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Isotopic evidence for mammalian diets and environment in Early Pliocene Yepómera, Mexico

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ABSTRACT

Concurrent expansion of grassland habitat in the Americas and first appearances of immigrant taxa to Mexico via the Great American Biotic Interchange (GABI) during the Late Miocene to Early Pliocene suggest a possible link between the timing of migrations and changes in the environmental conditions. However, the causes and environmental context of GABI migrations are not well understood. This study examined the stable isotope compositions of tooth enamel samples of the Yepómera fauna from western Chihuahua, Mexico, to explore environmental conditions of this region between 4.99 and 5.23 Ma, just after the arrival of C_4 plants in North and South America and before the first major migration of GABI. At Yepómera, there was distinct niche partitioning into C_3 diets, mixed diets, and C_4 diets. Despite expectations, no niche partitioning between equid species (*Dinohippus mexicanus, Nannippus aztecus, Astrohippus stockii,* and *Neohipparion eurystyle*) can be determined from carbon isotope ratios. The enamel carbon and oxygen isotope data suggest a relatively dry, open habitat dominated by either savanna or grassland, with a substantial C_4 vegetation component and a warmer and somewhat wetter climate than today. These reconstructions are consistent with a rise in C_4 biomass before 5.23 Ma and suggest that the conditions needed for growth of C_4 vegetation were prevalent in this region of Mexico. Future work along the GABI migration route will lead to a more complete understanding of the ecologic responses to changing climate and faunal interchange events.

1. Introduction

Significant climate and tectonic changes occurred during the Miocene that greatly affected ecology across the Americas in the Pliocene. Marine oxygen isotope records suggest a long-term cooling trend after the Mid-Miocene Climatic Optimum (MMCO) (Zachos et al., 2001) while terrestrial carbon isotope records from various localities around the world suggest a rapid expansion of grasses using C_4 photosynthetic pathway in the late Miocene (Cerling et al., 1997; Edwards et al., 2010). Given that C_4 photosynthesis is favored under low CO_2, high temperature, and water-stressed conditions (Ehleringer et al., 1991a), the late Miocene C_4 expansion was thought to be driven by a decline in atmospheric pCO_2 – the CO_2 hypothesis (Cerling et al., 1997). However, pCO_2 reconstructions based on geochemical proxies suggest no significant changes in pCO_2 during the Miocene (e.g., Pagani et al., 2005; Foster et al., 2017). These paleo-CO_2 estimates, along with the observed regional differences in the timing of the C_4 expansion, were used to argue against the CO_2 hypothesis and other forcing mechanisms have been proposed to explain the late Miocene C_4 expansion including increased aridity or increased fire frequency/disturbance (e.g., Tipple and Pagani, 2007; Edwards et al., 2010; Fox et al., 2012; Hoetzel et al., 2013). However, other recent pCO_2 reconstructions show declining pCO_2 that approached pre-industrial levels during the late Miocene (Tripati et al., 2009; Bolton et al., 2016; Mejía et al., 2017; Witkowski et al., 2018), around the time that C_4 biomass started to increase in Africa, providing support for the CO_2 hypothesis (Polissar et al., 2019). It is possible that low pCO_2 is the necessary condition or the key driver of C_4 grass expansion and regional differences in the timing and extent of C_4 expansion reflect the secondary influence of other environmental factors such as regional/local temperature and precipitation (Cerling et al., 1997; Polissar et al., 2019). If pCO_2 was indeed the key driver, one would expect C_4 grasses to spread earlier and to a greater extent in

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warmer and relatively dry low latitude regions (Cerling et al., 1997). C_4 abundances in the Late Miocene appear to progressively increase southward from records in the United States (Teeri and Stowe, 1976; Cerling et al., 1998; Tipple and Pagani, 2007; Passey et al., 2002) and this pattern seems to continue into Mexico from the limited studies of sites in this region (Cerling et al., 1998; MacFadden, 2006; Pérez-Crespo et al., 2012, 2016, 2017), suggesting that Mexico could have likely been the center of origin for C_4 plants in North America. Central to northern Mexico should be an ideal location for testing these hypotheses given the high average annual temperatures, lower latitude, and low average annual precipitation (Schneider et al., 2011; Lawrimore et al., 2016; IAEA/WMO, 2021) relative to the Great Plains region known for its thorough C_4 records (e.g., Edwards et al., 2010; Fox et al., 2012). With the expansion of grasslands in North America in the early Miocene, animals adapted to open environments (Maguire and Stigall, 2008; Edwards et al., 2010; Strömberg, 2011). All these changes in environment and adaptations to these environments would have set the stage for species interactions during the Great American Biotic Interchange (GABI) when migration of fauna across the Panama land bridge began (Woodburne, 2010).

While the timing of the final closure of the Central American Seaway remains contentious (e.g., Keigwin Jr, 1978; Marshall et al., 1982; Marshall, 1988; Coates et al., 1992; Webb, 2006; Woodburne, 2010; Montes et al., 2012; Coates and Stallard, 2013; Bacon et al., 2015; O'Dea et al., 2016), several first appearances of migrant taxa in Mexico occurred prior to the first major GABI pulse at 3 Ma and predate the traditionally accepted closure of the Panama Isthmus at 5–3 Ma (Flynn et al., 2005; Bloch et al., 2016). Reconciliation of this late closure with early exchanges can be accomplished through “rafting” (Houle, 1999; Carranza-Castañeda and Miller, 2004; de Queiroz, 2005; Jackson and O'Dea, 2013) and the initial collision of South America with Panama at ~25 Ma creating a narrow, crossable Central American Seaway (Farris et al., 2011; Montes et al., 2012; Bacon et al., 2015). Several open environment-adapted immigrant taxa from South America have been reported appearing earlier (in the late Hemphillian) in Mexico than in the temperate parts of North America (Flynn et al., 2005). Webb (1978) considered various migrant taxa (e.g., *Glossotherium*, *Glyptotherium*, *Dasypus*, *Hemiauchenia*, *Lama*, *Palaeolama*, *Hippidion*, *Onohippidion*, *Neochoerus*, *Hydrochoerus*, *Calomys*, *Stegomastodon*, *Argyrohyus*, *Platygonus*, *Erethizon*, *Arctotherium*, *Titanis*, and *Dusicyon*) involved in GABI exchanges to be savanna-adapted. Later work has corroborated that these taxa favored temperate grassland to savanna habitats (McDonald, 2005; Pérez-Crespo et al., 2012; Prado and Alberdi, 2014; Saarinen and Karme, 2017; Omena et al., 2020; Tomassini et al., 2020). While the involvement of *Stegomastodon* in GABI has been contested as a misidentification (Mothé et al., 2012; Mothé et al., 2019), recent studies presented unequivocal evidence that another proboscidean (*Cuvieronius hyodon*) that favored open environments (Pérez-Crespo et al., 2016) migrated during GABI (Prado and Alberdi, 2014; Mothé et al., 2019). Because many successful migratory taxa appear to have been savanna-adapted, there should have been corridors of open environment to allow for successful migration between North America and South America (Webb, 1991; Woodburne, 2010). The environment across the Central American land bridge is thought to have shifted between rainforest and grassland as tropical humidity changed in response to transient, regional-scale glacial events in the middle to late Pliocene and glacial cycles of the Pleistocene (Webb, 1978, 1991; Woodburne, 2010; Mudelsee and Raymo, 2005; De Schepper et al., 2014; Jiménez-Moreno et al., 2019). Fauna in Mexico should have diets reflecting prevalent grassland or savanna habitats since open habitats would be necessary for the savanna-adapted migrant taxon to have crossed between South America and the Great Plains or temperate North America. Recent studies have uncovered fossils of endemic North American tropical fauna from the early to middle Miocene strata in Panama (MacFadden et al., 2014; Wood and Ridgwell, 2015). Given the proximity of these fossil localities to rainforests in South America (Hoorn et al., 2010; Prado and Alberdi, 2014), there has also been exchange of rainforest-adapted fauna (e.g., an early Miocene monkey from South American discovered in Panama) (Bloch et al., 2016), but northward movement may have been restricted by more arid sections of Mexico. This highlights the importance of examining fossils across Mexico to determine how far different habitats across the Americas extended spatially and temporally.

In this study, we analyzed the stable carbon and oxygen isotopic ratios ($\delta^{13}C$ and $\delta^{18}O$) of 215 tooth enamel samples from a diverse group of fossil mammals from western Chihuahua, Mexico. The isotope data were used to examine the dietary habits of these ancient mammals and to reconstruct the local environmental conditions during the late Hemphillian. While the study area is far north of Central Mexico, previous efforts have focused on the Great Plains regions and studies of records in Mexico remain sparse. A complete understanding of the GABI exchanges will require studying the entire path over which migrations occurred.

2. Background

2.1. Stable isotopes in plants

C_3 and C_4 plants fractionate carbon isotopes differently due to the use of different photosynthetic pathways (Farquhar et al., 1982, 1989). C_3 plants are mainly woody plants and grasses with cool growing seasons and have more negative $\delta^{13}C$ values between −22 and − 36‰, with an average of −27‰ (Cerling et al., 1993, 1997; Kohn, 2010). Within C_3 plants, $\delta^{13}C$ values above the average value are typically associated with plants experiencing water stress, with values greater than −23‰ almost exclusively found in desert ecosystems, while $\delta^{13}C$ values less than −31‰ are found in the understories of closed-canopy forests (Farquhar et al., 1989; Cerling et al., 1997; Cerling, 1999; Cerling and Harris, 1999; Kohn, 2010). C_4 plants are mainly grasses with warm growing seasons that are more drought resistant and tend to have $\delta^{13}C$ values between −9 and −17‰, averaging to a value of −12.5‰ (Troughton et al., 1974; Vogel et al., 1978; Cerling et al., 1997; Smith et al., 2002). The C_4 photosynthetic pathway has greater photosynthetic efficiency than the C_3 photosynthetic pathway under low carbon dioxide, high temperature, and/or high aridity conditions (Ku et al., 1977; Jordan and Ogren, 1984; Brooks and Farquhar, 1985; Sharkey, 1988; Farquhar et al., 1989; Ehleringer et al., 1991a, 1991b, 1997; Cerling et al., 1997). As such C_4 plants would be expected to dominate in regions where these conditions prevail. The predominance of one vegetation type over another should reflect the prevailing environmental conditions and should be detectable through carbon isotope ratios in paleosols or in the hydroxyapatite of grazers or browsers.

