Geol. Mag. **155** (*1*), *2018, pp. 203–208.* © *Cambridge University Press 2017*
doi:10.1017/S0016756817000747

RAPID COMMUNICATION

The diet of *Leptomeryx* sp. from the Late Eocene Yolomécatl Formation, NW Oaxaca, Sierra Madre del Sur Morphotectonic Province, SE México and its palaeoecological significance

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(*Received* 8 May 2017; *accepted* 8 August 2017; *first published online* 11 September 2017)

Abstract

The diet and habitat of *Leptomeryx* sp. from the Late Uintan Yolomécatl Formation of NW Oaxaca, SE Mexico were inferred using dental enamel carbon and oxygen isotopic relationships, and compared with those of congeneric species from temperate North America. Results show that *Leptomeryx* sp. fed on C3 plants and lived in open forest or forest/savanna ecotone. The palynoflora and co-occurrence of perissodactyls and artiodactyls that live in an environment like that of *Leptomeryx* support this interpretation. Further, both records disclose that in NW Oaxaca (southern North America) tropical conditions prevailed at that time, unlike that of temperate North America.

Keywords: Mexico, Oaxaca, Yolomécatl Formation, stable isotopes, *Leptomeryx*

1. Introduction

1.a. Previous work and purpose

The Tertiary vertebrate record of México is scattered across the country. Spanning the Eocene–Pliocene interval (i.e. Early Wasatchian – Early Blancan North American Land Mammal Ages or NALMAs), it includes among others remains of marsupials, creodonts, perissodactyls, proboscideans, carnivores, rodents and lagomorphs (Montellano-Ballesteros & Jiménez-Hidalgo, 2006). In particular, the Eocene localities and faunas of Lomas las Tetas de Cabra (Wasatchian, Baja California; Novacek *et al*. 1991), Marfil (Bridgerian–Uintan, Guanajuato; Fries, Hibbard & Dunkle, 1955; Black & Stephens, 1973; Ferrusquía-Villafranca, 1989), Rancho Gaitan (Chadronian, Chihuahua; Ferrusquía-Villafranca, 1969; Ferrusquía-Villafranca, Galindo-Hernández & Barrios-Rivera, 1997; Ferrusquía-Villafranca *et al*. 2002) and Yolomécatl (Uintan, Oaxaca; Jiménez-Hidalgo *et al*. 2015; Ferrusquía-Villafranca *et al*. 2016) stand out for their biodiversity. It should be noted that the latter is the southernmost Eocene fauna of North America, and includes mammal species belonging to at least five Orders: Carnivora, Rodentia, Condylarthra, Artiodactyla and Perissodactyla (Jiménez-Hidalgo *et al*. 2015; Ferrusquía-Villafranca, unpublished data). Among the Artiodactyla species found, *Leptomeryx* sp. (Leptomerycidae) was previously known from the Chadronian Rancho Gaitan local fauna (Ferrusquía-Villafranca, 1969; Ferrusquía-Villafranca, Galindo-Hernández & Barrios-Rivera, 1997). This taxon is a small (rabbit-sized), primitive, hornless brachydont/mesodont ruminant, that lived during Middle–Late Eocene (Late Uintan) to Early Miocene time (Early Hemingfordian) (Damuth, 1990; Webb, 1998). Palaeoecologically, *Leptomeryx* is considered to be a forest-dwelling mammal that thrived on tree leaves and fruits (Clark, Beerbower & Kietze, 1967; Retallack, 1983; Wall & Collins, 1998).

The *Leptomeryx* sp. of this study was found in Yolomécatl, Oaxaca, some 1480 km south of its known former location in Mexico (Rancho Gaitan, near Ojinaga, Chihuahua), at *c.* 12° latitude, crossing the Tropic of Cancer. We decided to use the carbon and oxygen isotopic relationships recorded in the tooth enamel of an Oaxacan specimen referred to this taxon in order to infer its diet and habitat, compare them with those inferred from *Leptomeryx* species from temperate North America, and decide whether or not the latitudinal difference influenced the diet and habitat of *Leptomeryx* in southern (tropical) North America.

1.b. Study area

The study area includes *c.* 90 km^2 of rugged terrain within the Mixteca Region, NW Oaxaca State, Sierra Madre del Sur Morphotectonic Province, SE Mexico, between latitudes 17° 25′ and 17° 36′ N and longitudes 97° 29′ and 97° 36′ W (Fig. 1). The Cenozoic sequence unconformably overlies carbonate rock units of Late Jurassic – Late Cretaceous age. The area also includes the Mixteco/Oaxaca Terrane boundary, namely the Tamazulapam fault (Nieto-Samaniego *et al*. 2006; Morán-Zenteno, Cerca & Keppie, 2007).

