Diet and habitat of unique individuals of *Dinohippus mexicanus* and *Neohipparion eurystyle* (Equidae) from the late Hemphillian (Hh3) of Guanajuato and Jalisco, central Mexico: stable isotope studies

Víctor Adrián Pérez-Crespo1,2, Oscar Carranza-Castañeda2, Joaquín Arroyo-Cabrales3, Pedro Morales-Puente1,4, Edith Cienfuegos-Alvarado1,4 and Francisco J. Otero1,4

1 Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica S/N, Ciudad Universitaria, Del. Coyoacán, 04510, Ciudad de México, Mexico.
2 Centro de Geociencias, Universidad Nacional Autónoma de México, Campus UNAM Juriquilla, Querétaro, 76230, Mexico.
3 Laboratorio de Arqueozoología "M. en C. Tícul Álvarez Solórzano", Subdirección de Laboratorios y Apoyo Académico, Instituto Nacional de Antropología e Historia, Moneda 16 Col. Centro, 06060, Ciudad de México, Mexico.
4 Laboratorio Nacional de Geoquímica y Mineralogía-LANGEM, Mexico.

*vapc79@gmail.com*

**ABSTRACT**

Stable carbon and oxygen isotopes were determined in molar enamel from fossil Pliocene equids from Rancho El Ocote in the San Miguel Allende basin, Guanajuato, and from Santa María, Tecoxtotlán basin, Jalisco. At each locality, the source was one molar from an individual *Dinohippus mexicanus* and one molar from an individual *Neohipparion eurystyle*. Results indicated that the *N. eurystyle* individuals from both localities had been C3/C4 mixed feeders, and had lived in open-zone vegetation (δ13C: -3.1‰ to -1.3‰; δ18O: -4.9‰ to -6.4‰). On the other hand, the *D. mexicanus* from Rancho El Ocote had fed upon C4 plants and lived in open zones (δ13C: -1.3‰; δ18O: -4.9‰), whereas the *D. mexicanus* from Santa María was a C3/C4 mixed feeder with considerable consumption of C3 plants (δ13C: -7.7‰; δ18O: -6.4‰). These results could be contrasted to suggestions from previous isotopic work that *D. mexicanus* in Mexico predominantly fed on C3 plants and further samples analyses are warranted. This study contributes to the understanding of the Pliocene equid taxa from central Mexico and emphasizes the presence of different diets, ranging from exclusive C3 to mixed C3/C4 plants.

Key words: *Dinohippus mexicanus*; *Neohipparion eurystyle*; stable isotopes; late Hemphillian, Mexico.

**RESUMEN**

En este trabajo se analizó un molar de *Dinohippus mexicanus* y uno más de *Neohipparion eurystyle*, ambos recogidos de la localidad de Rancho el Ocote, en la Cuenca de San Miguel de Allende; de la misma forma también se analizaron un molar de cada una de las especies de équidos antes mencionadas, que fueron recogidos en la localidad de Santa María, de la cuenca de Tecoxtotlán, Jalisco. Los molares fueron analizados por isótopos estables de carbono y oxígeno presentes en el esmalte dental, los cuales revelan que en ambas localidades, *N. eurystyle* poseía una dieta mixta C3/C4 y habitaba en zonas de vegetación abierta (δ13C: -3.1‰ y -1.3‰; δ18O: -4.9‰ y -6.4‰). En cambio, *D. mexicanus* de Rancho El Ocote se alimentó de plantas C4 y vivió en zonas abiertas (δ13C: -1.3‰; δ18O: -4.9‰), mientras que el ejemplar de Santa María poseía una dieta mixta C3/C4 con un importante consumo de plantas C3 (δ13C: -7.7‰; δ18O: -6.4‰), lo que es contrario a otras propuestas basadas en isótopos estables que indican que los *D. mexicanus* de México sólo se alimentaban de plantas C3, a aquellos con dietas mixtas C3/C4.

Palabras clave: *Dinohippus mexicanus*; *Neohipparion eurystyle*; Henfiliano tardío; isótopos estables; México.

