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RECONSTRUCCIÓN PALEOAMBIENTAL DE DOS YACIMIENTOS PLEISTOCÉNICOS (RANCHOLABREANO) DEL CENTRO-OCCIDENTE DE MÉXICO CON PRESENCIA DE RUMIANTES FÓSILES.

TESIS PROFESIONAL

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Para

Tristán.

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Índice

Resumen

En este trabajo se presentan los resultados de una reconstrucción paleoambiental empleando como organismos modelo a la comunidad de rumiantes de dos sitios del Centro-Occidente de México (La Cinta-Portalitos y La Piedad-Santa Ana), así como una revisión crítica del registro fósil de rumiantes del país y un reporte de una localidad fosilífera con el registro más austral de bisonte gigante (*Bison latifrons*) en territorio nacional. Para llevar a cabo la reconstrucción se emplearon metodologías paleoecológicas (mesodesgaste, microdesgaste y análisis de isótopos estables de carbono), así como metodologías de contraste independiente (estratigrafía, mineralogía y análisis de isótopos estables de oxígeno). Los patrones de desgaste sugieren que los bisontes (*Bison antiquus*) y berrendos (*Tetrameryx shuleri*) fueron generalistas que solían consumir pastos de forma no estricta, lo que contrata con la dieta de bisontes y berrendos modernos. Los cérvidos (cf. *Navahoceros fricki* y *Odocoileus hemionus*) en cambio, mostraron dietas mixtas. El análisis de isótopos estables de carbono ($\delta^{13}C$) muestra que los bisontes (*B. antiquus* y *B. latifrons*) eran pacedores no estrictos que habitaron en pastizales y praderas heterogéneas (con presencia de asteráceas). Se encontró evidencia de competencia entre las especies de bisontes, y entre estos y las especies de caballo (*Equus mexicanus*, *E. conversidens* y *E. cedralensis*) de ambos sitios, pero no se encontró competencia entre bisontes y mamutes (*Mammuthus columbi*). Por otra parte, los análisis de isótopos estables de oxígeno ($\delta^{18}O$) y de estratigrafía y mineralogía mostraron que en la Cinta-Portalitos (LCPT), la temperatura media anual (TMA) era de 15.1° C y las condiciones prevalentes durante el Pleistoceno tardío eran de climas altamente estacionales y mésicos. Por otra parte, en la Piedad-Santa Ana (LPSA) se infirió una TMA de 13.4° C, con condiones plesitocénicas igualmente estacionales y de alta humedad. En cuanto a la evolución de los sitios, se aprecia que en LCPT los climas eran más secos antes de la aparición de la megafauna en el registro fósil (ca. 23 ka) y que estas condiciones cambiaron a húmedas, lo que provocó el aumento de los niveles del paleolago de Cuitzeo, hasta su posterior retroceso gradual. Para LPSA se observa un régimen constante de alta estacionalidad, marcada por evidentes avulsiones del río Lerma hasta formar lagos someros en las llanuras de inundación, proceso que se presentaba aún en tiempos recientes. Esta información contribuye al conocimiento de la evolución paleoclimática de esta zona del Centro de México y aporta nuevos datos acerca de la plasticidad dietaria de los rumiantes que habitaron el país.

Palabras clave: Ruminantia, mesodesgaste, microdesgaste, isótopos estables, paleoambiente.

Abstract

In this work, we present a paleoenvironmental reconstruction employing fossil ruminants from two Central-Western Mexico sites (LCPT: La Cinta-Portalitos, and LPSA: La Piedad-Santa Ana), as model organisms. We also present a critical review of the Mexican ruminant fossil record, and a report of a fossil locality with the southernmost record of giant bison (*Bison latifrons*). In order to make the paleoenvironmental reconstruction we employed paleoecological (mesowear, microwear, and stable carbon isotope analysis) and independent contrast methodologies (stratigraphy, mineralogy, and stable oxygen isotope analysis). The wear patterns suggest that the bison (*Bison antiquus*) and the pronghorns (*Tetrameryx shuleri*) were non-strict grazer generalists, which is dramatically different from the diet of modern bison and pronghorn. In contrast, the deer (cf. *Navahoceros fricki* and *Odocoileus hemionus*) showed a mixed feeder diet. The carbon stable isotope ($\delta^{13}C$) analysis showed that the bison species (*B. antiquus* and *B. latifrons*) were non-strict grazers who inhabited grasslands and non-grass-dominated prairies (with prevalence of Asteraceae). We found evidence of competition between bison species, as well as competition between Bison spp. and horses (*Equus mexicanus*, *E. conversidens*, and *E. cedralensis*) at both sites, but we found no evidence of this phenomenon between bison species and mammoth (Mammuthus columbi). On the other hand, the oxygen ($\delta^{18}O$) stable isotope analysis, stratigraphy and mineralogy showed that at LCPT during the Late Pleistocene, the mean annual temperature (MAT) was 15.1° C, and the climate was humid and heavily seasonal. Similarly, the Late Pleistocene climate at LPSA was also seasonal and humid, but the MAT was only 13.4° C. The climatic evolution showed that at LCPT the regimen was dryer than during the time period on which the megafauna was found (ca. 23 ka), but after it, the paleolake begun to grow and slowly retreated to its current levels. Conversely, we found that the climate at LPSA were always heavily seasonal with periodical avulsion of the Lerma river and the formation of shallow lakes at the floodplains until recent times. This information contributes to the knowledge of the paleoclimatic evolution of this area of Central Mexico and provides new information about the dietary plasticity of the ruminants that inhabited the Mexico.

Key words: Ruminantia, mesowear, microwear, stable isotopes, paleoenvironment.

1. Introducción general

El registro fósil de México abarca los últimos 560 Ma y va del Precámbrico, al Holoceno temprano (McMenamin and Awramik, 1983; Arroyo-Cabrales et al., 2008). En este lapso existen taxones mejor representados que otros y los mamíferos son el grupo de vertebrados mejor estudiado (Arroyo-Cabrales et al., 2008); especialmente para el Cuaternario (Ferrusquía-Villafranca et al., 2010), lapso en el que se encuentra su mayor riqueza taxonómica, particularmente para el Pleistoceno, época que cuenta con el mayor número de localidades fosilíferas del país (Arroyo-Cabrales et al., 2002, 2010).

El Pleistoceno fue una época con cambios climáticos que afectaron la estructura y distribución de las comunidades bióticas (Arroyo-Cabrales et al., 2002; Ceballos et al., 2010). En el caso de los mamíferos, la composición taxonómica de las faunas y su distribución estratigráfica son consideradas para el establecimiento de edades de mamíferos terrestres (Wood et al., 1941). Para el Pleistoceno de América del Norte se reconocen tres de estas edades (NALMAs por sus siglas): el Blancano (5.2-4.6 a 1.35 Ma), el Irvingtoniano (1.35 Ma a 160 Ka) y el Rancholabreano, que va desde hace 160 a 9.5 Ka (Bell et al., 2004). Durante esta última NALMA, tuvieron lugar dos cambios climáticos importantes: el Último Máximo Glacial y el Dryas Reciente (Haynes, 2008; Clark et al., 2009). Estos eventos produjeron grandes cambios en la estructura de las comunidades y son responsables del establecimiento de las biotas modernas de México (Ceballos et al., 2010).

La mayoría de los registros de mamíferos terrestres del Pleistoceno en México corresponden al Rancholabreano y están representados por más de 280 especies, agrupadas en 13 órdenes, siendo los más diversos: Rodentia (34.6%), Chiroptera (17.9%), Carnivora (13.6%) y Artiodactyla, con un 12.5% (Ferrusquía-Villafranca et al., 2010). Los artiodáctilos del Pleistoceno de México incluyen tres subórdenes: Suiformes, Tylopoda y Ruminantia (McKenna and Bell, 1997), de los que los rumiantes eran los más diversos, con un 60% del total de artiodáctilos reportados en México (Ferrusquía-Villafranca et al., 2010).

Los rumiantes son los ungulados más diversos y exitosos, cuentan con cerca de 197 especies recientes (Hernández-Fernández and Vrba, 2005), se distribuyen en casi todas las

masas continentales y habitan en una gran variedad de ecosistemas (Nowak and Paradiso, 1983).

Uno de los atributos ecológicos de los organismos es el hábito alimentario, que en mamíferos herbívoros suele clasificarse en tres categorías modelo: pacedor, ramoneador y de dieta mixta (Hofmann and Stewart, 1972; Leuthold, 1977). Esta diversidad de hábitos está relacionada a la estructura de la vegetación en la que habitan estos ungulados (Keast, 1968; Pienaar, 1974). Debido a esta relación, la inferencia de los patrones dietarios aporta información acerca de su uso de hábitat y por lo tanto, contribuye a la reconstrucción paleoambiental (Solounias et al., 1988).

La Cinta-Portalitos y la Piedad-Santa Ana son yacimientos fosilíferos pleistocénicos localizados entre los límites estatales de Michoacán y Guanajuato (García-Reyes, 2004; Servín-González, 2010). La estratigrafía de ambos sitios está representada por intercalaciones de sedimentos continentales de origen fluvial y lacustre en alternancia, con presencia de flujos volcánicos (García-Zepeda, 2006; Marín-Leyva, 2011; Díaz-Sibaja, 2013). La edad relativa asignada para estos sitios corresponde al Pleistoceno tardío y a la NALMA del Rancholabreano, por la presencia del taxón índice *Bison* sp. en coetaneidad con taxones restringidos a este lapso como: *Canis dirus, Platygonus compressus, Panthera atrox* y *Megalonyx jeffersoni* (García-Zepeda, 2006; Díaz-Sibaja, 2013; Eng-Ponce, 2017).

La fauna asociada de la Piedad-Santa Ana incluye a *Mammuthus columbi* (Servín-González, 2010; Gutiérrez Bedolla et al., 2016), *Equus mexicanus, E. conversidens*, *E. cedralensis* (Marín-Leyva, 2011; Marín-leyva et al., 2016; Marín-Leyva et al., 2016), *Camelops hesternus* (syn. *C. traviswhitei*), *Hemiauchenia macrocephala* (Plata-Ramírez, 2012; Plata-Ramírez et al., 2015), *Odocoileus virginianus*, *Tetrameryx shuleri*, *Bison antiquus* y *B. latifrons* (Díaz-Sibaja et al., 2012, 2014a, 2014b; Díaz-Sibaja, 2013).

Por otro lado, en la Cinta-Portalitos se presenta una fauna más diversa que incluye a *Mammuthus columbi* (García-Zepeda, 2006; Gutiérrez Bedolla et al., 2016), *Equus mexicanus*, *E. conversidens*, *E. cedralensis* (Marín-Leyva, 2011; Marín-leyva et al., 2016; Marín-Leyva et al., 2016), *Camelops hesternus*, *Hemiauchenia macrocephala*, *H. gracilis* (Plata-Ramírez, 2012; Plata-Ramírez et al., 2015), *Odocoileus virginianus*, *O. hemionus*, *Navahoceros fricki*, *Tetrameryx shuleri*, *Stockoceros conklingi*, *Capromeryx minor* (Díaz-

Sibaja et al., 2012, 2014a, 2014b; Díaz-Sibaja, 2013), *Neochoerus aesopi*, *Nothrotheriops shastensis*, *Paramylodon harlani*, *Megalonyx jeffersoni* (Eng-Ponce et al., 2015, 2016; Eng-Ponce, 2017), carnívoros de las familias Felidae, Canidae y Mustelidae (Cervantes-Barriga et al., 2016), pequeños mamíferos como roedores (Pérez-González and Godinez-García, 2007; Cervantes-Barriga et al., 2017) y soricomorfos (Eng-Ponce et al., 2017a), así como otros vertebrados que incluyen tortugas, serpientes (Moreno-Flores et al., 2017) y peces teleósteos (De la Paz-Ruíz et al., 2017).

Algunas de estas especies (e.g. los proboscídeos, équidos, capibaras y algunos perezosos gigantes) han sido objeto de diferentes estudios paleoecológicos, usando aproximaciones como el mesodesgaste dental (Marín-Leyva et al., 2016), el microdesgaste dental (Eng-Ponce et al., 2016, 2017b; Gutiérrez Bedolla et al., 2016; Marín-Leyva et al., 2016) y el análisis de isótopos estables de carbono y oxígeno (Gutiérrez Bedolla et al., 2016; Marín-leyva et al., 2016; Eng-Ponce et al., 2017b). Estos estudios sugieren la presencia de pastizales en las zonas bajas y bosques hacia las partes altas de los sitios de depósito (Gutiérrez Bedolla et al., 2016; Marín-leyva et al., 2016; Marín-Leyva et al., 2016). Esta interpretación ha sido reforzada mediante estudios de carácter sedimentológico y mineralógico (Marín-Leyva, 2011; Díaz-Sibaja, 2013).

Los estudios paleoecológicos previos en los sitios de estudio fueron llevados a cabo con las especies de megafauna más abundantes para ambos yacimientos (équidos y proboscídeos), encontrando en ambos casos una dieta pacedora o de hábitos mixtos con tendencia al consumo de poáceas, lo que sugiere la presencia de pastizales (Gutiérrez Bedolla et al., 2016; Marín-leyva et al., 2016; Marín-Leyva et al., 2016). Sin embargo, los rumiantes poseen una diversidad de dietas y un mayor uso de hábitat (Nowak and Paradiso, 1983). Dada la relación entre la dieta y el hábitat de este grupo de ungulados (Solounias et al., 1988), este componente faunístico puede aportar más información del paleoambiente. En este trabajo se presenta la información de los patrones de dieta y uso de hábitat de dos comunidades de rumiantes del Pleistoceno tardío (Rancholabreano) del Centro-Occidente de México, esta información contribuye a la reconstrucción paleoambiental de los yacimientos fosilíferos estudiados y aportan información nueva sobre la dieta de este grupo de mamíferos en América del Norte.

2. Marco teórico

A lo largo del desarrollo de este trabajo se emplearon tres metodologías principales para inferir el tipo de dieta y uso de hábitat, el microdesgaste dental, el mesodesgaste dental y el análisis de isótopos estables de carbono y oxígeno. Adicionalmente, se llevaron a cabo estudios de estratigrafía y composición mineralógica para inferir condiciones ambientales en los sitios de depósito.

El microdesgaste dental consiste en el estudio de los microdefectos del esmalte en la zona oclusal de determinadas piezas dentales (Walker et al., 1978). Dichos microdefectos se clasifican en estrías (depresiones lineales cuya longitud siempre es mayor a su ancho), hoyuelos (una depresión cuya longitud y ancho son casi iguales) y biselados (una depresión fuertemente curvada e irregular) (Gordon, 1982). La selección de la pieza dental analizada atiende a dos causas, la comparación con piezas dentales de especies modelo modernas con dietas conocidas (e.g. Solounias et al., 2000; Solounias and Semprebon, 2002) y a la zona de los dientes donde se produce principalmente la fase bucal I de masticación, en la que el diente entra en contacto con el alimento (Janis, 1990). El análisis de la densidad de estrías y hoyuelos para la predicción de la dieta en ungulados se lleva a cabo con datos de alta magnificación (500x) (Solounias et al., 2000) y baja magnificación (35x) (Solounias and Semprebon, 2002). Este método aporta información de la dieta de los organismos estudiados, en relación a horas y hasta 3-4 días antes de su muerte (Walker et al., 1978; Teaford and Oyen, 1989; Solounias et al., 1994), por lo que constituyen una fuente inmediata de reconstrucción de la estructura de la vegetación.

Por otra parte, el mesodesgaste ofrece información dietaria que corresponde con un periodo más largo de la vida de los organismos, dependiendo de la pieza dental analizada (Fortelius and Solounias, 2000). En los bisontes, el lapso representado por el mesodesgaste va de los 4 a los 12 años de edad (Skinner and Kaisen, 1947; Fuller, 1959), para los cérvidos de los 2 a los 6.5 años de edad (Severinghaus, 1949) y para los antilocápridos de 1.3 a 4.3 años de edad (Jiménez-Hidalgo and Carranza-Castañeda, 2011). En la metodología original, se evalúa la forma del relieve oclusal del ectolofo de molares superiores segundos (Fortelius and Solounias, 2000), en la región de la fase bucal I de

masticación y el ápice de las cúspides y de trituración del alimento (Janis, 1990). Este método fue ampliado para incluir los molares superiores terceros (Franz-Odendaal and Kaiser, 2003) y posteriormente, se generaron nuevas metodologías para inferir la dieta a partir del análisis de la dentición mandibular (Fraser et al., 2014) y de la región interna del paracono y metacono de molares segundos superiores (Solounias et al., 2014).

Otra metodología de inferencia de dieta que no implica el uso de los gradientes de desgaste es el análisis de isótopos estables de carbono y oxígeno. Un isótopo estable es un elemento químico con diferente masa atómica, pero el mismo número atómico y que no se transforman en otros elementos (Fry, 2010). En los elementos con masas inferiores a 40, se presenta el fenómeno de fraccionamiento isotópico, que involucra acumulación selectiva de variedades isotópicas, debido a procesos físicos y químicos (Koch, 1998). Los valores isotópicos de carbono y oxígeno se reportan en partes por mil (‰) y en proporción (δ) de isótopos pesados sobre ligeros ($\delta X_{std}= (R_{sample}/R_{std}-1)\cdot 100$), en relación a valores de referencia de carbonatos marinos y agua oceánica, siendo tales valores el Vienna PeeDee Belemnite (VPDB), con un valor de 0.01118 para carbono ($^{13}C/^{12}C$) y ya sea Standard Mean Ocean Water (SMOW) o VPDB con valores estándar de 0.0020052 y 0.0020672 respectivamente, para oxígeno ($^{18}O/^{16}O$). Los valores más negativos indican mayor proporción del isótopo ligero, mientras que valores positivos indican mayor proporción del isótopo pesado (O'Leary, 1988; Ehleringer and Rundel, 1989; Koch, 1998; Fry, 2010). En la naturaleza, la proporción del isótopo ligero siempre es mayor, en el caso del ^{12}C es de 98.89% y para el ^{16}O es de 99.76% (Ehleringer and Rundel, 1989; Fry, 2010).

Los valores de $\delta^{13}C$ en el CO_2 atmosférico previos a la era industrial eran de -8‰, este valor se hace cada vez más negativo (0.002 ‰/año) debido a la quema de combustibles fósiles (O'Leary, 1988; Hoefs, 2009). En las plantas modernas, los valores de $\delta^{13}C$ de los productos de la fotosíntesis tienen un fraccionamiento de Δ= 20‰ con respecto a los valores de CO_2 atmosférico (Fry, 2010). Estos valores de fraccionamiento varían dependiendo del tipo de metabolismo, las plantas C3 (árboles y arbustos principalmente) tienen valores de $\delta^{13}C$ promedio de -27 ±3‰, mientras que las plantas con metabolismo C4 (pocáceas principalmente) tienen valores promedio de -13 ±2‰ y finalmente, las plantas con metabolismo tipo CAM (cactáceas y otra vegetación xerófila) tienen valores entre -10 y

-20‰ (O'Leary, 1988; Koch et al., 1998). La fuente isotópica en los estudios de dieta y uso de hábitat es el hidroxiapatito ($Ca_2[PO_4, CO_3]_3[OH_3CO_3]$) dental, pues refleja fielmente la composición de la vegetación ingerida, en contraposición con el hidroxiapatito de otros tejidos que puede alterarse diagenéticamente con mayor facilidad (DeNiro and Epstein, 1978; Schoeninger and DeNiro, 1982; Koch, 1998). La firma isotópica de las plantas pasa por un proceso de fraccionamiento, producto del metabolismo de los herbívoros que en promedio es de 14‰ (Cerling and Harris, 1999), por lo que el esmalte de los ramoneadores (consumidores de plantas C3) modernos muestran valores de entre -16 y -10‰ y los pacedores (consumidores de plantas C4) modernos tienen un rango de -2 a 2‰ (Sponheimer et al., 2001; Feranec, 2003). Sin embargo, los valores actuales de $\delta^{13}C$ en el CO_2 atmosférico son distintos de los valores del Pleistoceno, presentando un enrriquecimieto medio de -6.5‰ (Marino et al., 1992). Por lo consiguiente, valores de $\delta^{13}C$ del esmalte fósil más negativos que -8.7‰ reflejan una dieta compuesta enteramente por plantas C3, mientras que valores más positivos que -0.5‰ reflejan una dieta compuesta exclusivamente por plantas C4 (Feranec, 2003).

En el caso del oxígeno, existe una estrecha relación entre los valores de $\delta^{18}O$ del esmalte dental y el agua meteórica (Longinelli, 1984; D'Angela and Longinelli, 1990). Los valores de $\delta^{18}O$ del agua meteórica se ven afectados por diferentes factores, siendo el principal el de la temperatura (Dansgaard, 1964). La relación entre el agua meteórica y el esmalte persiste a lo largo de 10^6 años en el hidroxiapatito dental, debido a que los enlaces entre el oxígeno y el fósforo son más estables y son más resistentes a la diagénesis que los enlaces entre el carbono y el oxígeno del carbonato (Bryant et al., 1994). El agua es la fuente de oxígeno para la síntesis de hidroxiapatito; esta agua es obtenida por los ungulados y otros organismos a partir de las plantas consumidas y del agua superficial ingerida, que se mantienen en equilibrio isotópico debido a la temperatura constante (≈37°C) de estos mamíferos (Luz et al., 1984; Koch et al., 1998). El efecto del metabolismo en el fraccionamiento del oxígeno guarda relación con la masa de los mamíferos euterios, siendo mayor el efecto en mamíferos de tallas pequeñas (<100 kg) (Ayliffe et al., 1992; Bryant and Froelich, 1995). Este efecto ha sido considerado y estudiado en diferentes grupos de mamíferos para los que existe evidencia empírica del valor de fraccionamiento (e.g. D'Angela and Longinelli, 1990). Dependiendo del tipo de muestreo del esmalte (muestra

seriada y muestra en volumen) se obtienen valores que corresponden a variación estacional o al promedio de varios años (Nunez et al., 2010; González-Guarda et al., 2017).

Los métodos paleobiológicos aportan evidencia sobre la estructura de la vegetación de los ambientes antiguos. Sin embargo, para llevar a cabo una reconstrucción paleoambiental se deben de tomar en cuenta las características abióticas del sitio de depósito. Una de las aproximaciones empleadas en este tipo de trabajo es el estudio de la mineralogía asociada a restos fósiles (Carrasco et al., 2008). En los diferentes estratos que componen la columna estratigráfica de los yacimientos fosilíferos se pueden diferenciar minerales heredados, transformados y neoformados (Eberl, 1984). La génesis de estos minerales atiende a condiciones ambientales y climáticas particulares que pueden ser inferidas mediante la identificación y caracterización de estos minerales (Fesharaki et al., 2007). Además, la prevalencia de los productos de alteración exógena de las arcillas está correlacionado con el régimen climático presente en el momento de su formación (Carrasco et al., 2008)

3. Hipótesis

Dado que el actualismo biológico sugiere que el tipo de dieta está vinculado a la estructura del hábitat, el estudio de la dieta de los rumiantes fósiles de este estudio proveerá una reconstrucción paleoambiental en términos de la estructura de la vegetación.

4. Objetivos

4.1. General

Inferir los hábitos alimentarios de los rumiantes fósiles de la Cinta-Portalitos y la Piedad-Santa Ana, así como las condiciones ambientales del sitio de depósito para llevar a cabo una reconstrucción paleoambiental.

4.2. Específicos

- Inferir la preferencia alimentaria de los rumiantes fósiles sujeto de estudio durante tres lapsos particulares de su ontogenia:
    - A lo largo del tiempo de mineralización de piezas dentales de adultos.
    - Durante el tiempo de uso de piezas dentales de adultos de mediana edad.
    - Al final de la vida de los organismos.
- Inferir el tipo de vegetación presente en los sitios de estudio a partir de la información de la preferencia alimentaria de los rumiantes estudiados.
- Inferir los patrones climáticos durante el depósito de los sedimentos que conforman las columnas estratigráficas de los sitios de estudio.

5. Descripción de los sitios de estudio

5.1. Ubicación

La Cinta-Portalitos y la Piedad-Santa Ana se encuentran entre los estados de Michoacán de Ocampo y Guanajuato (figura 1), en las coordenadas 20°03-06'N, 101°08-09'W y 20°23-19' N, 102°01-02' W, respectivamente (García-Zepeda, 2006; Servín-González, 2010; Marín-Leyva et al., 2016).

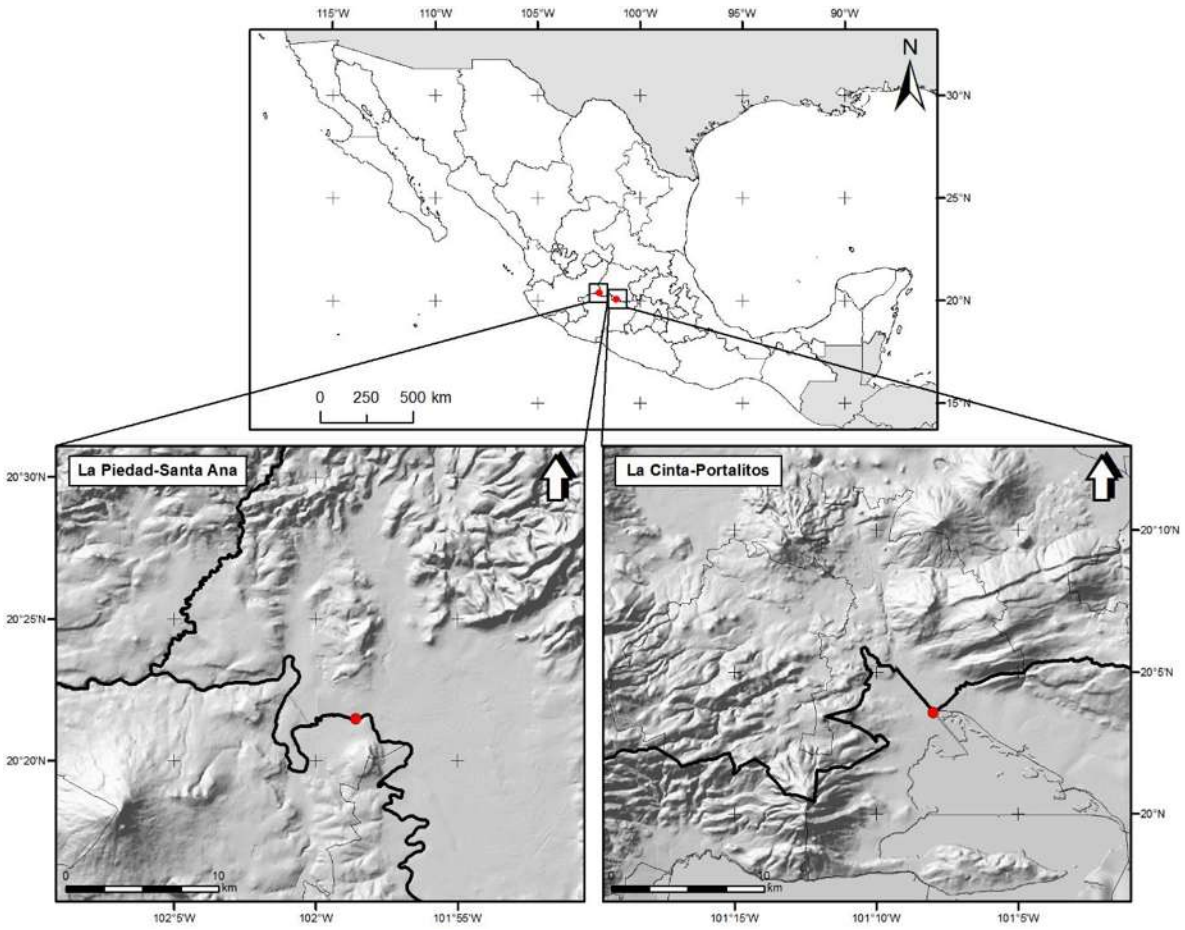

Figura 1. Localización e hipsografía de las áreas de estudio.

5.2. Geomorfología

Los sitios de estudio se encuentran ubicados en el sector central del Cinturón Volcánico Transmexicano, entre el sistema de fallas Taxco-Querétaro y el rift de Colima, en el Campo Volcánico Michoacán-Guanajuato (Ferrari, 2000).

La Cinta-Portalitos se halla entre elevaciones de 1750 a 2350 msnm (figura 1). Hacia el sur del yacimiento se encuentra el cuerpo del lago de Cuitzeo, compuesto de un semi graben con inclinación hacia el sur, hacia el suroeste se encuentran edificios volcánicos en escudo y semiescudo, mientras que al noroeste se encuentran edificios en escudo con un amplio fallamiento de tipo normal en sentido noroeste-sureste. Hacia el noroeste se presenta la depresión de Yuriria y hacia el noreste, aparatos volcánicos de tipo maars y de tipo cono de ceniza (Montiel-Escobar et al., 1998; Pérez-Flores et al., 1999; Marín-Leyva, 2011; Díaz-Sibaja, 2013).

Por otra parte, en la Piedad-Santa Ana las elevaciones van de los 1700 a los 2500 msnm. La geomorfología de la zona es variada (figura 1). Hacia el sur se encuentra el complejo volcánico de Zináparo, al suroeste el Cerro Grande o Cujaruato, hacia el oeste el sistema de fallas de la zona de la Piedad-Degollado, al noroeste la zona de lomeríos de los Altos de Jalisco, hacia el norte y noroeste el levantamiento neotectónico de Pénjamo y finalmente, hacia el este el graben de Penjamillo, que alberga la llanura de inundación del río Lerma (Darras, 1989; Pérez-Flores et al., 1999; Rosas-Elguera et al., 2000; Díaz-Sibaja, 2013).

5.3 Geología

La geología de la Cinta-Portalitos se compone de un basamento altamente fracturado de rocas andesíticas del Mioceno tardío, de entre 13 y 8 Ma. Sobreyaciendo a estas rocas se encuentran secuencias sedimentarias lacustres interestratificadas con depósitos epiclásticos, piroclásticos y depósitos fluviales compuestos de grava, arena y conglomerado aledaños a las zonas de falla, donde se registran periodos de subsidencia (Israde-Alcántara, 1997). En las zonas bajas que componen el lecho del lago y sus antiguos afluentes se encuentran zonas con aluvión Cuaternario, hacia el sur afloran ignimbritas, riolitas, andesitas y basaltos del Mioceno, hacia el este y oeste se presentan derrames de andesita y basalto correspondientes a vulcanismo del Pleistoceno y hacia el norte del yacimiento se encuentran afloramientos con andesitas y basaltos del Mioceno (Israde-Alcántara, 1997; Montiel-Escobar et al., 1998; Pérez-Flores et al., 1999).

El yacimiento de la Piedad-Santa Ana se encuentra en zonas con aluvión Cuaternario. Hacia el sur, se presentan andesitas y basaltos del Pleistoceno (con una edad

máxima de 1.68 Ma), hacia el oeste un bloque de arenisca y toba riolítica del Mioceno (<8.7 Ma) que subyace flujos de basalto y andesita del Plioceno (5-2.5 Ma); hacia el norte, pequeños afloramientos con andesitas, riolitas y tobas riolíticas del Oligoceno que subyacen flujos basálticos y andesíticos del Mioceno medio y finalmente hacia el este, en el graben de Penjamillo, tobas y areniscas basálticas del Pleistoceno con intercalaciones de depósitos piroclásticos (lapilli y bombas) con sedimentos de origen fluvial y lacustre, principalmente arenas, conglomerados y diatomita (Martínez-Reyes and Nieto-Samaniego, 1990; Pérez-Flores et al., 1999; Rosas-Elguera et al., 2000; Díaz-Sibaja, 2013).

5.4. Estratigrafía

La estratigrafía de la Cinta-Portalitos (figura 2) se compone de una secuencia fluviolacustre, con evidencia de vulcanismo que se describe a continuación de la base a la cima.

Estrato 1: 47 cm de diatomita de color café claro con un contacto superior neto. Estrato 2: 23 cm de toba basáltica de color obscuro con un contacto superior transicional. Estrato 3: 21 cm de arena limosa de color café amarillento con un contacto superior erosionado. Estrato 4: 41 cm de toba basáltica de color obscuro con un contacto superior erosionado. Estrato 5: 31 cm de paraconglomerado polimíctico con clastos de riolita, basalto, pumita, cuarzo y feldespato, con una matriz arenosa de color café amarillenta, con presencia de restos fósiles de gasterópodos (principalmente de la familia Polygyridae) y de vertebrados acuáticos y terrestres. Estrato 6: 90 cm de diatomita de color café claro, con presencia de concreciones de carbonato de calcio, con un contacto superior transicional. Estrato 7: 49 cm de arcilla limosa de color café obscuro rojizo, con presencia de nódulos de oxidación amarillentos y restos arqueológicos que incluyen abundante obsidiana trabajada y cerámica. Estrato 8: suelo resisual de color café obscuro a negro, producto de pedogénesis *in situ*, poco diferenciado hacia la base, con presencia de raíces y materia orgánica.

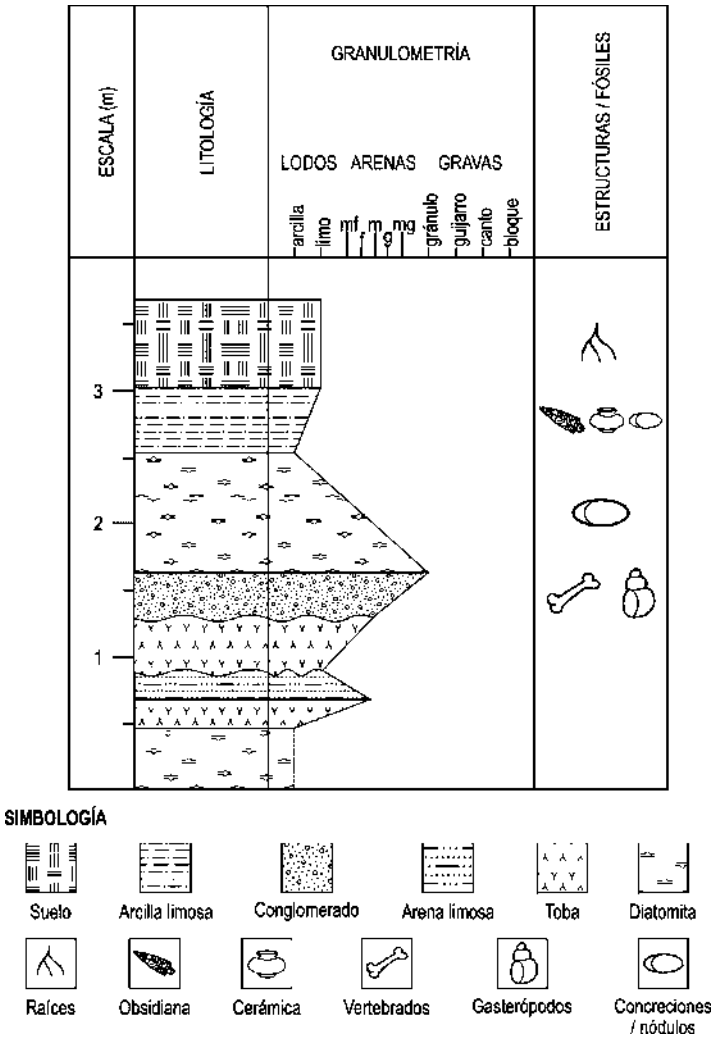

Figura 2. Estratigrafía general de la Cinta-Portalitos. Abreviaturas, mf: arena muy fina, f: arena fina, m: arena media, g: arena gruesa, mg: arena muy gruesa.

La estratigrafía de la Piedad-Santa Ana (figura 3) se compone de secuencias fluviales y lacustres intercaladas con vulcanismo hacia la base, descrita a continuación de la base a la cima.

Estrato 1: 48 cm de diatomita de color café claro, con un contacto superior ligeramente erosionado. Estrato 2: 28 cm de toba basáltica de color obscuro, con un contacto superior erosionado. Estrato 3: 60 cm de paraconglomerado polimíctico con clastos de riolita, basalto, cuarzo y obsidiana, con una matriz arenosa de color amarillenta con lentes de toba retrabajada y presencia de restos fósiles de vertebrados. Estrato 4: 100

cm de arenas medias a finas de color café a amarillenta, con oxidación y un contacto superior erosionado. Estrato 5: 110 cm de arenas limosas de color café, con un contacto superior neto. Estrato 6: 100 cm de diatomita de color café claro, con un contacto superior transicional. Estrato 7: 140 cm de arcilla limosa de color café, con vestigios arqueológicos que incluyen obsidiana trabajada y cerámica, con un contacto superior transicional. Estrato 8: 30 cm de suelo resisual de color café obscuro a negro, producto de pedogénesis *in situ*, poco diferenciado hacia la base, con presencia de raíces y materia orgánica.

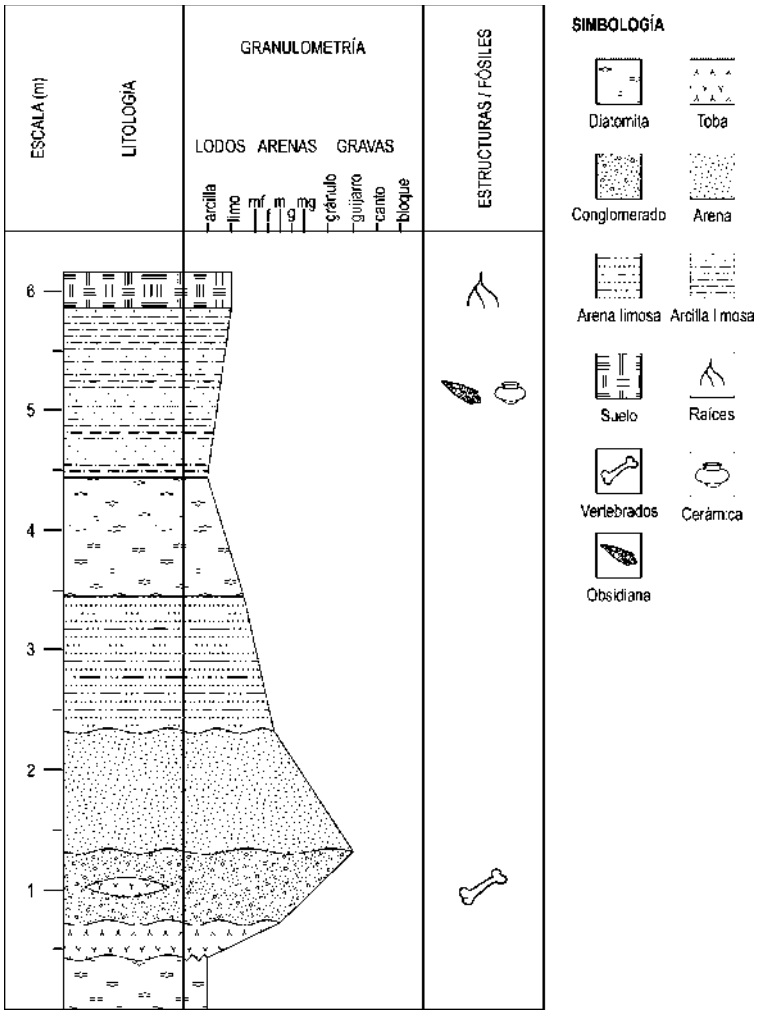

Figura 2. Estratigrafía general de la Piedad-Santa Ana. Abreviaturas, mf: arena muy fina, f: arena fina, m: arena media, g: arena gruesa, mg: arena muy gruesa.

6. Resultados

Como **primer capítulo** se expone una revisión crítica del registro fósil de los rumiantes (Artiodactyla: Rumiantia) de México. Este capítulo es de particular relevancia para el entendimiento de la taxonomía, evolución y patrones geográficos de este grupo de ungulados en territorio nacional. En dicha sección se proponen once nuevas sinonimias, un *nomen nudum* y la reasignación del material previamente identificado como *Bison alaskensis* (*Bison aguascalentensis*) a *Bison latifrons*. Este trabajo provee de un marco de referencia para el estudio de los rumiantes fósiles del país.

Como **segundo capítulo** se presenta el artículo requisito, titulado "A combined mesowear analysis of Mexican *Bison antiquus* shows a generalist diet with geographical variation" (en prensa), donde se infieren las condiciones estables de la dieta de las poblaciones de esta especie en los sitios de estudio y se comparan con los patrones de la misma en otras regiones del contienente y al sur del país, con la localidad oaxaqueña de Viko Vijin (la población más austral de esta especie). Como primera aproximación, se infiere una dieta pacedora no estricta y sugiere una estructura de la vegetación heterogénea en los sitios estudiados.

Para corroborar esta inferencia dietaria y ampliarla hacia otras especies de rumiantes presentes en los sitios de estudio, el **capítulo tres** muestra los resultados de los análisis de microdesgaste dental de baja magnificación (35x) y de isótopos estables de carbono ($\delta^{13}C$). En este capítulo también se presentan evidencias de competencia entre los bisontes y otras especies de megafauna de los sitios estudiados. Adicionalmente, se presentan los resultados del análisis de isótopos estables de oxígeno ($\delta^{18}O$) para inferir las temperaturas de ambos sitios y los resultados de los análisis mineralógicos para inferir las condiciones paleoclimáticas de los sitios durante el Pleistoceno, así como su evolución.

Finalmente, se presenta como **anexo** un estudio donde se publica una nueva localidad del sur de México con la presencia más austral de *Bison latifrons* (una de las especies de bisonte de nuestros sitios de estudio).

Capítulo 1. The fossil ruminants (Artiodactyla: Rumiantia) of Mexico, a critical review (artículo en preparación)

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Introduction

Ruminants (Artiodactyla: Ruminantia) originated in Asia, around 45 Ma, during the Middle Eocene (Vislobokova, 2001; Métais, 2006; Métais and Vislobokova, 2007). Today they encompasses more than 200 modern species, nested in six families (Hernández-Fernández and Vrba, 2005), and with at least nine more extinct families in the global fossil record (McKenna and Bell, 1997). The most remarkable and diagnostic character of advanced groups are the cranial appendages such as ossicones, pronghorns, antlers and horns (Davis et al., 2011).

Ruminants have successfully colonized almost all continental land masses, with exception of Australia and Antarctica (Vrba and Schaller, 2000a). Their biogeographic history includes two early independent dispersion events into North America during the Eocene, where the firsts fossil records suggests an appearance around 41.3 Ma (Webb, 1998a; Métais and Vislobokova, 2007). Since then, this group have generated one exclusive North American family, Antilocapridae (Janis and Manning, 1998; Davis, 2007), and have participated in several dispersion events from the Old Wold, during the Neogene and Pleistocene, with representatives of the families Palaeomerycidae (Janis et al., 1998a; Prothero and Liter, 2007), Cervidae, and Bovidae (Kurtén and Anderson, 1980; Webb, 1998b).

Systematic reviews on North American fossil ruminants are scarce (e.g. Frick, 1937) or are included on a larger taxonomic group reviews focusing on a specific time period (Kurtén and Anderson, 1980; Janis et al., 1998b; Prothero and Foss, 2007). This is the case for the Mexican ruminants, because only two systematic review works exists, and are focused on the Miocene (Jiménez-Hidalgo et al., 2002)and the Quaternary (Ferrusquía-Villafranca et al., 2010). In Mexico, mammals are one of the most common terrestrial fossil group (Arroyo-Cabrales et al., 2008), and they are present in more than 776 fossiliferous localities,

most of them restricted to the Pleistocene (Arroyo-Cabrales et al., 2002). The fossil ruminants of Mexico formed an important part of the mastofaunal assemblages, and their study is relevant to understand the evolution and radiation of this group in the meridional regions of North America.

In this work we present a critically assessment of the Mexican ruminant fossil record, and generate a broad taxonomic framework for future studies, proposing new synonymies and diagnostic characters for all species in this work.

Materials and methods

Sources of information

After performing an exhaustive compilation and revision of literature, we considered two kinds of sources of information: 1) primary sources and 2) secondary sources. The primary sources were the journal articles, academic/arbitrated books, chapters of books, and technical reports. The secondary sources were the conference abstracts/proceedings, theses, and databases. We mainly employed primary sources, and for the secondary ones, we tried to access the fossil material in order to identify it. The non-verifiable sources of information were discarded.

Temporal ranges

For the Periods and Epochs, we employed the ages of the International Chronostratigraphic Chart v2017/02 (Cohen et al., 2017). The North American Land Mammal Ages (NALMA) boundaries, definitions, and subdivisions were taken from Bell *et al*. (2004), Prothero and Emry (2004) and Tedford *et al*. (2004).

Geographical data

The distribution maps were elaborated considering two type of boundaries: political state divisions (Ita-Rubio de et al., 1990) and Mexican Biogeographic Provinces (CONABIO, 1997). The delimitation of each Mexican Biogeographic Provinces attends to four biotic distribution patterns: vascular plants, amphibians, reptiles, and mammals, as well as morphotectonic features (CONABIO, 1997). We paid special attention to morphotectonic criteria, specifically for Quaternary species, due to the importance of these in determining the distribution patterns of both flora and fauna, recent and fossil (Ferrusquía-Villafranca et al., 2010). The Biogeographic Provinces employed in this work are the Baja California (BCa), Balsas Depression (BaD), Cabo (Cab), Californian (Cal), Chiapas Highlands (ChH), Gulf of Mexico (GoM), North Plateau (NoP), Oaxaca (Oax), Pacific Coast (PaC), Peten (Pet), Sierra Madre del Sur (SMS), Sierra Madre Occidental (SMOc), Sierra Madre Oriental (SMOr), Soconusco (Soc), Sonoran (Son), South Plateau (SoP), Tamaulipecan

(Tam), Volcanic Axis (VoA), Yucatan (Yuc) (Figure 1). All of the maps employed in this work have a Lambert conformal conic projection, a GCS WGS 1984 Geographic Coordinate System, and a scale of 1:4,000,000.

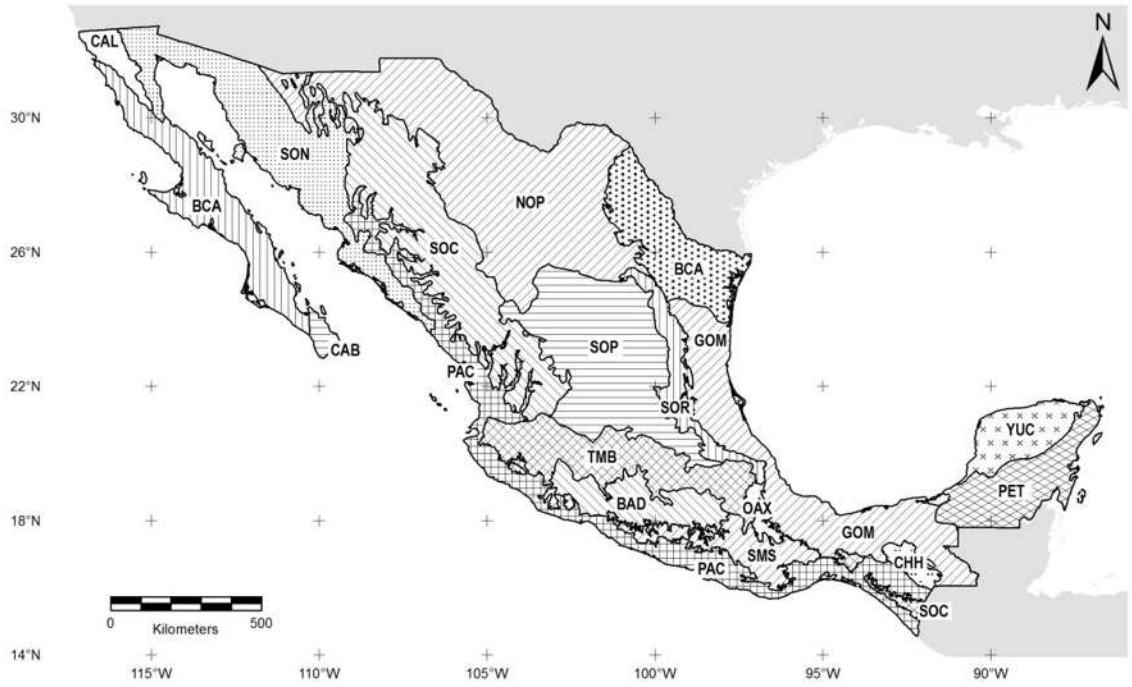

Figure 1. Biogeographic Provinces employed in this work Abbreviations in text.

For the analysis of the Mexican ruminant fossil record, we employed two concepts: fossil site and local fauna. We consider a fossil site to be a single locality and a local fauna as an aggregate of fossil species that are found in a number of closely grouped localities in a limited geographic area (Woodburne, 2004).

Anatomical terminology

Ruminant dental anatomy terminology employed through this manuscript follow the Bärmann and Rössner, (2011) standard terminological proposal. Also, we omitted the diagnosis for the species with no fossil record in Mexico.

