the incorporation of a higher percentage of C_4 plants in the diet of many of the analyzed taxa (or towards the consumption of C_3 plants from more open areas). This result is directly related to an increase in aridity and global development of more open areas where C_4 plants thrived since the beginning of the Pliocene (Cerling et al., 1997; Rabassa et al., 2005; Strömberg, 2011).

4.3. Predator–prey interactions

The carnivorous guild is represented herein by metatherians of the order Sparassodonta and includes the genera Stock et al. (2018) *Lycopsis* from the Chasicoan Stage/Age of Arroyo Chasicó, and *Thylacosmilus* from the Huayquerian Stage/Age of Salinas Grandes de Hidalgo and Quehué. The first records of the order Carnivora in South America were represented by specimens of Procyonidae found at Salinas Grandes de Hidalgo, Telén, and Quehué (Montalvo et al., 1998, 2008; Vizcaíno and Farina, 1999), although they have not been sampled in this work due to its scarcity in the fossil record.

Sparassodonta has a wide range of body masses (Tarquini et al., 2022). *Lycopsis*, a fox–like form, had an estimated mass of 11–18 kg (Ercoli and Prevosti, 2011; Prevosti et al., 2013; Suárez et al., 2015), while the Thylacosmilidae *Thylacosmilus*, a sabertooth–like form, had a 41 kg estimated body mass (Suárez, 2019; but also see Vizcaíno et al., 2004; Ercoli and Prevosti, 2011). Overall, their δ^{13}C data point to a consumption of prey from C_3 open areas (Figs. 2 and 3, Table 1).

Of late, Bayesian mixing models have been widely used to investigate trophic interactions in modern and ancient ecosystems based on isotopic data (e.g., Phillips and Gregg, 2003; Moore and Semmens, 2008; Parnell et al., 2010; Phillips et al., 2014; Stock et al., 2018). MixSIAR is a robust and widely- used Bayesian mixing model described by Stock et al. (2018) and we have employed it in previous studies (Domingo et al., 2020; Sanz-Pérez et al., 2020). However, one major limitation pointed out by Stock et al. (2018) is that the MixSIAR model finds it difficult to determine the most probable sources (prey) to a mixture (predator) when there are more than 7 sources for 2 isotopic systems. In our current case, we have one isotopic system directly routed by the dietary intake (δ^{13}C) and 5, 7 and 13 potential prey at Quehué, Arroyo Chasicó and Salinas Grandes de Hidalgo localities, respectively. Stock et al. (2018) suggested combining sources either a priori or a posteriori to overcome the model limitation due to an excess in the prey number. A priori combination could be done if prey lumped in groups with significant differences in the selected isotopic system. In our study, we cannot adopt this option as probable prey do not separate in statistically different groups. Therefore, we opted to discard the use of MixSIAR here and survey potential trophic interactions by i) graphically assessing the position of tooth enamel δ^{13}C values in the case of *Lycopsis* from Arroyo Chasicó or ii) statistically comparing δ^{13}C values of predator-prey pairs in the case of *Thylacosmilus* from Salinas Grandes de Hidalgo and Quehué.

At present, the only species of the genus *Lycopsis* recorded in Arroyo Chasicó is L. *viverensis* (Forasiepi et al., 2003). *Lycopsis* has been classified as a hypercarnivore according to Prevosti et al. (2013). Based on its anatomy, *Lycopsis* would have fed upon vertebrates smaller than itself (Argot, 2004a, 2004b; Prevosti et al., 2013). In fact, there is direct evidence this metatherian fed upon rodents, since broken bones and teeth of a dinomyid have been found in the body cavity of a Miocene specimen of *Lycopsis longirostrus* from La Venta locality in Colombia (Marshall, 1977). Other works also suggest large rodents (e.g., dinomyids or hydrochoerines) would have been common prey of this sparassodont (Argot, 2004a; Ercoli et al., 2014).

The low number of samples that could be recovered from *Lycopsis* (two samples) prevented us from making statistical tests to infer predator-prey relationships. In this case, we have opted to discuss the position of tooth enamel δ^{13}C values of *Lycopsis* with respect to potential prey in the graphical space (Fig. 5). The δ^{13}C values of *Lycopsis* are indicative of ingestion of prey from less open environments compared to *Thylacosmilus*. Some of the mammals analyzed as potential prey show very high body masses compared to *Lycopsis* and could be ruled out a priori as prey, such as the large notoungulates (>150 kg) *Chasicotherium* (Homalodotheriidae), *Thypotheriopsis* (Mesotheriidae), *Hemixotodon* and *Paratrigodon* (Toxodontidae). On the other hand, the δ^{13}C values of the notoungulates *Paedotheirum* (2 kg) and *Hemihegetotherium* (13 kg) are higher than those of the metatherian, indicating they possibly do not actively contribute to its diet. Rodents *Cardiatherium* (~12–30 kg) and *Tetrastylus* (~7.5–21 kg) and the litopterns *Cullinia* (~100 kg) and *Theosodon* (~44–100 kg) show ranges of δ^{13}C values that overlap with that of *Lycopsis* suggesting they may have been potential prey for this carnivore, as suggested by previous work (Argot, 2004a, 2004b). This is a tentative approach to the inference of potential prey for the sparassodont *Lycopsis* and we are aware more samples are needed to perform sound statistical tests with a trophic meaning.

Thylacomislus was classified as a hypercarnivore (Prevosti et al., 2013; Janis et al., 2020). Anatomical studies of this taxon have inferred skeletal adaptations to cursoriality and arboreal adaptive traits, although it seems it would be an ambush rather than a pursuit hunter, like lions (Argot, 2004a, 2004c; Ercoli et al., 2012; Prevosti and Forasiepi, 2018). Presumably, its forelimbs would have had manipulative capabilities to capture, hold and secure small and medium prey (Argot, 2004a, 2004b, 2004c). In addition, the femoral head had an orientation also found in bears, suggesting the possibility of adopting erect bipedal postures while attacking large prey (Argot, 2004a, 2004c). Therefore, *Thylacosmilus* was capable of hunting small– and medium–sized but could also take down large–sized prey.

The statistical analysis was performed by lumping together tooth enamel δ^{13}C values from Quehué and Salinas Grandes de Hidalgo. This can be done as i) both fossiliferous sites were assigned to the Huayquerian Stage/Age and although no contemporary, no major climatic and environmental events happened during the period spanned between both localities. Spatially, they are less than 200 kms away and topographically, no major altitude difference may have existed between them. Therefore, it can be inferred species sampled in these two localities were part of the same mammalian community within this relatively homogenous area of the Pampean region. δ^{13}C data were normally distributed and thus, a t-Student test was undertaken for each *Thylacosmilus*-prey pair. According to Argot (2004a), the most probable prey of *Thylacosmilus* may have been small–medium size notoungulates and litopterns, as well as large rodents (as dinomyids and hydrochoerines), mostly consistent with our results (although at the moment there is no record of hydrochoerines in these two localities). Argot (2004c) suggests throat–bite attack, frequently linked to sabretooth dentition development, would be effective at hunting ungulates or large rodents, but not in the case of armored glyptodonts or large ground sloths and toxodontids, which were equipped with very large claws. This agrees with the fact that t-Student tests only report significant differences in δ^{13}C values between *Thylacosmylus* and Toxodontidae indet. (t-Student $= 3.723$, $p = 0.008$), the mylodontid *Proscelidodon* (t-Student $= 5.194$, $p = 0.002$), and cingulate Glyptodontidae indet. (t-Student $= -3.405$, $p = 0.026$) (Fig. 5), suggesting these three herbivore genera poorly contributed to its diet. The rest of the taxa analyzed may have contributed to its diet on account of the lack of significant differences between their δ^{13}C values and those of *Thylacosmylus*. To sum up, *Thylacosmilus* would have discarded i) prey with the lowest mean δ^{13}C values and ii) large mammals (Fig. 5).

Preliminary isotopic analysis suggests these two sparassodonts exploited different prey, coinciding with inferred anatomical features.