**INTRODUCTION**

Taxonomic and biostatigraphic research in the Mexican Late Tertiary sedimentary basins has shown a highly diversified mammal fauna. Among the best known and important local faunas are those from Rancho El Ocote in the San Miguel Allende basin, Guanajuato, and from Santa María in the Tecoxtotlán basin, Jalisco. The faunal complex known for those late Hemphillian localities includes the following equids, *Namnippus aztecus*, *Neohipparion eurystyle*, *Astrohippus stockii* and *Dinohippus mexicanus*; rhinoceros, *Teleoceras fossilis*; carnivores, *Agriotherium schneideri*, *Boreophagus secundus*, *Canis ferus*, and *Machairodus* cf. *M. coloradensis*; camelids, *Hemiauchenia vera*, *Megatylopus matthewi*, and *Altorjas* sp.; rodents, *Spermophilus* sp., *Ammospermophilus* sp., *Paenemarmota* sp., *Perognathus* sp., *Phlegomys* sp., *Calomys* sp., *Bairmymys* sp., *Prosoedmon* sp. and *Neotoma* sp.; the xenarthran *Megalonyx* sp.; lagomorphs, *Hypolagus mexicanus* and *Notolagus velox*; and the proboscidean *Rhinotherium* sp. (Miller...

Carbon isotope values from dental enamel record the photosynthetic pathways of plants consumed by the animal in an early life stage when the molars were being formed (Koch, 2007). On the other hand, the mesowear method is based on the attrition (tooth-on-tooth contact) and abrasion (tooth-on-food contact) of the teeth (largely their cusps), regardless of the photosynthetic pathway used by the plant that generates it (Kaiser and Solounias, 2003). This method assesses the dental wear caused by the animal’s diet during months to years of its life span, i.e., the long-term alteration of the enamel (Fortelius and Solounias, 2000). The abrasion produced by the intake of abiotic material (e.g., sand, dust, or soil) could be many times more severe than the effect of enamel attrition (Sanson et al., 2007).

Analysis of carbon and oxygen stable isotopes in fossil molars of the equids Astrohippus stocki, Dinohippus mexicanus, Nanmis aztecus, and Neohippipon euryestyle from Yépomé, Chihuahua, and Rancho El Ocote, Guanajuato, suggested that these species fed predominantly on C₄ plants, such as grasses or other herbaceous plants (MacFadden, 2008). On the other hand, a mesowear analysis of molars from D. mexicanus and N. euryestyle from the Tecolutlán basin (Jalisco) indicated that N. euryestyle had specialized in feeding on abrasive material (such as grass or external grit), whereas D. mexicanus was a mixed feeder (Barrón-Ortiz and Guzmán, 2008). A combination of mesowear, microwear and stable isotope analyses (Bravo-Cuevas et al., 2015) suggested that A. stockii from Rancho El Ocote had a C₃/C₄ mixed diet; most C₃ plants are shrubs and trees, with a few C₄ grasses. Unfortunately, those authors did not provide the stratigraphic context of their specimens. Carbon and oxygen stable isotopes in molars of D. mexicanus and N. euryestyle from the Tecolutlán basin have not previously been analyzed. In the present study, enamel from the molar of an individual from each species from Tecolutlán basin was analyzed and the data were compared with those from the molar of an individual of each species from Rancho El Ocote. The objective was to detect differences and similarities in diet of the two species in comparison with the results recorded by MacFadden (2008).

Δ¹³C and Δ¹⁸O biogeochemical markers

Since 1980, the application of carbon and oxygen stable isotopes analysis has been important in inferring diet and habitat of Cenozoic herbivorous mammals and birds (Barrick, 1998; Koch, 1998; MacFadden and Higgins, 2004; Angst et al., 2014). Carbon is incorporated into animals by three plant photosynthetic pathways. The C₃ pathway has Δ¹³C values from -22‰ to -35‰ and is found in trees and shrubs, as well as in some cold-zone grasses (Smith and Epstein, 1971; O’Leary, 1981; Medina et al., 1986). The C₄ pathway has Δ¹³C values from -10‰ to -12‰ and is typical for grasses, and also for some dry-zone trees and shrubs (Stowe and Teeri, 1978; Cerling, 1999; Cerling and Ehleringer, 2000). Finally, the Grassulacean Acid Metabolism (CAM) pathway has Δ¹³C values from -35‰ to -12‰ and is found in succulent plants such as cacti and some orchids (Göröker, 1997; Andrade et al., 2007).