Taxonomic definitions above species level

For the arrangement of ruminant taxonomy, we followed mainly McKenna and Bell (1997), Davis (2007), and Groves and Grubb (2011). Also, we employed the following taxon definitions through this work:

Ruminantia: the least inclusive clade containing *Bos taurus* and *Tragulus napu* (Spaulding et al., 2009). Characterized by the fusion of the cuboid and navicular to form the naviculocuboid bone, the absence of upper incisors, and the possession of a procumbent incisiviform lower canine (Webb, 1998a; Métais and Vislobokova, 2007).

Leptomerycidae: the least inclusive clade containing *Hendryomeryx* and *Pseudoparablastomeryx* (based on Webb, 1998). Characterized by a low skull roof, elongated rostrum, centrally located orbits closed by a complete postorbital bar, limited to no exposure of the mastoid, brachydont premolars and molars with poorly developed labial ribs, isolated and reduced caniniform p1, three adjacent cuspids in p2, well-developed paraconids, metaconids, and hypoconids in p3-p4, well-developed metaconid with posterolingual cuspid in p4, not closed crescent-shaped cuspids in lower molars, P1 absent, lingual protocone in P2-P3, crescent-shaped protocone in P4, mesostyle in upper molars, reduced manual digits II and V, moderate spout like odontoid process in the axis, fused magnum and trapezoid, paraxonic tetradactyl manus, reduced fibula (malleolar bone, non-parallel trochleae of the astragalus (Webb, 1998a; Métais and Vislobokova, 2007).

Hypertragulidae: the least inclusive clade containing *Hypertragulus* and *Nanotragulus* (based on Webb, 1998) (*Parvitragulus*, *Simimeryx*, *Andegameryx*, and *Hypisodus* are excluded following Métais and Vislobokova, 2007). Characterized by high skull roof, short rostrum (larger than Leptomerycidae), posteriorly opened orbits, large lateral exposure of mastoid, isolated tusk-like caniniform p1, isolated secodont p2, tribosphenic p4 with sub circular heel, brachydont molars, complete crescent-shaped cuspids in lower molars, tusk-like upper canine (not present in *Nanotragulus*), isolated secodont P1, lingually conical protocone in P3-P4, mesostyle absent in upper molars, short peg-like odontoid process in the axis, pentadactyl manus, tetradactyl pes (digit I absent), digits II and V reduced, unfused magnum and trapezoid, complete fibula fused distally with the tibia, non-parallel trochleae of the astragalus (Webb, 1998a; Métais and Vislobokova, 2007).

Antilocapridae: the least inclusive clade containing *Paracosoryx* and *Capromeryx* (based on Janis and Manning, 1998). Characterized by permanent supraorbital horncores (*komecera*) covered by skin (in early forms) or a keratinous sheath (in derived forms), usually forked at the distal end (the ramifications are termed here as prongs); large and complete orbits, presence of antorbital vacuity, absence of lacrimal fossa, large and hollow auditory bulla, usually absence of upper canine (except in early forms), cheek teeth hypsodont and without accessory characteristics (except in *Paracosoryx*), molariform premolars, fibula reduced to a malleolar bone, fused metapodials III+IV with closed gully and complete distal keels (Janis and Manning, 1998).

"Merycodontinae": a paraphyletic assemblage of small antilocaprids with horncores circular in cross section, usually forked, branched or palmated horncores presumably covered by skin, apparently only males possessed horncores; possible retention of metapodials II and V. Includes the genera: *Paracosoryx*, *Ramoceros*, *Merriamoceros*, *Merycodus*, "*Merycodus*" (see discussion), and *Cosoryx* (Janis and Manning, 1998; Davis, 2007).

Cervidae: the least inclusive clade containing *Cervus* and *Hydropotes* (based on Zhang and Zhang, 2012; Kuznetsova et al., 2005). Except for *Hydropotes*, all of the members of the family are characterized by deciduous, postorbital cranial appendages (*epochocera*), which lack a permanent keratin or skin cover: the antlers. Branches on the antlers are termed here as "tines". The family is also defined by the combination of the following characters: an antorbital vacuity which excludes the lacrimal from articulation with the nasals, a lacrimal fossa, double lacrimal duct, unexpanded to slightly expanded auditory bulla, upper canine reduced or lost, brachydont to mesodont cheek teeth, absence of p1, posterolingual groove in p4 absent, ectostylid and metastylid in lower teeth, complete internal postprotocristid, protocone of the P3 in lingual position, metastyle present in upper teeth, moderate to large metaconule in M3, non-bifurcated metaconule, fused (III+IV) metapodials with closed distal gully by a distal bridge, complete distal keels, posterior tuberosity, cubonavicular facet raised with posterior lip and fusion of lateral (II and V) metapodials (Janis and Scott, 1987; Groves and Grubb, 2011).

The division of Cervidae into the subfamilies Capreolinae and Cervinae, considered in this work follow Gilbert *et al.* (2006).

Early *Odocoileus*: a wastebasket taxon employed here to designate Blancan to Irvingtonian *Odocoileus* species different from *Odocoileus virginianus* and *O. hemionus*, usually classified as *Odocoileus brachyodontus*, which status is dubious (see the discussion below).

Bovidae: the least inclusive clade containing *Bos taurus* and *Capra aegagrus* (based on Bibi, 2013; Vrba and Schaller, 2000). Characterized by postorbital, unbranched, and nondeciduous cranial appendages (true horns, *coelocera*) with pedicle (originating from the frontal bone), horn core (induced by the integument), and a keratinous horn sheat. The family is also defined by the combination of the following characters: one or two lacrimal orifices, upper canine reduced or lost, teeth with metastyle, protoconid/protocone of p3 and P3 in lingual position, large metaconid/metacone in m3 and M3, absence of p1, fused (III+IV) metapodials with open gully, complete distal keels; and lateral metapodials (II and V) lost (Janis and Scott, 1987).

Institutional abbreviations

CoMNH: Denver Museum of Nature and Science (formerly Colorado Museum of Natural Museum).

FAM: Frick Collection (American Mammals or) American Museum of Natural History.

FC: Fauna del Cedazo (Cedazo Fauna), from the personal collection of Oswaldo Mooser.

FM: Fossil Mammal Collection of the American Museum of Natural History.

FMNH: Field Museum of Natural History.

FV: Ismael Ferrusquía Villafranca's Field catalog.

HJ73: Arturo Hernández Junquera field collection of 1973.

IGCU, IG, IGM: Instituto de Geología (Geology Institute), Universidad Nacional Autónoma de México (National Autonomous University of Mexico), Oscar Carranza Castañeda personal catalog.

INAH: Instituto Nacional de Antropología e Historia (National Institute of Anthropology and History).

LACM: Los Angeles County Museum, California.

MNHN: Museo Nacional de Historia Natural de la Universidad Nacional de México (National Natural History Museum of the National University of Mexico, now in the IGM collections).

MPGJ: Paleontology Museum, Geosciences, Juriquilla (Museo de Paleontología Geociencias Juriquilla), Mexico.

SMU: Shuler Museum of Paleontology, Roy M. Huffington Department of Earth Sciences, Texas.

UAHMP: Paleontology Museum of the Autonomous University of the State of Hidalgo (Museo de Paleontología de la Universidad Autónoma del Estado de Hidalgo).

UCMP: University of California Museum of Paleontology.

UMMP: University of Michigan Museum of Paleontology.

YMP VP: Yale Peabody Museum of Natural History, Vertebrate Paleontology.

Results and discussion

The ruminant diversity (Figure 2) of Mexico encompasses 31 species in 5 families, 8 subfamilies, and 23 genera. The most diverse family is the Antilocapridae with 13 species (42%), followed by the Bovidae with 8 species (26%), and the Cervidae, with 7 species (23%). The less diverse families are the Hypertragulidae with 2 species (6%), and the Leptomerycidae with only one species (3%). The most diverse genus is *Bison* with 4 species, followed by *Capromeryx* with 3 species, and *Odocoileus*, *Mazama*, and *Ovis* with 2 species each (Table 1).

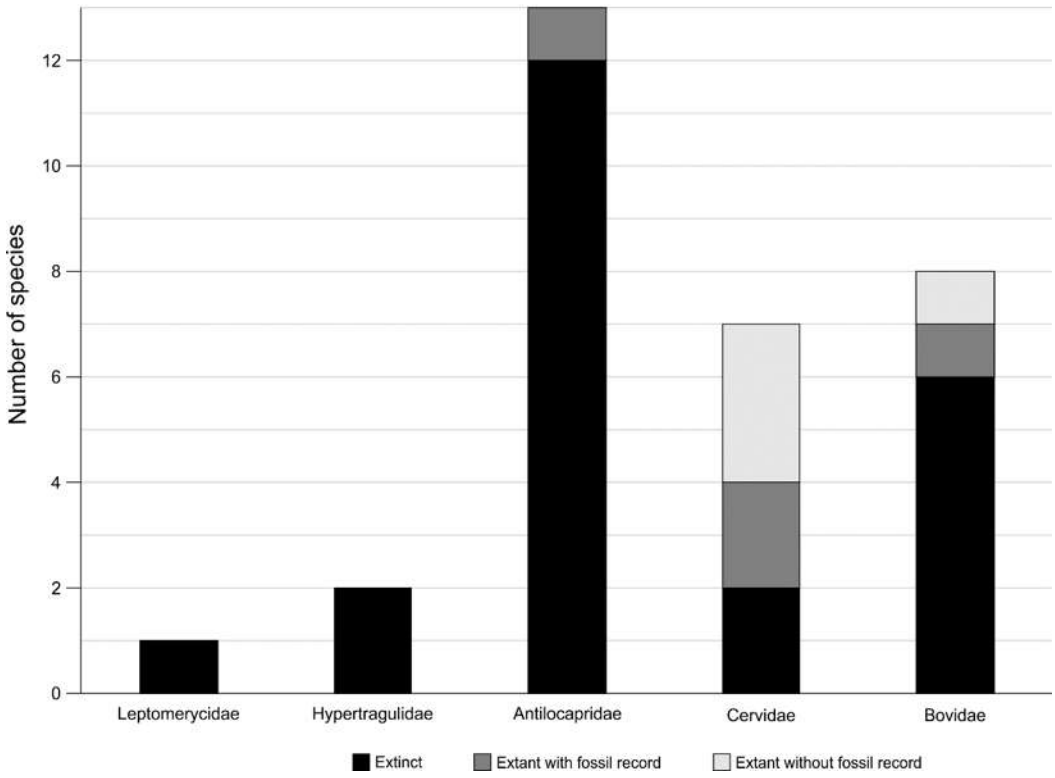

Figure 2. Mexican ruminant diversity per family.

Among the extant Mexican ruminants, 4 species have no fossil record in Mexico and are restricted to the Holocene: *Bison bison* (Bovidae), *Mazama pandora*, *M. temama*, and *Cervus canadensis* (Cervidae). On the other hand, 3 extant species are represented in the Mexican fossil record: *Antilocapra americana* (Antilocapridae), *Odocoileus virginianus* and *O. hemionus* (Cervidae). At suprageneric level, only the horned ruminant families (Antilocapridae, Bovidae, and Cervidae) have modern representatives, while the hornless leptomerycids and hypertragulids are extinct worldwide.

Table 1. Fossil and recent ruminant species of Mexico. Symbology: *extant species with fossil record; ^extant species without fossil record in Mexico.

	Range in Mexico
LEPTOMERYCIDAE	
Leptomerycinae	
Pseudoparablastomeryx sp.	Barstovian
HYPERTRAGULIDAE	
Hypertragulinae	
Hypertragulus heikeni	Chadronian
Nanotragulus sp.	Chadronian to Orellan
ANTILOCAPRIDAE	
"Merycodontinae"	
"Merycodus" sabulonis	Hemingfordian (He2) to Barstovian (Ba1)

	Cosoryx sp.	Hemphilian (Hh2)
Antilocaprinae		
	Plioceros sp.	Hemphilian (Hh2)
	Sphenophalos sp.	Hemphilian (Hh2)
	Subantilocapra garciae	Hemphilian (Hh3)
	Texoceros sp.	Hemphilian (Hh4)
	Hexobelomeryx fricki	Hemphilian (Hh2) to Blancan (Bl3)
	Capromeryx tauntonensis	Blancan (Bl3)
	Capromeryx furcifer	Irvingtonian (Ir2?)
	Capromeryx minor	Rancholabrean
	Stockoceros conklingi	Rancholabrean
	Tetrameryx shuleri	Rancholabrean
	*Antilocapra americana**	Rancholabrean to Recent
CERVIDAE		
Capreolinae		
	Capreolus constantini	Blancan (Bl3)
	Navahoceros fricki	Rancholabrean
	*Odocoileus virginianus**	Rancholabrean to Recent
	*Odocoileus hemionus**	Rancholabrean to Recent
	Mazama pandora^	Holocene to Recent
	Mazama temama^	Holocene to Recent
Cervinae		
	Cervus canadensis^	Holocene to Recent
BOVIDAE		
Caprinae		
	Euceratherium collinum	Rancholabrean
	Ovis sp. nov.	Irvingtoninan
	*Ovis canadensis**	Rancholabrean
	Oreamnos harringtoni	Rancholabrean
Bovinae		
	Bison alaskensis	Rancholabrean
	Bison latifrons	Rancholabrean
	Bison antiquus	Rancholabrean
	Bison bison^	Recent

In total, we recorded 81 localities (Table 2) and local faunas with presence of fossil ruminants in 14 Biogeographic Provinces (Figure 3). The best-represented province is the Volcanic Axis with 20 localities (25%), followed by the South Plateau with 16 localities (20%). On the other hand, the Californian, the Balsas Depression, the Chiapas Highlands, the Soconusco, and the Peten provinces have no ruminant fossil record.

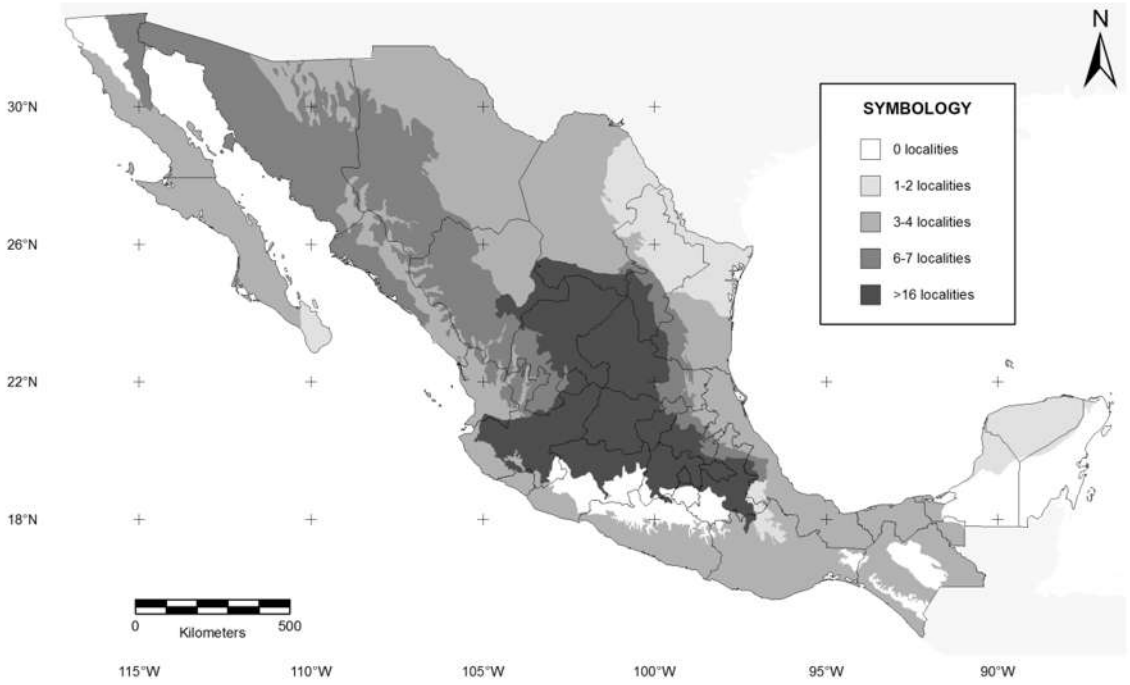

Figure 3. Number of localities per Biogeographic province.

As for the representativeness of the ruminant fossil record (Figure 4), the best-represented Epoch was the Pleistocene, with a total of 59 localities (74% of the total), followed by the Miocene with 11 localities (14%). And the least represented epochs are the Pliocene (3 localities) and the Eocene (2 localities). In the South Plateau and Yucatan provinces, we recorded one locality that may be Holocenic, Gruta de Loltún, Yucatán. Finally, we found that three localities with ruminant taxa from mixed ages, the Yepómera local fauna in the Sierra Madre Occidental province with Miocene and Pleistocene taxa, the San Miguel de Allende local fauna in the South Plateau province with Miocene and Pliocene taxa (and one possible Pleistocene taxon), and the Tecolotlán locality in the Volcanic Axis province, with Miocene and Pleistocene taxa.

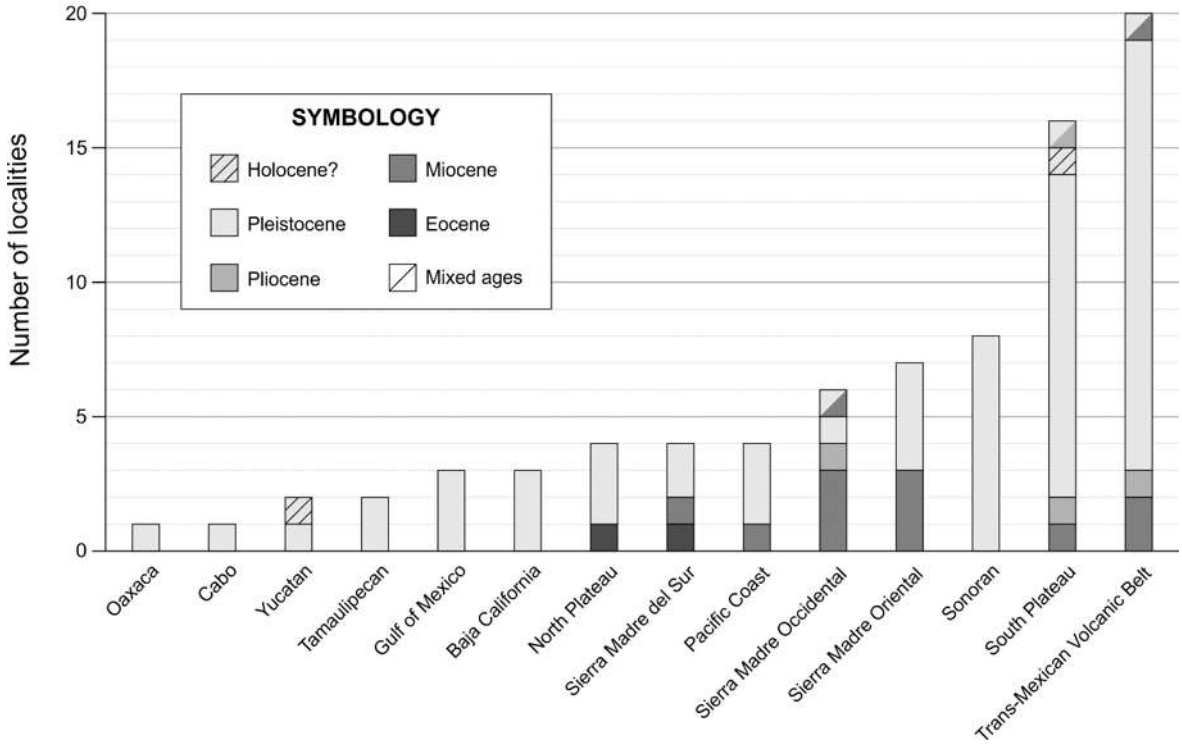

Figure 4. Number of localities per Biogeographic province, distributed by age.

The fossil ruminants are present in 20 States of the Republic, excluding Baja California, Campeche, Colima, Durango, Guerrero, Morelos, Nayarit, Quintana Roo, Sinaloa, and Tabasco. The State with the largest number of localities/local faunas with presence of fossil ruminants is Hidalgo, with 10 records (12% of all records), followed by Jalisco with 9 records (11%), and Sonora with 8 records (10%). The states with only one locality/local fauna are Aguascalientes (El Cedazo), Puebla (Valsequillo), Querétaro (Landa de Matamoros), Tamaulipas (Ejido San Lázaro), and Tlaxcala (San Mateo Huexoyucan).

Table 2. Distribution of fossil records in Mexican Biogeographic provinces. PSE: *Pseudoparablastomeryx* sp., HYP: *Hypertragulus heikeni*, NAN: *Nanotragulus* sp., MER: "*Merycodus*" *sabulonis*, COS: *Cosoryx* sp., PLI: *Plioceros* sp., SUB: *Subantilocapra garciae*, SPH: *Sphenophalos* sp., TEX: *Texoceros* sp., and HEX: *Hexobelomeryx fricki*. Gray cells: originally reported as cf., and *: local fauna represented by more than one locality.

Province	Locality	PSE	HYP	NAN	MER	COS	PLI	SUB	SPH	TEX	HEX
Sierra Madre Occidental	Yepómera*										X
	Matachic*										X
	Colotlán										X
	Juchipila Basin*					X	X		X		

North Plateau	Rancho Gaitán*		X								
South Plateau	Teocaltiche										X
	San Miguel de Allende*							X		X	X
Sierra Madre Oriental	Landa de Matamoros										X
	Tehuichila										X
	Potrero de Zietla										X
Volcanic Axis	Juchitlán										X
	Tecolotlán										X
	La Plegaria*									X	X
Sierra Madre del Sur	Iniyoo*			X							
	Matatlán	X									
Pacific Coast	Nejapa*				X						
TOTAL		**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**2**	**11**

Table 2. (continuation). CAT: *Capromeryx tauntonensis*, CAF: *Capromeryx furcifer*, CAM: *Capromeryx minor*, STO: *Stockoceros conklingi*, TET: *Tetrameryx shuleri*, ANT: *Antilocapra americana*, CAP: *Capreolus constantini*, NAV: *Navahoceros fricki*, MAZ: *Mazama* sp., OVI: *Odocoileus virginanus*. Gray cells: originally reported as cf., dark gray cells: possible holocenic record, blue cell: reassigned, and *: local fauna represented by more than one locality.

Province	Locality	CAT	CAF	CAM	STO	TET	ANT	CAP	NAV	MAZ	OVI
Sonoran	Golfo de Santa Clara		X		X				X		X
	San Clemente de Térapa			X	X						
	La Botana			X							
	La Playa			X							
Sierra Madre Occidental	Rancho La Brisca			X		X					
North Plateau	Mina						X				
	Cueva Jiménez			X			X				
Tamaulipecan	Cueva Bustamante								X		
	Cueva la Mina								X		
	El Cedral			X					X		
	Mina de San Antonio				X						
	Cueva La Presita			X	X						X
	Laguna de la Media Luna										X
South Plateau	El Cedazo*			X	X	X			X		
	San Miguel de Allende*	X									
	Santa María Amajac							X			
	El Barrio			X	X						X
	San Agustín Tlaxiaca				X						
Sierra Madre Oriental	San Josecito				X				X		
	Barranca del Berrendo			X							
Gulf of Mexico	La Mixtequilla			X	X	X				X	

	Tecolotlán					X					
	Zacoalco					X					X
	Chapala*					X			X		X
	La Piedad-Santa Ana					X					X
Volcanic Axis	La Cinta-Portalitos			X	X	X					X
	Tajo de Tequixquiac*			X	X						
	Los Reyes La Paz				X						
	Tlapacoya								X		X
	San Mateo Huexoyucan										
	Valsequillo*			X	X	X					
Oaxaca	Sótano de San Agustín								X		
Pacific Coast	Los Tanques					X					
	Villaflores										X
Yucatan	Cueva de Lara (Actun Lara)										X
	Gruta de Loltún									X	X
TOTAL		**1**	**1**	**14**	**13**	**10**	**2**	**1**	**9**	**2**	**12**

Table 2. (continuation). OHE: *Odocoileus hemionus*, OSP: *Odocoileus* sp., EUC: *Euceratherium collinum*, ORE: *Oreamnos harringtoni*, OCA: *Ovis canadensis*, ONS: *Ovis* sp. nov., BSP: *Bison* sp., BAL: *B. alaskensis*, BLA: *B. latifrons*, and BAN: *B. antiquus*. Gray cells: originally reported as cf., blue cell: reassigned, and *: local fauna represented by more than one locality.

Province	Locality	OHE	OSP	EUC	ORE	OCA	ONS	BSP	BAL	BLA	BAN
	Comondú										X
Baja California	Santa Rita							X			
	Unnamed BCS										X
Cabo	Rancho el Carrizal										X
	Golfo de Santa Clara	X	X				X				
	Ramos Arizpe									X	
	San Clemente de Térapa		X					X			
Sonoran	La Guitarra			X							
	Llano Prieto							X			
	La Botana		X					X			
	Chinobampo							X			
	Rancho La Brisca	X						X			
Sierra Madre Occidental	Yepómera*							X			
	Miñaca		X								
North Plateau	Mina Erupcion		X								
	Mina	X									X
Tamaulipecan	Cueva la Mina			?							
South Plateau	El Cedral			X				X			
	Mina de San Antonio	X									

	Unnamed Z2									X	
	Unnamed Z1									X	
	Unnamed SLP										X
	Laguna de las Cruces										X
	El Cedazo*									X	
	San Juan de los Lagos							X		X	
	San Miguel de Allende*		?								
	Las Cajas							X			
	San Agustín Tlaxiaca		X					X			
	San Josecito		X	X	X						
Sierra Madre Oriental	Cueva del Tiburón			X							
	Epazoyucan					X		X			
Gulf of Mexico	Ejido San Lázaro							X			
	Buenavista		X								
	Rancho San Miguel							X			
	Atotonilco el Bajo							X			
	Zacoalco	X								X	X
	Chapala*	X	X							X	X
	La Piedad-Santa Ana									X	X
	Ciudad Universitaria							X			
	La Cinta-Portalitos	X								X	X
	Uruétaro		X								
Volcanic Axis	Huachichil									X	
	Zumpango de Ocampo									X	
	Tajo de Tequixquiac*			X					X	X	X
	Los Reyes La Paz							X			
	Chimalhuacán							X			
	San Vicente Chicoloapan										X
	Tlapacoya										
	San Mateo Huexoyucan										X
	Valsequillo*										X
Sierra Madre del Sur	Viko Vijin*		X								X
	San Dionisio Ocotepec*							X		X	
Pacific Coast	Los Tanques							X			
	La Simpatía, Villa Corzo							X			
Yucatan	Gruta de Loltún							X			
TOTAL		**7**	**12**	**5**	**1**	**1**	**1**	**22**	**1**	**13**	**15**

Systematic paleontology

Order Ruminantia Scopoli, 1777

Family Leptomerycidae (Zittel, 1893)

Subfamily Leptomerycinae (Zittel, 1893)

Genus *Pseudoparablastomeryx* Frick, 1937

Synonyms: *Blastomeryx francescita* (Frick, 1937), *Parablastomeryx* (Frick, 1937) (in part, see discussion below).

Range in Mexico (Figure 5): Matatlán, Oaxaca, Sierra Madre del Sur province (Jiménez-Hidalgo et al., 2002).

Age range: In Mexico from the Middle Barstovian (Middle Miocene), 14.3 to 15.3 Ma (Ferrusquía-Villafranca, 1990; Jiménez-Hidalgo et al., 2002), and in North America from 18.8 to 11 Ma (Webb, 1998a).

Diagnosis: Upper premolars with larger cingulum than *Leptomeryx*, p1 absent, reduced mesiodistal length in the premolars, lower premolars labiolingually compressed, entostylid of m3 greatly reduced.

Included species: *P. scotti* (type species) and *P. francescita*.

Notes: *Pseudoparablastomeryx* was originally described as a subgenus of *Parablastomeryx* (Frick, 1937), and today is regarded as a separate valid genus (Webb, 1998a). The genus is known from Saskatchewan, South Dakota, Nebraska, California, New Mexico, and Texas (Webb, 1998a). The Mexican record represents the southernmost of its distribution, and extends its known geographical range southwards by more than 1,000 km.

The remains from the Matatlán Formation in Oaxaca consists in a right astragalus (FV 97-62) which possesses the diagnostic characters of a small leptomerycid, such as a navicular facet narrower than the cuboidal facet, the subsustentacular facet is not clearly differentiated from the cuboidal facet, in lateral view the distal trochlea is short and rounded, and the distal and proximal facets are parallel (Jiménez-Hidalgo, 2000). Besides this combination of characters, only this genus of leptomerycid was present during the Barstovian (Tedford et al., 2004).

Family Hypertragulidae Cope, 1879

Subfamily Hypertragulinae (Cope, 1879)

Genus *Hypertragulus* Cope, 1874

Species *Hypertragulus heikeni* Ferrusquía-Villafranca, 1969

Range in Mexico (Figure 5): 32 km NW of Ojinaga, Rancho Gaitán local fauna (Prietos Formation), Chihuahua, North Plateau province (Ferrusquía-Villafranca, 1969).

Age range: In Mexico, known only from the Early Chadronian (Ferrusquía-Villafranca, 1969), and in North America from the Middle Duchesnean (Late Eocene), ca. 39.5 Ma (Webb, 1998a).

Diagnosis: Smaller than the type species, *H. calcaratus*; anterior mental foramen below the diastema between p2 and the canine, posterior mental foramen below the contact between p3-p4, brachydont teeth, p2 isolated, p3 with small accessory mesial cusp, p4 bicuspid with distal talonid, secant premolars, selenodont molars with poorly defined stylids and well-defined shelves, m1-m2 with mesial and distal cingula, non-selenid talonid in m3 with a well-developed lingual crest (Ferrusquía-Villafranca, 1969).

Notes: *H. heikeni* is known from the Big Bend area of Texas, at the Devil's Graveyard Formation, in the Bandera Mesa member (Webb, 1998a). In Mexico, it was originally described from the Prietos Formation, closely to the Big Bend localities, which represents its southernmost record (Ferrusquía-Villafranca, 1969). Chronologically, *H. heikeni* is the earliest ruminant in Mexico, and its record in the Chadronian represents the latest appearance of this species in North America.

Genus *Nanotragulus* Lull, 1922

Synonyms: *Allomeryx* (Sinclair, 1905), *Hypertragulus ordinatus* (Matthew, 1907), *Hypertragulus fontanus* (Stock, 1935).

Range in Mexico (Figure 5): Iniyoo local fauna (Yolomécatl Formation), Oaxaca, Sierra Madre del Sur province (Jiménez-Hidalgo et al., 2015).

Age range: In Mexico, from the Chadronian to the Orellan (Late Eocene, probably Early Oligocene), with a minimal age between 35.7 and 32.9 Ma (Jiménez-Hidalgo et al., 2015). In North America, the genus is known from the Withneyan to the Arikareean, between 31.9 and 18.8 Ma (Webb, 1998a).

Diagnosis: Larger than *Hypertragulus*, subhypsodont teeth, teeth with small mesial cingula and crescent-shaped cuspids, upper molars with absence of mesostyles, p4 with paraconid (anterolingual conid), non-parallel trochleae in the astragulus (Frick, 1937; Webb, 1998a; Métais and Vislobokova, 2007; Jiménez-Hidalgo et al., 2015).

Included species: *N. loomisi* (type species), *N. fontanus*, *N. ordinatus*, and *N. planiceps*.

Notes: *Nanotragulus* is known from Oregon, South Dakota, Wyoming, Nebraska, California, Texas, and Florida. The Iniyoo local fauna record represents the southernmost known range of the genus in North America, and extends its presence by almost 1,000 km.

The age of the Iniyoo local fauna is currently under discussion. The Yolomécatl Formation, where the fossils are found, overlays the Yanhuitlán Formation, with an estimated minimal

age between 43 ± 1.2 and 40.5 ± 1.7 Ma, and conformably underlies the Cañada Maria Andesite, which has an age between 35.7 ± 1.0 and 32.9 ± 0.9 Ma (Martiny et al., 2000; Santamaría-Díaz et al., 2008). These ages and the taxonomic composition of the faunal assemblage suggest a Late Eocene age for the Iniyoo local fauna (Jiménez-Hidalgo et al., 2015, 2017), and expands the age range of *Nanotragulus* by almost 4 Ma from the Withneyan to the Chadronian NALMA.

Family Antilocapridae Gray, 1866

Subfamily "Merycodontinae" (Matthew, 1904)

Genus "*Merycodus*" Leidy, 1854

Species *"Merycodus" sabulonis* (Matthew and Cook, 1909)

Synonyms: *Merycodus necatus sabulonis* (Matthew and Cook, 1909), *Cosoryx* (*Subparacosoryx*) *savaronis* (Frick, 1937), *Cosoryx* (*Subparacosoryx*) *sabulonis* (Frick, 1937).

Range in Mexico (Figure 5): El Camarón, La Mancornada, El Gramal, and Las Ánimas, Nejapa local fauna (El Camarón Formation), Oaxaca, Sierra Madre del Sur province (Jiménez-Hidalgo et al., 1999; Jiménez-Hidalgo, 2000; Ferrusquía-Villafranca, 2003).

Age range: In Mexico, from the Barstovian (Middle Miocene), with a minimal age between 16 and 15.3 Ma (Ferrusquía-Villafranca, 2001). In North America, from the Early Hemingfordian to the Early Claredonian (Janis and Manning, 1998).

Diagnosis: When compared to *Merycodus necatus* (type species of the genus), "*M*". *sabulonis* has lower teeth less hypsodont, larger p4 with smaller lingual conids, shorter diastema, horncore shaft shorter, prongs larger, if present the burr is centrally placed, the horncore is circular to subelliptical in transversal section (Matthew and Cook, 1909; Frick, 1937; Skinner and Taylor, 1967; Janis and Manning, 1998).

Notes: "*Merycodus*" *sabulonis* was originally described as a subspecies of *Merycodus necatus*, based on a partial mandibular ramus with a complete dental series (Matthew and Cook, 1909). Later, it was recognized as a subspecies of *Cosoryx*, within the *Paracosoryx* subgenus and a partial associated skull was referred as a separate subspecies and subgenus: *Cosoryx* (*Subparacosoryx*) *savaronis* (Frick, 1937). *C. savaronis* is now considered as the same species of "*M*". *sabulonis* and a set of horncores was associated to this species (Skinner and Taylor, 1967). The status of "*M*". *sabulonis* within the *Merycodus* genus is dubious, and it depends on the identity of the original mandibular ramus and its association with the associated horncores and their morphology (Skinner and Taylor, 1967; Janis and Manning, 1998). The horncore morphology of the Nejapa fossil material is similar to *Meryceros warreni*, except in its transversal section, since the *Meryceros* horncores are flat while the *Merycodus* and *Cosoryx* are circular to subelliptical in transversal section (Janis and Manning, 1998; Jiménez-Hidalgo, 2000).

This species is known from Saskatchewan, Wyoming, Nebraska, Colorado, and New Mexico, from the Early Hemingfordian to the Earyl Claredonian (Janis and Manning, 1998). Its presence in the Nejapa local fauna extends its known range southwards in more than 2,400 km and represents one of the latest records of this species in North America.

Genus *Cosoryx* Leidy, 1869

Range in Mexico (Figure 5): Puente de Cofradía, El Mixtón, and La Pitahaya, Juchipila local fauna (Juchipila Formation), Zacatecas, Sierra Madre Occidental province (Carranza-Castañeda et al., 2013).

Age range: In Mexico from the Middle Hemphillian (Hh2), Late Miocene (Carranza-Castañeda et al., 2013). In North America, the genus is known from the Early Barstovian to the Late Claredonian, approximately from 15.8 to 9 Ma (Janis and Manning, 1998).

Diagnosis: Horncores tall and slender, shaft tilted laterally and anteriorly, with a circular to subelliptical transversal section, burr usually present near the base of the shaft, prongs elongated, subequal in size, arched and dorsally directed; anterior prongs rotated medially; when compared to *Meryceros* and *Merycodus*, the muzzle is shorter, with narrow nasals, wide and more hypsodont upper teeth, with reduced premolars (Leidy, 1869; Frick, 1937; Skinner and Taylor, 1967; Janis and Manning, 1998; Davis, 2007).

Included species: *Cosoryx furcatus* (type species), (?)*C. agilis*, *C. ilfonensis*, and *C. cerrosensis*.

Notes: The Juchipilla material consists in a partial skull with the base of both horncores (MPGJ 1633), a mandible fragment with m3-2, partial m1 and the alveolus of p4 (MPGJ 1762), a mandible with part of the m1, and the alveoli of p4-3 (MPGJ 1596), and a partial horncore (MPGJ 1634). These fossils exhibit the diagnostic features of the genus, including reduced premolars, horncore shaft tilted laterally and anteriorly, rounded in transversal section and the possible presence of a burr, located near the base of the shaft (Carranza-Castañeda et al., 2013).

Cosoryx is known from Montana, South Dakota, Wyoming, Nebraska, Nevada, Colorado, California, New Mexico and possibly Texas and Oklahoma (Janis and Manning, 1998). The Juchipilla basin *Cosoryx* extends the range of the genus in at least 1,500 km southwards, and it represents the earliest known record of this taxon, extending its geological range between 1.4 and 2.4 Ma. Other possibly record of the genus may be present at Cuicatlán, Oaxaca (Miocene), but those fossil remains are still undescribed and cannot be safely assigned to *Cosoryx* (Carranza-Castañeda et al., 2013).

Subfamily Antilocaprinae Brooke, 1876

Genus *Plioceros* Frick, 1937

Range in Mexico (Figure 5): El Mixtón, Juchipila local fauna (Juchipila Formation), Zacatecas, Sierra Madre Occidental province (Carranza-Castañeda et al., 2013).

Age range: In Mexico from the Middle Hemphillian (Hh2), Late Miocene (Carranza-Castañeda et al., 2013). In North America, the genus is known from the Late Barstovian to the Late Hemphilian, approximately from 14 to 6 Ma (Janis and Manning, 1998).

Diagnosis: Horncores laterally compressed, with a dumbbell shape in transversal section at the midshaft, posteriorly and laterally tilted, with two short prongs forked at the distal region, the anterior prong is smaller and its projected laterally, the posterior prong is larger and its apex is slightly oriented medially; p3-p4 mesolingual and posterolingual conid not connected, moderate-sized talonid of m3, relatively long diastema (Frick, 1937; Janis and Manning, 1998).

Included species: *Plioceros blicki* (type species), *P. dehlini*, and *P. flobairi*.

Notes: The *Plioceros* material from the Juchipila local fauna comprises a partial skull with the base of both horncores (MPGJ 1627) and an isolated horncore (MPGJ 1754) (Carranza-Castañeda et al., 2013). Its large size distinguish the Juchipila material from smaller and similar antilocaprids such as *Subantilocapra* (Webb et al., 2008). Also, the Juchipila horncores show a flat transversal section with a wide base which is one characteristic of *Plioceros* (Frick, 1937; Janis and Manning, 1998; Carranza-Castañeda et al., 2013) and distinguish it from other flat horned antilocaprines such as *Proantilocapra* and *Ottoceros*, and from the wide, but posteriorly twisted base of the horncore of *Sphenophalos* (Janis and Manning, 1998).

Plioceros is known from Montana, South Dakota, Nebraska, Kansas, California, and New Mexico (Janis and Manning, 1998). Its presence in the Juchipila local fauna extends its known range southwards in about 1,500 km.

Genus *Sphenophalos* Merriam, 1909

Range in Mexico (Figure 5): El Resbalón, Juchipila local fauna (Juchipila Formation), Zacatecas, Sierra Madre Occidental province (Carranza-Castañeda et al., 2013).

Age range: In Mexico from the Middle Hemphillian (Hh2), Late Miocene (Carranza-Castañeda et al., 2013). In North America, its exclusively reported for the Hemphillian, from 8.8 to 5.2 Ma (Janis and Manning, 1998).

Diagnosis: Horncores large and transversally compressed, posterolaterally positioned, the base width equals and sometimes exceeds the length of the upper curve of the orbits, in transversal section the base has a wedge shape, shaft twisted laterally along posterior margin forming a flange, the anterior prong is more compressed than the posterior prong,

cheek teeth almost as hypsodont as in *Antilocapra* (Merriam, 1909; Janis and Manning, 1998).

Included species: *Sphenophalos nevadanus* (type species) and *S. middleswarti*.

Notes: The Juchipila material consists in a partial left horncore (MPGJ 2042) which displays several diagnostic characters, including a transverse compression, the anterior prong is smaller than the posterior, and the posterior margin is twisted laterally forming a notorious flange (Carranza-Castañeda et al., 2013).

Sphenophalos is known from Oregon, Nevada, California, Nebraska, and Arizona (Janis and Manning, 1998). The record from Juchipila extends the range of this genus southwards in approximately 1,700 km, and its within its previously known geochronological distribution.

Genus *Texoceros* Frick, 1937

Synonyms: *Dorcameryx optimae* (Reed and Longnecker, 1932), *Capromeryx texanus* (Hesse, 1935).

Range in Mexico (Figure 5): La Plegaria, Tepexi del Río Basin, Hidalgo, Volcanic Axis province (Padilla-Gutiérrez, 2004; Carranza-Castañeda, 2006) and Coecillos, Arroyo de Emilio, Rancho el Ocote (Rhino layer), Rinconada, and María Elena sites, San Miguel de Allende local fauna (Rancho Viejo Beds), Guanajuato, South Plateau province (Jiménez-Hidalgo, 2005; Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013).

Age range: In Mexico from the late to latest Hemphilian (Hh3 to Hh4), Late Miocene (Padilla-Gutiérrez, 2004; Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013). In North America, its known from the Early late Hemphilian to the Late Hemphilian, approximately from 8.8 to 5.2 Ma, and with a possible record in the Benson local fauna (St. David Formation, Arizona) from the Early Blancan (Janis and Manning, 1998).

Diagnosis: Horncores with two prongs with a short shaft, anterior prong slightly smaller than the posterior prong, anterior prong laterally compressed with a subelliptical transversal section and rotated laterally, posterior prong with a circular transversal section and rotated medially, diastema twice the length of the premolar row, in most cases m3 lobe expanded (Hesse, 1935; Frick, 1937; Janis and Manning, 1998; Jiménez-Hidalgo, 2005).

Included species: *Texoceros guymonensis* (type species), *T. altidens*, *T. edensis*, (?)*T. minorei*, and (?)*T. vaughani*.

Notes: *Texoceros* was originally described by Frick (1937) under the species *T. guymonensis* from a partial skull with the base of the horncores, part of the skull roof and the dorsal part of the orbit (FM 31675). Later Dalquest (1983) suggested that *T. guymonensis* had no diagnostic characters to be consider as the type species for the genus, a view supported by Janis and Manning (1998). Nevertheless, *T. altidens* (previously known

as *Merycodus altidens*) was described from a lower jaw fragment and isolated upper molars (Matthew, 1924), and due to the lack of horncores in its original description, we consider that *T. guymonensis* should be consider as the type species of the genus, a view supported by Byrd (2007).

The *Texoceros* material from La Plegaria (IGCU 12151) consists in a partial left jaw with the m3, and its referred to this genus on the basis of a streamlined jaw, a short diastema and by the measurements of the alveoli and the preserved molar (Padilla-Gutiérrez, 2004). On the other hand, the material from San Miguel de Allende comprises several upper and lower teeth (IGCU 5633, 12239, 12240, 5631, 12241, 12242, 11048) and jaw fragments (IGCU 12238, 5649) that are referred to *Texoceros* in the basis of its size (smaller than *Hexobelomeryx*, and larger than *Subantilocapra*) and its morphology, such as a p3 with shallow posterior valley, a narrow p4 with deep anterior valley, poor developed stylids in lower molars, P4 with a well-developed posterior style, well-developed mesostyle in M1, well-developed parastyle and mesostyle in M2 and M3, and a M3 without a talon (Jiménez-Hidalgo, 2005). These records of *Texoceros* in Mexico represent its southernmost known distribution and extends the geographical range of the genus in about 1,400 km.

Genus *Subantilocapra* (Webb, 1973)

Species *Subantilocapra garciae* (Webb, 1973)

Synonyms: *Antilocapra* (*Subantilocapra*) *garciae* (Webb, 1973), *Sphenophalos* sp. (Richards and McCrossin, 1991).

Range in Mexico (Figure 5): María Elena and Coecillos sites, San Miguel de Allende local fauna (Rancho Viejo Beds), Guanajuato, South Plateau province (Jiménez-Hidalgo, 2005; Carranza-Castañeda et al., 2013).

Age range: In Mexico from the early Late to the latest Hemphilian (Hh3 to Hh4), Late Miocene (Jiménez-Hidalgo, 2005). In North America is known only from the latest Hemphilian (Hh4) (Webb, 1973; Janis and Manning, 1998; Webb et al., 2008).

Diagnosis: Horncores, elongated and laterally compressed, with the anterior region narrower than the posterior region; wide shaft, slightly curved laterally along its main axis, convex in the medial side and flat in the lateral side; slight bifurcation at the tip, anterior prong smaller and projecting anteriorly from the main axis of the horncore, posterior prong larger and in line with the axis of the shaft or slightly pointing backwards; cheek teeth less hypsodont than in *Antilocapra*, with persistent fossae, with well-developed styles, but weak ribs; the anterior and mesolingual conids in the premolars does not close to form an anterior fossa, posterior fossa present in advanced wear stages; lower teeth with poorly-developed (almost flat) stylids and ribs (Webb, 1973; Janis and Manning, 1998; Webb et al., 2008).

Notes: *Subantilocapra garciae* was originally described as a subgenus of *Antilocapra* (Webb, 1973). Later it was considered as a subjective junior synonym of *Sphenophalos*

(Richards and McCrossin, 1991; Janis and Manning, 1998). Recently, its status as a valid species has been supported on the basis of a smaller size than *Sphenophalos* and its distinctive teeth and horncore morphology (Webb et al., 2008).

The Mexican fossil material of *Subantilocapra* consists on fragments of the maxilla (IGCU 12243, 5625) and isolated upper teeth (IGCU 5943, 5634, 5635, 5644, 12244, 5642, 5624, 12245, 12246, 12247), which bear the diagnostic characteristics of upper molars described before (Jiménez-Hidalgo, 2005). We assigned this material to the only species described for the genus: *S. garciae*. Outside Mexico, this genus is only recorded at the Palmetto and Gardinier mines, Upper bone Valley, Florida (Webb et al., 2008), its presence in San Miguel de Allende local fauna extends its range in more than 2,000 km southwards.

Genus *Hexobelomeryx* Furlong, 1941

Species *Hexobelomeryx fricki* Furlong, 1941

Range in Mexico (Figures 5 and 6): Arroyo Huachin, Arroyo de las Burras, Arroyo de los Poños, Rincón, Yepómera 5 and 6 sites, Yepómera local fauna, Chihuahua, Sierra Madre Occidental province (Furlong, 1941; Lance, 1950; Barrios-Rivera, 1985; Lindsay et al., 2006); Matachic 1, and Arroyo de los Gises, Matachic local fauna, Chihuahua, Sierra Madre Occidental province (Furlong, 1941; Lindsay et al., 2006); Los Vélez, Colotlán, Jalisco, Sierra Madre Occidental province (Solorzano, 2002; Padilla-Gutiérrez, 2004; Carranza-Castañeda, 2006); Teocaltiche, Unit A (Basal Unit), Jalisco, South Plateau province (Montellano-Ballesteros, 1997); Landa de Matamoros, Querétaro, Sierra Madre Oriental province (Carranza-Castañeda, 2006); Potrero de Zietla, Tehuichila, Zacualtipán Basin, Hidalgo, Sierra Madre Oriental province (Carranza-Castañeda and Miller, 1993; Carranza-Castañeda, 2006); Tecolotlán, and Juchitlán, Jalisco, Volcanic Axis province (Solorzano, 2002; Padilla-Gutiérrez, 2004); La Plegaria, Tepexi del Río Basin, Hidalgo, Volcanic Axis province (Padilla-Gutiérrez, 2004; Carranza-Castañeda, 2006); Rancho El Ocote, Arroyo La Carreta, Arrastracaballos, Coecillos, Ferrocarril 2, Perros Bravos, Rancho San Martín, La Rinconada, La Presa, Porkchop, Cara Cara, Earthwatch, Arroyo Tepalcates, and Candado sites, San Miguel de Allende local fauna (Rancho Viejo Beds), Guanajuato, South Plateau province (Carranza-Castañeda and Ferrusquía-Villafranca, 1978; Dalquest and Mooser, 1980; Miller and Carranza-Castañeda, 1984; Carranza-Castañeda, 2006; Jiménez-Hidalgo and Carranza-Castañeda, 2011).

Age range: from the Late Early Hemphilian (Hh2) to the Middle Blancan (Bl3), Late Miocene to Late Pliocene (Jiménez-Hidalgo and Carranza-Castañeda, 2011).

