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

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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 C3 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 C4 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.

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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 Bartsovan (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 Valero 2008, 2016; Laurito et al. 2005), and this has motivated taxonomic, biostratigraphical, and paleoecological studies (Laurito and Valero 2010; Valero 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 Valero 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 Valero (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 C3, C4 and Crassulacean Acid Metabolism (CAM) (O’Leary 1988). The C3 photosynthetic pathway is present in trees and shrubs, and some temperate grasses, with δ13C values ranging between -34‰ and -22‰ (van der Merwe and Medina 1989; Cerling et al. 1997; Koch 1998; Drucker and Bocherens 2009). The C4 pathway is usually found in grasses as well as trees and shrubs from warm regions and has δ13C values between -14‰ and -10‰ (Smith and Epstein 1971; Koch 1998; Cerling 1999; Medrano and Flexas 2000). Several factors may affect the abundance of C3 and C4 plants in the ecosystem. At localities with temperatures lower than 25°C, C3 plants increase in numbers while C4 plants decrease (Medrano and Flexas 2000). Also, C4 plants are able to cope with lower atmospheric CO2 and humidity levels than C3 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 C3 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 δ13C values between -35‰ and -12‰. However, due to the carbon isotope values range, it is difficult to separate these plants from C3 and C4 plants based on δ13C 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 C3 plants have carbon isotope values from -19‰ to -9‰, whereas those that have consumed C4 plants have values from -2‰ to +2‰. The C3/C4 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 δ18O 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, δ18O dental enamel can be used to infer past climatic conditions at a location and certain ecological characteristics of the analyzed species (Ayliffe et al. 1992; Sánchez-Chillón et al. 1994; Bryant and Froelich 1996; Kohn et al. 1996; Sponheirmer 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 (Valero 2010; Fig. 2). The vertebrate fauna, as well as scarce plant remains
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).

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(CH₃CO₂)₂ – CH₃COOH 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 rejoined to the mass spectrometer (Révész and Landwehr 2002). Results were reported as δ¹⁸OVPDB and δ¹³CVPDB, 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 δ13C values, reference was made to MacFadden and Cerling (1996) in order to infer the diet of the animal. The relationship between the δ13C and δ18O 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 δ18O values were converted to Vienna Standard Mean Ocean Water (V-SMOW) using the Faure (1977) formula: \( \delta^{18}O_{\text{V-SMOW}} = \delta^{18}O_{\text{V-PDB}} \times \frac{0.997}{0.998} + 0.986 \), to be compared with the rainwater δ18O 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 δ13C values for the whole set of species (DF 17, F 0.94, p < 0.471092; H 3.140302, p < 0.534627) nor among δ18O values (DF 17, F 2.74, p < 0.074511; H 7.57045, p < 0.108643). The relationship between δ13C and δ18O values showed three groups: (i) most of the gomphotheres, Dinohippus mexicanus, and some Protohippus gidleyi specimens; (ii) Calippus hondurensis, one gomphothere and most of the Protohippus gidleyi specimens; and (ii) the llamas (Fig. 3).

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

<table>
<thead>
<tr>
<th>Species</th>
<th>δ13C VPDB</th>
<th>δ18O VPDB</th>
<th>δ18O V-SMOW Water</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calippus hondurensis</td>
<td>-14.7</td>
<td>-8.4</td>
<td>-11.4</td>
</tr>
<tr>
<td>Calippus hondurensis</td>
<td>-13.1</td>
<td>-8.8</td>
<td>-11.8</td>
</tr>
<tr>
<td>Dinohippus mexicanus</td>
<td>-11.0</td>
<td>-5.4</td>
<td>-6.3</td>
</tr>
<tr>
<td>Dinohippus mexicanus</td>
<td>-11.6</td>
<td>-5.1</td>
<td>-8.0</td>
</tr>
<tr>
<td>Gomphotherium hondurensis</td>
<td>-11.2</td>
<td>-6.6</td>
<td>-9.6</td>
</tr>
<tr>
<td>Gomphotherium hondurensis</td>
<td>-15.2</td>
<td>-8.0</td>
<td>-11.0</td>
</tr>
<tr>
<td>Gomphotherium hondurensis</td>
<td>-10.0</td>
<td>-6.9</td>
<td>-11.4</td>
</tr>
<tr>
<td>Gomphotherium hondurensis</td>
<td>-7.4</td>
<td>-8.3</td>
<td>-11.8</td>
</tr>
<tr>
<td>Hemiauchenia vera</td>
<td>-14.6</td>
<td>-5.0</td>
<td>-7.9</td>
</tr>
<tr>
<td>Hemiauchenia vera</td>
<td>-16.1</td>
<td>-6.1</td>
<td>-9.0</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-7.8</td>
<td>-4.9</td>
<td>-7.8</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-16.7</td>
<td>-8.3</td>
<td>-11.3</td>
</tr>
<tr>
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<td>-10.0</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-9.7</td>
<td>-4.6</td>
<td>-7.4</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-7.2</td>
<td>-7.2</td>
<td>-10.1</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-11.1</td>
<td>-6.1</td>
<td>-9.1</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-16.6</td>
<td>-8.5</td>
<td>-11.5</td>
</tr>
<tr>
<td>Protohippus gidleyi</td>
<td>-15.5</td>
<td>-8.2</td>
<td>-11.2</td>
</tr>
</tbody>
</table>

