Geol. Mag. **149** (*1*), 2012, pp. 153–157. © Cambridge University Press 2011
doi:10.1017/S0016756811000951

RAPID COMMUNICATION

Diet and habitat definitions for Mexican glyptodonts from Cedral (San Luis Potosí, México) based on stable isotope analysis

VICTOR ADRIÁN PÉREZ-CRESPO*†, JOAQUÍN ARROYO-CABRALES‡, LUIS M. ALVA-VALDIVIA§, PEDRO MORALES-PUENTE¶ & EDITH CIENFUEGOS-ALVARADO¶

*Posgrado en Ciencias Biológicas, UNAM, Ciudad Universitaria, Del. Coyoacán, 04150, México, D. F.
‡Laboratorio de Arqueozoología 'M. en C. Ticul Álvarez Solórzano', Subdirección de Laboratorios y Apoyo Académico, INAH, Moneda 16 Col. Centro, 06060, México, D. F.
§Laboratorio de Paleomagnetismo, Instituto de Geofísica, UNAM, Ciudad Universitaria, Del. Coyoacán, 04150, México, D. F.
¶Instituto de Geología, Universidad Nacional Autónoma de México, Circuito de la Investigación Científica S/N, Ciudad Universitaria, Del. Coyoacán, 04150, México, D. F.

(*Received* 13 September 2010; *accepted* 6 September 2011; *first published online* 18 October 2011)

Abstract

Values for $\delta^{13}C$ and $\delta^{18}O$ obtained from molar samples from three individuals pertaining to *Glyptotherium* sp. from Cedral (San Luis Potosí, México) are provided and are utilized to infer general aspects of glyptodont diet and habitat. On average this animal showed a C_3/C_4 mixed diet, with a high consumption of C_4 plants. Comparisons of the $\delta^{13}C_{VPDB}$ and $\delta^{18}O_{VPDB}$ values for glyptodonts with horses, mastodons, mammoths and tapirs from the same locality show that glyptodonts from Cedral lived in an open habitat.

Keywords: México, glyptodonts, diet, habitat, $\delta^{13}C$, $\delta^{18}O$.

1. Introduction

Cingulata is an order of mammals (Mammalia) originating in South America, which dispersed into North America during the Great American Biotic Interchange (Tonni & Pasquali, 2002; MacFadden, 2006). In México, the oldest remains of the order Cingulata are pampatheres found in Lower Pliocene sediments with an estimated age of between 4.8 and 4.7 Ma, while the earliest record of glyptodonts was found in Upper Pliocene sediments dated at around 2.8 Ma (Carranza-Castañeda & Miller, 2004; Woodburne, Cione & Tonni, 2006).

In the Pleistocene of México there were three families within the order Cingulata: armadillos (Dasypodidae, *Cabassous centralis* and *Dasypus novemcinctus*), glyptodonts (Glyptodontidae, *Glyptotherium cylindricum*, *G. floridanum* and *G. mexicanus*) and pampatheres (Pampatheriidae, *Holmesina septentrionales* and *Pampatherium mexicanum*) (Arroyo-Cabrales, Polaco & Johnson, 2007). Currently, armadillos are the only surviving family in the Americas (Wilson & Reeder, 2005). Diet and general habitat for the two extinct families of Cingulata are the focus of great debate. Presently, armadillos are considered omnivores, having a quite varied diet including insects and fruits, and live in a great variety of habitats (McDonough & Loughry, 2008); as for the extinct families, pampatheres have been considered insectivores or open-zone grazers (De Iuliis, Bargo & Vizcaíno, 2000), while glyptodonts are considered either browsers, inhabiting areas near water springs, similar to the preferred habitat of extant capybaras (Gillette & Ray, 1981), or grazers utilizing open areas, as suggested by others (Vizcaíno, 2000; Vízcaíno *et al.* 2004). The above inferences were proposed based on the dental morphology, of which there is no equivalent in any modern mammal (Fariña & Vizcaíno, 2001). The objective of this study is to determine the diet and habitat of *Glyptotherium* sp. based on the analysis of $\delta^{13}C$ and $\delta^{18}O$ in three specimens from the archaeological–palaeontological site at Cedral (San Luis Potosí, México). We analysed the stable isotopes of carbon, reported as $\delta^{13}C$, and oxygen, $\delta^{18}O$, from the osteodentine carbonate (Ferigolo, 1985) obtained from the molars of three individuals.