2.2. Stable isotopes in tooth enamel as paleoecological and paleoclimatic indicators

Stable isotope analysis of vertebrate tooth enamel has found substantial use in paleoenvironmental and paleodietary reconstruction (e.g., Cerling and Harris, 1999; Kohn and Cerling, 2002; Smith et al., 2002; Fox and Fisher, 2004; MacFadden and Higgins, 2004; MacFadden, 2005; Nunez et al., 2010; Hynek et al., 2012; Pérez-Crespo et al., 2017). Carbon isotope ratios of consumed plants (or animals for carnivores) are incorporated into the structural carbonate of bone and dental tissue with an enrichment factor (ε). This enrichment has commonly been taken as 14.1 ± 0.5‰ for ruminant mammals (Krueger and Sullivan, 1984; Cerling and Harris, 1999) or 13‰ for non-ruminant mammals (Passey et al., 2005). However, this is likely an oversimplification. Recent studies (Tejada-Lara et al., 2018; Cerling et al., 2021) suggest that species have varied enrichment factors depending on body size and metabolism differences.

In addition to determining food sources, differences between specimens with a similar diet can be used to interpret water stress, which can shift the carbon isotope ratio in plants (Freudenthal et al., 2014). The

$\delta^{13}C$ of enamel of C_3 consumers can also be used to constrain mean annual precipitation (MAP) by using the offset between dietary and atmospheric carbon isotope ratios (Kohn, 2010; Drewicz and Kohn, 2018). Enamel $\delta^{13}C$ thus has great potential use in assessing the ecological and climatic conditions of a study site.

Oxygen isotopes are preserved in the structural carbonate and in the phosphate of enamel hydroxyapatite (Longinelli, 1984; Luz et al., 1984; Kohn and Cerling, 2002; Hillson, 2005). Enamel $\delta^{18}O$ values reflect the $\delta^{18}O$ of body water, which ultimately comes from ingested water (Longinelli, 1984; Luz et al., 1984; Makarewicz and Pederzani, 2017). Herbivore $\delta^{18}O$ can reflect the $\delta^{18}O$ of meteoric water if the organism is an obligate drinker or that of leaf water if from the enamel of drought-tolerant species (Kohn et al., 1996; Levin et al., 2006; Makarewicz and Pederzani, 2017). Leaf water is generally enriched in ^{18}O relative to local meteoric water due to evapotranspiration (Dongmann et al., 1974; Epstein et al., 1977). The oxygen isotope ratios of obligate drinkers are strongly correlated with the oxygen isotopic composition of local meteoric water; and the latter varies with temperature in mid to high latitude regions or with precipitation amount at low latitudes (Dansgaard, 1964; Rozanski et al., 1993; Bowen and Wilkinson, 2002). The oxygen isotope ratios of nonobligate drinkers vary with humidity and leaf evapotranspiration rates, with higher transpiration resulting in more enrichment in ^{18}O in the leaf water and thus the enamel (Dongmann et al., 1974; Fricke and O'Neil, 1999; Hillson, 2005; Levin et al., 2006; Ripullone et al., 2008; Drewicz and Kohn, 2018). Changes in enamel $\delta^{18}O$ of obligate drinkers, if unaltered by diagenesis, can thus be used to infer temperature or precipitation changes (Fricke and O'Neil, 1996; Fricke et al., 1998). As drinking habits of fossil taxa are difficult to verify, drinking habit is assumed to be identical between fossil taxon and extant relatives. While the main drivers of oxygen isotope fractionation in precipitation are temperature and amount of precipitation ("amount effect"), other factors such as latitude, altitude, distance to coast ("continental effect"), and moisture source/circulation changes can also affect the $\delta^{18}O$ of precipitation (Dansgaard, 1964; Sharp, 2007). Higher latitudes, higher altitudes, and/or greater distances to coast in general lead to lower oxygen isotope ratios in precipitation (Sharp, 2007). As such, these factors must also be accounted for in comparisons to other sites.

Enamel is normally the best preserved of hard tissues because of its dense crystalline structure, low organic and water content, and low porosity, making enamel the best suited tissue for paleo-environmental studies (Quade et al., 1992; Wang and Cerling, 1994; Koch et al., 1997; Koch, 1998; Cerling and Harris, 1999; Kohn et al., 1998; Hillson, 2005). Unlike bone tissue, dental tissues do not experience turnover, so the isotopic signature is not being altered after crystallization is completed (Hillson, 2005). Enamel grows incrementally from the crown of the tooth toward the root—with layers or bands representing material formed at roughly the same time—and can be used to create a time series of environmental changes throughout tooth formation (Fricke and O'Neil, 1996; Fricke et al., 1998; Hillson, 2005; Brookman and Ambrose, 2012).

3. Study site

Several localities in the Yepómera area (center of Yepómera—29°03′20″ N, 107°51′15″ W, elevation: 1942 m) of western Chihuahua, Mexico, were the focus of this research (Lindsay, 1984; Lindsay et al., 2006; McLeod, 2006). Most of the specimens sampled for this study came from one of two sites within the river valley called Arroyo Huachin (CIT 275) (site 1: 29°06′40″ N, 107°51′56″ W, elevation: 1973 m; site 2: 29°07′15″ N, 107°51′18″ W, elevation: 2008 m). The mean annual precipitation (MAP) recorded at a station in Temósachic (MXN00008208—28°57′00″ N, 107°50′00″ W, elevation: 1869 m) from 1961 to 1986 was 512 ± 172 mm/yr (±1σ). The study area is bordered by the arid conditions of the Chihuahuan Desert to the north and east and wetter conditions to the south and west (Schneider et al., 2011; Lawrimore et al., 2016) (Fig. 1). The MAP recorded at the IAEA-GNIP (International Atomic Energy Agency Global Network for Isotopes in Precipitation) station in Chihuahua, Chihuahua, Mexico (28.63°N, 106.07°W, elevation: 1423 m) is 358 ± 159 mm/yr (±1σ) (IAEA/WMO, 2021). The mean annual temperature (MAT) recorded at the station in Temósachic, Chihuahua, Mexico from 1961 to 1986 was 12.6 ± 0.7 °C (±1σ), with average minimum and maximum temperatures of 2.1 ± 1.0 °C and 23.2 ± 0.7 °C (±1σ), respectively (Lawrimore et al., 2016). MAT recorded at the IAEA-GNIP (International Atomic Energy Agency Global Network for Isotopes in Precipitation) station in Chihuahua, Chihuahua, Mexico (28.63°N, 106.07°W, elevation: 1423 m) from 1962 to 1988 was 18.1 ± 1.2 °C (±1σ) (IAEA/WMO, 2021). While the IAEA-GNIP station in Chihuahua is much lower in elevation than modern Yepómera, it was likely closer to the elevation of this study site during the Pliocene when the elevation of the North American Cordillera was thought to be only ~50% of its modern elevation (Thompson and Fleming, 1996; Dowsett et al., 1999; Haywood and Valdes, 2004). Under the Köppen-Geiger climate classification system, Yepómera is classified as a cool, arid steppe (BSk) (Kottek et al., 2006). This is the same category as much of the Great Plains region, but at lower latitude and higher elevation. Average MAT in Temósachic from 1961 to 1986 is slightly higher than average MAT recorded at several stations (USC00257830 [NE], USC00291963 [NM], USC00299156 [NM], USC00343628 [OK], USC00395090 [SD], USC00411267 [TX], USC00480270 [WY],

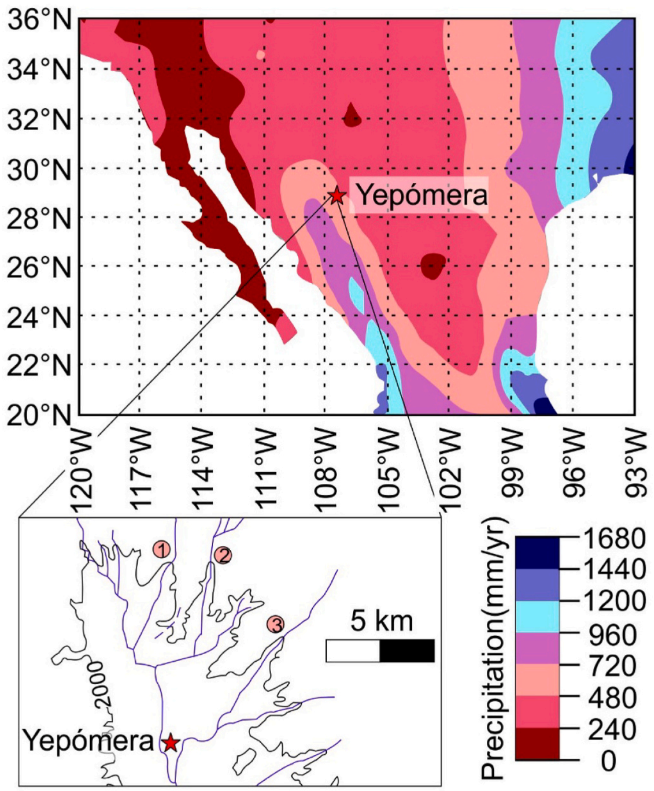

Fig. 1. Map of the Yepómera locality and modern precipitation.
The mean annual precipitation was estimated by multiplying the average monthly precipitation (from 1891 to 2016) by 12. The red star represents the study site, which is enlarged in the lower panel. The localities shown are (1) Arroyo Huachin (LACM CIT 275), (2) Arroyo de las Burras (LACM CIT 276), and (3) Arroyo de los Poños (LACM CIT 289). Sites 1 and 2 represent the most productive sites and the ones from which most of the samples in this study were taken.
GPCC Precipitation data provided by the NOAA/OAR/ESRL PSL, Boulder, Colorado, USA, from https://psl.noaa.gov/ (Schneider et al., 2011). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

USC00483855 [WY], USW00003024 [TX], USW00003932 [OK], USW00003936 [KS], USW00003954 [OK], USW00013967 [OK], USW00023007 [TX], USW00023052 [NM], USW00023062 [CO], USW00023065 [KS], USW00024090 [SD], USW00093058 [CO]) across the Great Plains for the same period (11.2 ± 0.6 °C) (Lawrimore et al., 2016), but this difference is not statistically significant. Average MAT recorded at the IAEA-GNIP station in Chihuahua from 1962 to 1988, on the other hand, is significantly higher than modern Yepómera and the Great Plains region. If the elevation of Yepómera was indeed lower during the Late Miocene and Early Pliocene than today, then this area should be more similar in climate to Chihuahua and would be much warmer than the Great Plains region because of its lower latitude.

