

# Feeding habits and habitat of herbivorous mammals from the Early–Late Hemphillian (Miocene) of Costa Rica

VÍCTOR ADRIÁN PÉREZ-CRESPO, CÉSAR A. LAURITO, JOAQUÍN ARROYO-CABRALES, ANA L. VALERIO, PEDRO MORALES-PUENTE, EDITH CIENFUEGOS-ALVARADO, and FRANCISCO J. OTERO



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Carbon and oxygen stable isotope values in the dental enamel of fossils were used to infer the diet and habitat of the extinct equids *Calippus hondurensis*, *Dinohippus mexicanus*, and *Protohippus gidleyi*, the gomphothere *Gomphotherium hondurensis*, and the llama *Hemiauchenia vera* of the Early–Late Hemphillian (Hh2) from San Gerardo de Limoncito, Puntarenas province, Costa Rica. The results suggest that these mammals fed mainly on C<sub>3</sub> plants and lived in clearings of rainforests. This contrasts with previous studies from North America that indicated that the same species lived in forest savannas and fed mainly on C<sub>4</sub> plants, but it is similar to the results obtained from the palynological record of the area, as well as with several vegetation models suggesting the presence of humid tropical forest during the Miocene in Central America.

Key words: Mammalia, carbon and oxygen stable isotopes, Neogene, Hemphillian, Costa Rica.

Víctor Adrián Pérez-Crespo [vapc79@gmail.com], Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica S/N, Ciudad Universitaria, Del. Coyoacán, 04150, México.

César A. Laurito [clauritomora@ina.ac.cr], Instituto Nacional de Aprendizaje, La Uruca, San José, Costa Rica; Departamento de Historia Natural, Museo Nacional de Costa Rica, 749-1000, San José, Costa Rica.

Joaquín Arroyo-Cabrales [arromatu@hotmail.com], Laboratorio de Arqueozoología “M. en C. Ticul Álvarez Solórzano”, Subdirección de Laboratorios y Apoyo Académico, INAH, Moneda 16 Col. Centro, 06060, México.

Ana L. Valerio [avalerio@museocostarica.go.cr], Departamento de Historia Natural, Museo Nacional de Costa Rica, 749-1000, San José, Costa Rica.

Pedro Morales-Puente [mopuente@unam.mx], Edith Cienfuegos-Alvarado [edithca@unam.mx], and Francisco J. Otero [fotero@geologia.unam.mx], Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica S/N, Ciudad Universitaria, Del. Coyoacán, 04150, México; Laboratorio de Isótopos Estables, Laboratorio Nacional de Geoquímica y Mineralogía, LANGEM-UNAM, Ciudad Universitaria, Coyoacán, 04150, México.

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## Introduction

The vertebrate fossil record of Central America is mainly confined to Cenozoic outcrops and particularly Miocene and Pleistocene ones (Lucas 2014). Studies in the region have focused on taxonomy (Cisneros 2005; Mead et al. 2012; MacFadden et al. 2015), paleobiogeography (MacFadden 2006; Kirby et al. 2008; Lucas and Alvarado 2010; Laurito and Valerio 2012), and biostratigraphy (Lucas 2014). The few studies with a paleoecological perspective have included analyses of carbon and oxygen stable isotope values in Pleistocene horses of several localities (MacFadden et al.

1999), in mammals from the Bartsovian (early Miocene) of Panama (MacFadden and Higgins 2004), and in some toxodonts from the Pleistocene of Honduras and Panama (MacFadden 2005).

This contrasts with North and South America, where a wide range of paleoecological studies using biogeochemical markers and morphofunctional methods have yielded far more information about Cenozoic mammals (MacFadden and Higgins 2004).

In the case of Costa Rica, several localities contain fossils from the Pleistocene (Lucas et al. 1997) and Miocene Epochs. Remains of fish, reptiles, birds, and terrestrial and

marine mammals have been found in the Late Hemphillian North American Land Mammal Age (NALMA) outcrop of San Gerardo de Limoncito (Laurito and Valerio 2008, 2016; Laurito et al. 2005), and this has motivated taxonomic, biostratigraphical, and paleoecological studies (Laurito and Valerio 2010; Valerio 2010).