1.a. Stable isotopes $\delta^{13}C$ and $\delta^{18}O$

There are three photosynthetic pathways in plants, which are distinguished by differences in their $\delta^{13}C$ values. C_3 plants (−22 ‰ to −30 ‰) are the most abundant and include most dicotyledonous trees and shrubs, and a few temperate grasses. C_4 plants (−10 ‰ to −14 ‰) include monocotyledonous grasses, pterydophytes and a few dicotyledonous trees and shrubs from tropical habitats. The CAM pathway is found in bromeliads, cacti, orchids and other succulent plants. The $\delta^{13}C$ values are between −10 ‰ and −30‰, and therefore are not easily separated from the other two pathways (Smith & Epstein, 1971; Vogel, 1978; Ehleringer *et al.* 1986; Cerling *et al.* 1997; Keeley & Rundel, 2003). These values are then passed onto herbivorous animals, with 14 % enrichment with respect to the plant's original values (Cerling & Harris, 1999; Sánchez, 2005). These final values can be assigned to the different feeding habits: browser species from −9 to −19 ‰; grazers, −2 to +2 ‰; and mixed diet organisms from −2 to −9 ‰ (MacFadden & Cerling, 1996).

While oxygen is incorporated into a mammal's bones through food, the main source is ingested water, and its composition of $\delta^{18}O$ is affected mainly by environmental temperature (Dansgaard, 1964; Sánchez *et al.* 1994; Bryant

†Author for correspondence: vapc79@gmail.com

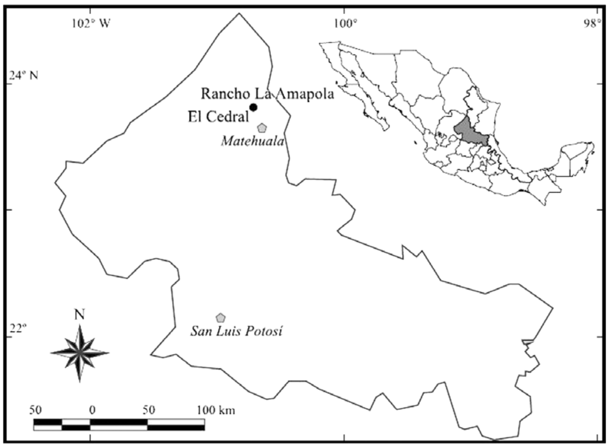

Figure 1. Geographic location of the Pleistocene fossiliferous locality at El Cedral, San Luis Potosí, México (after Pérez-Crespo *et al.* 2009).

& Froelich, 1995; Kohn, 1996). Based on the previous statement, $\delta^{18}O$ values are mainly used for palaeoclimatic inferences (Ayliffe, Lister & Chivas, 1992; Iacumin *et al.* 1996; Kohn, Schoeninger & Valley, 1998; Grimes *et al.* 2008).

2. Materials and methods

2.a. Study area

The Cedral archaeological–palaeontological site is located in the state of San Luis Potosí, México, at 23° 49′ N and 100° 43′ W, at 1700 m asl (Fig. 1). This site contains several ancient springs, which could have been used for drinking water by Late Pleistocene mammals, including the glyptodont, *Glyptotherium* sp.; mylodont, *Paramylodon harlani*; tapir, *Tapirus haysii*; wolf, *Canis dirus*; lion, *Panthera atrox*; camel, *Camelops hesternus*; mastodon, *Mammut americanum*; mammoth, *Mammuthus columbi*; and horses, *Equus mexicanus*, *E. conversidens* and *Equus* sp., as well as smaller mammals and other vertebrates (Álvarez & Polaco, 1982; Lorenzo & Mirambell, 1986). Stratigraphically controlled excavations at the site were able to identify the presence of three fossiliferous levels, based on 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 8 000 years BP (Fig. 2). It is important to recognize that two of the three glyptodont samples are from unknown layers, while the third one was collected in Layer XIV (Fig. 2).

