Geol. Mag. **155** (*3*), *2018, pp. 674–684.* © *Cambridge University Press 2016*
doi:10.1017/S0016756816000935

Diet and habitat of mesomammals and megamammals from Cedral, San Luis Potosí, México

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(*Received* 19 June 2016; *accepted* 1 September 2016; *first published online* 10 November 2016)

Abstract – Using carbon and oxygen isotopic relationships from dental enamel, diet and habitat were inferred for both mesomammals and megamammals that lived in Cedral (San Luis Potosi, north-central México) during Late Pleistocene time. $\delta^{13}C$ and $\delta^{18}O$ values show that bison, some horses and mammoth were eating C_4 plants and lived in open areas, while tapir, camel and some llamas ate C_3 plants and inhabited closed areas. All other studied herbivores (pronghorn, glyptodont, mylodont ground sloth, javelina, mastodon, and other llamas, horses and mammoth) had a C_3/C_4 mixed diet, living in areas with some percentage of tree coverage. On the other hand, American lion and dire wolf ate either C_4 or mixed-diet herbivores, and short-faced bear ate C_3 herbivores. At Cedral, more humid conditions existed than presently, allowing the presence of a forested area near the grassland.

Keywords: Cedral, stable isotopes, herbivores, carnivores, diet, habitat.

1. Introduction

In México, many Late Pleistocene palaeontological localities are distributed all over the country. A few of them appear to be archaeological sites with evidence of human activity (Mirambell, 1982; Mirambell & Lorenzo, 2012; Sánchez *et al.* 2014). One of those is Cedral, San Luis Potosí (México), where the earliest evidence of human presence in México has been found (Lorenzo & Mirambell, 1986; Mirambell & Lorenzo, 2012). Remains of molluscs, reptiles, birds and mammals are associated with such evidence. These remains have been the objective of several studies, mainly focused on the identification and taxonomic studies of the different taxa, especially the mammals that inhabited the Cedral region (Alberdi, Arroyo-Cabrales & Polaco, 2003; Álvarez, Ocaña & Arroyo-Cabrales, 2012; Alberdi *et al.* 2014). In addition, environmental conditions have been inferred for the site during the time range in which the birds and mammals occurred (Corona-M, 2012; Olivera-Carrasco, 2012). The presence of three fossiliferous levels is based on stratigraphically controlled excavations with associated radiocarbon dates (modified from Lorenzo & Mirambell, 1986). These levels are: (1) between 30 000 and 25 000 years BP (before present); (2) between 17 000 and 11 000 years BP, and (3) between 10 000 and 8000 years BP (Fig. 1). Some studies have inferred the diet and habitat of five megaherbivore mammal species (horses (*Equus conversidens*, *E. mexicanus* and *E. cedralensis*), glyptodont (*Glyptotherium* sp.) and mammoth (*Mammuthus columbi*)) using either the carbon/oxygen isotopic relationships found in dental enamel (Pérez-Crespo *et al.* 2009, 2012*b*) or micro/mesowear analyses (Barrón-Ortíz, Theodor & Arroyo-Cabrales, 2014).

In this study, the diet and habitat of several large herbivore and carnivore species from Cedral are inferred using carbon/oxygen isotopic relationships. This information is added to the other mammal data. The combined data are contrasted with data from previous studies using birds and molluscs to infer the palaeoenvironmental conditions that were present at Cedral during Late Pleistocene time.

1.a. Stable isotopes

Three main approaches are used for inferring the diet and habitat of Pleistocene extinct mammals: biological actualism, morphofunctional analyses and biochemical carbon/oxygen markers (Wing *et al.* 1992; Andrews & Hixson, 2014). Carbon is incorporated into plants through photosynthesis via the three pathways of C_3, C_4 and CAM (Crassulacean Acid Metabolism) (O'Leary, 1988).

The C_3 photosynthetic pathway is present in trees and shrubs, and some temperate grasses, with carbon isotopic values ranging between −34‰ and −22‰ (van der Merwe & Medina, 1989; Cerling *et al.* 1997; Koch, 1998; Drucker & Bocherens, 2009). On the other hand, the C_4 photosynthetic pathway has $\delta^{13}C$ values between −14‰ and −10‰, and is usually found in grasses as well as trees and shrubs from warm regions

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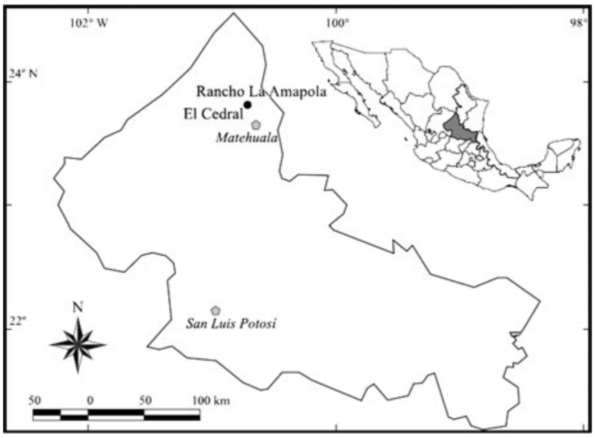

Figure 1. Geographic location of the Pleistocene locality at Cedral, San Luis Potosí, México.