Herbivores incorporate the carbon of the plants on which they feed into their organs and tissues, so they have carbon isotope values reflecting those of the plants they feed upon. In the case of tooth enamel, the tissue is enriched by 14.1‰ relative to the plant value (Cerling and Harris, 1999). Animals that feed on C₃ plants have carbon isotopic values from -19‰ to -9‰, while herbivores that have consumed C₄ plants have carbon isotopic values from -2‰ to +2‰. The C₃/C₄ mixed feeders show values from -9‰ to -2‰ (MacFadden and Cerling, 1996).

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 CO₂ exhalation, feces, urine and sweat (Koch et al., 1994; Sánchez, 2005). Given that ingested water comes from meteoric water, its composition is affected primarily by temperature, but also by altitude, latitude and the amount of rain fall in a zone (Dansgaard, 1964). The oxygen composition of dental enamel from mammals is used mainly for inferring the paleoclimatic conditions that prevailed in a locality in the past (Longinelli and Nuti, 1973; Kohn, 1996; Kohn et al., 1998; Schoeninger et al., 2000; Mahboubi et al., 2014).

STUDY LOCALITIES

Rancho El Ocate is located at 21°05´28"N and 100°41´01"W in the San Miguel Allende basin, Guanajuato. The ashes found in the stratigraphic sequence were dated by fission tracks, and provided ages of 4.8 Ma for the lower sediments (the Rhino layer) formed during the late Hemphillian, and 4.7 Ma for the upper ash from the early Blancan (Kowallis et al., 1998). These ages provide the limits of the North American Land Mammal Ages (NALMA), late Hemphillian and early Blancan (Figures 1 and 2) (Flynn et al., 2005; Carranza-Castañeda, 2006; Cohen et al., 2013). Four equid species, D. mexicanus, N. eurystyle, A. stockii, and N. aztecus occur in the Rhino level, with lithology and sedimentation rates showing a more humid environment than those of the overlying Blanco level, where only D. mexicanus and N. neustyle are found (Carranza-Castañeda, 2006).

The molars from Rancho El Ocate were collected at the GTO-2A locality. Carranza-Castañeda et al. (2013) recorded that Dinohippus mexicanus and Neohippipon euryestyle were found in the Rhino level, and to Hh3 in the Mammalian Chronology proposed by Tedford et al. (2004). On the other hand, N. eurystyle was not found above the Rhino level. This implies that the level above the Rhino level represents the final portion of the late Hemphillian (Hh4) (Figure 2).

The Tecolutlán basin is 100 km southeast of Guadalajara, in the state of Jalisco (Figure 1; the late Hemphillian stratigraphic sequence is divided by lacustrine strata). The best faunal representation is from the Santa María locality and the studied molars were collected at this site (Figure 3). Lower ash has been dated by ⁴⁰Ar/³⁹Ar at 4.89 Ma (Kowallis et al., 1998). Carranza-Castañeda et al. (2013) have shown that the Santa María area belongs to Hh3. As an erosional discordance, the late Blancan-Irvingtonian, Buenaventura sequence contains gravel and sands, with an internal ash dated at 2.6 Ma (Kowallis et al., 1998). Santa María has a stratigraphic sequence in the Tecolutlán basin that terminates at the bottom of the lacustrine strata. Lithology and sedimentation rates at Santa María indicate the presence of a humid environment, containing remains of D. mexicanus, N. eurystyle, A. stockii and N. aztecus. The last two species are not found in the San José stratigraphic sequence that is overlying the lacustrine sands, with lithology and sedimentation rates typical for a dry environment (Carranza-Castañeda et al., 2013).

MATERIALS AND METHODS

Sample extraction, preparation and statistical analysis of the results

A bulk sample was taken from isolated teeth from Rancho El Ocate: MPGJ-2056 (Dinohippus mexicanus), MPGJ-2026 (Neohippipon euryestyle) and Tecolutlán Basin: MPGJ-2956 (D. mexicanus), MPGJ-2959 (N. eurystyle), each of them representing a single individual. The samples were taken at the crown-root joint following the protocol of
Figure 1. Late Hemphillian fossiliferous localities in the Tecolotlán basin (1) and Rancho El Ocote (2), Mexico.

Figure 2. Stratigraphic column for Rancho El Ocote (GTO 2A). Investigated specimens came from the Rhino layer. Taken from Pacheco-Castro and Carranza-Castañeda (2015).
Feranec and MacFadden (2000) and belong to the Palaeontological Collection of the Centro de Geociencias of the Universidad Nacional Autónoma de México (UNAM), Campus Juriquilla, Querétaro.