2.b. Sample extraction and preparation

Samples from tooth osteodentine were taken from the following isolated teeth: DP-2489 (Layer XIV), DP-2490 and DP-2491 (backdirt), each of them representing a unique individual. They are housed at the Palaeontological Collection of the Archaeozoology Lab 'M. en C. Ticul Álvarez Solórzano', Subdirección de Laboratorios y Apoyo Académico del Instituto Nacional de Antropología e Historia. Osteodentine is the main component of glyptodont teeth (Ferigolo, 1985), and it has a similar chemical composition to dental enamel, but in different proportions, since enamel has 3 % water, 1 % organic matter (collagen) and 96 % hydroxyapatite (Hillson, 1986; Koch,

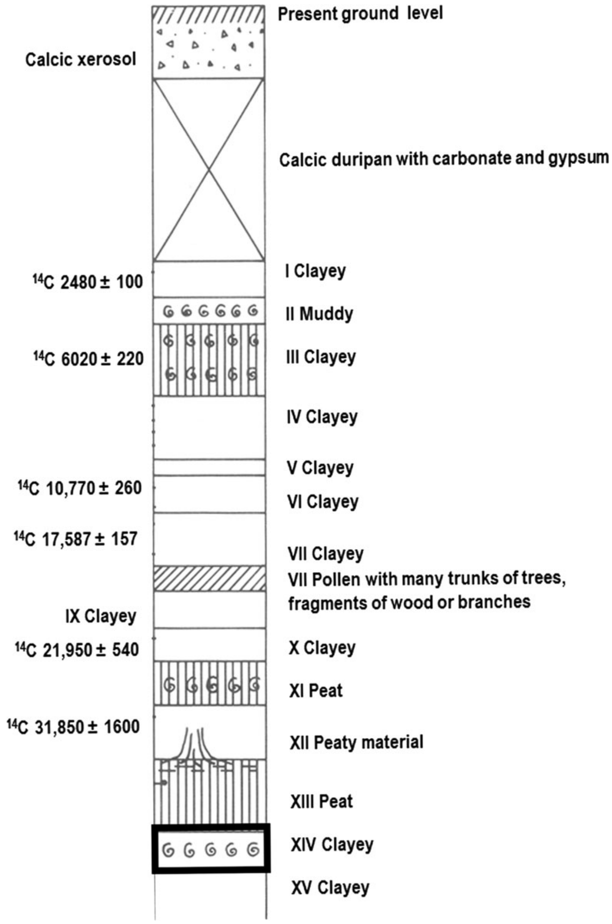

Figure 2. Stratigraphic column for El Cedral. In the column, the level where excavations found the remains of glyptodonts is indicated with a bold box (modified from Lorenzo & Mirambell, 1986).

2007), and osteodentine is composed of 4–20 % water, 18–21 % organic matter and 75 % hydroxyapatite (Hillson, 1986; MacFadden *et al.* 2010), being more susceptible to diagenetic processes than the enamel. However, recent analyses on molars from different extinct 'Xenarthrans' suggested that their osteodentine could provide $\delta^{13}C$ and $\delta^{18}O$ signals that are reliable enough to propose inferences on food habits and palaeoclimates (MacFadden *et al.* 2010).

The preparation of the samples and analyses were performed in the Stable Isotopes Mass Spectrometry Lab at the Geology Institute, National University of México. The preparation procedure follows the method proposed by Koch, Tuross & Fogel (1997). First, 20 mg of osteodentine 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 left for a period of 2 hours; later the samples were centrifuged and the distilled water decanted. This procedure was executed three times. Once the washing was finished, 5 ml of a buffer solution made of $CaCH_3CO_2$–CH_3COOH 1M, pH = 4.75, was added and allowed to rest for nine hours. Later 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 hours in an

https://doi.org/10.1017/S0016756811000951 Published online by Cambridge University Press

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 $\delta^{13}C_{VPDB}$, 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) as well as Werner & Brand (2001). For this technique, the standard deviation was 0.2 ‰ for oxygen and 0.2 ‰ for carbonates.