The Tertiary sequence (Ferrusquía-Villafranca *et al*. 2016) consists of five lithostratigraphic units: two volcanic and one shallow intrusive of Eocene–Oligocene age, as

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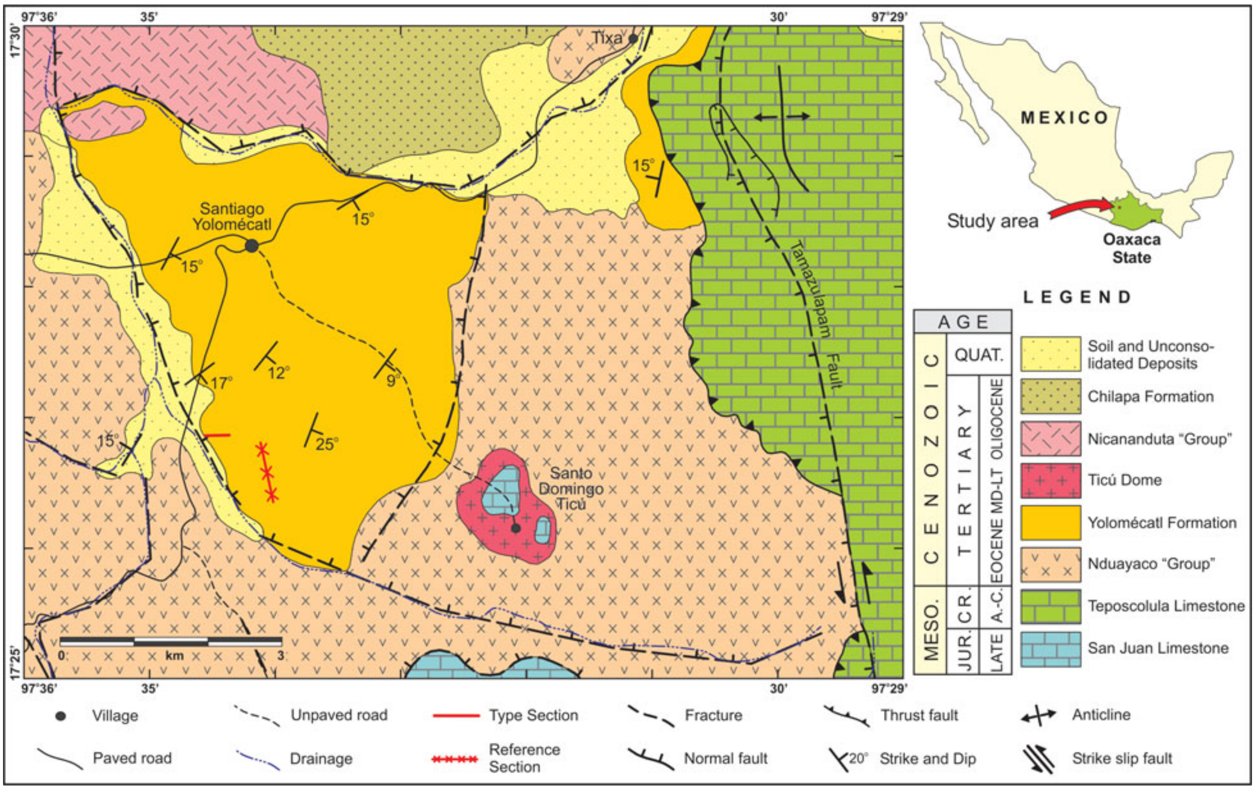

Figure 1. (Colour online) Location and geology of the study area.

well as two epiclastic and subordinately pyroclastic units of Eocene – early Late Oligocene age. Finally, Quaternary deposits and soils unconformably overlie the preceding units (Fig. 1). The structural record chiefly includes folds in the Mesozoic units and faults in the Tertiary units. Palaeontologically, the most interesting unit is the Yolomécatl Formation, an *c.* 650 m thick, vertebrate-bearing, red clastic lacustrine/fluvial succession that fills the namesake triangular graben, which is genetically related to the Tamazulapam fault dynamics. Felsic tuff sheets interbed this succession; one yielded an ^{39}Ar–^{40}Ar age of 40.7 Ma (Ferrusquía-Villafranca *et al.* 2016), which dates this unit and its fauna as of late Middle Eocene age (i.e. Late Uintan NALMA).