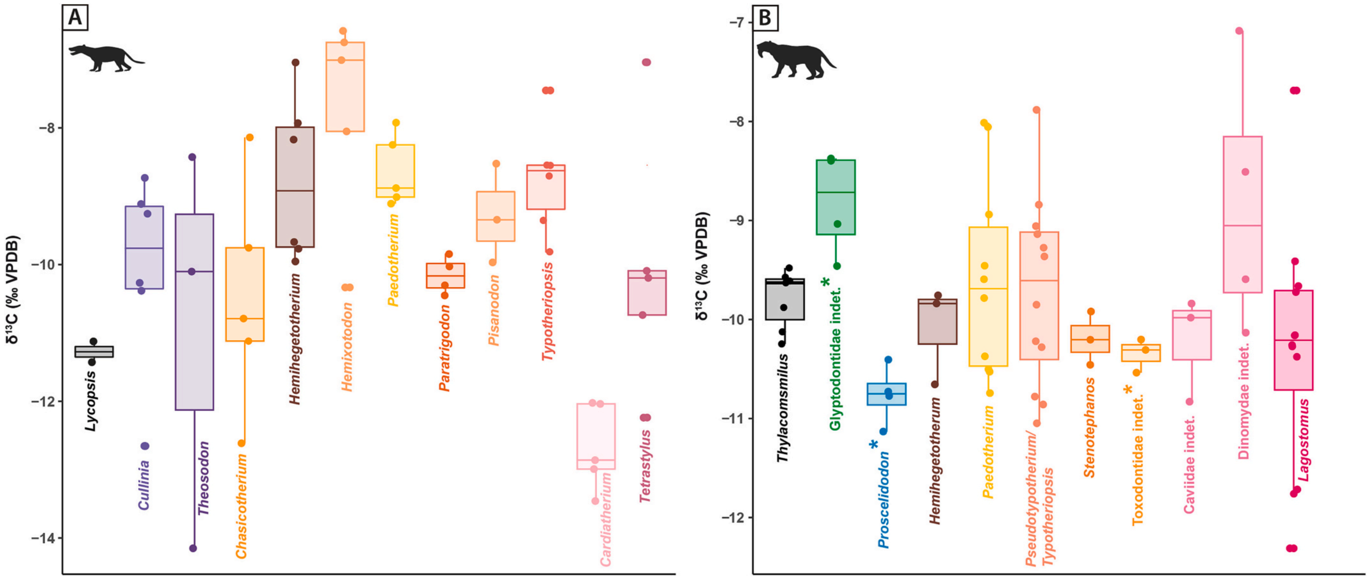

Fig. 5. Boxplot comparing the distribution and median $\delta^{13}C$ values of the studied sparassodonts and their potential prey. A) *Lycopsis* and its potential prey from Chasicoan Stage/Age (Arroyo Chasicó locality), and B) *Thylacosmilus* and its potential prey from Huayquerian Stage/Age (Quehué and Salinas Grandes de Hidalgo localities). Prey with significant differences with *Thylacosmilus* are indicated with *. Sparassodonta $\delta^{13}C$ values have been corrected for the trophic offset, adding 1.3‰ to the raw values (Fox–Dobbs et al., 2006; Clementz et al., 2009).

Although both were ambush predators, *Thylacosmilus* had a robust composition with adaptations to incipient cursorial specialization and arboreal traits (Argot, 2004a; Ercoli et al., 2012), whereas *Lycopsis* was more slender and lighter, a more terrestrial predator less adapted to an arboreal life and without cursorial specialization traits (Argot, 2004a; Prevosti and Forasiepi, 2018). *Thylacosmilus* show $\delta^{13}C$ values indicative of prey from more open environments than *Lycopsis*. In addition, the higher body mass of *Thylacosmilus* allowed it access to larger prey.

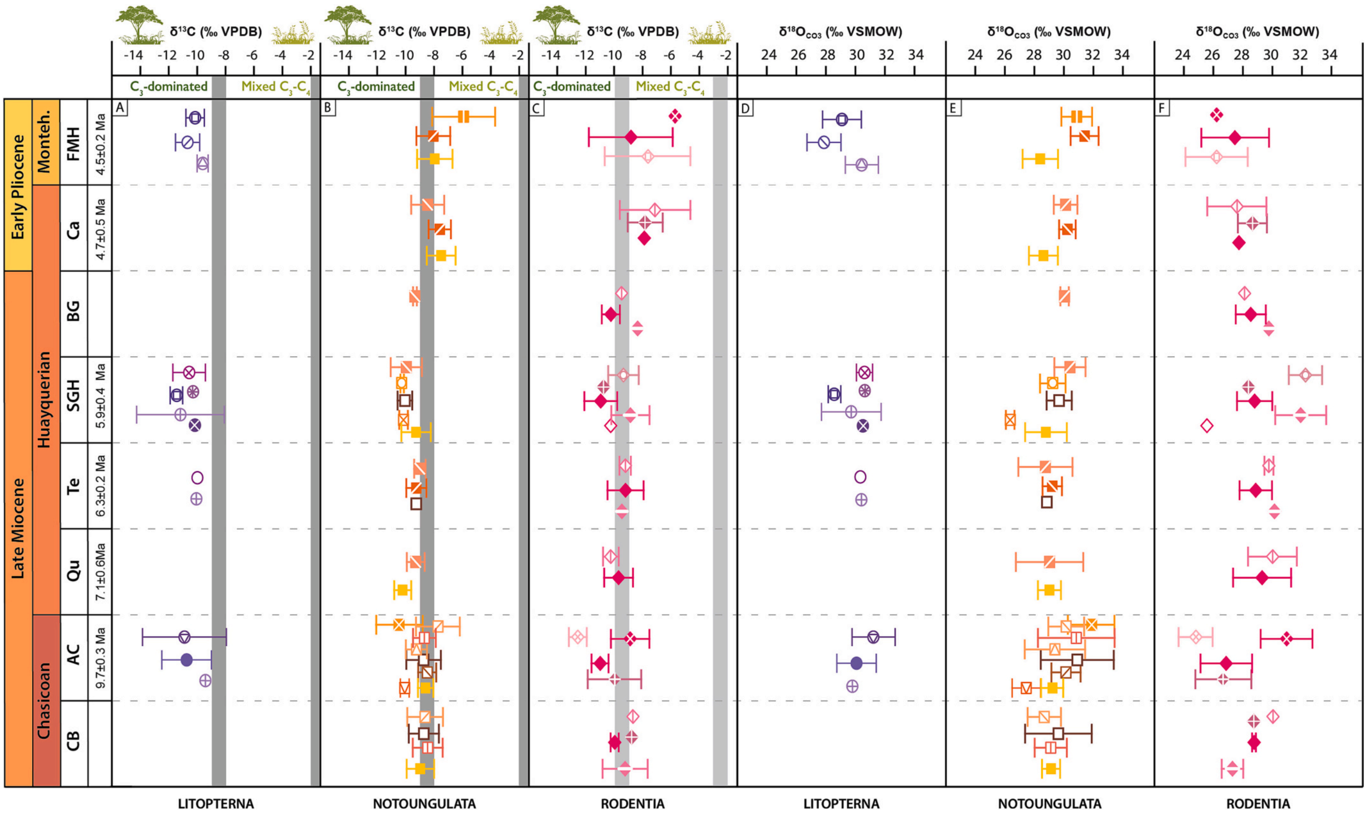

Fig. 6. Temporal evolution of litoptern, notoungulate and rodent isotopic data according to the new chronological framework proposed in this work. A–C) $\delta^{13}C$ (‰ VPDB) mean ± 1 standard deviation values and D–F) $\delta^{18}O_{CO3}$ (‰ VSMOW) mean ± 1 standard deviation values. The gray vertical bars depict the vegetation $\delta^{13}C$ cut–off values between a C_3–dominated diet and an intermediate C_3–C_4 diet. For the legend of taxa symbols see Figs. 2 to 4.

4.4. Paleoenvironmental inferences through the GABI

In this section we evaluate the paleoenvironmental evolution of the region during the Late Miocene–Early Pliocene interval (ca. 5 Ma) using the new radiometric ages and isotopic data (Fig. 6). For this evaluation, we focus on litoptern, notoungulate, and rodent data, considering they are the best represented groups over the studied timespan.