Samples were processed in the Stable Isotope Laboratory at the Instituto de Geología, UNAM, with the method proposed by Koch et al. (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). Once the washing was finished, 5 ml of a buffer solution, Ca(CH₃COO)₂·CH₃COOH 1.0 M, pH 4.75, was added and allowed to rest for 9 h. The buffer solution was decanted and the samples were washed again 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 aluminum plate adjoined 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.

RESULTS

Carbon and oxygen isotopic values for D. mexicanus from Rancho El Ocote are more positive than those from Tecolotlán (Table 1, Figure 4). The δ¹⁴C values for specimens of N. eurystyle from the two sites are similar to each other, although somewhat higher from Rancho El Ocote than from Tecolotlán (Table 1, Figure 4).

DISCUSSION

Diet

The carbon isotope value (δ¹³C: -1.3‰) for Dinohippus mexicanus (MPGJ-2056) from Rancho El Ocote implies that this individual was a specialist feeding on C₄ plants such as grasses or other herbs (Table 1), also observed by MacFadden (2008) for Rancho El Ocote and Yepomera locations. In contrast, individuals found in Florida and Texas were mixed C₃/C₄ feeders (MacFadden, 2008), but consumed an important amount of C₃ plants, such as C₃ grasses, tree leaves and shrubs. On this basis, MacFadden (2008) assumed that, during the late Hemphillian, C₄ plants were abundant in Mexican ecosystems, whereas C₃ plants were abundant further north. However, the present results with specimen MGPJ-2956 from Santa María (Tecolotlán basin) differ in that they show a δ¹³C value that characterize it as a C₃/C₄ mixed feeder, but with an important component of C₃ plants (Table 1).

Figure 3. Statigraphic column for the Tecolotlán basin (Santa María). Investigated specimens came from the bone layer. B: Bone layer, K: Cretaceous. Taken from Carranza-Castañeda (2006).
Mesowear studies on specimens of \textit{D. mexicanus} from the Tecolotlán basin (Barrón-Ortiz and Guzmán, 2008) found both browsers and mixed feeders.

The present isotope analysis has suggested that specimen MPGJ-2956, pertaining to \textit{D. mexicanus} from Tecolotlán, may have fed on trees, shrubs and \textit{C}_4 grasses, a diet similar to that proposed by Barrón-Ortiz and Guzmán (2008) for other Tecolotlán specimens. MPGJ-2956 was collected in the lower stratigraphic sequence of the Tecolotlán basin (Carranza-Castañeda, 2006), whereas Barrón-Ortiz and Guzmán (2008) assumed that their specimens likely came from the upper part of the sequence. Their lack of stratigraphic data precludes direct comparison of the two studies; it is uncertain whether the individuals represented by the different specimens were contemporaneous and whether the diet of this species remained constant through time. In Costa Rica, \textit{D. mexicanus} seems to have had a generalist, not a specialized, diet based on morphological ground (Laurito and Valerio, 2010), similar to that suggested by the isotope values in specimens from Texas, Yépomera and Rancho El Ocote (MacFadden, 2008).

In the case of \textit{N. eurystyle}, carbon isotope values for both MPGJ-2026 from Rancho El Ocote and MPGJ-2959 from the Tecolotlán basin show that these animals were \textit{C}_3/\textit{C}_4 mixed feeders, with in the case of MPGJ-2956, an emphasis on the intake of \textit{C}_3 plants (Table 1). This pattern is different from what was found by MacFadden (2008) with specimens from Rancho El Ocote and Yépomera, which fed exclusively on \textit{C}_4 plants. Mesowear analyses (Barrón-Ortiz and Guzmán, 2008) suggested that \textit{N. eurystyle} from the Tecolotlán basin was a grazer, but the lack of stratigraphic control makes it difficult to ascertain whether the diet variation between individuals was due to different locations from the same time period, or whether the differences were due to environmental change.

Since the individuals of \textit{N. eurystyle} analyzed here appear to have been \textit{C}_3/\textit{C}_4 mixed feeders like some individuals in Florida (MacFadden, 2008), both \textit{N. eurystyle} and \textit{D. mexicanus} from the Mexican late Hemphillian appear to have been generalists in their diet.