The moisture sources of this area are the Gulf of Mexico and the Pacific Ocean (Hales, 1974; Barlow et al., 1998; Fawcett et al., 2002; Lachniet and Patterson, 2009; Durán-Quesada et al., 2010). The long-term (1962–1988) precipitation isotope record from the IAEA-GNIP station in Chihuahua show that winter precipitation in the study region has lower $\delta^{18}O$ values (−9.7 ± 2.6‰; ±1σ) than summer precipitation (−5.6 ± 0.4‰; ±1σ) (IAEA/WMO, 2021) (Fig. 2). The amount weighted long-term average precipitation $\delta^{18}O$ in the region is −7.1 ± 2.8‰ (±1σ) (IAEA/WMO, 2021). A difference in proportion of moisture sources could change the oxygen isotope composition of precipitation without a change in temperature or amount of rainfall. One of the assumptions made in this study is that the moisture sources and circulation patterns around this study area in the Late Miocene-Early Pliocene are comparable to modern patterns based on the isotope work of Billups et al. (1998) and modelling by Micheels et al. (2007). Admittedly, the North American Monsoon is not well understood, and the proportion of each moisture source is still debated (Barlow et al., 1998; Seth et al., 2019). It has also been suggested that shifts in moisture sources occurred during transitions between stadials and interstadials (Asmerom et al., 2010; Wagner et al., 2010; An et al., 2015); this, however, should not be relevant during the early Pliocene. If the assumption of a moisture source analogous to modern is found to be incorrect, then reconstructed MAT (relying on modern relationships between MAT, latitude, and oxygen isotope distribution) and reconstructed MAP (relying on modern relationships between MAP, carbon isotopes, altitude, and latitude) would need to be reevaluated. This is not a necessary assumption for the interpretation of ecology and niche partitioning.

Yepómera is a series of sub-localities with similar faunal assemblages (Lindsay et al., 2006; MacFadden, 2006). This fauna includes a large abundance and diversity of equids, with lesser amounts of pronghorn, camels, and proboscideans (Lindsay et al., 2006; McLeod, 2006). The Yepómera fauna in the Yepómera region, as defined by Lindsay et al. (2006), are correlated to the latest Hemphillian (Hh4) North American Land Mammal age (Tedford et al., 2004), and most of the sites fall within the Thvera Subchron (C3n.4n) aged to between 4.99 and 5.23 Ma (Cande and Kent, 1995; Lindsay et al., 2006; Hilgen et al., 2012) (Fig. 3).

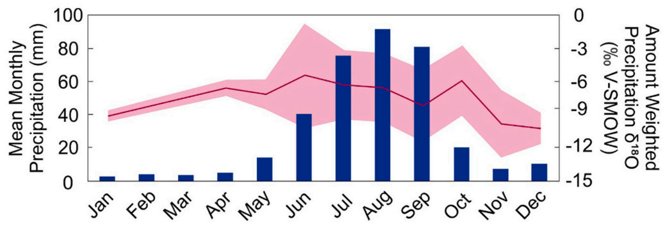

Fig. 2. Monthly Precipitation and Precipitation Oxygen Isotope Composition in Chihuahua, Mexico, for the period of 1962–1988.
Bars correspond to average monthly precipitation. The solid red line corresponds to amount weighted mean monthly $\delta^{18}O$ of precipitation. The light red area represents the 90% confidence interval of monthly average $\delta^{18}O$ of precipitation. (Precipitation and isotope data from IAEA/WMO, 2021). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

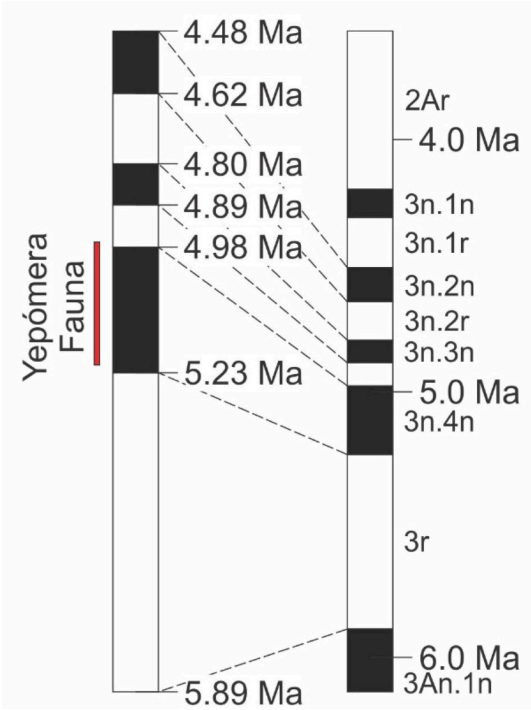

Fig. 3. Magnetostratigraphy of Yepómera sites.
The estimated temporal range of the Yepómera fauna is drawn in against the Geomagnetic Polarity Time Scale (GPTS). LACM CIT 275 (Arroyo Huachin, Y-13) and LACM CIT 276 (Arroyo de las Burras, Y-3) fit within the Thvera Subchron (C3n.4n). LACM CIT 277, CIT 278, CIT 280, CIT 281, CIT 289, and CIT 447 are known to be Hemphillian and thus older than the Concha fauna (Clarendonian), which appears by the Sidufjall Subchron (4.8 to 4.89 Ma). LACM CIT 274 may have Pleistocene fossils, making it more difficult to determine the age of this site. Since the majority of specimens come from LACM CIT 275, this study should reflect conditions between 4.98 and 5.23 Ma, but the possibility of samples as young as 4.89 Ma cannot be excluded. (Based on Lindsay et al., 2006).

The Yepómera assemblage does extend slightly out of the Thvera Subchron into the subsequent reversal, but no strata from which samples were collected are younger than 4.99 Ma (the start of the next normal polarity interval) (Cande and Kent, 1995; Lindsay et al., 2006; Hilgen et al., 2012). As such, the age of samples in this study can best be constrained between 4.99 Ma to 5.23 Ma. Strata are roughly horizontal, fine grained, and well sorted, but with some discontinuous fluvial sands, siltstones, gravel, marls, and diatomites (Lindsay et al., 2006). In the 1930s to 1940s, the California Institute of Technology collected an extensive quantity of specimens from Yepómera, a collection that has been transferred to the Natural History Museum of Los Angeles County where it is being curated and is available for study (MacFadden, 2006; McLeod, 2006). For these specimens, field photographs and communication with Chester Stock, who directed the collection, have been used to reconstruct most of the collection information because no field notes, no locality descriptions, and only a single field map has survived (MacFadden, 2006; McLeod, 2006).

4. Methods

4.1. Sample selection

Fossil teeth housed in the collections of the Natural History Museum of Los Angeles County (LACM) were sampled for this study. This collection is not well constrained stratigraphically due to the limited notes of the CalTech fieldwork team. A total of 215 enamel powder samples were collected from 65 fossil teeth (63 from unique specimens of a given taxa, 2 duplicate teeth from 2 of these specimens from which a tooth had already been sampled) for carbon and oxygen isotope analyses (Suppl. Table 1). The specimens in this study come from several LACM localities from Yepómera, Temósachic, and Matachic areas: LACM CIT 274 (Orozco Ranch) ($n = 1$), LACM CIT 275 (Arroyo Huachin) ($n = 33$, 31 unique and 2 duplicates), LACM CIT 276 (Arroyo de las Burras) ($n = 10$), LACM CIT 277 (Hernández Quarry) ($n = 6$), LACM CIT 278 (Arroyo Vacío) ($n = 2$), LACM CIT 280 (Arroyo de las Tinajas) (n = 1), LACM CIT 281 (Matachic 1) (n = 1), LACM CIT 286 (Arroyo de las Barrancas Blancas) (n = 1), LACM CIT 289 (Arroyo de los Poños) ($n = 8$), and LACM CIT 447 (Morales Ranch) (n = 2) (Lindsay et al., 2006). The specimens include a variety of mammalian herbivores typical of the Yepómera assemblage, including equids, pronghorns, camelids, proboscideans, and peccaries, plus one presumed omnivore, *Agriotherium* (Lindsay, 1984). Teeth from as many specimens of each taxon as possible were sampled (Table 1). Sample sizes (number of specimens) of each taxon are below the number suggested by Clementz and Koch (2001) to be a statistically robust sample size for terrestrial mammals ($n = 16$). Thus, the interpretations of Early Pliocene ecology at this site should be taken as preliminary and revised as more complementary or comprehensive work is completed. The last molars to erupt (M3s or m3s) were chosen for sampling whenever possible because these are produced later in life and avoid any possible lactation effect (Bryant et al., 1994; Zazzo et al., 2000; Jenkins et al., 2001; Hillson, 2005). However, other studies seem to suggest that there is no lactation effect on isotopes (Kohn et al., 1998; Gadbury et al., 2000; Nelson, 2005). As such, other molars and premolars were sampled when third molars were not available. It is worth noting that this is an assumption based on eruption of teeth and nursing in modern animals as analogues (Fricke and O'Neil, 1996; Hoppe et al., 2004; Rountrey et al., 2012). Teeth may have erupted earlier or later in fossil taxa and duration of nursing in extinct taxa may have been different from extant relatives (Metcalfe et al., 2010). Two teeth from a single bear (*A. schneideri*) were sampled to determine the predominant prey source.

Taxonomy of sampled taxa mostly follow those by Lindsay et al. (2006) and MacFadden (2006). The sampled teeth were identified to either the species-level or genus-level (depending on which taxon) with confidence. No teeth that were beyond a reasonable level of confidence in classification were sampled. However, with exception of the horses, which mostly fall into discrete size classes, taxonomic identifications for other mammals based on enamel fragments do carry at least a small element of uncertainty. Samples coming from a tooth that was partly fragmented or damaged are identified in Suppl. Table 1.

4.2. *Sampling and isotope analyses*

The outer surfaces were cleaned, and non-enamel material was removed from the sampling surface prior to enamel collection with a rotary tool. Serial samples of enamel were collected through drilling at 23 mm intervals along the growth axis (in bands following the curvature of growth rings). Bulk samples were collected from specimens not suited for serial sampling by drilling parallel to the growth axis of each tooth. Enamel samples were treated following a commonly used procedure (e.g., Bowman et al., 2017) and prepared for isotope analysis following the carbonate acid digestion methodology of McCrea (1950). Samples were treated with a 5% sodium hypochlorite to remove organic matter, followed by a 1 M acetic acid to remove non-structural carbonate. The treated samples were then cleaned with distilled water and freeze-dried. Phosphoric acid (100%) was used to react with the sample powders at 25 °C to release carbon dioxide. A GasBench II Auto-carbonate device connected to a Finnigan MAT Delta Plus XP stable isotope ratio mass spectrometer (IRMS) via continuous flow helium stream was used to analyze the released carbon dioxide for carbon and oxygen isotope ratios. Average accuracy and precision for these measurements were 0.0 and 0.1‰ (1σ), respectively, for carbonate δ^{13}C and δ^{18}O, based on repeated analyses of lab standards. Several carbonate standards including NBS-19 ($\delta^{13}C = 1.95$‰ and $\delta^{18}O = -2.2$‰) and intra-lab standards (MB-cc: $\delta^{13}C = -10.5$‰ and $\delta^{18}O = -3.14$‰; ROY-cc: $\delta^{13}C = 0.67$‰ and $\delta^{18}O = -12.02$‰; and MERK: $\delta^{13}C = -35.5$‰ and $\delta^{18}O = -16.2$‰) calibrated to the international standard Vienna Peedee Belemnite (V-PDB) were used as a control. All enamel carbonate results are reported in the standard δ notation as δ^{13}C and δ^{18}O values in permil (‰) relative to V-PDB.