As mentioned above, carbon isotope composition allows us to reconstruct the diet of fossil herbivores and consequently the vegetation cover and in turn, the environment. All litopterns presented a diet based on C_3 plants from woodland and wooded C_3 grassland throughout the study's time interval (Fig. 6A), and statistical analyses report no significant differences among fossil sites ($\chi^2 = 0.700$, $p = 0.737$, SM6). Conversely, significant differences were recorded in the case of notoungulates and rodents ($\chi^2 = 55.651, p < 0.001$ and $\chi^2 = 28.142, p = 0.005$, respectively, SM6), suggesting a change in their diets over time.

A general trend towards diets based on more open environments can be observed during the Early Pliocene in notoungulates and rodents (Fig. 6B–C), indicative of a shift to more arid conditions. This increase in aridity has been recorded globally and is explained as a consequence of the expansion of an ice sheet in Patagonia (7–5 Ma) causing a drop-in sea level, an increase in continentality, and a decrease in precipitation (Rabassa et al., 2005). Selective pressures driven by the development of more open environments due to an increase in aridity at this time favored hypsodont lineages (e.g., Janis et al., 2000; Strömberg, 2011). Precisely, an increase in hypsodonty is observed in both, notoungulates and rodents during the Miocene–Pliocene boundary encompassing their dietary change (Verzi et al., 2008; Piñero et al., 2021). On the contrary, litopterns maintained brachydont molars (Carlini et al., 2006), dental feature that may have conditioned their specialization as consumers of non-abrasive plant items, such as leaves and did not experience a diet shift over time. On the contrary, there was an increase in hypsodonty during the Miocene–Pliocene boundary in both notoungulates and rodents (Verzi et al., 2008; Piñero et al., 2021).

In addition, at that time, the expansion of C_4 plants had already occurred and they began to dominate the environments (Domingo et al., 2020). However, diets incorporating C_4 plants are recorded in the region by notoungulates and rodents already since the Chasicoan Stage/Age in the Late Miocene (Fig. 6B–C), suggesting the existence of favorable conditions for the development of C_4 plants before their great expansion and even evidences of the presence of grasses since 44 Ma (Eocene) in Patagonia (Strömberg, 2011; Hynek et al., 2012; Bellosi et al., 2021).

For the Huayquerian Stage/Age, the tooth enamel $\delta^{13}C$ values of rodents also suggest mixed C_3–C_4 diets, in contrast to notoungulates (except those from Caleufú, the locality with the most modern assemblage assigned to the latest Huayquerian Stage/Age), showing a clear preference for a C_3–based diet. Notoungulates ́ preference for C_3 diets between 7.5 and 6.3 Ma may indicate climatic conditions were more favorable for the C_3 photosynthesis pathway compared to previous (Chasicoan Stage/Age) and more modern faunas (latest Huayquerian/ Montehermosan stages/ages), when notoungulates showed mixed C_3–C_4 diet values. During the Messinian (∼ 7.2–5.3 Ma) a global cooling took place, linked with a decrease in pCO_2 values (Herbert et al., 2016). Although pCO_2 seems to be the primary driver of the C_4 pathway, a combination of other controlling factors may benefit the C_3 pathway in semi-arid environments, such as decreases in growing season temperature and/or in warm season precipitation (Koch et al., 2004). The record of C_4 plants in the diet of rodents during the complete time interval studied points to an early specialization of rodents to mixed diets, probably due to their high evolutionary adaptability (Hernández Fernández, 2001; Moreno Bofarull et al., 2008; Babarinde and Saitou, 2020; Hernández Fernández et al., 2022).

Regarding tooth enamel $\delta^{18}O$ values, litopterns and large notoungulates are assumed to be obligate drinkers (see discussion in section 4.2), therefore their values reflect the isotopic composition of the water masses directly related to hydrological conditions. In the case of small-medium notoungulates, they may or may not be obligate drinkers, depending on diet and water availability. No major differences were observed in litopterns throughout the studied sequence (Fig. 6D; $\chi^2 = 3.544$, $p = 0.170$, SM6), while significant differences were recorded in notoungulates ($\chi^2 = 57.728$, $p < 0.001$, SM6). All notoungulates were included in this analysis, since we cannot discard the possibility they were obligate drinkers. In the case of notoungulate $\delta^{18}O$ values, a similar trend to carbon isotope composition can be noticed (Fig. 6E), with higher $\delta^{18}O$ values during the Chasicoan Stage/Age and latest Huayquerian–Montehermosan stages/ages. This is indicative of more arid conditions or higher temperatures, and lower $\delta^{18}O$ values supporting lower temperatures during most of the Huayquerian Stage/Age. Litoptern $\delta^{18}O$ values do not show a clear trend (Fig. 6D), probably because they may be better recording global hydrological conditions (Domingo et al., 2020) and probably during the time period studied, there were no significant changes in the hydrological cycle. On the contrary, according to Domingo et al. (2020), notoungulates would be representative of regional hydrological conditions, recording an increase in $\delta^{18}O$ values (Fig. 6E) related to a rise in aridity and/or temperature during the Early Pliocene compared to the Huayquerian in Argentina as pointed out by some authors (Hynek et al., 2012; Domingo et al., 2020). Finally, $\delta^{18}O$ values of rodents show a great variability, wide ranges in some taxa, and a slight trend towards lower $\delta^{18}O$ values can be identified from the Huayquerian Stage/Age to the Montehermosan Stage/Age (Fig. 6F). These results can be explained by the fact rodents obtain part of their water needs by eating (representing evaporation in plants and not in water bodies) and since they have narrower home ranges than large mammals, they could be recording more local environmental conditions when compared to litopterns and notoungulates.

5. Conclusions

In this work we provide new zircon ages for the Neogene of Argentine Pampas, including first numerical values for some South American classic localities such as Salinas Grandes de Hidalgo in La Pampa Province, and Arroyo Chasicó and Farola Monte Hermoso in Buenos Aires Province, covering a period of ca. 5 million years (Late Miocene–Early Pliocene), in a relatively small area (∼90,000 km^2). Dated localities are relevant as they hold mammalian assemblages linked to the last stages of South American isolation and to the first pulses of the GABI. Among the latter localities, those with fossil remains of the families Procyonidae (Carnivora) and Cricetidae (Rodentia) stand out as they are “Herald” Northamerican taxa. The new dating provides novel information that help to chronologically adjust the presence of the first Holarctic immigrants in the Argentine Pampas.

The chronological arrangement obtained herein has allowed us to propose a solid temporal frame to evaluate the paleoenvironmental and paleoecological evolution of the region based on stable isotope data of mammalian fossils. Furthermore, this study is one of the few isotopic works that cover such a wide time span in South America. In addition, the genus-level study of the taxa allows us to improve the paleoecological and paleoenvironmental interpretations made in previous works. During the Chasicoan Stage/Age (Late Miocene), $\delta^{13}C$ herbivore data point to mixed C_3–C_4 diets, implying the existence of favorable habitats for C_4 plants before their full expansion. However, during the Huayquerian Stage/Age (Late Miocene), taxa showed a preference for C_3 plants, possibly due to favorable climatic conditions for this photosynthetic pathway, except for some rodents that continued to include C_4 plants in their diets (maybe related to an early specialization of this group). In the latest Huayquerian–Montehermosan stages/ages (Early Pliocene), there is a significant change in diets with taxa incorporating a higher percentage of C_4 plants, supported by the statistical analyses. This result shows the expansion of C_4 plants is recorded in the study region at the Early Pliocene. The notoungulates, which during most part of the Huayquerian Stage/Age (Quehué, Telén, and Salinas Grandes de Hidalgo) showed a preference for C_3–based diets, in the latest

Huayquerian–Montehermosan stages/ages (Caleufú and Farola Monte Hermoso) switched to mixed C_3–C_4 diets indicative of more open environments. This change in diets reflects an increase in aridity and/or temperature since the Late Miocene–Pliocene in the region. Regarding δ^{18}O values, we have detected different results in litopterns, notoungulates and rodents. Litopterna values show no trend, while Notoungulata showed an increase in δ^{18}O values during the Early Pliocene possibly related to an increase in aridity and/or temperature. However, Rodentia values for this time period showed a slight decrease in δ^{18}O values. This difference may be due to rodents recording more local conditions and obtaining part of the water they need by eating as opposed to notoungulates that need to drink to meet their physiological needs. Finally, this study also evaluated, for the first time, the trophic behavior of two metatherian sparassodonts (*Lycopsis* and *Thylacosmilus*) based on stable isotope analysis. Preliminary results suggest these Late Miocene hypercarnivores exploited different prey, and *Thylacosmilus* probably did not include large ground sloths and armored glyptodonts in its diet, agreeing well with their anatomical features, hunting strategies and body mass. This new information allows us to investigate in more depth the paleoecological behavior of this group of mammals, which constituted (together with the Phorusrhacidae “terror birds”) one of the main components of the vertebrate predator guild from the Neogene of South America.