Morphofunctional aspects of three equid species found at San Gerardo, *Calippus hondurensis*, *Dinohippus mexicanus*, and *Protohippus gidleyi*, have been analyzed by extrapolation of information derived from specimens found in the USA (Laurito and Valerio 2010). However, such an approach is not ideal, since populations of a same species that lived in different geographic zones would have experienced different environmental conditions and would therefore have modified their feeding habits and the habitat itself (MacFadden 2005, 2008).

Laurito and Valerio (2010) concluded that the fossil mammal assemblage found in San Gerardo de Limoncito indicated that a wooded savanna existed there during the Miocene and that the equids and llamas fed mainly on grasses, whereas gomphotheres fed on leaves of trees and shrubs. The present study tests this view with carbon and oxygen stable isotope analyses of dental enamel for the same equid species, the gomphothere *Gomphotherium hondurensis*, and the llama *Hemiauchenia vera*, all from San Gerardo de Limoncito.

*Other abbreviations.*—CAM, Crassulacean Acid Metabolism; DF, degree of freedom; F, Fisher statistics; H, H statistic; NALMA, North American Land Mammal Age; p, probability level.

## Carbon and oxygen stable isotopes

Carbon is incorporated into plants through photosynthesis in the three pathways C<sub>3</sub>, C<sub>4</sub>, and Crassulacean Acid Metabolism (CAM) (O'Leary 1988). The C<sub>3</sub> photosynthetic pathway is present in trees and shrubs, and some temperate grasses, with  $\delta^{13}\text{C}$  values ranging between -34‰ and -22‰ (van der Merwe and Medina 1989; Cerling et al. 1997; Koch 1998; Drucker and Bocherens 2009). The C<sub>4</sub> pathway is usually found in grasses as well as trees and shrubs from warm regions and has  $\delta^{13}\text{C}$  values between -14‰ and -10‰ (Smith and Epstein 1971; Koch 1998; Cerling 1999; Medrano and Flexas 2000). Several factors may affect the abundance of C<sub>3</sub> and C<sub>4</sub> plants in the ecosystem. At localities with temperatures lower than 25°C, C<sub>3</sub> plants increase in numbers while C<sub>4</sub> plants decrease (Medrano and Flexas 2000). Also, C<sub>4</sub> plants are able to cope with lower atmospheric CO<sub>2</sub> and humidity levels than C<sub>3</sub> plants (McInerney et al. 2011). In temperate areas, the two kinds of plants co-exist throughout the year, but at locations with different microhabitat conditions for temperature and humidity. Furthermore, the carbon isotope composition of C<sub>3</sub> plants can be influenced by factors such as saline soils, low light intensity, water

availability, efficient use of water and lack of nutrients, and the particular conditions in the habitat or microhabitat (Ehleringer et al. 1987; Mooney et al. 1989; Bocherens 2003; Codron et al. 2005).

The third photosynthetic pathway, CAM, is found in succulent plants such as cacti, bromeliads, and agaves, with  $\delta^{13}\text{C}$  values between -35‰ and -12‰. However, due to the carbon isotope values range, it is difficult to separate these plants from C<sub>3</sub> and C<sub>4</sub> plants based on  $\delta^{13}\text{C}$  values alone (Decker and De Wit 2005; Andrade et al. 2007).

When herbivores feed on plants, the carbon from those plants is incorporated into their tissues and structures such as dental enamel. Hence, the isotope values are correlated with those of the plants; nevertheless, there is a 14.1‰ increment (Cerling and Harris 1999). Animals that feed on C<sub>3</sub> plants have carbon isotope values from -19‰ to -9‰, whereas those that have consumed C<sub>4</sub> plants have values from -2‰ to +2‰. The C<sub>3</sub>/C<sub>4</sub> mixed feeders show values from -9‰ to -2‰ (MacFadden and Cerling 1996).

In contrast to carbon, oxygen enters the body of animals during inhalation, in water derived from food, and in drinking water. It is in balance with oxygen that is lost through exhalation, feces, urine, and sweat (Koch et al. 1994; Koch 2007). The main source is drinking water, often derived from rain water that is affected by altitude, latitude, amount of precipitation and environmental temperature (Dansgaard 1964). The equilibrium between ingested and exhaled water could also be modified by the animals' physiology and habitat (Sánchez 2005). However, herbivores inhabiting humid and closed (forest) zones generally show lower  $\delta^{18}\text{O}$  values than those living in arid and open (grassland, savannas, or prairies) zones (Ambrose and DeNiro 1986; Feranec and MacFadden 2006). Because of that situation,  $\delta^{18}\text{O}$  dental enamel can be used to infer past climatic conditions at a location and certain ecological characteristics of the analyzed species (Ayliff et al. 1992; Sánchez-Chillón et al. 1994; Bryant and Froelich 1996; Kohn et al. 1996; Sponheimer and Lee-Throp 1999; Schoeninger et al. 2000; Harris and Cerling 2002; Levin et al. 2006).