(Smith & Epstein, 1971; Koch, 1998; Cerling, 1999; Medrano & Flexas, 2000). Several factors may affect the abundance of C_3 and C_4 plants in the ecosystems. At localities with temperatures lower than 25 °C, C_3 plants increase in numbers while C_4 plants diminish (Medrano & Flexas, 2000). Also, C_4 plants are able to cope with lower atmospheric CO_2 and humidity levels than C_3 plants (McInerney, Strömberg & White, 2011). Ehleringer & Monson (1993) have shown that in desert areas of the southern USA and northern México, where rain is plentiful in winter, C_3 plants are more abundant while C_4 plants are more abundant during summer. In temperate areas, both kinds of plants coexist throughout the year, but at locations with different microhabitat conditions for temperature and humidity. Furthermore, several factors like saline soils, low light intensity and lack of nutrients may influence the carbon isotopic composition of C_3 plants (Bocherens, 2003).

The third photosynthetic pathway, CAM, is found in succulent plants, like cacti, bromeliads or agaves, with $\delta^{13}C$ values between −35 ‰ and −12 ‰ (Decker & de Wit, 2005; Andrade *et al.* 2007).

Herbivores eat plants, incorporating the carbon from those plants into their tissues and structures such as dental enamel. As such, the isotopic values are correlated with those of the plants, but with a 14.1 ‰ increment (Cerling & Harris, 1999). Based on that difference, modern animals that eat C_4 plants will have $\delta^{13}C$ values between −2 ‰ and 2 ‰. Carbon isotopic values between −9 ‰ and −19 ‰ will be found in herbivores eating C_3 plants, while those eating both types of plants will have $\delta^{13}C$ values between −2 ‰ and −9 ‰ (MacFadden & Cerling, 1996). These carbon isotope values are based on modern atmospheric CO_2 in which the $\delta^{13}C$ value has decreased from −6.5 ‰ to −8.0 ‰ owing to anthropocentric released CO_2 (Marino & McElroy, 1991; Marino *et al.* 1992). The $\delta^{13}C$ values of dental enamel for Late Pleistocene animals, therefore, are between 0.5 and 1.3 more positive than in current herbivorous mammals (Koch, Hoppe & Webb, 1998).

Based on the above, Feranec (2004) pointed out that carbon isotopic values for Pleistocene herbivore dental enamel greater than −1.3 ‰ are typical for C_4 plants; those lower than −7.9 ‰ indicate C_3 plants; and those feeding on both types of plants show values between −1.3 ‰ and −7.9 ‰. In the case of carnivores, carbon isotopic values will depend upon the prey eaten, as well as the part of the carcass eaten, like muscle, organs or bone (Coltrain *et al.* 2004; Kohn, McKay & Knight, 2005; Palmqvist *et al.* 2008; Feranec & DeSantis, 2014). As such, carnivore values will show enrichment between 1.3 ‰ and −2 ‰ in relation to the isotopic values of the herbivores they feed upon (Clementz *et al.* 2009). On the other hand, oxygen is mainly ingested via the water that is drunk. Additionally, some oxygen is ingested via the eaten and inhaled food oxygen. All these ways of ingestion are in equilibrium with water lost from exhalation, sweating, urine and faeces (Koch, Fogel & Tuross, 1994). Factors like physiology, climate and habitat can modify such a balance (Sánchez, 2005). The ingested oxygen mostly comes from the ingested water that is derived from rain water, which is affected by latitude, longitude and rain quantity, but mainly temperature (Dansgaard, 1964; Castillo, Morales & Ramos, 1985). Oxygen isotopic composition is frequently used for palaeoclimatic and palaeoecological studies (Bocherens *et al.* 1996; Sponheirmer & Lee-Thorp, 1999; Schoeninger, Kohn & Valley, 2000).

2. Materials and methods

2.a. Study area

The Cedral site is located in the state of San Luis Potosí, México, at 23° 49′ N and 100° 43′ W, and 1700 m asl (metres above sea level) (Fig. 2). This site contains several ancient source water springs that could have been used as drinking water by Late Pleistocene mammals and others (Álvarez, Ocaña & Arroyo-Cabrales, 2012; Corona-M, 2012).

