



Diet and habitat of *Mammuthus columbi* (Falconer, 1857) from two Late Pleistocene localities in central western Mexico



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ABSTRACT

In recent decades, methods such as stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) present in tooth enamel and dental microwear produced by food have been shown to be more precise in providing data about diet and habitat of extinct and extant animals. In Mexico, the results of these two methods have not been compared for proboscideans. It is considered important to apply both methods to complement the information obtained in each case. This study aimed to infer the diet and habitat of *Mammuthus columbi* from two Late Pleistocene localities, La Cinta-Portalitos and La Piedad-Santa Ana (Michoacan-Guanajuato) in west-central Mexico, to provide reliable data about paleoenvironments. The isotopic analysis showed no significant differences in the values of $\delta^{13}\text{C}$, but there were significant differences for $\delta^{18}\text{O}$. Furthermore, the isotopic values indicated that populations of *M. columbi* of both sites had, on average, a mixed diet (C_3/C_4), with some grazer individuals (C_4) and habitat preference for open areas. Dental microwear analysis suggested that populations of *M. columbi* in both sites were grazers (grasses). The use of both techniques provided more reliable information about the eating habits and habitat preferences of extinct animals. With the trophic spectrum found in the study populations and associated taxa in both sites, both localities had a heterogeneous environment with open grassland areas and forests in higher altitude zones.

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1. Introduction

The First Pleistocene fossils in Mexico were documented over 400 years ago, among the most important and frequent discoveries, due to the large size of the bones, were those pertaining to mammoths (Order Proboscidea) (Corona et al., 2005). In Mexico, the genus *Mammuthus* is known in most of the country, except the Yucatan Peninsula (Arroyo-Cabrales et al., 2007). Mexico's west central region is characterized by many lake basins of great importance because they provided the right environment for the fossilization of various vertebrates belonging to the Late Pleistocene (Marín-Leyva, 2011). Especially in Michoacan, the Columbian mammoth *Mammuthus columbi* were distributed in lacustrine and

fluvial basins belonging to the Trans-Mexican Volcanic Belt (García-Zepeda and Garduño-Monroy, 2006).

Mammoths, similarly to modern elephants (genera *Elephas* and *Loxodonta*), had molars that were adapted for the consumption of abrasive food (grasses). However, most modern elephants are mixed feeders; they eat both C_3 and C_4 plants (Cerling et al., 1999). Knowledge about paleoecological data, such as diet and habitat, of several species in different geographical locations is important because it could provide insights into the composition and changes of past vegetation, which are a key component of climate change and provide a way for testing the different hypotheses about Pleistocene megafaunal extinctions (Metcalf, 2011).

1.1. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) and dental microwear

The species *M. columbi* is classified as a grazer due to the dental morphology of the genus *Mammuthus*, and as such an inhabitant of

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grassland areas (Maglio, 1973). However, in recent decades other techniques to describe paleodiets have been used. These include stable isotopes of Carbon and Oxygen, as well as dental microwear. Stable isotopes, present in tooth enamel, help to infer the diet of extinct animals, climate, and indirectly the vegetation that existed in their habitat (Sánchez et al., 2004). Dental microwear is based on microscopic scars left by food on the enamel surface (pits and scratches), which allows more reliable approximations about the diet of extinct animals (Solounias and Moelleken, 1992; Solounias and Hayek, 1993).

In Mexico, there are a few studies including both stable isotopes of carbon and oxygen (Pérez-Crespo, 2007; Pérez-Crespo et al., 2007, 2010, 2012a; 2012b, 2014) and dental microwear (Marín-Leyva et al., 2013; Barrón-Ortiz et al., 2014) for inferring the diet and habitat of fossil mammal populations, while in the world there are more studies using the two methods (Filippi et al., 2001; Palombo et al., 2005; Ecker et al., 2013; Münzel et al., 2014). It is considered important to apply both methods to complement the information obtained in each case.

We inferred the diet and habitat of mammoths from two Late Pleistocene localities from western-central Mexico: La Cinta-Portalitos (hereafter abbreviated as LC-PT) and La Piedad-Santa Ana (hereafter abbreviated as LP-SA) (Michoacan-Guanajuato, Mexico). We used both methods in order to know if our mammoth populations had a grazer diet based on their dental morphology (hypsodont), if they had the same type of diet throughout their life and if they preferred to live in open or closed environments.

2. Study localities

The study localities were LC-PT located on the northern side of Cuitzeo Lake (20° 05' 09" N; 101° 09' 31" W), and LP-SA located on the banks of the Lerma river (20° 21' 38" N; 101° 58' 13" W), separated by approximately 100 km (Fig. 1). Fossil vertebrates from these localities were assigned to the Rancholabrean North American Land Mammal Age–NALMA (ca. 160 ka to 9.5 ka) (Bell et al., 2004). The faunal assemblage was varied and extensive, with numerous vertebrate taxa (including amphibians and reptiles), of which 14 were large mammals (those above 44 kg according to Koch and Barnosky, 2006). The mammoth remains were an important component of the terrestrial ecosystems.

The locality of LC-PT has a heterogeneous geomorphology subdivided into four zones: NE (shield type volcanic outcroppings with normal faults, northern part of Cuitzeo graben), NW (shield type monogenetic volcanic outcroppings), SW (oldest volcanic rocks) and S (drainage altered by agricultural activity and a portion of the extant lake) (Marín-Leyva, 2011). Six lithological and paleontological facies were recognized for this locality: Facies I: lacustrine, clay with diatoms; Facies II: igneous, volcanic activity, Facies III: fluvial-lacustrine, sand and clay; Biofacies IV: fluvial-lacustrine, micro-conglomerate, fossil vertebrates; Facies V: lacustrine, clay with diatoms; and Facies VI: soils and silt.