Declaration of Competing Interest

We declare that we have no conflicts of interest regarding the contents of this study.

Data availability

I have shared the data in the supplementary material of the article

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2023.111917.

References

Argot, C., 2004a. Evolution of South American mammalian predators (Borhyaenoidea): anatomical and palaeobiological implications. Zool. J. Linnean Soc. 140, 487–521. https://doi.org/10.1111/j.1096–3642.2004a.00110.x.

Argot, C., 2004b. Functional–adaptive analysis of the postcranial skeleton of a Laventan borhyaenoid, *Lycopsis longirostris* (Marsupialia, Mammalia). J. Vertebr. Paleontol. 24, 689–708. https://doi.org/10.1671/0272–4634(2004b)024[0689:FAOTPS]2.0.CO;2.

Argot, C., 2004c. Functional–adaptive features and palaeobiologic implications of the postcranial skeleton of the late Miocene sabretooth borhyaenoid *Thylacosmilus atrox* (Metatheria). Alcheringa Australas. J. Palaeontol. 28, 229–266. https://doi.org/10.1080/03115510408619283.

Babarinde, I.A., Saitou, N., 2020. The dynamics, causes, and impacts of mammalian evolutionary rates revealed by the analyses of capybara draft genome sequences. Genome Biol. Evol. 12 (8), 1444–1458. https://doi.org/10.1093/gbe/evaa157.

Barreto, G.R., Quintana, R.D., 2013. Foraging strategies and feeding habits of Capybaras. In: Moreira, J.R., Ferraz, K.M.P.M.B., Herrera, E.A., Macdonald, D.W. (Eds.), Capybara. Springer New York, New York, NY, pp. 83–96. https://doi.org/10.1007/978–1–4614–4000–0_4.

Bellosi, E., Genise, J.F., Zucol, A., Bond, M., Kramarz, A., Sánchez, M.V., Krause, J.M., 2021. Diverse evidence for grasslands since the Eocene in Patagonia. J. S. Am. Earth Sci. 108, 103357 https://doi.org/10.1016/j.jsames.2021.103357.

Borges, P.A., Dominguez–Bello, M.G., Herrera, E.A., 1996. Digestive physiology of wild capybara. J. Comp. Physiol. B. 166, 55–60. https://doi.org/10.1007/BF00264639.

Bruner, A., Leier, A.L., Barbeau Jr., D.L., Pullen, A., Fidler, M.K., Stubbins, B., 2022. Detrital zircon provenance and transport pathways of Pleistocene–Holocene eolian sediment in the Pampean Plains, Argentina. GSA Bull. 135, 435–448. https://doi.org/10.1130/B36267.1.

Buckley, M., 2015. Ancient collagen reveals evolutionary history of the endemic South American ‘ungulates’. P. Roy. Soc. B. 282, 20142671.

Carlini, A.A., Gelfo, J.N., Sánchez, R., 2006. A new Megadolodinae (Mammalia, Litopterna, Protherotheriidae) from the Urumaco Formation (Late Miocene) of Venezuela. J. Syst. Palaeontol. 4, 279–284. https://doi.org/10.1017/S1477201906001830.

Carrillo, J.D., Faurby, S., Silvestro, D., Zizka, A., Jaramillo, C., Bacon, C.D., Antonelli, A., 2020. Disproportionate extinction of South American mammals drove the asymmetry of the Great American Biotic Interchange. Proc. Natl. Acad. Sci. U. S. A. 117, 26281–26287.

Catena, A.M., Croft, D.A., 2020. What are the best modern analogs for ancient South American mammal communities? Evidence from ecological diversity analysis (EDA). Palaeontol. Electron. 23, a03.

Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. Oecologia 120, 347–363. https://doi.org/10.1007/s004420050868.

Cerling, T.E., Harris, J.M., MacFadden, B.J., Leakey, M.G., Quade, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. Nature 389, 153–158. https://doi.org/10.1038/38229.

Cione, A.L., Tonni, E.P., Bargo, S., Bond, M., Carlini, A.A., Deschamps, C.M., Dozo, M.T., Goin, F.J., Montalvo, C.I., Nasif, N., Noriega, J.I., Jaureguizar, E.O., Pascual, R., Prado, J.L., Scillato–Yané, G.J., Soibelzon, L., Verzi, D.H., Carolina, E., 2007. Mamíferos continentales del Mioceno tardío a la actualidad en la Argentina: cincuenta años de estudios. Asociación Paleontológica Argentina. Publicación Especial 11, 258–278.

Cione, A.L., Gasparini, G.M., Soibelzon, E., Soibelzon, L.H., Tonni, E.P., 2015. The Great American Biotic Interchange, Springer Briefs in Earth System Sciences. Springer, Netherlands, Dordrecht. https://doi.org/10.1007/978–94–017–9792–4.

Clauss, M., Hagen, K.B., Frei, S., Ortmann, S., Lawrenz, A., Głogowski, R., Fritz, J., Flach, E., Kreuzer, M., 2019. Digestive anatomy, physiology, resting metabolism and methane production of captive maras (*Dolichotis patagonum*). Comp. Biochem. Physiol. A Mol. Integr. Physiol. 235, 82–89. https://doi.org/10.1016/j.cbpa.2019.05.023.

Clementz, M.T., Koch, P.L., 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. Oecologia 129, 461–472. https://doi.org/10.1007/s004420100745.

Clementz, M.T., Holroyd, P.A., Koch, P.L., 2008. Identifying aquatic habits of herbivorous mammals through stable isotope analysis. PALAIOS 23, 574–585. https://doi.org/10.2110/palo.2007.p07–054r.

Clementz, M.T., Fox–Dobbs, K., Wheatley, P.V., Koch, P.L., Doak, D.F., 2009. Revisiting old bones: coupled carbon isotope analysis of bioapatite and collagen as an ecological and palaeoecological tool. Geol. J. 44, 605–620. https://doi.org/10.1002/gj.1173.

Corriale, M.J., Loponte, D., 2015. Use of stable carbon isotope ratio for foraging behavior analysis of capybara (*Hydrochoerus hydrochaeris*) from Esteros del Iberá, Argentina. Mamm. Biol. 80, 73–80. https://doi.org/10.1016/j.mambio.2014.12.007.

Cortés, A., Tirado, C., Rosenmann, M., 2003. Energy metabolism and thermoregulation in *Chinchilla brevicaudata*. J. Therm. Biol. 28, 489–495. https://doi.org/10.1016/S0306–4565(03)00049–4.

Coutts, D.S., Matthews, W.A., Hubbard, S.M., 2019. Assessment of widely used methods to derive depositional ages from detrital zircon populations. Geosci. Front. 10, 1421–1435.

Croft, D.A., 2001. Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). Divers. Distrib. 7, 271–287.

Croft, D.A., 2006. Horned Armadillos and Rafting Monkeys: The Fascinating Fossil Mammals of South America. Indiana University Press, 320 pp.

Dantas, M.A.T., Cherkinsky, A., Lessa, C.M.B., Santos, L.V., Cozzuol, M.A., Omena, É.C., Lopes Da Silva, J.L., Sial, A.N., Bocherens, H., 2020. Isotopic paleoecology (δ^{13}C, δ^{18}O) of a late Pleistocene vertebrate community from the Brazilian Intertropical Region. Rev. Bras. Paleontol. 23, 138–152. https://doi.org/10.4072/rbp.2020.2.05.