2.b. Sample preparation and analyses

The preparation of the samples and analyses were performed in the Stable Isotopes Mass Spectrometry Lab at the Geology Institute, National Autonomous University of México. The preparation procedure followed the method proposed by Koch, Tuross & Fogel (1997). First, 20 mg of enamel was ground and screened with a 125 μm mesh to obtain a fine and uniform dust. As sloths lack dental enamel, 20 mg of osteodentine was taken from their molariforms for analysis. Then, 10 ml of 30 % hydrogen peroxide (H_2O_2) was added to eliminate the organic matter and was left for a period of 2 hours. Subsequently, the samples were centrifuged and the hydrogen peroxide decanted and washed with distilled water three times. Once this wash cycle was completed, 5 ml of a buffer solution made of $Ca(C_2H_3O_2)_2$–H_3C_2OOH 1M, pH = 4.75 was added and allowed to sit for 9 hours. Afterwards, the buffer solution was discarded, and samples were washed three times again with distilled water. Finally, to eliminate

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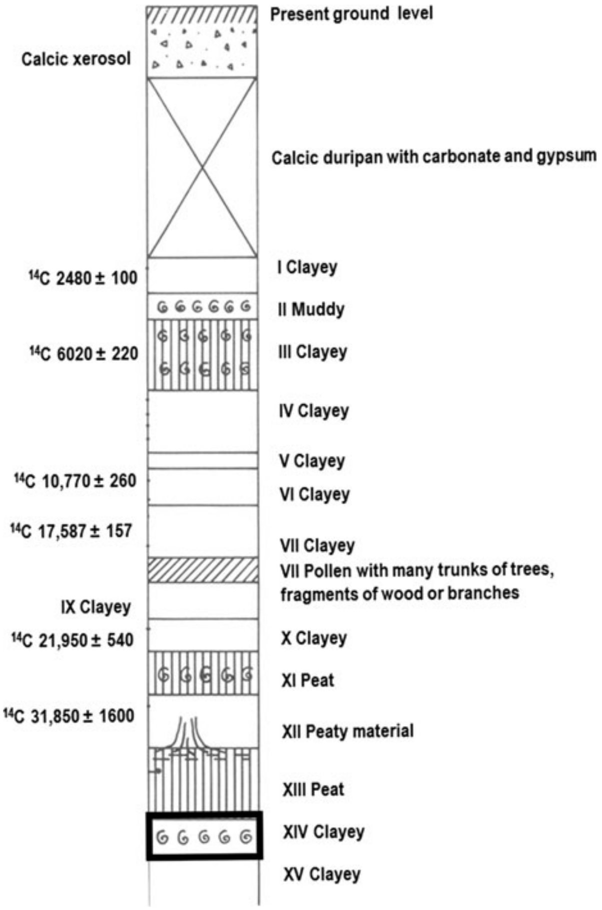

Figure 2. Stratigraphic column for Cedral (modified from Lorenzo & Mirambell, 1986).

any remaining water, absolute ethanol was added, and the solution was left to rest for 12 hours 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 aluminium plate adjoined to the mass spectrometer (Révész & Landwehr, 2002). Results were reported as $\delta^{18}O_{VPDB}$ and $\delta^{13}C_{VPDB}$. 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) and Coplen *et al.* (2006), as well as Werner & Brand (2001). For this technique, the standard deviation was 0.2 ‰ for oxygen and 0.2 ‰ for carbon. Additionally, isotopic values recorded by Pérez-Crespo *et al.* (2009, 2012*b*) for the horses *Equus conversidens*, *E. mexicanus* and *E. cedralensis*, glyptodont *Glyptotherium* sp. and mammoth *Mammuthus* were included in the study.

Mean, maximum and minimum values were assayed for $\delta^{13}C$ and $\delta^{18}O$. In the case of the herbivore $\delta^{13}C$ values, these were compared with values provided by Feranec (2004) for inferring diet type. Carbon and oxygen isotopic values were compared using an analysis of variance, the Kruskall-Wallis test and the Tukey-Kramer test, and graphed following the Feranec & MacFadden (2006) and White *et al.* (2009) models (Fig. 2).

Table 1. Carbon and oxygen isotopic values for carnivores and herbivores from Cedral