The associated large fauna included the equids *Equus mexicanus*, *E. conversidens*, *E. cedralensis*, the bovid *Bison* sp., the camelids *Camelops hesternus* and *Hemiauchenia* sp., the cervid *Odocoileus virginianus* and the tayassuid *Platygonus* sp. Other fauna included the rodents *Microtus* sp., *Neotoma* sp., *Sigmodon* sp. and *Spermophilus* sp., the snake *Elaphe guttata* and the amphibians *Lithobates pipiens* and *Ambystoma* sp. (García-Zepeda, 2006; Pérez and Godínez, 2007; Marín-Leyva, 2008, 2011; Plata-Ramírez, 2012; Díaz-Sibaja, 2013).

The locality of LP-SA had a homogeneous geomorphology subdivided into four zones: NW (Lerma River between highland and hills), W (Chapala plains), SW (volcanic outcroppings from Cerro Grande), SE (Lerma River Great Plains). Six lithological and

paleontological facies were recognized for this site: Facies I: fluvio-lacustrine, clay with sands; Facies II: volcanic, sand; Biofacies III: micro and macro-conglomerate, with fossil macro-vertebrates; Facies IV: fluvial, sand and silt; Facies V: lacustrine, clay with diatoms; Facies VI: soils, silt. The equids *Equus mexicanus*, *E. conversidens*, *E. cedralensis*, the bovid *Bison* sp., the camelids *Camelops hesternus* and *Hemiauchenia* sp., and the cervids *Odocoileus virginianus* and *Cervus elaphus canadensis* were also present (García-Zepeda, 2006; Plata-Ramírez, 2012; Díaz-Sibaja, 2013).

In both study areas, we observed similar fossil fauna despite the different environments of each site. Studies of pollen and diatoms in LC-PT showed that the lake and adjacent areas presented several environmental changes in the past 130 ka. Cuitzeo lake had five humidity phases and in nearby areas the environment experienced several changes; in cold and humid periods vegetation was dominated by temperate forest (pine-oak type) in higher altitudes and herb elements in low areas, while in cold and dry stages elements of xerophytic scrub were present (Israde-Alcántara et al., 2002, 2010; Caballero et al., 2010). There are no such studies for LP-SA.

3. Materials and methods

3.1. Stable isotopes

For this study, 11 fossil molars of *Mammuthus columbi* were used, from the Palaeontological Collection of the Biology College (Universidad Michoacana de San Nicolás de Hidalgo) and the local Museum of La Piedad, Michoacan were used, five from LP-SA and six from LC-PT (Table 1). To extract samples, each molar plate was drilled close to the root towards the occlusal area, removing 40–50 mg of enamel per molar (Pérez-Crespo, 2007). The samples were prepared according to MacFadden and Cerling (1996) and were analyzed in a mass spectrometer (LUGIS, Geology Institute, Universidad Nacional Autónoma de México) to obtain isotopic ratios of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from the carbonates in Viena Pee Dee Belemnite (VPDB).

Table 1

Individual values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ expressed in ‰ VPDB and % of C_4 consumed by populations of *M. columbi* from LP-SA and LC-PT. Abbreviations: M2/3 = second or third upper molar; m2/3 = second or third lower molar; $\text{C}_4\%$ = percentage of C_4 plants consumed, based on the equation $(100) \delta^{13}\text{C}_{\text{sample}} = (100-X) \delta^{13}\text{C}_{100\% \text{C}_3\text{enamel}} + (X) \delta^{13}\text{C}_{100\% \text{C}_4\text{enamel}}$, where the enamel $\delta^{13}\text{C}_{100\% \text{C}_3}$ value is -12.5% and the enamel $\delta^{13}\text{C}_{100\% \text{C}_4}$ value is 2.5% , corresponding to estimates for the Late Pleistocene (Koch et al. 2004).

Catalog number	Molar	Locality	$\delta^{13}\text{C}$ VPDB (‰)	$\delta^{18}\text{O}$ VPDB (‰)	% C_4
CPOEI 282	M2/M3	LP-SA	-5.75	-7.74	44.98
CPOEI 283	M3	LP-SA	-4.27	-5.96	54.89
CPOEI 284	m2/m3	LP-SA	-4.23	-6.51	55.10
CPOEI 285	M2/M3	LP-SA	-4.09	-5.80	56.07
CPOEI 286	m3	LP-SA	-3.77	-6.03	58.23
UM 725	M3	LC-PT	-4.60	-4.23	52.66
UM 726	M3	LC-PT	-4.35	-5.49	54.32
UM 52	M2/M3	LC-PT	-3.36	-5.63	60.94
UM 8	M3	LC-PT	-4.12	-3.81	55.88
UM 9	M2/M3	LC-PT	-1.05	-4.80	76.33
UM 148	M2	LC-PT	-2.13	-4.25	69.12

A Chi-square test (χ^2) was performed to compare the isotopic values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ between the localities of LP-SA and LC-PT. Then, they were compared to populations of *M. columbi* from the USA: Florida, New Mexico and Texas (Koch et al., 1998, 2004) and from Mexico: El Cedral and Laguna de las Cruces (San Luis Potosí), Valsequillo (Puebla), Jicotlán (Oaxaca), Metepec (State of México), Santa Isabel (State of México), Culhuacan (Distrito Federal), Tocuila

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