Diagnosis: Horncores with three tapering prongs (resulting from the division of the posterior prong into two unequal prongs); anterior prong smaller and emerges from the main shaft from the middle region, posterior prongs less divergent than the anterior prong, the middle prong is directed medially, the anterior and posterior prongs are directed slightly laterally, the base of the shaft is subelliptical in transversal section and is located above the

orbits, but displaced medially; P4 with well-developed styles, while the rib of the mesolabial crista is present only in early stages of wear, unlike *Anilocapra*; m3 with three major lobes, and a small variable fouth lobe; rami relatively short, large diastema, deep jaw, with the longitudinal axis of the diastema below m3 (Furlong, 1941; Janis and Manning, 1998; Jiménez-Hidalgo and Carranza-Castañeda, 2011).

Notes: *Hexobelomeryx fricki* is almost unique to Mexico, its only reliable record outside Mexican territory belongs to the Late Hemphilian of the Goodnight Beds of Texas-Oklahoma, and a second dubious record is reported for the Golgotha Watermill Pothole Quarry, from the Late Hemphilian of Nevada (Janis and Manning, 1998). Considering this record, the Mexican *Hexobelomeryx* bearing sites are separated from the US record by more than 900 km southwards.

In Mexico, *H. fricki* is identified as cf. in Teocaltiche (Montellano-Ballesteros, 1997), Landa de Matamoros (Carranza-Castañeda, 2006; Lindsay et al., 2006), Colotlán (Solorzano, 2002), and Tehuichila (Carranza-Castañeda and Miller, 1993), but since *Hexobelomeryx* has only one recognized species, we consider all these records as *Hexobelomeryx fricki*.

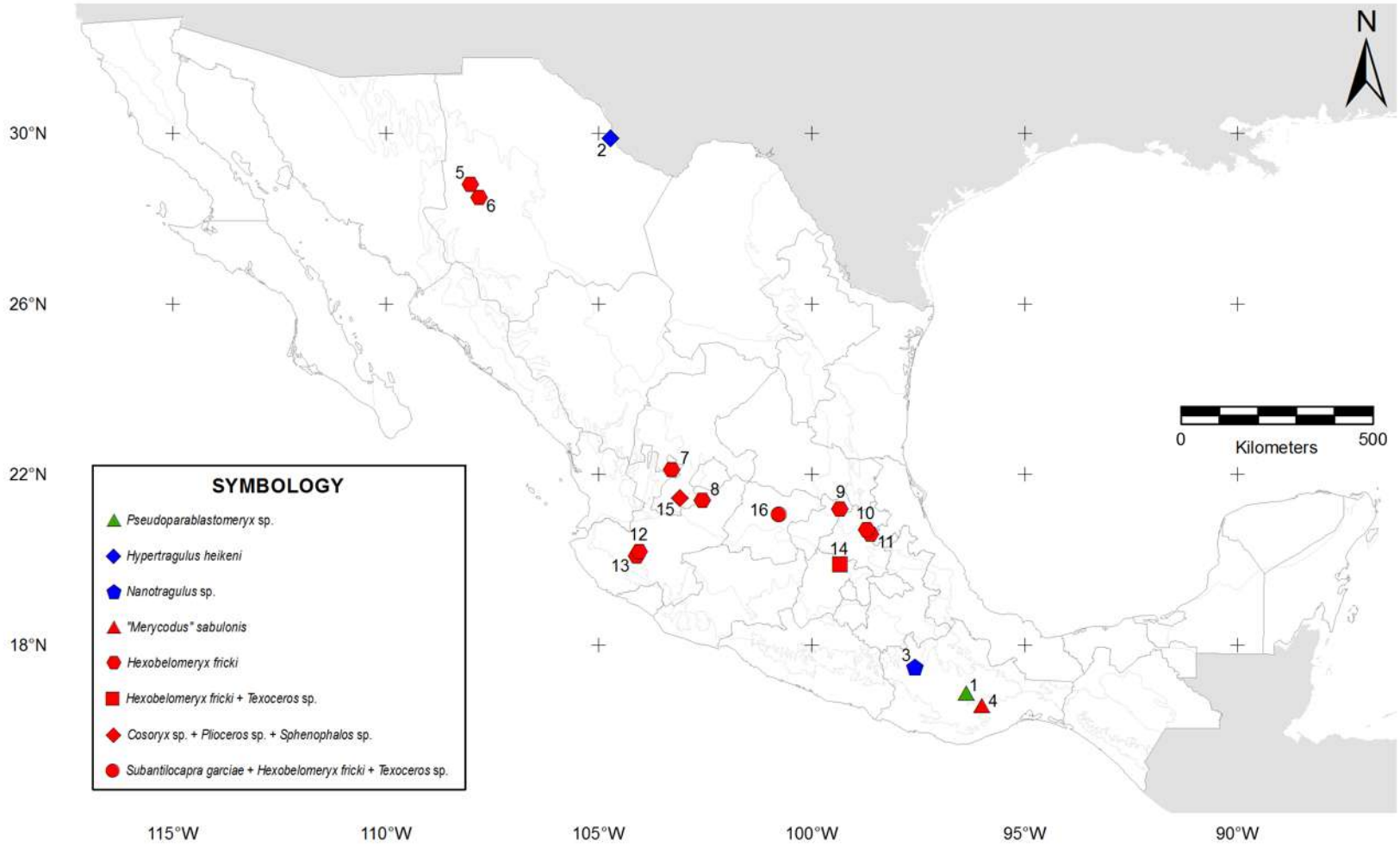

Figure 5. Distribution map of fossil ruminant-bearing localities from the Eocene to the Miocene. Green: Leptomerycidae, blue: Hypertragulidae, red: Antilocapridae. (1) Matatlán, (2) Rancho Gaitán, (3) Iniyoo, (4) El Camarón, (5) Yepómera, (6) Matachic, (7) Colotlán, (8) Teocaltiche, (9) Landa de Matamoros, (10) Tehuichila, (11) Potrero de Zietla, (12) Tecolotlán, (13) Juchitlán, (14) La Plegaria, (15) Juchipila, (16) San Miguel de Allende.

Genus *Capromeryx* Matthew, 1902

Species *Capromeryx tautonensis* Morgan and Morgan, 1995

Range in Mexico (Figure 6): El Tanque, Arrastracaballos, Ferrocarril 2, and Cara Cara sites, San Miguel de Allende local fauna (Rancho Viejo Beds), Guanajuato, South Plateau province (Jiménez-Hidalgo et al., 2004). In North America is known from the Kiem Formation, Nebraska, and the Ringold Formation, Tauton local fauna, Washington (Morgan and Morgan, 1995; Janis and Manning, 1998).

Age range: In Mexico from the Blancan III, approximately between 3.6 and 3.3 Ma (Jiménez-Hidalgo and Carranza-Castañeda, 2001); in North America from the Blancan IV (Morgan and Morgan, 1995).

Diagnosis: Large species of *Capromeryx*, base of the horncores large, unconstricted and placed above the orbit, posterior porng larger than the anterior one, posterior prong subcircular in transversal section, posterior margin of the posterior prong slightly constrained and straight; p4 with a deep posterolingual conid (when heavily worn, unites with the mesolingual conid to form a fossa), M3 without a posterior heel (Morgan and Morgan, 1995).

Notes: *Capromeryx tautonensis* is only known in two localities outside Mexico, from Nebraska and Washington (Janis and Manning, 1998), the San Miguel de Allende record is the southernmost record of *C. tautonensis* and extends its range in about 2,400 km southwards. This Mexican record is also the earliest for the species and the genus, and represents the first genus of antilocaprid besides *Hexobelomeryx* in Mexico reported for the Pliocene (Jiménez-Hidalgo and Carranza-Castañeda, 2001).

Species *Capromeryx furcifer* Matthew, 1902

Synonyms: *Capromeryx minimus* (Meade, 1942).

Range in Mexico (Figure 6): El Golfo de Santa Clara, El Golfo local fauna, Arroyo Diablo Formation (?), Sonora, Sonoran province (Croxen et al., 2007; White et al., 2010).

Age range: In Mexico is known only for the late Irvingtonian (Ir2) (Croxen et al., 2007). In North America from the late Irvingtonian to the Rancholabrean (Janis and Manning, 1998; White and Morgan, 2011).

Diagnosis: Small pronghorn, with paired horncores emerging from a common shaft located above the orbits, and slightly compressed laterally; prongs are straight, parallel, and separated near the base of the shaft, tilted anteriorly (but not curved forwards as *C. minor*); posterior prong subcircular in transversal section, considerably larger than the anterior, with a deep posterior sulcus, and a usually present lateral sulcus near the base, and lateral constrictions near the apex; anterior prong small (in Rancholabrean specimens is so reduced that is almost lost), with an anterior margin rounded at the base, and usually a lateral sulcus;

the fronto-parietal suture form a procumbent posterior ridge; the p4 is long, simple and trenchant, lacking the mesolingual conid; the cheek teeth are as hypsodont as in *Antilocapra americana*, but about 2/3 its size (Matthew, 1902; White and Morgan, 2011).

Notes: White and Morgan (2011) reported and described specimens of *Capromeryx furcifer* from the late Rancholabrean of New Mexico, and they synonymized this species with *C. minor*. Nevertheless, we consider that the size, and diagnostic characteristics of *C. furcifer* described early in this work (especially those of the horncores), are different enough from those of *C. minor* (see below) to separate them at specific level, thus rejecting those species as synonyms, a view supported by Bravo-Cuevas et al. (2013).

Besides Hay Springs, Nebraska (Matthew, 1902), its type locality, *Capromeryx furcifer* is recorded at Angus, Nuckolls County (Martin, 1969), Gordon Fossil Quarry, and Rushville Quarry, Nebraska (Hintlian, 1975); Cragin Quarry, Kingsdown Formation, Kansas (Hibbard and Taylor, 1960), Fowlkes Cave (Dalquest and Stangl, 1967), Slaton Quarry, Texas (Dalquest, 1967), Tramperos Creek fauna, Union County; Shelter Cave, Doña Ana County; Pendejo Cave, Otero County, New Mexico (White and Morgan, 2011). The records of Muskox Cave and Slaughter Canyon (based upon the *C. furcifer* and *C. minor* synonymy) reported by White and Morgan (2011) could not be corroborated by us, and are therefore, omitted. Its presence in El Golfo local fauna represents the most western record of the species by more than 700 km.

Species *Capromeryx minor* Taylor, 1911

Synonyms: *Capromeryx mexicana* (Furlong, 1925), *Breameryx minor* (Furlong, 1946), *Breameryx mexicana* (Furlong, 1946), *Capromeryx mexicanus* (Morgan and Morgan, 1995).

Range in Mexico (Figure 6): San Clemente de Térapa (Mead et al., 2006), La Botana, Tesopaco local fauna (Mead et al., 2007), and La Playa, Sonora, Sonoran province (White et al., 2010); Rancho La Brisca, Sonora, Sierra Madre Occidental province (Van Devender et al., 1985); Cueva Jiménez, Chihuahua, North Plateau province (Messing, 1986); Rancho La Amapola, El Cedral (Álvarez et al., 2012), Cueva La Presita (Polaco and Butrón, 1997), San Luis Potosí, South Plateau Province; Arroyo el Cedazo, El Cedazo local fauna (Tacubaya Formation), Aguascalientes, South Plateau province (Mooser and Dalquest, 1975); El Barrio and Barranca del Berrendo (Bravo-Cuevas et al., 2013), Hidalgo, South Plateau and Sierra Madre Oriental provinces respectively; La Mixtequilla, Veracruz, Gulf of Mexico province (Polaco, 1995); La Cinta-Portalitos, Michoacán-Guanajuato (Díaz-Sibaja, 2013; Díaz-Sibaja et al., 2014a), Tequixquiac, Tajo de Tequixquiac local fauna (Becerra Formation), State of Mexico (Freudenberg, 1922; Furlong, 1925; Maldonado-Koerdell, 1955), Hueyatlaco, Valsequillo local fauna, Puebla (Pichardo, 1997), Volcanic Axis province.

Age range: Restricted to the Rancholabrean, Late Pleistocene (Janis and Manning, 1998).

Diagnosis: Smallest of pronghorns, paired horncores rising from the base of a common shaft, the shaft is compressed laterally and is located above the orbits, slightly displaced to its posterior margin; the prongs are vertical and parallel, anterior prong smaller than the posterior prong, slightly displaced medially, with a sinuous axis, a cylindrical (and sometimes triangular) transversal section, with a flat posterior margin; posterior prong slightly curved forward, subcircular in transversal section, with a flat lateral side, a deep posterior sulcus and a shallow basal fossa in the posterolateral margin; fronto-parietal suture forming a well-defined ridge arched dorsally, cheek teeth hypsodont and small, with a reduced premolar row, M3 with a well-developed heel (Chandler, 1916; Furlong, 1925, 1946; Bravo-Cuevas et al., 2013).

Notes: *Capromeryx mexicana* (occasionally misspelled as *C. mexicanus*) was originally described by Furlong (1925) from the skull and a large part of an allegedly adult individual (holotype UCMP 26648), and a partial skull and limb bones of an allegedly immature individual (paratype UCMP 26649). The immature status of the paratype is based on the presence of physis (growth lines) in the humeri, radii, femora, tibiae, metapodials, proximal region of the proximal phalanges, and the tuberosity of the calcaneus. Nevertheless, when dental wear is taking into account (Lubinski, 2001; Jiménez-Hidalgo and Carranza-Castañeda, 2011), the holotype display a stage V tooth wear stage, correlated with a very old individual of more than 9 years old, and the paratype display a stage III, corresponding with a mature individual of 3.3 years old. Also, the paratype display pathological features not mentioned by Furlong, such as twisted bones and bone outgrowths in the diaphysis, which correlates with malnutrition and osteoid osteomas (Waldron, 2009). The physis present in this individual may be due to its malnutrition or a neotenic character retention. Finally, the dental characters of *C. mexicana* are not diagnostic (Hibbard and Taylor, 1960), and the allegedly horncores diagnostic characters of this species can be found in several specimens of *C. minor* from Rancho La Brea, California (White and Morgan, 2011; Bravo-Cuevas et al., 2013). Thus, we consider *C. mexicana* as a junior synonym of *C. minor* (1999, 2012: Article 23).

The fossil material from Térapa, La Botana, Rancho La Brisca, Cueva Jiménez, Rancho La Amapola, Cueva La Presita, and La Playa are stated as cf. *Capromeryx*, *Capromeryx* sp., *Capromeryx* cf. *minor* or *Capromeryx mexicana*, but since *C. minor* is the only Rancholabrean species of small pronghorn in Mexico, we decided to include those records as *Capromeryx minor*.

In the United States, *Capromeryx minor* is known from Blackwater Draw, Formation, Nebraska, Ingleside, Texas (Davis, 2007), Schuilling Cave (Jefferson, 1991a), Lone Tree Point (Rodeo Pecten Point), McKittrick-Asphalto (Jefferson, 1991b), Rancho La Brea (its type locality), California (Taylor, 1911), and a number of New Mexico sites reported by White and Morgan (2011). The Mexican record of this species form a continuum, connecting the Pacific Coast and Great Plains records, extending as south as the Valsequillo local fauna, in Puebla.

Genus *Stockoceros* (Frick, 1937)

Species *Stockoceros conklingi* (Stock, 1930)

Synonyms: (?)*Tetrameryx conklingi* (Stock, 1930), *Tetrameryx onurosagris* (Roosevelt and Burden, 1934), *Stockoceros onurosagris* (Roosevelt and Burden, 1934).

Range in Mexico (Figure 6): El Golfo de Santa Clara, El Golfo local fauna, Arroyo Diablo Formation (?) (Lindsay, 1984; Croxen et al., 2007) and San Clemente de Térapa, Sonora, Sonoran province (Mead et al., 2006); Mina de San Antonio (Bravo-Cuevas et al., 2013) and Cueva La Presita, San Luis Potosí (Polaco and Butrón, 1997; Arroyo-Cabrales and Polaco, 2003), Arroyo el Cedazo, El Cedazo local fauna (Tacubaya Formation), Aguascalientes (Mooser, 1958; Mooser and Dalquest, 1975), El Barrio and San Agustín Tlaxiaca? (Bravo-Cuevas et al., 2009b, 2013), South Plateau province; San Josecito Cave, Nuevo León, Sierra Madre Oriental province (Furlong, 1943; Arroyo-Cabrales and Johnson, 2008); La Mixtequilla, Veracruz, Gulf of Mexico province (Polaco, 1995); La Cinta-Portalitos, Michoacán-Guanajuato (Díaz-Sibaja et al., 2014a), Tequixquiac, Tajo de Tequixquiac local fauna (Becerra Formation) (Maldonado-Koerdell, 1955) and Los Reyes La Paz, State of Mexico (García, 1975), Hueyatlaco, Valsequillo local fauna, Puebla, Volcanic Axis province (Pichardo, 1997).

Age range: Restricted to the Rancholabrean, Late Pleistocene (Kurtén and Anderson, 1980; Davis, 2007).

Diagnosis: Medium size pronghorn (larger than *Capromeryx* and smaller than *Antilocapra* and *Tetrameryx*), with paired, subequal, and divergent horncores rising from a common supraorbital base displaced to the posterior margin of orbit; prongs subcircular to elliptical in transversal section and flared laterally, the anterior prong is displaced more laterally and possess a small sulcus in the lateral margin; near the base, the posterior prong is slightly flat in its lateral margin and occasionally presents a small sulcus; as age advances, the prongs are more divergent and the posterior prong tends to grow larger and curves forwards; a well-defined supraorbital foramen is present near the anterior base of the prongs; antorbital vacuity narrower than *Antilocapra*; proximal margin of the nasals convergent an placed more anteriorly than in *Antilocapra*; ramus less curved ventrally, with long diastema and an a greater angle of divergence than *Antilocapra*; teeth smaller and more hypsodont than *Antilocapra* and *Tetrameryx*, styles are not as strongly developed as in *Antilocapra*, P2 with strongly developed medial fold and lacking a fossa, lower premolars less hypsodont than *Antilocapra* and with well-defined double roots; m3 with either 3 or 4 lobes; tibiae larger than *Antilocapra* (Roosevelt and Burden, 1934; Skinner, 1942; Kurtén and Anderson, 1980).

Notes: *Stockoceros conklingi* was originally described as *Tetrameryx*(?) *conklingi* by Stock (1930) from Shelter Cave, New Mexico, and it was referred to *Tetrameryx* tentatively, as Stock suspected that this new species could have belonged to a new genus. Before the generic status of *T.*(?). *conklingi* can be examined, Roosevelt and Burden (1934) described a second, related species: *Tetrameryx onurosagris* from a skull with both horncores, and

P4-M3 dental series, from Sonoita Cave, Arizona. Afterwards, Frick (1937) created *Stockoceros* as a subgenus of *Tetrameryx*, establishing *T.*(?) *conklingi* as the subgenotypic species, and *T. onurosagris* as the only other species included in the subgenus. This view was supported by Colbert and Chafee (1939), who distinguished between *Tetrameryx sensu* lato (*T.*(?) *conklingi* and *T. onurosagris*), and *Tetrameryx sensu stricto* (*T. shuleri*). Finally, Skinner (1942) raised the subgenus *Stockoceros* to the genus category, and established *S. conklingi* from Papago Springs as the genotypic species.

The main differences between *S. conklingi* and *S. onurosagris* are related to their size and the angle of divergence between prongs, being *S. onurosagris* larger and with more divergent prongs (Roosevelt and Burden, 1934; Skinner, 1942; Kurtén and Anderson, 1980). Nevertheless, in a study with a large sample of both species, from San Josecito Cave (Nuevo León, México), Shelter Cave (New Mexico), and Papago Springs (Arizona), Furlong (1943) suggested that those differences may be due to ontogenetic variation. This view was supported by Bravo-Cuevas et al. (2013). Finally, the holotype of *S. onurosagris* (FM 22488) display a dental wear pattern in stage IV, corresponding with a fully mature adult individual between 3.5 and 4.3 years old (Lubinski, 2001; Jiménez-Hidalgo and Carranza-Castañeda, 2011), while the holotype of *S. conklingi* (LACM 174), corresponds with a juvenile individual (Furlong, 1943, plate I, figs. 2 and 2a). The differences between the biological age of the holotypes support the hypothesis of ontogenetic differences, rather than specific ones. Thus, we consider *S. onurosagris* as a junior synonym of *S. conklingi* (ICZN, 1999: Article 23).

The original material from El Cedazo IGM 5268 (originally as IGM 56-204), was identified as *Tetrameryx* (Mooser, 1958), despite being reassigned to *S. conklingi* by Mooser and Dalquest (1975), and still identified as such in the collection of the Geology Institute (UNAM), it represents a young adult of *S. conklingi*. The record of San Agustín Tlaxiaca may be the same as El Barrio. In Valsequillo, the species is originally reported as *T. conklingi* (Pichardo, 1997). The Mexican records of this species from El Golfo and Térapa connect the records from New Mexico and Arizona, forming a continuum.

Genus *Tetrameryx* Lull, 1921

Species *Tetrameryx shuleri* Lull, 1921

Synonyms: *Tetrameryx mooseri* (Dalquest, 1974), *Tetrameryx tacubayensis* (Mooser and Dalquest, 1975).

Range in Mexico (Figure 6): Rancho La Brisca, Sonora, Sierra Madre Occidental province (Van Devender et al., 1985); Arroyo San Francisco, El Cedazo local fauna (Tacubaya Formation), Aguascalientes, South Plateau province (Dalquest, 1974; Mooser and Dalquest, 1975); La Mixtequilla, Veracruz, Gulf of Mexico province (Polaco, 1995); Tecolotlán, Zacoalco (Solorzano, 2002), and Lago de Chapala (Chapala local fauna), Jalisco (Downs, 1956; Rufolo, 1998; Solorzano, 2002; Lucas, 2008a), La Piedad-Santa Ana and La Cinta-

Portalitos, Michoacán-Guanajuato (Díaz-Sibaja et al., 2014a), Hueyatlaco, Valsequillo local fauna, Puebla, Volcanic Axis province (Pichardo, 1997); Los Tanques, Zacatecas, Pacific Coast province (Lozano-Ramos et al., 2006).

Age range: Restricted to the Rancholabrean, Late Pleistocene (Kurtén and Anderson, 1980; Davis, 2007).

Diagnosis: Large pronghorn, almost the same size of *Antilocapra americana*; paired, unequal, and divergent horncores rising from a common supraorbital base (shaft) displaced to the posterior margin of orbit; posterior prong considerably larger (approximately >250%) than the anterior prong; posterior prong with a circular to subcircular transversal section, anterior prong with subcircular to elliptical transversal section; anterior prong with lateral non-terminal sulcus of variable length, generally restricted to the base; posterior prong with a shallow groove, laterally placed in the base, and anteriorly placed as it closes to the apex of the prong; cheek teeth as large as in *Antilocapra*, and with weak styles (except for M3 mesostyle), M2-M3 slightly larger (Lull, 1921; Kurtén and Anderson, 1980; Janis and Manning, 1998).

Notes: The material from Rancho La Brisca, Tecolotlán, and Zacoalco is referred as *Tetrameryx* sp., but since *Tetrameryx shuleri* is the only known Rancholabrean valid species, we decided to include these records as *T. shuleri*.

Dalquest (1974), and Mooser and Dalquest (1974) described two news species of *Tetrameryx* for the Rancholabrean of El Cedazo local fauna, in Aguascalientes, Mexico: *T. mooseri* (holotype FC 624) and *T. tacubayensis* (holotype FC 615) respectively. These species are not recorded anywhere else, but in the Arroyo San Francisco site, and are not represented by any other horned specimens rather than the holotypes, and questionable associated cranial remains and isolated teeth (found as far from the holotypes as 4 km). The diagnostic characters defined for each of these species are variations in the lateral sulcus of the posterior prong, and the divergence angle between prongs. As noted by other authors, the angle of divergence between prongs of four-horned antilocaprids varies with age, and cannot be used as a diagnostic character (Lull, 1921; Furlong, 1943). For example, the angle of divergence is greater in *T. tacubayensis*, which is regarded as larger than other *Tetrameryx* species, this agrees with the hypothesis of *T. tacubayensis* as an old individual, while the holotype of *T. shuleri* (SMU 60004) is regarded as a young individual (Lull, 1921). Besides, the external sulcus is variable and highly modified and thus, is not consider diagnostic (Janis and Manning, 1998). The holotype of *T. tacubayensis* display this sulcus only at the base, as the holotype of *T. shuleri* (Lull, 1921). Given this evidence, we consider *T. mooseri* and *T. tacubayensis* as junior synonyms of *T. shuleri* (ICZN, 1999: Article 23).

Genus *Antilocapra* (Ord, 1815)

Species *Antilocapra americana* (Ord, 1815)

Synonyms: *Antilope americanus* (Ord, 1815), *Antilope furcifer* (Hamilton-Smith, 1827), *Capra americana* (Richardson, 1829), *Antilocapra anteflexa* (Gray, 1855), †*Neomeryx finni* (Parks, 1925).

Range in Mexico (Figure 6): Mina, Nuevo León, (Franzen, 1993, 1994) and Cueva Jiménez, Chihuahua, both in the North Plateau province (Messing, 1986; Arroyo-Cabrales and Polaco, 2003).

Age range: In Mexico is known only for the Pleistocene(?)-Holocene (see discussion below). In North America, its known only from the Pleistocene to the present (Janis and Manning, 1998; Davis, 2007).

Diagnosis: Large species of pronghorn, with a large, undivided horncore; supraorbital placed shaft, displaced to the posterior margin of the orbits; the anterior prong is vestigial and its preserved as a lump in the anterior region of the posterior prong, and its separated of it by a shallow sulcus; posterior prong larger and bladelike, with the posterior region larger and extending narrowing to the tip; horncore triangular in transversal section; sexually dimorphic, the females display shorter horncores; highly hypsodont teeth, including premolars; upper premolars with well-developed styles and a "mesostyle"; lower premolars with poorly-developed double roots, p4 with connected conids, forming a persistent fossa; M3 with poorly-developed metastyle, m3 with 4 lobes; absence of digits II and V (O'Gara, 1978; Kurtén and Anderson, 1980; Janis and Manning, 1998; Davis, 2007).

Notes: *Neomeryx finni* was described by Parks (1925) based on several isolated teeth in which, the only diagnosable character was the presence of a fourth "lobe" in the distal region of the m3. Nevertheless, this character is not diagnostic, as it appears in very old individuals (>9 years old) of *Antilocapra americana* (Lubinski, 2001), such as the one described by Parks. Thus, we consider *N. finni* as a junior synonym of *A. americana* (ICZN, 1999: Article 23).

The fossil records of *Antilocapra americana* in Mexico are dubious. Some of them belong to the Holocene, rather than the Pleistocene. The caves CM68 and CM37, located at the east and west respectively of the Cuatro Ciénegas basin, Coahuila belong to the Holocene (Gilmore, 1947). Additionally, the Coxcatlan Cave (Puebla) bears *A. americana* in three different zones (Flannery, 1967); nevertheless, the oldest dates of the cave indicate a maximum age of 7 ka BP, thus belonging to the Holocene. Other records are highly questionable as well, such as the cf. *Antilocapra americana* from Laguna de la Media Luna, San Luis Potosí, identified from a partial jaw ramus without teeth (HJ73-166) and an incomplete metacarpal (HJ73-154) by Hernández-Junquera (1977). These remains are not diagnostic and are referred to *Antilocapra* by its general morphology and size, which is the same as for *Tetrameryx shuleri* for the referred specimens. As no radiometric age or stratigraphic control is known for the Laguna de la Media Luna, the antilocaprid remains and age are dubious. In other instances, *Antilocapra* is recorded, but no figures are presented, and the fossil material and specific locality are now lost. Such is the case for *Antilocapra* sp. nov. reported for the Valley of Mexico (Freudenberg, 1921, 1922).

The two records presented in this work have some issues too. The most reliable is the one from Mina, where at least 3 individual fossils were assigned to this species, and are known from the same beds as common Late Pleistocene (Rancholabrean) fauna, such as *Canis dirus*, *Equus conversidens*, and *Camelops hesternus* (Franzen, 1994). But in this work those specimens are not referred to any specific or diagnostic elements, and could not be tracked by us to corroborate its identity. Finally, the Cueva Jiménez site have some issues too. This cave site was originally described as Late Pleistocene-Holocene, but no stratigraphic control is presented and the remains of *A. americana* are not described (Messing, 1986). Thus, we recommend caution when considering *A. americana* as a Rancholabrean species with fossil record in Mexico.

Antilocapridae indet.

Some antilocaprids with no specific determination have being reported for Mexico; from Rancho las Tunas (Early Blancan), Baja California Sur (Miller, 1980); El Golfo de Santa Clara (Irvingtonian), Sonora (Lindsay, 1984); and La Botana (Rancholabrean), Marlett Locality (Desemboque de los Seris, undetermined age), and Quitovac (Irvingtonian-Rancholabrean?), Sonora (White et al., 2010). Also, White et al. (2010) reported from the El Golfo, Sonora, a new species of antilocaprid (Antilocapridae gen. et sp. nov.) yet to be described formally. These records were not mapped, and they were not included in our analyses.

Family Bovidae Gray, 1821

Subfamilia Caprinae (Gray, 1821)

Genus *Ovis* Linnaeus, 1758

Species *Ovis canadensis* Shaw, 1804

Synonyms: *Ovis cervina* (Desmarest, 1804), *O. montana* (Schreber, 1804), *O. pygargus* (Hamilton-Smith, 1827), *O. californianus* (Douglas, 1829), *O. nelsoni* (Merriam, 1897), *O. mexicanus* (Merriam, 1901a), *O. sheldoni* (Merriam, 1916), *O. catclawensis*? (see discussion below) (Hibbard and Wright, 1956).

Age and range in Mexico (Figure 6): It is found only at the Holocene of Cuatro Ciénegas Basin (Gilmore, 1947), and Cueva de la Candelaria, Coahuila, North Plateau province (Aveleyra-Arroyo de Anda, 1956), as well as in Tula, Hidalgo, Sierra Madre Oriental province (Valadez and Paredes, 1988).

Diagnosis: sexually dimorphic, with females smaller and with reduced horncores; tip of the horncores blunt, lachrymal pit shallow and weakly defined (Shackleton, 1985); large and wide skull, with wide rostrum; with a long, broad and subhypsodont teeth, and long, thick, broad-based, and little divergent horncores (Kurtén and Anderson, 1980).

Notes: *Ovis catclawensis* was originally described from the Late Pleistocene of Catclaw Cave, Arizona, based upon a partial right jaw with p3-m3, with the diagnostic characters based upon the robust m3 morphology (Hibbard and Wright, 1956). Afterwards, *O. catclawensis* material form a natural trap cave in Wyoming was regarded as larger than *O. canadensis*, and with larger legs (Gilbert and Martin, 1984), but no information on how this long-legged sheep was the same species as the Catclaw Cave was provided. The robust m3 is not enough to justify the species rank of *O. catclawensis*, and as other authors have suggested, this character is found in different modern subspecies, and this species may represent a temporal subspecies of *O. canadensis* (Hibbard and Wright, 1956; Harris and Mundel, 1974; Kurtén and Anderson, 1980). Additionally, non-published communications suggest that the *O. catclawensis* of Wyoming present a different postcranial morphology than *O. canadensis* (Kurtén and Anderson, 1980), but this evidence was never published. Thus, we consider *O. catclawensis* as a junior synonym of *O. canadensis*, and a *species inquirenda* (ICZN, 1999: Articles 23 and 67).

Most of the records of *Ovis canadensis* in Mexico are associated with human remains, clearly assignable to the Holocene, except for the remains of Epazoyucan, Hidalgo, which are found in association with Late Pleistocene (Rancholabrean) fauna (Bravo-Cuevas et al., 2009b; Pineda-Maldonado et al., 2017). Upon detailed examination of the assigned remains (UAHMP 329, a left calcaneum) of *O. canadensis* from this locality, we concluded that it belonged to a large pronghorn (cf. *Tetrameryx shuleri*), and thus, *O. canadensis* is not present in the fossil record of Mexico.

Genus *Euceratherium* Sinclair and Furlong, 1904

Species *Euceratherium collinum* Sinclair and Furlong, 1904

Synonyms: *Preptoceras sinclairi* (Furlong, 1905), *Aftonius calvini* (Hay, 1912), *Taurotragus americanus* (Gidley, 1913), *Euceratherium bizzelli* (Stovall, 1937).

Range in Mexico (Figure 6): La Guitarra, Sonora, Sonoran province (Hibbard, 1955; Barrios-Rivera, 1985); Rancho La Amapola, El Cedral, San Luis Potosí, South Plateau province (Álvarez et al., 2012); Cueva del Tiburón, San Luis Potosí (Alarcón and Arroyo-Cabrales, 2015), and San Josecito Cave, Nuevo León, Sierra Madre Oriental province (Cushing, 1945; Álvarez, 1969; Silva-Bárcenas, 1969; Barrios-Rivera, 1985); Cueva de La Boca (Cueva la Mina? See discussion below), Nuevo León, Tamaulipecan province (Arroyo-Cabrales and Polaco, 2003); and Tequixquiac, Tajo de Tequixquiac local fauna (Becerra Formation), State of Mexico (Freudenberg, 1921; Hay, 1930; Frick, 1937; Maldonado-Koerdell, 1948; Arellano, 1951; Hibbard, 1955; Silva-Bárcenas, 1969; Kurtén and Anderson, 1980; Barrios-Rivera, 1985; Carranza-Castañeda and Miller, 1987).

Age range: In Mexico is known only for the Rancholabrean, in North America, its known from the Irvingtonian to the Rancholabrean (Kurtén and Anderson, 1980).

Diagnosis: large sheep species, almost 75% the size of modern *Bison* (Kurtén and Anderson, 1980), frontals at a steep angle with respect of the nasals, forming a swollen area above the orbits; parietal restricted to the occiput, forming no part of the cranial roof; hypsodont large teeth with no cement, and no accessory cuspules but occasionally with a median accessory style on the lingual portion of the upper teeth (Sinclair and Furlong, 1904; Furlong, 1905); the bases of the horncores are large and divergent, situated close together at the posterior region of the frontals, behind the orbits, burr of the horncores widely separated, the base has an elliptical cross-section, while the middle region is laterally compressed and the tip has a circular or elliptical cross-section, the base is wide and it decreases its width towards the tip, the main axis is spiraled and directed posteriorly at the base and afterwards anteriorly to the tip.

Notes: In Mexico, this sheep species is elusive and it is found primarily in cave deposits, with the notable exception of the Becerra Formation, Tequixquiac (Hibbard, 1955). The similarities between size and overall morphology of *E. collinum* with *Bison*, especially in the metapodials (Kurtén and Anderson, 1980) calls for attention to carefully identify these elements. Finally, the reference of *Euceratherium* sp. at Cueva de La Boca, Nuevo León (Arroyo-Cabrales and Polaco, 2003), has the same geographical coordinates of the locality Cueva la Mina, recorded originally by Kurten (1975), here we consider both as the same locality since local people use to call La Boca cave as La Mina (the mine), as pointed by Arroyo-Cabrales and Polaco (2003).

Genus *Oreamnos* (Rafinesque, 1817a)

Species *Oreamnos harringtoni* Stock, 1936

Age and range in Mexico (Figure 6): known only for the Rancholabrean of San Josecito Cave, Nuevo León, Sierra Madre Oriental province (Wilson, 1942; Rideout and Hoffmann, 1975; Kurtén and Anderson, 1980; Mead et al., 1987).

Diagnosis: two thirds the size of *O. americanus*, horncores larger and more curved, metacarpal III with larger *extensor carpi radialis* surface, metatarsals III+IV narrow in the proximal region of the diaphysis, and deeper anterior median groove (Stock, 1936).

Notes: The Mexican record of *Oreamnos harringtoni* in San Josecito Cave, does not support the hypothesis that this species lived in cold adapted environments of the last Wisconsin glaciation (Wilson, 1942; Kurtén and Anderson, 1980), due to the lack of cold adapted species in association with this extinct mountain goat. Further investigation on the southern distribution of this species may clarify its geographical and climatic patterns in the south of its distribution.

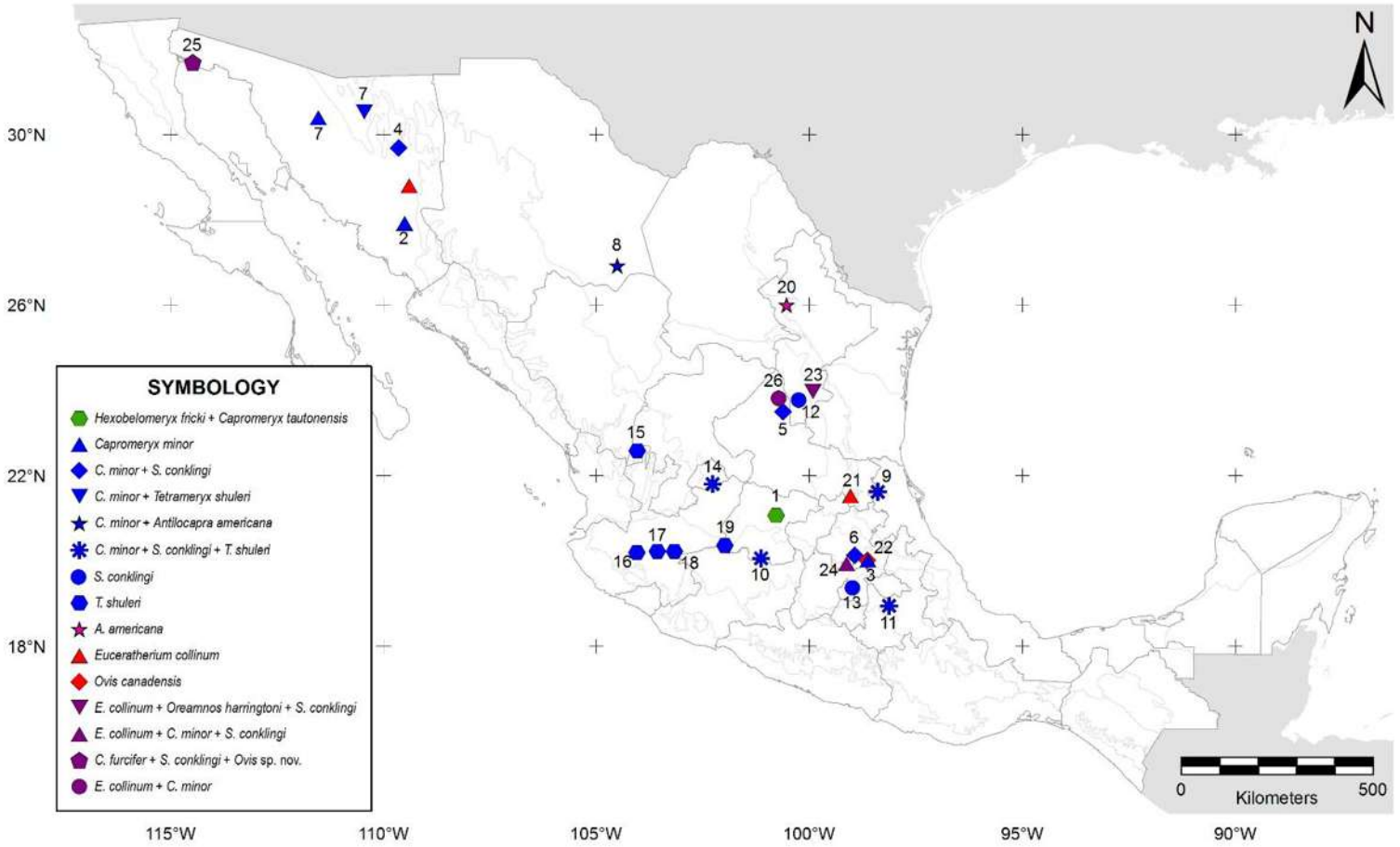

Figure 6. Pliocene to Pleistocene sites with presence of Antilocapridae and Bovidae (*Bison* spp. excluded). Green: Pliocene antilocaprids, blue: Pleistocene antilocaprids, pink: possible Holocene, red: Holocene, purple: Pleistocene Bovidae+Antilocapridae. (1) San Miguel de Allende, (2) La Botana, (3) Barranca del Berrendo, (4) San Clemente de Térapa, (5) Cueva La Presita, (6) El Barrio, (7) Rancho La Brisca, (8) Cueva Jiménez, (9) La Mixtequilla, (10) La Cinta-Portalitos, (11) Valsequillo, (12) Mina de San Antonio, (13) Los Reyes La Paz, (14) Arroyo El Cedazo, (15) Los Tanques, (16) Tecolotlán, (17) Zacoalco, (18) Chapala, (19) La Piedad-Santa Ana, (20) Mina, (21) Cueva del Tiburón, (22) Epazoyucan, (23) San Josecito, (24) Tequixquiac, (25) Golfo de Santa Clara, (26) El Cedral.

Subfamily Bovinae Gill, 1872

Genus *Bison* (Hamilton-Smith, 1827)

Range in Mexico (Figure 7): Santa Rita, Baja California state and province (Ferrusquía-Villafranca and Torres-Roldán, 1980); San Clemente de Térapa (Mead et al., 2006; Carranza-Castañeda and Roldán-Quintana, 2007; Nunez et al., 2010), Llano Prieto, La Botana and Chinobampo (Mead et al., 2007), Sonora, Sonoran province; Rancho la Brisca, Sonora (Van Devender et al., 1985), Yepómera, Chihuahua (Lindsay et al., 2006), Sierra Madre Occidental; El Cedral, San Luis Potosí (Álvarez et al., 2012), San Juan de los Lagos, Jalisco (Dugès, 1897), Las Cajas, and San Agustín Tlaxiaca, Hidalgo (Bravo-Cuevas, 2001; Bravo-Cuevas et al., 2009a), South Plateau province; Epazoyucan, Hidalgo, Sierra Madre Oriental province (Pineda-Maldonado et al., 2017); Ejido San Lázaro, Tamaulipas, Gulf of Mexico province (Reynoso and Montellano-Ballesteros, 2004); Rancho San Miguel (Lucas, 2008b), and Atotonilco el Bajo, Jalisco (Solorzano, 2002), Ciudad Universitaria, Morelia, Michoacán (García-Zepeda et al., 2015), Chimalhuacán (García, 1968), and Los Reyes La Paz (García, 1975), State of Mexico, Volcanic axis province; San Dionisio Ocotepec, Oaxaca, Sierra Madre del Sur province (Díaz-Sibaja et al., 2018); Los Tanques, Valparaíso, Zacatecas (Lozano-Ramos et al., 2006), and La Simpatía, Villa Corzo, Chiapas (Carbot-Chanona and Vázquez-Bautista, 2006); and Gruta de Loltún, Yucatán, Yucatan province (Álvarez, 1982a; Arroyo-Cabrales and Álvarez, 2003).

Notes: Most of the materials of *Bison* sp. are not described, not figured or are not diagnostic, which difficult its assignation to any known species, but a few cases are notable. Such as the record from San Juan de los Lagos, Jalisco, where Dugès (1897) explicitly reported *Bison latifrons* and another unidentified species of which, only postcranial elements were found. This highlights the importance in studies focusing on differences between postcranial elements of Pleistocene *Bison* spp. (e.g. Díaz-Sibaja et al. 2018). At the Cedral locality a *Bison* sp. of small horncores is reported (Álvarez et al., 2012), due to the age of this site (Late Pleistocene), this is likely *B. antiquus*, the only small horned species in Mexico during this age. Nevertheless, more detailed analysis of the *Bison* of this site is required to provide an identification.

The most unusual record of *Bison* comes from the cave of Gruta de Loltún, a system that contains vertebrate remains from the Late Pleistocene to the Holocene, and its located at the Yucatan Peninsula, at only 40 m above the sea level (Arroyo-Cabrales and Álvarez, 2003). Fossil bats suggests that during the Pleistocene and Holocene, the vegetation structure was composed by tropical deciduous forest (Arroyo-Cabrales and Álvarez, 1990), a highly unusual habitat for modern *Bison* (Meagher, 1986). The original report if this taxon was made by Álvarez (1982), who assigned the remains to *Bison bison*. Nonetheless, as evidence suggest, this species had not yet evolved, see discussion on *Bison* "occidentalis" in the *B. antiquus* section below. The tooth fragment reported is a mesial upper selenid of a right M2/3, the scale bar accompanying the tooth figure is wrong, and its size (transversal width of 46.8 mm) is overestimated, well above the upper limit of known *B. latifrons* teeth (35 mm) (Green and Martin, 1960), the largest bison species in North America. Unfortunately, we weren't unable to locate this material in the INAH collection of the Loltún cave, and all other remains we examined were holocenic *Bos primigenius taurus* postcranial elements. Thus, we assigned the remains to *Bison* sp. until further investigation is carried out.

Species *Bison alaskensis* Rhoads, 1897

Synonyms: *Bison alleni* (Marsh, 1877) (in part, see discussion below), *B. chaneyi* (Cook, 1928), *B. latifrons* Harlan, 1825 (in part, see discussion below).

Age and range in Mexico (Figure 7): Known only in the Rancholabrean of Tequixquiac, Tajo de Tequixquiac local fauna (Becerra Formation), State of Mexico (Hibbard and Villa-Ramírez, 1950).

General diagnosis: Large spiral-horned bison species; for the horn cores: posterior margin sinuous, longitudinal axis sinuous (rotated rearwards to the coronal plane of the occipitals), growth spiraled along longitudinal axis, base asymmetrical (scalene for males, circular to elliptical for females) with the greatest dorsoventral diameter at the anterior region, distal tip curved, length along upper curve >425 mm (McDonald, 1981).

Notes: *Bison alaskensis* was originally described by Rhoads (1897) from a partial skull (FMNH P 25226) collected from northern Alaska (Plate XII, fig. 3 and 6, in Rhoads, 1897, and plate 24, fig. 3, 3A, 3B, in Skinner and Kaisen, 1947). This specimen has the typical female morphology, with slender horn cores, a convex posterior margin and straight growth along a semi-spiraled axis (McDonald, 1981). Subsequently, *B. alaskensis* was synonymized subjectively with *B. crassicornis* (syn= *B. priscus*) by Guthrie (1966), and with *B. priscus* (as *B. priscus alskensis*) by Kurtén and Anderson (1980). Later, it was considered as a valid species by McDonald (1981), who considered *B. chaneyi* and *B. aguascalentensis* as junior synonyms of *B. alaskensis*.

Bison alleni was another giant bison species, originally described by Marsh (1877) from a single horn core (YMP VP 11911), collected from Blue River, Riley County, Kansas. It was synonymized with *B. latifrons* by McDonald (1981). The type specimen can be referred as *B. latifrons*, but the specimen reported by Lucas (1899) does not possess the morphological characteristics of this species. Instead, the second specimen (plate LXXIX and LXXX in Lucas, 1899) can be assigned to *B. alaskensis*, it possesses the following diagnosable characteristics: posterior margin sinuous, longitudinal axis sinuous (rotated rearwards to the coronal plane of the occipitals), and an incomplete distal tip curved backwards.

Bison chaneyi was described by Cook (1928) from a partial skull (CoMNH VP 1147) collected from Vernon, Texas (fig. 1 and 2, in Cook, 1928, and plate 24, fig. 1, 1A, 1B in Skinner and Kaisen, 1947). The holotype of *B. chaneyi* exhibits the typical male morphology of *B. alaskensis*, with robust horn cores, sinuous posterior margin, and a strongly spiraled axis (McDonald 1981).

Bison aguascalentensis (misspelled as *B. aguascalientensis* and *B. aguascalientes*) was described by Mooser and Dalquest (1975) from a partial skull (FC 658) collected from Arroyo San Francisco, (Cedazo local fauna) Aguascalientes (fig. 12 in Mooser and Dalquest, 1975). This species was synonymized subjectively with *B. alaskensis* by McDonald (1981). Mooser and Dalquest (1975) originally described *B. aguascalentensis* as follows: "…The horn core of the left side (…) leaves the cranium at right angles to the longitudinal axis of the skull and dips down only slightly, rather than greatly, before curving outward smoothly to the recurved, untwisted tip", these characters plus a straight posterior margin, straight longitudinal axis, and

straight growth, as seen in the figure 12 are all characters of *B. latifrons*. Thus, we consider *Bison aguascalentensis* as a junior synonym of *Bison latifrons* (ICZN, 1999: Article 23) and not as a junior synonym of *B. alaskensis* as stated previously.