Catalogue number	Species	$\delta^{13}C$	$\delta^{18}O$
DP2517	*Arctodus simus*	−11.8	−5.1
DP2358	*Bison* sp.	−1.3	−6.8
DP2359	*Bison* sp.	−1.3	−6.6
DP2390	*Bison* sp.	−3.2	−7.4
DP4311	*Bison* sp.	−1.2	−5.5
DP3332	*Camelops hesternus*	−9.3	−5.6
DP4814	*Camelops hesternus*	−9.3	−4.6
DP4250	*Camelops hesternus*	−8.8	−5.9
DP3666	*Canis dirus*	−6.7	−7.2
DP3322	*Capromeryx mexicana*	−5.7	−4.6
DP3328	*Capromeryx mexicana*	−8.8	−4.4
DP4527	*Equus cedralensis*	−2.7	−3.6
*DP2631	*Equus cedralensis*	−1.5	−2.4
*DP2719	*Equus cedralensis*	−2.1	−2.4
*DP4564	*Equus cedralensis*	−3.0	−1.6
*DP2744	*Equus cedralensis*	−4.4	−1.4
*DP2752	*Equus conversidens*	−1.9	−1.8
*DP2318	*Equus conversidens*	−2.6	−2.9
*DP4577	*Equus conversidens*	−1.7	−4.8
*DP3926	*Equus mexicanus*	−4.4	−1.4
*DP3874	*Equus mexicanus*	−5.9	−2.4
*DP3865	*Equus mexicanus*	−4.7	−4.0
*DP2755	*Equus mexicanus*	−6.9	−3.2
*DP2678	*Equus mexicanus*	−4.3	−3.6
*DP2752	*Equus mexicanus*	−5.1	−1.9
*DP2318	*Equus mexicanus*	−2.7	−4.0
*DP2490	*Glyptotherium* sp.	−4.5	−7.6
*DP2489	*Glyptotherium* sp.	−4.6	−5.8
*DP2491	*Glyptotherium* sp.	−3.7	−7.0
DP4245	*Hemiauchenia* sp.	−10.3	−5.6
DP3333	*Hemiauchenia* sp.	−8.0	−6.1
DP3331	*Hemiauchenia macrocephala*	−5.6	−7.2
DP4237	*Hemiauchenia vera*	−9.5	−4.5
DP2299	*Mammut americanum*	−8.7	−3.9
DP3737	*Mammut americanum*	−7.2	−4.7
DP5247	*Mammut americanum*	−9.2	−4.6
*DP3729	*Mammuthus columbi*	−3.8	−5.1
DP2299	*Mammuthus columbi*	−1.8	−4.4
DP2298	*Mammuthus columbi*	−3.3	−3.8
DP2383	*Mammuthus columbi*	−0.9	−4.5
DP3457	*Megalonyx* cf. *M. jeffersoni*	−3.1	−4.5
DP3658	*Nothrotheriops shastensis*	−9.8	−3.8
DP4424	*Panthera atrox*	−4.3	−4.3
DP4387	*Paramylodon harlani*	−4.8	−7.7
DP3217	*Platygonus* sp.	−9.1	−4.8
DP3182	*Tapirus haysii*	−10.7	−5.3
DP3184	*Tapirus haysii*	−10.5	−5.9
DP3190	*Tapirus haysii*	−10.6	−5.3

*Values taken from Pérez-Crespo *et al.* (2009, 2012*b*).

Significance level for the statistical tests was set at $p < 0.05$, and NCCS and PASS (Hintze, 2004) was the utilized software.

3. Results

Table 1 contains carbon and oxygen isotopic values for each one of the studied specimens, and Table 2 has average values for each studied species. The most negative carbon isotopic value is for the short-faced bear (*Arctodus simus*), while bison (*Bison* sp.) has the most positive average isotopic values.

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Table 2. Means, maximum and minimum values of $\delta^{13}C$ and $\delta^{18}O$

Species	n	$\delta^{13}C_{VPDB}$	δ^{13}CMax	δ^{18}CMin	$\delta^{18}O_{VPDB}$	δ^{18}OMax	δ^{18}OMin
Arctodus simus	1	− 11.8	− 11.8	− 11.8	− 5.1	− 5.1	− 5.1
Bison sp.	4	− 1.7	− 3.2	− 1.2	− 6.5	− 7.4	− 5.5
Camelops hesternus	3	− 9.1	− 9.3	− 8.8	− 5.3	− 5.9	− 4.6
Canis dirus	1	− 6.7	− 6.7	− 6.7	− 7.2	− 7.2	− 7.2
Capromeryx mexicana	2	− 7.2	− 8.8	− 5.7	− 4.5	− 4.6	− 4.3
Equus cedralensis	4	− 2.3	− 3.0	− 1.5	− 3.8	− 3.6	− 1.6
Equus conversidens	3	− 2.0	− 2.6	− 1.7	− 3.1	− 4.8	− 1.8
Equus mexicanus	7	− 4.8	− 6.9	− 2.7	− 2.5	− 4.0	− 1.4
Glyptotherium sp.	3	− 4.3	− 4.6	− 3.7	− 6.8	− 7.6	− 5.8
Hemiauchenia sp.	2	− 9.2	− 10.3	− 8.0	− 5.9	− 6.1	− 5.8
Hemiauchenia macrocephala	1	− 5.6	− 5.6	− 5.6	− 7.2	− 7.2	− 7.2
Hemiauchenia vera	1	− 9.5	− 9.5	− 9.5	− 4.5	− 4.5	− 4.5
Mammut americanum	3	− 8.3	− 9.2	− 7.2	− 4.4	− 4.7	− 3.9
Mammuthus columbi	4	− 2.4	− 3.8	− 0.9	− 4.4	− 5.1	− 3.8
Megalonyx cf. *M. jeffersoni*	1	− 3.1	− 3.1	3.1	− 4.5	− 4.5	− 4.5
Nothrotheriops shastensis	1	− 9.8	− 9.8	− 9.8	− 3.8	− 3.8	− 3.8
Panthera atrox	1	− 4.3	− 4.3	− 4.3	− 4.3	− 4.3	− 4.3
Paramylodon harlani	1	− 4.8	− 4.8	− 4.8	− 7.7	− 7.7	− 7.7
Platygonus sp.	1	− 9.1	− 9.1	− 9.1	− 4.8	− 4.8	− 4.8
Tapirus haysii	3	− 10.6	− 10.7	− 10.5	− 5.5	− 5.9	− 5.3

n – number of individuals; delta values expressed in ‰.