Thirteen samples were randomly selected for analysis of oxygen isotope ratios in phosphate (Suppl. Table 2) to check for diagenetic alteration. Sample treatment for phosphate oxygen isotope analysis followed the methodology of Crowson et al. (1991) and LaPorte et al. (2009). Samples were treated with a 5% sodium hypochlorite to remove organic matter, followed by a 1 M acetic acid to remove non-structural carbonate. The samples were then treated with 2 M hydrofluoric acid and allowed to sit in an ultrasonic bath overnight. The solution was further treated with 20% ammonium hydroxide to bring it to neutral. Next, a solution of 2 M silver nitrate was added to precipitate tri-silver phosphate crystals. The crystals were then cleaned with distilled water and freeze-dried. The crystals were loaded into silver capsules and pyrolyzed at high temperature (1450 °C) in a thermal conversion elemental analyzer (TC/EA) coupled to the IRMS via continuous flow helium stream to analyze for oxygen isotope ratios. Average accuracy and precision for these measurements were 0.1 and 0.1‰ (1σ) (based on multiple analyses of lab standards), respectively, for phosphate oxygen isotope data. Several standards including NBS-120c ($\delta^{18}O = 21.7$‰), IAEA-601($\delta^{18}O = 23.14$‰), IAEA-602 ($\delta^{18}O = 71.28$‰), and intra-lab phosphate standards (UMS-1: $\delta^{18}O = 12.0$‰; Karen-H: $\delta^{18}O = 16.65$‰; Karen-L: $\delta^{18}O = 8.92$‰) calibrated to the international standard Vienna Standard Mean Ocean Water (V-SMOW) were used as a control. All phosphate results are reported as $\delta^{18}O_{PO4}$ values in permil relative to V-SMOW.

4.3. *Reconstructing δ^{13}C of diet base*

Published body masses (BM) were used for those taxa for which estimations exist: *Prosthennops serus* (88 ± 26 kg; ±1σ) (Lambert, 2006),

Table 1

Summary of results of carbon and oxygen isotope analyses of tooth enamel samples from Yepómera, Mexico.

Taxa	Common name	No. of enamel samples	No. of individuals	Mean δ^{13}C (‰)	±1σ (‰)	Mean δ^{18}O (‰)	±1σ (‰)
Agriotherium schneideri	bear	2	1	−5.7	0.3	−4.2	0.1
Paracamelus sp.	camel	18	7	−7.6	1.6	−1.9	0.9
Hemiauchenia sp.	llama	16	7	−5.5	3.0	0.0	2.7
Astrohippus stockii	horse	27	7	0.3	1.2	−2.3	0.6
Dinohippus mexicanus	horse	43	7	−0.7	1.4	−2.3	1.3
Nannippus aztecus	horse	17	7	−1.3	0.6	−2.3	0.8
Neohipparion eurystyle	horse	33	7	−0.2	2.0	−3.5	0.9
Prosthennops serus	peccary	7	5	−4.8	2.9	−2.1	0.9
Stegomastodon sp.	proboscidean	21	7	−4.2	2.0	−3.6	1.4
Hexobelomeryx fricki	pronghorn	31	8	−4.3	1.7	−2.1	0.8

Hexobelomeryx fricki (30 ± 9 kg; ±1σ) (Jiménez-Hidalgo and Carranza-Castañeda, 2011), *Hemiauchenia* sp. (200 ± 60 kg; ±1σ) and *Paracamelus* sp. (600 ± 180 kg; ±1σ) (Dalquest, 1992; Janis et al., 2002; Lambert, 2006), *Astrohippus stockii* (127 ± 38 kg; ±1σ), *Dinohippus mexicanus* (245 ± 74 kg; ±1σ), *Nannippus aztecus* (previously *N. minor*) (89 ± 27 kg; ±1σ), and *Neohipparion eurystyle* (141 ± 42 kg; ±1σ) (MacFadden, 1986; Alberdi et al., 1995; MacFadden et al., 1999; Lambert, 2006), and *Stegomastodon* (6030 ± 1809 kg; ±1σ) (Christiansen, 2004; Larramendi, 2015). The body mass of *Agriotherium schneideri* was calculated using the carnivore tooth crown area-body mass regression and measured crown area of teeth sampled (900 mm^2) to calculate a body mass of 510, which seems reasonable given similar estimates of other species of *Agriotherium* (Legendre and Roth, 1988; Sorkin, 2006).

Body masses of herbivores were used to calculate species specific enamel-diet enrichment factors using one of the following equations given in Tejada-Lara et al. (2018):

$$\text{Foregut fermenters}: ln(\varepsilon) = 2.34 + 0.05 \times ln(\text{BM}) \tag{1}$$

$$\text{Hindgut fermenters}: ln(\varepsilon) = 2.42 + 0.032 \times ln(\text{BM}) \tag{2}$$

Where ε is the enrichment factor (in ‰) and the BM is the body mass (in kg). The basis of the equation is the link between body mass and quantity of methane produced. In this way, taxa with hindgut fermentation and foregut fermentation are expected to differ in enrichment factor (ε) despite similar size. Fermentation types in extinct taxa are inferred from extant relatives: those related to modern camels, llamas, and pronghorns are considered foregut fermenters; those related to modern horses, proboscideans, and peccaries are considered hindgut fermenters. The calculated enrichment factors are shown in Table 2.

Measured enamel δ^{13}C value was adjusted by an enrichment factor ($\mathcal{E}_{\text{enamel-diet}}$) to reconstruct the δ^{13}C value of the diet base. It was then corrected for the difference in atmospheric carbon isotopic ratios ($\delta^{13}C_{\text{atm}}$) between the modern and the Latest Miocene-Early Pliocene. Assuming a modern $\delta^{13}C_{\text{atm}}$ value of between −7.5% and − 8% (based on NOAA MLO records) and the Latest Miocene-Early Pliocene estimate of −6.25‰ from the $\delta^{13}C_{\text{atm}}$ reconstruction of Tipple et al. (2010), vegetation in the past should be enriched in ^{13}C by approximately 1.5‰ relative to modern vegetation of the same type. The corrected δ^{13}C values of diet bases ($\delta^{13}C_{\text{diet base}} = \delta^{13}C_{\text{enamel}} - \mathcal{E}_{\text{enamel-diet}} - 1.5‰$) can be sorted into C_3 ($\delta^{13}C_{\text{diet base}} \leq -23.0‰$), mixed ($-23.0‰ < \delta^{13}C_{\text{diet base}} < -17.0‰$), and C_4 ($\delta^{13}C_{\text{diet base}} \geq -17.0‰$) categories based on the δ^{13}C ranges of modern C_3 and C_4 plants reported by Troughton et al. (1974), Vogel et al. (1978), Cerling et al. (1997), and Kohn (2010). All further mentions of diet base include this correction for $\delta^{13}C_{\text{atm}}$ differences. Niche specialization was assessed based on paired *t*-tests between each taxon (Table 3; Suppl. Tables 3, 4, 5).

4.4. Reconstructing δ^{18}O of local water

Published equations linking phosphate and environmental water δ^{18}O listed below were used to calculate the δ^{18}O of the water source from enamel phosphate δ^{18}O. Taxon-specific equations from modern relatives were used when available. A general equation was used for the taxa in which no fractionation data for their modern relatives have been published (i.e., camelids) (Bryant et al., 1994; Ayliffe et al., 1992; Pietsch and Tütken, 2015).

$$\text{Equid}: \delta^{18}O_{\text{water}} = 0.69 \times \delta^{18}O_{\text{PO4}} + 22.9 \tag{3}$$

$$\text{Elephant}: \delta^{18}O_{\text{water}} = 1.06 \times \delta^{18}O_{\text{PO4}} + 24.3 \tag{4}$$

$$\text{General}: \delta^{18}O_{\text{water}} = 0.68 \times \delta^{18}O_{\text{PO4}} + 21.7 \tag{5}$$

In the above equations, $\delta^{18}O_{\text{water}}$ and $\delta^{18}O_{\text{PO4}}$ are the δ^{18}O of water and phosphate, respectively, on the V-SMOW reference scale. For enamel samples whose phosphate component was not analyzed, their phosphate δ^{18}O values were calculated from the δ^{18}O values of structural carbonate in enamel using the relationship for modern mammals given in Iacumin et al. (1996).

Table 2

Estimated body sizes, enamel-diet enrichment factors (ε), and δ^{13}C values of diet base for Yepómera fauna.*

Taxa	Body Mass (kg)	ε (‰)	Mean enamel δ^{13}C (‰)	Mean diet δ^{13}C (‰)	Modern-equivalent diet δ^{13}C (‰)	Diet type
Agriotherium schneideri	510 ± 153	+8.0	−5.7 ± 0.3	−13.7 ± 0.3	−15.2 ± 0.3	Prey with C_4 Diet
Paracamelus sp.	600 ± 180	+14.5 ± 1.7	−7.6 ± 1.1	−22.1 ± 2.0	−23.6 ± 2.0	C_3
Hemiauchenia sp.	200 ± 60	+13.5 ± 1.6	−5.5 ± 0.6	−19.0 ± 1.7	−20.5 ± 1.7	Mixed
Astrohippus stockii	127 ± 38	+13.1 ± 1.3	0.3 ± 0.5	−12.8 ± 1.4	−14.3 ± 1.4	C_4
Dinohippus mexicanus	245 ± 74	+13.4 ± 1.3	−0.7 ± 0.5	−14.1 ± 1.4	−15.6 ± 1.4	C_4
Nannippus aztecus	89 ± 27	+13.0 ± 1.3	−1.3 ± 0.2	−14.3 ± 1.3	−15.8 ± 1.3	C_4
Neohipparion eurystyle	141 ± 42	+13.2 ± 1.3	−0.2 ± 0.8	−13.4 ± 1.5	−14.9 ± 1.5	C_4
Prosthennops serus	88 ± 26	+13.0 ± 1.3	−4.8 ± 1.3	−17.8 ± 1.8	−19.3 ± 1.8	Mixed
Stegomastodon sp.	6030 ± 1809	+14.9 ± 1.4	−4.2 ± 0.8	−18.6 ± 1.6	−20.6 ± 1.6	Mixed
Hexobelomeryx fricki	30 ± 9	+12.3 ± 1.5	−4.1 ± 0.6	−16.6 ± 1.6	−18.1 ± 1.6	Mixed

* Published body mass (BM) estimates for herbivores are reported with enrichment factors calculated using the equations from Tejada-Lara et al. (2018). The calculated body size for *A. schneideri* is also reported, but because there is no known relationship between carnivore body mass and diet-enamel enrichment, it is not used to calculate an enrichment factor. The enrichment is instead taken from Krueger and Sullivan (1984). Lambert (2006) produced body mass estimates for several of the taxon (average 20%, range of 15 to 30%), but did not specify what value in the range of 15 to 30% is associated with which specific body mass estimate. Other papers cited for body mass report similar or lower percent errors for their estimates. To be as conservative as possible, we assume a percent error of 30% for all body mass estimates. Error is given as ±1 standard error (S.E.) for all reported values. Standard error is calculated using the equation: S.E. $= \sigma_{\text{sample}} \div \text{sqrt}(n)$. Standard error for $\mathcal{E}$ is calculated by propagating standard error of the regression ($\text{S.E.}_{\text{regression}} = \sigma_{\text{errors}} \times \text{sqrt}((n-1) \div (n-2))$, where $\sigma_{\text{errors}} = \text{sqrt}(1 - R^2) \times \sigma_{\text{sample, y}}$) and standard error of calculated $\mathcal{E}$ values using $\mu_{\text{BM}} + (3 \times \sigma_{\text{BM}})$ and $\mu_{\text{BM}} - (3 \times \sigma_{\text{BM}})$ in the appropriate equations of Tejada-Lara et al. (2018). Standard deviation within each taxon (Table 1) is divided by the square root of number of individuals (Table 1) to determine standard error on enamel δ^{13}C averages. Standard error for $\mathcal{E}$ and standard error of enamel samples from each taxon are propagated to determine the standard error on average diet δ^{13}C and modern-equivalent diet δ^{13}C. Preferred diet type is determined based on the average modern-equivalent diet δ^{13}C.