Defler, T., 2019. History of Terrestrial Mammals in South America: How South American Mammalian Fauna Changed from the Mesozoic to Recent Times, Topics in Geobiology. Springer International Publishing, Cham. https://doi.org/10.1007/978–3–319–98449–064463.

Deschamps, M.C., Tomassini, R.L., 2016. Late Cenozoic vertebrates from the southern Pampean Region: systematic and bio–chronostratigraphic update. Publicación Electrónica de la Asociación Paleontológica Argentina 16, 202–225. https://doi.org/10.5710/PEAPA.16.05.2016.113.

Domingo, L., Prado, J.L., Alberdi, M.T., 2012. The effect of paleoecology and paleobiogeography on stable isotopes of Quaternary mammals from South America. Quat. Sci. Rev. 55, 103–113. https://doi.org/10.1016/j.quascirev.2012.08.017.

Domingo, L., Koch, P.L., Hernández Fernández, M., Fox, D.L., Domingo, M.S., Alberdi, M. T., 2013. Late Neogene and Early Quaternary Paleoenvironmental and Paleoclimatic Conditions in Southwestern Europe: Isotopic analyses on Mammalian Taxa. PLoS One 8, e63739. https://doi.org/10.1371/journal.pone.0063739.

Domingo, L., Tomassini, R.L., Montalvo, C.I., Sanz–Pérez, D., Alberdi, M.T., 2020. The Great American Biotic Interchange revisited: a new perspective from the stable isotope record of Argentine Pampas fossil mammals. Sci. Rep. 10, 1608. https://doi.org/10.1038/s41598–020–58575–6.

Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., Smith, S.A., 2010. The origins of C$_4$ grasslands: integrating evolutionary and ecosystem science. Science 328, 587–591. https://doi.org/10.1101/583625.

Ercoli, M.D., Prevosti, F.J., 2011. Estimación de masa de las especies de Sparassodonta (Mammalia, Metatheria) de Edad Santacrucense (Mioceno Temprano) a partir del tamaño del centroide de los elementos apendiculares: inferencias paleoecológicas. Ameghiniana 48, 462. https://doi.org/10.5710/AMGH.v48i4(347).

Ercoli, M.D., Prevosti, F.J., Álvarez, A., 2012. Form and function within a phylogenetic framework: locomotory habits of extant predators and some Miocene Sparassodonta (Metatheria). Zool. J. Linnean Soc. 165, 224–251. https://doi.org/10.1111/j.1096–3642.2011.00793.x.

Ercoli, M.D., Prevosti, F.J., Forasiepi, A.M., 2014. The structure of the mammalian predator guild in the Santa Cruz Formation (late Early Miocene). J. Mamm. Evol. 21, 369–381. https://doi.org/10.1007/s10914–013–9243–4.

Farinati, E.A., Manera, T., Tomassini, R.L., 2010. La Bahía que iluminó a Darwin. Spanish J. Palaeontol. 25, 35–41. https://doi.org/10.7203/sjp.25.1.18906.

Farquhar, G.D., Ehleringer, I.J.R., Hubick, K.T., 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Biol. 40 (1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443.

Felix, G., Almeida Paz, I., Piovezan, U., Garcia, R., Lima, K., Nääs, I., Salgado, D., Pilecco, M., Belloni, M., 2014. Feeding behavior and crop damage caused by capybaras (*Hydrochoerus hydrochaeris*) in an agricultural landscape. Braz. J. Biol. 74, 779–786. https://doi.org/10.1590/1519–6984.02113.

Feranec, R., García, N., Díez, J.C., Arsuaga, J.L., 2010. Understanding the ecology of mammalian carnivorans and herbivores from Valdegoba cave (Burgos, northern Spain) through stable isotope analysis. Palaeogeogr. Palaeoclimatol. Plaeoecol. 297, 263–272.

Folguera, A., Zárate, M., 2009. La sedimentación neógena continental en el sector extrandino de Argentina central. Rev. Asoc. Geol. Argent. 64, 692–712.

Forasiepi, A.M., Goin, F.J., di Martino, V., 2003. Una nueva especie de *Lycopsis* (Metatheria, Prothylacyninae) de la Formación Arroyo Chasicó (Mioceno tardío) de la provincia de Buenos Aires. Ameghiniana 40, 249–253.

Fox–Dobbs, K., Wheatley, P.V., Koch, P.L., 2006. Carnivore specific bone bioapatite and collagen carbon isotope fractionations: Case studies of modern and fossil grey wolf populations 2006. AGU Fall Meeting Suppl. B53C–0366.

Hagen, K.B., Besselmann, D., Cyrus-Eulenberger, U., Vendl, C., Ortmann, S., Zingg, R., Kienzle, E., Kreuzer, M., Hatt, J.M., Clauss, M., 2015. Digestive physiology of the plains viscacha (*Lagostomus maximus*): a large herbivorous hystricomorph rodent. Zoo Biol. 34, 345–359. https://doi.org/10.1002/zoo.21216.

Hayes, J.M., Walley, John, W.C., David, R., 2001. 3. Fractionation of the isotopes of carbon and hydrogen in biosynthetic processes. In: Stable Isotope Geochemistry, Reviews in Mineralogy & Geochemistry, pp. 225–277.

Herbert, T.D., Lawrence, K.T., Tzanova, A., Peterson, L.C., Caballero-Gill, R., Kelly, C.S., 2016. Late Miocene global cooling and the rise of modern ecosystems. Nat. Geo. 9, 843–847.

Hernández Fernández, M., 2001. Bioclimatic discriminant capacity of terrestrial mammal faunas. Glob. Ecol. Biogeogr. 10, 189–204.

Hernández Fernández, M., Pelegrin, J.S., Gómez Cano, A.R., García Yelo, B.A., Moreno-Bofarull, A., Sánchez-Fontela, N., Rodríguez-Ruiz, C., Ramiro Camacho, A., Domingo, L., Menéndez, I., Martín-Perea, D.M., Bazán, C.M., Alcalde, G.M., Domingo, M.S., Luna, B., Peinado Cortés, M.M., Arias, A., González Couturier, G., Márquez Villena, A., Anaya, N., Blanco, F., Galli, E., Gamboa, S., Quesada, A., Sanz-Pérez, D., Varela, S., Cantalapiedra, J.L., 2022. Macroevolution and climate changes: a global multi-family test supports the resource-use hypothesis in terrestrial mammals. Hist. Biol. 34 (8), 1471–1479. https://doi.org/10.1080/08912963.2022.2042807.

Hynek, S.A., Passey, B.H., Prado, J.L., Brown, F.H., Cerling, T.E., Quade, J., 2012. Small mammal carbon isotope ecology across the Miocene–Pliocene boundary, northwestern Argentina. Earth Planet. Sci. Lett. 321–322, 177–188. https://doi.org/10.1016/j.epsl.2011.12.038.

Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R: Bayesian isotopic niche metrics. J. Anim. Ecol. 80, 595–602. https://doi.org/10.1111/j.1365–2656.2011.01806.x.

Janis, C.M., Damuth, J., Theodor, J.M., 2000. Miocene ungulates and terrestrial primary productivity: Where have all the browsers gone? Proc. Natl. Acad. Sci. 97, 7899–7904.

Janis, C.M., Figueirido, B., DeSantis, L., Lautenschlager, S., 2020. An eye for a tooth: *Thylacosmilus* was not a marsupial "saber-tooth predator". PeerJ 8, e9346. https://peerj.com/articles/9346/.

Jochum, K.P., Weis, U., Stoll, B., Kuzmin, D., Yang, Q., Raczek, I., Enzweiler, J., 2011. Determination of Reference Values for NIST SRM 610–617 Glasses Following ISO Guidelines. Geostand. Geoanal. Res. 35, 397–429. https://doi.org/10.1111/j.1751–908x.2011.00120.x.

Kim, H.Y., 2015. Statistical notes for clinical researchers: post-hoc multiple comparisons. Restor. Dent. Endod. 40 (2), 172–176. https://doi.org/10.5395/rde.2015.40.2.172.

