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Dietary analysis of Late Cenozoic Mexican equids from three different geographic/geologic settings using stable carbon isotopes: Coincidences, differences and paleobiologic significance

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ABSTRACT

The development of Vertebrate Paleontology in Mexico is uneven, so that there is a strong bias in favor of Neogene/Quaternary mammals largely collected in the Trans-Mexican Volcanic Belt (TMVB hereafter) and Central Plateau (CeP hereafter) Morphotectonic Provinces [MP hereafter]; however, the time is ripe for pursuing research in other than taxonomic areas. Here we investigate C_3/C_4 plant consumption in the equid lineage in three such provinces, which provide different geographic/geologic and paleoecologic scenarios during the Barstovian, Hemphillian and Rancholabrean times.

Our results show that the Barstovian equids from Oaxaca, Sierra Madre del Sur MP *Cormohipparion* aff. *C. quinni*, *Merychippus* cf. *M. sejunctus* and *Pliohippus* sp. largely fed on C_3 plants, which were the chief food stuff of horses in Mexico, particularly in the Southeast. On the other hand, the Hemphillian equid from Guanajuato, CeP *Astrohippus stocki*, was an unbalanced C_3/C_4 mixed feeders in favor of C_4 plants, a fact that indicates a profound plant diversification due to the inception and rapid diversification of C_4 plants that occurred there at this time, as it occurred in temperate North America, resulting in the differential consumption of C_4 plants over that of C_3 plants. Such trend prevailed until the Rancholabrean, as born out by the inferred diet for *Equus conversidens* and *Equus* sp. from Hidalgo, TMVB.

Clearly then, the coeval diet change observed in Mexico and temperate North America implies a correlative vegetation change resulting in the appearance and rapid diversification of C_4 plants, which largely formed the preferred food stuff of equids since the Hemphillian, although some C_3 plant consumption was maintained till the Rancholabrean. It should be noted that the development of hypsodonty in equids and many artiodactyls, has long been interpreted as the adaptive mammalian response to the new feeding conditions.

1. Introduction

Vertebrate Paleontology in Mexico spans some 150 years, from an early start carried out by foreign paleontologists (e.g. E.D. Cope, H. F. Osborn, W. Freudenberg), to its present stage with a small, but very active native community loosely associated to paleontologists from many countries. The development has been quite uneven, so that some groups (e.g. mammals and dinosaurs) have been more attended than others; likewise, some epochs/periods (e.g. Pleistocene and Tertiary), have received more attention than others. Geographically, there is a strong bias toward the Trans-Mexican Volcanic Belt and the Central Plateau Morphotectonic Provinces.

Understandably then, in some disciplinary areas, Vertebrate Paleontology is mature enough to make feasible research avenues other than the taxonomic one. Such is the case with Late Cenozoic mammals. In fact, the diet of some Pleistocene, Pliocene and Late Miocene taxa has been established through geochemical isotope studies (Arroyo-Cabrales et al., 2014; Pérez-Crespo et al., 2014), or through micro/mesowear analysis (Barrón-Ortíz and Guzman, 2008; Bravo-Cuevas and Priego-Vargas, 2009; Bravo-Cuevas et al., 2011; Barrón-Ortíz et al., 2014). Here we report the results of geochemical stable isotope studies in six equid taxa from different morphotectonic

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provinces and geologic ages, aimed at detect the similarities/differences of the data, and see how they conform to different to geographic/geologic and chronologic scenarios, observing if the diet changed through time, as it did in temperate North America (MacFadden, 1997), or if the change occurred at a different time in Mexico. To the best of our knowledge, this is the first time that a study involving taxa of a given lineage, but from different morphotectonic provinces, and ages is attempted in Mexico.

1.1. On the stable isotopes of carbon

The use of carbon stable isotopes to infer diets of Cenozoic herbivore mammals has been an important tool, allowing an independent assessment of hypotheses based on morphological data (Bocherens et al., 1996; Koch, 1998; MacFadden, 2000; Clementz et al., 2003; Kohn et al., 2005). Carbon is fixed through plant photosynthesis that has three pathways: C_3 (Hatch–Slack cycle); C_4 (Calvin–Benson cycle); and CAM (Crassulacean Acid Metabolism) (Smith and Epstein, 1971; Dawson et al., 2002; Andrade et al., 2007).

The C_3 pathway is found mainly in dicotyledonous trees and shrubs, as well as some temperate grasses and has $\delta^{13}C$ values from −22‰ to −35‰, and an average value around −27.8‰ (O'Leary, 1988; Ehleringer and Cerling, 2002). On the other hand, the C_4 pathway is typical of monocotyledoneae grasses, as well as some trees and shrubs from warm regions. This photosynthesis way showing carbon isotopic values between −10‰ and −14‰, with an average around −13.5‰ (Cerling et al., 1997; Keeley and Rundel, 2003). Several factors affect the abundance of C_3 and C_4 plants in the ecosystems, like temperature, since at localities with temperature lower than 25 °C, C_3 plants increase their numbers while C_4 plants presence diminish (Medrano and Flexas, 2000). Also, C_4 plants are able to cope with lower atmospheric CO_2 and humidity levels than C_3 plants (McInerney et al., 2011). Finally, the third pathway, CAM, is found in succulent plants, like cacti and bromeliads, with values between −10‰ and −35‰. These values are not useful in distinguishing either C_3 or C_4 plants (Gröcke, 1997). CAM plants distribution is limited due to its low temperature tolerance and by aridity, splitting into two groups: those that inhabit arid or semi-arid zone, like cacti, and those that prefer tropical or subtropical zones, like orchards (Ehleringer and Monson, 1993).