4.5. Reconstructing mean annual temperature

Mean annual temperature (MAT) in mid-latitude regions can be estimated from the δ^{18}O of reconstructed water based on the modern relationships between air temperature and precipitation δ^{18}O found by Fricke and O'Neil (1999). However, regional scale differences may shift true values of air temperature and precipitation δ^{18}O away from the estimates from these global relationships. This problem can be mitigated by using the relationship between modern monthly precipitation δ^{18}O and air temperature data collected at stations near the study site (Tütken et al., 2007). Linear regression analysis of modern unweighted monthly precipitation δ^{18}O and air temperature data from the IAEA station in Chihuahua (IAEA/WMO, 2021) near our study site produced the

Table 3

t-tests of taxa by dietary group.*

Diet groups	Abs. difference in means (‰)	*df*	*t*	*p*	Significant difference at 95% CI
C_3 Specialist Dietary $\delta^{13}C$ vs Generalist Dietary $\delta^{13}C$	4.1	14	−5.21	0.0001	Yes
C_4 Specialist Dietary $\delta^{13}C$ vs Generalist Dietary $\delta^{13}C$	4.4	41	−7.94	0.0000	Yes
C_3 Specialist Dietary $\delta^{13}C$ vs C_4 Specialist Dietary $\delta^{13}C$	8.5	8	−12.60	0.0000	Yes
C_3 Specialist Dietary $\delta^{18}O$ vs Generalist Dietary $\delta^{18}O$	0.4	25	0.53	0.5981	No
C_4 Specialist Dietary $\delta^{18}O$ vs Generalist Dietary $\delta^{18}O$	2.3	37	−3.33	0.0020	Yes
C_3 Specialist Dietary $\delta^{18}O$ vs C_4 Specialist Dietary $\delta^{18}O$	2.7	10	4.72	0.0008	Yes

* Alpha for rejection of null is corrected for multiple pairwise comparisons with the Bonferroni correction; $\alpha = 0.016$.

following equation:

$$T\ (^\circ C) = \left(2.2449 \times \delta^{18}O_{water}\right) + 34.439\ \left(R^2 = 0.5406\right) \tag{6}$$

The $\delta^{18}O_{water}$ values derived from the enamel $\delta^{18}O$ values obligate drinkers were used, together with the above equation, to reconstruct a range of temperatures that were then averaged to approximate MAT under the assumption that the evaporative origin and the seasonality of precipitation in the region remain unchanged since the latest Miocene. Although climate model simulations suggest that circulation patterns in the Late Miocene were like modern (Micheels et al., 2007, 2011) and thus our assumption may be valid, the equation only accounts for half of the variability in the data, creating additional uncertainty in the MAT estimate. Given these uncertainties, the estimated MAT should not be considered definitive.

4.6. *Reconstructing annual precipitation and water deficit*

Mean annual precipitation (MAP) was estimated from the reconstructed diet $\delta^{13}C$ values of taxa with a C_3 diet using the modern relationship between $\delta^{13}C$ values of C_3 plants and MAP given in Kohn (2010):

$$\delta^{13}C = -10.29 + 1.90 \times 10{-}4 \times \mathrm{Altitude}\,(\mathrm{m}) - 5.61 \times log10(\mathrm{MAP} - 300;\mathrm{mm/yr}) - 0.0124 \times \mathrm{Abs}\,(\mathrm{latitude};^\circ) \tag{7}$$

For all sub-localities, latitude was taken to be 29.1° N. Altitude was taken to be 1000 m (50% of the modern altitude of 2000 m) based on PRISM2 data (Thompson and Fleming, 1996; Dowsett et al., 1999; Haywood and Valdes, 2004). Cautions were taken to carefully assess possible C_4 consumption as diet- $\delta^{13}C$ values within the $\delta^{13}C$ range of C_3 plants may reflect consumption of some C_4 plants rather than aridity in an environment containing C_4 plants (Kohn, 2010). Only samples with $\delta^{13}C$ lower than −24.5‰ (and thus are well in the range of pure C_3 consumers in arid environments) were used to estimate MAP and the impact of possible C_4 consumption on the calculated MAP are discussed later in Section 6.2.

Another hydroclimate index, water deficit (WD), was calculated from the oxygen isotope data using the method of Levin et al. (2006). This method requires classification of taxa as either evaporation sensitive (ES) or evaporation insensitive (EI). EI taxa are obligate drinkers, while ES taxa are nonobligate drinkers. As drinking habits of fossil taxa are difficult to verify, drinking habit is assumed to be uniform between fossil taxon and extant relatives. The assumption of *Stegomastodon* being an obligate drinker (and thus evaporation insensitive) like modern proboscideans should be reasonable given that water intake is expected to increase, and metabolic water production is proposed to decrease, with increasing body weight, necessitating obligate drinking at this size (Bryant and Froelich, 1995). The assumption of camelids being nonobligate drinkers depends far more on assuming similar physiology to descendants. *Hemiauchenia* sp. is considered ancestral to guanacos and vicuñas (Webb, 1974; González et al., 2006; Stahl, 2008; Marin et al., 2013). Guanacos are drought tolerant, nonobligate drinkers while vicuñas are obligate drinkers (Franklin, 1982; Samec et al., 2014). *Paracamelus* sp. in North America is ancestral to Bactrian and Dromedary camels (Pickford et al., 1995; Khan et al., 2003; Yam and Khomeiri, 2015), both of which are well adapted to aridity (Schmidt-Nielsen, 1959; Cloudsley-Thompson, 1995; Khan et al., 2003; Yam and Khomeiri, 2015; Hoter et al., 2019; Du et al., 2021). If the assumption of uniformitarianism between fossil and extant taxon is incorrect, then this estimate may underestimate true precipitation in the region. Assuming that these proboscideans were EI taxa and that the camelids were ES taxa, just like their modern relatives, the following equation given by Levin et al. (2006) for ES taxa relative to elephants was used to estimate water deficit.

$$\varepsilon_{ES-Elephant} \simeq \delta^{18}O_{ES} - \delta^{18}O_{Elephant} = 4.07 \times 10^{-3} \times \mathrm{WD}\ (\mathrm{in\ mm}) - 1.64 \tag{8}$$

5. Results and interpretation

5.1. *$\delta^{18}O$ of tooth enamel and assessment of sample preservation*

The isotopic integrity of a fossil enamel sample can be assessed by measuring the $\delta^{18}O$ values of both the structural carbonate and phosphate in the enamel as these two components have different susceptibility to dissolution and recrystallization during diagenesis (e.g., Iacumin et al., 1996). The expected difference between unaltered $\delta^{18}O$ (V-SMOW) of carbonate and phosphate ($\Delta_{\text{calcite-phosphate}}$) should be around 9.0‰, with the possibility of reaching 7‰ if temperature of the system exceeds 30 °C (Longinelli and Nuti, 1973; Bryant et al., 1996; Iacumin et al., 1996). Given that modern mammalian body temperatures vary between 30 and 40 °C depending on species and individual, a range of 7 to 10‰ was accepted as indicating minimal to no alteration (Bryant et al., 1996; Iacumin et al., 1996; Clarke and Rothery, 2008). Samples evaluated had a $\Delta_{\text{calcite-phosphate}}$ between 7.0 and 9.7‰, except for one specimen of *H. fricki* (LACM 78589) ($\Delta_{\text{calcite-phosphate}} = 4.6$‰) and one specimen of *D. mexicanus* (LACM 65502) ($\Delta_{\text{calcite-phosphate}} = 6.9$‰) (Fig. 4). A specimen of *Hemiauchenia* sp. (LACM 78009) had a $\Delta_{\text{calcite-phosphate}}$ of exactly 7.0‰. To be cautious when extrapolating these results to the full dataset, this specimen will be considered altered, although whether this sample is altered or pristine remains unclear. Of the samples checked for diagenesis, 10 of 13 (77%) could be classified as unaltered. These results suggest generally good preservation for the dataset. Significant intra-tooth oxygen isotopic variations observed in individual fossil teeth (Fig. 5) may reflect seasonal variations in the isotopic composition of water ingested by the animals (Sharp and Cerling, 1998; Higgins and MacFadden, 2004) and suggest the good preservation of enamel as diagenesis tends to smooth out seasonal signals in a specimen (Sharp, 2007). In addition, the generally low intraspecific variation and observable interspecific differences (Figs. 6, 7) suggest that the Yepómera assemblage is likely largely unaltered, and that variation reflects minor life habit variation within each taxon rather than alteration effects or locality differences.

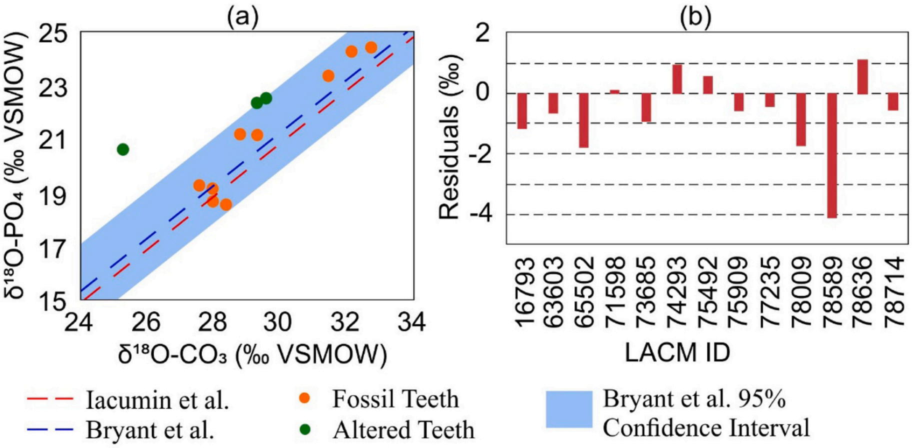

Fig. 4. (a) Comparison of the oxygen isotope compositions of co-occurring phosphate and carbonate in tooth enamel samples from Yepómera with the linear regressions of the relationship between the two phases in extant mammals (Iacumin et al., 1996; Bryant et al., 1996), and (b) residuals between the predicted regression value and measured $\delta^{18}O$ values. Samples outside or on the margin of the 95% confidence interval of the regression in (a) are considered altered teeth. Residuals greater than 1.8‰ in (b) are indicative of alteration.