2.c. Statistical analysis of the results

The mean and standard deviation were obtained for the $\delta^{13}C$ and $\delta^{18}O$ values of the three individuals. Also, the type of diet was assigned in accordance with the $\delta^{13}C$ values by comparison with the proposed classification of MacFadden & Cerling (1996).

To infer the habitat type, first a variance analysis for the glyptodont $\delta^{13}C_{VPDB}$ values was performed against both typical browser species from closed areas, like mastodons (*Mammut americanum*) and tapirs (*Tapirus haysii*), as well as grazing species that inhabited open areas, like horses (*Equus* sp.) and the Columbian mammoth (*Mammuthus columbi*), from Cedral (Pérez-Crespo *et al*. 2009; Pérez-Crespo, unpub. data). A comparison between the isotopic data from Cedral using a Tukey-Kramer test (Hammer & Harper, 2006) showed statistical differences between these groups. The glyptodont $\delta^{13}C_{VPDB}$ and $\delta^{18}O_{VPDB}$ values were compared to other members of the Cedral fauna, and plotted on a graph to visually display the analysis results from the analysis of variance (ANOVA) and Tukey-Kramer tests. The probability level for the statistical samples was $p < 0.05$, and the software used was NCCS and PASS (Hintze, 2004).

Table 1. Result of the Tukey-Kramer test between the glyptodonts and the El Cedral fauna

	E	G	Ma	Mc	T
E	−3.53	−3.53	−3.53*	−3.53	−3.53*
G		−4.32	−4.32*	−4.32	−4.32*
Ma			−8.38	−8.38*	−8.38
Mc				−2.48	−2.48*
T					−10.67

* Groups with significant differences. E – *Equus* sp., G – *Glyptotherium* sp., Ma – *Mammut americanum*, Mc – *Mammuthus columbi* and T – *Tapirus haysii*.

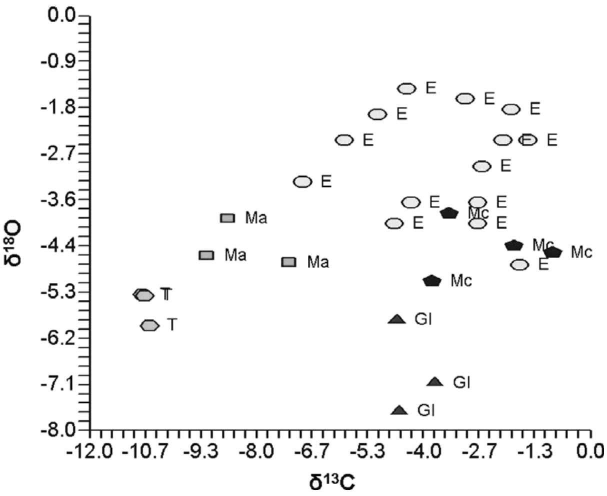

Figure 3. Graph of the $\delta^{13}C$ v. $\delta^{18}O$ values for *Glyptotherium* sp. and the faunal complex of El Cedral, México. E – *Equus* sp., G – *Glyptotherium* sp., Ma – *Mammut americanum*, Mc – *Mammuthus columbi* and T – *Tapirus haysii*.