Carbon in plants becomes incorporated into herbivorous tissue, such as dental enamel, when those plants are eaten (Koch, 1998, 2007). Because of that situation, herbivores will have similar plant $\delta^{13}C$ values, but enriched at 14.1‰ (Cerling and Harris, 1999). Based on classifications proposed by MacFadden and Cerling (1996), C_4 plant eaters show values from −2 to 2‰; C_3 plant eaters have values from −9 to −19‰; and C_3/C_4 mixed-diet herbivores show values between −2 and −9‰.

2. Material and methods

2.1. Geologic aspect

The geologic summaries presented for each area (Figures A1–A4), namely Matatlán and Nejapa, Oaxaca State, as well as Rancho El Ocote, Guanajuato State, were taken from Ferrusquía-Villafranca and Ruiz-González (2015), the maps themselves were slightly modified; that of the Epazoyucan Area Hidalgo State were modified from SGM (1997, 2002).

2.2. Geochemical aspect

To perform the isotope analysis, we selected 13 molars referred to these taxa (Table 1): *Merychippus* cf. *M. sejunctus*, *Cormohipparion* aff. *C. quinni*. and *Pliohippus* sp. (Barstovian of Oaxaca, Sierra Madre del Sur Morphotectonic Province, MP hereafter); *Astrohippus stockii* (Hemphillian of Guanajuato, Central Plateau MP); *Equus conversidens* and *Equus* sp. (Rancholabrean of Hidalgo, Trans-Mexican Volcanic Belt MP). The enamel sampling was as follows: Specimen IGM-6726 yielded three samples; Specimen FV-9628 yielded one sample; Specimen IGM-7972 yielded one sample; Specimen UAHPP409 yielded two samples; Specimen UAHMP2711 yielded three samples; Specimen IGCU-1325 1 yielded four samples; Specimen IGM-9143 yielded one sample; Specimen IGM-9148 yielded six samples; Specimen UAHM CR-32 yielded one sample; and Specimen CR-7 yielded two samples (Table 1).

The material from the first three taxa is housed in the Coleccioón Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México; that of the last three is lodged in the Sección de Microvertebrados, Museo de Paleontología de la Universidad Autónoma del Estado de Hidalgo. Later, each molar was drilled (using a Dremel Power Drill) to extract the enamel; one to four enamel samples were taken per tooth.

2.3. Sample preparation of dental enamel for isotopes analyses

The preparation of the samples and analyses were performed in the Stable Isotopes Mass Spectrometry Lab at the Instituto de Geología, Universidad Nacional Autónoma de Mexico. The preparation procedure follows the method proposed by Koch et al. (1997), which is briefly outlined. First, 20 mg of enamel was ground and screened with a 125-μm mesh to obtain a fine and uniform dust. Then 10 ml of 30% distilled water (H_2O) was added to eliminate the organic matter and was left for a period of 2 h. Subsequently, the samples were centrifuged and the distilled water decanted. This procedure was executed three times. Once the washing was completed, 5 ml of a buffer solution made of $CaCH_3$-CO_2–H_3COOH 1 M, pH = 4.75, was added and allowed to sit for 9 h. Afterwards, the buffer solution was discarded, and samples were washed three times again with distilled water. Finally, to eliminate any remaining water, ethanol was added, and the solution was left to rest for 12 h in an oven at 90 °C. Determination of simple isotopic abundance was executed in a Finnigan MAT 253 mass spectrometer with a dual inlet system, and GasBench auxiliary equipment with a GC Pal autosampler that has a temperature-controlled aluminum plate adjoined to the mass spectrometer (Révész and Landwehr, 2002). Results were reported as $\delta^{13}C_{VPDB}$, and they were normalized using NBS-19, NBS-18 and LSVEC to the Vienna Pee Dee Belemnite scale in accordance with the corrections described by Coplen et al. (2006) as well as Werner and Brand (2001). For this technique, the standard deviation was 0.2‰ for carbon.

2.4. Statistical analysis

The maximal, minimal and average $\delta^{13}C$ values were calculated for each taxon, and later compared with the standard values proposed by MacFadden and Cerling (1996) to infer diet type. Finally, we plotted such values, to compare/detect similarities/differences among the various horse species (Fig. 2).

2.5. Terms and abbreviations

δ: isotopic relationship of $^{13}C/^{12}C$,‰: per thousand. V-PDB: Vienna Pee Dee Belemnite. IGM, Instituto Geológico de México (Colección Nacional de Paleontología, housed at the Instituto de Geología, Universidad Nacional Autónoma de México). IGCU, part of the Colección Nacional temporarily housed in the Centro de Geociencias, Juriquilla, Queretaro. FV, specimen field number assigned by I. Ferrusquía-Villafranca to material not yet incorporated to the Colección Nacional Nacional. NALMA, North American Land