Kleinert, K., Strecker, M.R., 2001. Climate change in response to orographic barrier uplift: Paleosol and stable isotope evidence from the late Neogene Santa Maria basin, northwestern Argentina. Geol. Soc. Am. Bull. 113, 728–742. https://doi.org/10.1130/0016–7606(2001)113<0728:CCIRTO>2.0.CO;2.

Koch, P.L., 1998. Isotopic reconstruction of past continental environments. Annu. Rev. Earth Planet. Sci. 26, 573–613. https://doi.org/10.1146/annurev.earth.26.1.573.

Koch, P.L., 2007. Isotopic Study of the Biology of Modern and Fossil Vertebrates. In: Michener, R., Lajtha, K. (Eds.), Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing Ltd, Oxford, UK, pp. 99–154. https://doi.org/10.1002/9780470691854.ch5.

Koch, P.L., Diffenbaugh, N.S., Hoppe, K.A., 2004. The effects of late Quaternary climate and pCO$_2$ change on C$_4$ plant abundance in the south-central United States. Palaeogeogr. Palaeoclimatol. Palaeoecol. 207 (3–4), 331–357. https://doi.org/10.1016/j.palaeo.2003.09.034.

Kohn, M.J., Cerling, T.E., 2002. Stable Isotope Compositions of Biological Apatite. Rev. Mineral. Geochem. 48, 455–488. https://doi.org/10.2138/rmg.2002.48.12.

Latorre, C., Quade, J., McIntosh, W.C., 1997. The expansion of C$_4$ grasses and global change in the late Miocene: Stable isotope evidence from the Americas. Earth Planet. Sci. Lett. 146, 83–96. https://doi.org/10.1016/S0012–821X(96)00231–2.

Leigh, E.G., O'Dea, A., Vermeij, G.J., 2014. Historical biogeography of the Isthmus of Panama: Historical biogeography. Biol. Rev. 89, 148–172. https://doi.org/10.1111/brv.12048.

Levin, N.E., Cerling, T.E., Passey, B.H., Harris, J.M., Ehleringer, J.R., 2006. A stable isotope aridity index for terrestrial environments. Proc. Natl. Acad. Sci. 103, 11201–11205. https://doi.org/10.1073/pnas.0604719103.

Linares, E., Llambías, E.J., Latorre, C.O., 1980. Geología de la provincia de La Pampa y geocronología de sus rocas metamórficas y eruptivas. Rev. Asoc. Geol. Argent. 35, 87–146.

Lopes, R.P., Ribeiro, A.M., Dillenburg, S.R., Schultz, C.L., 2013. Late middle to late Pleistocene paleoecology and paleoenvironments in the coastal plain of Rio Grande do Sul State, Southern Brazil, from stable isotopes in fossils of *Toxodon* and *Stegomastodon*. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 385–394. https://doi.org/10.1016/j.palaeo.2012.10.042.

Luz, B., Cormie, A.B., Schwarcz, H.P., 1990. Oxygen isotope variations in phosphate of deer bones. Geochim. Cosmochim. Acta 54, 1723–1728. https://doi.org/10.1016/0016–7037(90)90403–8.

MacFadden, B.J., Cerling, T.E., Prado, J., 1996. Cenozoic Terrestrial Ecosystem Evolution in Argentina: evidence from Carbon Isotopes of Fossil Mammal Teeth. PALAIOS 11, 319–327. https://doi.org/10.2307/3515242.

Marshall, L.G., 1977. A New Species of *Lycopsis* (Borhyaenidae: Marsupialia) from the La Venta Fauna (late Miocene) of Colombia, South America. J. Paleontol. 51, 633–642.

Marshall, L.G., Webb, S.D., Sepkoski Jr., J.J., Raup, D.M., 1982. Mammalian evolution and the Great American Interchange. Science 215 (4538), 1351–1357. https://doi.org/10.1126/science.215.4538.1351.

Montalvo, C.I., Verzi, D.H., Vucetich, M.G., Visconti, G., 1998. Nuevos Eumysopinae (Rodentia, Echimyidae) de la Formación Cerro Azul (Mioceno tardío) de La Pampa, Argentina. Quintas Jornadas Geológicas y Geofísicas Bonaerenses, Actas I 57–64.

Montalvo, C.I., Melchor, R.N., Visconti, G., Cerdeño, E., 2008. Vertebrate taphonomy in loess–paleosol deposits: a case study from the late Miocene of Central Argentina. Geobios 41, 133–143.

Montalvo, C.I., Tomassini, R.L., Sostillo, R., Cerdeño, E., Verzi, D.H., Visconti, G., Folguera, A., Schmidt, G.I., 2019. A Chasicoan (late Miocene) vertebrate assemblage from Cerro Azul Formation, central Argentina. Geomorphological and biochronological considerations. J. S. Am. Earth Sci. 95, 102218 https://doi.org/10.1016/j.jsames.2019.102218.

Montalvo, C.I., Folguera, A., Cerdeño, E., Verzi, D.H., Pérez, M.E., Sostillo, R., Tomassini, R.T., 2023. The oldest Andean synorogenic fossiliferous deposits of the Miocene Cerro Azul Formation, central Argentina. J. South A. Earth Sci. 123, 104235 https://doi.org/10.1016/j.jsames.2023.104235.

Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J.C., Valencia, V., Ayala, C., Perez–Angel, L.C., Rodriguez–Parra, L.A., Ramirez, V., Nino, H., 2015. Middle Miocene closure of the Central American Seaway. Science 348, 226–229. https://doi.org/10.1126/science.aaa2815.

Moore, J.W., Semmens, B.X., 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecol. Lett. 11 (5), 470–480. https://doi.org/10.1111/j.1461-0248.2008.01163.x.

Moreno Bofarull, A., Arias Royo, A., Hernández Fernández, M., Ortiz–Jaureguizar, E., Morales, J., 2008. Influence of continental history on the ecological specialization and macroevolutionary processes in the mammalian assemblage of South America: differences between small and large mammals. BMC Evol. Biol. 8, 1–18.

Mukherjee, P.K., Souders, A.K., Sylvester, P.J., 2019. Accuracy and precision of U–Pb zircon geochronology at high spatial resolution (7–20 μm spots) by laser ablation–ICP–single–collector–sector–field–mass–spectrometry. JAAS 34, 180–192. https://doi.org/10.1039/c8ja00321a.

Norris, A., Danyushevsky, L., 2018. Towards Estimating the Complete Uncertainty Budget of Quantified Results Measured by LA–ICP–MS. Goldschmidt, Boston.

O'Dea, A., Lessios, H.A., Coates, A.G., Eytan, R.I., Restrepo–Moreno, S.A., Cione, A.L., Collins, L.S., de Queiroz, A., Farris, D.W., Norris, R.D., Stallard, R.F., Woodburne, M. O., Aguilera, O., Aubry, M.–.P., Berggren, W.A., Budd, A.F., Cozzuol, M.A., Coppard, S.E., Duque–Caro, H., Finnegan, S., Gasparini, G.M., Grossman, E.L., Johnson, K.G., Keigwin, L.D., Knowlton, N., Leigh, E.G., Leonard–Pingel, J.S., Marko, P.B., Pyenson, N.D., Rachello–Dolmen, P.G., Soibelzon, E., Soibelzon, L., Todd, J.A., Vermeij, G.J., Jackson, J.B.C., 2016. Formation of the Isthmus of Panama. Sci. Adv. 2, e1600883 https://doi.org/10.1126/sciadv.1600883.

Ortiz Jaureguizar, E., 1998. Paleoecología y evolución de la fauna de mamíferos de América del Sur durante la «edad de las planicies australes» (Mioceno superior–Plioceno superior). https://doi.org/10.3989/egeol.98543–4215.

Parnell, A.C., Inger, R., Bearhop, S., Jackson, A.L., 2010. Source Partitioning Using Stable Isotopes: Coping with Too Much Variation. PLoS One 5, e9672. https://doi.org/10.1371/journal.pone.0009672.