1.c. Stable isotopes

Three main approaches are used for inferring the diet and habitat for Pleistocene and earlier extinct mammals: biological actualism, morphofunctional analyses and biochemical carbon/oxygen markers (Andrews & Hixson, 2014). Carbon is incorporated into plants through photosynthesis in three pathways: C3, C4 and CAM (O'Leary, 1988).

The C3 photosynthetic pathway occurs in trees and shrubs and some temperate grasses, with carbon isotopic values ranging between –34 ‰ and –22 ‰ (van der Merwe & Medina, 1989, 1991; Cerling *et al.* 1997; Koch, 1998). On the other hand, the C4 photosynthetic pathway has δ^{13}C values between –14 ‰ and –10 ‰, and is usually found in grasses as well as trees and shrubs from warm regions (Smith & Epstein, 1971; Cerling, 1999; Medrano & Flexas, 2000). The third photosynthetic pathway, CAM (crassulacean acid metabolism), is found in succulent plants such as cacti, bromeliads or agaves, with δ^{13}C values between –35 ‰ and –12 ‰ (Gröcker, 1997; Andrade *et al.* 2007).

Herbivores eat plants, incorporating the carbon from those plants into their tissues and structures such as dental enamel. The isotopic values are correlated with those of the plants, but vary in carbon isotopic composition by as much as a 14.1 ‰ increment (Cerling & Harris, 1999). Based on that variation, modern animals that eat C4 plants will have δ^{13}C values between –2 ‰ and 2 ‰. Carbon isotopic values between –9 ‰ and –19 ‰ will be found in herbivores eating C3 plants, while those eating both types of plants will have δ^{13}C values between –2 ‰ and –9 ‰ (MacFadden & Cerling, 1996). However, given that C4 plants became dominant by Hemphillian time (*c.* 8 Ma ago), this classification is not readily applied to older, pre-Hemphillian mammal taxa. Zanazzi & Kohn (2008) have therefore proposed that δ^{13}C values of –15 ‰ to –21 ‰ indicate the presence of mesic, closed-canopy forest; –13 ‰ to –8 ‰ woodlands; and –8 ‰ xeric grasslands.

On the other hand, oxygen is incorporated into animals by inhalation, from water in food and mainly by ingested water. Such oxygen is in equilibrium with what is lost through CO_2 exhalation, faeces, urine and sweat. Other factors such as physiology, climate and habitat can modify such balance (Sánchez, 2005). The ingested oxygen mostly comes from the ingested water that is present from rain water, in turn affected by latitude, longitude and rain quantity, but mainly temperature (Dansgaard, 1964; Castillo, Morales & Ramos, 1985). Oxygen isotopic composition (^{18}O/^{16}O) is frequently used for palaeoclimatic and palaeoecological studies (Bocherens *et al.* 1996; Kohn, 1996; Sponheirmer & Lee-Thorp, 1999; Schoeninger, Kohn & Valley, 2000).

2. Materials and methods: sample extraction and preparation

A bulk sample (belonging to the Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México) was taken from isolated chick teeth

Table 1. Carbon and oxygen isotopic values of *Leptomeryx* sp. from the Yolomécatl Formation, *L. speciosus* and *L. evansi* from the White River Group. The $\delta^{18}O_{VSMOW}$ values of specimens from White River Group were transformed to $\delta^{18}O_{VPDB}$ using Faure's (1977) equation: $\delta^{18}O_{VPDB} = (0.97002 \times \delta^{18}O_{VSMOW}) - 29.98$. $\delta^{18}O$ values are expressed in VPDB ‰. White River Group values were taken from Zanazzi & Kohn (2008).

Species	$\delta^{13}C$ mean	Maximum value	Minimum value	$\delta^{18}O$ mean	Maximum value	Minimum value
Leptomeryx sp.	− 12.5	0	0	− 4.1	0	0
L. speciosus	− 9.8	− 8.3	− 12.5	− 6.1	− 3.3	− 9.0
L. evansi	− 8.5	− 9.6	− 7.8	− 6.9	− 5.4	− 8.7