## Material and methods

*Location.*—San Gerardo de Limoncito is in the Coto Brus Canton, the 4th district of Limoncito, Puntarenas province, Costa Rica, between 8°51'19.6" N and 83° 04'51.9" W and at 760 m above sea level (Fig. 1). Remains of fossil sharks, stingrays, turtles, crocodiles, birds, dolphins, whales, equids, gomphotheres, llamas, pampatheres, sloths, and peccaries have been recovered there. The sedimentological context of the fossil material considered in the present study encompasses littoral and fluvial environments, associated with a fan delta sequence, and characterized by reworked sedimentary intraclasts deposited as conglomerates from which most of the vertebrate remains have been obtained (Valerio 2010; Fig. 2). The vertebrate fauna, as well as scarce plant remains

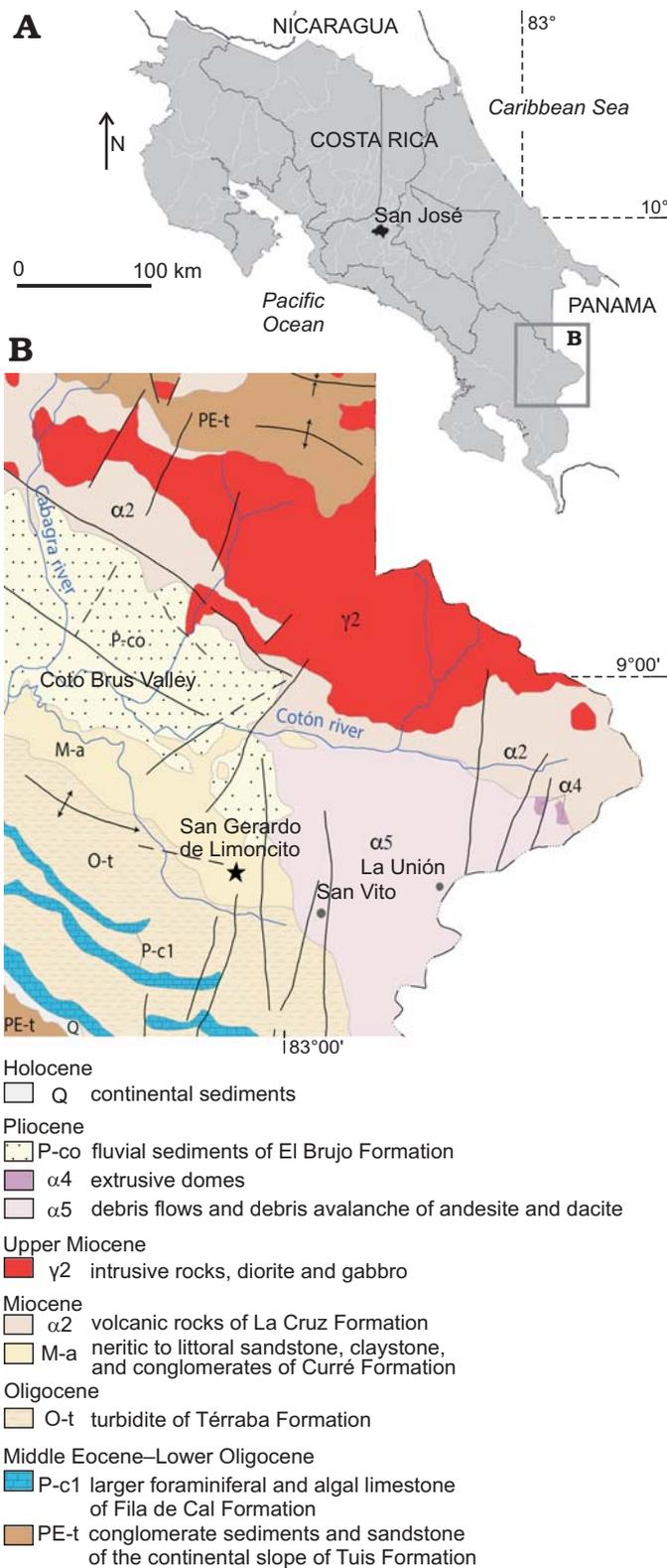


Fig. 1. A. Geographic location of studied area. B. Geological map of the San Gerardo de Limoncito area, modified from Denyer and Alvarado (2007).

and sedimentological data, suggest a tropical estuary associated with ancient ecosystems of wooded savannas, with a predominance of grasslands in lowlands near the coast (Laurito and Valerio 2010).