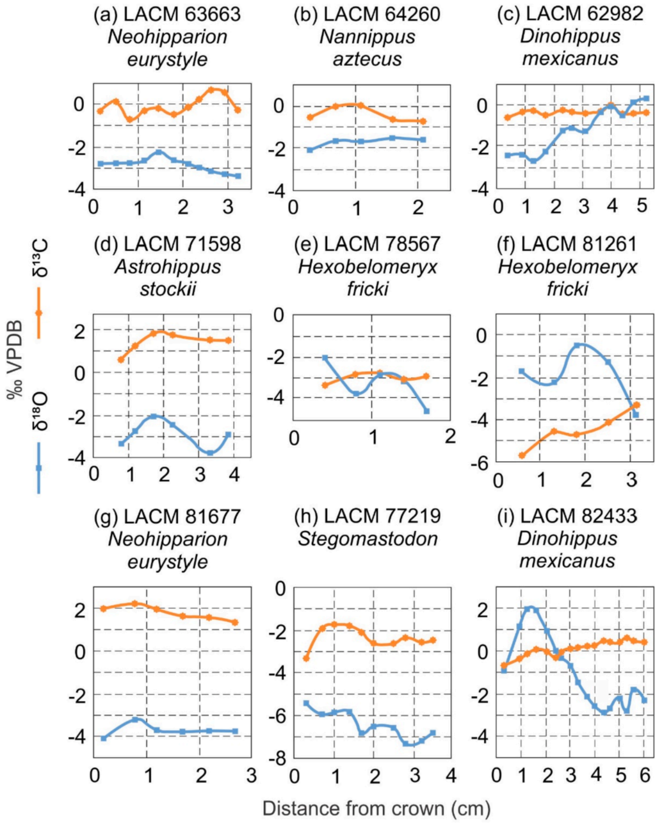

Fig. 5. Seasonal $\delta^{13}C$ and $\delta^{18}O$ records from Yepómera herbivore teeth.

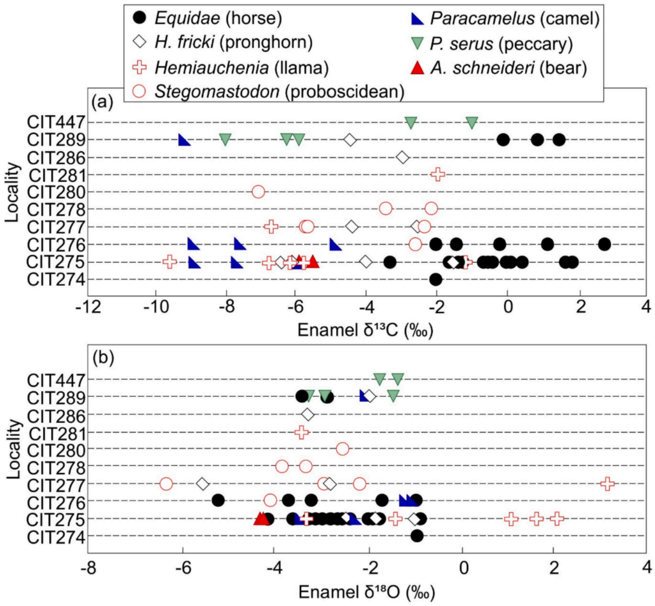

Fig. 6. Bulk enamel $\delta^{13}C$ (a) and $\delta^{18}O$ values (b) of mammals analyzed from different fossil localities in Yepómera, Mexico.

5.2. $\delta^{13}C$ and $\delta^{18}O$ of enamel, diet, and water compositions of fossil mammals

Enamel isotope data from the Yepómera fauna show that there is a general overlap of enamel $\delta^{13}C$ and $\delta^{18}O$ within taxonomic groups from different sites (Fig. 6; Suppl. Table 1), suggesting similar dietary and drinking behaviors within each taxon. The minor differences among sites seem to reflect differences in the proportion of each type of taxa at the sites rather than major environmental differences between the sites (Fig. 6). The reconstructed diet $\delta^{13}C$ values vary from −25‰ to −12‰ (Fig. 7), indicating a variety of diets (C_3, mixed, and C_4 diets) existed in the Yepómera area in the late Hemphillian. The isotopic similarity and differences among taxonomic groups reflect similarities and differences in food and water resources utilized by these ancient animals (Fig. 7; Tables 1 and 2).

5.2.1. Equids

The reconstructed diet $\delta^{13}C$ values indicate that the equids had C_4 diets except for two individuals (one *Dinohippus mexicanus* and one *Nannippus aztecus*) with mixed diets (Fig. 7). There is a general similarity in $\delta^{13}C$ values among the different equid taxa (Fig. 7). Most of these samples came from LACM CIT 275, but there does not appear to be any major differences based on locality (Fig. 6). The oxygen isotopic ratios were also very similar among equids, suggesting consumption of isotopically similar water. *Neohipparion eurystyle* did tend toward more negative $\delta^{18}O$ values than the other equids (Fig. 7). This trend is consistent at each of the three localities with equids but is not statistically significant (Suppl. Table 3). Whether this is a difference in physiology or water source is unclear. Using the equid-specific fractionation equation of Bryant et al. (1994) (i.e., Eq. (3)) with the measured phosphate $\delta^{18}O_{PO4}$ values of 19.0 ± 0.3‰ (vs. V-SMOW) from well-preserved equid enamel samples, the water source (meteoric water) should have a $\delta^{18}O$ of −5.6 ± 0.4‰ (V-SMOW).

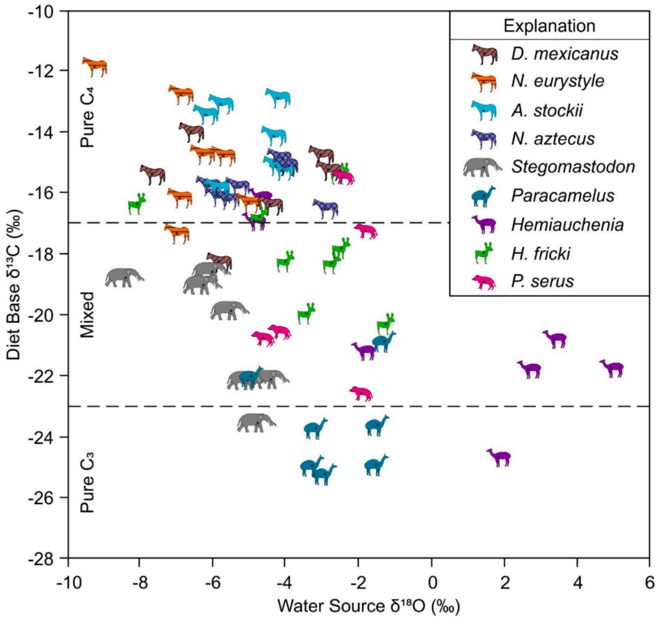

Fig. 7. Reconstruction of Yepómera herbivore ecology and water source. Dashed lines divide $\delta^{13}C$ domains that define the modern diet types (pure C_3 diets, mixed diets, and pure C_4 diets). Each species represented fits predominantly into one of these feeding groups with varying degrees of adaptability in diet. Among the equids, small variations occur, but none are substantial enough to suggest a significant difference in life habit between species. Only one of seven specimens of *D. mexicanus* and one of seven of *N. eurystyle* had a C_3 component to the diet, which may relate to accommodation of the additional equid species in this niche or dietary preference for a specific C_3 plant when it was available (such as a specific fruit). However, this is not abundant enough in the sampling population to suggest this was a common occurrence. Similar $\delta^{18}O$ values between equid species suggest a similar water source.

5.2.2. *Stegomastodon*

The reconstructed $\delta^{13}C$ values for *Stegomastodon* indicate that these ancient elephant-like animals had mixed diets except one individual had a pure C_3 diet (Fig. 7). There are no major differences between localities for these samples, except for one sample from LACM CIT 277 with a lower $\delta^{18}O$ (Fig. 6b). There were no other proboscideans from this site, so it is unclear whether this is due to alteration or if this site truly did have slightly less evaporative conditions or a greater range of seasonality. Using the elephant-specific fractionation equations of Ayliffe et al. (1992) (i.e., Eq. (4)) with the phosphate $\delta^{18}O_{PO4}$ values of 18.9 ± 0.5‰ from pristine proboscidean enamel, the water source should have a $\delta^{18}O$ of −5.1 ± 0.5‰. This suggests a similar water source to that of the equids.

5.2.3. *Hexobelomeryx fricki*

Hexobelomeryx fricki enamel yielded $\delta^{13}C$ values indicating that five of the specimens had mixed diets while three specimens had pure C_4 diets (Fig. 7). There are no major differences between localities for these samples after removing the known altered sample (Fig. 6). Using the general equation (i.e., Eq. (5)) for placental mammals from Pietsch and Tütken (2015) with the phosphate $\delta^{18}O_{PO4}$ value of 19.0‰ from the pristine sample of pronghorn enamel, the water source should have a $\delta^{18}O$ of −4.0‰. This suggests a water source within the 95% confidence interval of the water source of the equids and of *Stegomastodon*.

5.2.4. Camelids

Hemiauchenia sp. enamel $\delta^{13}C$ values indicate that four of the specimens had mixed diets, one specimen had a C_3 diet, and two specimens had a C_4 diet (Fig. 7), suggesting a flexible diet. The $\delta^{18}O$ values occur in two clusters: one relatively enriched in ^{18}O, while the other is depleted in ^{18}O (Fig. 5b). While the ^{18}O-enriched samples are only from one locality (LACM CIT 275), the same locality produced a specimen showing depleted values and the other localities (LACM CIT 277 and CIT 281) each are represented by only one specimen. As such, this is likely not a locality difference, but rather a lifestyle difference between the two groups or possibly a temporal difference within the taxa, capturing a transition from either a dry to wetter climate or a wetter to drier climate. The former is expected, given that the taxonomy of camelids is poorly defined and *Hemiauchenia* sp. may very well represent more than one taxon, but the latter cannot be excluded as a possible explanation. For the purposes of this work—and in the absence of a method to distinguish these subgroups—*Hemiauchenia* sp. will be assumed to represent a single taxon that lived contemporaneously. A general equation (i.e., Eq. (5)) for placental mammals from Pietsch and Tütken (2015) was used with the phosphate $\delta^{18}O_{PO4}$ of 24.4 ± 0.1‰. This suggested a water source with a $\delta^{18}O$ of 3.0 ± 1.6‰. This would suggest a different water source than that of the previously discussed taxa (or possibly a combination of two different ones based on the large variability).