Pascual, R., Bondesio, P., 1982. Un roedor Cardiatheriinae (Hydrochoeriidae) de la Edad Huayqueriense (Mioceno tardío) de La Pampa. Sumario de los ambientes terrestres en la Argentina durante el Mioceno. Ameghiniana 19, 19–35.

Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO2, and bioapatite in different mammals. J. Archaeol. Sci. 32, 1459–1470. https://doi.org/10.1016/j.jas.2005.03.015.

Pelegrin, J.S., Gamboa, S., Menéndez, I., Hernández Fernández, M., 2018. El Gran Intercambio Biótico Americano: una revisión paleoambiental de evidencias aportadas por mamíferos y aves neotropicales. Ecosistemas 27, 5–17.

Phillips, D.L., Gregg, J.W., 2003. Source partitioning using stable isotopes: coping with too many sources. Oecologia 136 (2), 261–269. https://doi.org/10.1007/s00442-003-1218-3.

Phillips, D.L., Inger, R., Bearhop, S., Jackson, A.L., Moore, J.W., Parnell, A.C., Semmens, B.X., Ward, E.J., 2014. Best practices for use of stable isotope mixing models in food–web studies. Can. J. Zool. 92, 823–835. https://doi.org/10.1139/cjz–2014–0127.

Piñero, P., Verzi, D.H., Olivares, A.I., Montalvo, C.I., Tomassini, R.L., Fernández–Villoldo, A., 2021. Evolutionary pattern of *Metacaremys* gen. nov. (Rodentia, Octodontidae) and its biochronological implications for the late Miocene and early Pliocene of southern South America. Pap. Palaeontol. 7, 1895–1917. https://doi.org/10.1002/spp2.1368.

Prado, J.L., Sánchez, B., Alberdi, M.T., 2011. Ancient feeding ecology inferred from stable isotopic evidence from fossil horses in South America over the past 3 Ma. BMC Ecol. 11, 15. https://doi.org/10.1186/1472–6785–11–15.

Prevosti, F.J., Forasiepi, A.M., 2018. Evolution of South American Mammalian Predators During the Cenozoic: Paleobiogeographic and Paleoenvironmental Contingencies. In: Springer Geology. Springer International Publishing, Cham. https://doi.org/10.1007/978–3–319–03701–1.

Prevosti, F.J., Forasiepi, A., Zimicz, N., 2013. The evolution of the Cenozoic terrestrial mammalian predator guild in South America: competition or replacement? J. Mamm. Evol. 20, 3–21. https://doi.org/10.1007/s10914–011–9175–9.

Prevosti, F.J., Romano, C.O., Forasiepi, A.M., Hemming, S., Bonini, R., Candela, A.M., Cerdeño, E., Madozzo Jaén, M.C., Ortiz, P.E., Pujos, F., Rasia, L., Schmidt, G.I., Taglioretti, M., MacPhee, R.D.E., Pardiñas, U.F.J., 2021. New radiometric 40Ar–39Ar dates and faunistic analyses refine evolutionary dynamics of Neogene vertebrate assemblages in southern South America. Sci. Rep. 11, 9830. https://doi.org/10.1038/s41598–021–89135–1.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rabassa, J., Coronato, A.M., Salemme, M., 2005. Chronology of the Late Cenozoic Patagonian glaciations and their correlation with biostratigraphic units of the Pampean region (Argentina). J. S. Am. Earth Sci. 20, 81–103. https://doi.org/10.1016/j.jsames.2005.07.004.

Rasia, L.L., 2016. Los Chinchillidae (Rodentia, Caviomorpha) fósiles de la República Argentina: sistemática, historia evolutiva y biogeográfica, significado bioestratigráfico y paleoambiental. PhD Thesis, Facultad de Ciencias Naturales y Museo. Universidad Nacional de La Plata, La Plata, 381 pp.

Reguero, M.A., Candela, A.M., Galli, C.I., Bonini, R., Voglino, D., 2015. A new Hypsodont Notoungulate (Hegetotheriidae, Pachyrukhinae) from the late Miocene of the Eastern Cordillera, Salta province, Northwest of Argentina. Andean Geol. 42, 56–70. https://doi.org/10.5027/andgeoV42n1–a04.

Romano, C.O., Bonini, R., Hemming, S., Cenizo, M., Pardiñas, U.F., Prevosti, F.J., 2023. Advances in the understanding of Neogene mammalian fauna in the Pampean region (Central Argentina) through revising "biozone" hypotheses based on new dates and biochronological analyses. Ameghiniana 60 (5), 465–491.

Saarinen, J., Mantzouka, D., Sakala, J., 2020. Aridity, cooling, open vegetation, and the evolution of plants and animals during the Cenozoic. In: Martinetto, E., Tschopp, E., Gastaldo, R.A. (Eds.), Nature through Time. Springer Textbooks in Earth Sciences, Geography and Environment. Springer, Cham. https://doi.org/10.1007/978–3–030–35058–1_3.

Sanz-Pérez, D., Hernández Fernández, M., Muñoz-García, M.B., Pérez-Dios, P., Morales, J., Domingo, L., 2020. Palaeoecological and palaeoenviromental reconstruction of the upper Miocene vertebrate karstic site of Corral de Lobato, central-eastern Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 556, 109877. https://doi.org/10.1016/j.palaeo.2020.109877.

Schultz, P.H., Zárate, M., Hames, W.E., Harris, R.S., Bunch, T.E., Koeberl, C., Renne, P., Wittke, J., 2006. The record of Miocene impacts in the Argentine Pampas. Meteorit. Planet. Sci. 41, 749–771. https://doi.org/10.1111/j.1945–5100.2006.tb00990.x.

Simpson, G.G., 1950. History of the fauna of Latin America. Am. Sci. 38, 261–389.

Simpson, G.G., 1980. Splendid Isolation: The Curious History of South American Mammals. Yale University Press, New Haven y Londres, p. 266.

Sláma, J., Košler, J., Condon, D.J., Crowley, J.L., Gerdes, A., Hanchar, J.M., Horstwood, M.S.A., Morris, G.A., Nasdala, L., Norberg, N., Schaltegger, U., Schoene, B., Tubrett, M.N., Whitehouse, M.J., 2008. Plesovice zircon – A new natural reference material for U–Pb and Hf isotopic microanalysis. Chem. Geol. 249, 1–35. https://doi.org/10.1016/j.chemgeo.2007.11.005.

Sostillo, R., Montalvo, C.I., Verzi, D.H., 2014. A new species of *Reigechimys* (Rodentia, Echimyidae) from the late Miocene of Central Argentina and the evolutionary pattern of the lineage. Ameghiniana 51, 284–294. https://doi.org/10.5710/AMGH.24.04.2014.2741.

Sostillo, R., Montalvo, C.I., Cerdeño, E., Schmidt, G.I., Folguera, A., Cardonatto, M.C., 2021. Updated knowledge on the Notoungulata (Mammalia) from the late Miocene Cerro Azul Formation, La Pampa Province, Argentina. Hist. Biol. 33, 1247–1265. https://doi.org/10.1080/08912963.2019.1689239.

Stock, B.C., Jackson, A.L., Ward, E.J., Parnell, A.C., Phillips, D.L., Semmens, B.X., 2018. Anayzing mixing systems using a new generation of Bayesian tracer mixing models. PeerJ 6, e5096.

Stock, B., Semmens, B., 2016. Mixsiar: V3.1.2. Zenodo. https://doi.org/10.5281/ZENODO.47719.

Strömberg, C.A.E., 2011. Evolution of Grasses and Grassland Ecosystems. Annu. Rev. Earth Planet. Sci. 39, 517–544. https://doi.org/10.1146/annurev–earth–040809–152402.

Stubbins, B., Leier, A.L., Barbeau, D.L., Pullen, A., Nie, J., Zárate, M.A., Fidler, M.K., 2023. Global climate forcing on late Miocene establishment of the Pampean aeolian system in South America. Nat. Commun. 14, 6899. https://doi.org/10.1038/s41467-023-42537-3.