Before McDonald (1981), Barrios-Rivera (1985) considered the Mexican giant bison with flat horncore bases as *B. channeyi* (syn= *B. alaskensis*), following Hibbard and Villa-Ramírez (1950), who stated this as a character for the species. Nevertheless, the flatness of the horncore base is a sexual character, present in several males of different North American bison species (McDonald, 1981), and thus it cannot be used as a specific character. Many authors have followed Hibbard and Villa-Ramírez (1950) proposal, thus referring several giant bison with flat horncore bases as *B. alaskensis*. For example, in San Juan de los Lagos and Lago de Chapala sites (Jalisco), Solorzano (2002) listed *B. alaskensis*, without any description of the fossil material. The reference of *B. alaskensis* from Lago de Chapala date back from Downs (1956), who listed the species as *B. cheneyi* (sic) and did not provide either any description or figures either. This specimen (LACM 1767) was examined later by Rufolo (1998), and he determined it to be referred to *B. alleni* (syn= *B. latifrons*), a conclusion rejected by Lucas (2008a), despite that the horn core does actually have characters of *B. latifrons* and none of *B. alaskensis* except for large horncores. A possibly *B. chaneyi* was also reported from Huachichil, State of Mexico (De Terra 1953), but no further detail is provided. Finally, some of the specimens (IG 49-33, IG 14) found in the Tajo de Tequixquiac site were reported as *B. chaneyi* by Hibbard and Villa-Ramírez (1950) and later, were referred to *B. alaskensis* by McDonald (1981), despite they clearly possess *B. latifrons* morphology, such as straight axis, straight growth, straight posterior margin and untwisted tips (Hibbard and Villa-Ramírez 1950, plate 1, fig. D; Plate II fig. B, C; and Plate III, fig. A), and are similar to the specimen reported by Hopkins (1951). Thus, we assign all these specimens to *B. latifrons*.

The only reliable record of *B. alaskensis* in Mexico comes from a partial skull (MNHN 15, now IGM 5251) collected from the Upper Becerra Formation, in the Tajo de Tequixquiac site (Hibbard and Villa-Ramírez 1950). This specimen is very similar to the holotype of *B. chaneyi* and confidently represents a male *B. alaskensis*. Other records of this species in Mexico such as Duraznillo, San Gerardo (Aguascalientes), Santa Isabel Ixtapan (State of Mexico), and Zoatecpan (Puebla) in databases (Arroyo-Cabrales et al. 2002) without specimen number or related published paper, should be regarded with caution and be examined in order to determine if they truly represent *B. alaskens*is or a misidentified *B. latifrons*.

Species *Bison latifrons* (Harlan, 1825)

Synonyms: *Bison ferox* (Marsh, 1877), *B. alleni* (Marsh, 1877), *Bos crampianus* (Cope, 1895), *B. arizonica* (Blake, 1898), *Bison regius* (Hay, 1913), *B. angularis* (Figgins, 1933), B. rotundus (Figgins, 1933), *B. aguascalentensis* (Mooser and Dalquest, 1975).

Range in Mexico (Figure 7): Range in Mexico: Ramos Arizpe, Sonora, Sonoran province (Cracraft, 1968); two unnamed sites at Zacatecas (Skinner and Kaisen, 1947), Arroyo el Cedazo, El Cedazo local fauna (Tacubaya Formation), Aguascalientes (Mooser and Dalquest, 1975), South Plateau province; Zacoalco (Solorzano, 2002; Lucas, 2008b), and Chapala, Jalisco (Downs, 1956; McDonald, 1981; Solorzano, 2002), La Piedad-Santa Ana, and La Cinta-

Portalitos, Michoacán-Guanajuato (Díaz-Sibaja et al., 2012), Huachichil (De Terra, 1953), Zumpango de Ocampo (Osborn, 1905), and Tequixquiac, Tajo de Tequixquiac local fauna (Becerra Formation), State of Mexico (Cope, 1884; Villada, 1903), State of Mexico, Volcanic Axis province; San Dionisio Ocotepec, Oaxaca, Sierra Madre del Sur province (Díaz-Sibaja et al., 2018).

Age range: Restricted to the Rancholabrean (McDonald, 1981).

General diagnosis: Very large straight-horned bison species; for the horn cores: posterior margin straight (slightly convex in females), longitudinal axis straight (usually directed at right angle to the coronal plane of the occipitals), growth straight along longitudinal axis, base symmetrical (isosceles in males, circular to elliptical for females), distal tip straight, length along upper curve >500 mm (McDonald, 1981).

Notes: As stated previously (see discussion of *Bison alaskensis*), many specimens of *B. latifrons* are often confused with *B. alaskensis*, and many others are left without identification due to the lack of associated horn cores to provide a positive diagnosis. However, *B. latifrons* postcranial elements can be distinguished from *B. alaskensis* from morphology and morphometry, since the latter is more similar to *B. priscus*, and display a larger size (Austin, 2005; Díaz-Sibaja, 2013; Díaz-Sibaja et al., 2018).

Bison latifrons is the oldest autochthonous bison species, its first appearance was during the early Late Pleistocene (Sangamonian interglacial stage), with a date between 141 ±14 and 138±13 Ka, (Miller et al., 2014). This species persisted until the early Holocene, with its latest record in Avery Island, Louisiana, dated between 6.4 to 7.7 Ka (Gagliano, 1967; Dillehay, 1974). Thus, its presence cannot be used to infer a Sangamon age as previously suggested by several authors (e.g. Hibbard 1955; Kurtén and Anderson 1980).

The Ramos Arizpe record was stated as *B.* cf. *alleni* (Cracraft, 1968), which was synonymized with *B. latifrons* (McDonald, 1981), thus we reassigned it to the latter. The Chapala material of this species is problematic (see Lucas, 2008a) and needs further study, here we consider the most reliable identifications based upon horncores (Downs, 1956) as *B. latifrons*.

Species *Bison antiquus* Leidy, 1852

Synonyms: *Bison californicus* (Rhoads, 1897), *B. occidentalis* (Lucas, 1898), *Bos scaphoceras* (Cope, 1895), *Bison kansensis* (McClung, 1905), *B. pacificus* (Hay, 1927), *B. figginsi* (Hay and Cook, 1928), *B. taylori* (Hay and Cook, 1928), *B. texanus* (Hay and Cook, 1928), *Simobison figginsi* (Hay and Cook, 1930), *Bison oliverhayi* (Figgins, 1933), *Stelabison occidentalis* (Figgins, 1933), *S. occidentalis francisi* (Figgins, 1933), *Bison bison antiquus* (Wilson, 1974), *B. bison* (in part) (Kurtén and Anderson, 1980), *B. antiquus occidentalis* (McDonald, 1981).

Range in Mexico (Figure 7): Comondú (McDonald, 1981), and an unnamed locality (Skinner and Kaisen, 1947), Baja California Sur, Baja California province; Rancho el Carrizal, Baja California, Cabo province (Ferrusquía-Villafranca and Torres-Roldán, 1980); Mina, Nuevo León, North Plateau province (Franzen, 1993, 1994); Laguna de las Cruces (Álvarez, 1982b; Barrios-Rivera, 1985), and an unnamed locality (Skinner and Kaisen, 1947), San Luis Potosí,

South Plateau province; Chapala (Chapala local fauna) (Lucas 2008a; McDonald 1981; Solorzano 2002), and Zacoalco (Solorzano, 2002; Lucas, 2008b), Jalisco, La Piedad-Santa Ana, and La Cinta-Portalitos, Michoacán-Guanajuato (Díaz-Sibaja et al., 2012; Díaz-Sibaja, 2013), Tequixquiac, Tajo de Tequixquiac local fauna (Becerra Formation) (Hibbard, 1955; Carranza-Castañeda and Miller, 1987), and San Vicente Chicoloapan (McDonald, 1981), State of Mexico, San Mateo Huexoyucan, Tlaxcala (Sánchez Salinas et al., 2016), Hueyatlaco, Valsequillo local fauna (McDonald, 1981; Barrios-Rivera, 1985; Pichardo, 1997, 1999), Puebla, Volcanic Axis province; Viko Vijin local fauna (Jiménez-Hidalgo et al., 2013), Oaxaca, Sierra Madre del Sur province.

Age range: Restricted to the Rancholabrean (McDonald, 1981).

General diagnosis: Small straight-horned bison species; for the horn cores: posterior margin straight, longitudinal axis arched, growth straight along the longitudinal axis, base symmetrical (isosceles in males, circular to elliptical for females), distal tip slightly curved upwards, the length along upper curve >175 and <400 mm (McDonald, 1981).

Notes: *Bison antiquus* (ancient bison) is the best-known North American fossil bison. It was originally described from a partial right horn core with an attached frontal bone, from Big Bone Lick, Kentucky (Leidy, 1852), and today its recognized from several complete skeletons (Frison and Todd, 1987). The earliest record of this species dates from 41.5 Ka and comes from the Unit C2 of Jones Spring, Missouri (FAUNMAP Working Group, 1994). This date is in agreement with recent molecular estimates for the first appearance of *B. antiquus*, and a second wave of bison dispersal into continental North America around 45 to 21 Ka (Froese et al., 2017), and can be used to provide a minimum relative age constraint for the sites with the presence of this species.

Bison occidentalis (western bison) was described by Frederick Lucas in 1898 from a partial skull from Fort Yukon, Alaska. This species was regarded as separate from *B. antiquus* (e.g. Lucas 1899; Skinner and Kaisen 1947) and also as a synonym of *B. bison* (e.g. Kurtén and Anderson 1980). However, McDonald (1981) considered it as a subspecies of *B. antiquus*, and a transitional form to *B. bison*. This hypothesis is supported by molecular data, which points to a transition from *B. antiquus antiquus* to *B. bison*, through *B. antiquus occidentalis* around 4 to 5 Ka in southern Canada (Wilson et al., 2008). However, *B. antiquus* "antiquus" and *B. antiquus* "occidentalis" are bot non-monophyletic and thus, we do not consider them as valid subspecies. Although, the "occidentalis" morphology can be distinguished from the "antiquus" form. Western bison has slender, posteriorly directed horn cores, with a curved tip which has a circular to elliptical cross section, the posterior margin is straight or slightly concave, and have a reduction or lack of the dorsal groove (Lucas 1899; McDonald 1981; Skinner and Kaisen 1947). Since the first appearance of the occidentalis form has an age of 11.37 ±170 Ka (Harington, 2003), and it is not typically found in association with typical Late Pleistocene fauna such as mammoths and horses, it is useful to provide a minimum relative age. Nonetheless, caution is advised, since females of the antiquus form can be confused with males of the occidentalis form.

Some authors consider that the Pleistocene bison species *Bison antiquus* and *Bison* "occidentalis" (here considered as *B. antiquus*) can be synonymized with *Bison bison* and

consider them as subspecies (e.g. Wilson, 1974; Kurtén and Anderson, 1980). Nevertheless, as McDonald (1981) pointed out, these forms can be distinguished by their horncore morphology and dimensions. Even if they form a big anagenetic line that ends in *Bison bison* (Wilson et al., 2008; Froese et al., 2017), their ecological behavior (Rivals et al., 2007; Rivals and Semprebon, 2012) and selection regimes were completely different and are better understood if *B. bison* and *B. antiquus* are considered separate species.

The Laguna de las Cruces (Álvarez, 1982b) and La Cinta-Portalitos (García-Zepeda, 2006) bison were originally reported as *Bison bison*, but since this species was not present in the Late Pleistocene (Wilson et al., 2008) and its morphology can be confused with its parent taxon, we decided to include this record as *B. antiquus*. Similarly, the Rancho el Carrizal (Ferrusquía-Villafranca and Torres-Roldán, 1980) report was originally made as cf. but since this fauna is composed of typical Rancholabrean fauna, we decided to report it as *B. antiquus*.

Finally, *Bison priscus* is considered as a valid Mexican species in recent review works (Ferrusquía-Villafranca et al., 2010). But, we found that this is not the case. Franzen (1993) reported the presence of *B. priscus* in Mina, Nuevo León. This report was expanded and the material was figured in Franzen (1994), fig 12. The referred skull has diagnostic characters of *B. antiquus*, but none of *B. priscus* except for the small size of the horncores. The posterior margin is straight, the longitudinal axis slightly arched, the growth is straight and the tips are not strongly twisted (McDonald, 1981). The other report of this species was from San Vicente Chicoloapan, Mexico State, which was several hundreds of kilometers away from other known *B. priscus* (McDonald, 1981). But after we examined the specimen (INAH DP 516), we found no diagnostic features of *B. priscus* in it, but it does have characters of *B. antiquus* such as straight posterior margin and growth straight along the longitudinal axis. Thus, we assigned this partial skull as *B. antiquus* and consider that *B. priscus* has no presence in Mexico.

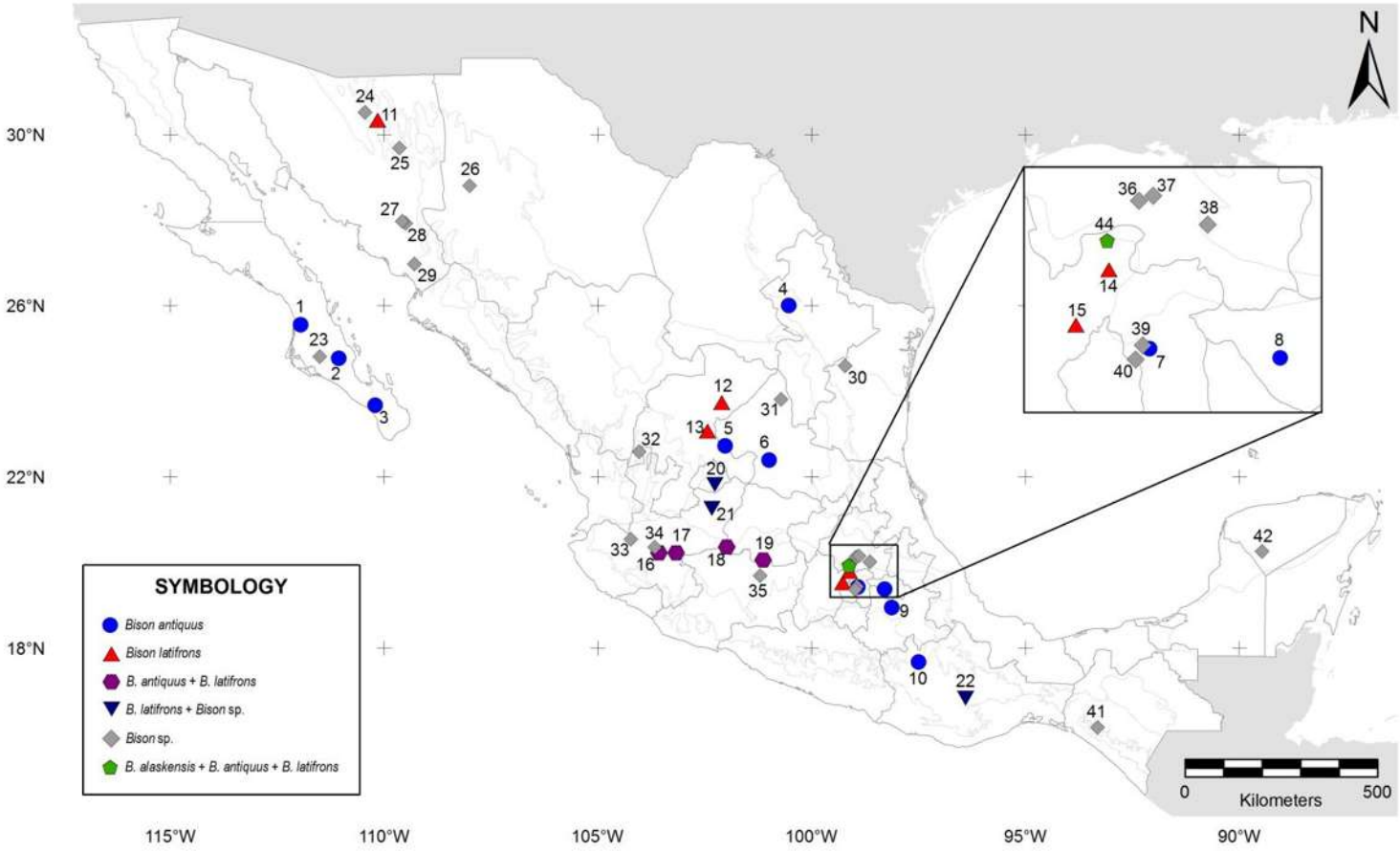

Figure 7. *Bison* spp. fossil record. (1) Comondú, (2) Unnamed BC, (3) Rancho el Carrizal, (4) Mina, (5) Laguna de las Cruces, (6) Unnamed SLP, (7) San Vicente Chicoloapan, (8) San Mateo Huexoyucan, (9) Valsequillo, (10) Viko Vijin, (11) Ramos Arizpe, (12) Unnamed Z2, (13) Unnamed Z1, (14) Zumpango de Ocampo, (15) Huachichil, (16) Zacoalco, (17) Chapala, (18) La Piedad-Santa Ana, (19) La Cinta-Portalitos, (20) Arroyo el Cedazo, (21) San Juan de los Lagos, (22) San Dionisio Ocotepec, (23) Santa Rita, (24) Rancho La Brisca, (25) San Clemente de Térapa, (26) Yepómera, (27) Llano Prieto, (28) La Botana, (29) Chinobampo, (30) Ejido San Lázaro, (31) El Cedral, (32) Los Tanques, (33) Rancho San Miguel, (34) Atotonilco el Bajo, (35) Ciudad Universitaria (36) Las Cajas, (37) San Agustín Tlaxiaca, (38) Epazoyucan, (39) Chimalhuacán, (40) Los Reyes La Paz, (41) La Simpatía, Villa Corzo, (42) Gruta de Loltún.

Family Cervidae (Goldfuss, 1820)

Subfamily Capreolinae (Brookes, 1828)

Genus *Capreolus* Gray, 1821

Species *Capreolus constantini* Vislobokova et al., 1995

Range in Mexico (Figure 8): Known only from Santa María Amajac (El Grande Formation), Hidalgo, South Plateau Province (Jiménez-Hidalgo and Bravo-Cuevas, 2013).

Age range: In Mexico, it has a minimal age between 4.57 ±0.02 and 4.2 ±0.3 Ma, Blancan III(?), Pliocene (Jiménez-Hidalgo and Bravo-Cuevas, 2013). In the Old World is known from the Late Pliocene (Villafranchian zone MN16, 3.5 to 2.7 Ma) to the Early Pleistocene (Early-Middle Villafranchian) (Vislobokova et al., 1995).

Diagnosis: Almost the same size than *C. pygargus*; pedicles far apart, antlers long and lyre-shaped; the antler is strongly ornamented and have a sigmoid shape from the pedicle to the first tine, first tine long and situated far apart from the pedicle; premolars less molariform, long premolar row, p4 with closed back valley; lower molars with isolated hypoconid (when heavily worn, this character is lost); upper molars with well-developed pillar of the paracone and metacone, and fold of the protocone; crown of the upper molars trapezoidal in shape, crown of the p2 triangular in shape; strong anterior stylid in p3 (Vislobokova et al., 1995).

Notes: The Mexican record of *C. constantini* represents one of the earliest records of cervids in Mexico. This species is not known anywhere in North America, and the only other known fossil sites are Udunga and Beregovaja, in the Trans-Baikal region of Russia (Vislobokova et al., 1995). The presence of *C. constantini* in the Pliocene of Mexico reinforces the hypothesis of at least two Miocene-Pliocene dispersal events for the Cervidae (Jiménez-Hidalgo and Bravo-Cuevas, 2013).

Early *Odocoileus*

Range in Mexico (Figure 8): Miñaca, Chihuahua, Sierra Madre Occidental province (Lindsay, 1984), and Uruétaro, Michoacán, Volcanic Axis province (Gutiérrez-Bedolla, 2011; Gutiérrez-Bedolla et al., 2012).

Notes: The genus *Odocoileus* appears in the Blancan of North America, and due to the absence of diagnostic features of the fossil remains from this age, many are referred just as *Odocoileus* sp. (Webb, 1998b). Nevertheless, one species have been described for the Pliocene, *Odocoileus brachyodontus*, based on a M2-M3 (UMMP 28140) dental series from Rexroad Formation, Meade County, Kansas (Oelrich, 1953). The diagnostic characters of *O. brachyodontus* include brachydont teeth, and a M3 with protocone and metaconule separated from the paracone and metacone respectively (Oelrich, 1953). These characters are found in other specimens of the genus *Odocoileus* and the only difference

between them is the slightly larger size of *O. brachyodontus* (often less than 1 mm), thus are not diagnostic to species level (Wheatley and Ruez Jr., 2006). Because of this, we consider *O. brachyodontus* as a *nomen nudum* (ICZN, 1999: Article 13) until new specimens show diagnostic features to differentiate it from other species of *Odocoileus*.

We consider as early *Odocoileus* only the Blancan records of the genus. The age of Miñaca is not specified, but the presence of *Nannippus*, *Prosthennops*, *Chasmaporthetes*, and *Stegomastodon* (Lindsay, 1984) suggest an Early Blancan age (Bell et al., 2004). Also, the age of Uruétaro is not specified (Gutiérrez-Bedolla, 2011), but the presence of *Rhynchotherium falconeri* (reassigned here from *Cuvieronius* sp. following Lucas and Morgan, 2008), *Paenemarmota* sp., and *Nannippus* sp., and suggest a Blancan IV age (Bell et al., 2004).

Genus *Odocoileus* Rafinesque, 1832

Species *Odocoileus virginianus* (Zimmermann, 1780)

Fossil synonyms: *Odocoileus speleus* (Rafinesque, 1832), *Cariacus dolichopsis* (Cope, 1878), *C. ensifer* (syn= *Odocoileus hemionus*) (in part, see discussion on *O. hemionus* below) (Cope, 1889), *C. laevicornis* (Cope, 1896), *Dama laevicornis* (Hay, 1902), *Odocoileus laevicornis* (Rhoads, 1903), *O. osceola* (Hay, 1916) (see discussion below), *O. sellardsiae* (Hay, 1917), *Palaeodocoileus gracilis* (Spillmann, 1931), *Palaeodocoileus salinae* (Frick, 1937), (?)*Odocoileus doclichopsis* (Frick, 1937), *O. cooki* (Frick, 1937), *O. sheridanus* (Frick, 1937), *O. cascensis* (in part, see discussion on *O. hemionus* below) (Frick, 1937). For a detailed synonym list of modern species see Smith (1991).

Range in Mexico (Figure 8): El Golfo de Santa Clara, Sonora, Sonoran province (Croxen et al., 2007; White et al., 2010); Cueva La Presita (Arroyo-Cabrales and Polaco, 2003) and Laguna de la Media Luna, San Luis Potosí (Hernández-Junquera, 1977), El Barrio, Hidalgo, South Plateau Province (Bravo-Cuevas, 2001); Zacoalco (Solorzano, 2002; Lucas, 2008b), and Chapala (Chapala local fauna), Jalisco (Solorzano, 2002), La Piedad-Santa Ana, and La Cinta-Portalitos, Michoacán-Guanajuato (Díaz-Sibaja, 2013; Díaz-Sibaja et al., 2014b), Tlapacoya, Estado de México, Volcanic Axis province (Álvarez, 1969); Villaflores, Chiapas, Pacific Coast province (Montellano-Ballesteros and Carbot-Chanona, 2010; Gómez-pérez and Carbot-chanona, 2012); Cueva de Lara (Actún Lara) (Arroyo-Cabrales and Polaco, 2003), and Gruta de Loltún, Yucatán, Yucatan province (Arroyo-Cabrales and Álvarez, 2003; Arroyo-Cabrales and Polaco, 2003).

Age range: In Mexico, from the Late Pleistocene (Rancholabrean) to the Present. In North America appears in the Late Blancan (Webb, 1974; Kurtén and Anderson, 1980).

Diagnosis: Medium to small-sized deer, shallow lachrymal fossae, small brachydont teeth, three premolars and molars, absence of upper canines (Smith, 1991), helical main beam with a strong, continuous curving structure from which several vertical tines arise, usually with a basal candle (brow tine), with little to none ornamentation (Gustafson, 1985; Smith,

1991), p4 molariform, with an anterior fossetid formed by the closure of the mesolingual conid with the anterior conid (in some young individuals the fossetid is not complete, but the contact still exists); anterior conid forming a poorly developed anterior style, the mesolingual conid expands distally into a posterolingual crista; with an entostylid between a strongly developed mesolabial and posterolabial conids; posterolingual crista and conid separated by a deep posterior valley, a shallow back valley is present between the posterolingual conid and the posterior stylid, a distal style is formed by the posterolingual conid instead of the posterolabial conid.

Notes: *Odocoileus laevicornis* was described by Cope (1896) as *Cariacus laevicornis*; this species is based on upper right P4-M2 series, and the basal parts of associated antlers from Port Kennedy Cave of the Pleistocene (Irvingtonian) of Pennsylvania. Nevertheless, it is unlikely that the antlers belong to the same individual and only the upper molars are taken as the holotype (Spamer et al., 1995). The diagnostic features of the holotype include the lack of folds in the fossae and the relatively small size of the premolar (Cope, 1896). Nevertheless, these features fall within the variation of *O. virginianus*, and thus, we consider *O. laevicornis* as a junior synonym of *O. virginianus* (ICZN, 1999: Article 23).

Odocoileus osceola was originally described by Bangs (1896) as a modern species of *Odocoileus* inhabiting Florida. It was later identified for the Pleistocene of Florida by Hay (1916), and stated as very similar to *O. virginianus*, except by the labiolingual diameter of the teeth by 2 mm, a difference produced by the moderate worn of the teeth. Thus, *Odocoileus osceola* is regarded as a junior synonym of *O. virginianus* (Smith, 1991).

Odocoileus sellardsiae was described by Hay (1917) from an isolated fifth cervical vertebra, recovered from Vero, Florida (Late Pleistocene). Hay compared the vertebra (7923) to a fifth cervical of *O. hemionus* and concluded this was a new species. Later, Weigel (1962) subjectively considered it as a junior synonym of *O. virginianus*. We compared the vertebra with cervical series of *O. virginianus* housed in the osteological collection (Colección Osteológica del Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano") of the Instituto Nacional de Antropología e Historia (INAH), Mexico, and found that *O. sellardiae* falls within the variation and size of *O. virginianus*. Thus, we consider this species as synonyms (ICZN, 1999: Article 23).

Cariacus dolichopsis was described from a left mandibular ramus found in Rancholabrean lacustrine deposits from Vandenburg County, Indiana (Cope, 1878). Afterwards, Frick (1937) placed *C. dolichopsis* within the genus *Odocoileus*. The diagnostic characters of *O. dolichopsis* include a shorter teeth row and a slightly larger diastema, these characters fall within the range of variation of *O. virginianus*. Because of this, we consider *O. dolichopsis* as a junior synonym of *O. virginianus* (ICZN, 1999: Article 23).

Palaeodocoileus gracilis was originally described by Spillmann (1931) from a crushed partial skull with antlers from the Late Pleistocene of Quebrada Chalang, Ecuador. This species was considered a synonym of *O. virginianus* by Wilson and Reeder (2005). After the description of *P. gracilis*, Frick (1937) described *Palaeodocoileus salinae* from a partial left ramus (FM 28284) from Salinas, Ecuador, with no diagnosis. Afterwards, Simpson

(1945) assigned the genus *Palaeodocoileus* to *Odocoileus*; and after, Churcher (1962) presented more specimens with antlers. The referred specimens by Frick (1937) and others (e.g. Churcher, 1962; and Tomiati and Abbazzi, 2002) have no diagnostic characteristics that distinguish them from *O. virginianus*, other than a slightly smaller size (which falls within the range of variation of modern populations and subspecies of *O. virginianus* such as *O. v. yucatanensis*), and have the same antler pattern and p4 morphology of this species (Gustafson, 1985). Thus, we consider *Odocoileus salinae* as a junior synonym of *O. virginianus* (ICZN, 1999: Article 23).

The specimen of Laguna de la Media Luna (HJ73 162) was reported as *Odocoileus* sp. and it was assigned to *O. virginianus* by us, following (Gustafson, 1985).

Species *Odocoileus hemionus* (Rafinesque, 1817b)

Fossil synonyms: *Cariacus ensifer* (in part, see discussion below) (Cope, 1889), *Cervus brevitrabalis* (in part, see discussion below) (Cope, 1889), *Odocoileus cascensis* (in part, see discussion below) (Frick, 1937). For a detailed synonym list of modern species see (Anderson and Wallmo, 1984).

Range in Mexico (Figure 8): El Golfo de Santa Clara, Sonora, Sonoran province (Croxen et al., 2007; White et al., 2010); Rancho la Brisca, Sonora, Sierra Madre Occidental province (Van Devender et al., 1985); Mina de San Antonio, San Luis Potosí (Arroyo-Cabrales and Polaco, 2003), Mina, Nuevo León, North Plateau province (Franzen, 1993, 1994); Zacoalco (Solorzano, 2002; Lucas, 2008b), and Chapala (Solorzano, 2002), Jalisco, La Cinta-Portalitos, Michoacán-Guanajuato (Díaz-Sibaja, 2013; Díaz-Sibaja et al., 2014b), Volcanic Axis province.

Age range: In Mexico, from the Late Pleistocene (Rancholabrean) to the Present. In North America it is doubtfully recorded since the Irvingtonian of Bautista, El Casco, and Irvington, California (Kurtén and Anderson, 1980).

Diagnosis: Medium-sized deer species, deep lachrymal fossa (Smith, 1991), medium sized brachydont teeth, absence of upper canines, three premolars and molars (Anderson and Wallmo, 1984), antlers dichotomously branched in a non-spiraled main axis, main axis at the first branching flat in transversal section, basal tine (brow tine) sometimes absent (Anderson and Wallmo, 1984; Gustafson, 1985; Smith, 1991), p4 molariform, incomplete anterior fossa, united to the posterior valley; posterolingual conid and posterior stylid contacting distally and lingually, posterolingual conid at 45° and expanded lingually; when heavily worn, the mesolabial and posterolabial conids form a posterolabial cristid; very small to absent entostylid.

Notes: *Cariacus ensifer* was described by Cope (1889), from a partial base of an antler (AMNH 8660). It was later ascribed to *Odocoileus ensifer* by Frick (1937), and later it was considered as a subjective synonym of *O. hemionus* by Kurtén and Anderson (1980). The morphology of the holotype antler (AMNH 8660) does not correspond with typical *O.*

hemionus specimens, it has a large brow tine, projected anteriorly and no other diagnostic features. This morphology was similar to a young anomalous specimen of *O. hemionus* (Fry and Gustafson, 1974), but the rest of the associated specimens show clear *O. virginanus* morphology and size (Frick, 1937). And thus, we consider *O. ensifer* (holotype only) it as a junior synonym of *O. hemionus*, and the rest of the referred specimens as *O. virginianus* (ICZN, 1999: Article 23).

Another species described by Cope (1889) was *Alces brevitrabalis*, based on a series of basal isolated antlers from Adams County, Washington. The holotype (AMNH 8654) and one of the referred specimens (AMNH 8655) are very large (similar in size to *Cervus canadensis*), are transversally flattened, but does not bear any of the brow tines characteristic of *Cervus canadensis*, but this may be due to abnormalities during development (Goss, 1983). Kurtén and Anderson (1980) consider this species tentatively as *Cervus* (?) *brevitrabalis*. Nevertheless, one of the referred specimens (AMNH 8658) is completely different from the holotype and the referred specimen of *Cervus* (?) *brevitrabalis*, it is considerably smaller, bears no brow tine and it is preserved until the first branching, which is dichotomic and flat, both diagnostic characteristics of *O. hemionus*. And thus, we consider this specimen as referable to *O. hemionus* (ICZN, 1999: Article 23).

Odocoileus cascensis was described by Frick (1937) from a series of mandibular elements and isolated antlers. This species was later considered as a subjective synonym of *O. hemionus* by Kurtén and Anderson (1980). The mandibular elements assigned and figured by Frick (1937) as *O. cascensis* (FAM 17813, and FAM 17811) bears the typical p4 morphology of *O. hemionus*, and the maxillary elements (FAM 17810A) is similar in size to *O. hemionus*. However, the antlers assigned to this taxon, and specially the FAM 17834A show the typical size and spiraled morphology of O. virginianus. Thus, we consider the mandibular and maxillary elements of *O. cascensis* as *O. hemionus*, and the antlers as *O. virginianus* (ICZN, 1999: Article 23).

Genus *Navahoceros* Kurtén, 1975

Species Navahoceros fricki *(Schultz and Howard, 1935)*

Synonyms: *Rangifer fricki* (Schultz and Howard, 1935), *Cervus lascrucensis*? (Frick, 1937), *Odocoileus halli* (Álvarez, 1969).

Range in Mexico (Figure 8): Golfo de Santa Clara, Sonora, Sonoran province (Croxen et al., 2007); Cueva Bustamante, and Cueva La Mina or Cueva de La Boca, Nuevo León, Tamaulipecan province (Kurtén, 1975; Arroyo-Cabrales and Polaco, 2003); Rancho La Amapola, El Cedral, San Luis Potosí (Álvarez et al., 2012), Arroyo el Cedazo, El Cedazo local fauna (Tacubaya Formation), Aguascalientes, South Plateau province (Mooser and Dalquest, 1975); San Josecito Cave, Nuevo León, Sierra Madre Oriental province (Kurtén, 1975; Kurtén and Anderson, 1980; Arroyo-Cabrales and Polaco, 2003; Arroyo-Cabrales and Johnson, 2008); Chapala, Jalisco (Rufolo, 1998; Solorzano, 2002; Lucas, 2008a),

Tlapacoya, Estado de México, Volcanic Axis province (Álvarez, 1969; Kurtén, 1975; Kurtén and Anderson, 1980); Sótano de San Agustín, Oaxaca, Oaxaca province (Kurtén, 1975; Arroyo-Cabrales and Polaco, 2003).

Age range: In Mexico its known only for the Rancholabrean. In North America its known from the Blancan (Morgan et al., 2008) to the Rancholabrean.

Diagnosis: Medium to large-sized deer species, with very thick-set limb bones and short metapodials, females antlerless, males with simple forked antlers (Kurtén, 1975); the antlers are three tined (Kurtén and Anderson, 1980), with a large basal tine (brow tine) pointing medially and backwards, the other tines are dichotomously branched, with the area of divergence wide and flat, the tines are subequal but the posterior one tends to be more cylindrical and large, whereas the anterior tine is usually slightly hook-shaped, bending upwards and with a more flat transversal section, but never palmate. Brachydont teeth with heavy-crenulated enamel. Upper molars with well-developed styles. P4 with complicated-shaped fossa, with sinuous enamel, usually with a fosseta in the posterolingual crista, and if present, a central fold located anteriorly. The p4 is molariform, with a well-developed entostyle, and anterior and posterior fossetids, the posterior "selenid" is smaller and mesiodistally compressed, with a deep posterolabial conid.

Notes: The Golfo de Santa Clara record of this species is stated as cf. and no other information about the referred specimens is provided (Croxen et al., 2007). This fossil fauna is regarded as Irvingtonian (Morgan, 2008), nevertheless the presence of *Bison* (a fossil index for the Rancholabrean) in many localities suggest a mixture of Irvingtonian and Rancholabrean faunas (White et al., 2010). And since, no stratigraphic analysis of the *Navahoceros* remains from this area was conducted, we consider it as Rancholabrean.

Previous works in La Cinta-Portalitos local fauna, Michoacán-Guanajuato report the presence of *Navahoceros fricki* (Díaz-Sibaja, 2013; Díaz-Sibaja et al., 2014b). But after thorough comparison with the material described by Álvarez (1969) housed at the Instituto Nacional de Antropología e Historia (INAH), and the material of San Josecito Cave housed at the Natural History Museum of Los Angeles County, we came to the conclusion that the fossils from La Cinta-Portalitos does not represent *Navachoceros fricki* and are instead, are a collection of large *Odocoileus hemionus*.

Genus *Mazama* Rafinesque, 1817

Modern species present in Mexico: *Mazama pandora* Merriam, 1901, *Mazama temama* (Kerr, 1792).

Genus synonyms: *Moschus* (Erxleben, 1777), *Cervus* (Kerr, 1792).

Range in Mexico (Figure 8): La Mixtequilla, Veracruz, Gulf of Mexico province (Polaco, 1995); Gruta de Loltún, Yucatán, Yucatan province (Arroyo-Cabrales and Álvarez, 2003; Arroyo-Cabrales and Polaco, 2003).

Age range: In Mexico it is known since the Rancholabrean (Polaco, 1995; Arroyo-Cabrales and Álvarez, 2003; Arroyo-Cabrales and Polaco, 2003). In South America it is known since the Lujanian, Late Pleistocene (Churcher, 1962).

Diagnosis: small deer species, with simple, small unbranched antlers (Goss, 1983). The p4 is molariform, and it is very similar to *Odocoileus* spp., nevertheless, the posterolingual conid lacks the connection to the posterolabial cristid, and is connected directly to the posterior stylid; this union forms the posterior fossa.

Notes: Some authors recognize the presence in Mexico of *Mazama pandora* and *Mazama americana* (e.g. Ceballos and Arroyo-Cabrales, 2012). Nevertheless, phylogenetic and karyogenic studies have showed that *M. americana* and *M. temama* are different species (Jorge and Bernirschkle, 1977; Escobedo-Morales et al., 2016), with the latter in Mexico. Thus, we follow the Groves and Grubb (2011) criteria and consider them as separate species.

The material of La Mixtequilla is found in association with *Capromeryx minor*, *Stockoceros conklingi*, and *Tetrameryx shuleri* (Polaco, 1995), all restricted to the Rancholabrean. On the other hand, the material of Gruta de Loltún comes from several layers from the latest Rancholabrean, to the Early Holocene (Arroyo-Cabrales and Álvarez, 2003). These records are within the modern geographical range of both *Mazama pandora* and *M. temama*, the brocket deer recognized for Mexico. Also, are the earliest appearance of *Mazama* sp. in the fossil record of North America.

Subfamily Cervinae Goldfuss, 1820

Genus *Cervus* Linnaeus, 1758

Species *Cervus canadensis* (Erxleben, 1777)

Synonyms: *Cervus elaphus* (in part, see discussion below) Linnaeus, 1758, *C. merriami* (Nelson, 1902).

Age and range in Mexico: It is found only in the Holocene of Cuatro Ciénegas Basin, Coahuila, North Plateau province (Gilmore, 1947).

Diagnosis: Large-sized deer species, only the males carry antlers, the antlers can be as large as 1.5 m in length, and have 12-14 points (Goss, 1983), antlers highly ornamented, the main beam is scalloped, with the valleys and crests, ventrally and dorsally placed, respectively; tines emerge from every crest of the main beam, and are dorsally and medially oriented; the basal tine (brow tine) is large, placed close to the burr, and anteriorly directed; a second tine (bez tine) may be present close to the basal tine, giving the appearance of a pair of basal tines; a distal "crown" may be present, the "crown" is a highly reduced repetitive structure, subequal to the scalloped pattern of the middle beam. The p4 is not molariform, the anterior, mesolingual, and posterolingual conids are well differenciated; an anterior and posterior conids are present; the posterolabial cristid is narrow, and the

anterolingual and posterolingual cristids are well-developed, although the anterolingual is larger (Frick, 1937; Hillson, 2005).

Notes: In this work, we recognize the status of the wapiti (*C. canadensis*) as a separate species from the red deer (*C. elaphus*), based upon recent molecular and morphological studies which points to a Miocene divergence between these species (Ludt et al., 2004; Groves and Grubb, 2011; Lorenzini and Garofalo, 2015). And thus, the records of *C. elaphus* in North America are referred to *C. canadensis*.

The wapiti has no fossil record in Mexico, as stated by previous authors (Ferrusquía-Villafranca et al., 2010). Although, this species had historical range in northern Mexico, as *Cervus canadensis merriami* (Leopold, 1959). The record of Cuatro Ciénegas, Coahuila, in the North Plateau province comes from several cave sites used as human habitation; the remains of *C. canadensis* are subfossils from the Holocene, and were deposited through human agency (Gilmore, 1947). Other allegedly *C. canadensis* records includes Zacoalco (Solorzano, 2002; Lucas, 2008b), and Chapala (Downs, 1956; Rufolo, 1998; Solorzano, 2002; Lucas, 2008a), in the state of Jalisco. The records of Zacoalco appear just listed and no fossil material is referred or presented in figures. The Chapala record was originally made by Downs (1956) under similar conditions, until Rufolo (1998) reported an antler (LACM 1781), and a radius (LACM 141365). The radius is also not represented in either, figures or tables, and it is not discussed either, making its assignation difficult to test. On the other hand, the antler is figured and its measurements are presented in the table 9 (Rufolo, 1998). Both the greatest anteroposterior (39.8 mm) and transversal (34 mm) diameter of the pedicel are within the range of *Odocoileus hemionus* and large *O. virginianus* (Díaz-Sibaja, 2013), and the element (depicted in figure 13D) has no diagnostic features of *Cervus* sp. but it does possess the overall morphology of *Odocoileus* spp., and thus, we assign this element to this genus. This makes the Jalisco's record of *Cervus* in the late Pleistocene dubious.

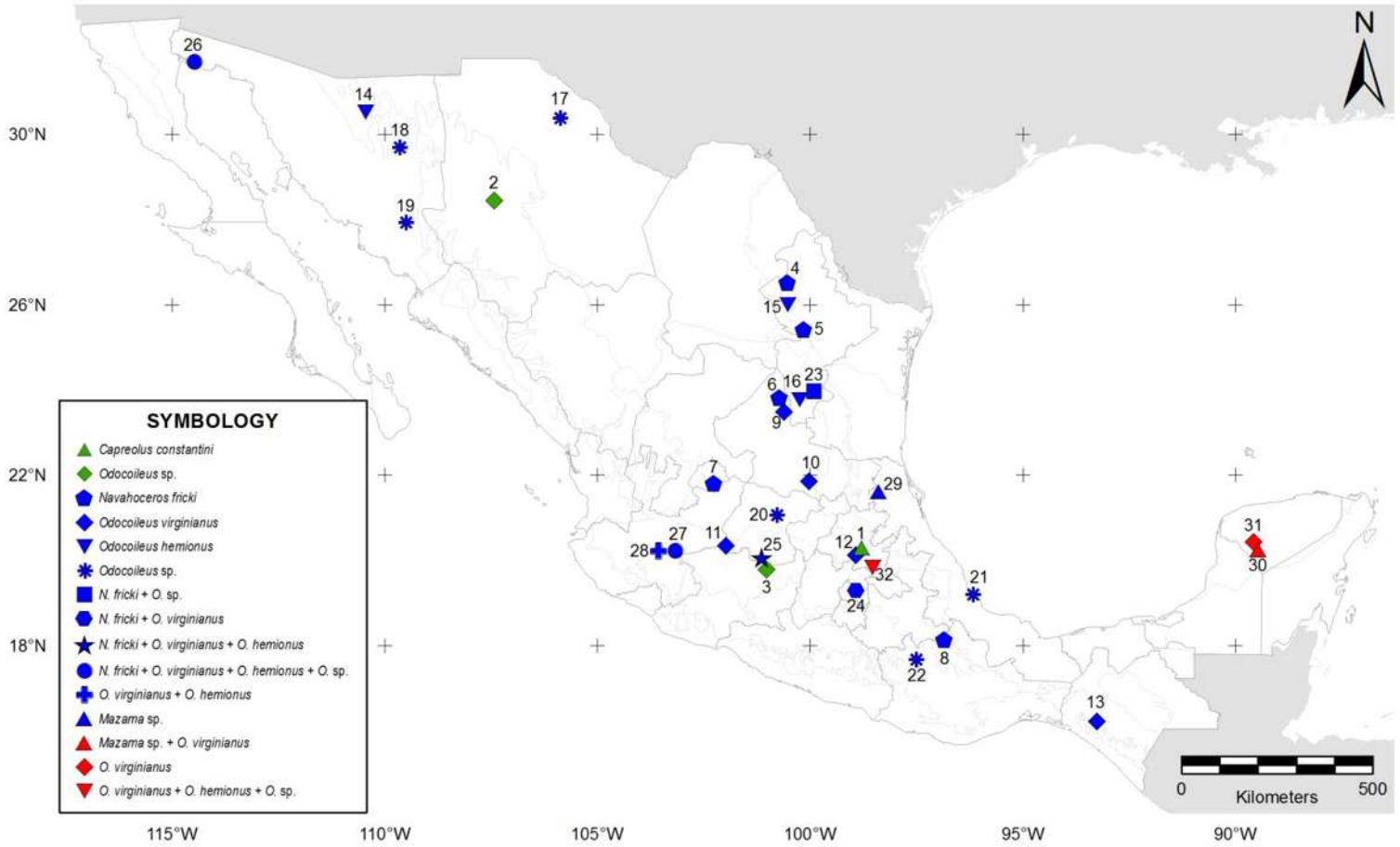

Figure 8. Pliocene to Pleistocene sites with fossil Cervidae. Green: Pliocene records, blue and red: Pleistocene records. (1) Santa María Amajac, (2) Miñaca, (3) Uruétaro, (4) Cueva Bustamante, (5) Cueva La Mina, (6) El Cedral, (7) Arroyo el Cedazo, (8) Sótano de San Agustín, (9) Cueva La Presita, (10) Laguna de la Media Luna, (11) La Piedad-Santa Ana, (12) Las Cajas, (13) Villaflores, (14) Rancho La Brisca, (15) Mina, (16) Mina de San Antonio, (17) Mina Erupción, (18) San Clemente de Térapa, (19) La Botana, (20) San Miguel de Allende, (21) Buenavista, (22) Viko Vijin, (23) San Josecito, (24) Tlapacoya, (25) La Cinta-Portalitos, (26) Golfo de Santa Clara, (27) Chapala, (28) Zacoalco, (29) La Mixtequilla, (30) Gruta de Loltún, (31) Cueva de Lara (Actun Lara), (32) Tepeapulco.

Conclusion

In total, we recognize the validity of 28 fossil taxa (Table 1), including the records of Blancan *Odocoileus* of unknown species, and a yet to be described *Ovis* species from the Irvingtonian of the Golfo de Santa Clara beds. Of these taxa, six (*Pseudoparablastomeryx*, *Nanotragulus*, *Plioceros*, *Sphenophalos*, *Texoceros*, and *Mazama*) are maintained at genus level due to the lack of diagnostic fossil material to assign them to a particular species. A similar scenario is frequent for *Bison*, and *Odocoileus* records.

In this work we found no evidence of Mexican fossil record for *Cervus canadensis* and *Bison bison* as reported in previous works. These species are present only in the Holocene archaeological record, and only *C. canadensis* is a suitable candidate to be found as fossil in Mexico, since molecular evidence suggests that *B. bison* arose during the early Holocene (4-5 Ka) in southern Canada. The allegedly records of *B. bison* may be of its Latest Pleistocene-Early Holocene ancestor, *Bison antiquus* with the "occidentalis" morphology.

Finally, we synonymize a total of 11 taxa: *Tetrameryx mooseri* and *T. tacubayensis* (syn= *T. shuleri*), *Neomeryx finni* (syn= *Antilocapra americana*), *Ovis catclawensis* (syn= *O. canadensis*), *Odocoileus laevicornis*, *O. sellardsiae*, *O. dolychopsis*, and *O. salinae* (syn = *O. virginianus*), *O. ensifer* and *O. cascensis* (syn = *O. virginianus* in part, and *O. hemionus* in part, see discussion on these taxa), and *Cervus brevitrabalis* (syn = *O. hemionus*). We also considered *O. brachyodontus* as a *nomen nudum*. And we reassigned *Bison aguascalentensis* from *B. alaskensis* synonym to *B. latifrons*.

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Capítulo 2. A combined mesowear analysis of Mexican *Bison antiquus* shows a generalist diet with geographical variation (artículo en prensa)

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A combined mesowear analysis of Mexican *Bison antiquus* shows a generalist diet with geographical variation

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Running Header: Mexican *Bison antiquus* diet.

Abstract.—*Bison antiquus* was one of the largest and most widely distributed megafaunal species during the Late Pleistocene in North America, giving rise to the modern plains bison in the middle Holocene. Despite the importance of the ancient bison, little is known about its feeding ecology. We employed a combination of extended mesowear, and mesowear III to

infer the dietary preference and habitat use of three Mexican samples of *B. antiquus*. Two northern samples from the Transmexican Volcanic Belt morphotectonic Province: La Piedad-Santa Ana and La Cinta-Portalitos, as well as one southern sample from the Sierra Madre del Sur morphotectonic province: Viko Vijin. We found that the northern Mexican samples were primarily non-strict grazers, while the southern sample displays a pattern consistent with mixed feeding habits. This suggests variability among the diets of these bison samples, caused by different paleoenvironments. This evidence complements the paleoenvironmental reconstructions in the studied localities; for the northern samples, open prairies composed of patches of woodland or shrubland and for the southern locality a fluvial floodplain with short-lived vegetation. In both scenarios, grasses (Poaceae) were non-dominant. The dietary habits of our samples of ancient bison in Mexico are the southernmost dietary inference for the species in North America and expand our knowledge of the dietary habits of *Bison antiquus* during the late Pleistocene.