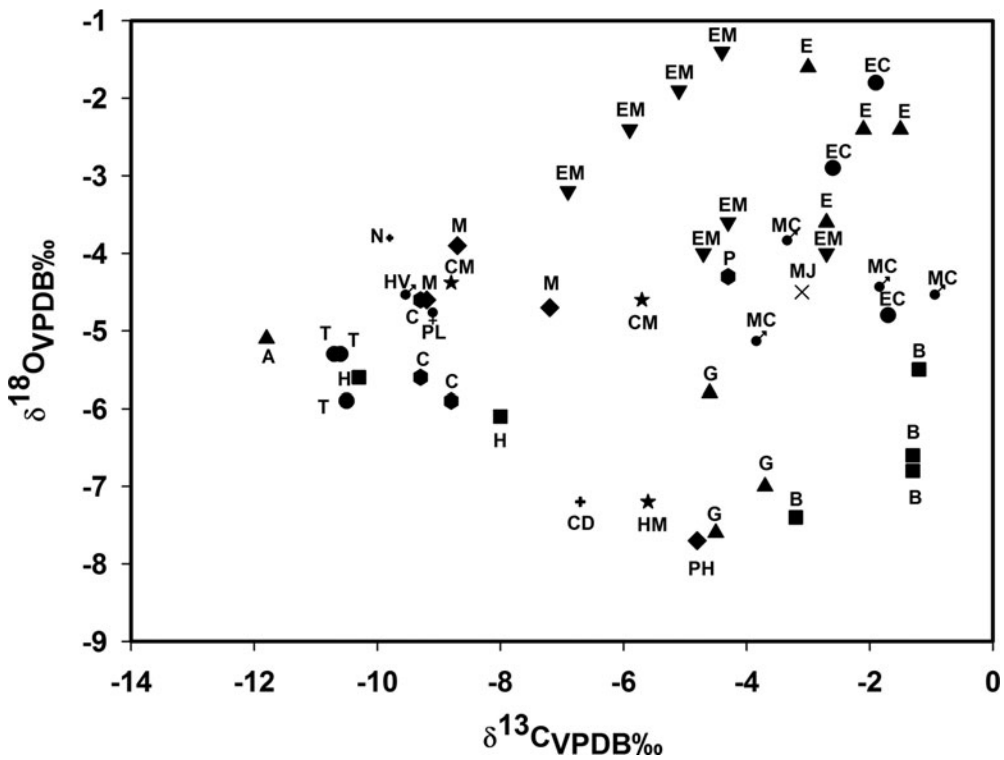

Figure 3. Graph of the $\delta^{13}C$ v. $\delta^{18}O$ values for Cedral fauna. A – *Arctodus simus*; B – *Bison* sp.; C – *Camelops hesternus*; CD – *Canis dirus*; CM – *Capromeryx mexicana*; E – *Equus cedralensis*; EC – *Equus conversidens*; EM – *Equus mexicanus*; G – *Glyptotherium* sp.; H – *Hemiauchenia* sp.; HM – *Hemiauchenia macrocephala*; HV – *Hemiauchenia vera*; MM – *Mammut americanum*; MC – *Mammuthus columbi*; MJ – *Megalonyx* cf. *M. jeffersoni*; N – *Nothrotheriops shastensis*; P – *Panthera atrox*; PH – *Paramylodon harlani*; PL – *Platygonus* sp.; T – *Tapirus haysii*.

Both analysis of variance and Kruskall-Wallis tests assayed between $\delta^{13}C$ and $\delta^{18}O$ values show that significant differences exist among the analysed species ($p < 0.00001$; Degree of Freedom: 46; Fisher test: 17.61; $p < 0.001685$; Degree of Freedom: 46; H test: 42.1652); see online Supplementary Material Tables S1 and S2 available at http://journals.cambridge.org/geo for the results from the Tukey-Kramer tests for both isotopic relationships. In the graph (Fig. 3), most values for bison, some horses and mammoth are located to the right, which indicates these animals lived in areas of open vegetation. Values for short-faced bear, tapir (*Tapirus* sp.), some llamas (*Hemiauchenia* sp. and *H. vera*), camel (*Camelops hesternus*), mastodon (*Mammut americanum*), javelina (*Platygonus* sp.) and Shasta ground sloth (*Nothrotheriops shastensis*) are to the

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left, which suggests those animals preferred areas of closed vegetation. The American lion (*Panthera atrox*), dire wolf (*Canis dirus*), ground sloth (*Paramylodon harlani*), glyptodont (*Glyptotherium* sp.), some horses, llamas (*H. macrocephala*) and mammoth values are located between those two groups, indicating that those animals lived in areas with some degree of tree coverage.