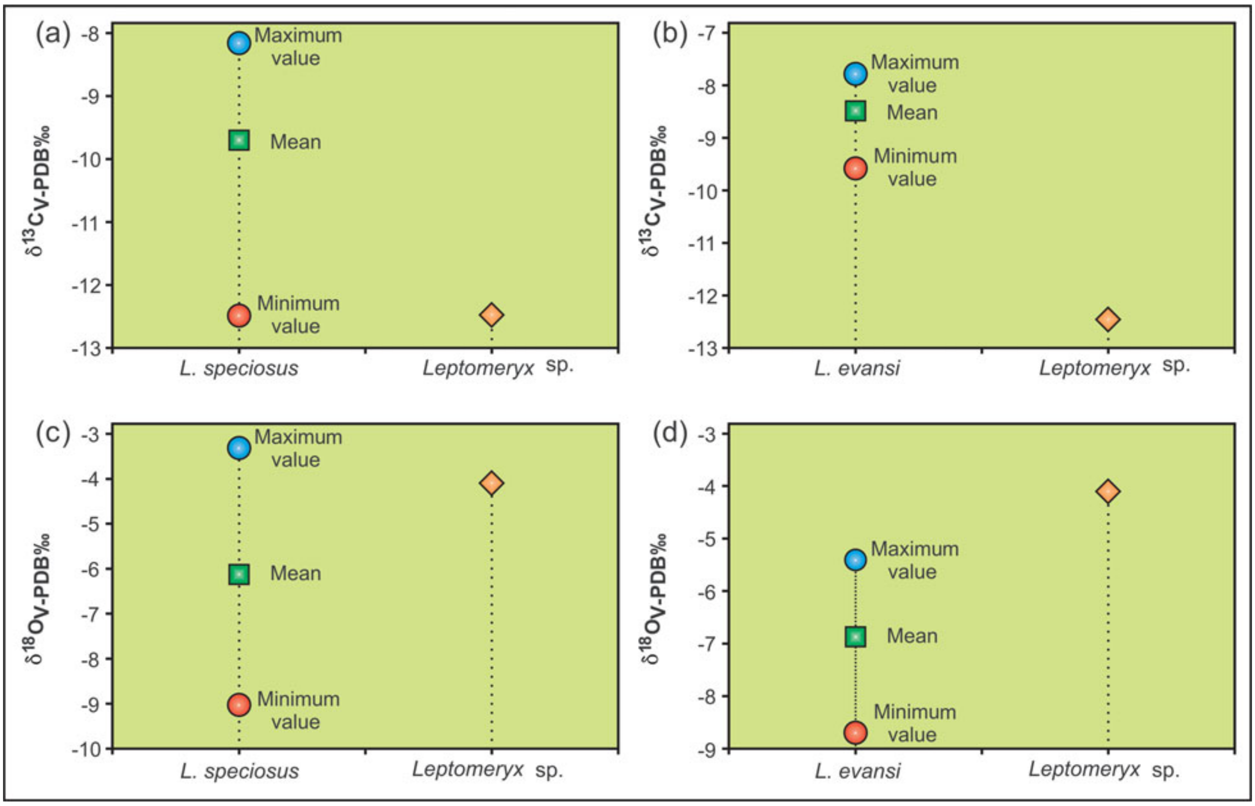

Figure 2. (Colour online) Comparison of (a, b) carbon and (c, d) oxygen isotopic values of *Leptomeryx specious* and *L. evansi* from the White River Group and *Leptomeryx* sp. from the Yolomécatl Formation.

and processed in the Stable Isotope Laboratory at the Instituto de Geología, UNAM, by the method proposed by Koch, Tuross & Fogel (1997). First, 20 mg of enamel was ground and sieved (125 µm mesh) to obtain a fine and uniform powder. Then 10 mL of hydrogen peroxide at 30 % was added to eliminate the organic matter. After 2 h, the samples were centrifuged and the hydrogen peroxide decanted and washed again three times with water type I (grade HPLC 18.2 MΩ).

After the washing, 5 mL of a buffer solution, $Ca(CH_3CO_2)_2$-CH_3COOH 1.0 M, pH 4.75, was added and the mixture was allowed to rest for 9 h. The buffer solution was decanted and the samples were washed another three times with water type I. Finally, to eliminate any remaining water, ethanol was added and the solution was left for 20 h in an oven at 90 °C. Isotopic ratios were determined with a Finnigan MAT 253 mass spectrometer with a dual inlet system, and auxiliary Gas Bench equipment with a GC Pal autosampler with a temperature-controlled aluminium plate adjoined to the mass spectrometer (Révész & Landwehr, 2002). Results were reported as $\delta^{18}O_{VPDB}$ and $\delta^{13}C_{VPDB}$, 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 & Brand (2001) and Coplen *et al.* (2006). For this technique, the standard deviation was 0.2 ‰ for oxygen and carbon.

Finally, we compared the isotopic values of carbon and oxygen with those obtained by Zanazzi & Kohn (2008) of *Leptomeryx speciosus* from the Late Eocene (Chadronian) White River Group and *L. evansi* from the Orellan part of this group (Table 1).