Introduction

Dental mesowear is a useful tool to infer the diet of extinct herbivores. It was originally developed for herbivorous mammals with lophodont teeth and labiolingual mandibular excursion, and it was based on the analysis of the relief (high or low) and shape (sharp, rounded or blunt) of the ectoloph's cusps of second upper molars (Fortelius and Solounias, 2000). Later, the original method was extended to include the analysis of the upper third molar in ruminants (Franz-Odendaal and Kaiser, 2003). Also, three univariate scales of dental wear have been developed to facilitate the comparison between mesowear patterns; one ranges from 0 to 3 and it

is used for upper dentition (Rivals et al., 2007a), the second goes from 0 to 4 and it is employed for upper postcanine dentition (Kaiser, 2011; Kaiser et al., 2013), and the other goes from 1 to 5 and it is used in both upper and lower teeth (Fraser et al., 2014). Recently, mesowear III was developed to analyze the lingual enamel band of the paracone and metacone; this method has a scoring system that considers four wear stages (1 to 4) of the mesial and distal enamel bands, and the shape of its junction (also 1 to 4), where each stage is associated with the attrition signal, linked to a particular dietary guild (Solounias et al., 2014). The original mesowear score, its modifications, and the mesowear III method can be used together to better predict ruminant diet than any single variable (Danowitz et al., 2016).

Mesowear is considered one of the main dietary approaches to infer diet (Fortelius and Solounias, 2000; Hoffman, 2006; Semprebon and Rivals, 2007; Rivals et al., 2009a, 2009b; Blondel et al., 2010), along with other approaches, such as stable carbon isotope analysis and dental microwear. In ruminants, mesowear provide additional information, such as the geographical (Rivals et al., 2007a) and temporal variation of diet (Rivals and Semprebon, 2006; Fraser and Theodor, 2013).

One of the most conspicuous ruminants in the North American Pleistocene was the bison (*Bison* spp.), it was the largest, numerous and the most widely distributed ruminant (McDonald, 1981; Shapiro et al., 2004). Bison ranged from Baillie Island in the Yukon, Canada (Harrington, 1990) to Matagalpa, Nicaragua (Howell and MacDonald, 1969). In this wide geographical range, the bison mesowear studies are scarce, and are focused on topics such as diet quality in *Bison bison* (Berini, 2010), ontogenetic diet variation in *B. priscus* (Rivals et al., 2007b) and geographical diet variation in some species of the genus (Rivals et al., 2007a). Such studies were

performed with fossil samples from mid and high latitudes of North America, while the diets of the southern bison species are unknown.

Five species of Bison have been reported from the Quaternary of Mexico: *Bison alaskensis*, *B. antiquus*, *B. bison*, *B. latifrons*, and *B. priscus* (Arroyo-Cabrales et al., 2002; Ferrusquía-Villafranca et al., 2010). Of these species, *B. bison* appears between 4,000 and 5,000 years before present, during the Early Holocene in Southern Canada (Wilson et al., 2008). Among Pleistocene species, *B. antiquus* has the widest geographic range in Mexico, with fossil material from Baja California (Skinner and Kaisen, 1947; Ferrusquía-Villafranca and Torres-Roldán, 1980; McDonald, 1981), Baja California Sur (McDonald, 1981), Estado de México (Hibbard, 1955), Jalisco (Downs, 1956; McDonald, 1981; Lucas, 2008), Puebla (McDonald, 1981), San Luis Potosí (Skinner and Kaisen, 1947; McDonald, 1981), Michoacán (Díaz-Sibaja, 2013), and Oaxaca (Jiménez-Hidalgo et al., 2013).

Since *Bison antiquus* is the most abundant bison in North America and Mexico and given the scarce knowledge of its dietary patterns in its southernmost range, the main objectives of this paper are 1) to infer the diet of three Mexican samples of *B. antiquus*: two from West Central Mexico and one from Southern Mexico, and 2) to compare it with the diet of *B. antiquus* from temperate North America and with the modern bison.

Materials and methods

Locality and stratigraphic information.—Specimens of *Bison antiquus* for this study comes from three local faunas in West-Central and Southern Mexico, named "La Piedad-Santa Ana", "La Cinta-Portalitos" and "Viko Vijin" (Fig. 1).

92 La Piedad-Santa Ana is located between the municipalities of La Piedad de Cabadas
93 (Michoacán state) and Pénjamo (Guanajuato state). In the east, its geomorphology is dominated
94 by the alluvial plain of the Lerma river and volcanic hills to the west. Also, there are small
95 extinct monogenetic volcanoes in the North and South of the study area. Stratigraphy (Fig. 2) is
96 composed of an alternation of fluvial and lacustrine sequences with some volcanic tuffs at the
97 base, and archaeological elements to the top. Fossils are embedded in a yellowish conglomerate
98 with a sandy matrix (Díaz-Sibaja 2013; Díaz-Sibaja et al. 2012; Marín-Leyva, De Miguel, et al.
99 2016).
100 La Cinta-Portalitos is located between the municipalities of Cuitzeo (Michoacán state) and
101 Uriangato (Guanajuato state). The geomorphology is dominated by extinct shield volcanoes to
102 the West and Northwestern, the latter one with faults of NE-SW direction. To the North, ash-
103 cinder, and maars volcanoes occur, and into the south, there is the recent bottom of Cuitzeo
104 Lake. Stratigraphy (Fig. 2) is mainly composed of lacustrine sequences, dominated by diatomite
105 beds; between these facies, there are some fluvial beds with sand and some sandy tuffs. To the
106 top, there are archaeological remains. The fossils occur disarticulated in an extensive bed of
107 brown conglomerates with silt and sandy matrix (García-Zepeda 2006; Marín-Leyva, De Miguel,
108 et al. 2016).
109 The Viko Vijin local fauna comes from six localities from the municipalities of Concepción
110 Buenavista, San Antonio Acutla, Teotongo, and Villa Tejupam de la Unión, and is located in the
111 northwestern region of the Oaxaca state. The area's geomorphology is dominated by hills and
112 gullies from the Mixteca Alta Oaxaqueña. Stratigraphy (Fig. 2) is composed mainly of fluvial
113 sequences with abundant silty to sandy strata; in the base of the sequence, there are volcanic tuffs

or breccias. Fossils occur in clayey and sandy strata with some silt and abundant caliches or nodular calcretes (Jiménez-Hidalgo et al., 2011, 2013).

Taxonomic identification.—Selected molars were identified as *Bison antiquus* by morphological and morphometric comparison with teeth from the literature (Allen, 1876; Chandler, 1916; Hillson, 2005), by direct comparison with osteological collections (such as the one of the Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano", Instituto Nacional de Antropología e Historia), and by their association with several isolated horn cores and complete skulls of this species in the localities of this study (McDonald, 1981; Jiménez-Hidalgo et al., 2013).

Mesowear.—We selected second (Fortelius and Solounias, 2000) and third upper molars (Franz-Odendaal and Kaiser, 2003) of adult individuals in an intermediate wear stage, between the stages S-1b to S-3 for M2, and S2 to S4a for M3 (Skinner and Kaisen, 1947). Our sample size consisted of 9 specimens for “La Cinta-Portalitos”, 11 specimens for “La Piedad-Santa Ana” and 16 for “Viko Vijin” (Supplementary dataset 1). Although it was originally suggested that the minimum number of observations to get a robust mesowear signal should be 10 (Fortelius and Solounias, 2000; Kaiser et al., 2000), posterior studies suggested that smaller sample sizes are enough to offer insights into paleodiet and paleoecology (Bernor et al., 2014). Since then, many studies have offered paleodietary and paleoecological inferences with small sample sizes, ranging from 9 to 3, and even 1 (Danowitz et al., 2016).

For the scoring of mesowear variables (Fig. 3), the labial portion of the ectoloph’s cusps of the paracone and metacone were observed and categorized by its relief (high or low) and its

shape (sharp, rounded or blunt) (Fortelius and Solounias, 2000). To control the interobserver error when scoring the relief, we employed the methodological proposal of Merceron et al. (2007) in which the relief state (high or low) was obtained by dividing the distance that connects the highest point of the evaluated cusp and the lowest point of the intercuspidal area (x in Fig. 3.1) by the cusp height (y in Fig.3.1); when the value was greater than 2, we consider it as a low cusp. We employed the software ImageJ 1.50i for these measurements. Also, we scored the cusp shape according to the degree of facet development; when no facets were distinguishable, we consider the cusp as blunt; when there was no distinguishable junction between facets, we consider the cusp as rounded, and when this junction was distinguishable, we consider the cusp as sharp (Fortelius and Solounias, 2000; Kaiser et al., 2000; Merceron et al., 2007).

We also evaluated the lingual facets (mesial and distal) of the paracone and its junction (Fig. 3), categorizing the facets as 1) flat surface with no gouges, 2) surface nearly flat and with some gouges, 3) rounded surface with abundant gouges, 4) smooth rounded surface with no gouges and poorly defined edges. The j-junction was categorized in 1) well defined and sharp edge, 2) poorly defined edge, with some gouges, 3) rounded edge, poorly defined, smooth but still differentiated edge, 4) undifferentiated mesial and distal cusps, j-junction lost (Solounias et al., 2014; Danowitz et al., 2016). We observed the analyzed molars with a stereoscopic microscope to discard those with taphonomical alterations such as mechanical fractures (Fortelius and Solounias, 2000) or abrasion caused by sand (Blondel et al., 2010). To minimize subjectivity when recording the mesowear variables, we compared our scorings with the original diagrams and photographs of Fortelius and Solounias (2000) and Danowitz et al. (2016), making sure we obtained similar results to those of experienced observers, since mesowear is less prone to observer variation than other methods such as dental microwear (Loffredo and DeSantis, 2014).

160 To identify the mesowear pattern associated with a particular dietary category (browser,
161 mixed feeder, strict grazers and non-strict grazers) of the *B. antiquus* samples of this study, we
162 performed a cluster analysis with 27 model species with known dietary preferences taken from
163 the Fortelius and Solounias (2000) original database and with the variables Per-High, Per-Sharp,
164 and Per-Blunt (percentages of high, sharp, and blunt cusps in the total sample), using the
165 complete linkage (without standardization of the data) clustering method, and Euclidean distance
166 for scaling (Fortelius and Solounias, 2000; Franz-Odendaal and Kaiser, 2003; Clauss et al.,
167 2007).
168 In addition to the cluster analysis, we transformed the original Fortelius and Solounias (2000)
169 database to the univariate 0-3 scale of mesowear to compare the signatures of our three samples
170 of *B. antiquus* with known dietary categories (browser, grazer and mixed feeder) of model and
171 extinct *Bison* species as follows: high and sharp cusps were assigned with a 0 score, high and
172 rounded with 1, low and sharp, and low and rounded with 2, and blunt cusps were assigned with
173 a 3 score (Rivals et al., 2007a). Additionally, we performed Pearson's chi-squared tests ($\alpha = 0.05$)
174 to compare the mesowear patterns of the 0-3 univariate scale (Fortelius and Solounias, 2000;
175 Rivals et al., 2007a) and the mesowear III (Solounias et al., 2014) with our samples, to determine
176 the similarities in the wear patterns with the model dietary groups (i.e. grazer, browser, mixed
177 feeder).
178 Although we recognized that the relief and cusp shape can be affected by phylogenetic signal
179 creeping in (Fortelius and Solounias, 2000), independent data suggest that when a phylogenetic
180 control is introduced, the correct classification of a samples only improves by only one percent
181 (Fraser and Theodor, 2011), and thus, we did not consider any use of a phylogenetic control.

182 Finally, to predict the dietary guild with more accuracy, we combined the data of extended
183 mesowear (0-3 univariate scale) and mesowear III (scores of the mesial, distal and j-junction) to
184 perform a discriminant analysis (see Supplementary data set 2 for raw data). This combination of
185 analyses can predict better the diet of a fossil sample than just one variable because they
186 encompass different parts of the chewing cycle (Danowitz et al., 2016; Janis, 1990). Mesowear
187 univariate data was transformed from Fortelius and Solounias (2000), mesowear III data was
188 taken from Danowitz et al. (2016), and for the Mexican data, an average per sample was
189 employed. Originally, the combination of extended mesowear and mesowear III (Danowitz et al.,
190 2016) employed the 0-6 univariate mesowear scale developed by Mihlbachler et al. (2011). This
191 scale was developed for Equoidea, but since horses have unique traits in their wear patterns, and
192 given that the 0-3 univariate mesowear scale (Rivals et al. 2007) was developed for its use in
193 bison, and encompasses most of the possible cusp relief and shape combinations seen in nature,
194 we employed the 0-3 scale, transforming the dataset of Danowitz et al. (2016) to this scale. The
195 selected discriminant method was linear and common covariance, because our extended
196 mesowear and mesowear III data came from the same order of magnitude (i.e. scales) and were
197 in covariance (i.e. the same teeth were scored both in the lingual and labial part of the ectoloph).
198 Dietary category (browser, grazer or mixed feeder) was the grouping variable (Danowitz et al.,
199 2016). Finally, in order to test statistic differences among the multivariate centroids of the dietary
200 categories, we performed a Wilks' lambda test ($\alpha = 0.05$). The cluster analysis was performed
201 with Statistica 10 software, while the discriminant analysis, chi-square, and Wilk's lambda tests
202 were carried out with JMP 8.0.
203

204 *Repositories and institutional abbreviations*.—The fossil specimens from La Piedad-Santa Ana
205 and La Cinta-Portalitos are housed at the Colección del Laboratorio de Paleontología,
206 Universidad Michoacana de San Nicolás de Hidalgo (UM, CPOEI, PMB) located at the Faculty
207 of Biology. Specimens from Viko Vijin are housed at the Colección Científica del Laboratorio
208 de Paleobiología, campus Puerto Escondido, Universidad del Mar (UMPE).
209

210 ## Results

211

212 The analyses showed that the mesowear patterns in the Mexican samples of *Bison antiquus* were
213 similar to those of non-strict grazers and mixed feeders. A summary of these mesowear patterns
214 is shown in Table 1 (see raw mesowear values in Supplementary data set 1). Extended mesowear
215 signatures in both La Cinta-Portalitos and La Piedad-Santa Ana showed a majority of low cusps
216 (66.6% and 54.5 %), whereas the opposite was found in Viko Vijin, where the total sample
217 displayed high cusps. Rounded cusps where the predominant among the samples. On the other
218 hand, mesowear III signatures showed a large proportion of abrasiveness, with indices above 2.8,
219 and in some cases, the maximum wear index is reached (see Viko Vijin's j-junction score).
220 The cluster analysis (Fig. 4.1) grouped the three Mexican samples within the non-strict
221 grazers. Samples from La Cinta-Portalitos and La Piedad-Santa Ana formed one cluster close to
222 the one of *Connochaetes taurinus* and *Alcelaphus buselaphus*. Meanwhile, the Viko Vijin sample
223 formed a cluster with *Kobus ellipsiprymnus*. The univariate mesowear analysis (Fig. 4.2) showed
224 the highest values for La Cinta-Portalitos sample (1.66), followed by La Piedad-Santa Ana
225 sample (1.54) and ending with the Viko Vijin sample (0.93).

There were no statistically significant differences between the mesowear univariate scores (0-3) of La Cinta-Portalitos and La Piedad-Santa Ana with the grazer guild ($p = 0.32$, $p = 0.1$, respectively), but there were statistically significant differences with the mixed feeder ($p = 0.0002$, $p = 0.0003$, respectively) and browser guilds ($p < 0.0001$, in both cases). On the other hand, the Viko Vijin scores show no statistically significant differences with the mixed feeder guild ($p = 0.29$), but statistically significant differences with the grazer ($p < 0.0001$) and browser ($p = 0.005$) guilds.

The mesowear III analysis (Fig. 4.3) showed no statistically significant differences between the scores of La Cinta-Portalitos and the grazer ($p = 0.54$) and mixed feeder ($p = 0.1$) guilds, but there were differences with the browser guild ($p < 0.0001$). As for the scores of La Piedad-Santa Ana, we found no statistically significant differences between the mesowear III scores and the grazer guild ($p = 0.75$), but we found differences with the mixed feeder ($p = 0.02$) and browser ($p < 0.0001$) guilds. The Viko Vijin scores showed no statistically significant differences with the mixed feeder guild ($p = 0.6$), but statistically significant differences with the grazer ($p = 0.01$) and browser ($p < 0.0001$) guilds.

Finally, the discriminant analysis (Fig. 4.4) classified the samples of La Cinta-Portalitos and La Piedad-Santa Ana as grazers with posterior probabilities of 88% and 81% respectively, while the Viko Vijin sample was classified as a mixed feeder, with a probability of 75%. Also, the multivariate centroids of the dietary categories showed statistically significant differences between groups (Prob > F = < 0.0001).

Discussion

249 *Cluster analysis.*—In the cluster analysis (Fig. 4.1) the samples from Michoacán-Guanajuato
250 comprised one cluster, and this was close to the one formed by *Connochaetes taurinus* and
251 *Alcelaphus buselaphus*, which are identified as non-strict grazers (Fortelius and Solounias,
252 2000). The Viko Vijin sample formed a cluster with the waterbuck (*Kobus ellipsiprymnus*). The
253 blue wildebeest (*C. taurinus*) diet consists of 87.5% of monocots, 12% dicots, and 0.5% of fruits
254 (Gagnon and Chew, 2000). The blue wildebeest preferred habitat consists of open bushland and
255 short grassy plains, always with a close (< 20 km) water source (Kingdon, 2013). On the other
256 hand, the hartebeest (*A. buselaphus*) diet comprises of 75% monocots, 20% dicots, and 5% fruits
257 (Gagnon and Chew, 2000). Hartebeests are considered as an ecotone species (Kingdon, 2013),
258 their preferred habitat are boundaries between open grassy plains (or glades) and parkland,
259 woodland or scrub; their movements are often within the drainage lines in the dry season and in
260 more open plains during the rainy season (Booth, 1985; Kingdon, 2013). Similarly, *Kobus*
261 *ellipsiprymnus* is regarded as a non-strict grazer (Fortelius and Solounias, 2000), its diet consists
262 of 84% monocots, 15% dicots, and 1% of fruits (Gagnon and Chew, 2000) and its preferred
263 habitat consists of mosaics of savanna woodlands and forest-savanna, with permanent water
264 sources (Kingdon, 2013).

265 Also, the cluster analysis showed that the modern plains bison (*Bison bison*) is classified
266 within the strict grazer category (Fortelius and Solounias, 2000), and it is not near the mesowear
267 pattern of our samples of *Bison antiquus* (Fig. 4.1, bb: *Bison bison*). These data suggests a
268 distinct and broader dietary niche for the ancient Mexican bison populations analyzed when
269 compared to its alleged modern plains analog and a wider range of habitat use by the Pleistocene
270 *Bison antiquus* individuals analyzed in this study.
271

Age of studied bison samples.—The age of the bison samples used in this study is important in order to compare them. The radiometric age of la Piedad-Santa Ana site is unknown, but the age of the other two sites has been inferred. *Bison* material of Viko Vijin has been dated by the uranium series based on 230Th-234U-238U method, providing an estimated age of 36 ka for the fossil localities (Ordoñez-Regil et al., 2016). We inferred the age of la Cinta-Portalitos by the relationship of dated radiocarbon sections of a core made in the Cuitzeo Lake (Israde-Alcántara et al., 2010) and the depth in which the fossil bed was found, thus providing an estimate age of 24.05 ka (with a maximum of ca. 35 ka and a minimum of ca. 18 ka). This shows that both northern and southern Mexican samples are of comparable age, both occurring during the middle Wisconsin glacial stage. Under this scenario, caution must be taken when comparing different univariate bison scores from the literature. For example, *B. antiquus* from New Mexico and New Mexico-Texas samples, date back to 10.5 ka (Rivals et al., 2007a) and 10-15 ka (Barrón-Ortíz, 2016), both close to the Younger Dryas event ca. 10-11.6 ka, and the Bølling-Allerød warm period respectively (Björck, 2007), and far from the estimated ages of our study sites. Other bison samples also have this age pattern, *B. priscus* from Alaska dates from 11.99 ka (Rivals et al., 2007a). Only two dated bison samples are known from both glacial (21-60 ka) and late glacial (10-13 ka) stages, unfortunately these samples were not identified to species level (Barrón-Ortíz, 2016), thus obscuring the paleoecological inference of those mesowear scores, since they can represent the signal of various species.

Modern and extinct bison wear patterns.—Our results suggest that the Mexican samples analyzed display a mixed feeder pattern, rather than a strict grazer pattern. This is similar to the diet of *Bison antiquus* from Rancho La Brea, inferred from dental boluses in which, the

consumption of grasses was only 13.4% of the diet, compared with an 86.6% of gymnosperms and dicotyledons (Akersten et al. 1988).

On the other hand, our extended mesowear univariate scores show two patterns, more abrasive scores for La Cinta-Portalitos (1.66) and La Piedad-Santa Ana (1.54), and a less abrasive score for Viko Vijin (0.93). The scores from the northern Mexican samples (Fig. 4.2) are similar to one previously known *Bison antiquus* score (1.56) from Plainview Quarry (BaPV), Hale County, Texas (Rivals and Semprebon, 2012); and are lower than the 1.83 score from Ingleside (BaIP), San Patricio County, Texas (Rivals and Semprebon, 2012), the 1.93 score from Blackwater Draw (BaBC), Clovis Pit, Curry County of (Rivals and Semprebon, 2012), and the 1.88 score from Blackwater Draw (BaBD), Dry Cave, and Dark Canyon Cave, New Mexico and Lubbock Lake, and Scharbauer Ranch, Texas (Barrón-Ortíz, 2016). Also, our scores from northern Mexico are higher than the 1.31 score from Folsom Quarry, Union County, New Mexico (Rivals et al., 2007a). In contrast, the Viko Vijin sample score is the lowest for the species (0.93). The low latitude provenance of the sample and the association of the diet and the different environment and vegetation structure can explain this low score, as was explained above.

Mesowear univariate scores from other bison fossil species are known. Two samples of *Bison* sp. from Dalhart Sideroad Pit, Channing, Hartley County, Texas, and Seminole Field Station B, Pinellas County, Florida display a 1.05 mesowear score (Rivals et al., 2007a). There are two known *Bison* sp. fossil samples from Alberta, Canada, with mesowear data at two different times, one preglacial sample with a 1.67 score, and one postglacial sample with a 1.86 score (Barrón-Ortíz, 2016). A sample of steppe bison, *B. priscus* from the Fairbanks Area, Alaska, displays a score of 1.1 (Rivals et al., 2007a). Despite this mesowear spectrum, the genus *Bison*

318 and its fossil species still fall within the grazer univariate score range (Rivals et al., 2007a). The
319 northern Mexican samples display the highest values, and the Viko Vijin sample has the lowest
320 values. The differences between the Mexican samples are probably due to dissimilarities in the
321 diet and habitat use between these more middle to higher latitude species and our sample's
322 individuals.
323 The univariate wear pattern of modern *Bison bison* ecotypes is also different from our sample
324 patterns. Modern plains bison (*Bison bison bison*) grouped with the strict grazer guild in the
325 cluster analysis (Fig. 4.1), and display a very high mesowear score (2.73), the highest value
326 among the extant model species (Fortelius and Solounias, 2000; Rivals et al., 2007a). On the
327 other hand, the wood bison (*Bison bison* "athabascae") grouped within the mixed feeder guild in
328 the cluster analysis (Fig. 4.1), and display a mesowear score of 1.0, which is outside the range of
329 typical grazers (Rivals et al., 2007a). We consider these modern scores as two different
330 ecological behaviors of the same species since the modern status of wood bison as a separate
331 subspecies is dubious (Geist, 1991; Groves and Grubb, 2011). The modern bison and its ecotypes
332 display a wide range of variation among its wear signals. Our samples display a similar wear
333 spectrum and this may reflect as well, notable differences between the diets of our northern and
334 southern Mexican samples and niche plasticity as wide as is seen in modern bison. The Viko
335 Vijin sample has the lowest wear values of all known bison (extant and extinct), although is very
336 similar to the pattern of modern wood bison (Fig. 4.2). This may reflect a similar composition in
337 the abrasiveness in the diet of modern wood bison and extinct *B. antiquus* from Viko Vijin, as
338 well as important differences between the feeding behavior between northern Mexican samples
339 of *B. antiquus* and modern plains bison, making the latter a non-suitable ecological analog for

340 *Bison antiquus*, as apparently its diet is more abrasive and restricted to grasses. This is supported
341 by the analysis of dental boluses of *B. antiquus* from California (Akersten et al. 1988).
342
343 *Dietary geographical variation and grit consumption.*—A cline of wear (Fig. 4.2-3) of the
344 studied samples (both for extended mesowear and mesowear III) is apparent and seems to be
345 associated with the latitude (i.e. the northern samples show more wear in their teeth than the
346 southern ones). This can be explained by differences in the vegetation structure and the diet of
347 the individuals (Rivals et al., 2007a) or by the presence of exogenous materials ingested by the
348 northern bison individuals (Damuth and Janis, 2011; Hoffman et al., 2015). There is some
349 evidence against dust, quartz sand and other exogenous materials as the main source of the wear
350 patterns observed. For example, *Antilocapra americana* inhabits highly dusty and open
351 environments and its mesowear signature contains a very high proportion (88.6%) of sharp cusps
352 (Fortelius and Solounias, 2000). Also, there is an experimental approach that shows the
353 importance of vegetal endogenous SiO2 particles in the abrasion of enamel, pointing out that
354 wear is mainly caused by the mechanical forces involving chewing of the vegetal material rather
355 than just ingesting exogenous grit (Xia et al., 2015). However, we cannot completely discard that
356 volcanic ash, dust and other quartz-related exogenous materials were involved to some degree in
357 the shaping of the observed wear patterns. Also, these exogenous particles are more abundant in
358 open areas (Janis and Fortelius, 1988; Fortelius and Solounias, 2000), such as the ones
359 previously inferred for the fossil localities of the northern samples (Gutiérrez Bedolla et al.,
360 2016; Marín-Leyva et al., 2016), which supports the ingestion of grasses. Given that the studied
361 sites have similar elevations, La Cinta-Portalitos ranges from 1750 to 2350 masl (metres above
362 sea level), La Piedad-Santa Ana ranges from 1700 to 2500 masl, and Viko Vijin ranges from

363 1800 to 240 masl (Díaz-Sibaja, 2013; Jiménez-Hidalgo et al. 2011), altitude seems not to be
364 related to the observed dietary trends.
365
366 *Mesowear and previous paleoenvironmental reconstructions of localities.*—Our data support and
367 expand on previous paleoenvironmental scenarios for La Cinta-Portalitos and La Piedad-Santa
368 Ana. The evidence suggests the main presence of open areas with dominance of grasses. All in
369 agreement with isotopic (δ13C and δ18O) and microwear data from *Equus* spp. and *Mammuthus*
370 *columbi* (Gutiérrez Bedolla et al., 2016; Marín-Leyva et al., 2016), mesowear data from horses
371 (Marín-Leyva et al., 2016), palynological data (Israde-Alcántara et al., 2010), and the scarcity of
372 typical closed-habitat mammals in these paleocommunities such as tapirs. Our mesowear bison
373 data expands this scenario and suggest the presence of a more heterogeneous vegetation
374 structure, mainly for La Cinta-Portalitos, where previous palynological data points to the
375 presence of other botanical elements such as Cheno-Am, *Ambrosia*, Asteraceae indet., *Cirsium*
376 and *Thalictrum* during the time interval in which bison inhabited the area (Israde-Alcántara et al.,
377 2010), and several typical mixed feeder mammals such as pronghorns and camelids (Díaz-Sibaja
378 et al., 2014a, 2014b; Plata-Ramírez et al., 2015).
379 Also, our mesowear data support previous paleoenvironmental scenarios for Viko Vijin local
380 fauna. The bison samples of this fauna come from localities Oax-3 La Pedrera and Oax-7 Río
381 Tejupam. The inferred paleoenvironment for Oax-3 is a floodplain (Jiménez-Hidalgo et al.,
382 2011) with the presence of short-lived vegetation in a wetland setting (Guerrero-Arenas et al.,
383 2013). Locality Oax-7 was fluvial, possibly a meandering system in an open setting (Jiménez-
384 Hidalgo et al., 2011). Our mesowear data support these environmental settings and suggest a
385 more heterogeneous vegetation structure, with mosaic vegetation, and little dominance of

386 grasses. This is supported by the presence of typical open habitat mammals such as *Equus* and
387 *Mammuthus*, as well as typically closed habitat mammals such as *Odocoileus* and *Cuvieronius*,
388 coexisting with some genera identified as mixed feeders such as *Hemiauchenia* and *Camelops*
389 (Jiménez-Hidalgo et al., 2011).
390

391 ## Conclusions

392

393 The combined mesowear analysis showed that our northern Mexican samples of *Bison antiquus*
394 fall within the grazer guild and the southern one within the mixed feeder guild. These mesowear
395 signatures are different from those of most of the previously reported samples of *B. antiquus*, and
396 from modern *B. bison*. The Viko Vijin mesowear score is close to the wood bison (*B. bison*
397 "athabascae") suggesting similar dietary behavior. These mesowear patterns show broader
398 dietary habits for *B. antiquus* and a low abrasive ingestion in the southernmost populations.
399 These interpretations fit within a more generalist diet than previously assumed for this species.
400 The difference among mesowear scores is related to latitude, reflecting different
401 environmental conditions. Based on previous evidence (i.e. isotopic, microwear, mesowear,
402 palynological, and sedimentological data, as well as the composition of vertebrate and
403 invertebrate-associated fauna), we agree that the Mexican studied sites were open areas with
404 scarce dominance of grasses and probably a more heterogeneous landscape. These
405 paleoenvironments were coetaneous, occurring during the early and middle Wisconsin glacial
406 stage.

Our paleoecological inferences on the diet of these bison samples require further testing. Future studies must be focused on other species found in these fossil mammal assemblages, and in other proxies such as microwear and stable carbon isotope analyses.

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Accessibility of supplemental data

Data http://datadryad.org/review?doi=doi:10.5061/dryad.bn15d

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606

607 **Figures and Figure Captions**

608

609 **Figure 1.** The geographic location of the study areas.

610

611 **Figure 2.** General stratigraphy of the fossil localities in this study.

612

613 **Figure 3.** Mesowear variables. **(1)** Categorization of traditional and extended mesowear
614 variables: shape and relief. The relief is considered high when x/y= ≤ 2, and low when x/y= > 2.
615 **(2)** Mesowear III variables: j-junction (where mesial and distal enamel bands meet) and
616 mesial/distal enamel band scoring system.

617

618 **Figure 4.** Summary of results. **(1)** Hierarchical cluster diagram of mesowear signatures of 27
619 extant model species with known diet and our samples. **(2)** Mesowear univariate scores of 50
620 extant model species with known dietary preferences against *Bison antiquus* samples from
621 previous studies. **(3)** Mesowear III scores of extant model species and our samples. **(4)** Canonical
622 plot of the discriminant analysis combining extended mesowear univariate signatures with
623 mesowear III signatures. Color code: red, grazers; orange, non-strict grazers; green, mixed
624 feeders; blue, browsers. Abbreviations: PBb: plains *Bison bison*, WBb: wood *Bison bison*, BaLC:
625 *B. antiquus* from La Cinta-Portalitos, BaLP: *B. antiquus* from La Piedad-Santa Ana, BaVV: *B.*
626 *antiquus* from Viko Vijin, BaBD: *B. antiquus* from Blackwater Draw, Dry Cave, and Dark
627 Canyon Cave, New Mexico and Lubbock Lake, and Scharbauer Ranch, Texas (Barrón-Ortíz,
628 2016), BaFQ: *B. antiquus* from Folsom Quarry, New Mexico (Rivals et al. 2007a), BaBC: *B.*
629 *antiquus* from Blackwater Draw, Clovis Pit, Curry County, New Mexico; BaIP: *B. antiquus* from
630 Ingleside, San Patricio County, and BaPV: *B. antiquus* from Plainview Quarry, Hale County,
631 Texas (Rivals and Semprebon, 2012). Cluster abbreviations: bb, *Bison bison*; cs, *Ceratotherium*

632 *simum*; eq, *Equus quagga*; Eg, *Equus grevyi*; dl, *Damaliscus lunatus*; ct, *Connochaetes taurinus*;
633 ab, *Alcelaphus buselaphus*; hn, *Hippotragus niger*; he, *Hippotragus equinus*; rr, *Redunca*
634 *redunca*; ke, *Kobus ellipsiprymnus*; Me, *Aepyceros melampus*; Cs, *Capricornis sumatraensis*;
635 To, *Taurotragus oryx*; Ts, *Tragelaphus scriptus*; Cc, *Cervus canadensis*; Ng, *Nanger granti*; Et,
636 *Eudorcas thomsonii*; Om, *Ovibos moschatus*; GC, *Giraffa camelopardalis*; OH, *Odocoileus*
637 *hemionus*; DS, *Dicerorhinus sumatrensis*; OJ, *Okapia johnstoni*; OV, *Odocoileus virginianus*;
638 DB, *Diceros bicornis*; AA, *Alces alces*; RS, *Rhinoceros sondaicus*.
639

640 **Tables**

641

642 **Table 1.** Summary of mean mesowear patterns of the fossil *Bison antiquus* of this study.
643 Abbreviations: %high, percentage of high cusps; %low, percentage of low cusps; %sharp,
644 percentage of sharp cusps; %round, percentage of rounded cusps; Mesial, mesial enamel band
645 score; Distal, distal enamel band score; J-junction, score of the intersection of mesial and distal
646 enamel bands.

Fossil sample	% high	% low	% sharp	% round	Mesial	Distal	J-junction
La Cinta-Portalitos	33.3	66.6	0	100	3.8	3.7	3.3
La Piedad-Santa Ana	45.5	54.5	0	100	3.9	3.7	3.7
Viko Vijin	100	0	6.2	93.75	2.8	2.8	4

647

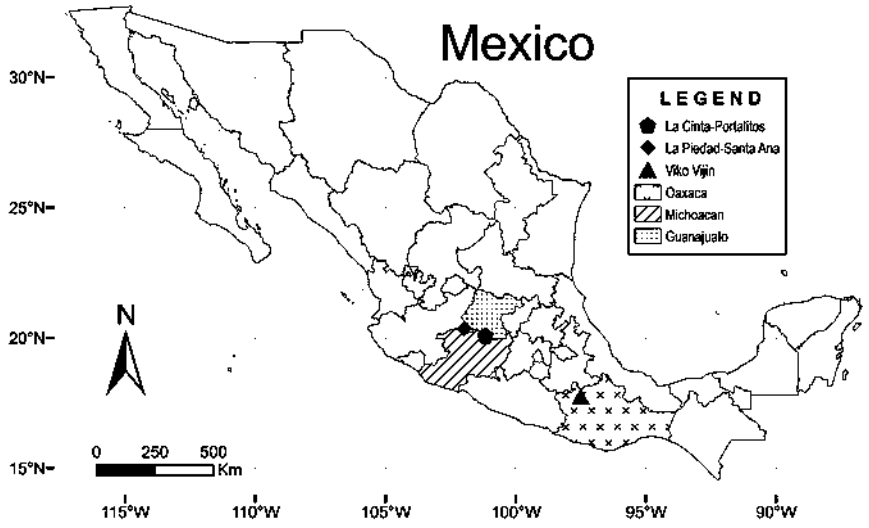

Figure 1

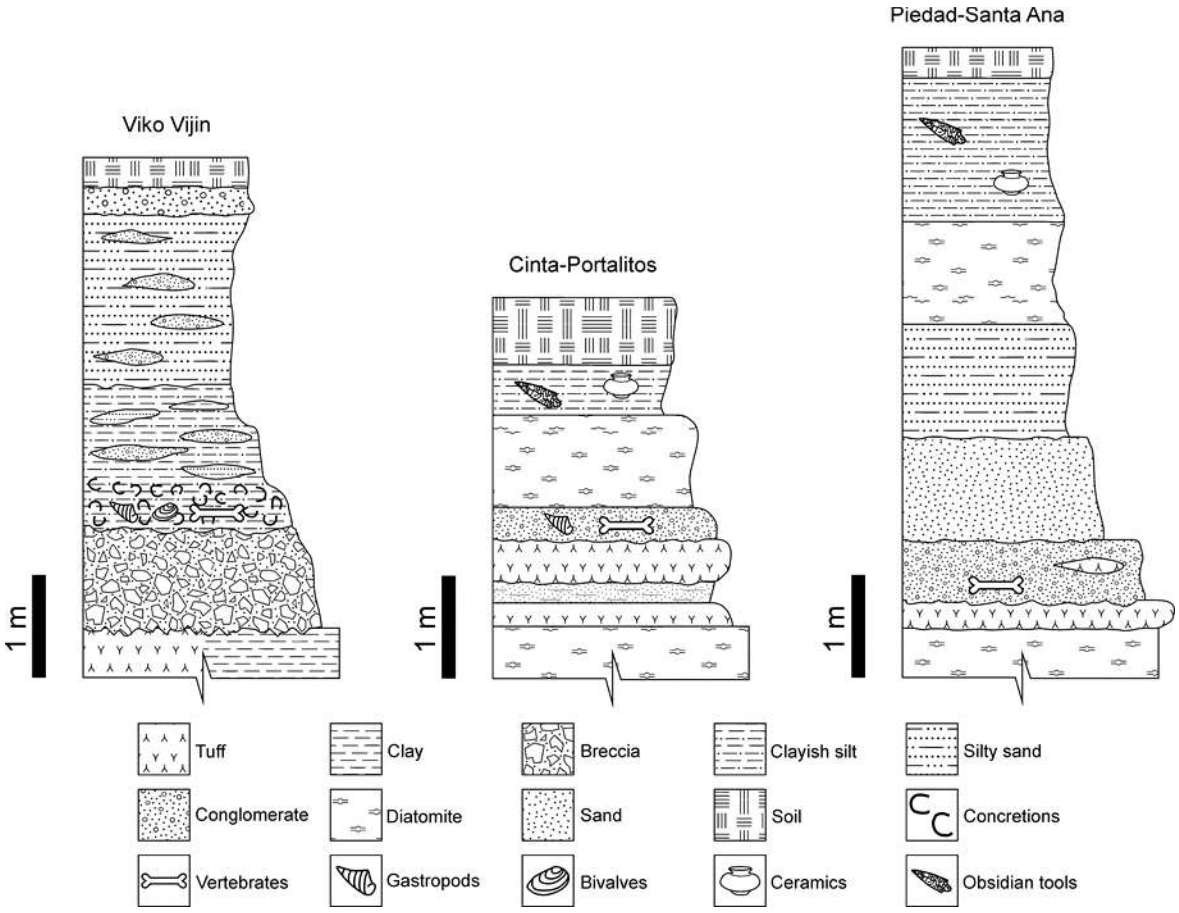

Figure 2

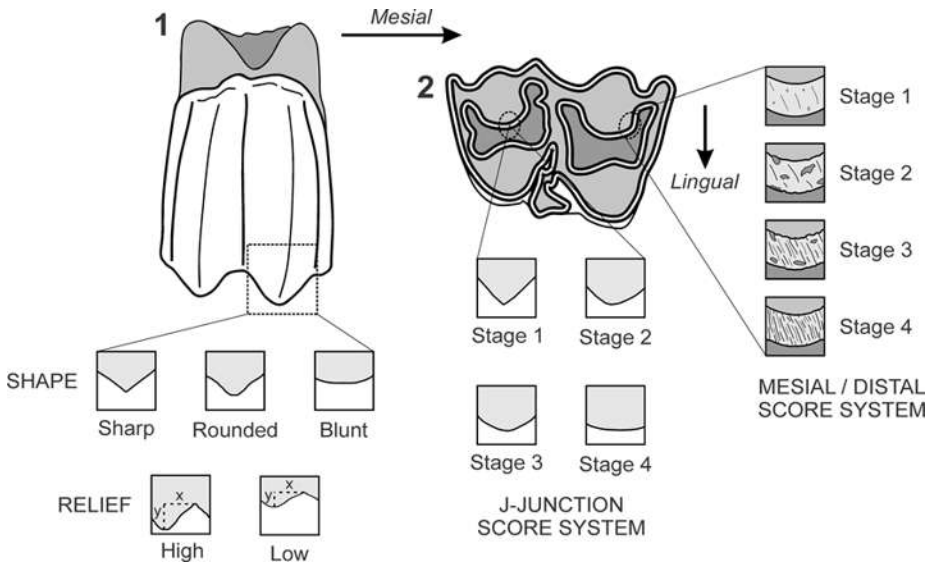

Figure 3

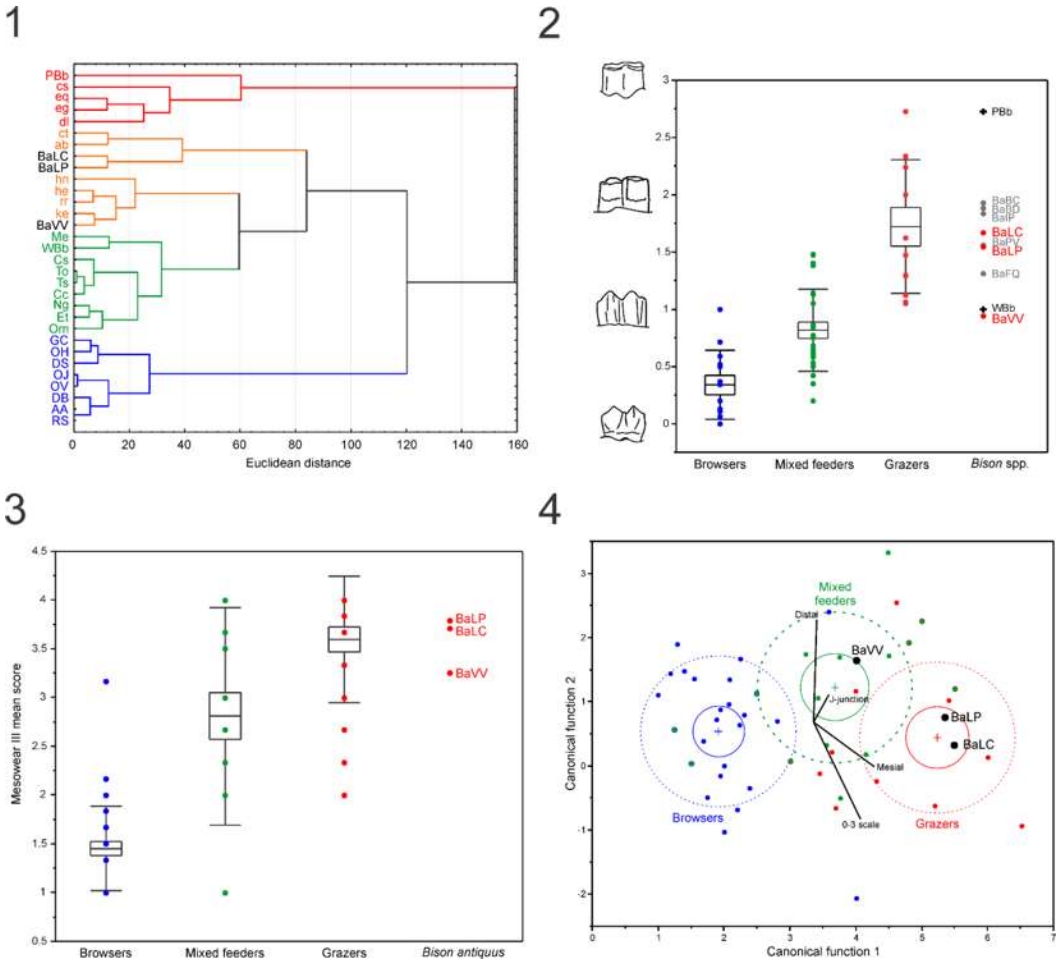

Figure 4

Capítulo 3. Diet, habitat and climatic inferences of two sites with fossil Ruminants in Central Mexico: a multiproxy analysis employing stable isotopes ($\delta^{13}C$, $\delta^{18}O$), microwear, and mineralogy

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Introduction

La Cinta-Portalitos (LCPT) and La Piedad-Santa Ana (LPSA) are two fossil sites located at the occidental region of the Trans-Mexican volcanic belt morphotectonic province, between the states of Michoacán and Guanajuato (García-Zepeda, 2006; Servín-González, 2010; Díaz-Sibaja, 2013). Their associated fauna places both sites at the Late Pleistocene, into the Rancholabrean Land Mammal Age (Bell et al., 2004). In the present, LCPT represents an abandoned channel within the Cuitzeo lake basin (García-Zepeda, 2006; Marín-Leyva et al., 2016a), whereas LPSA belongs to the Lerma river hydrological system (Servín-González, 2010; Díaz-Sibaja, 2013). Although a few paleobiological studies have been carried out in both sites with horses (Marín-Leyva et al., 2016a, 2016b) and mammoths (Gutiérrez-Bedolla et al., 2016), very little is known about the ruminants (Artiodactyla: Ruminantia), a major component in the faunas of both sites (Díaz-Sibaja, 2013). Most ruminants are habitat specialists (Vrba and Schaller, 2000), having a tight link between their diet and the vegetation structure in which they live (Keast, 1968; Pienaar, 1974), and having more diverse habitats than horses and mammoths (Nowak and Paradiso, 1983). This makes them very useful to reconstruct past environments (Solounias et al., 1988).

Several proxies to reconstruct ruminant paleodiet exists, which includes dental mesowear (Fortelius and Solounias, 2000; Franz-Odendaal and Kaiser, 2003; Rivals et al., 2007; Kaiser, 2011; Kaiser et al., 2013; Fraser et al., 2014; Danowitz et al., 2016), dental microwear (Walker et al., 1978; Solounias et al., 2000; Solounias and Semprebon, 2002), morphological proxies (Fraser and Theodor, 2011) and carbon stable isotope ($\delta^{13}C$) analysis (Koch, 1998). Additionally, other proxies provide independent support for the reconstructions generated through dietary studies, such as the carbon (e.g. Domingo et al., 2013) and oxygen stable isotope ($\delta^{18}O$) analysis (e.g. González-Guarda et al., 2017), the clay mineralogical analysis (e.g. Fesharaki et al., 2007; Carrasco et al., 2008), among others.

Due to enamel remodelation, dental microwear provide information of the last days on the life of the studied organisms (Teaford and Oyen, 1989; Solounias et al., 1994). Stable isotope analysis provides information of the diet during the mineralization of the dental piece analyzed (Gadbury et al., 2000; Hoppe et al., 2004). In combination, this data provides a wide framework to better understand paleodiets. In this work we infer the diet, habitat, resource competition, mean annual temperature, and depositional evolution of two sites from central Mexico with a multiproxy analysis of dental microwear, oxygen and carbon stable isotope analysis, and mineralogy.

Methods

Dental microwear

In total, we obtained 24 viable epoxy casts following the methodology described by Solounias and Semprebon (2002), after we discarded those with visible taphonomical effects such as sand abrasion, following King et al. (1999). For the acquisition of the raw number of pits and scratches we observed the second enamel band of the paracone in upper molars and the second enamel band of the protoconid in lower molars (Solounias and Semprebon, 2002; Merceron et al., 2004). We obtained digital photographs of the teeth casts with a stereo-light microscope at low magnification (35x on a Leica LAS EZ, Leica Microsystems©), afterwards we processed the images to obtain the 0.4 mm x 0.4 mm (95.9 ppp) area for the count of enamel microdefects (Solounias and Semprebon, 2002) and employed the semiautomatizated software Microware 4.02 (Ungar, 2002), following the definitions of features of (Gordon, 1982). All features were taken by one observer to minimize the inter-observer error rates (Grine et al., 2002).

We obtained the density of pits and scratches by dividing the number of features between the observed area, and proceeded to perform a bivariate analysis with these densities. Additionally, we performed a function discriminant analysis (FDA) with the average number of pits and scratches for each taxon with the guilds as the grouping variable. The statistically significant differences between groups centroids were tested with a Wilk's Lambda's test. We also calculated the 0-17% scratch low raw range by calculating the original percentage of individuals with less than 17 scratches per observable area, in samples of six or more. This 0-17% *scale* was plotted excluding the frugivores to better

interpret the results obtained by the bivariant and function discriminant analyses (Solounias and Semprebon, 2002). All statistical analyses and graphs were made in JMP 8.0 software.

Stable isotope analysis

We selected dental pieces in which the amelogenesis process (enamel deposition by ameloblasts) begun around and after the weaning of the calves to represent the diet and habitat of adults, and to avoid isotopically offset relative to adult values (Hoppe et al., 2004). In *Bison* the weaning occurs in a a window of age between 8 and 10 months (Meagher, 1986). A time in which the base of the crown of the second permanent molars, and almost the totality of the third molar crown has developed (Gadbury et al., 2000). Thus, we selected those molar positions to obtain our samples. We excluded all permanent premolars, since we were unable to identify them at species level. We obtained bulk samples from the middle region of the crown (≈ 25 mm from the base of the crown), to collect only mature enamel with >75% of hydroxyapatite content (Passey and Cerling, 2002). These bulk samples are the average $\delta^{13}C$ value of an individual, thus representing broadly its diet (Koch et al., 1998).