This plasticity in equid diets may be explained by different factors. For example, in desert areas in the southern USA and northern Mexico, \textit{C}_3 plants are more abundant in winter, the rainy season, whereas \textit{C}_4 plants are more abundant in summer (Ehleringer and Monson, 1993). In temperate areas in general, the two kinds of plants co-inhabit year-around, but in microhabitats that differ in temperature and humidity. Isotope analysis has shown that present-day feral horses in southern New Mexico feed on leaves and grasses that differ in proportion according to seasonal availability (Hansen, 1976; Smith et al., 1998). Furthermore, factors such as soil salinity, light intensity and soil nutrients may influence the carbon isotope composition of plants (Bocherens, 2003) and hence the composition of the dental enamel of herbivores. Competition with other herbivore species may in part explain the wide feeding spectra shown by these equids; Late-Pleistocene bison and horses at Rancho La Brea, California, fed mainly on \textit{C}_3 plants, but bison more frequently preferred \textit{C}_4 plants (Feranec et al., 2009), suggesting the presence of resource partitioning. The small sample size in the present study precludes further speculation.

### Table 1. Carbon and oxygen isotopic values of molar enamel from fossil equids in Mexico.

<table>
<thead>
<tr>
<th>Catalogue number</th>
<th>Species</th>
<th>(\delta^{13}C_{VPDB})</th>
<th>(\delta^{18}O_{VPDB})</th>
<th>Locality</th>
<th>Diet suggested by MacFadden (2008)</th>
<th>Present study</th>
</tr>
</thead>
<tbody>
<tr>
<td>MPGJ-2056</td>
<td>\textit{Dinohippus mexicanus}</td>
<td>-1.3</td>
<td>-3.3</td>
<td>Rancho El Ocote</td>
<td>\textit{C}_3 feeder</td>
<td>\textit{C}_3 feeder</td>
</tr>
<tr>
<td>MPGJ-2956</td>
<td>\textit{Dinohippus mexicanus}</td>
<td>-7.7</td>
<td>-6.4</td>
<td>Tecolotlán</td>
<td>\textit{C}_3 feeder</td>
<td>\textit{C}_3/\textit{C}_4 feeder</td>
</tr>
<tr>
<td>MPGJ-2026</td>
<td>\textit{Neohipparion eurystyle}</td>
<td>-3.1</td>
<td>-4.8</td>
<td>Rancho El Ocote</td>
<td>\textit{C}_3 feeder</td>
<td>\textit{C}_3/\textit{C}_4 feeder</td>
</tr>
<tr>
<td>MPGJ-2959</td>
<td>\textit{Neohipparion eurystyle}</td>
<td>-4.9</td>
<td>-6.4</td>
<td>Tecolotlán</td>
<td>\textit{C}_3 feeder</td>
<td>\textit{C}_3/\textit{C}_4 feeder</td>
</tr>
</tbody>
</table>

![Figure 4. \(\delta^{13}C\) vs \(\delta^{18}O\) for equid molars from Rancho El Ocote (GTO 2A) and the Tecolotlán basin (Santa María). O: Rancho El Ocote; T: Tecolotlán.](image-url)
Lake and water channels (Carranza-Castañeda, 2006). Fossil freshwater gastropods, teeth of Crocodylus sp., all aquatic animals, and remains of the rhinoceros Teleoceras fossiger, have been found there (Carranza-Castañeda et al., 2005). Although T. fossiger has been defined as a browser, isotopic analyses of specimens from Florida showed its diet to be more generalist (MacFadden, 1998), so its presence would not necessarily indicate the existence of C4 plants in the locality. Nevertheless, the wet environment would have been favorable to C4 plants (Ehleringer and Monson, 1993). Abundance of C4 plants at Santa Maria did not depend on the presence of a latitudinal gradient, but on specific conditions at each locality.

The conclusions above are supported by the oxygen isotope values: D. mexicanus from Santa Maria shows a δ18O value of -6.4‰, whereas from Rancho El Ocote it is -3.3‰. For N. eurystyle from Santa Maria it is -6.4‰, whereas from Rancho El Ocote it is -4.8‰. With increasing amounts of rain, oxygen isotope values become more negative (Dansgaard, 1964). Because Santa Maria and Rancho El Ocote are at different altitudes and latitudes, differences in δ18O values are to be expected. Additionally, the location of Santa Maria on the foothills of the Sierra Madre Occidental implies that it received more precipitation, creating more humidity favorable for the establishment of C4 plants, as reflected by the lacustrine sediments (Carranza-Castañeda, 2006). Another factor, however, could explain the different oxygen isotope values. Both D. mexicanus and N. eurystyle may have migrated from place to place in search of food (MacFadden, 2008). They drank water from different feeding areas, and hence the isotopic composition could differ, as found for bison in the eastern Great Plains (Widga et al., 2010).