Paracamelus sp. enamel $\delta^{13}C$ values indicate that five of the specimens had C_3 diets and two specimens had mixed diets (Fig. 7). A general equation (Eq. (5)) for placental mammals from Pietsch and Tütken (2015) was used with the phosphate $\delta^{18}O_{PO4}$ of 21.2 ± 0.0‰. This suggested a water source with a $\delta^{18}O$ of −0.7 ± 0.0‰. This is clearly a different water source than that of the previously discussed taxa, or rather, likely a mixed use of the two previously discussed water sources.

5.2.5. *Prosthennops serus*

Prosthennops serus enamel $\delta^{13}C$ values indicate that one of the specimens had a C_4 diet, one specimen had a C_3 diet, and the other three specimens had mixed diets. Samples from LACM CIT 289 had a less negative $\delta^{18}O$ than those from LACM CIT 447, and a wider range of $\delta^{13}C$ (Fig. 6). Whether this is a true difference in locality conditions cannot be confirmed because LACM CIT 289 had multiple taxa and a wide range, while LACM CIT 447 had only these two samples to represent it and fit within the range of LACM CIT 289. This difference can likely be attributed to sampling bias. No phosphate work was done for *P. serus* samples, so the water source of these specimens cannot be properly assessed.

5.2.6. *Agriotherium schneideri*

The diet base of *Agriotherium schneideri*, assuming a carnivorous lifestyle and the associated +8‰ enrichment (Krueger and Sullivan, 1984), would have a dietary $\delta^{13}C$ value of −15.2‰, indicating a prey that consumed only C_4 vegetation (Table 2). This would suggest a large proportion of the diet comes from equid meat, which was contrary to our expectations assuming that grizzly bears (*Ursus arctos horribilis*) are an adequate modern analogue. While modern grizzly bears are expected to hunt and scavenge meat from ungulates, current research leans toward these prey species being the predominantly larger ungulates like moose, elk, and bison (Mattson, 1997; Fortin et al., 2013; Cristescu et al., 2014). The hunting method of grizzlies in this case also tends to favor use of tree cover for ambushing prey (Cristescu et al., 2014). Our results do not suggest that this type of cover was common in Yepómera nor do these results suggest that *A. schneideri* consumed the largest animals (proboscideans and camelids)—either through hunting calves, hunting juveniles, or scavenging carrion. With a diet of primarily equids in an open environment, these bears either chased prey far more than modern bears or scavenged the remains of equids preferentially. Perhaps this is related to the difference in environment between Yepómera and the current habitats of grizzlies. Lack of tree cover at Yepómera may have required a different hunting strategy than modern analogues, including choosing smaller prey that could be chased down more easily rather than using ambush tactics. An alternative is that the size of the smaller equids and the larger equid calves made them a dietary staple instead of calves of larger taxon without the risk of being confronted by parent proboscideans and camelids defending their young. Determination of the actual cause for this preference would require further research beyond stable isotopes.

It has been suggested that *Agriotherium* was primarily a carnivore, based on dentition, but other researchers have suggested that it was an omnivorous scavenger (McLellan and Reiner, 1994; Miller and Carranza-Castañeda, 1996; Sorkin, 2006). As such, an omnivorous diet was also considered, using an enamel-diet enrichment of +12‰ (Krueger and Sullivan, 1984). The plant component of the diet is assumed to be C_3 based on diet studies of modern grizzly bears (Mowat and Heard, 2006). With a $\delta^{13}C_{vegetation}$ value of −23.6‰ (based on values from the C_3 consumers at this site), the diet base of −17.2‰ would still suggest that most of the dietary meat comes from prey taxa consuming C_4 vegetation and that over 75% of the diet comes from meat. While these calculations exclude the possibility of fish in the diet, modern grizzly bears typically have more terrestrial meat than fish in the diet, especially further inland (Mowat and Heard, 2006). Assuming behaviors match with these modern analogues, this inland site would likely have made fish a negligible dietary component. Equids are the only sampled taxa to be predominantly C_4 consumers and thus would have to be the dominant food source.

However, there are uncertainties that cannot be ruled out regarding *Agriotherium schneideri*: (1) the prey of *A. schneideri* may have been a C_4 consuming taxon not sampled in this study, (2) the carbon isotope ratios of both sampled *A. schneideri* teeth had been significantly altered by diagenesis to higher values, or (3) the fractionation factor used is not accurate for *A. schneideri*. The first issue can be a result of the inherent incompleteness of the fossil record or a result of sampling bias toward fossils of larger animals. Study of modern analogues may help elucidate what other prey could have been utilized that are not represented by the fossils in this study. The second was presumed not to be an issue because both teeth looked well preserved and generated similar isotope data; however, no phosphate work was done on either tooth to verify the degree of preservation. The third issue can be resolved with the study of diet and enamel isotopes in modern analogues. Unlike for herbivores, far less work has been done on fractionation factors of modern carnivore diet and enamel. Accurate fractionation factors would allow for proper interpretation of ancient carnivore diets from enamel isotope data. These uncertainties highlight the need for more studies of modern carnivore diet and enamel.

5.3. Serial $\delta^{13}C$ and $\delta^{18}O$ compositions of tooth enamel

Fluctuations in carbon and oxygen isotope compositions of diet and water can be observed through serial sampling of individual teeth. Most teeth analyzed show a ± 2.2‰ (±2σ) intra-tooth isotopic variation in water source $\delta^{18}O$ (Fig. 5), smaller than the seasonal range of modern precipitation $\delta^{18}O$ variation in the region (±4.0‰, ±2σ) (IAEA/WMO, 2021) (Fig. 2). While it is possible that this variation could reflect seasonality, lack of information on tooth growth rates prevents confirmation of seasonal $\delta^{18}O$ values. A few specimens (a *Nannippus aztecus*, LACM 64260, a *Neohipparion eurystyle*, LACM 81677, and possibly another *Neohipparion eurystyle*, LACM 63663) show long-term stability in oxygen isotope ratios, which may suggest these individuals drank from an isotopically buffered water source such as a river or a lake. Some of the samples have patterns that have a moving baseline (such as LACM 77219 and LACM 62982), which indicate a shift in the isotopic composition of environmental water supply, either due to changing conditions of the environment or migration into environments with different conditions. This trend, however, is rare in the serial samples and never included a change in diet as shown in relatively steady carbon isotope ratios, suggesting that migration into adjacent areas was not common among Yepómera fauna and that it would have been limited to areas with similar vegetation types (i.e., similar habitats) when it did occur.

6. Discussion

6.1. Niche space of the Yepómera fauna

The stable isotope results from Yepómera show a clear dietary separation between three groups: the equids (C_4 specialists), *Paracamelus* sp. (C_3 specialists), and the rest of the taxa (the generalists) (Fig. 7; Table 3). While the equids are clearly distinct in resource use from the other taxa in this study, the four species had very similar diets (Fig. 7). Difference in body size is often suggested as a main driver for resource partitioning in mammalian herbivores, such that similar-sized organisms in an area with limited resources should have to partition resources to survive (Hutchinson, 1958, 1959; Bell, 1970, 1971; Klein and Bay, 1994; Feranec and MacFadden, 2000; Kleynhans et al., 2011). Among the equids analyzed in this study, two species—*Neohipparion eurystyle* and *Astrohippus stockii*—had a similar body mass and should be expected to utilize different niches to avoid exhausting resources (Hutchinson, 1958, 1959; Feranec and MacFadden, 2000). The enamel $\delta^{13}C$ data, however, reveal no significant difference in the diets of these species (Fig. 7; Suppl. Table 3). These results contrast with expectations from the niche theory of Hutchinson (1959) because *A. stockii* and *N. eurystyle* seem to fill the same niche space (food source, feeding method, and body size) without either species generating enough competitive pressure to push the other out of the area. Neither is there a unique specialization in one of the species that would allow it to utilize the marginal space of this niche not already in use for the larger and smaller equid niche spaces. Nor are these species small enough to utilize spaces only transiently used by the larger equids. One possible explanation is that *N. eurystyle* and *A. stockii* did not co-occur in this area and that each taxon held its grazing niche at a different time. Another possibility is that populations of these two species were small and never reached the carrying capacity of local habitats. Future collection with better stratigraphic control may help resolve which of these is more plausible. These results are consistent with the larger scale observations of Parker et al. (2018) that equids with more-derived traits (large body size, hypsodonty, and monodactyly, such as *Dinohippus mexicanus* in our study) across Cenozoic North America show no difference in habitat distribution from those with less-derived traits and that those adaptations did not necessarily reflect habitat use. While Parker et al. (2018) did not exclude the possibility that there may have been differences in resource use between the more-derived and less-derived equids at finer resolutions, our study site shows that the variety in adaptations among equids may not necessarily affect resource use within a community of these equids.

The overlap of niche space for *Stegomastodon*, *Hexobelomeryx fricki*, *Prosthennops serus*, and *Hemiauchenia* sp. (Fig. 7) is consistent with niche theory as each is unique in size and has a broad range of possible food sources. Mixed feeding strategies would allow these species greater flexibility in consuming available resources and in mitigating competition between each other and the specialists when a specific resource became scarce. This could include consumption of different plant species and different plant parts (stems, leaves, roots) (Bell, 1970; Kleynhans et al., 2011). As different plant parts can have slightly different (up to 3‰ difference) $\delta^{13}C$ signatures from the whole plant due to differences in the proportion of each biochemical component, this could also contribute to the wide range of $\delta^{13}C$ values in each of these taxa (Craig, 1953; Wilson and Grinsted, 1977; Benner et al., 1987; Boutton, 1996; Loader et al., 2003; Cernusak et al., 2009).

The similarity in reconstructed water $\delta^{18}O$ values supports that the equids, proboscideans, and antilocaprids shared a water source (Fig. 7). This is in line with expectations given that modern relatives of these taxa are obligate drinkers and the water source (local meteoric water and its derivatives such as streams or rivers) should be isotopically similar. The camelid oxygen isotope ratios show a much different water source than the other taxa (Fig. 7). A positive $\delta^{18}O$ suggests a highly evaporated water source such as leaf water or lake/pond water (Dongmann et al., 1974; Gonfiantini, 1986). This implies that at least the examined individuals of *Hemiauchenia* sp. were nonobligate drinkers and derived most of their body water from plants and/or a lake/pond (Table 4).