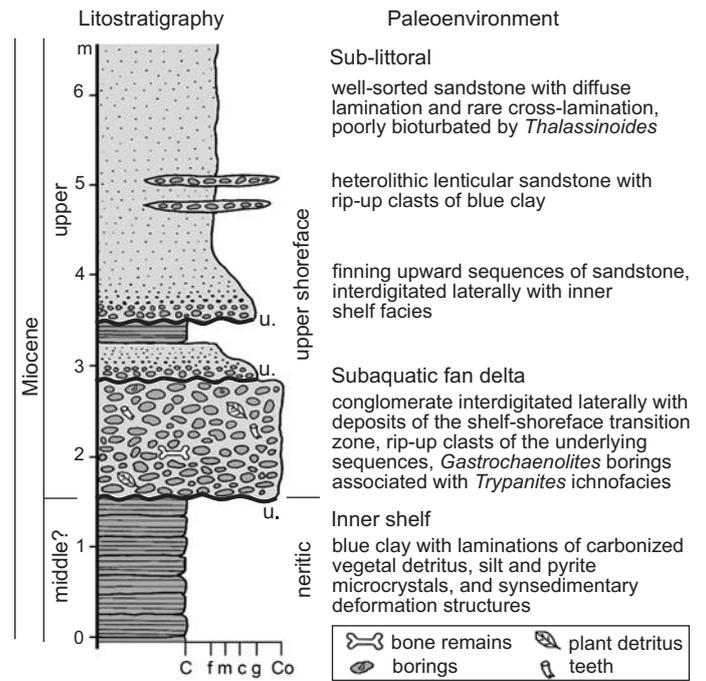


Fig. 2. Stratigraphic column of the fossil-bearing locality, San Gerardo de Limoncito, modified from Laurito and Valerio (2010). Abbreviations: C, clay; c, coarse sandstone; Co, conglomerate; f, fine; g, gravel; m, middle; u., unconformity.

The locality is part of the Curré Formation, from the middle–upper Miocene. Given the presence of *Calippus hondurensis*, *Dinohippus mexicanus*, and *Protohippus gidleyi*, Laurito and Valerio (2010) and Valerio and Laurito (2012) deduced that the site is from the Early–Late Hemphillian NALMA (6.57 Ma), corresponding to Stage Hh2 according to the chronology proposed by Tedford et al. (2004).

**Extraction and preparation of samples.**—Samples were processed in the Stable Isotope Laboratory at the Instituto de Geología, Universidad Nacional Autónoma de México, México, using the method proposed by Koch et al. (1997). First, 20 mg of diagenetically unaltered tooth enamel was ground and sieved (125 μm mesh) to obtain a fine and uniform powder. Then 0.5 ml of hydrogen peroxide at 30% was added to eliminate the organic matter. After two hours, the samples were centrifuged and the hydrogen peroxide was decanted and washed again three times with type I water (grade HPLC 18.2 MΩ). Once the washing was finished, 5 ml of a buffer solution, Ca(CH<sub>3</sub>CO<sub>2</sub>)<sub>2</sub> – CH<sub>3</sub>COOH 1.0 M, pH 4.75, was added and allowed to rest for nine hours. The buffer solution was decanted and the samples were washed again three times with type I water. Finally, to eliminate any remaining water, ethanol was added, and the solution was left for 20 hours in an oven at 90°C. Isotope ratios were determined with a Finnigan MAT 253 mass spectrometer with a dual inlet system and auxiliary Gas Bench equipment with a GC Pal auto-sampler with a temperature-controlled aluminum plate adjoined to the mass spectrometer (Révész and Landwehr 2002). Results were reported as δ<sup>18</sup>O<sub>VPDB</sub> and δ<sup>13</sup>C<sub>VPDB</sub>, and

they were normalized using NBS-19, NBS-18, and LSVEC to the Vienna Pee Dee Belemnite (VPDB) scale in accordance with the corrections described by Coplen (1988), Werner and Brand (2001), and Coplen et al. (2006). For this technique, the standard deviation was 0.2‰ for oxygen and carbon.