Carbon isotope analyses on the two other equid species found at Rancho El Ocote, A. stocki and N. azte cus, showed that some of these individuals were C3/C4 mixed feeders, suggesting that this area was drier than at the Florida and Texas localities, and favored the presence of C3 plants (MacFadden, 2008). However, no inference could be made regarding whether during the late Hemphillian grassland with some trees or shrubs existed.

On the basis of the diversity of fossil herbivorous species found at Rancho El Ocote or in the Tecolotlán basin, other species should be included in subsequent studies in order to draw more precise inferences regarding the vegetation type and environmental conditions that existed at each locality during the late Hemphillian.

CONCLUSIONS

At Rancho El Ocote, the diet of the Dinohippus mexicanus specimen was primarily based on C4 plants, and this animal preferred open zones, such as grasslands or savannas. In contrast, the Neohipparion eurystyle was a C3/C4 mixer feeder with an emphasis on C3 plants, living in open zones.

In the Tecolotlán basin, the Dinohippus mexicanus and Neohipparion eurystyle were C3/C4 mixed feeders and lived in areas with some tree coverage; this suggests that conditions here were more favorable for C3 plants than at Rancho El Ocote.

These preliminary conclusions require substantiation by analyses of more specimens and from a wider range of species.

ACKNOWLEDGEMENTS

We thank the Centro de Geociencias, UNAM, Campus Juriquilla Querétaro, for permit us to obtain the enamel samples from the equids. Also, thanks to CONACyT (#132620), PAPIIT (IN109814), PAPIIT (IN404714) and PAPIIT (IA104017) for grants, and to the Laboratorio de Isótopos Estables of the Instituto de Geología, UNAM, as well as R. Puente M. for analyzing the samples. Dr. Eileen Johnson, Museum of Texas Tech reviewed the English writing. We also acknowledge to Ann Grant who helped to improve the writing. Adolfo Pacheco helped with Figure 2. Reviews by Víctor Manuel Bravo Cuevas and an anonymous reviewer on the second version helped to improve considerably the scientific content of this paper.

REFERENCES


Carranza-Castañeda, O., 2006, Late Tertiary fossil localities in Central Mexico, between 19°-23° N. in Carranza-Castañeda, O., Lindsay, E.H. (eds.), Advances in late Tertiary vertebrate paleontology in Mexico and the Great American Biotic Interchange: México, Universidad Nacional Autónoma de México, Instituto de Geología and Centro de Geociencias, Publicación Especial 4, 45-60.


Coplen, T.B., 1988, Normalization of oxygen and hydrogen isotope data: Chemical Geology, 72, 293-297.


Feranec, R.S., Hadley, E.A., Paytan, A., 2009, Stable isotopes reveal seasonal competition for resources between Late Pleistocene Bison (Bison) and Horse (Equus) from Rancho La Brea, Southern California: Palaeogeography, Palaeoclimatology, Palaeoecology, 271, 153-160.


MacFadden, B.J., Cerling, T.E., Harris, J.M., Prado, J.L., 1999b, Ancient latitudinal gradients of C3/C4 grasses interpreted from stable carbon isotopes of New World Pleistocene horses (Equus) teeth: Global Ecology and Biogeography, 8, 137-149.


Miller, W.E., Carranza-Castañeda, O., 1998, Late Tertiary canids from Central Mexico: Journal of Paleontology, 72, 546-556.


Sanchez, B., 2005, Reconstrucción del ambiente de mamíferos extintos a partir del análisis isotópico de los restos esqueléticos, in Alcorno, P., Redondo, R., Toledo, J. (eds.), Nuevas técnicas aplicadas al estudio de los sistemas ambientales: los isótopos: Madrid, Universidad Autónoma de Madrid, 49-64.


Manuscript received: october 8, 2015
Corrected manuscript received: november 14, 2016
Manuscript accepted: january 13, 2017