3. Results

The $\delta^{13}C$ value of the *Leptomeryx* sp. specimen from Yolomécatl is −12.5 ‰ and that of $\delta^{18}O$ is –4.1 ‰. The carbon isotopic value falls within the range reported by Zanazzi & Kohn (2008) for *Leptomeryx speciosus* and *L. evansis* from the Chadronian and Orellanian portions of the White River Group. In the case of $\delta^{18}O$ value, this is similar to that of *Leptomeryx speciosus* but different from that shown by *L. evansi* (Fig. 2a–d).

4. Discussion

4.a. Diet

The carbon value of *Leptomeryx* sp. indicates that this individual fed only on C3 plants; Wall & Collins (1998) and

Webb (1998) had pointed out that *Leptomeryx* was a small herbivore that fed on leaves and fruit, which are C3 plants (Medrano & Flexas, 2000). Zanazzi & Kohn (2008) mentioned that the Late Eocene (Chadronian) *Leptomeryx speciosus* from the White River Group fed on C3 plants as observed in the Yolomécatl specimen. The Early Oligocene (Orellan) *Leptomeryx evansi* from the same group had a mixed C3/C4 diet however, which indicates that C4 plants were ingested or, alternatively, that the C3 plants on which *L. evansi* fed were water-stressed (due to a scarcity/lack of water), an environmental condition that altered its δ^{13}C values; this is confirmed by microwear studies (see Zanazzi & Kohn, 2008; Mathis & MacFadden, 2010; Shackelton, 2016). Further, Zanazzi & Kohn (2008) indicated that the δ^{18}O values of *Leptomeryx* are consistent with these mammals having had an incompletely developed anterior intestine fermentation system, or that they depended on water to accomplish anterior intestine fermentation, and that they possibly fed at night, when humidity is greater, behaving just as the extant Indonesian *Tragulus javanicus* (mouse deer).

4.b. Habitat

The oxygen isotopic value of the Yolomécatl individual is similar to that of *Leptomeryx speciosus* (Chadronian, White River Group) and different from *L. evansis* (Orellan, same group), as shown in Table 1. However, the δ^{18}O values of *L. evansi* fall within the range of *L. speciosus* values (see Table 1).

Likewise, the isotopic results obtained from the Yolomécatl *Leptomeryx* sp. indicate that it was a forest or forest/savanna ecotone dweller, as was the Chadronian *L. speciosus* from the White River Group, and clearly different that the Orellan *L. evansi* from the same group which preferred open, somewhat xeric vegetation areas (Zanazzi & Kohn, 2008; Lukens, 2013).

On the other hand, Webb (1998) indicated that the Late Eocene *Leptomeryx* species lived in open forests. The palynologic record obtained from the Yolomécatl Formation discloses the presence of arboreal and herbaceous taxa in NW Oaxaca at that time, lending credence to this assertion (see online Supplementary Table S1, available at http://journals.cambridge.org/geo). In addition, the record of *Amynodontopsis* sp., *Merycoidodon* sp., *Miohippus* sp., *Perchoerus probus*, *Poebrotherium* sp. and *Trigonias* sp. from the same formation (Jiménez-Hidalgo *et al.* 2015; Ferrusquía-Villafranca, unpublished data), which were dwellers of forests, open forests or savannas (Zanazzi & Kohn, 2008; Bottrell, 2009; Boardman, 2013; Boardman & Secord, 2013; Evans & Janis, 2014), also strengthens this theory.

5. Conclusions

The results of this study lead us to conclude that the *Leptomeryx* sp. from the Late Eocene (Uintan) Yolomécatl Formation fed only on C3 plants and lived in a forest or in a forest/savanna ecotone. This scenario is consistent with the palynologic record of this formation, which indicates the presence of arboreal and herbaceous vegetation cover, and with the presence of mammal taxa known to lived in an environment similar to that of *Leptomeryx* sp. Both records disclose a tropical environment in northwestern Oaxaca during Late Eocene time.

Acknowledgements. We are indebted to the Instituto de Geología, Universidad Nacional Autónoma de México (UNAM) for its support, and to the Dirección General de Asuntos del Personal Académico de la UNAM (DGAPA) for their financial assistance through grants PAPIIT IN110614 and IA10407 to develop this project. The analysis was carried out in the Laboratorio de Isótopos Estables and Laboratorio Universitario de Geoquímica Isotópica (LUGIS) of Institutos de Geología and Geofísica, UNAM by our colleagues Edith Cienfuegos Alvarado and Francisco J. Otero Trujano, to whom we are grateful. We also thank two anonymous reviewers for their suggested changes that contributed to the improvement of this publication.

Declaration of interests

None

Supplementary material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0016756817000747.

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