**Data analyses.**—Average values were obtained for carbon and oxygen isotopes. For the  $\delta^{13}\text{C}$  values, reference was made to MacFadden and Cerling (1996) in order to infer the diet of the animal. The relationship between the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values was assessed by Analysis of Variance (ANOVA), a Kruskal-Wallis test, and a Tukey-Kramer test. Significance was set at  $p < 0.05$  and the utilized software was NCCS and PASS (Hintze 2004). The  $\delta^{18}\text{O}$  values were converted to Vienna Standard Mean Ocean Water (V-SMOW) using the Faure (1977) formula:  $\delta^{18}\text{O}_{\text{V-SMOW}} = 0.1030901 * \delta^{18}\text{O}_{\text{V-PDB}} + 30.91$ , and transformed into  $\delta^{18}\text{O}$  of water through the Iacumin et al. (1996) formula:  $\delta^{18}\text{O}_{\text{water}} = \delta^{18}\text{O}_{\text{V-SMOW}} - 33.63/0.998$ , to be compared with the rainwater  $\delta^{18}\text{O}$  values calculated for this locality (Bowen and Wilkinson 2002; Bowen and Revenaugh 2003; Bowen et al. 2005; Bowen 2008).

## Results

Table 1 shows carbon and oxygen isotope values for the five species analyzed. There were no differences observed among  $\delta^{13}\text{C}$  values for the whole set of species (DF 17, F 0.94,  $p < 0.471092$ ; H 3.140302,  $p < 0.534627$ ) nor among  $\delta^{18}\text{O}$  values (DF 17, F 2.74,  $p < 0.074511$ ; H 7.57045,  $p < 0.108643$ ). The relationship between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values showed three groups: (i) most of the gomphotheres, *Dinohippus mexicanus*, and some *Protohippus gidleyi* specimens; (ii) *Calippus hon-*

Table 1. Carbon and oxygen isotope values (‰) from dental enamel of fossil herbivorous mammals from the Early–Late Hemphillian of San Gerardo de Limoncito, Costa Rica (after Laurito and Valerio 2016).

Species	$\delta^{13}\text{C}_{\text{V-PDB}}$	$\delta^{18}\text{O}_{\text{V-PDB}}$	$\delta^{18}\text{O}_{\text{V-SMOW Water}}$
<i>Calippus hondurensis</i>	-14.7	-8.4	-11.4
<i>Calippus hondurensis</i>	-13.1	-8.8	-11.8
<i>Dinohippus mexicanus</i>	-11.0	-5.4	-8.3
<i>Dinohippus mexicanus</i>	-11.6	-5.1	-8.0
<i>Gomphotherium hondurensis</i>	-11.2	-6.6	-9.6
<i>Gomphotherium hondurensis</i>	-15.2	-8.0	-11.0
<i>Gomphotherium hondurensis</i>	-10.0	-6.9	-11.4
<i>Gomphotherium hondurensis</i>	-7.4	-8.3	-11.8
<i>Hemiauchenia vera</i>	-14.6	-5.0	-7.9
<i>Hemiauchenia vera</i>	-16.1	-6.1	-9.0
<i>Protohippus gidleyi</i>	-7.8	-4.9	-7.8
<i>Protohippus gidleyi</i>	-16.7	-8.3	-11.3
<i>Protohippus gidleyi</i>	-11.5	-7.1	-10.0
<i>Protohippus gidleyi</i>	-9.7	-4.6	-7.4
<i>Protohippus gidleyi</i>	-11.0	-7.2	-10.1
<i>Protohippus gidleyi</i>	-11.1	-6.1	-9.1
<i>Protohippus gidleyi</i>	-16.6	-8.5	-11.5
<i>Protohippus gidleyi</i>	-15.5	-8.2	-11.2