4. Discussion

4.a. Herbivore diets

The results show that most of the bison at Cedral were feeding on C_4 plants. One, however, shows a mixed C_3/C_4 diet, but with an important C_4 plant intake. Based on data $\delta^{13}C$ secured for *Bison* species by Chisholm *et al*. (1986), Connin, Betancourt & Quade (1998), Gadbury *et al*. (2000), Leyden & Oetelaar (2001), Koch, Diffenbaugh & Hoppe (2004) and Feranec (2007) in the USA and Canada, bison were feeding primarily on C_4 plants, with a few individuals being C_3/C_4 mixed feeders. Furthermore, meso- and microwear studies have shown that Pleistocene bison were more flexible in their diet than previously considered (Rivals, Solounias & Mihlbachler, 2007).

For the camels, assays showed that their diet was mainly based on C_3 plants. Similarly, Pérez-Crespo *et al*. (2012*b*) analysed the diet for this animal from Laguna de las Cruces, a locality near Cedral. They found that some individuals were C_3/C_4 mixed feeders with a large intake of C_4 plants, while others exclusively fed upon C_4 plants. Dompierre & Churcher (1996) and Semprebon & Rivals (2010) pointed out that camels were mainly mixed-diet feeders. Some individuals or even populations, however, showed either grazing or browsing diets, like the Cedral individuals. These results suggested that these animals were generalists rather than specialists in their diet.

Individuals of *Capromerxy mexicana* showed a C_3/C_4 mixed diet, similar to results based on mesowear by Barrón-Ortíz *et al*. (2014) for the same samples. This small pronghorn was characterized as a grassland browser and grazer based on morphological inferences (Johnson, Arroyo-Cabrales & Polaco, 2006). Studies by Connin, Betancourt & Quade (1998), Coltrain *et al*. (2004), Rivals & Semprobon (2006) and Semprobon & Rivals (2007) on different genera of Cenozoic antilocaprids showed that these animals had a wider feeding spectrum than previously proposed.

For the horses, on average the three known species at Cedral were C_3/C_4 mixed-diet feeders. Small differences, however, occurred in the amount of C_3 or C_4 plant consumption for each species. *Equus cedralensis* had a C_3/C_4 mixed diet, while one individual ate C_4 plants exclusively. *E. conversidens* was a C_3/C_4 mixed feeder, but with some preferences for C_4 plants. Finally, *E. mexicanus* had a mixed diet, but with a larger consumption of C_3 plants than the other two species. One individual, however, had a mixed diet with a larger intake of C_4 plants. Barrón-Ortíz, Theodor & Arroyo-Cabrales (2014) evaluated the same individuals using both meso- and microwear analyses and found a similar pattern. They proposed that the pattern may be due to microhabitats at the site as well as to size differences among the horse species.

The glyptodont $\delta^{13}C$ values indicated a C_3/C_4 mixed diet with a large consumption of C_4 plants. Gillete & Ray (1981) proposed that this genus had a browsing feeding habit. Later, Fariña & Vizcaíno (2001) questioned such a proposal, and indicated that glyptodont teeth were hypsodont and had ostedentine rings that mimicked enamel function, as well as skull morpho-functional adaptations (Vizcaíno, De Iuliis & Bargo, 1998; Vizcaíno *et al.* 2004). These lines supported the suggestion that the genus mainly ate grasses. Johnson, Arroyo-Cabrales & Polaco (2006) characterized the glyptodont as a browser along waterways. Isotopic data, however, obtained during the present study supports the proposal by Vizcaíno (2000) and Fariña & Vizcaíno (2001). The Cedral individuals primarily ate C_4 grasses.

For the Cedral llamas, two individuals assigned to *Hemiauchenia* sp. and an individual of *Hemiauchenia vera* showed a diet mainly based on C_3 plants, while *H. macrocephala* had a C_3/C_4 mixed diet, but with an important intake of C_3 plants. The current isotopic analysis and meso- and microwear studies (Barrón-Ortíz, Theodor & Arroyo-Cabrales, 2014) indicated that these animals were generalists in their diet. Individuals were eating either C_3 or C_4 plants only, or with C_3/C_4 mixed diets (Feranec, 2003; Semprebon & Rivals, 2010), as previously proposed by Honey *et al*. (1998).

For Cedral mastodons, the study individuals only ate C_3 plants. Isotopic studies by Koch, Hoppe & Webb (1998) and Metcalfe (2011) with mastodon samples from Ontario (Canada) and New York and Florida (USA) indicated that this species was a browser (exclusively eating C_3 plants). This interpretation was supported by dental microwear studies by Green & Hulbert (2005), Green, Semprebon & Solounias (2005), Green (2006) and Rivals, Semprebon & Lister (2012) using specimens from South Carolina, Florida and Texas (USA). Coprolite analysis of samples from Aucilla River, Florida pertaining to this animal assayed by Leeper *et al*. (1991) and Newson & Mihlbachler (2006), however, found small quantities of herbs.

For the other proboscidean group at Cedral, three mammoths had a C_3/C_4 mixed diet, while one individual exclusively ate C_4 plants. Another study with Mexican mammoth samples also showed that this animal had a C_3/C_4 mixed diet with an important consumption of C_4 plants (Pérez-Crespo *et al.* 2012*a*), similar to the findings at Cedral.