6.2. Paleoclimatic conditions and habitats of the Yepómera fauna

Enamel $\delta^{18}O$ values of obligate drinkers can be used to reconstruct the $\delta^{18}O$ values of local meteoric water (e.g., Longinelli, 1984; Bryant et al., 1994; Kohn and Cerling, 2002; Pietsch and Tütken, 2015). In the modern world, precipitation $\delta^{18}O$ values are strongly correlated with air temperature in mid and high latitude regions (e.g., Dansgaard, 1964; Rozanski et al., 1993; Fricke and O'Neil, 1999) including the study region (Eq. (6)). The $\delta^{18}O_{water}$ values reconstructed, using Eqs. (3) and (4), from the enamel $\delta^{18}O$ values of all horses and elephants (presumably obligate drinkers) are $-5.4 \pm 1.6‰$ ($\pm 1\sigma$), which is higher than the weighted annual mean $\delta^{18}O_{water}$ ($-7.1 \pm 2.8‰$) of modern precipitation recorded at the IAEA station in the region. This suggests that the area was warmer ~5 Ma than today. However, it is difficult, if not impossible, to reliably reconstruct temperature for a locality using only precipitation $\delta^{18}O_{water}$ values because the modern $\delta^{18}O_{water}$ -temperature relationships may not be applicable in the distant past due to changes in the climate system such as changes in circulation pattern, moisture sources, etc. (e.g., Dansgaard, 1964; Fricke and O'Neil, 1999). Climate model simulations suggest that circulation patterns in the Late Miocene and Pliocene were like modern patterns (Haywood et al., 2000; Haywood and Valdes, 2004; Micheels et al., 2007, 2011). Thus, we assume that precipitation in the early Pliocene had a similar seasonal isotope pattern as observed today (i.e., similar moisture sources and seasonality of precipitation) and estimated the paleo-temperatures in the region using the reconstructed $\delta^{18}O_{water}$ values and the modern relationship between precipitation $\delta^{18}O$ and temperature in the area (Eq. (6)). The MAT estimated by averaging all the calculated temperatures is 22 ± 3 °C ($\pm 1\sigma$), which is significantly warmer than modern MAT in Chihuahua (18.1 ± 1.2 °C; $\pm 1\sigma$). The reconstructed temperatures at the study site ~5 Ma were consistent with the results of model simulations suggesting a 3–5 °C higher temperature in the Pliocene than modern along the North American Cordillera (Haywood et al., 2000; Haywood and Valdes, 2004). However, future work should include fossil fish from near the site to calculate MAT more accurately as suggested in Fricke and Wing (2004) and Eberle et al. (2010), after which the estimates from Eq. (6) can be assessed for accuracy.

The $\delta^{13}C$ data indicate that *Paracamelus* sp. had pure or nearly pure C_3 diets, suggesting that they were primarily browsers, which is consistent with the inference from relatively low-crowned teeth of *Paracamelus* sp. (Zazzo et al., 2000; Rybczynski et al., 2013). Their reconstructed diet-$\delta^{13}C$ values of $-23.6 \pm 1.6‰$ ($\pm 1\sigma$) are consistent with those of C_3 plants commonly found in open habitats experiencing water stress (Farquhar et al., 1989; Cerling, 1999; Kohn, 2010). The pure or nearly C_4 diets of co-occurring equids suggest significant C_4 biomass in area, which in turn also implies a relatively dry and open habitat. Reconstruction of mean annual precipitation using Eq. (7) and the $\delta^{13}C$ values of three individual *Paracamelus* sp. with pure C_3 diets (assuming $\delta^{13}C \leq -24.5‰$ is representative of a pure C_3 diet) yielded an average value of 684 ± 33 mm/yr ($\pm 1\sigma$), which falls within 2σ of the present-day mean annual precipitation range of the study area (512 ± 172 mm/yr; $\pm 1\sigma$) and is significantly higher than the amount (358 ± 159 mm/yr; $\pm 1\sigma$) recorded at the IAEA station at a lower elevation in the region (IAEA/WMO, 2021). It is important to note that in ecosystems containing C_4 plants, a diet-$\delta^{13}C$ value of $-24.5‰$ (the cut-off value used in our precipitation reconstruction) may reflect consumption of a small amount of C_4 vegetation and potentially bias the estimate of MAP to lower values (Kohn, 2010). While the presence of C_4 in large enough abundance to be a dietary staple of nearly every taxon sampled (Fig. 7) suggests that the environment should be relatively dry and therefore coexisting C_3 plants should have higher-than-average $\delta^{13}C$ perhaps approaching $-23.0‰$ (Farquhar et al., 1989; Cerling, 1999), we cannot completely rule out the possibility that the diet-$\delta^{13}C$ values (below the cut-off for a pure C_3 diet) used in our MAP reconstruction may reflect consumption of a small amount of C_4 plants. Given this possibility, we consider our reconstruction as a conservative estimate of annual precipitation in the region. Our reconstruction agrees with the models of Haywood et al. (2000), Salzmann et al. (2008), and Micheels et al. (2011) suggesting that MAP was slightly elevated relative to modern in the Early Pliocene.

Vegetation distribution is controlled by climatic conditions, specifically temperature and precipitation (Woodward et al., 2004; Mucina, 2019). As shown in Fig. 8, the MAT (22 ± 3 °C; $\pm 1\sigma$) and MAP (684 ± 33 mm/yr; $\pm 1\sigma$) estimated from the isotopic compositions of the Yepómera fauna suggest that the area was most likely dominated by either grassland (<10% tree coverage) or savanna (10–30% tree coverage) (Woodward et al., 2004) in the latest Miocene and early Pliocene. Even if C_3 vegetation in the area had $\delta^{13}C$ closer to $-27‰$, the MAP estimate

Table 4
t-tests of taxa by dietary water source.*

Drinking habit	Abs. difference in means (‰)	*df*	*t*	*p*	Significant difference at 95% CI
Obligate Drinker Water $\delta^{18}O$ vs Nonobligate Drinker Water $\delta^{18}O$	3.4	24	−4.75	0.0001	Yes
Obligate Drinker Dietary $\delta^{13}C$ vs Nonobligate Drinker Dietary $\delta^{13}C$	4.8	30	6.03	0.0000	Yes

* Alpha for rejection of null is corrected for multiple pairwise comparisons with the Bonferroni correction; $\alpha = 0.025$.

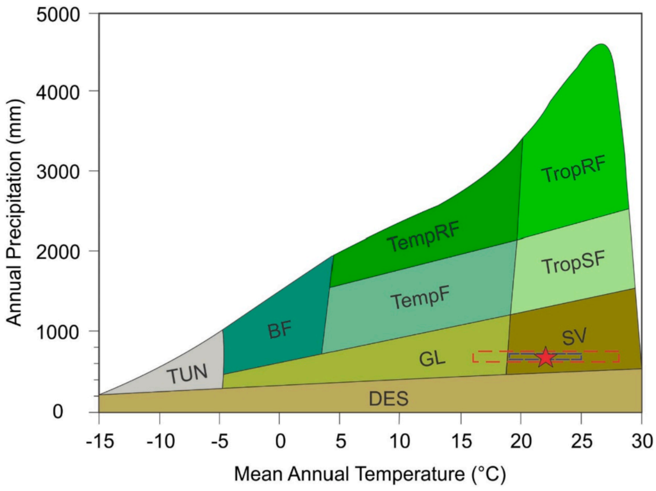

Fig. 8. Mean annual temperature and annual precipitation ranges of modern North American biomes (adapted from Woodward et al., 2004).
DES = desert; TUN = tundra; BF = boreal forest; GL = grassland; SV = savanna; TempF = temperate forest; TempRF = temperate rainforest; TropSF = tropical seasonal forest; and TropRF = tropical rain forest. The red star marks the reconstructed MAP and MAT of Yepómera, with the area bounded by the dashed blue line representing the 68% confidence interval and the area bounded by the dashed red line representing the 95% confidence interval. In both cases, the most likely biomes are grassland and savanna. High uncertainty in mean annual temperature estimates likely reflects the strong seasonality in the area. The low uncertainty in mean annual precipitation suggests a consistent dryness. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

would be under 1200 mm/yr and the interpretation of habitat would not change. The possibility of temperate forests cannot be fully excluded, and likely existed as small pockets within savanna or riparian areas. Related to this low precipitation, the relatively high δ^{13}C values of these taxa also suggest an open environment lacking canopy cover and containing substantial C_4 biomass (Kohn, 2010), consistent with the above interpretation of the prevalent biomes as grassland and savanna. This interpretation is consistent with modern descriptions of Chihuahua as being predominantly xeric shrubland and grassland, with temperate mixed forest on higher slopes (Sanders, 1921; Lindsay et al., 2006; Rzedowski, 2006; Colditz et al., 2012).

A water deficit can be estimated using the δ^{18}O of *Hemiauchenia* sp. (as an ES taxa) and *Stegomastodon* (in the role of elephants) with Eq. (8). Excluding an outlier of each species (each with a significantly lower δ^{18}O than the other samples of each taxon), the estimated water deficit is 1532 ± 156 mm/yr. Comparing these values to modern measures of water deficit, based on the work of Stephenson (1990), the biome can be classified as a shortgrass prairie or a shrubland depending on the amount of evapotranspiration. Under either classification, this is a relatively dry and open environment. These various lines of evidence, including the water deficit, water stress observed in C_3 plants, existence of substantial C_4 biomass, and reconstruction of MAP, all suggest an open, savanna to grassland-like environment, in agreement with the predominance of savanna ecomorphs in GABI migrations. This is consistent with expectations of an open environment GABI route between middle latitude South America and North America. Further fossil collection and analysis throughout Mexico is needed to verify spatial and temporal trends along the GABI migration route. Additional sites with a fossil record of GABI migrant taxon coexisting with the taxon of this study could be used to determine effects of GABI on niche partitioning and resource use in Mexico using these results as a pre-mixing baseline. Mapping the distribution of migrant taxa fossils through increased collection efforts and performing environmental reconstructions for each collection site will yield crucial information about how environment encourages or inhibits the migration of specific species.

7. Conclusions

The Yepómera fauna show distinct niche partitioning into three groups based on varying degrees of consumption of C_4 biomass. Horses had predominantly C_4 diets while camels had a pure or nearly pure C_3 diet. All other herbivores (including peccary, llama, proboscidean, and pronghorn) had predominantly mixed diets consisting of both C_3 and C_4 plants. This indicates that C_4 biomass must have been a major component of the local environment during the Late Miocene-Early Pliocene. No niche partitioning between equid species is demonstrated by the ranges of carbon isotope ratios. While these results are generally consistent with previous observations, further sampling to expand sample sizes of each taxon to robust levels would help minimize margin of error. Both the carbon and oxygen isotope data suggest a relatively dry, open habitat akin to a savanna or grassland. Despite the dominance of C_4 vegetation at this site, broader scale conclusions are limited as regions adjacent to Yepómera may have had substantially different vegetation due to differences in environmental conditions such as temperature, altitude, and humidity (factors that vary drastically along this latitude in Mexico today). The isotopic ratios of the Yepómera fauna provide evidence for a rise in C_4 biomass in northern Mexico before 5.23 Ma, though how much earlier remains unclear. Future work in this area and across Mexico will allow for a more complete understanding of the timing and controls on the GABI exchanges. Developing a higher resolution fossil record and pursuing additional isotope studies will be instrumental in the future study of long-term environmental and biotic changes during the GABI.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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