3. Results

The $\delta^{13}C_{VPDB}$ values were for specimen DP-2489, −4.65 ‰, DP-2490, −4.59 and DP-2491, −3.73 ‰, with a mean of −4.32 ‰ and a standard deviation of 0.51 ‰. The $\delta^{18}O$ values had a mean of −6.85 ‰ and a standard deviation of 0.90 ‰, with the individual values as follows: DP-2489, −4.65 ‰; DP-2490, −7.62 ‰ and DP-2491, −7.08 ‰. An ANOVA test was performed between glyptodonts and the remaining assayed mammal herbivores from Cedral, showing significant differences ($p < 0.000000$*, F: 22.80, DF: 26), while the Tukey-Kramer test showed that glyptodonts were statistically different from the mastodons and tapirs, but similar to the horses and mammoths (Table 1). A graph showing $\delta^{13}C_{VPDB}$ v. $\delta^{18}O_{VPDB}$ values for the glyptodonts and remaining Cedral fauna confirms such analysis results (Fig. 3).

4. Discussion

4.a. Diet

Glyptodont $\delta^{13}C_{VPDB}$ values show a mixed C_3/C_4 diet, with large quantities of C_4 plants being consumed. Gillette & Ray (1981) had previously proposed that the animal was a preferred browser. Fariña & Vizcaíno (2001) questioned such a proposal since glyptodont molars are hypselenodont, with morphofunctional adaptations indicative of a grazer (Vizcaíno, De Iuliis & Bargo, 1998; Vizcaíno *et al*. 2004; Vízcaíno, 2009). The isotopic data obtained from the Cedral glyptodonts suggest that this animal ate mainly grasses.

Data provided by this study in regard to $\delta^{13}C_{VPDB}$ values supports the latter proposal, showing that the three sampled individuals had a mixed diet, but ate a large amount of C_4 plants. This is also supported by the statistical analyses, since ANOVA and Tukey-Kramer test results for glyptodont $\delta^{13}C_{VPDB}$ values and those of mastodons and tapirs are significantly different, while the glyptodont values are similar to those of mammoths and horses from Cedral, which also show a C_3/C_4 mixed diet, but with a larger consumption of C_4 plants. The palynological history for the region, recorded by Sánchez-Martínez & Alvarado (in press), shows the existence of herbaceous plants from the families Poacea, Amaranthacea and Quenopodiacea, all of which are C_4 plants (Keeley & Rundel, 2003), and could have been consumed by the glyptodonts.

4.b. Habitat

Based on the remains of these animals being found in lacustrine sediments, Gillette & Ray (1981) proposed that they occurred in habitats associated with rivers, lakes and other water sources, similar to those used by living capybara. Our comparison of the $\delta^{13}C_{VPDB}$ and $\delta^{18}O_{VPDB}$ values of the studied glyptodonts and browsing species from Cedral shows quite different values, with glyptodonts being more similar to the grazing Cedral species. This is similar to the suggestions by Fariña & Vizcaíno (2001) and Rincón, White & McDonald (2008), who have indicated that this species inhabited savannas or grassland; however, the presence of springs in Cedral, as well as near other glyptodont findings

https://doi.org/10.1017/S0016756811000951 Published online by Cambridge University Press

in México (Mead *et al*. 2007; Bravo-Cuevas, Ortíz-Caballero & Cabral-Perdomo, 2009), could point out that Cedral glyptodonts were living in open areas close to water sources, matching what Gillette & Ray (1981) mentioned, with a diet mainly based on C_4 plants rather than C_3 plants.

5. Conclusions

Glyptodonts (*Glyptotherium* sp.) from Cedral had a C_3/C_4 mixed diet, dominated by the consumption of C_4 plants, shown by the $\delta^{13}C_{VPDB}$ values. This species in Cedral was an inhabitant of open areas close to water sources, similar to extant capybaras. However, this hypothesis would need to be tested with a larger number of specimens in order to predict any pattern in their food habits, as well as in the kind of habitat. Furthermore, the studied specimens need to be specifically identified and dated.

Acknowledgements. We thank the Consejo de Arqueología from INAH for granting the permit to obtain the osteodentine samples from the studied glyptodonts. Also, the senior author thanks CONACYT and Posgrado en Ciencias Biologícas, UNAM for the graduate-studies scholarship (# 200441), and the Laboratorio Universitario de Geoquímica Isotópica (LUGIS) from the Institute of Geology, UNAM, as well as F. J. Otero and R. Puente M. for analysing the samples. Dr Michael Pasenko, University of Arizona, kindly reviewed an earlier version of this manuscript, and provided useful comments to improve it. Drs Begoña Sanchez Chillón, Sergio Vizcaíno and two anonymous reviewers also contributed with useful comments.