The one javelina sample from Cedral showed a diet exclusively of C_3 plants. Previously, this animal was thought to have eaten leaves and fruits, as well as succulent plants (Kurtén & Anderson, 1980). Isotopic analysis of specimens from California and Florida (USA) showed that these animals had a C_3/C_4 mixed diet, with some individuals exclusively eating C_3 plants (Feranec, 2005; Trayler, 2012).

Ground sloths at Cedral had a wide variety of diets depending upon species. The mylodont had a C_3/C_4 mixed diet, with an important C_3 plant intake. Kurtén & Anderson (1980) mentioned that the species ate grasses, short shrubs and roots, while Johnson, Arroyo-Cabrales & Polaco (2006) characterized *Paramylodon harlani* as a grassland mixed browser. Morphometric analyses undertaken by McDonald (2005), McDonald & Pelikan (2006) and Bargo & Vizcaíno (2008), however, suggested that this species ate mainly grasses and other herbs. Isotopic analysis of Texan specimens by Reuz (2005) showed a mixed diet similar to the individual from Cedral.

On the other hand, the nothrotheriop sloth at Cedral exclusively ate C_3 plants. Microwear studies showed that those animals fed upon leaves (Green, 2009), but isotopic analysis indicated that these animals mostly had a C_3/C_4 mixed diet (Bonde, 2013). Similarly, coprolite analysis from materials pertaining to this species indicated that these animals ate tree leaves, herbs and cacti (Thompson *et al.* 1980; Poinar *et al.* 1998). In the case of *Megalonyx* cf. *M. jeffersoni*, this individual had a C_3/C_4 mixed diet, with an important intake of C_4 plants. Such a finding was different from that based on the morphological inference (Kurtén & Anderson, 1980; McDonald, 2005; Johnson, Arroyo-Cabrales & Polaco, 2006) that these animals ate fruit and tree leaves. Isotopic data from individuals elsewhere in North America (Kohn, McKay & Knight, 2005) showed that this animal ate C_3 plants. Bonde (2013), however, found individuals from California (USA) had a C_3/C_4 mixed diet. He proposed that the species had different feeding strategies, allowing it to eat a wide diversity of plants.

Finally, tapirs at Cedral had a diet based on C_3 plants. Tapirs today are known to eat mainly leaves, stems, fruits, bark and flowers (Naranjo, 2009; Talamoni & Assi, 2009). Isotopic analyses of present and fossil (Florida) specimens (Koch, Hoppe & Webb, 1998; DeSantis & MacFadden, 2007; DeSantis, 2011) indicate that these animals were specialized in consumption of C_3 plants, similar to what was found for the Cedral specimens.

4.b. Carnivore diets

The carbon isotopic value for the Pleistocene lion *Panthera atrox* at Cedral shows that this felid fed upon mixed-diet herbivores or C_4 grazers such as bison, horses, pronghorn and mammoth. Fox-Dobbs, Leonard & Koch (2008) suggested that individuals of the Pleistocene lion from Beringia ate bison, horses, moose and young mammoth, species that fed on C_3 herbs. Cedral herbivores, like those from Beringia, ate herbs with different photosynthetic pathways and their diets should not be considered much different. Furthermore, Trayler (2012) found that some specimens from California ate C_3 herbivores, like cervids and mastodon, as well as some horses. These data suggest, as with all other information, that the American lion had a wide variety of prey.

For the one dire wolf *Canis dirus* at Cedral, the $\delta^{13}C$ value suggests that it fed upon horses, llamas, mastodon and camel. Kurtén & Anderson (1980) and Binder & Van Valkenburgh (2010) characterized the dire wolf as a scavenger. On the other hand, Wang & Tedford (2008), Anyonge & Baker (2005) and Meloro (2012) suggested that the species was an active hunter that also ate carrion, similar to grey wolf behaviour today. Fox-Dobbs *et al.* (2007) noted that dire wolf from Rancho La Brea scavenged mastodon and sloth carcasses, but actively hunted bison, camel and horses. Coltrain *et al.* (2004) found that other Rancho La Brea dire wolf had isotopic values that suggested they ate C_3 herbivores. Trayler's (2012) results from two California locations had isotopic values pointing to them eating C_4 herbivores. These data showed that dire wolf had a wide variety of prey upon which it could feed, providing enough resources to inhabit the same area with other large predators, like the Pleistocene lion or sabre-toothed cat. Because Pleistocene lions also were present at Cedral, the dire wolf being more of a generalist would help it to coexist with the felid. With only one sample for each species, this hypothesis could not be tested.