Discussion

Diet.—The δ13C values from the equid Calippus hondurensis indicate that those animals fed on C3 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 C3 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 C3 plants, while Laurito and Valerio (2010) indicated that D. mexicanus was more generalist in its diet, citing mesowear studies (Barrón-Ortíz and Guzmán-Gutiérrez 2008) that indicated that D. mexicanus at Rancho El Ocote, Mexico, were grazers, whereas individuals from Tecolotlán, México, 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 C4 plants, whereas those in Florida mainly fed on C3 plants (MacFadden 2008). Specimens from Tecolotlán had a C3/C4 mixed diet but with higher proportion of C3 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 δ13C values of the three individuals of Gomphotherium hondurensis indicate that two of them fed only on C3 plants, whereas the third had a mixed diet of C3/C4 plants.
Because gomphotheres had brachiodont molars, they have been thought to have eaten only leaves of trees and shrubs, i.e., mainly C₃ 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 C₃ or C₄ plants; they mainly had a mixed C₃/C₄ diet, such as the one for *G. hondurensis* from San Gerardo de Limoncito.

The llama *Hemiauchenia vera* analyzed here specialized on C₃ plants, whereas Laurito and Valerio (2016) indicated that this species from San Gerardo de Limoncito had a mixed C₃/C₄ 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 C₃ plants or were browsers, and that this habit was maintained in some specimens from two of the three most recent chronostatigraphic units NALMAs: Blancon and Rancholabrean. Among the latter, some llamas with mixed diets coexisted with others that specialized on C₃ 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 C₃/C₄ plants, with a high proportion of C₃ plants, whereas most equids only fed on C₃ 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 C₃ 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 (Sanson 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 C₃ grasses.

**Habitat.**—These herbivorous mammals lived in a closed zone (Fig. 3). Closed habitats include jungles or forests where C₃ plants are abundant and animals that lived in this type of vegetation had δ¹³C and δ¹⁸O values more negative that those inhabited in grasslands (Feranec and MacFadden 2006). However, ecosystems where C₃ 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).

C₃ habitats can be divided into tropical undergrowth, tropical rainforest, subtropical rainforest with closed canopy, 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). δ¹³C 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 δ¹³C values (-26.0‰ to -20.2‰) more negative than mammals inhabiting forest gaps (-17.5‰ to -16.2‰) (Cerling et al. 2004). The negative δ¹³C 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 C₃/C₄ 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 C₄ plants.

Two individuals of *Protohippus gidleyi* had isotope values that were more positive than for the others (δ¹³C -7.8‰ and -9.7‰; δ¹⁸O -4.4‰ and -4.6‰) (Table 1). Variation in the δ¹⁸O of the water in a locality may influence the δ¹⁸O 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 δ¹⁸O values differing from those of the other animals from the same locality (Pellegreni et al. 2008; Widge et al. 2010). The δ¹⁸O 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.

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**Table 2. Oxygen isotopic values (δ¹⁸O_V-SMOW‰) 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.**

<table>
<thead>
<tr>
<th>Month</th>
<th>January</th>
<th>February</th>
<th>March</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
<th>October</th>
<th>November</th>
<th>December</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Value</td>
<td>-6.1</td>
<td>-5.5</td>
<td>-5.5</td>
<td>-5.6</td>
<td>-3.8</td>
<td>-3.3</td>
<td>-3.9</td>
<td>-3.2</td>
<td>-5.5</td>
<td>-6.1</td>
<td>-6.7</td>
<td>-7.0</td>
<td>-5.4</td>
</tr>
</tbody>
</table>
the δ13C 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 C3 plants. Together with the δ13C and δ18O 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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