References

Álvarez, S. T. & Polaco, O. J. 1982. Restos pleistocénicos de dos especies de *Microtus* (Rodentia: Muridae), del norte de San Luís Potosí, México. *Anales de la Escuela Nacional de Ciencias Biológicas México* **26**, 47–53.

Arroyo-Cabrales, J., Polaco, O. & Johnson, E. 2007. An overview of the Quaternary mammals from México. *Courier Forschungsinstitut Senckenber*, **259**, 191–203.

Ayliffe, L. K., Lister, A. M. & Chivas, A. R. 1992. The preservation of glacial-interglacial climatic signatures in the oxygen isotopes of elephant skeletal phosphate. *Palaeogeography, Palaeoclimatology, Palaeoecology* **99**, 179–91.

Bravo-Cuevas, V. M., Ortíz-Caballero, E. & Cabral-Perdomo, M. A. 2009. Gliptodontes (Xenarthra, Glyptodontidae) del Pleistoceno Tardío (Rancholabreano) de Hidalgo, Centro de México. *Boletin de la Sociedad Geologíca Mexicana* **61**, 267–76.

Bryant, J. D. & Froelich, P. N. 1995 A model of oxygen isotope fractionation in body water of large mammals. *Geochemical et Cosmochimica Acta* **59**, 4523–37.

Carranza-Castañeda, O. & Miller, W. E. 2004. Late Tertiary terrestrial mammals from Central México and their relationships to South America immigrants. *Revista Brasileira de Paleontologia* **7**, 249–61.

Cerling, T. E. & Harris, J. M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* **120**, 347–63.

Cerling, T. E., Harris, J. M., MacFadden, B. J., Leakey, M. G., Quade, J., Eisenman, V. & Ehleringer, J. R. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**, 152–8.

Coplen, T. B. 1988. Normalization of oxygen and hydrogen isotope data. *Chemical Geology* **72**, 293–7.

Dansgaard, W. 1964. Stable isotopes in precipitation. *Tellus* **16**, 436–68.

De Iuliis, G., Bargo, S. M. & Vizcaíno, S. F. 2000. Variation in skull morphology and mastication in the fossil giant armadillos *Pampatherium* spp. and allied genera (Mammalia: Xenarthra: Pampatheriidae), with comments on their systematic and distribution. *Journal of Vertebrate Paleontology* **20**, 743–54.

Ehleringer, J. R., Field, C. B., Liz, Z. F. & Kuo, C. Y. 1986. Leaf carbon isotope ratio and mineral composition in subtropical plants along an irradiance cline. *Oecologia* **70**, 520–6.

Fariña, R. A. & Vizcaíno, S. F. 2001. Carved teeth and strange jaws: how glyptodonts masticated. *Acta Paleontologica Polonica* **46**, 219–34.

Ferigolo, J. 1985. Evolutionary trends of histological pattern in the teeth of edentata (Xenarthra). *Archives of Oral Biology* **30**, 71–82.

Gillette, D. D & Ray, C. E. 1981. Glyptodonts of North America. *Smithsonian Contributions to Paleobiology* **40**, 1–255.

Grimes, S. T., Collinson, M. E., Hooker, J, J. & Mattey, D. P. 2008. Is small beautiful? A review of the advantages and limitations of using small mammal teeth and direct fluorination analysis technique in the isotopic reconstruction of past continental climate change. *Palaeogeography, Palaeoclimatology, Palaeoecology* **256**, 39–50.

Hammer, Ø. & Harper, D. 2006. *Paleontological Data Analysis*. Oxford: Blackwell Publishing, 351 pp.

Hillson, S. 1986. *Teeth*. Cambridge, UK: Cambridge University Press, 376 pp.