We collected bulk samples between 9 and 15 mg of enamel with a rotative hand drill equipped with a diamond-head dental bur. The samples were pulverized with an agate mortar and then, sifted with a sieve with a 149 µm mesh opening. These samples were sent for processing to the Stable Isotope Laboratory of the University of California, Santa Cruz, prior processing according to the Carbonate Preparation for Enamel Apatite Samples protocol, which consisted in:

1. Weigh out 5-10 mg of powdered enamel into a microcentrifuge tube.
2. Add 1 ml of 30% H_2O_2 for 10 mg of sample.
3. Seal the microcentrifuge tube and agitate (vortex genie) each sample for 30-60 seconds.
4. Loosen the lids (so that gas can escape) and allow samples to sit and react for 24 hours (agitate often).
5. Centrifuge the samples and aspirate the H_2O_2 away taking care to leave the powder behind.
6. Rinse the sample by adding 1 ml of Milli-Q® and agitating. Then centrifuge and repeat for a total of 5 rinses.
7. Once samples have been rinsed 5 times, add 2 ml of 1M acetic acid buffered with calcium acetate to pH of ~5* for 25 mg of sample (scale according to the sample weight). Currently the acetic acid buffered with calcium acetate is found in the flammables cabinet.
8. Agitate samples and allow them to react for 24 hours.
9. Centrifuge the samples and aspirate the acetic acid buffer solution away taking care to leave the powder behind.

10. Rinse the sample by adding 1 ml of Milli-Q® water and agitating. Then centrifuge and aspirate as in step 9. Repeat four additional times leaving the powder only (no water) after the final aspiration.
11. Uncap each sample and cover with aluminum foil. Use a sharp to make a small hole in the foil covering each sample tube.
12. Freeze the samples for ~25 minutes or longer.
13. Place samples on a freeze dryer overnight.
14. Weigh out between 0.5 and 1 mg for a Kiel run into sample boats.
15. Vacuum roast the samples for ~ 1 hour at 65°C before running them on a mass spectrometer.

* Buffer solution should be made by mixing a 1M solution of acetic acid with a 1M solution of calcium acetate. Using the Henderson-Hasslebach equation this yields a solution of ~pH 5. Confirm this pH periodically. Do not use buffer solution if pH falls below 4.5.

The isotope compositions are presented in δ values, with the $R_{standard}$ term:

$$\delta^{H}X = \left[\left(R_{sample} - R_{standard}\right)/R_{standard}\right] \times 1000$$

Where X is the element, H is the mass of the heavy stable isotope (13 for C, 18 for O), and R is the ratio of the heavy isotope to the light isotope for the element ($^{13}C/^{12}C$, $^{18}O/^{16}O$) (Fry, 2010). The values of $\delta^{13}C$ and $\delta^{18}O$ are presented in parts per thousand (‰), and in Vienna Pee Dee Belemnite (VPDB) values, with a standard carbon ($^{13}C/^{12}C$) value of 0.01118 and a standard oxygen ($^{18}O/^{16}O$) value of 0.0020672 (Hayes, 2002; Fry, 2010).

The samples were processed in a Thermo Finnigan MAT 253 mass spectrometer with a dual-inlet system, and an attached Finnigan Kiel IV Carbonate Device. The standards used were Carrara Marble (CM), IAEA-603 calcite ($\delta^{13}C$ = 1.97‰ and $\delta^{18}O_{CO3}$ = -1.61‰, VPDB), NBS-18, calcite ($\delta^{13}C$ = -5.03‰ and $\delta^{18}O_{CO3}$ = -23.01‰, VPDB), NBS-19, calcite ($\delta^{13}C$ = 1.95‰ and $\delta^{18}O_{CO3}$ = -2.2‰, VPDB).

The isotopic carbon values were used to infer the diet of the *Bison* spp. samples. The fractionation of carbon isotopes in atmospheric CO_2 of the Pleistocene is around -6.5‰ (Marino et al., 1992; Tipple et al., 2010). Due to this effect, we considered that $\delta^{13}C_{VPDB}$ values more negative than -8.7‰ are consistent with a C_3 diet, and values more positive than -0.5‰ reflect a diet of C_4 plants, with intermediate values representing mixed feeder habits (Feranec, 2003).

To infer the habitat use, we employed $\delta^{13}C$ values of bioapatite, considering the following categorization for the $\delta^{13}C_{vegetation}$: 1) closed canopy forest (< -14.5‰), 2) woodland to woodland-mesic C_3 grassland (-14.5 to -9.5‰), 3) open woodland-xeric C_3 grassland (-9.5 to -6.5‰), 4) mixed C_3-C_4 grassland (-6.5 to -1.5‰), and 5) C_4 grassland (> -1.5‰) (Domingo et al., 2013).

Additionally, we calculated $\delta^{13}C$ values of original vegetation consumed from bioapatite values, as a modern equivalent (for fine diet comparison), employing the following equation (Cerling and Harris, 1999):

$$\delta^{13}C_{vegetation} = \delta^{13}C_{leaf} + \left(\delta^{13}C_{modernatmCO_2} - \delta^{13}C_{ancientatmCO_2}\right)$$

Where: $\delta^{13}C_{leaf} = \delta^{13}C_{tooth} - 14.1‰$, $\delta^{13}C_{modernatmCO_2} = -8‰$, $\delta^{13}C_{ancientatmCO_2} = -6.5‰$ (Domingo et al., 2013). Modern C_3 (-22 to -35‰), C_4 (-19 to -9‰) and CAM (-10 to -20‰) $\delta^{13}C$ from O'Leary (1988).

Additionally, we estimated the percentage of C_4 plants consumed by each individual and average sample of each species by using the following formula (Koch et al., 2004):

$$(100)\delta^{13}C_{sample} = (100 - X)\delta^{13}C_{100\%C3enamel} + (X)\delta^{13}C_{100\%C4enamel}$$

Where X is the $\%C_4$ consumed, $\delta^{13}C_{100\%C3enamel}$ = -12.6‰, and $\delta^{13}C_{100\%C4enamel}$ = 2.4‰, based on pre-LGM and LGM values, which correspond to the values of the Pleistocene (Koch et al., 2004). To better appreciate the possible effects on the competition for resources, we obtained the percentage of similarity in the consumption of C4 by comparing the differences of means between taxa.

We also transformed the raw isotopic oxygen values ($\delta^{18}O_{CO3(VPDB)}$) provided by the Stable Isotope Laboratory (UC Santa Cruz) to Vienna Standard Mean Ocean Water (VSMOW) values, with the formula (Coplen, 1988):

$$\delta^{18}O_{CO_3(VSMOW)} = \left(1.03091 \times \delta^{18}O_{CO_3(VPDB)}\right) + 30.91$$

The VSMOW oxygen values were transformed from carbonate ($\delta^{18}O_{CO3}$) to phosphate ($\delta^{18}O_{PO4}$) values with the following formula (Iacumin et al., 1996):

$$\delta^{18}O_{PO_4(VSMOW)} = \left(0.98 \times \delta^{18}O_{CO_3(VSMOW)}\right) - 8.5$$

Due to the constant core temperature of mammals (≈37°C), there is an oxygen isotopic equilibrium between biogenic phosphate and meteoric water values, especially for large bodied mammals (>100 kg) (Luz et al., 1984; Koch et al., 1998). The ingested meteoric water ($\delta^{18}O_{mw}$) isotopic values were calculated employing the following modern model species equations:

Large bovines (R = 0.99): $\delta^{18}O_{mw\ (VSMOW)} = \left(\delta^{18}O_{PO_4(VSMOW)} - 24.5\right)/1.01$ (D'Angela and Longinelli, 1990).

Horses (R = 0.87): $\delta^{18}O_{mw\ (VSMOW)} = \left(\delta^{18}O_{PO_4(VSMOW)} - 22.6\right)/0.71$ (Delgado Huertas et al., 1995).

Proboscideans (R = 0.92): $\delta^{18}O_{mw\ (VSMOW)} = \left(\delta^{18}O_{PO_4(VSMOW)} - 23.3\right)/0.94$ (Ayliffe et al., 1992).

Finally, to obtain the mean annual temperature (MAT °C), we used the following linear equation (R = 0.84) (Rozanski et al., 1993):

$$MAT(°C) = \left(\delta^{18}O_{mw(VSMOW)} + 12.68\right)/0.36$$

In order to compare our results with previously published isotopic data from the localities studied, we employed the data from Gutiérrez Bedolla *et al.* (2016), and Marín-leyva *et al.* (2016). To compare differences of feeding habits and raw habitat use we employed the data of Koch *et al.* (1998), which contains several well-documented taxa with known feeding habits. We also employed the Koch *et al.* (1998) data to plot the bioapatite $\delta^{13}C$ (VPDB) and $\delta^{18}O_{CO3}$ (VSMOW) values to make a raw comparison of habitat use following the Feranec and MacFadden (2006) model of carbon and oxygen isotope distributions. We made comparisons by oneway analysis of variance (ANOVA) by population, comparing means with Tukey-Kramer tests ($\alpha = 0.05$). All statistical analyses and graphs were made in JMP 8.0 software.

Mineralogy

We employed qualitative mineralogical analyses to infer paleoenvironmental and depositional conditions in our study sites. We selected representative samples (with exception of volcanoclastic sediments) from a typical stratigraphic column, and probed the fossil bed with three independent repetitions (different samples). For the preparation of the samples, we proceeded to sift the samples in a sieve with a mesh aperture of 149 µm, to obtain only the clay, due to its representativeness of the environmental conditions (Fesharaki et al., 2007; Carrasco et al., 2008). After sieving the samples, each one was pulverized in an agate mortar and then sent to analysis to the X-ray Laboratory, and Chemical Analyses Laboratory of the Instituto de Investigación en Metalurgía y Materiales, of the Universidad Michoacana de San Nicolás de Hidalgo.

Mineralogical characterization was performed by X-ray powder diffraction (XRD) using a Bruker D8 ADVANCE Plus - X-ray Powder Diffractometer, DAVINCI.DESIGN, with a Locked Coupled scan type, to obtain complete diffractograms (5-70.0001°, at a standard 2Φ) at a constant 25°C room temperature. The analysis of the raw data was carried out in the DIFFRAC PLUS EVA and OPUS 6.5 Spectroscopy Software, and compared our powder diffraction patterns to the Powder Diffraction File (PDF) database of the International Centre for Diffraction Data (ICDD), previous atmospheric compensation of each analysis (Ostrooumov, 2009). We also performed a DXR analysis on modern flood plain soil (E12) at LPSA to test our hypothesis of temperate and plain flood origin of montmorillonite in association with kaolinite group minerals.

To validate the results obtained by the XRD analysis, we carried out an infrared spectroscopy analysis (IRS) with the same samples, and preparation employed in the XRD. Prior to the analysis, we mixed 3 mg of sample with 0.3 mg of potassium bromide (KBr), and proceeded to generate a tablet, by compressing the sample with 20 tons for one minute.

Afterwards, we proceed to its analysis in a Burke Tensor 27 FT-IR Spectrometer. We searched in an interval of 4,000-400cm^{-1} wavelength, and proceed to compensate for atmospheric H_2O and CO_2 in the sample. We searched the characteristic transmittance (%) bands in the literature based on the mineralogical content found in the DXR analysis.

Results and discussion

Dental microwear

For low magnification dental microwear (35x), we analyzed a total of 7 *B. antiquus* from La Cinta-Portalitos (LCPT), 6 from La Piedad-Santa Ana (LPSA), one *B. latifrons* from LCPT, one *Tetrameryx shuleri* from LPSA, 6 from LCPT, and one individual of *Odocoileus hemionus* and two of cf. *Navahoceros frikcki* from LCPT. The raw dental microwear data is presented in the Table 1.

Table 1. Dental microwear data of this study.

Taxon	Collection ID	Site	Total number of pits	Total number of scratches	Pit density (n/mm2)	Scratch density (n/mm2)
Bison antiquus	UM 167	La Cinta-Portalitos	13	25	325	625
Bison antiquus	UM 613	La Cinta-Portalitos	15	15	375	375
Bison antiquus	UM 619	La Cinta-Portalitos	7	41	175	1025
Bison antiquus	UM 1268	La Cinta-Portalitos	9	26	225	650
Bison antiquus	UM B003	La Cinta-Portalitos	5	32	125	800
Bison antiquus	UM B005	La Cinta-Portalitos	5	15	125	375
Bison antiquus	UM B006	La Cinta-Portalitos	7	24	175	600
Bison antiquus	CPOEI 153	La Piedad-Santa Ana	10	18	250	450
Bison antiquus	CPOEI 154	La Piedad-Santa Ana	7	20	175	500
Bison antiquus	CPOEI 157	La Piedad-Santa Ana	11	32	275	800
Bison antiquus	PMB 008	La Piedad-Santa Ana	9	21	225	525
Bison antiquus	UM 972	La Piedad-Santa Ana	6	28	150	700
Bison antiquus	UM B007	La Piedad-Santa Ana	14	26	350	650
Bison latifrons	UM 116	La Cinta-Portalitos	14	14	350	350
Tetrameryx shuleri	UM 932	La Cinta-Portalitos	11	24	275	600
Tetrameryx shuleri	UM 933	La Cinta-Portalitos	8	30	200	750
Tetrameryx shuleri	UM 934	La Cinta-Portalitos	16	27	400	675
Tetrameryx shuleri	UM 937	La Cinta-Portalitos	16	26	400	650
Tetrameryx shuleri	UM 939	La Cinta-Portalitos	15	20	375	500
Tetrameryx shuleri	UM 1111	La Cinta-Portalitos	17	30	425	750
Tetrameryx shuleri	UM 943	La Piedad-Santa Ana	22	32	550	800
Odocoileus hemionus	UM 977	La Cinta-Portalitos	21	25	525	625
cf. Navahoceros fricki	UM 172	La Cinta-Portalitos	10	20	250	500
cf. Navahoceros fricki	UM 978	La Cinta-Portalitos	15	24	375	600

The bivariate analysis (Figure 1) shows that the *Bison antiquus* samples from La Piedad-Santa Ana and La Cinta-Portalitos falls within the grazer and the regional/seasonal mixed feeder guilds. A similar pattern is observed for the cf. *Navahoceros fricki* and *Odocoileus hemionus* individuals from La Cinta-Portalitos. Similarly, the B. latifrons individual falls between the leaf browser and the regional/seasonal mixed feeder guilds. On the other hand, both the individual of *Tetrameryx shuleri* from La Piedad-Santa Ana and the sample of *T. shuleri* from La Cinta-Portalitos falls within the grazer guild.

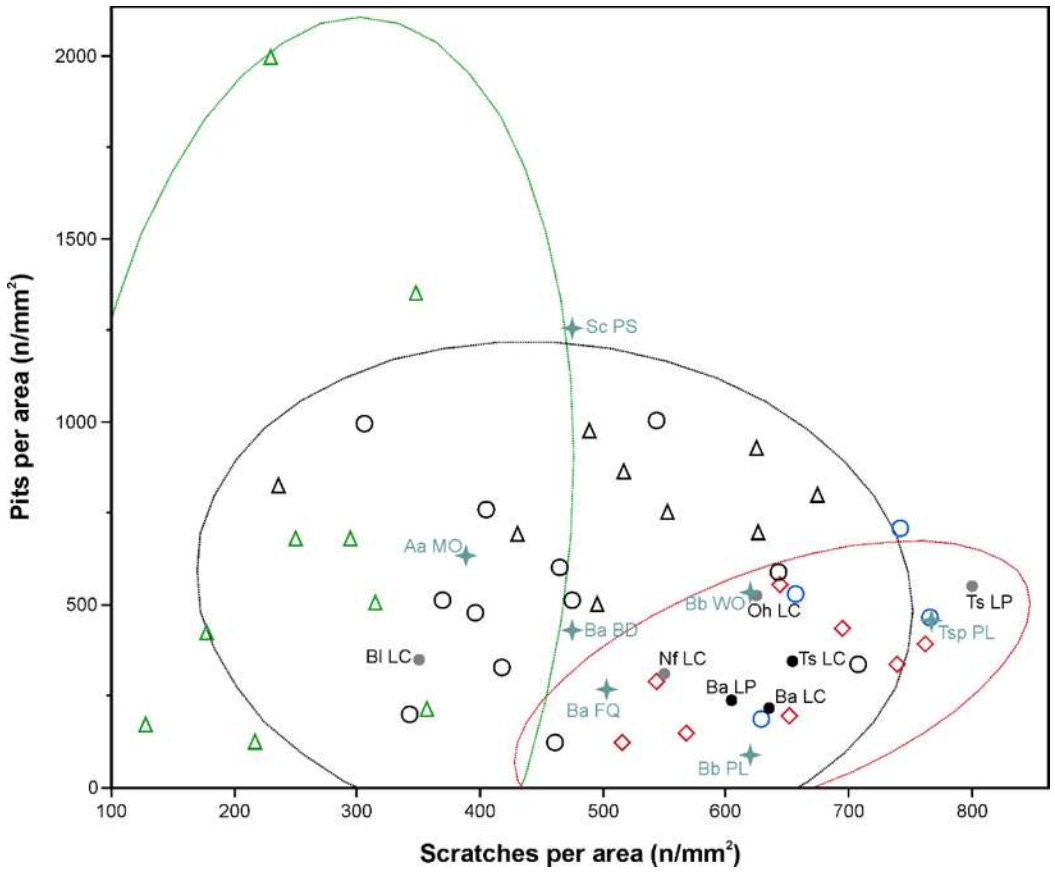

Figure 1. Dental microwear (35x) bivariate analysis. Green triangles: leaf browsers, black triangles: fruit browsers, black circles: regional/seasonal mixed feeders, blue circles: meal by meal mixed feeders, red diamonds: grazers. All ellipses represent 95% confidence. Black dots: samples of six or more, gray dots: samples of one or two individuals. Ba LC: *Bison antiquus* from La Cinta-Portalitos (LCPT), Ba LP: *B. antiquus* from La Piedad-Santa Ana (LPSA), Bl LC: *B. latifrons* from LCPT, Ts LC: *Tetrameryx shuleri* from LCPT, Ts LP: *T. shuleri* from LPSA, Oh LC: *Odocoileus hemionus* from LCPT, and Nf LC: cf. *Navahoceros fricki* from LCPT. Aa MO: modern *Antilocapra americana*, Bb PL: modern plains *Bison bison*, Bb WO: modern wood *B. bison*, Ba FQ: *B. antiquus* from Folsom Quarry, New Mexico, Ba BD: *B. antiquus* from Black Water Draw Curry, Sc PS: *Stockoceros conklingi* from Papago Springs Cave, Tsp PL: *Tetrameryx* sp. from the Pliocene of Arizona and San Timoteo Beds, California. Microwear data from Solounias and Semprebon (2002), Rivals *et al.* (2007), Rivals and Semprebon (2012).

Our dental microwear analysis (Figure 1) showed that the sample of *B. antiquus* from LCPT was near to the *Equus grevyi* and *Capra ibex* signals. *E. grevyi* is a species that prefers stony plains with short grasses and scattered, short (3-4 m) *Acacia* trees (Churcher, 1993); while C. ibex has sexually segregated habitat, the males are habitat generalists and the females usually lives in steep terrains, both usually found in meadows (Parrini et al., 2009). *B. antiquus* from LPSA is found near the signals of C. ibex and *Hippotragus niger*. The latter species inhabits seasonally burnt woodlands and woodland-grassland edges, always with a near water source (Nowak and Paradiso, 1983; Kingdon, 2013). Meanwhile, *B. latifrons* individual signal was found in a space near the *Diceros bicornis* microwear signal. This rhinoceros is an habitat generalist, dwelling in forests, prairies, grasslands, and deserts (Hillman-Smith and Groves, 1994). In contrast, previous *B. antiquus* data from Folsom Quarry (Rivals et al., 2007), and Blackwater Draw Curry (Rivals and Semprebon, 2012), both in New Mexico, are not similar to the microwear signals of our samples of this species, which suggest a wide variety of dietary habits. Similarly, modern *B. bison* microwear signals are also different from those of our extinct bison samples. Modern plains bison is a strict grazer (Meagher, 1986; Solounias and Semprebon, 2002), while the modern wood bison is a mixed feeder (Meagher, 1986; Rivals et al., 2007). These data suggest that *Bison antiquus* display a wider arrange of ecological behaviors than its modern descendant, and we consider this as an indicative of a generalist diet, as previously suggested (Díaz-Sibaja et al., in press).

On the other hand, the *Tetrameryx shuleri* from LCPT is near the microwear signal of *Kobus ellipsiprymnus*, and *Axis axis*, a grazer and seasonal mixed feeder with a major consumption of grasses, respectively (Solounias and Semprebon, 2002). *K. ellipsiprymnus* inhabits woodland with a near water source (Nowak and Paradiso, 1983; Kingdon, 2013). *A. axis* habitat is grasslands and open forests (Nowak and Paradiso, 1983). Our individual of *T. shuleri* from LPSA is near the microwear signal of *Cervus canadensis* and *Rucervus duvaucelii*, a mixed feeder and a grazer respectively (Solounias and Semprebon, 2002). C. canadensis is a habitat generalist, while *R. duvaucellii* usually inhabits undulating grasslands with scattered with trees (Lydekker, 1901). Our antilocaprids does not have a similar wear pattern that modern *Antilocapra americana*, which is a browser that inhabits grasslands, grassland-bushlands and deserts (O'Gara, 1978; Solounias and Semprebon, 2002). Similarly, its Pleistocene relative, *Stockoceros conklingi* (syn= *S. onurosagris*) from Papago Springs cave, have a distinctive microwear signal, similar to those of modern mixed feeders (Rivals and Semprebon, 2006). Finally, *Tetrameryx* sp. from the Blancan of New Mexico and California display a similar pattern to the *T. shuleri* of LPSA (Semprebon and Rivals, 2007), nonetheless, a larger sample size is required to provide additional ecological inferences.

The *Odocoileus hemionus* individual was near the microwear signals of *Tetracerus quadricornis, Rusa unicolor*, and modern wood *Bison bison*, a grazer and a mixed feeders, respectively (Solounias and Semprebon, 2002; Rivals et al., 2007). *T. quadricortnis* is a habitat generalist that prefers dry deciduous mixed forest with open patches (Leslie and Sharma, 2009), similarly *R. unicolor* is also a generalist, but it prefers the tall-grass ecotone

with open grasslands (Leslie, 2011). This is similar to the preferred habitat and diet of modern *O. hemionus* (Anderson and Wallmo, 1984). Finally, the individuals of cf. *Navahoceros fricki* have a microwear signal similar to *Equus burchelli*, a strict grazer that inhabits mesic open areas with predominance of grass (Grubb, 1981).

The initial FDA analysis showed 16 misclassified species, with statistically significant differences between guilds (Prob>F = <0.0001), and it classified the *B. antiquus* samples within the grazer guild, the *B. latifrons* was classified as a seasonal mixed feeder, while *Tetrameryx shuleri* and both deer species were classified as mixed feeders. On the other hand, the 0-17% *scale* (Figure 2) showed that the *B. antiquus* sample from LCPT is close to the regional/seasonal mixed feeder microwear signal, while the *B. antiquus* from LPSA is closer to both, the meal by meal mixed feeder and grazer guilds. Finally, the *T. shuleri* from LCPT was similar to the grazer guild.

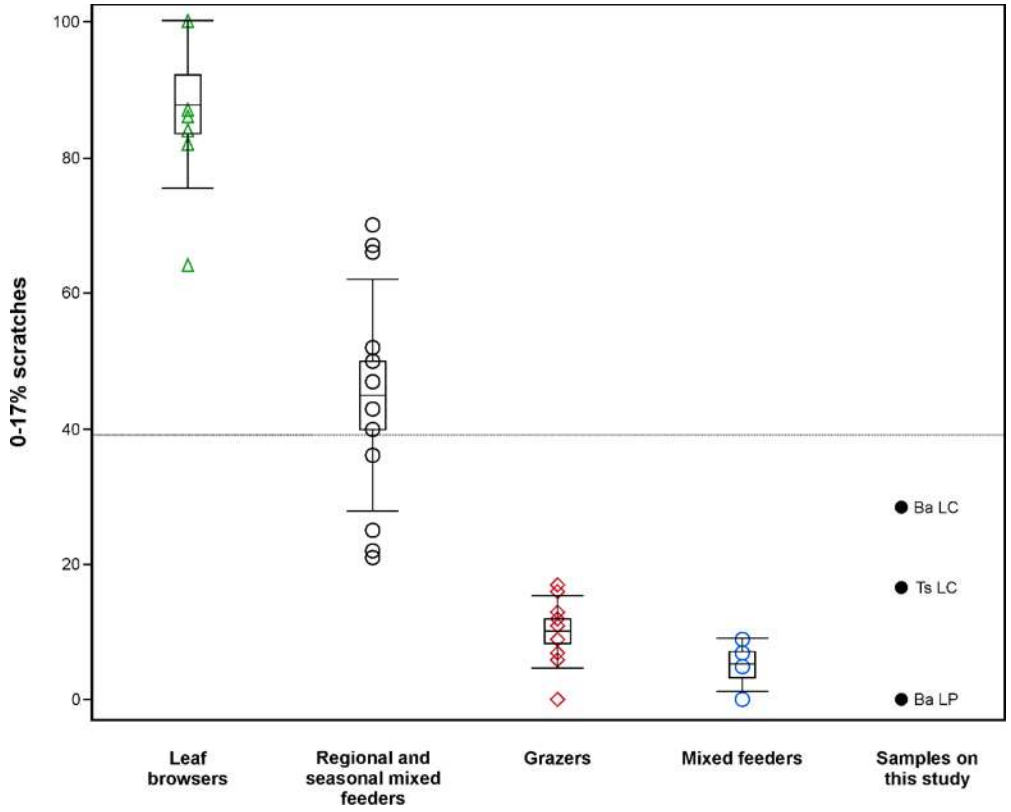

Figure 2. 0-17% scratches analysis. The boxes represent the standard deviation, and mean with error bars of each guild (frugivores excluded). The symbology is the same as in Figure 1.

As a whole, the microwear data suggests that the LCPT site was a heterogeneous prairie with bushes of short trees. While the LPSA site was a heavily seasonal open grassland with presence of woodland and a near water source. These inferences are in partial agreement

with other data, such as the sedimentology and stratigraphy of both sites (Marín-Leyva, 2011; Díaz-Sibaja, 2013). But the new microwear data suggests more heterogeneity on the sites as previously stated (Gutiérrez-Bedolla et al., 2016; Marín-Leyva et al., 2016a, 2016b).

Stable isotope analysis

In total we obtained 14 enamel samples of *Bison* spp. for our study (Table 2). We discarded one sample due to possible diagenetic alterations. Descriptive statistics of these populations shows the following values for $\delta^{13}C$: *B. antiquus* from LCPT (n = 10), x = -1.06, σ = 1.1, *B. antiquus* from LPSA (n = 9), x = -0.26, σ = 1.22, and *B. latifrons* from LCPT (n = 5), x = -0.91, σ = 1.8. We found no statistically significant differences between *Bison* spp. populations (Prob>F = 0.4).

Table 2. Summary of isotopic values of *Bison* spp. samples.

Taxon	Collection ID	Site	$\delta^{13}C_{VPDB}$	$\delta^{18}O_{VPBD}$	$\delta^{13}C_{vegetation}$	$\%C_4$ consumed	MAT °C
Bison antiquus	UM B009	La Cinta-Portalitos	-0.85	-4.10	-16.45	78.3	16.4
Bison antiquus	UM 1288	La Cinta-Portalitos	-0.84	-3.39	-16.45	78.35	18.3
Bison antiquus	UM 124	La Cinta-Portalitos	-0.53	-2.78	-16.13	80.46	20.0
Bison antiquus	UM 170	La Cinta-Portalitos	-2.36	-1.41	-17.96	68.23	23.8
Bison antiquus	UM 120	La Cinta-Portalitos	1.15	-2.16	-14.45	91.67	21.8
Bison antiquus	UM 167	La Cinta-Portalitos	-2.69	-4.61	-18.30	66.02	15.0
Bison antiquus	UM 615	La Cinta-Portalitos	-0.96	-5.77	-16.57	77.56	11.7
Bison antiquus	UM B005	La Cinta-Portalitos	-1.85	-6.79	-17.46	71.61	8.9
Bison antiquus	UM 616	La Cinta-Portalitos	-0.26	-4.89	-15.86	82.24	14.2
Bison antiquus	UM 166	La Cinta-Portalitos	-1.43	-3.71	-17.03	74.43	17.5
Bison antiquus	UM 969	La Piedad-Santa Ana	-0.14	-5.60	-15.74	83.05	12.2
Bison antiquus	CPOEI B019	La Piedad-Santa Ana	-0.23	-4.39	-15.84	82.41	15.6
Bison antiquus	CPOEI B023	La Piedad-Santa Ana	0.72	-4.66	-14.88	88.8	14.8
Bison antiquus	CPOEI B017	La Piedad-Santa Ana	0.67	-4.99	-14.92	88.51	13.9
Bison antiquus	CPOEI 31	La Piedad-Santa Ana	0.99	-5.04	-14.61	90.62	13.8
Bison antiquus	UM 676	La Piedad-Santa Ana	-2.62	-5.92	-18.22	66.53	11.3
Bison antiquus	UM 611	La Piedad-Santa Ana	0.41	-2.87	-15.18	86.78	19.8
Bison antiquus	UM 970	La Piedad-Santa Ana	-1.86	-5.87	-17.46	71.58	11.5
Bison antiquus	UM 610	La Piedad-Santa Ana	-0.36	-7.02	-15.96	81.56	8.2
Bison latifrons	UM 119	La Cinta-Portalitos	1.69	-5.39	-13.90	95.32	12.8
Bison latifrons	UM 59	La Cinta-Portalitos	-1.87	-6.06	-17.48	71.48	10.9
Bison latifrons	UM 118	La Cinta-Portalitos	-2.98	-4.49	-18.59	64	15.3
Bison latifrons	UM 1285	La Cinta-Portalitos	-1.35	-2.21	-16.96	74.96	21.6
Bison latifrons	UM 619	La Cinta-Portalitos	-0.03	-3.88	-15.64	83.76	17.0

The $\delta^{13}C$ and $\delta^{18}O$ values show a clear distinction between the Florida samples and the LCPT and LPSA sites (Figure 3), especially in the oxygen isotope ratio, due to differences between climate and humidity in these environments. The data from LCPT and LPSA show similar values, possibly due to its geographical proximity.

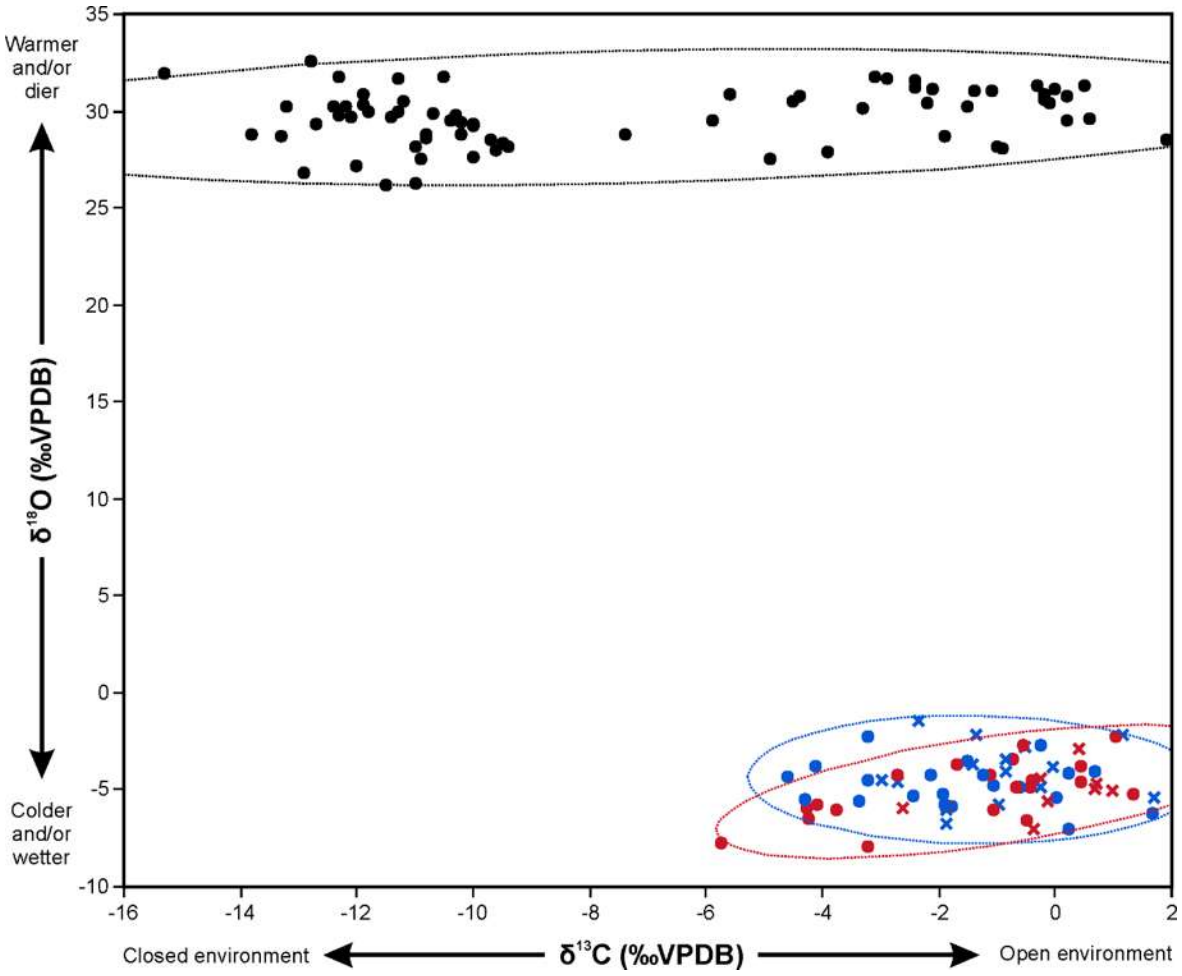

Figure 3. Bivariant plot of carbon and oxygen isotopic values comparing Florida data (black dots) against LCPT (blue dots) and LPSA (red dots) in western-central Mexico. The crosses represent *Bison* spp. data. The non-bison dots are *Mammuthus columbi* (Gutiérrez-Bedolla *et al*., 2016), *Equus mexicanus*, *E. conversidens*, and *E. cedralensis* (Marín-Leyva *et al*., 2016b).All ellipses represent 95% confidence.

The carbon stable isotopes ($\delta^{13}C$) show the *Bison* spp. samples between the range of grazers and mixed feeders (Figure 4), suggesting a broad dietary niche. *Bison antiquus* from LPSA show more individuals within the grazer guild (n = 7, 77%). On the contrary, *B. antiquus* from LCPT show more prevalence of mixed feeder individuals (n = 8, 80%). On the other

hand, *B. latifrons* from LCPT only show two individuals in the grazer guild, and most within the mixed feeder guild (40%).

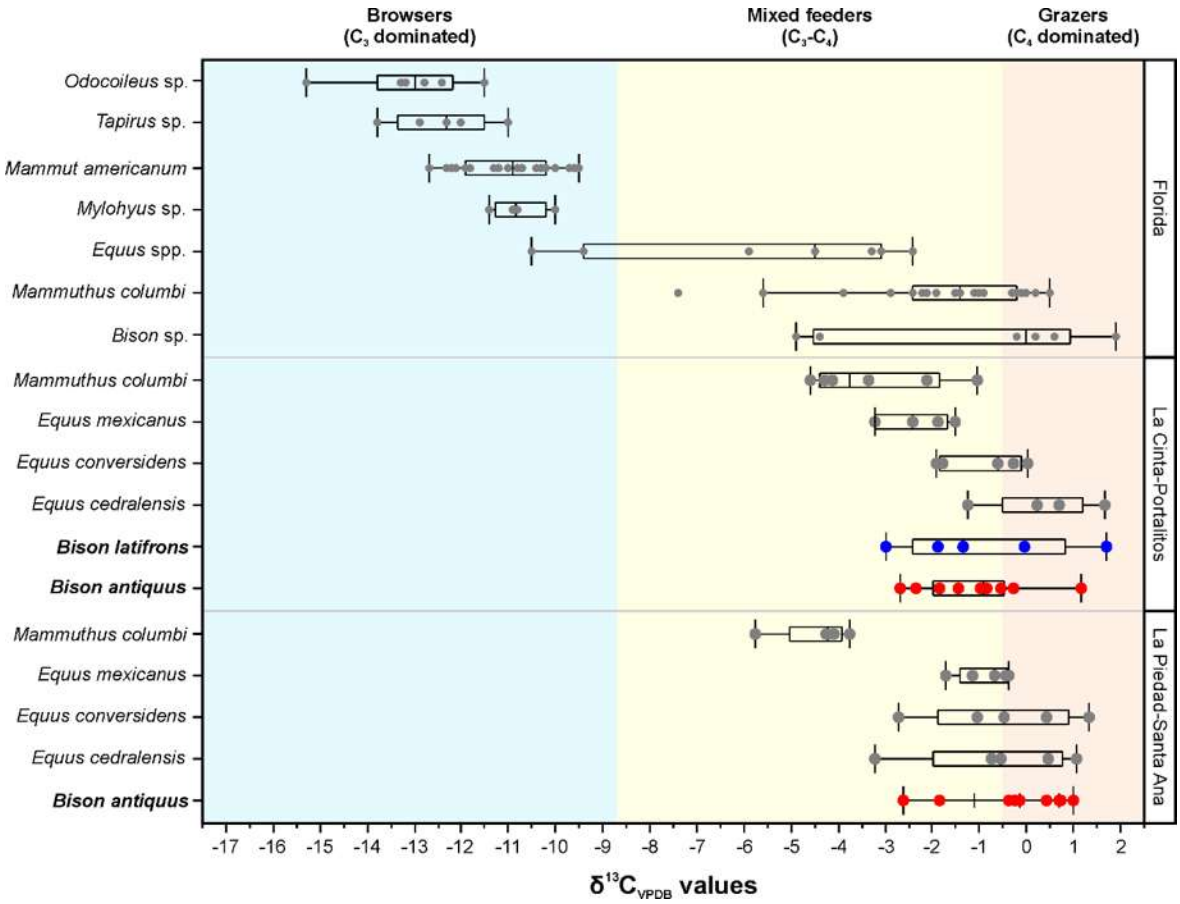

Figure 4. Carbon stable isotope signatures. Red: *Bison antiquus*, blue: *B. latifrons*, big dots: taxa in our study sites, small dots: model taxa from Florida, *Cuvieronius* excluded. Horses and mammoth data from Gutiérrez-Bedolla *et al*. (2016), and Marín-Leyva *et al*. (2016); Florida data from Koch *et al*. (1998).

As for the percentage of consumption of C_4 plants, *B. antiquus* from LCPT show a mean value of 76.8% (σ = 7.3%), *B. antiquus* from LPSA have a mean value of 82.2% (σ = 8.1%), and *B. latifrons* from LCPT display a mean of 77.9% (σ = 12%). We also compared the $\%C_4$ consumed by our samples of *Bison* spp., against other known grazing megafauna of the same sites (Figures 5 and 6). At LCPT we found no statistically significant differences between the diets of *Bison antiquus* and *B. latifrons* ($p = 0.99$), nor amongst *B. antiquus* and all species of *Equus* ($p > 0.34$ in all comparisons), a similar pattern was found between *B. latifrons* and all *Equus* species ($p > 0.39$). On the other hand, we found statistically significant differences between *B. antiquus* and *Mammuthus columbi* ($p = 0.01$) and between *B. latifrons* and *M. columbi* ($p = 0.03$).

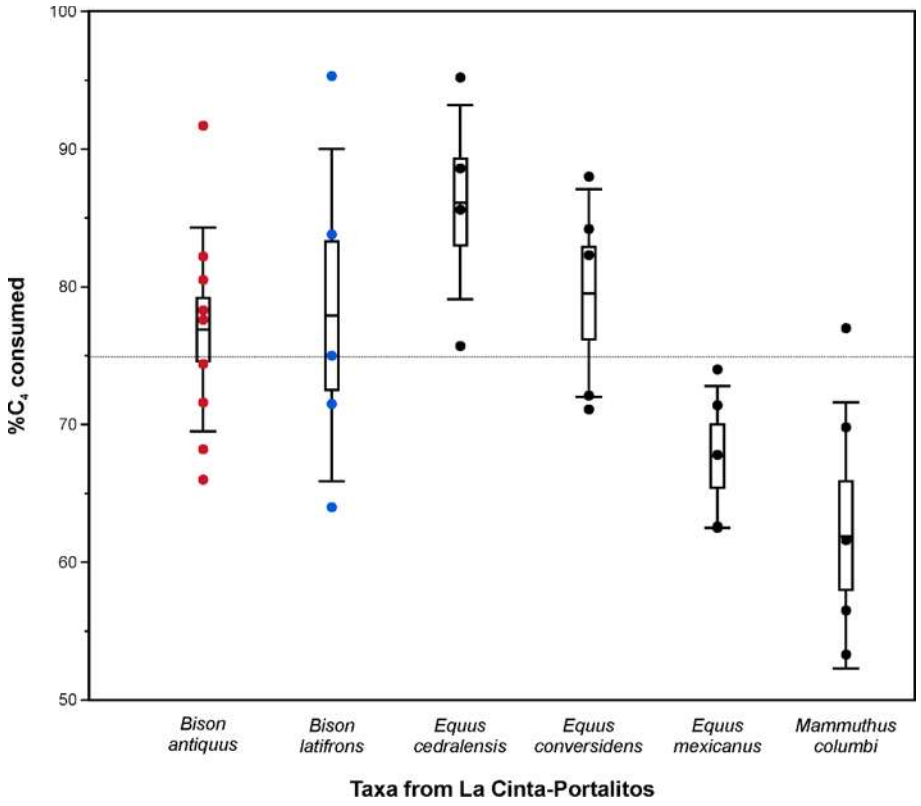

Figure 5. Percentage of C_4 plants consumed by major megafaunal representatives from La Cinta-Portalitos. Gray dotted line represents the grand mean. Box plots represent the means and standard deviation of each group. Horses and mammoth data from Gutiérrez-Bedolla *et al*. (2016), and Marín-Leyva *et al*. (2016).

On the other hand, in LPSA *B. antiquus* show no statistically significant differences in its consumption of C_4 with *E. mexicanus* ($p = 0.9$), *E. conversidens* ($p = 0.99$) and *E. cedralensis* ($p = 0.98$), but it showed statistically significant differences with *M. columbi* ($p < 0.0001$).

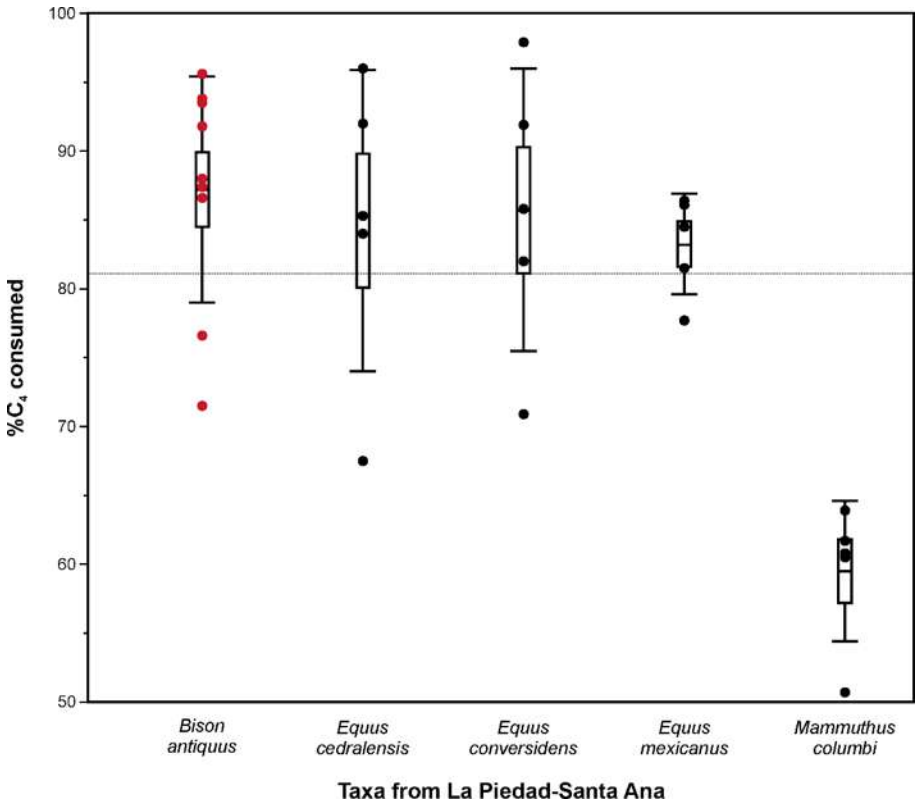

Figure 6. Percentage of C_4 plants consumed by major megafaunal representatives from La Piedad-Santa Ana. Gray dotted line represents the grand mean. Box plots represent the means and standard deviation of each group. Horses and mammoth data from Gutiérrez-Bedolla *et al*. (2016), and Marín-Leyva *et al*. (2016).

Additionally, we found high percentages of overlap in the consumption of C_4 plants (Table 3) between *B. antiquus* and *Equus* spp. at LPSA (97.4%), but relatively low percentage among *B. antiquus* and *M. columbi* (72.3%). On the other hand, *Bison* spp. and *Equus* spp. show high percentage overlap at LCPT (93.9%), and relatively low overlap percentages between *Bison* spp. and *M. columbi* (84.5%). Finally, the percentage of overlap amongst bison species was very high (98.9%). This data suggests that there was an intense competition between *B. antiquus* and *B. latifrons* at LCPT, and also a high competition between bison species and *Equus* spp. This pattern is more evident at LPSA, possibly due to a less heterogeneous habitat in that site. This pattern of competition between horses and bison is also found at Rancho La Brea, California (Feranec et al., 2009), where these species competed seasonally, but with a strong selection for C_3 plants, instead of C_4 plants as we found at our sites. Finally, we found low values of overlap in the consumption of C_4 vegetation between the bison and the mammoths (80.4%). The lowest values are from LPSA (72.3%), while the highest are from LCPT (84.5%), suggesting that *M. columbi* exploited a wider variety of resources at LPSA, due to its ability to consume higher vegetation.

Table 3. Overlap percentages in the consumption of C_4 vegetation amongst megafauna from LCPT and LPSA. Percentages over 95% are highlighted in bold.

La Cinta-Portalitos

	B. antiquus	*B. latifrons*	*E. mexicanus*	*E. conversidens*	*E. cedralensis*	*M. columbi*
B. antiquus	100					
B. latifrons	**98.9**	100				
E. mexicanus	90.7	89.7	100			
E. conversidens	**97.3**	**98.3**	88.1	100		
E. cedralensis	90.7	91.7	81.5	93.3	100	
M. columbi	85	84	94.2	82.3	75.7	100

La Piedad-Santa Ana

	B. antiquus	*E. mexicanus*	*E. conversidens*	*E. cedralensis*	*M. columbi*
B. antiquus	100				
E. mexicanus	**96**	100			
E. conversidens	**98.5**	**97.5**	100		
E. cedralensis	**97.7**	**98.2**	**99.2**	100	
M. columbi	72.3	76.2	73.8	74.5	100

The predicted habitat from $\delta^{13}C$ enamel values as vegetation type, locate our samples of *Bison* spp. between a C_4 grassland and a C_3-C_4 grassland (Figure 7). *B. antiquus* of LPSA had 77% (n = 7) of individuals in a Poaceae-dominated grassland likewise, *B. antiquus* of LCPT had a similar pattern with 70% (n = 7) individuals, while *B. latifrons* had 60% (n = 3) of individuals in this type of ecosystem, suggesting a widest foraging spectrum than modern plains *Bison bison*. The *Bison* spp. values present a wide overlap with the values of *Equus* spp., suggesting a similar habitat use of these herbivores. On the contrary, *Bison* spp. and *M. columbi* show little to no overlap in their inferred habitat type, with only 83% of individuals for LCPT, and 100% of individuals of LPSA foraging in a C_3-C_4 grassland. We also calculated the original bulk plant $\delta^{13}C$ signature and obtained that all *Bison* spp. samples fall within the C_4 signature, as do the *Equus* spp. On the other hand, *M. columbi* show a dissimilar pattern, with the population from LCPT between C_4 and C_3-C_4 bulk plant diet, and the population of LPSA with a clear C_3-C_4 signature. Finally, we plotted the CAM $\delta^{13}C$ estimated values (O'Leary, 1988), and found that every taxon examined has the potential signature of this type of plants. Nevertheless, palynological studies of LCPT (Israde-Alcántara et al., 2010) show an abundance (≈ 40%) of *Pinus*, *Alnus*, Poaceae, *Ambrosia*, as well as a moderate amount (≈ 20%) of *Quercus*, Cheno-Am, and *Monoletes*, neither of which are CAM. But there was a small amount (<10%) of Agavaceae pollen, a CAM type plant. Due to its low prevalence, we assume that CAM plants were not an important part of the vegetational structure in LCPT. We assume a similar scenario for LPSA, since it is in near vicinity, and it was part of the same hydrological system during the Pleistocene (Marín-Leyva, 2011). Additionally, CAM plants dominate in arid ecosystems (Koch, 1998), but the analysis of $\delta^{13}C$ of an *Odocoileus* sp. tooth (following

Kohn, 2010) yielded a mean annual precipitation value of 507.9 mm/year for LCPT, which is consistent with semi-arid values from Mexico (García, 1998a, 1998b). However, more data is necessary to establish a clear precipitation pattern.