Kurtén & Anderson (1980) and Christiansen (1999) classified the short-faced bear *Arctodus simus* as an active predator. Based on isotopic analysis, Matheus (1995, unpub. Ph.D. thesis, Univ. Alaska Fairbanks, 1997) identified it as a scavenger. Figuerido *et al.* (2010) and Donohue *et al.* (2013) noted it as an omnivore. Owing to having only one sample from Cedral and the lack of nitrogen isotopic values, it is difficult at this point to infer whether the short-faced bear was an omnivore or solely fed upon meat. The $\delta^{13}C$ value, however, showed that this individual fed upon C_3 herbivores, different from those eaten by the American lion and the dire wolf. The value did not overlap with any of the known herbivores from the site, but was close to tapir and llama values. Those animals could have been included in their diet, along with other C_3 herbivores like camel, javelina, *Nothrotheriops* and mastodon. For Alaska and California (Fairmed Landfill) specimens, Fox-Dobbs, Leonard & Koch (2008) and Trayler (2012) proposed that this animal ate mammoth, horse, bison and cervid. Trayler (2012), however, noted for other California locations (McKittrick and Asphalt Seep) that short-faced bear had a diet based on deer and tapir, similar to the one inferred for the Cedral individual.

4.c. Habitat

In regard to the oxygen isotopic values, taxa differences may be due to the species' particular physiology (Bryant & Froelich, 1995; Fricke & O'Niel, 1996; Zanazzi & Kohn, 2008), as well as to movements the animals may have undertaken. These animals would have a

https://doi.org/10.1017/S0016756816000935 Published online by Cambridge University Press

water isotopic composition from the areas where they previously fed (Hoppe, 2004).

Cedral herbivores lived in diverse habitats. Bison, some horse species and some mammoth preferred inhabiting open areas, while tapir, nothrotherid sloths, javelina, llamas, camel and mastodon preferred closed areas. All other herbivores preferred areas with some tree coverage such as Pleistocene pronghorn, glyptodont, mylodont and megalonichid sloths, and some mastodon, horse and mammoth (Fig. 3).

For carnivores, the American lion at Cedral inhabited areas with sparse tree coverage. Christiansen & Harris (2009) indicated that *Panthera atrox* mainly lived in open areas, while Trayler (2012) also included closed areas. The combined findings suggested that this species occupied a wide variety of habitats. Likewise, the dire wolf *Canis dirus* individual preferred open areas with some tree coverage. Johnson, Arroyo-Cabrales & Polaco (2006) mentioned that this animal was an inhabitant of grasslands or savannas. California specimens also showed that they inhabited tree covered areas (Trayler, 2012).

On the other hand, short-faced bear at Cedral inhabited closed areas. Kurtén & Anderson (1980), P. E. Matheus (unpub. Ph.D. thesis, Univ. Alaska Fairbanks, 1997) and Johnson, Arroyo-Cabrales & Polaco (2006) considered that this animal lived in grasslands or savannas. Trayler (2012) found bear individuals living in forested areas and others in areas with open vegetation. This variation suggested that this species was capable of living in a variety of habitats and fed upon animals living there. The lack of a larger sample, however, precluded testing that proposal.

Habitat differential preferences for Cedral carnivores and herbivores indicated that an open forest existed at this site. The fossil pollen record showed the presence of trees, herbs and cacti (Sánchez-Martínez & Alvarado, 2012). That record supported the proposal by Corona-M (2012) and Olivera-Carrasco (2012) that a wetland existed along with the spring, with a gallery forest near to grassland or scrub. This vegetation mosaic supported a diverse mammalian herbivore and carnivore fauna that inhabited Cedral during Late Pleistocene time. This pattern was similar to that found in northwestern Sonora and southwestern USA (Hall, Van Devender & Olson, 1988; Metcalfe, 2006; Clark *et al.* 2012). A humid climate allowed the presence of this vegetation mosaic. The warming environment in Holocene time allowed the rise of the xerophilous scrub that is present today (Flores, 2012).

5. Conclusions

For Cedral, north-central México, the herbivorous mammal fauna was constituted by three groups of animals. One group fed on C_3 plants and lived in open areas, like camel and some llamas. Another group fed on C_4 plants in open areas, like some bisons, horses and mammoths. The third group had a mixed diet, living in areas with some tree coverage, like pronghorn, glyptodont, mastodon, javelina, mylodont ground sloth, and other bison, horses, llamas and mammoth. On the other hand, American lion and dire wolf preyed on herbivores that lived in areas with some tree coverage, while short-faced bear ate herbivores living in closed areas. Based on these data and the pollen record, these animals lived in a forest with a nearby grassland. During Late Pleistocene time, environmental conditions were wetter than present, providing the best conditions for the settling of the first Mexican humans.

Acknowledgements. We thank the Consejo de Arqueología from INAH for granting the permit to obtain the enamel samples from the studied horses. Also, Consejo Nacional de Ciencia y Tecnologia and (#132620) and Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica-UNAM (#IN404714) provided supportive grants. Laboratorio de Isotópos Estables from the Instituto de Geologia, UNAM, as well as R. Puente M. analysed the samples. Also, Dr Eileen Johnson very kindly reviewed the English writing, but any mistakes are from the authors. Maria Teresa Alberdi and one anonymous review also contributed with useful comments.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0016756816000935

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https://doi.org/10.1017/S0016756816000935 Published online by Cambridge University Press