Hintze, J. 2004. NCSS and PASS. Kaysville, Utah: Number Cruncher Statistical Systems. Available at http://www.ncss.com.

Iacumin, P., Bocherens, H., Mariotti, A. & Longinelli, A. 1996. Oxygen isotope analyses of co-existing carbonate and phosphate in biogenic apatite: a way to monitor diagenetic alteration of bone phosphate? *Palaeogeography, Palaeoclimatology, Palaeoecology* **142**, 1–6.

Keeley, J. E. & Rundel, P. W. 2003. Evolution of CAM and C4 carbon-concentrating mechanisms. *International Journal Plants Science* **164**, (supplement 3) S55–S77.

Koch, P. L. 2007. Isotopic study of the biology of modern and fossil vertebrates. In *Stable Isotopes in Ecology and Environmental Science* (eds R. H. Micherner & K. Lajtha), pp. 99–154. Baltimore: Blackwell Publishing.

Koch, P. L., Tuross, N. & Fogel., M. L. 1997. The effects of sample treatment and diagenesis on the isotopic integrity of carbon in biogenic hydroxylapatite. *Journal of Archaeological Science* **24**, 417–29.

Kohn, M. J. 1996. Predicting animal $\delta^{18}O$: accounting for diet and physiological adaptation. *Geochemical et Cosmochimica Acta* **60**, 4811–29.

Kohn, M. J., Schoeninger, M. J. & Valley, J. W. 1998. Variability in oxygen isotope composition of herbivore teeth: reflections of seasonality or developmental physiology? *Chemical Geology* **152**, 97–112.

Lorenzo, J. L. & Mirambell, L. 1986. Preliminary report on archeological and paleoenvironmental studies in the area of El Cedral, San Luis Potosí, México. In *New Evidence for the Pleistocene Peopling of the Americas* (ed A. L. Bryan) pp. 107–13. Orono, Maine: Center for the Study of the Early Man, University of Maine, Peopling of the Americas Symposia Series.

https://doi.org/10.1017/S0016756811000951 Published online by Cambridge University Press

MACFADDEN, B. J. 2006. Extinct mammalian biodiversity of the ancient New World tropic. *Trends in Ecology and Evolution* **21**, 157–65.

MACFADDEN, B. & CERLING, T. E. 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10 million–year sequence from the Neogene of Florida. *Journal of Vertebrate Paleontology* **16**, 103–15.

MACFADDEN, B. J., DESANTIS, L. R. G., HOCHSTEIN, J. L. & KAMENOV, G. D. 2010. Physical properties, geochemistry, and diagenesis of xenarth teeth: prospects for interpreting the paleoecology of extinct species. *Palaeogeography, Palaeoclimatology, Palaeoecology* **291**, 180–9.

MCDONOUGH, C. M. & LOUGHRY, W. J. 2008. Behavioral ecology of armadillos. In *The Biology of Xenarthra* (eds S. Vizcaíno & W. J. Loughry), pp. 281–93. Gainsville: University Press of Florida.

MEAD, J. I., SWIFT, S. L., WHITE, R. S., MCDONALD, H. G. & BAEZ, A. 2007. Late Pleistocene (Rancholabrean) Glyptodont and Pampathere (Xenarthra, Cingulata) from Sonora, México. *Revista Mexicana de Ciencias Geológicas* **24**, 39–449.

PÉREZ-CRESPO, V. A., SÁNCHEZ-CHILLÓN, B., ARROYO-CABRALES, J., ALBERDI, M. T., POLACO, O. J., SANTOS-MORENO, A., BENAMMI, M., MORALES-PUENTE, P. & CIENFUEGOS-ALVARDO, E. 2009. La dieta y el hábitat del mamut y los caballos del Pleistoceno tardío de El Cedral con base en isótopos estables ($\delta^{13}C$, $\delta^{18}O$). *Revista Mexicana de Ciencias Geológicas* **26**, 347–55.