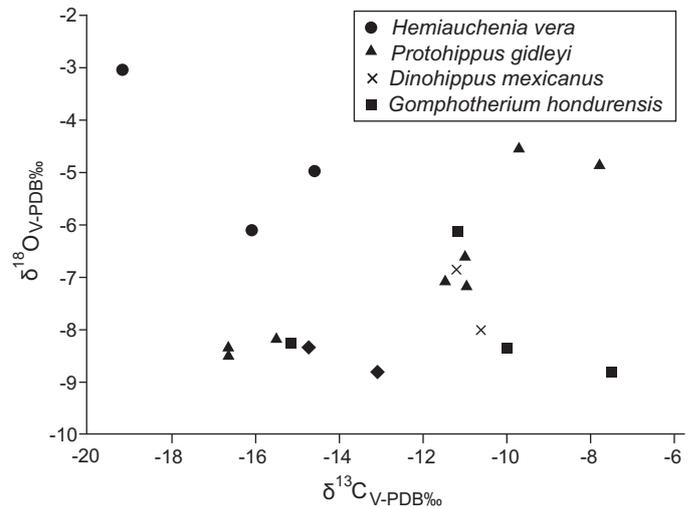


Fig. 3. Comparative analysis of carbon and oxygen stable isotope values in dental enamel from fossil herbivorous mammals of the San Gerardo de Limoncito locality.

*durensis*, one gomphothere and most of the *Protohippus gidleyi* specimens; and (ii) the llamas (Fig. 3).

The most negative  $\delta^{13}\text{C}$  value was in a llama that also had the most positive  $\delta^{18}\text{O}$  value; the highest positive  $\delta^{13}\text{C}$  value was from a gomphothere; and the lowest  $\delta^{18}\text{O}$  value was from a *Protohippus gidleyi* specimen (Table 1).

## Discussion

**Diet.**—The  $\delta^{13}\text{C}$  values from the equid *Calippus hondurensis* indicate that those animals fed on  $\text{C}_3$  plants. Because the wear on molars was only moderate, Laurito and Valerio (2010) concluded that this equid species was a browser; this is supported by the present data, since  $\text{C}_3$  plants are mainly trees and shrubs (Koch 1998).

In the case of the other equid *Dinohippus mexicanus*, data from studied individuals also suggest a diet based on  $\text{C}_3$  plants, while Laurito and Valerio (2010) indicated that *D. mexicanus* was more generalist in its diet, citing mesowear studies (Barrón-Ortiz and Guzmán-Gutiérrez 2008) that indicated that *D. mexicanus* at Rancho El Ocote, Mexico, were grazers, whereas individuals from Tecolotlán, Mexico, were mixed feeders or grazer-browsers. Isotope analyses of *D. mexicanus* populations from Rancho El Ocote and Yepomera (also in Mexico), and from Texas and Florida (USA), indicated that specimens from Mexican and Texan localities mainly fed on  $\text{C}_4$  plants, whereas those in Florida mainly fed on  $\text{C}_3$  plants (MacFadden 2008). Specimens from Tecolotlán had a  $\text{C}_3/\text{C}_4$  mixed diet but with higher proportion of  $\text{C}_3$  plants (Pérez-Crespo et al. 2017). Overall it seems that populations of *Dinohippus mexicanus* varied widely in their feeding habits, depending upon the region where they lived.

The  $\delta^{13}\text{C}$  values of the three individuals of *Gomphotherium hondurensis* indicate that two of them fed only on  $\text{C}_3$  plants, whereas the third had a mixed diet of  $\text{C}_3/\text{C}_4$  plants.

Because gomphotheres had brachiodont molars, they have been thought to have eaten only leaves of trees and shrubs, i.e., mainly C<sub>3</sub> plants; however, the Pleistocene gomphotheres *Cuvieronius* and *Stegomastodon* in North and South America (Sánchez et al. 2004; Pérez-Crespo et al. 2016) and *Rhynchotherium* in Florida and Mexico (MacFadden and Cerling 1996; Pérez-Crespo et al. 2015) had not specialized exclusively on either C<sub>3</sub> or C<sub>4</sub> plants; they mainly had a mixed C<sub>3</sub>/C<sub>4</sub> diet, such as the one for *G. hondurensis* from San Gerardo de Limoncito.

The llama *Hemiauchenia vera* analyzed here specialized on C<sub>3</sub> plants, whereas Laurito and Valerio (2016) indicated that this species from San Gerardo de Limoncito had a mixed C<sub>3</sub>/C<sub>4</sub> diet. Analyses of several populations of camelids from the Eocene to Pleistocene of North America (Feranec 2003; Semprebon and Rivals 2010) indicated that Hemphillian llamas fed on C<sub>3</sub> plants or were browsers, and that this habit was maintained in some specimens from two of the three most recent chronostratigraphic units NALMAs: Blancan and Rancholabrean. Among the latter, some llamas with mixed diets coexisted with others that specialized on C<sub>4</sub> plants or were grazers, so that these animals can be considered more generalist than specialist in their diet.