Suárez, C., 2019. Estudios taxonómicos y paleobiológicos sobre los Metatheria (Mammalia) del Mioceno medio de La Venta, Colombia. PhD Thesis, Facultad de Ciencias Naturales y Museo. Universidad Nacional de La Plata, La Plata, p. 292. https://doi.org/10.35537/10915/75246.

Suárez, C., Forasiepi, A.M., Goin, F.J., Jaramillo, C., 2015. Insights into the Neotropics prior to the Great American Biotic Interchange: new evidence of mammalian predators from the Miocene of Northern Colombia. J. Vertebr. Paleontol. 36, e1029581 https://doi.org/10.1080/02724634.2015.1029581.

Tarquini, S.D., Ladevèze, S., Prevosti, F.J., 2022. The multicausal twilight of South American native mammalian predators (Metatheria, Sparassodonta). Sci. Rep. 12, 1224. https://doi.org/10.1038/s41598–022–05266–z.

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. Proc. R. Soc. B Biol. Sci. 285, 20181020. https://doi.org/10.1098/rspb.2018.1020.

Tipple, B.J., Meyers, S.R., Pagani, M., 2010. Carbon isotope ratio of Cenozoic CO_2: A comparative evaluation of available geochemical proxies. Paleoceanography 25. https://doi.org/10.1029/2009PA001851.

Tomassini, R.L., Montalvo, C.I., 2013. Taphonomic modes on fluvial deposits of the Monte Hermoso Formation (early Pliocene), Buenos Aires province, Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. 369, 282–294. https://doi.org/10.1016/j.palaeo.2012.10.035.

Tomassini, R.L., Montalvo, C.I., Deschamps, C.M., Manera, T., 2013. Biostratigraphy and biochronology of the Monte Hermoso Formation (early Pliocene) at its type locality, Buenos Aires Province, Argentina. J. S. Am. Earth Sci. 48, 31–42. https://doi.org/10.1016/j.jsames.2013.08.002.

Trayler, R.B., Kohn, M.J., Bargo, M.S., Cuitiño, J.I., Kay, R.F., Strömberg, C.A., Vizcaíno, S.F., 2020. Patagonian Aridification at the Onset of the Mid-Miocene Climatic Optimum. Paleoceanogr. Paleoclimatol. 35 https://doi.org/10.1029/2020PA003956 e2020PA003956.

Tütken, T., 2011. The diet of sauropod dinosaurs: Implications from carbon isotope analysis of teeth, bones, and plants. In: Klein, K., Remes, K., Gee, C.T., Sander, P.M. (Eds.), Understanding the lifeof giants. The biology of the sauropod dinosaurs. Indiana University Press, Bloomington, pp. 57–79.

Vermeesch, P., 2018. Isoplot R: a free and open toolbox for geochronology. Geosci. Front. 9, 1479–1793. https://doi.org/10.1016/j.gsf.2018.04.001.

Vermeesch, P., 2021. Maximum depositional age estimation revisited. Geosci. Front. 12, 843–850. https://doi.org/10.1016/j.gsf.2020.08.008.

Verzi, D.H., Montalvo, C.I., 2008. The oldest South American Cricetidae (Rodentia) and Mustelidae (Carnivora): late Miocene faunal turnover in central Argentina and the Great American Biotic Interchange. Palaeogeogr. Palaeoclimatol. Palaeoecol. 267, 284–291. https://doi.org/10.1016/j.palaeo.2008.07.003.

Verzi, D.H., Montalvo, C.I., Deschamps, C.M., 2008. Biostratigraphy and biochronology of the Late Miocene of central Argentina: Evidence from rodents and taphonomy. Geobios 41, 145–155. https://doi.org/10.1016/j.geobios.2006.09.005.

Visconti, G., 2007. Sedimentología de la Formación Cerro Azul (Mioceno superior) de la provincia de La Pampa, Argentina. PhD Thesis, Facultad de Ciencias Exactas y Naturales. Universidad de Buenos Aires, Ciudad de Buenos Aires, 203 pp.

Vizcaíno, S.F., Farina, R.A., 1999. On the flight capabilities and distribution of the giant Miocene bird *Argentavis magnificens* (Teratornithidae). Lethaia 32, 271–278. https://doi.org/10.1111/j.1502–3931.1999.tb00546.x.

Vizcaíno, S.F., Fariña, R.A., Zárate, M.A., Bargo, M.S., Schultz, P., 2004. Palaeoecological implications of the mid–Pliocene faunal turnover in the Pampean Region (Argentina). Palaeogeogr. Palaeoclimatol. Palaeoecol. 213, 101–113. https://doi.org/10.1016/j.palaeo.2004.07.004.

Vrba, E.S., 1992. Mammals as a key to Evolutionary Theory. J. Mammal. 73, 1–28.

Vucetich, M.G., Deschamps, C.M., Pérez, M.E., 2013. Paleontology, Evolution and Systematics of Capybara. In: Moreira, J.R., Ferraz, K.M.P.M.B., Herrera, E.A., Macdonald, D.W. (Eds.), Capybara. Springer New York, New York, NY, pp. 39–59. https://doi.org/10.1007/978–1–4614–4000–0_2.

Webb, S.D., 1985. Late Cenozoic Mammal Dispersals between the Americas. In: Stehli, F. G., Webb, S.D. (Eds.), The Great American Biotic Interchange, Topics in Geobiology. Springer US, Boston, MA, pp. 357–386. https://doi.org/10.1007/978–1–4684–9181–4_14.

Webb, S.D., 2006. The Great American Biotic Interchange: patterns and processes. Ann. Mo. Bot. Gard. 93, 245–257. https://doi.org/10.3417/0026–6493(2006)93[245:TGABIP]2.0.CO;2.

Welker, F., Collins, M.J., Thomas, J.A., Wadsley, M., Brace, S., Cappellini, E., Turvey, S. T., Reguero, M., Gelfo, J.N., Kramarz, A., Burger, J., Thomas–Oates, J., Ashford, D. A., Ashton, P.D., Rowsell, K., Porter, D.M., Kessler, B., Fischer, R., Baessmann, C., Kaspar, S., Olsen, J.V., Kiley, P., Elliott, J.A., Kelstrup, C.D., Mullin, V., Hofreiter, M., Willerslev, E., Hublin, J.–.J., Orlando, L., Barnes, I., MacPhee, R.D.E., 2015. Ancient proteins resolve the evolutionary history of Darwin's South American ungulates. Nature 522, 81–84. https://doi.org/10.1038/nature14249.

Wiedenbeck, M., Hanchar, J.M., Peck, W.H., Sylvester, P., Valley, J., Whitehouse, M., Kronz, A., Morishita, Y., Nasdala, L., Fiebig, J., Franchi, I., Girard, J.–.P., Greenwood, R.C., Hinton, R., Kita, N., Mason, P.R.D., Norman, M., Ogasawara, M., Piccoli, P.M., Rhede, D., Satoh, H., Schulz Dobrick, B., Skår, O., Spicuzza, Mj, Terada, K., Tindle, A., Togashi, S., Vennemann, T., Xie, Q., Zheng, Y.–.F., 2004. Further Characterization of the 91500 Zircon Crystal. Geostand. Geoanal. Res. 28, 9–39. https://doi.org/10.1111/j.1751–908X.2004.tb01041.x.

Woodburne, M.O., 2010. The Great American Biotic Interchange: Dispersals, Tectonics, climate, Sea Level and Holding Pens. J. Mamm. Evol. 17, 245–264. https://doi.org/10.1007/s10914–010–9144–8.

Zárate, M.A., Schultz, P.H., Blasi, A., Heil, C., King, J., Hames, W., 2007. Geology and geochronology of type Chasicoan (late Miocene) mammal–bearing deposits of Buenos Aires (Argentina). J. S. Am. Earth Sci. 23, 81–90. https://doi.org/10.1016/j.jsames.2006.09.018.

Zavala, C., 1993. Estratigrafía de la localidad de Farola Monte Hermoso (Plioceno–Reciente), Provincia de Buenos Aires. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos 2, 228–235.

Zavala, C., Navarro, E., 1993. Depósitos fluviales en la Formación Monte Hermoso (Plioceno inferior–medio). Provincia de Buenos Aires. XXII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos 2, 236–244.