RÉVÉSZ, K. M. & LANDWEHR, J. M. 2002. $\delta^{13}C$ and $\delta^{18}O$ isotopic composition of $CaCO_3$ measured by continuous flow isotope ratio mass spectrometry: statistical evaluation and verification by application to Devils Hole core DH – 11 calcite. *Rapid Communications in Mass Spectrometry* **16**, 2102–14.

RINCÓN, A. D., WHITE, R. S. & MCDONALD, H. G. 2008. Late Pleistocene cingulates (Mammalian: Xenarthra) from Mene de Inciarte tar pits, Sierra de Perijá, Western Venezuela. *Journal of Vertebrate Paleontology* **28**, 197–207.

SÁNCHEZ, B. 2005. Reconstrucción del ambiente de mamíferos extintos a partir del análisis isotópico de los restos esqueléticos. In *Nuevas técnicas metodológicas aplicadas al estudio de los sistemas ambientales: los isótopos estables* (eds P. Alcorno, R. Redondo & J. Toledo), 49–64. Universidad Autónoma de Madrid, España.

SÁNCHEZ-CHILLÓN, B., ALBERDI, M. T., LEONE, G., BONADONNA, F. P., STENNI, B. & LONGINELLI, A. 1994. Oxygen isotopic composition of fossil equid tooth and bone phosphate: an archive of difficult interpretation. *Palaeogeography, Palaeoclimatology, Palaeoecology* **107**, 317–28.

SÁNCHEZ-MARTÍNEZ., F. & ALVARADO, J. L. In press. Análisis palinológico del sitio El Cedral, San Luis Potosí, México. *Instituto Nacional de Antropología e Historia, Colección Científica*, México, D.F. 10 pp.

SMITH, B. N. & EPSTEIN, S. 1971. Two categories of $^{13}C/^{12}C$ ratios for higher plants. *Plant Physiology* **47**, 380–4.

TONNI, E. & PASQUALI, R. 2002. El gran intercambio faunístico americano. *Cartilla de Difusión de Ciencias Naturales, Centro de Investigación Científicas CICYTTP-Diamante* **2**, 9.

VIZCAÍNO, S. F. 2000. Vegetation partitioning among Lujanian (Late-Pleistocene/Early-Holocene) armored herbivores in the Pampean region. *Current Research in the Pleistocene* **17**, 135–6.

VIZCAÍNO, S. F. 2009. The teeth of the "toothless": novelties and key innovations in the evolution of xenarthrans (Mammalian: Xenarthra). *Paleobiology* **35**, 343–66.

VIZCAÍNO, S. F., DE IULIIS, G. & BARGO, M. S. 1998. Skull shape, masticatory apparatus, and diet of *Vassallia* and *Holmesina* (Mammalia: Xenarthra: Pampatheridae); when anatomy constrains destiny. *Journal of Mammalian Evolution* **5**, 291–322.

VIZCAÍNO, S. F., FARIÑA, R. A., BARGO, M. S. & DE IULIIS, G. 2004. Functional and phylogenetic assessment of the masticatory adaptations in Cingulta (Mammalia, Xenarthra). *Ameghiniana* **41**, 651–64.

VOGEL, J. C. 1978, Isotopic assessment of the dietary habitats of ungulate. *South African Journal of Science* **74**, 298–301.

WERNER, R. A. & BRAND, W. A. 2001. Referencing strategies and techniques in stable isotope ratio analysis. *Rapid Communications in Mass Spectrometry* **15**, 501–19.

WILSON, D. E. & REEDER, D. A. M. 2005. *Mammals Species of the World. A taxonomical and geographic reference.* Baltimore: Johns Hopkins University Press, 2142 pp.

WOODBURNE, M. O., CIONE, A. L. & TONNIN, E. P. 2006. Central American provincialism and the Great American Biotic Interchange. In *Advances in Late Tertiary Vertebrate Paleontology in México and the Great American Biotic Interchange* (eds O. Carranza-Castañeda & E. H. Lindsay), pp. 73–101. Universidad Nacional Autónoma de México, Instituto de Geología y Centro de Geociencias, Publicación Especial 4.