In contrast, one of the eight *Protohippus gidleyi* specimens analyzed in the present study had a mixed diet of C<sub>3</sub>/C<sub>4</sub> plants, with a high proportion of C<sub>3</sub> plants, whereas most equids only fed on C<sub>3</sub> plants. This contrasts with the conclusion based on cuspid morphology of molars (Laurito and Valerio 2010) that *P. gidleyi* was a browser-grazer with a mixed diet. This apparent difference can be explained by the following: (i) isotope analysis reveals the diet of an individual at the time when the molars were formed (Koch 2007); (ii) although most of the C<sub>3</sub> plants were trees and shrubs, some were grasses (Koch 1998); and (iii) the wear at the tops of molars may be caused not only by food, but also by other abrasive material, such as sand particles (Sansón et al. 2007). Hence, neither the molar morphology (Laurito and Valerio 2010) nor the present isotope analyses eliminate the possibility that *P. gidleyi* fed on trees, shrubs, and also C<sub>3</sub> grasses.

**Habitat.**—These herbivorous mammals lived in a closed zone (Fig. 3). Closed habitats include jungles or forests where C<sub>3</sub> plants are abundant and animals that lived in this type of vegetation had  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values more negative than those inhabited in grasslands (Feranec and MacFadden 2006). However, ecosystems where C<sub>3</sub> plants are dominant are not necessarily wooded zones, but can be other types of habitat or diverse microhabitats (Drucker et al. 2008; Drucker and Bocherens 2009).

C<sub>3</sub> habitats can be divided into tropical undergrowth, tropical rainforest, subtropical rainforest with closed can-

opy, forest with canopy and gaps, subtropical rainforest with open canopy, savanna with dense riparian vegetation, warm temperate forest, subtropical savanna, and tropical deciduous forest (Secord et al. 2008).  $\delta^{13}\text{C}$  values in enamel can indicate the habitat where animals lived (Zanazzi and Kohn 2008): < -21‰ to -15‰ for forest with a closed canopy, 15‰ to -8‰ for forest, and > -8‰ for xeric grasslands.

On this basis, since the most negative value found in the mammalian fauna of San Gerardo de Limoncito was -16.7‰ and the most positive was -7.6‰, some of these animals may have lived in a forest with a canopy and openings.

This contrasts with a suggestion by Laurito and Valerio (2010) that the area nearby San Gerardo de Limoncito probably included a wooded savanna with grasslands, where the size of *Calippus hondurensis* allowed it to feed on young leaves and buds in wooded zones, whereas *Protohippus gidleyi* inhabited the boundary of the savanna and the wooded zone, and *Dinohippus mexicanus* lived on the savanna; meanwhile, gomphotheres, llamas, peccaries, and sloths would have lived in the forest or on the savanna.

Herbivores currently living beneath the canopy in the Ituri forest in Africa have  $\delta^{13}\text{C}$  values (-26.0‰ to -20.2‰) more negative than mammals inhabiting forest gaps (-17.5‰ to -16.2‰) (Cerling et al. 2004). The negative  $\delta^{13}\text{C}$  values recorded in the present study for the three species of equids, the gomphotheres, and the llamas from the upper Miocene of southern Central America suggest that members of this megafaunal assemblage also inhabited forest gaps because of their large size, but fed on leaves of trees, fruits, and some herbaceous plants beneath the canopy.

However, one of the three gomphotheres in the present study, as well as one of the eight *Protohippus gidleyi* specimens, had isotope values that indicate mixed C<sub>3</sub>/C<sub>4</sub> feeders. There are two possible explanations for this: the first is that these mammals used to feed on CAM plants, such as orchids, bromeliads, or cacti, which are found in tropical zones (Andrade et al. 2007; Lüttge 2010); the second is that these individuals were not natives of the area and came from other localities with C<sub>4</sub> plants.

Two individuals of *Protohippus gidleyi* had isotope values that were more positive than for the others ( $\delta^{13}\text{C}$  -7.8‰ and -9.7‰;  $\delta^{18}\text{O}$  -4.4‰ and -4.6‰) (Table 1). Variation in the  $\delta^{18}\text{O}$  of the water in a locality may influence the  $\delta^{18}\text{O}$  values in dental enamel (Hoppe et al. 2004a, b). Because some individuals may have drunk water in places other than those where they fed, these individuals may have accumulated  $\delta^{18}\text{O}$  values differing from those of the other animals from the same locality (Pellegrini et al. 2008; Widga et al. 2010).