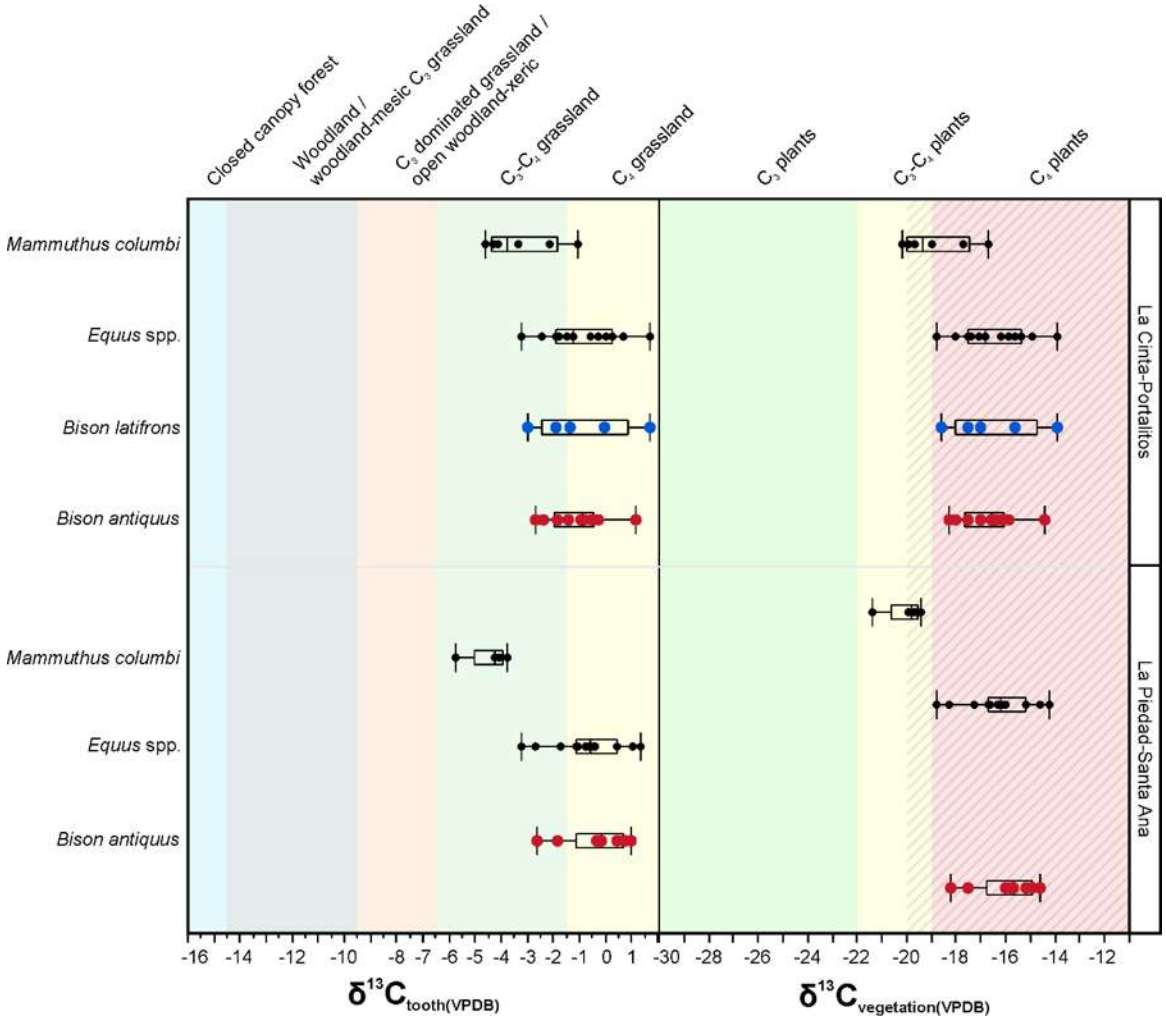

Figure 7. Left: $\delta^{13}C$ of tooth enamel as predictor of habitat. Right: modern equivalent of $\delta^{13}C$ of the bulk plant material ingested by megaherbivores at our study sites. Horses and mammoth data from Gutiérrez-Bedolla *et al*. (2016), and Marín-Leyva *et al*. (2016).

Finally, we estimated the mean annual temperature (MAT °C) for both sites (Figure 8). LCPT show a MAT of 15.1°C (n = 36, σ = 4.59), while LPSA a mean of 13.4 °C (n = 29, σ = 4.58). The temperatures present during the Pleistocene are similar to those found in the south of the localities (<1° latitude). When we compared these values, we found no statistically significant differences between them (Prob > F = 0.12), suggesting an isotherm displacement to the south. The modern MAT of LCPT is 17 ±1°C, which is 0.9°C higher

than the mean Pleistocene estimate. On the other hand, modern MAT of LPSA is 19 ±1°C, more than 4.6°C higher than the Pleistocene values. This difference in temperature may be explained by the change of the drainage regimen of the Lerma basin in the latest Pleistocene and early Holocene (Roy et al., 2009; Marín-Leyva, 2011).

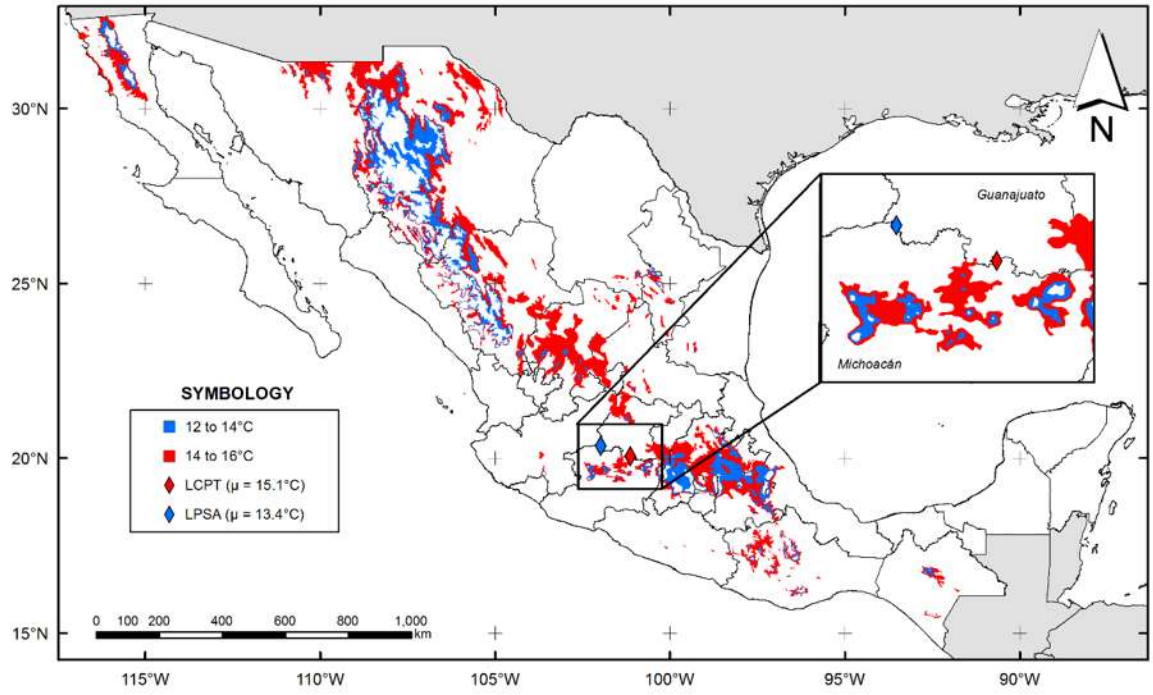

Figure 8. Modern temperatures within the range of the estimated temperature from our study areas. Data from García (1998c).

Mineralogy

In total, we analyzed 9 stata for both LCPT and LPSA. In the DXR analysis we found evidence of α-quartz (trigonal structure), and abundant silicates, mainly tectosilicates and phyllosilicates, as well as calcite and feldspar potassian. Summary abundance of minerals by stratum (with number), and site is as follows: Quartz 9 LCPT, 7 LPSA; Andesine 6 LCPT, 9 LPSA; Tridymite 8 LCPT, and LPSA; Montmorillonite 6 LCPT, 9 LPSA; Sanidine 3 LCPT, 7 LPSA; Halloysite 4 LCPT, 5 LPSA; Cristobalite 6 LCPT, and LPSA; Albite 5 LCPT; Mordenite 1 LCPT, 2 LPSA; Calcite 1 LCPT, and LPSA; Feldspar potassian 2 LPSA; Beidellite 1 LCPT; and Enstatite 1 LCPT (see Table 4 for a detailed summary).

Table 4. Mineralogical composition (DXR) of each stratum reported in this study. Bold text represents the fossil strata.

ID	Column/strata	Lithology	Content
		La Cinta-Portalitos	
E1	"Cerca nopal"/1	Diatomite	Quartz, Tridymite, Halloysite, Albite, Cristobalite, Beidellite
E2	"Cerca nopal"/2	Clayish silt	Quartz, Tridymite, Albite, Cristobalite, Andesine, Montmorillonite
E4	"Cerca nopal"/4	Silty sand	Halloysite, Quartz, Tridymite, Albite, Mordenite
E4.1	**"Portalitos 06"/2**	**Conglomerate with silt and sandy matrix**	**Halloysite, Quartz, Albite, Andesine, Cristobalite, Montmorillonite**
E5	**"Cerca nopal"/5**	**Conglomerate with silt and sandy matrix**	**Quartz, Tridymite, Halloysite, Calcite, Cristobalite, Andesine, Montmorillonite**
E6	"Cerca nopal"/6	Diatomite	Quartz, Tridymite, Halloysite, Sanidine, Albite, Cristobalite
E7	"Cerca nopal"/7	Diatomite	Quartz, Montmorillonite, Tridymite, Cristobalite, Andesine, Enstatite, Sanidine
E8	"Cerca nopal"/8	Silty sand	Quartz, Tridymite, Halloysite, Andesine, Montmorillonite
E9	**New sample**	**Conglomerate with silt and sandy matrix**	**Quartz, Tridymite, Andesine, Montmorillonite, Sanidine**
		La Piedad-Santa Ana	
E10	"Cárcamo"/1	Silty sand	Tridymite, Quartz, Cristobalite, Andesine, Sanidine, Montmorillonite
E11	"Cárcamo"/2	Silty sand	Mordenite, Andesine, Sanidine, Montmorillonite
E12	"Cárcamo"/8	Modern alluvial sediments	Quartz, Cristobalite, Tridymite, Calcite, Halloysite, Sanidine, Andesine, Montmorillonite
E13	**"Cárcamo"/4**	**Conglomerate with silt and sandy matrix**	**Quartz, Halloysite, Tridymite, Cristobalite, Andesine, Sanidine, Montmorillonite**
E14	**New sample**	**Conglomerate with silt and sandy matrix**	**Halloysite, Quartz, Tridymite, Cristobalite, Andesine, Sanidine, Montmorillonite**
E15	**New sample**	**Conglomerate with silt and sandy matrix**	**Quartz, Halloysite, Tridymite, Sanidine, Andesine, Montmorillonite**
E16	"Cárcamo"/3	Silty sand	Tridymite, Cristobalite, Mordenite, Halloysite, Andesine, Feldspar potassian, Montmorillonite
E17	"Cárcamo"/5	Silty sand	Quartz, Tridymite, Halloysite, Cristobalite, Sanidine, Andesine, Montmorillonite
E18	"Cárcamo"/6	Diatomite	Quartz, Andesine, Tridymite, Feldspar potassian, Montmorillonite

The sampled strata within our typical lithological columns are presented in the Figure 9. The minerals found are described in order of abundance (with exception of montmorillonite), and Dana classification system, as follows:

1) Tectosilicates: A) Andesine belongs to the plagioclase series, and it is commonly found as detrital grains in sedimentary rocks derived from Andesite (Anthony et al., 2003). It is commonly found at both sites due to the weathering of Andesite, a common volcanic rock of Miocene origin at LCPT (Israde-Alcántara, 1997), and Oligocene (Pérez-Flores et al., 1999) and Pliocene (5-2.5 Ma) origin at LPSA (Rosas-Elguera et al., 2000). Suggesting its presence as an authigenic mineral. B) Tridymite is commonly found as phenocrysts in felsic rocks, and sometimes in basalt (Anthony et al., 2003). Nevertheless, the absence of mafic rocks such as granite in the Cuitzeo basin and Lerma hydrological system near the fossil sites (Montiel-Escobar et al., 1998; Pérez-Flores et al., 1999; Rosas-Elguera et al., 2000), suggest that its origin is within basaltic rocks. C) Sanidine is usually form from rhyolites,

phonolites and trachytes, as well as felsic rocks. The abundance of rhyolites in LCPT of Miocene origin (Israde-Alcántara, 1997; Montiel-Escobar et al., 1998), and of Oligocene rhyolites at LPSA at the upper region of the basin (Pérez-Flores et al., 1999; Rosas-Elguera et al., 2000), also suggest an authigenic origin. D) Cristobalite is formed as a late-crystallizing phase in basaltic to rhyolitic volcanic rocks (Anthony et al., 2003), both common in both sites, also suggesting an in-situ origin. E) Mordenite is an authigenic mineral derived from volcanic rocks and glass (Anthony et al., 2003). F) Albite is only found at LCPT, and is a detrital authigenic product of basalt and granite alteration, as well as potassium metasomatism (Anthony et al., 2003), the absence of paleosols and sandstones for the metasomatism to be of relevance (Fedo et al., 1995) leaves basalt and granites as candidates for the origin of this mineral. Geological data show that granites are absent from LCPT area, which suggest basalt as candidate for the parental rock.

2) Phyllosilicates: A) Halloysite is formed by direct precipitation of aluminosilicates during weathering (Anthony et al., 2003), it can be used in determining paleoenviromental conditions when is found in association with other clay minerals (see discussion on montmorillonite below). B) Beidellite is derived from mafic rocks such as basalt under watery conditions (Anthony et al., 2003), which is abundant in the area. This mineral is only found at LCPT, at the base of the column in a Diatomite level, suggesting a slow in situ transformation.

3) Inosilicate: A) Enstatite is only found at LCPT in a diatom level, near the top of the column. This mineral forms from inclusions in mafic rocks (Anthony et al., 2003). As these rocks are very common in the area (Pérez-Flores et al., 1999), as well as olivine inclusions, we consider this to be also of authigenic origin.

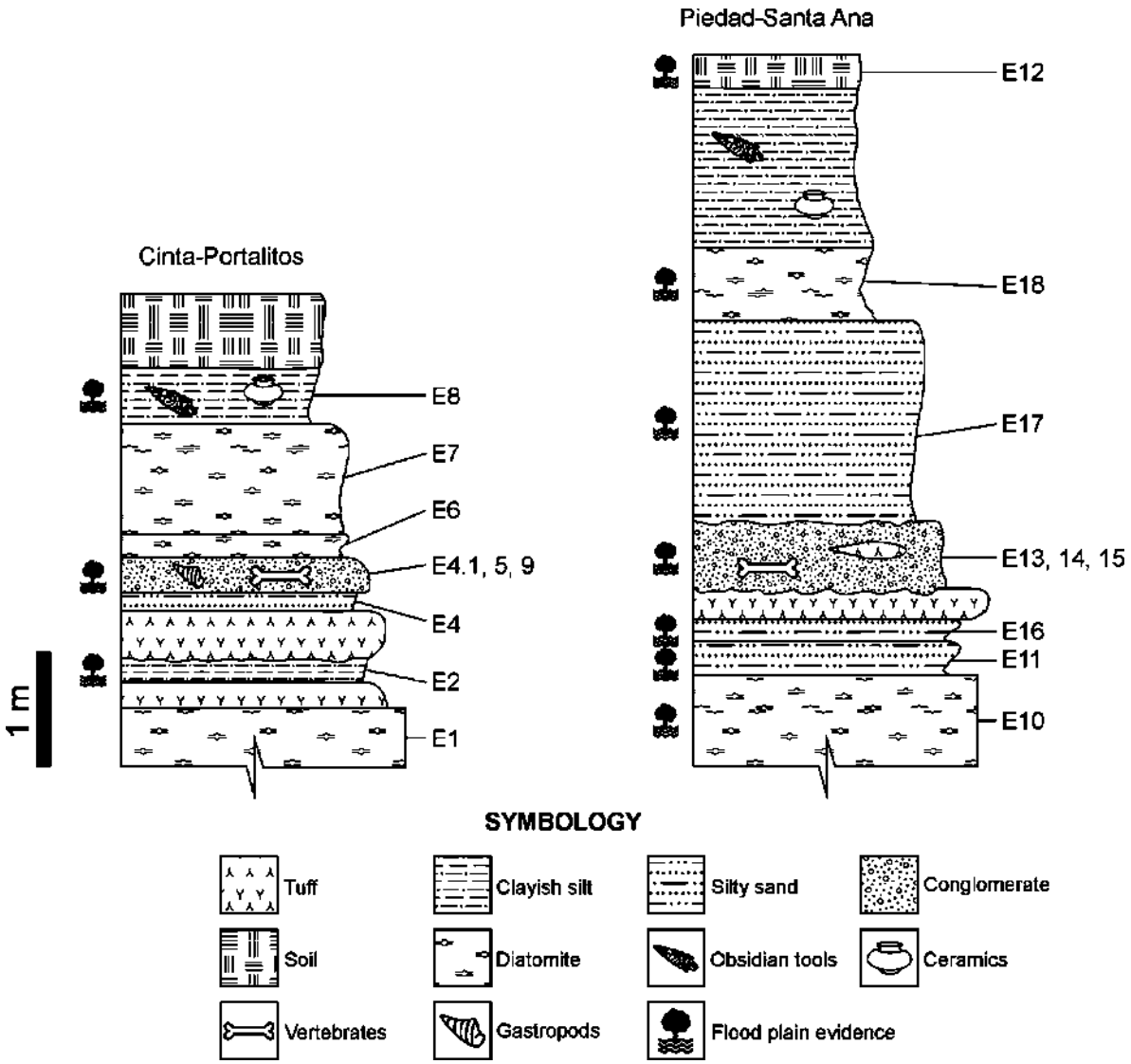

Figure 9. Typical stratigraphy from the study sites with samples taken for DXR and IRS analyses.

Montmorillonite is a phyllosilicate of the smectite group, typically as an alteration product of volcanic tuff and ash under alkaline conditions of poor drainage, and in association with Mg, Ca, Na, and K (Anthony et al., 2003). The typical elemental association is found within LCPT, being in higher concentration near the base of the stratigraphic column, where the tuff and ash are found (Marín-Leyva, 2011), suggesting an authigenic origin for this mineral. Tuffs are also, common at LPSA (see Figure 9), at the base of the fossiliferous stratum (Díaz-Sibaja, 2013), and in the near vicinity (Pérez-Flores et al., 1999; Rosas-Elguera et al., 2000). Montmorillonite alone is a classical indicative of flood plain areas (Junk et al., 1989), usually in warm, dry climates but as evidence suggest, low-temperature environments can also generate this mineral (Altschuler et al., 1963). Montmorillonite is usually associated with halloysite in the fossil strata, a condition that suggest tropical semi-

arid transitional and typical temperate climates (Carrasco et al., 2008). Our soil sample (E12) from LPSA supports this scenario within a temperate climate. Also, our stable isotope analysis suggests a similar climate.

The IRS analysis shows most of the strata of LCPT below the fossil bed with strong transmittance peaks of montmorillonite (figure 10) between 3451.51 and 3624.33 cm^{-1}. These strata reflects warm conditions with poor drainage (Singer, 1984).

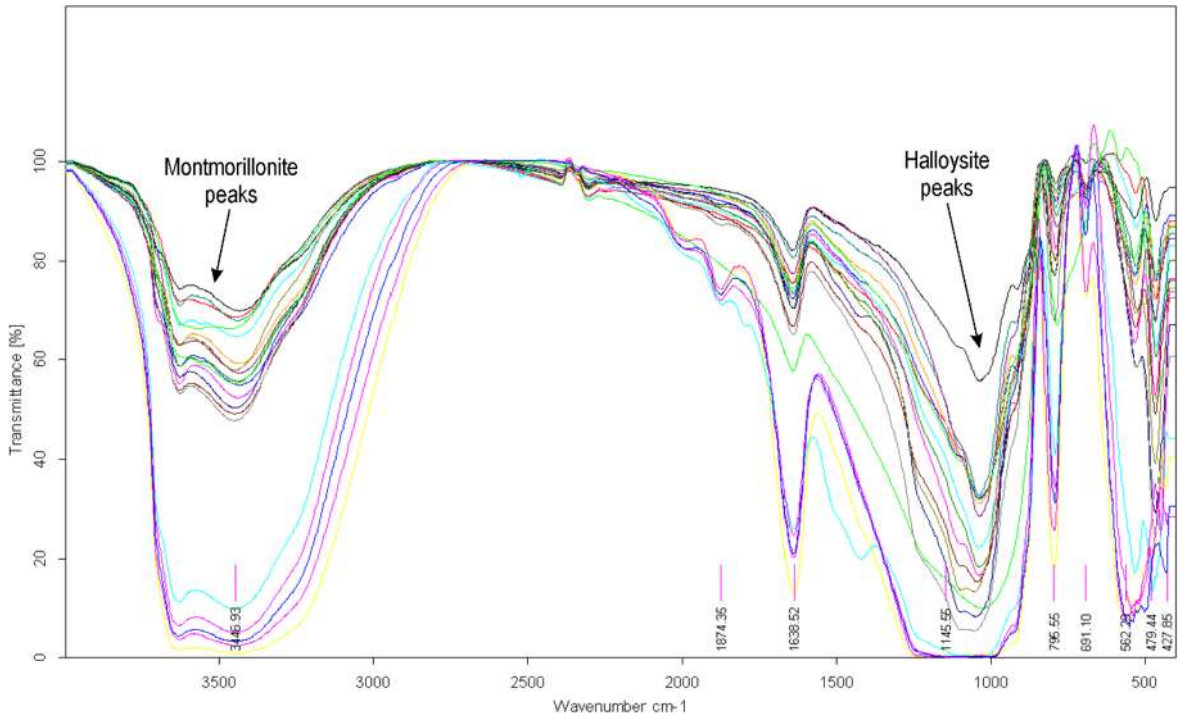

Figure 10. IRS spectra from LCPT and LPSA.

On the other hand, the rest of the strata have strong peaks close to 1000 cm^{-1}, a value related to characteristic bands for kaolinite with Si-O-Si vibrational mode (Ostrooumov, 2009), which represents halloysite with an interlayer of water (Bordeepong et al., 2011); this configuration suggest highly humid conditions for the precipitation of halloysite (Anthony et al., 2003). In these samples is also noticeable a weak peak between 3446.69 and 3625.02 cm^{-1}, suggesting the presence of montmorillonite, and thus, shallow waters, evidenced by the presence of thick packages of diatomite and clayish silt. At LPSA these conditions are within the proposed cycle of avulsion of the Lerma river and the inundation of the alluvial plain (Díaz-Sibaja, 2013). On the other hand, this scenario suggest a transgression event from the Cuitzeo lake, and its posterior slow regression to its present basin. This is similar to previously proposed scenario, but without evidence of the proposed erosive events (Marín-Leyva, 2011), due to the presence of authigenic minerals and absence of external mineralogical sources. It is noticeable that during this period of high

humid conditions, there was presence of human settlements, revealed by a high abundance of obsidian tools and ceramics.

Conclusions

Dental microwear analysis shows that *Bison antiquus* samples fall within the grazer and seasonal mixed feeder guilds, and had different patterns than previously known *B. antiquus* data from higher latitude. Also, *B. antiquus* show different microwear patterns than either ecotype of *Bison bison* (i.e. wood and plains bison), suggesting a different, and wider niche. At our sites, *B. antiquus* had a more abrasive diet at LPSA, a conclusion supported by $\delta^{13}C$ analysis, where the majority of individuals had a C_4-composed diet, while the majority of LCPT individuals had a C_3-C_4 diet, consistent with meal by meal mixed feeder habits (instead seasonal or regional mixed feeder ones). The only available individual of *B. latifrons* for dental microwear analysis fall within the regional/seasonal mixed feeder guild, a conclusion supported by $\delta^{13}C$ analysis, where *B. latifrons* population showed a wider dietary spectrum than *B. antiquus* within the C_3-C_4 and C_4 diet signatures. The habitat use inferred from $\delta^{13}C$ values suggests that both *Bison* species inhabited between C_4 and C_3-C_4 grasslands, a conclusion supported by palynological analyses at LCPT, where the herbaceous C_3 plants were present and by the reconstructed $\delta^{13}C$ vegetation values, where C_4 plants were more prevalent. These analyses also show that LCPT had major environmental heterogeneity than LPSA, where C_4 grasslands were dominating.

The $\delta^{13}C$ analysis showed competition for C_4 plants between *Bison antiquus* and *Bison latifrons*, as well as with *Equus* species at both sites. This competition was more intense at LPSA, where more homogeneous habitat (C_4 dominated grasslands) was inferred. The competition between *Bison* species is an indicative that both species lived in similar habitats, contrary to the traditional assumption that *B. latifrons* lived only at forested habitats. On the other hand, *Bison* and *Equus* species show a minor competition with *Mammuthus columbi*, and this elephant species showed mixed feeder habits in a more heterogeneous habitat, specially at LPSA. This competitive exclusion is likely due to the ability of *M. columbi* for feeding at higher level.

Dental microwear data of *Tetrameryx shuleri* and cf. *Navahoceros fricki* at LCPT supports similar environmental heterogeneity as the stable isotope analyses suggests. *T. shuleri* also shows a different microwear signature than previous known *Tetrameryx* (Pliocene), *Stockoceros conlingi* (Pleistocene) and *Antilocapra americana* (Holocene) data, suggesting a different, dietary behavior consisting in a mixed feeder diet.

The $\delta^{18}O$ analysis show that LCPT had higher mean annual temperatures than LPSA, 15.1 against 13.4°C respectively. These temperatures are present southwards, at less than 1° of latitude suggesting an isothermal displacement from the Late Pleistocene to the present. Mean precipitation data are insufficient to determine humidity conditions at studied sites, and further investigation on pure C_3 plants values is required. The temperatures inferred are consistent with mineralogical data, supporting more seasonal conditions for LPSA than

LCPT. The high prevalence of montmorillonite associated with halloysite suggest that humid seasonal floodplain conditions was prevalent at LPSA. On the other hand, high prevalence of montmorillonite with low halloysite values suggests dryer conditions at LCPT, before the late Pleistocene fauna, and a shift towards mesic conditions during the time the fauna fossilized. The stratigraphy shows that the lake conditions at LCPT were shifting from transgressive levels to drier conditions at the end of the Pleistocene and beginning of the Holocene, while LPSA was dominated by seasonal floodplanis that supported a less diverse vegetation structure.

Together, our data supports a temperate, mesic climate for LCPT at the Late Pleistocene, and a deeply seasonal climate from semi-arid to temperate at LPSA. The vegetation structure of LCPT was also more diverse than the vegetation at LPSA in which, C_4 grasslands was dominant. When we consider the palynological record at LCPT for the reconstruction of the C_3-C_4 grasslands inferred from $\delta^{13}C$, a meadow with Asteraceae, and presence of scattered *Pinus* and *Quercus* is suggested.

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7. Conclusión general

La revisión de los rumiantes fósiles de México permitió establecer un total de 28 taxones fósiles válidos. Estos taxones tienen registro fósil desde el Eoceno tardío y hasta la actualidad, con hiatos importantes durante el Oligoceno y Mioceno temprano. Las regiones geográficas mejor representadas siguen el patrón general de los mamíferos de México y se concentran en el centro del país, lo que resalta la importancia de nuevos descubrimientos en otras regiones (como el presentado como anexo en la zona sur de México). La mayor diversidad de rumiantes se presenta durante el Pleistoceno tardío, particularmente durante la edad de mamíferos del Rancholabreano, misma a la que pertenecen nuestros sitios de estudio.

Los análisis de mesodesgaste muestran que, durante gran parte de su vida los individuos de las poblaciones de *Bison antiquus* de La Cinta-Portalitos y La Piedad-Santa Ana fueron pacedores no estrictos, consumiendo no sólo pastos, sino además herbáceas y arbustos. Esta inferencia es similar a la obtenida mediante el estudio de los isótopos estables de carbono, que muestra un patrón similar, pero con tendencia hacia el consumo preferente de pastos. Finalmente, el análisis de microdesgaste muestra que, en los últimos días de vida los individuos de *B. antiquus* se alimentaban de poáceas casi de forma estricta. Esto apunta a que esta especie era generalista y que su plasticidad dietaria le permitía vivir no sólo en pastizales dominados por plantas C_4 (poáceas), sino también en praderas C_3-C_4.

De forma similar, se infiere que el bisonte gigante (*B. latifrons*) de la Cinta-Portalitos era un mixto estacional con consumo preferente de poáceas. Su dieta es muy similar a la del bisonte antiguo (98.9%), lo que apunta a una fuerte competencia entre estas especies y descarta hipótesis previas que sugerían una dieta ramoneadora y un hábitat forestal para el bisonte gigante.

La competencia en el consumo de plantas con metabolismo C_4 fue alta entre los bisontes y los équidos (*Equus mexicanus*, *E. conversidens* y *E. cedralensis*) de ambos sitios. Este patrón fue más intenso en LCPT (97.4%) que en LPSA (93.9%). Por otro lado, la competencia entre los bisontes y los mamutes (*Mammuthus columbi*) en ambos sitios fue baja (72.3-85%), lo que sugiere una mayor exclusión competitiva entre estos grupos de megaherbívoros.

Los análisis de microdesgaste dental sugieren que los cérvidos (cf. *Navahoceros fricki* y *Odocoileus hemionus*) de LCPT se alimentaban de forma mixta. Esta es la primera vez que se obtienen datos de dieta para *Navahoceros fricki*, mientras que para *O. hemionus*, se obtuvieron resultados similares a la composición moderna de la dieta de esta especie, lo que sugiere que no ha tenido cambios drásticos en su dieta desde el Pleistoceno tardío. Estos datos son preliminares, pues el microdesgaste revela únicamente la abrasividad de la dieta en los últimos días (3-4) de vida, por lo que este patrón puede variar de forma estacional u ontogenética.

El análisis de los isótopos estables de oxígeno en el hidroxiapatito del esmalte en los bisontes y otros taxones de la megafauna en ambos sitios sugieren una temperatura media anual para LCPT de 15.1° C, mientras que para LPSA, la temperatura media anual se estima en 13.4° C. Estas temperaturas no se encuentran actualmente en los sitios de estudio que son, 2° C más altas para LCPT y 6° C más altas para LPSA. Sin embargo, las temperaturas inferidas para el Pleistoceno tardío (ca. 23 ka) se encuentran desplazadas hacia el sur en menos de un grado de latitud, lo que sugiere un cambio moderado en el patrón de isotermas del Pleistoceno a la actualidad.

Los estudios de la estratigrafía y mineralogía de los sitios revelan que durante el tiempo en el que la megafauna vivió, las condiciones eran marcadamente estacionales y con abundancia de humedad. Los tectosilicatos y filosilicatos presentes en la fracción de arcillas de las columnas de ambos sitios de estudio sugieren una génesis *in situ*, por lo que su estudio revela condiciones locales. En LCPT dichas condiciones eran por lo general, áridas antes del depósito fosilífero. Dichas condiciones cambiaron hacia un ambiente más húmedo, con evidencia de transgresión del paleolago de Cuitzeo y su posterior regresión paulatina hasta su cuerpo actual. En cambio, las condiciones de LPSA se han mantenido con una marcada estacionalidad constante, antes y después del depósito fosilífero. Dichas condiciones estaban acompañadas de ciclos de avulsión del río Lerma hacia las planicies aluviales, mismas que sirvieron para el establecimiento de cuerpos de agua someros y relativamente estables, en los que se depositaron paquetes de diatomita. Estas condiciones lacustres cambiaron de forma intermitente hacia condiciones predominantemente fluviales, lo que es similar a las condiciones modernas en la estación de lluvias.

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Anexo. Una nueva localidad fosilífera en Oaxaca (México) y el registro más austral de *Bison latifrons*. Implicaciones paleobiogeográficas, paleoecológicas y paleoambientales (artículo publicado)

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Una nueva localidad fosilífera en Oaxaca (México) y el registro más austral de *Bison latifrons*. Implicaciones paleobiogeográficas, paleoecológicas y paleoambientales

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RESUMEN

Se reporta el registro más austral de *Bison latifrons* para América del Norte. El registro procede de una nueva localidad fosilífera en el municipio de San Dionisio Ocotepec, localizado en los Valles Centrales de Oaxaca. La fauna asociada incluye a *Mammuthus columbi*, *Equus* cf. *E. conversidens* y *Bison* sp. Por la presencia de bisontes y de mamut, se infiere una edad correspondiente al Rancholabreano (Pleistoceno tardío). Adicionalmente, se llevó a cabo un análisis de mesodesgaste para proboscídeos y un análisis de microdesgaste de baja magnificación (35x) a los restos dentales de mamut. Los resultados de estos análisis sugieren que el individuo de *M. columbi* era un pacedor. Debido a los hábitos dietarios del mamut y del hábitat inferido para caballos y bisontes de México, inferimos que, durante el Pleistoceno, en el sitio debieron existir zonas abiertas con pastizales en las partes planas. El presente registro de *Bison latifrons* es el primero de la especie para Oaxaca (México) y para la provincia morfotectónica del Cinturón Volcánico Transmexicano; con ello, su rango de distribución geográfica conocida se extiende en más de 447 km, desde Tequixquiac en el Estado de México hasta el centro de Oaxaca. Esta nueva localidad fosilífera contribuye al conocimiento de las faunas del Pleistoceno tardío de la porción sur de México y en particular del centro de Oaxaca, lo que mejora nuestro entendimiento de los cambios bióticos y climáticos ocurridos durante el inicio del Holoceno.

Palabras clave: Rancholabreano, Oaxaca, *Bison*, *Mammuthus*, *Equus*.

ABSTRACT

We report the southernmost record of Bison latifrons in North America. This is the first record for the species in Oaxaca (Mexico), and for the Transmexican Volcanic Belt morphotectonic province; the known geographic distribution range of Bison latifrons is extended in more than 447 km, from Tequixquiac in the State of Mexico to central Oaxaca. This finding comes from a new fossiliferous locality at the municipality of San Dionisio Ocotepec, located in the Central Valleys region of the state of Oaxaca, Mexico. The associated fauna includes: Mammuthus columbi, Equus cf. E. conversidens, and Bison sp. By the presence of bison as well as mammoth, a Rancholabrean land mammal age (Late Pleistocene) is assigned to the fossil fauna. In addition, we performed a proboscidean mesowear analysis as well as a low magnification microwear analysis (35x) to the dental elements of the mammoth. Our findings suggest that the mammoth individual was a grazer. Due to the mammoth's feeding habits and the habitat described for Mexican samples of bison and horses, we concluded that during the Late Pleistocene, San Dionisio Ocotepec was dominated by open grassland in the lowlands. This new fossil site and its fauna contribute to improve the knowledge of the Rancholabrean in southern Mexico, and particularly in the Central Valleys of Oaxaca. This improves our understanding of the biotic and climatic changes during the foundation of the Holocene.

***Keywords:* Rancholabrean, Oaxaca, Bison, Mammuthus, Equus.**

1. Introducción

El género *Bison* tiene una historia evolutiva corta y compleja. Evolucionó en Indochina durante el Plio-Pleistoceno, entre hace 3.4 y 2.6 Ma (Kurtén, 1968; McDonald, 1981; Khan *et al.*, 2010; Castaños *et al.*, 2012). Los bisontes se dispersaron por Eurasia hace aproximadamente 700 Ka, durante el Pleistoceno medio y arribaron a Beringia entre hace 300 y 130 Ka (Shapiro *et al.*, 2004). Finalmente, invadieron América del Norte continental entre hace 160 y 75 Ka (McDonald, 1981; Haynes, 1985; Bell *et al.*, 2004; Shapiro *et al.*, 2004), donde evolucionaron dos especies autóctonas: *Bison antiquus* (syn= *B. occidentalis*, *sensu* McDonald, 1981; Wilson *et al.*, 2008) y *Bison latifrons* (Guthrie, 1970). Estas dos especies de bisontes se presentan de forma simpátrica con dos especies de origen eurasiático: *B. priscus* y *B. alaskensis* (Guthrie, 1970; McDonald, 1981). Todas estas especies coexistieron durante el Pleistoceno tardío de América del Norte, incluyendo México (McDonald, 1981; Ferrusquía-Villafranca *et al.*, 2010), con excepción de *B. bison*, que se originó durante el Holoceno temprano (4 – 5 Ka) en el sur de Canadá (McDonald, 1981; Wilson *et al.*, 2008).

El bisonte gigante (*B. latifrons*) es uno de los bisontes menos conocidos de México. Se tienen registros de la especie en San Juan de los Lagos (Dugès, 1894; Solorzano, 2002), Zacoalco (Solorzano, 2002; Lucas, 2008) y Chapala, Jalisco (McDonald, 1981; Solorzano, 2002); la Piedad-Santa Ana y la Cinta-Portalitos, Michoacán-Guanajuato (Díaz-Sibaja *et al.*, 2012); Zumpango de Ocampo (Osborn, 1905) y Tequixquiac, Estado de México (Cope, 1884; Villada, 1903) y dos localidades sin nombrar en Zacatecas (Skinner y Kaisen, 1947). En Oaxaca sólo se tienen registros probables en la Mixteca alta, al norte del estado y en los Valles Centrales (Ferrusquía-Villafranca, 1976; Ferrusquía-Villafranca *et al.*, 2010).

Los bisontes del Pleistoceno formaron parte de un ensamblaje mastofaunístico diverso, de cerca de 286 especies reportadas (Arroyo-Cabrales *et al.*, 2002; Ferrusquía-Villafranca *et al.*, 2010). Esta riqueza de especies es comparable a la actual, aunque la composición y estructura de las comunidades es distinta (Ceballos *et al.*, 2010; Ferrusquía-Villafranca *et al.*, 2010; Ceballos y Arroyo-Cabrales, 2012). La mayoría de los registros de mamíferos cuaternarios en México corresponden a la NALMA (*North American Land Mammal Age*, edad de mamíferos terrestres norteamericanos) del Rancholabreano (Arroyo-Cabrales *et al.*, 2002), la cual se caracteriza por la presencia del taxón índice *Bison* y corresponde al Pleistoceno tardío (160 – 9.5 Ka) (Savage, 1951; Bell *et al.*, 2004). Durante el Rancholabreano se presentaron cambios climáticos importantes como por ejemplo, el Último Máximo Glaciar y el Dryas Reciente (Haynes, 2008; Clark *et al.*, 2009). Estos cambios alteraron la composición de las comunidades mastofaunísticas, lo que se toma como referencia para establecer los inicios del Holoceno (Ceballos *et al.*, 2010). El estudio de las faunas correspondientes al Rancholabreano contribuye al entendimiento de la fundación del Holoceno y de la respuesta de las comunidades de mamíferos al cambio climático (Arroyo-Cabrales *et al.*, 2008).

Las faunas del Pleistoceno tardío en Oaxaca corresponden en su mayoría a la región de la Mixteca alta, localizada al noroeste del estado (Pérez-Crespo *et al.*, 2008; Jiménez-Hidalgo *et al.*, 2011) y a la región de los Valles Centrales (Pérez-Crespo *et al.*, 2008). En este trabajo presentamos el registro más austral de *Bison latifrons*, su fauna asociada y el análisis de dieta de un ejemplar de mamut, procedente de una nueva localidad fosilífera del Rancholabreano en los Valles Centrales de Oaxaca.

2. Área de estudio

San Dionisio Ocotepec se localiza en el municipio del mismo nombre, al este de los Valles Centrales de Oaxaca. La localidad se encuentra entre las coordenadas 16°48' – 16°47' N y 96°24' – 96°22' O, con afloramientos fosilíferos en un par de arroyos de flujo intermitente denominados "El Pedregal" y "La Salina". La fisiografía de la zona

es heterogénea, con presencia de zonas planas utilizadas con fines agrícolas y ganaderos, así como una amplia representatividad de arroyos y cañadas (Figura 1).

El yacimiento se localiza en una zona con aluvión Cuaternario que sobreyace a tobas andesíticas y andesitas del Neógeno y secuencias de areniscas y lutitas de la Formación Teposcolula-Ocotlán (Cenomaniano-Albiano) y sólo en el sureste del sitio se encuentran calizas y lutitas de la Formación Yucu-

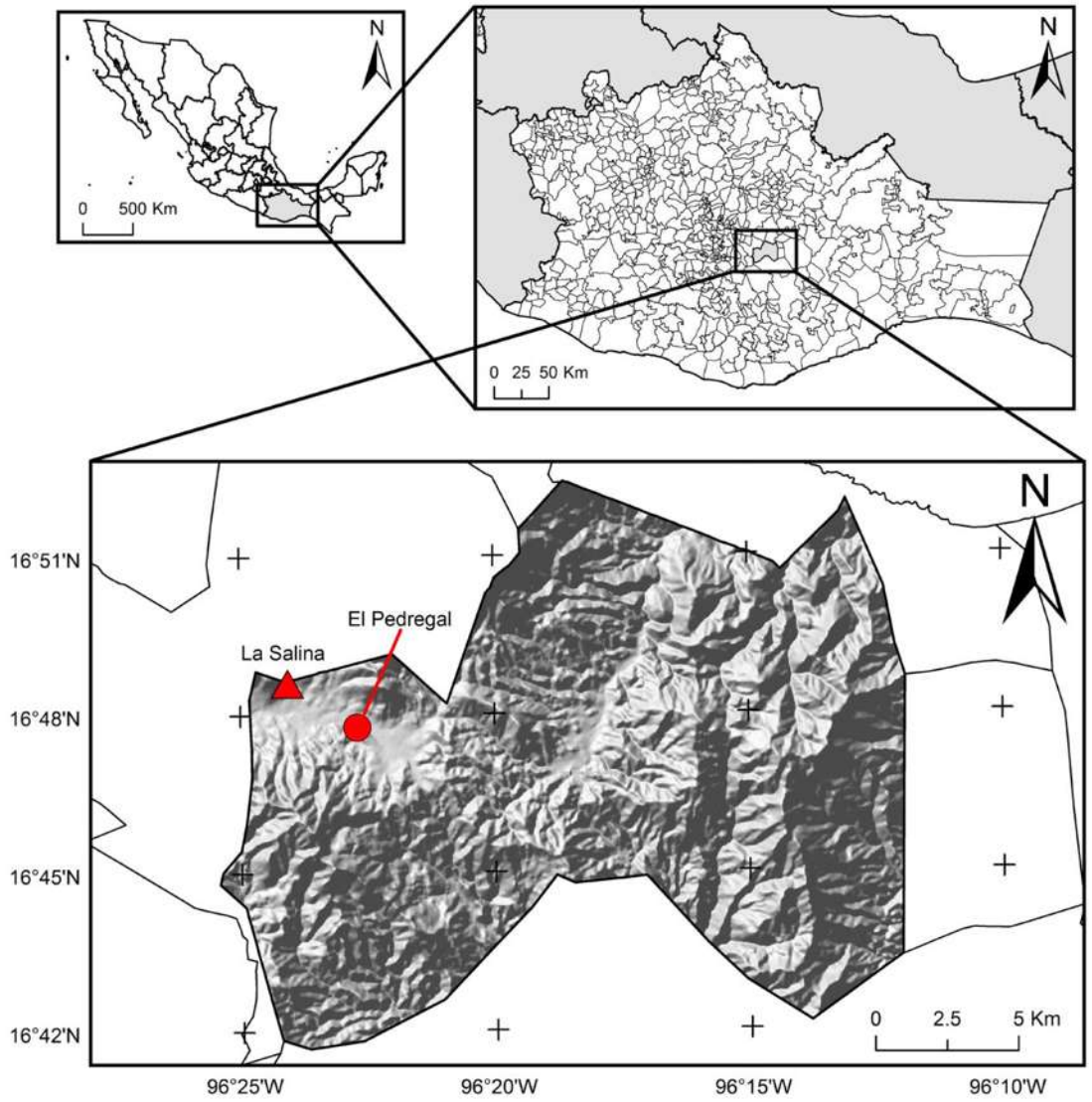

Figura 1 Ubicación geográfica y mapa hipsográfico de los yacimientos que forman la fauna local de San Dionisio Ocotepec.

nama (Sánchez-Rojas *et al.*, 2000).

La estratigrafía del sitio se compone principalmente por una alternancia de secuencias fluviales y volcanoclásticas (Figura 2). La columna tipo de la localidad se describe de base a cima en la Tabla 1.

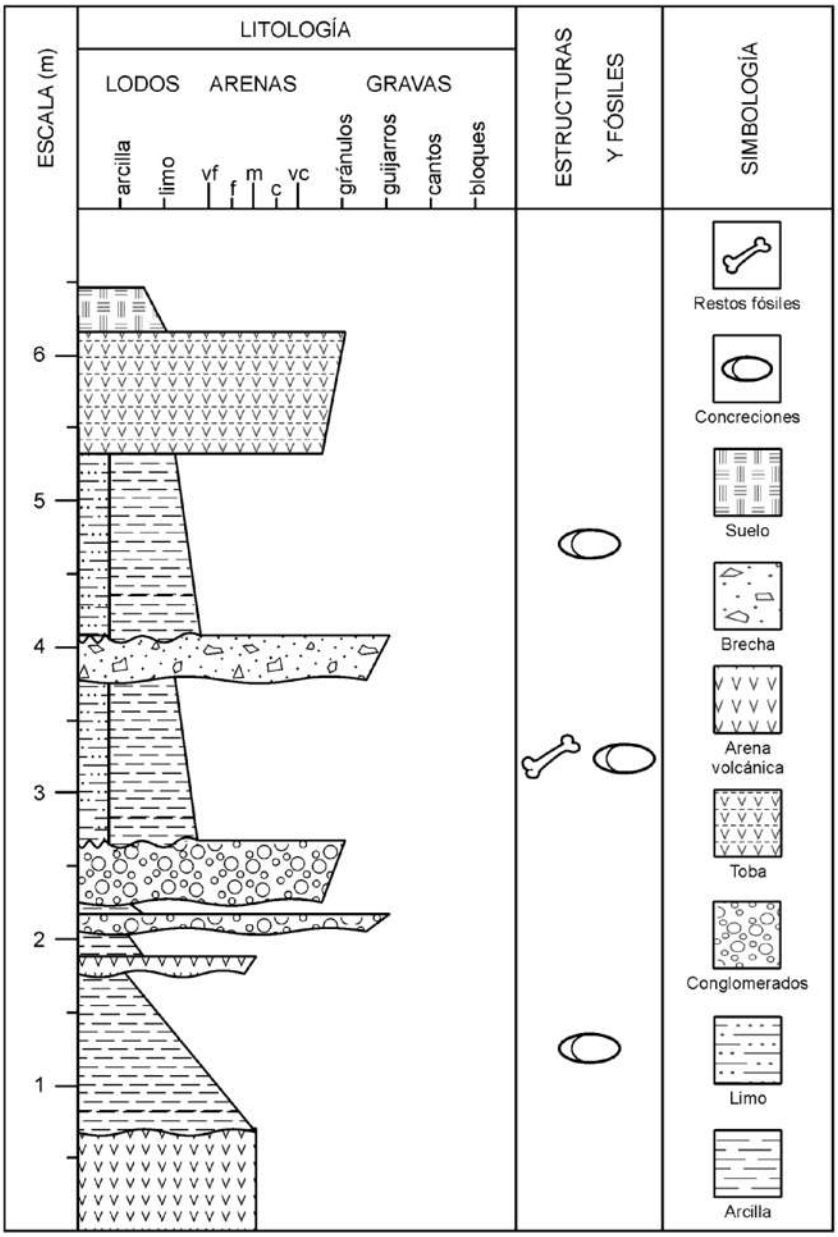

Figura 2 Columna estratigráfica tipo de la localidad.