The  $\delta^{18}\text{O}$  values of water obtained from the studied herbivorous mammals of San Gerardo de Limoncito are more negative than those of water calculated by Bowen and Wilkinson

Table 2. Oxygen isotopic values ( $\delta^{18}\text{O}_{\text{V-SMOW}}\text{‰}$ ) for water at San Gerardo de Limoncito at the present day. Data from Bowen and Wilkinson 2002; Bowen and Revenaugh 2003; Bowen et al. 2005; Bowen 2008.

January	February	March	April	May	June	July	August	September	October	November	December	Average
-6.1	-5.5	-5.5	-5.6	-3.8	-3.3	-3.9	-3.2	-5.5	-6.1	-6.7	-7.0	-5.4

(2002), Bowen and Revenaugh (2003), Bowen et al. (2005), and Bowen (2008) for this site at the present day (Tables 1, 2). Variation in the  $\delta^{18}\text{O}$  values of water in Costa Rica may be due to variation in rainfall and, to a lesser extent, to variations of temperature and altitude, as well as aridity (Lachniet and Patterson 2002; Reynolds-Vargas and Fraile 2009; Sánchez-Murillo et al. 2013). The  $\delta^{18}\text{O}$  values in present day water are most positive from May to August, the dry season, and more negative from October to December, the season with the highest precipitation (Table 2).

Comparison of the  $\delta^{18}\text{O}$  values from dental enamel of these fossils with the present day values for the same site suggests that during the Early–Late Hemphillian San Gerardo de Limoncito had a higher level of precipitation and was more humid than today. Humidity influences the global distribution of  $\text{C}_3$  and  $\text{C}_4$  plants (Medina et al. 1999; Medrano and Flexas 2000; Yamori et al. 2013); high humidity favors  $\text{C}_3$  plants over  $\text{C}_4$  plants. For example, in some desert areas of the southern USA and northern Mexico, where rain is more abundant in winter,  $\text{C}_3$  plants are more abundant at that season, while  $\text{C}_4$  plants are more abundant during summer (Ehleringer and Monson 1993).

However, carbon and oxygen isotopes data for some North American localities of same or close age indicate the abundance of  $\text{C}_4$  plants (MacFadden 2000). For example, at Rancho El Ocote (Guanajuato) and Tecolotlán (Jalisco), both from the Mexican Late Hemphillian (Hh3), the closest localities to Limoncito, carbon and oxygen isotope analyses indicates either abundance of  $\text{C}_4$  plants and grassland, with arid conditions at Rancho El Ocote, or humid conditions and higher abundance of  $\text{C}_3$  plants in Tecolotlán, including mixed forest and grassland (Pérez-Crespo et al. 2017). These results indicate that local environmental conditions may govern the abundance of  $\text{C}_3$  and  $\text{C}_4$  plants on a site more than the geographic parameters (latitude, elevation, and the like), as it was found at San Gerardo de Limoncito (Pérez-Crespo et al. 2017).

The pollen of 40 plant taxa recovered from sediments of the lower Miocene Uscari Formation indicated the presence of a tropical rainforest (Graham 1987). Although these outcrops of the Uscari Formation are relatively close to San Gerardo de Limoncito, they are allochronic with respect to the Curré Formation. Nevertheless, models for Central America during the late Miocene (Micheels et al. 2007; Pound et al. 2011) indicated that tropical rainforests were also present; this is consistent with the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of the fossil herbivorous mammal fauna analyzed here and with these pollen records.

## Conclusions

The horses *Calippus hondurensis*, *Dinohippus mexicanus*, and *Protohippus gidleyi*, the gomphothere *Gomphotherium hondurensis*, and the llama *Hemiauchenia vera* from San Gerardo de Limoncito, all fed on  $\text{C}_3$  plants; this is shown by

the  $\delta^{13}\text{C}$  in the dental enamel from fossils, and it suggests that during the Early–Late Hemphillian the site was more humid than today, thus favoring the presence of  $\text{C}_3$  plants. Together with the  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values of the dental enamel in these fossils, the paleovegetation reconstructions made for this geological period suggest that these herbivorous mammals lived in a tropical rainforest, but in clearings of the forest where they fed on plants that developed there.

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