Tabla 1. Estratigrafía generalizada de San Dionisio Ocotepec, elaborada a partir de cuatro columnas litológicas.

Número de estrato	Descripción
1	70 cm de arena volcánica andesítica fuertemente compactada. Contacto superior erosionado.
2	109 cm de arcilla con arena de color verde y con presencia de concreciones de carbonato de calcio de hasta 20 cm de diámetro. Contacto superior erosionado.
3	9 cm de arena volcánica andesítica de color rojizo fuertemente consolidada, con lentes de arcilla color café. Contacto superior neto.
4	20 cm de arcilla con limo de color café. Contacto superior erosionado.
5	9 cm de ortoconglomerados polimícticos con clastos de hasta 2 cm de diámetro. Contacto superior neto, con presencia de oxidación.
6	10 cm de arcilla de color café. Contacto superior erosionado.
7 – 11	40 cm de una intercalación de ortoconglomerados con brechas, ambos polimícticos y compuestos de clastos de riolita, basalto, granito y feldespatos, con contactos netos entre niveles y un contacto superior para el bloque de carácter fuertemente erosivo.
12	112 cm de arcilla con limo, de color café obscuro, con algunos clastos riolíticos y basálticos embebidos en la matriz y presencia de carbonatación hacia la base. Presencia de restos fósiles de vertebrados. Los fósiles se presentan tanto en la base como en la cima. Contacto superior erosionado.
13	28 cm de brecha de color amarillento, con clastos de hasta 10 cm de diámetro. Contacto superior erosivo.
14	125 cm de arcilla con limo de color negro, con lentes de arcilla rojiza con oxidación y concreciones calcáreas de hasta 10 cm de diámetro máximo. Contacto superior neto, ligeramente oxidado.
15	83 cm de toba retrabajada blanquecina con abundante oxidación. Contacto superior neto.
16	30 cm de suelo (regosol eútrico) residual moderno, con evidencia de pedogénesis *in situ* .

3. Material y método

Los fósiles se hallaron fortuitamente durante la construcción de un pozo de riego. En la zona del hallazgo se llevó a cabo el levantamiento de columnas litológicas para corroborar la ubicación estratigráfica de los restos fósiles. Adicionalmente, se llevaron a cabo salidas al campo para el levantamiento de la estratigrafía de la zona y la colecta de material fósil adicional en zonas aledañas al hallazgo original y en las barrancas y los arroyos de San Dionisio Ocotepec. El material colectado fue depositado en la Colección Paleontológica del Laboratorio de Paleontología de la Universidad Michoacana de San Nicolás de Hidalgo (con las iniciales UM) y en la colección del proyecto de Museo de Sitio de San Dionisio Ocotepec (con las iniciales MSDO), el cual se encuentra bajo resguardo de la presidencia municipal.

Para la identificación de los restos fósiles se empleó bibliografía especializada y comparación directa. La comparación directa se llevó a cabo con los materiales de la Colección Científica del Laboratorio de Paleobiología, Instituto de Recursos, Universidad del Mar; la Colección Paleontológica del Laboratorio de Paleontología, Universidad Michoacana de San Nicolás de Hidalgo (UMSNH); la colección virtual del Museo de Paleontología de la Universidad de Michigan (UMMP VP); el material del Museo Estatal de Indiana (ISM) y del

Museo Nacional de Historia Natural del Instituto Smithsoniano (USNM).

También se realizó un análisis de microdesgaste dental de baja magnificación a las piezas dentales de *Mammuthus columbi* (UM 1340, UM 1338), siguiendo el protocolo de Solounias y Semprebon (2002). En total, se llevaron a cabo tres moldes por pieza dental (maxilar y mandibular), de tres zonas: mesial, media y distal. Los moldes se observaron en un microscopio esteroscópico a 35x, del que se obtuvieron fotografías que fueron procesadas en el software Microware 4.02 (Ungar, 2002). Posteriormente, se obtuvo un promedio de hoyuelos y estrías para cada fotografía, que fue vertido en una base de datos de ungulados modelo modernos, tomada de Solounias y Semprebon (2002). Se hizo un análisis bivariante de promedio de estrías contra promedio de hoyuelos, así como análisis de funciones discriminantes canónicas (AFDC). Para el AFDC se usó un modelo de discriminación lineal y covarianza común, con las variables: promedio de hoyuelos y promedio de estrías; el soporte estadístico fue evaluado mediante una prueba de Lambda de Wilk, para corroborar la separación de categorías dietarias (pacedor, mixto y ramoneador). Finalmente, se llevó a cabo un análisis de mesodesgaste para proboscídeos, según la metodología propuesta por Saarinen *et al.* (2015); donde se promediaron los ángulos de los valles de dentina entre láminas de esmalte de seis zonas en los dos dientes reportados. Estos análisis se llevaron a cabo para inferir el tipo de hábitat en el que vivió la fauna de esta nueva localidad.

4. Resultados

En total se estudiaron más de 50 restos fósiles de los cuales, sólo 15 resultaron ser diagnósticos. La mayor parte de los restos procede del arroyo El Pedregal y sólo tres proceden de La Salina. Se reportan cuatro taxones en total: *Mammuthus columbi*, *Equus* cf. *E. conversidens*, *Bison* sp. y *Bison latifrons*.

4.1. PALEONTOLOGÍA SISTEMÁTICA

Orden Proboscidea Illigeri, 1811
Familia Elephantidae Gray, 1821
Mammuthus Brookes, 1828
Mammuthus columbi (Falconer, 1858)

Material referido. UM 1340, M2 derecho completo, con fragmentos del maxilar; UM 1338, m2 derecho completo; UM 1339, vértebra lumbar (L1); UM 1341 unciforme derecho completo; UM 1342, costilla izquierda; MSDO 001, fragmento distal de defensa izquierda; MSDO 002, MSDO 003 (Figura 3) y MSDO 004, fragmentos de escápulas y MSDO 005, epífisis parcial de un húmero derecho.

Descripción y asignación taxonómica. Los molares (Figura 3 a-d) presentan la morfología típica de un elefántido elefantino, con dientes hipsodontes y loxodontes de láminas compactas (Agenbroad y Brunelle, 1992; Osborn, 1942). Las piezas presentan 6.5 placas por cada 100 mm, lo que concuerda con el número diagnóstico para *Mammuthus columbi* de 6 – 7/100 mm en M2 y 5.5 – 6.5/100 mm en m2 (Osborn, 1942). La edad biológica del ejemplar corresponde con 26 ± 1 años, según el patrón de desgaste en las láminas que conforman los molares (Agenbroad y Brunelle, 1992).

La vértebra lumbar (Figura 3 e-g) presenta la morfología típica de un mamut, con procesos transversales delgados y no incorporados al centro vertebral, el cual posee una forma ovalada y presenta un margen inferior en forma de U (Hodgson *et al.*, 2008; Olsen, 1972). Su comparación con el ejemplar UMMP VP 116967, permitió identificarla como una lumbar 1 (L1), ya que en ambas el centro vertebral es más alto que ancho, la faceta articular de los procesos articulares craneales tienen forma de V en vista dorsal, los procesos transversos están orientados de forma caudal y son delgados, el margen dorsal de los procesos articulares caudales es redondeado y finalmente, la por-

ción anterior del proceso espinoso inicia alrededor del 50 % del ancho del centro vertebral.

Por su parte, en vistas ventral y posterior el unciforme (Figura 3 h-i) presenta una forma subpiramidal, en vista anterior presenta una forma cuadrangular (Olsen, 1972); en vista medial, las superficies articulares del *os magnum* son anchas y se encuentran separadas por un istmo amplio hacia la zona volar; finalmente, la superficie articular inferior tiene un margen recto poco prominente (Hodgson *et al.*, 2008).

Asumiendo que el dimorfismo sexual de defensas de mamut es similar al de elefántidos modernos, el fragmento de defensa (Figura 3 k-l) es referido como perteneciente a un macho, debido a la forma fuertemente triangular de la sección transversal de la misma, en contraposición con la sección oval de las hembras (Elder, 1970).

Al comparar la costilla de mamut asociada a los restos diagnósticos con costillas de *Mammut americanum* (ISM 71.3.261) y *Mammuthus primigenius* (USNM 23792), el elemento UM 1342 (Figura 3j) se asigna al género *Mammuthus*. La costilla de *M. columbi* referida es larga, delgada (Hodgson *et al.*, 2008) y en sección transversal, presenta una marcada forma de S, con prominentes cabeza y faceta articular caudal, un cuello relativamente largo, un tubérculo costal prominente y una tuberosidad íleo-costal con zonas de inserción muscular para el músculo íleo-costal torácico prominentes, además de un surco costal profundo. Es probable que la costilla proceda de la región media del cuerpo

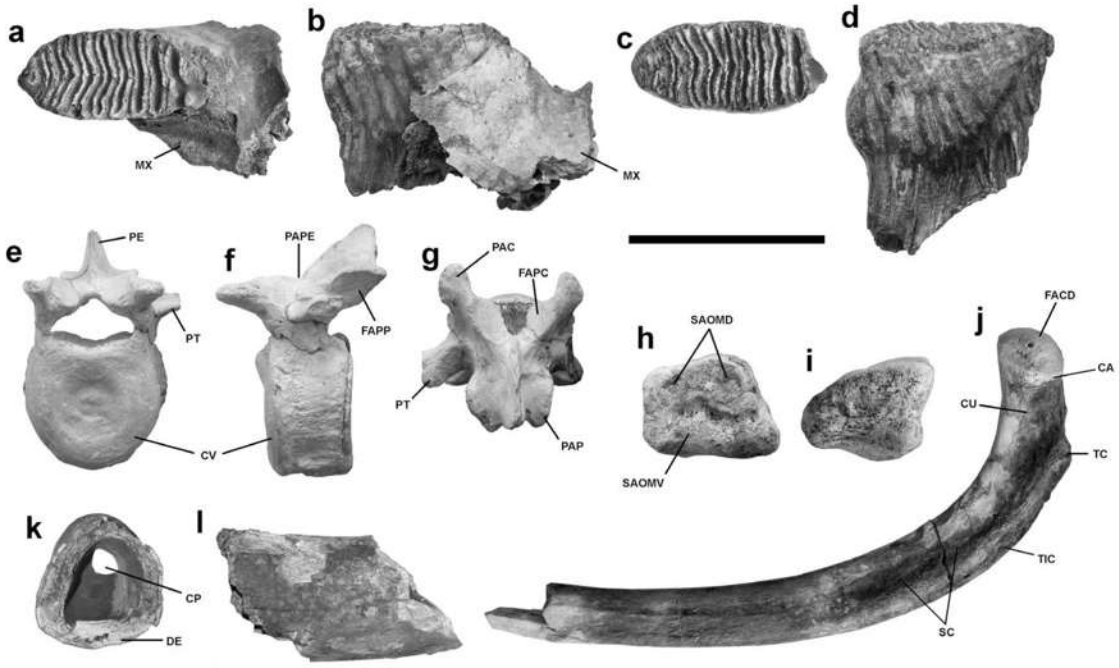

Figura 3 Restos fósiles de *Mammuthus columbi*. a, b) UM 1340 en vistas oclusal y labial; c, d) UM 1338 en vistas oclusal y labial; e, f, g) UM 1339 en vistas craneal, lateral izquierda y dorsal; h, i) UM 1341 en vistas medial y anterior; j) UM 1342 en vista especular posterior; k, l) MSDO 001 en vistas posterior y medial. Abreviaturas: MX, maxilar; PE, proceso espinoso; PT, proceso transverso; CV, centro vertebral; PAPE, porción anterior del proceso espinoso; FAPP, faceta articular de los procesos articulares caudales (posteriores); PAP, proceso articular caudal; PAC, proceso articular craneal; FAPC, faceta articular del proceso articular craneal; SAOMD, superficies articulares dorsales del *os magnum*; SAOMV, superficie articular ventral del *os magnum*; CP, cavidad pulpar; DE, dentina; FACD, faceta articular caudal; CA, cabeza; CU, cuello; TC, tubérculo costal; TIC, tuberosidad íleo-costal; SC, surco costal. Barra de escala: 10 cm..

por la curvatura del ángulo (Hodgson *et al.*, 2008). El resto de las piezas se encontraron asociadas a las piezas diagnósticas, y presentan la morfología típica de *Mammuthus* (Olsen, 1972) por lo que se infiere que pertenecieron al mismo individuo.

Orden Perissodactyla Owen, 1848
Familia Equidae Gray, 1821
Equus Linneo, 1758
Equus cf. E. *conversidens* Owen, 1869

Material referido. UM 1343, una vértebra cervical (C4-5) y UM 1344, una vértebra torácica de la región anterior (T5-7) (Figura 4).

Descripción y asignación taxonómica. La vértebra cervical (Figura 4) presenta las características típicas del género. Posee un centro vertebral inclinado en plano sagital anteroposteriormente, con forma acorazonada en las extremidades craneal y caudal; el proceso transverso sigue el eje del centro vertebral y se encuentra roto en su base; el proceso neural es corto y poco pronunciado, único en la región anterior y bifurcado en la posterior (formando una W); posee una cresta ventral bien desarrollada hacia la región posterior y presenta forámenes laterales bien definidos (Barone, 1995; Klaus-Dieter *et al.*, 2009; Pales y Garcia, 1981). Sólo se conserva el proceso articular caudal derecho, el cual rebasa el margen distal del centro vertebral en vista dorsal y posee una forma oval e inclinada medialmente.

La vértebra torácica (Figura 4) no posee el arco neural; presenta un centro vertebral inclinado en plano sagital anteroposteriormente y comprimido lateralmente en la región central; el centro posee forma semicircular, el margen dorsal es recto. Se reconoce como vértebra torácica por la posesión de las facetas costales craneal y caudal derechas y como séptima a quinta dorsal por la ausencia del foramen vascular, típico de vértebras torácicas posteriores (Barone, 1995; Klaus-Dieter *et al.*, 2009). Se comparó la altura y la longitud del

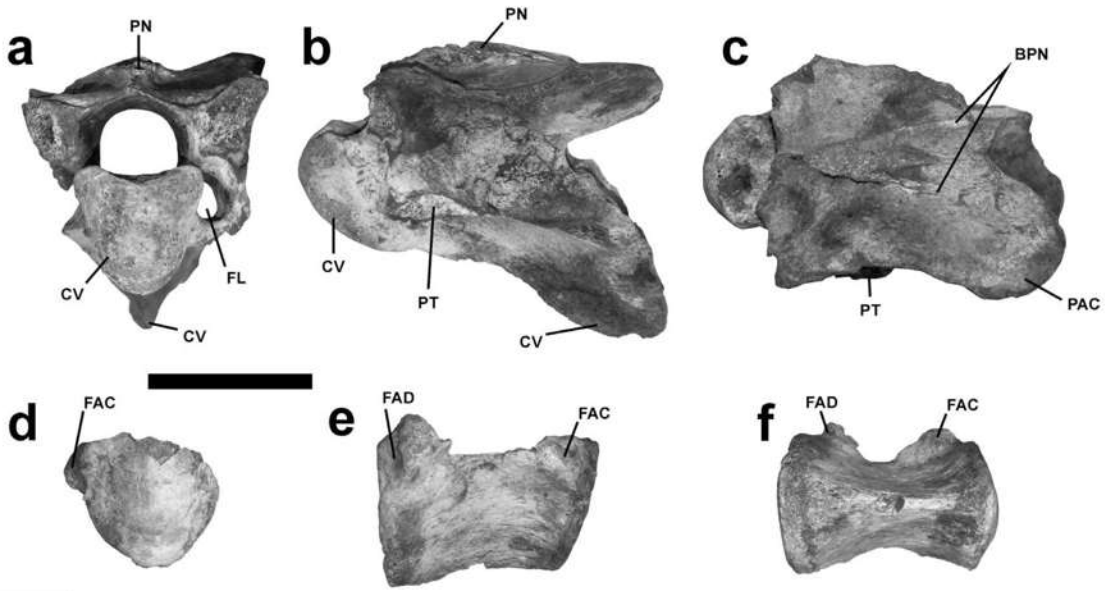

Figura 4 Restos fósiles de *Equus* cf. *E. conversidens*. a-c) UM 1343, en vistas craneal, lateral izquierda y dorsal. d-f) UM 1344, en vistas craneal, lateral derecha y ventral. Abreviaturas: PN, proceso neural; CV, centro vertebral; CV, cresta ventral; FL, foramen lateral; PT, proceso transversal; BPN, bifurcaciones del proceso espinoso; PAC, proceso articular caudal; FAC, faceta articular craneal; FAD, faceta articular caudal (distal). Barra de escala: 5 cm.

centro vertebral del elemento UM 1344 con *Equus conversidens* y *Equus* cf. *E. cedralensis* de la Colección Paleontológica de la UMSNH y el elemento UM 1344 es similar en dimensiones a *E. conversidens* (Tabla 2).

Debido a la similitud de talla entre los elementos UM 1343 y UM 1344 y debido a que *Equus conversidens* es el équido de talla media reportado para el Rancholabreano de México (Priego-Vargas *et al.*, 2016), ambos elementos se asignan a este taxón.

Orden Artiodactyla Owen, 1848
Familia Bovidae Gray, 1821
Bison (Hamilton-Smith, 1827)
Bison sp.

Material referido. UM 1345, un acetábulo derecho.

Descripción y asignación taxonómica. El acetábulo (Figura 5) muestra la morfología típica de un bovino de gran talla, que se corresponde con *Bison* (McCuaig-Balkwill y Cumbaa, 1992). Posee un borde acetabular semicircular, la superficie semilunar es amplia y se encuentra casi cerrada, con una incisura acetabular estrecha y una fosa acetabular profunda y notoria. La superficie semilunar del pubis emerge de una eminencia íleo-púbica notoria y amplia; en vista cenital, el borde acetabular se encuentra hendido en su porción dorsal, lo que permite apreciar parte de la superficie semilunar inferior (Barone, 1995; Schmid, 1972).

Bison latifrons (Harlan, 1825)

Material referido. UM 1346, parte proximal del radio derecho de un macho adulto, preservado desde el sulco tendíneo y hasta la zona articular proximal y con la cabeza completa (Figura 6).

Descripción y asignación taxonómica. El radio presenta las características típicas de un bovino de gran talla y se identifica como *Bison* por su morfología general (McCuaig-Balkwill y Cumbaa, 1992). Por debajo de la repisa de la tuberosidad radial y hacia la zona medial, se presenta una cicatriz para el músculo bíceps braquial bien desarrollada. Ésta posee forma cuadrada y se extiende hacia la zona posterior. La repisa de la tuberosidad radial es amplia y se encuentra expandida medialmente. La tuberosidad lateral o externa es amplia y posee un relieve lateral de inserción en un ángulo aproximado de 45° con respecto al eje articular. Este relieve es amplio y la zona de inserción del extensor dorsal del dedo (*extensor digiti quarti propius*) es mayor y dispuesta de forma más anterior que la zona de inserción del extensor lateral del dedo (*digitorum communis*). El proceso coronoide es redondeado y poco prominente; la hendidura central es

Tabla 2. Medidas de vértebras torácicas seleccionadas de *Equus* de México. Abreviaturas: LCDe, longitud máxima del cuerpo vertebral, incluyendo el diente; BFcr, ancho máximo en la facies articularis cranialis; BFcd, ancho máximo en la facies articularis caudalis. Medidas en mm.

Elemento	Taxón	LCDe	BFcr	BFcd	Altura del centro	Largo del centro
UM 1344	*Equus* cf. *E. conversidens*	64.9	48.2	51.2	48.1	70.6
UM 1346	*E. cedralensis*	33.6	32.1	35.1	27.5	39.9
UM 1347	*E. cedralensis*	37.8	28.8	31	25.2	36.3
UM 1348	*E. cedralensis*	40.9	30.6	32.5	29.6	44.4
UM 1349	*E. cedralensis*	40.9	33.8	32.2	28.7	40.6
UM 1350	*E. cedralensis*	40.1	29.8	29.2	26.8	42.3
UM 1351	*E. conversidens*	63.9	37.5	45.6	43.3	68.4
UM 1352	*E. conversidens*	58.2	45.3	49.2	50.8	68.2
UM 1353	*E. conversidens*	51.6	42.3	47.4	48.8	61.8

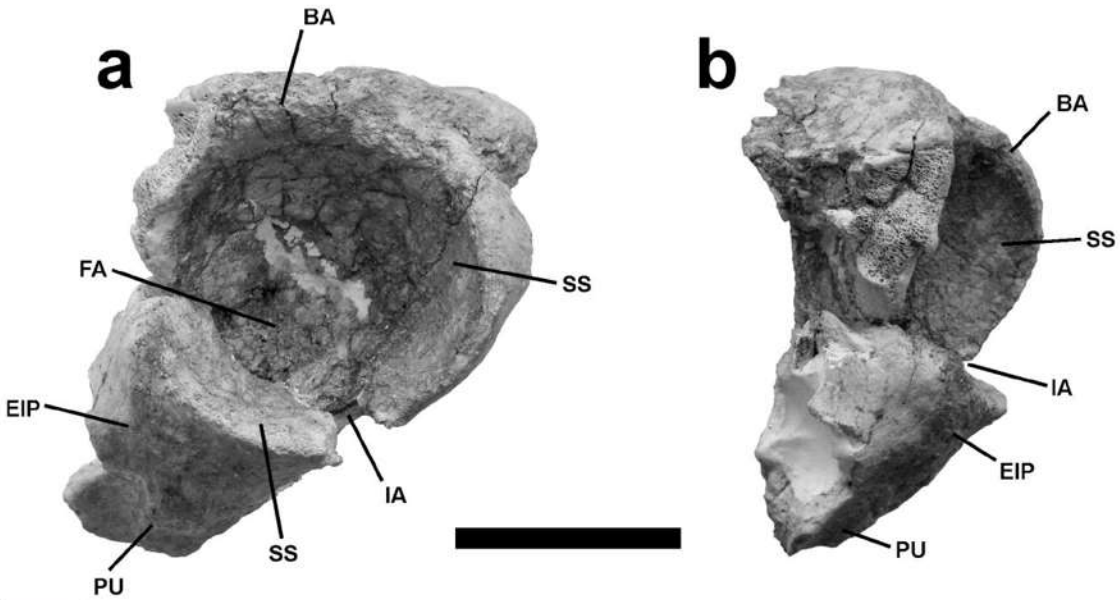

Figura 5 Acetábulo de *Bison* sp. UM 1345. a) Vista lateral, b) vista caudal. Abreviaturas: BA, borde acetabular; SS, superficie semilunar; IA, incisura acetabular; FA, fosa acetabular; EIP, eminencia ileo-púbica; PU, pubis. Barra de escala: 5 cm.

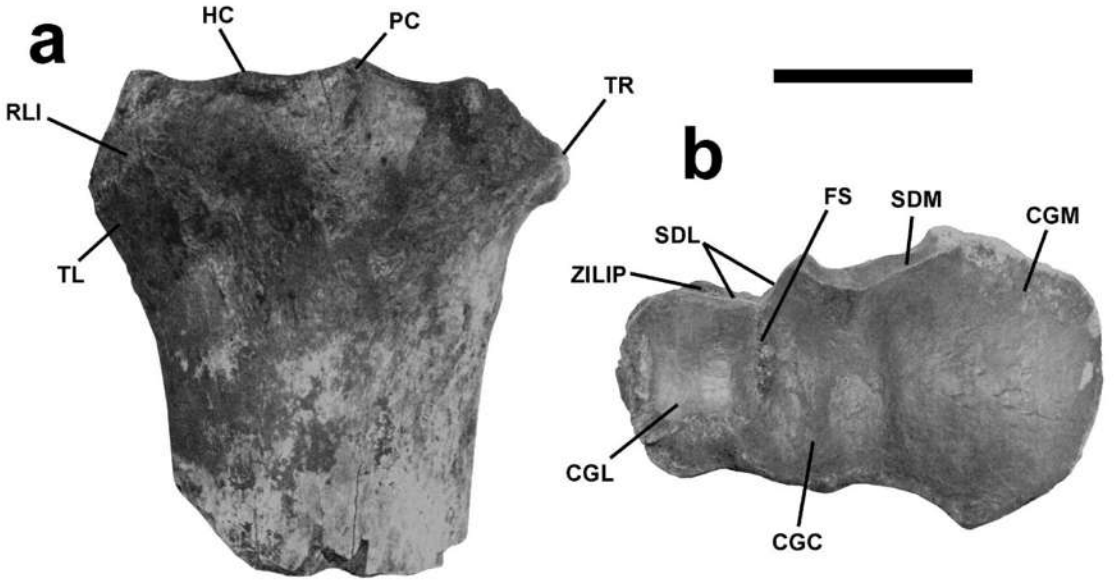

Figura 6 Radio de *Bison latifrons*, UM 1346. a) Vista anterior, b) vista dorsal. Abreviaturas: RLI, relieve lateral de inserción; TL, tuberosidad lateral; HC, hendidura central; PC, proceso coronoides; TR, repisa de la tuberosidad radial; ZILIP, zona de inserción del ligamento interóseo proximal; SDL, superficies diartrodiales laterales; SDM, superficie diartrodial medial; FS, foseta sinovial; CGM, cavidad glenoidea medial; CGC, cavidad glenoidea medial (central); CGL, cavidad glenoidea lateral. Barra de escala: 5 cm.

amplia y presenta una curva suave; en vista cenital, la faceta articular proximal presenta una cavidad glenoidea medial (o fosa capitular) amplia y separada de la cavidad glenoidea media y lateral, que son más pequeñas y cuadrangulares. Finalmente, la hendidura articular de la ulna es amplia y presenta un ángulo obtuso de aproximadamente 135° (Olsen, 1960; McCuaig-Balkwill y Cumbaa, 1992; Barone, 1995; Pales y Garcia, 1981; France, 2009). Para el Rancholabreano de Norteamérica y México se reportan cuatro especies de bisontes (McDonald, 1981; Ferrusquía-Villafranca *et al.*, 2010), de los cuales dos eran gigantes: el eurasiático *Bison alaskensis* y el autóctono *Bison latifrons*. Sin embargo, consideramos que este radio perteneció a *B. latifrons* por sus rasgos morfológicos. Comparamos la morfología de radios descrita para *B. priscus* debido a que *B. alaskensis* es conocido únicamente de cráneos y algunos autores lo refieren como una subespecie de *B. priscus* (*e.g.* Guthrie, 1966), además de que es parte del grupo de bisontes de origen eurasiático (McDonald, 1981).

Los radios de *B. priscus* son largos y gráciles, pero con epífisis gruesas, lo que les da un aspecto de tener una cabeza amplia (Shpansky *et al.*, 2016), en contraposición, el elemento UM 1346 no presenta una región epifisiaria notablemente expandida (Figura 6). En *B. priscus* la ulna se encuentra fuertemente anquilosada al radio (Prat *et al.*, 2010; Shpansky *et al.*, 2016), mientras que en UM 1346, se observan claramente la superficie de sinostosis radio-ulnar y la zona de inserción del ligamento interóseo proximal y no existe evidencia de anquilosis, lo que sugiere la presencia de un espacio interóseo proximal bien desarrollado. Además, en *B. priscus* (Figura 7) el relieve lateral de inserción se presenta en un ángulo cercano a 90°, presenta una tuberosidad lateral muy grande, alta y ligeramente hendida, con un borde dorsal que se encuentra a la misma altura del proceso coronoide y en algunos ejemplares, incluso lo excede en altura (Prat *et al.*, 2010). Ninguna de estas características está presente en UM 1346.

En Oaxaca, se ha reportado la presencia de *Bison antiquus* (Jiménez-Hidalgo *et al.*, 2011, 2013). El espécimen UM 1346 se asigna a un ejemplar macho de *B. latifrons* por su talla (Figura 6) y por comparación con radios de *B. latifrons* (UM 1264) y *B. antiquus* (UM 1347 y UMPE 0004). *B. antiquus* presenta una foseta sinovial en forma de moño, que ingresa a las cavidades glenoideas (medial y media) desde el punto intermedio de las superficies diartrodiales, mientras que la foseta de *B. latifrons* es recta, está dirigida hacia la parte anterior e ingresa únicamente a la cavidad glenoidea media desde el punto central de las superficies diartrodiales laterales. En *B. antiquus* el margen anterior de la cavidad glenoidea medial es ligeramente subtriangular, mientras que en *B. latifrons* forma un ángulo bastante prominente. En *B. latifrons* la repisa de la tuberosidad radial está más acentuada y el proceso coronoide es más redondeado. En la región posterior, la superficie diartrodial medial de *B. latifrons* es más grande y larga, rebasando el

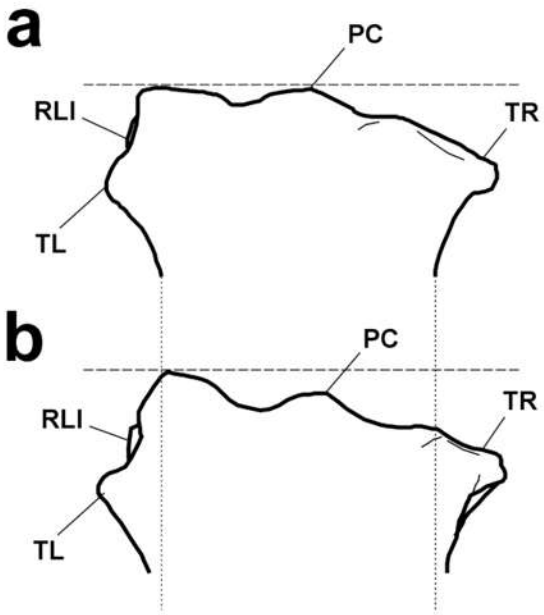

Figura 7 Comparación de la región proximal en radios de a) *Bison latifrons* y b) *B. priscus* en vista anterior. La línea punteada gruesa representa el punto más alto del tubérculo lateral. La línea punteada delgada indica el ancho relativo de la diáfisis en *B. latifrons*. Abreviaturas igual que en la figura 6. Los diagramas no están a escala.

margen ventral de las superficies diartrodiales laterales. Además, la superficie diartrodial medial de *B. latifrons* es menos pronunciada que en *B. antiquus*. Adicionalmente, la inserción del ligamento interóseo proximal es mucho más amplia y expandida posteriormente en *B. antiquus*. Finalmente, el ancho y largo de las superficies articulares proximales del radio UM 1346 se corresponden en sus dimensiones con las reportadas de *B. latifrons* machos (Figura 8).

4.2. INFERENCIA ALIMENTARIA

El único taxón analizado fue *Mammuthus columbi*, dado que fue el único con piezas dentales conservadas. El análisis de microdesgaste dental (Figura 9) sugiere que, en los últimos días de su vida, el individuo de mamut fue pacedor. Esta asignación dietaria se soporta con el análisis de funciones discriminantes, donde la pieza mandibular se asigna a dicho gremio con una probabilidad de 61 % y la maxilar con una probabilidad de 45.3 %. Además, la prueba de Lambda de Wilk muestra diferencias estadísticamente significativas entre gremios (ramoneadores, mixtos, pacedores), reforzando así esta asignación.

A diferencia del análisis de microdesgaste dental, el análisis de mesodesgaste representa la preferencia dietaria a lo largo de la vida de un individuo (For-

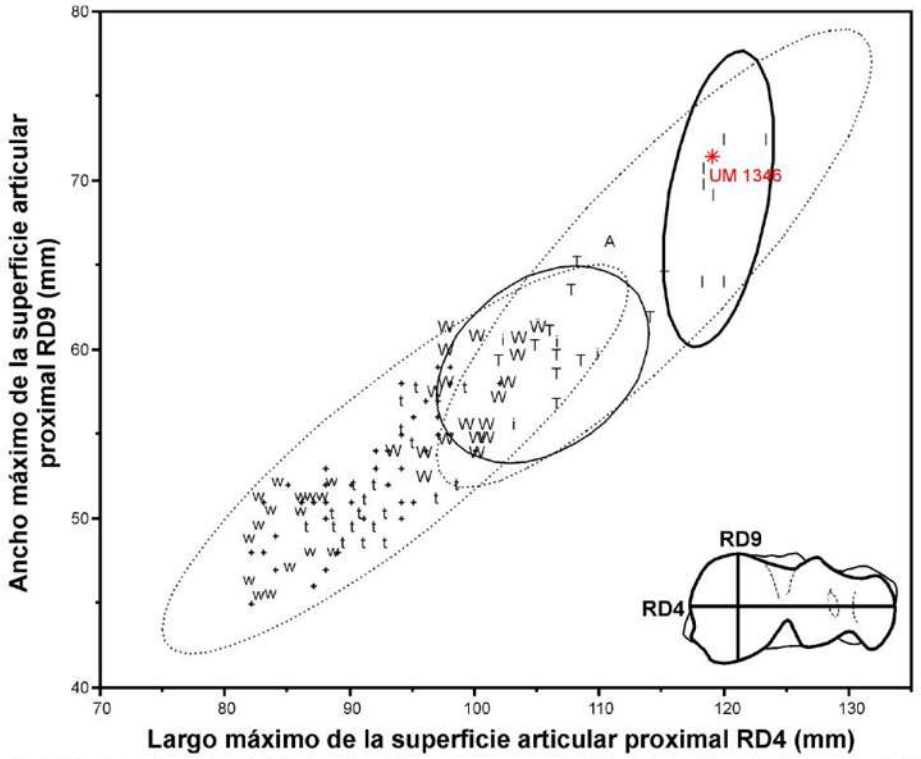

Figura 8 Análisis bivariante de radios de bisontes. Las elipses representan el 95 % de la confianza. Elipse punteada inferior de *B. antiquus*, elipse punteada superior de *B. latifrons*. Elipse sólida delgada de hembras de *B. latifrons*. Elipse sólida gruesa de machos de *B. latifrons*. Simbología i, I: hembras y machos (respectivamente) de Reserva de American Falls, Idaho; t, T: hembras y machos (respectivamente) de Lipscomb, Texas; w, W: hembras y machos (respectivamente) de Horner II, Wyoming; A: macho de Gallelli Gravel Pit, Alberta; +: Horner II, Wyoming (datos sin sexo especificado). I, i: *Bison laifrons*. T, t, W, w, A, +: *Bison antiquus*. Datos tomados de (Stevens, 1978; Todd, 1987; Todd *et al.*, 1992; Wilson *et al.*, 2008).

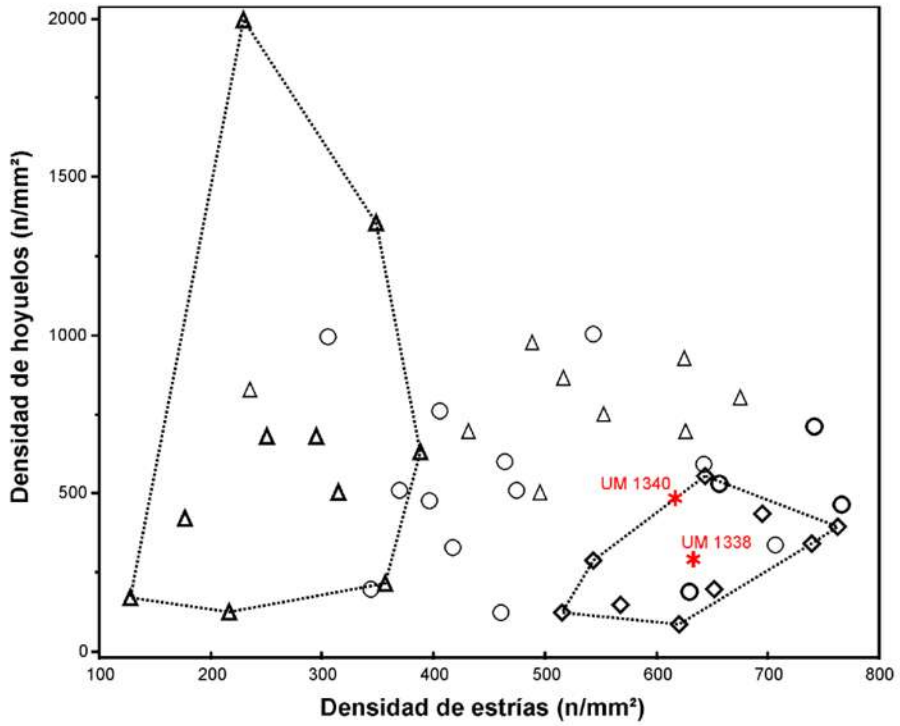

Figura 9 Análisis bivariante de microdesgaste dental de baja magnificación (35x), datos de Solounias y Semprebon (2002). Simbología: triángulos con línea gruesa: ramoneadores, triángulos con línea delgada: frugívoros, círculos con líneas delgadas: mixtos estacionales, círculos con líneas gruesas: mixtos no estacionales, rombos:pacedores. Ecoespacios principales delimitados por polígonos punteados.

telius y Solounias, 2000; Saarinen *et al.*, 2015). Los fósiles analizados poseen un promedio de ángulos de 125.7° (m2) y de 125.5° (M2). Estos valores (Figura 10) sugieren que el ejemplar de *M. columbi* de este estudio tenía una dieta dominada por plantas C4 (>70 %), lo cual es consistente con un hábito pacedor no estricto (Saarinen *et al.*, 2015).

5. Discusión

5.1. ORIGEN DE BISON LATIFRONS Y EDAD RELATIVA DE SAN DIONISIO OCOTEPEC

Se considera que el Rancholabreano inició hace 160 Ka antes del presente, usando como taxón índice al género *Bison* y en particular a *B. latifrons* (Bell *et al.*, 2004). Sin embargo, los registros tempranos usados para establecer esta edad son dudosos (Scott y Lindvall, 1970; Scott *et al.*, 1982; Haynes 1985). Por otro lado, la evidencia molecular apunta a que los bisontes invadieron América del Norte en dos oleadas, la más temprana situada entre 195 y 135 Ka, pero representada únicamente en Beringia por formas eurasiáticas como *Bison priscus* (Froese *et al.*, 2017). Los autóctonos americanos como *Bison latifrons* aparecieron posteriormente en América continental (McDonald, 1981). Esta especie se conoce de un intervalo de entre 120 Ka (Froese *et al.*, 2017; Miller *et al.*, 2014) y 6.4 a 7.7 Ka antes del presente (Dillehay, 1974; Gagliano, 1967). Por consiguiente, asignamos la fauna local de San Dionisio Ocotepec a la edad de mamíferos terrestres norteamericanos del Rancholabreano (Savage, 1951; Bell *et al.*, 2004).

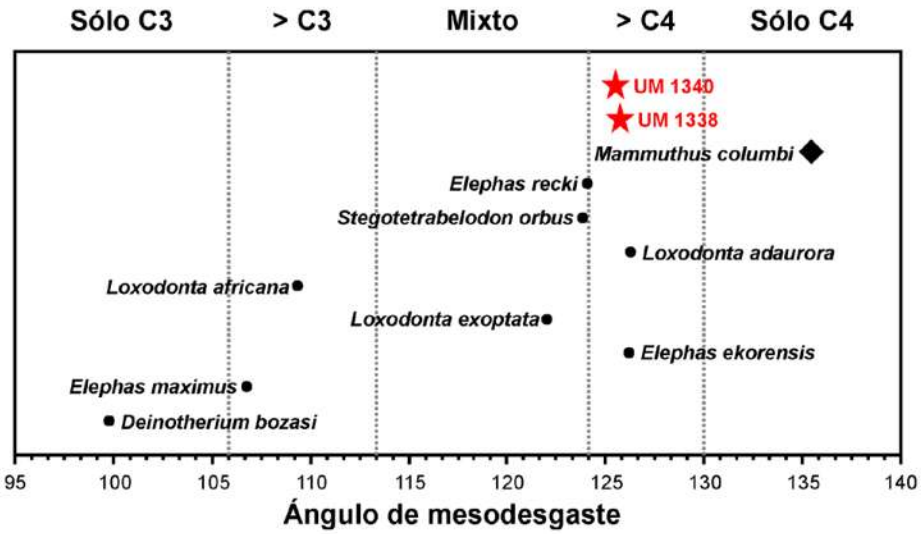

Figura 10 Mesodesgaste de proboscídeos y su relación con valores isotópicos de carbono y gremios conocidos. Modificado de Saarinen *et al.* (2015).

5.2. DISTRIBUCIÓN GEOGRÁFICA

Mammuthus columbi se ha reportado en casi todos los estados del país, con excepción de Quintana Roo, Yucatán, Campeche, Tabasco, y Colima (Arroyo-Cabrales *et al.*, 2007). Para Oaxaca se tienen al menos seis reportes de la especie (Arroyo-Cabrales *et al.*, 2003; Pérez-Crespo *et al.*, 2008), de los que dos registros (Guadalupe Victoria y San Pablo Etla) son referibles a la región noroeste de los Valles Centrales (Pérez-Crespo *et al.*, 2008). El registro de este trabajo extiende la distribución de la especie hacia el sur en aproximadamente 55 Km.

Por otra parte, el género *Equus* se ha registrado en casi todas las provincias morfotectónicas del país, con excepción de la Sierra Madre Occidental y la Planicie Costera del Golfo-Sur (Priego-Vargas *et al.*, 2016). *Equus conversidens* se presenta en las provincias morfotectónicas de: Sierras y Planicies del Noroeste, Cordilleras y Planicies de Chihuahua-Coahuila, Meseta Central, Sierra Madre Oriental, Cinturón Volcánico Transmexicano, Planicie Costera del Golfo-Norte, Península de Yucatán, Sierra Madre de Chiapas y Sierra Madre del Sur (Priego-Vargas *et al.*, 2016). En Oaxaca se ha reportado previamente la presencia de *E. excelsus* en Ejutla y Tehuantepec (Pérez-Crespo *et al.*, 2008), *E. mexicanus* en Teposcolula (Pérez-Crespo *et al.*, 2008) y la Mixteca Alta (Jiménez-Hidalgo *et al.*, 2012). Finalmente, *E. conversidens* ha sido reportado únicamente para la Mixteca (Jiménez-Hidalgo *et al.*, 2012). El posible registro de *E. conversidens* de San Dionisio Ocotepec conecta las localidades de la Mixteca Alta con las de la depresión central de Chiapas (Carbot-Chanona y Gómez-Pérez, 2014). Los bisontes (*Bison* spp.) están más o menos bien representados en México, sus registros son abundantes en las provincias morfotectónicas de Meseta Central, Sierra Madre Oriental y Cinturón Volcánico Transmexicano; mientras que hay pocos registros en las provincias de Península de Baja California, Sierras y Planicies del Noroeste, Cordilleras y Planicies de Chihuahua-Coahuila y Península de Yucatán (Ferrusquía-Villafranca *et al.*, 2010). Por otro lado, se presenta sólo un registro de *Bison* tanto en la provincia de la Sierra Madre del Sur (Jiménez-Hidalgo *et al.*, 2011, 2013) como en la Sierra Madre de Chiapas (Carbot-Chanona y Vázquez-Bautista, 2006). En Oaxaca, este registro

corresponde con la fauna local de Viko Vijin en la Mixteca alta, donde se reporta la presencia de la especie más abundante en México, *Bison antiquus* (Jiménez-Hidalgo *et al.*, 2013).

5.3. ESTRATIGRAFÍA

El análisis estratigráfico sugiere que los depósitos de San Dionisio son de carácter predominantemente fluvial. La presencia de concreciones de carbonato de calcio en forma de caliche y carbonatación sugiere la presencia de condiciones áridas (Schlesinger, 1982). Estas condiciones se encuentran en facies someras dominadas por el depósito de arcillas finas (en los estratos 2, 12 y 14), que sobreyacen sedimentos alóctonos de origen volcánico y perturbaciones estocásticas del régimen fluvial evidenciadas por la presencia de conglomerados y brechas. Estas condiciones sugieren que las facies someras presentaban pedogénesis *in situ* incompleta, que no dio origen a paleosuelos, pues este proceso se vio interrumpido en varias ocasiones por el depósito de nuevos sedimentos, culminando hacia la cima por el arrastre de sedimentos volcánicos alóctonos y la formación de suelos modernos.

5.4. TAFONOMÍA

Los restos fósiles de San Dionisio Ocotepec sugieren que el efecto de ponderación temporal (*Time-averaging*) es mínimo, particularmente en el sitio "El Pedregal", donde se encuentran los taxones: *Mammuthus columbi*, *Equus* cf. *E. conversidens* y *Bison latifrons*. Estos restos fósiles presentan escasas evidencias de intemperismo: poseen una superficie ósea con poco agrietamiento, no se presenta descamación y las superficies articulares presentan grietas en mosaico; lo que sugiere que los restos tuvieron un tiempo de exposición al medio que va de los días a los tres años como máximo (Behrensmeyer, 1978). Adicionalmente, la evidencia muestra que el arrastre de las piezas fue escaso, los bordes son completos y hay presencia de fracturas en espiral (causadas por compresión) con márgenes angulosos (Fernández-Jalvo y Andrews, 2003; 2016). El radio de *Bison latifrons* se encuentra dentro del grupo II de Voorhies, lo que indica que su transporte fue moderado, principalmente como carga tractiva (Voorhies, 1969). Finalmente, los restos de *M. columbi* descritos tienen índices de transporte fluvial de entre 53.9 % y 86.8 % (Frison y Todd, 1986), estos elementos corresponden a un único individuo adulto y fueron encontrados asociados. Sin embargo, el resto del esqueleto no se pudo rescatar debido a la construcción de un pozo de riego.

5.5. DESGASTE DENTAL

El microdesgaste dental representa la preferencia dietaria con un margen de horas a días antes de la muerte (Solounias y Semprebon, 2002). Estos patrones reflejan el tipo de vegetación disponible cercana a la zona de depósito (Solounias y Moelleken, 1994). Por otro lado, el mesodesgaste refleja la preferencia dietaria a lo largo de la vida útil de la pieza dental analizada (Saarinen *et al.*, 2015). Estos patrones de desgaste se emplean para llevar a cabo inferencias paleoambientales y predicciones dietarias para las especies con muestras de al menos diez individuos (Fortelius y Solounias, 2000). Estas aproximaciones ofrecen información ambiental limitada con tamaños de muestra inferiores a 10, incluyendo en ocasiones un individuo (Bernor *et al.*, 2014; Danowitz *et al.*, 2016; Hayek *et al.*, 1992). Sin embargo, estas inferencias deben ser tomadas como tentativas y no ser empleadas para hacer generalizaciones paleoecológicas de las especies o del sitio de depósito.

Los resultados de los análisis de desgaste en el ejemplar de *M. columbi* indican que el individuo fue un pacedor no estricto que se alimentó preferentemente de pastos en los últimos días a horas antes de su muerte. Esto se corresponde con lo que muestran otros estudios de microdesgaste llevados a cabo con esta especie en otras regiones de México (Gutiérrez Bedolla *et al.*, 2016). En el caso del mesodesgaste, el promedio de ángulos de los molares de *M. columbi* de este estudio fue de 125.6°, lo que sugiere una dieta mixta, dominada por plantas C4 (poáceas). Esto es distinto a lo encontrado para

la misma especie en Rancho la Brea (Saarinen *et al.*, 2015), con un promedio de ángulos de 135.5° y a lo encontrado en ejemplares del centro-este de Puebla, donde se obtuvo un promedio de 135° (Carbot-Chanona *et al.*, 2018), lo que sugiere que en estos sitios *M. columbi* era un pacedor casi estricto, con un consumo de plantas C4 de más de 90 % (Saarinen *et al.*, 2015). A pesar de sugerir la presencia de pastizales, la información del desgaste no es suficiente, por lo que se requieren de estudios adicionales, tales como mineralógicos y palinológicos.

5.6. PALEOAMBIENTE

Actualmente el relieve de la zona es irregular, con elevaciones pronunciadas hacia el sur (donde inicia la Sierra Madre del Sur) y hacia el norte, planicies que se conectan a la región fisiográfica de valles y lomeríos del centro del estado. Esta topografía debió de haber sido similar durante el Pleistoceno tardío, pues los afloramientos aledaños pertenecen a formaciones que datan del Cretácico tardío (*ca.* 91 – 71.5 Ma) y existen pocos indicios de depósitos posteriores más recientes.

La ocurrencia conjunta de *M. columbi* y *Equus* cf. *E. conversidens* también sugiere la presencia de zonas abiertas con pastizales en las partes planas, como lo indican diversos estudios con estos taxones en México (Bravo-Cuevas *et al.*, 2011; Gutiérrez Bedolla *et al.*, 2016; Marín-Leyva *et al.*, 2016). Aparentemente esto entra en contraposición con el hábitat forestal sugerido para *Bison latifrons* (McDonald, 1981). Sin embargo, no existe evidencia que sugiera que efectivamente, este era el ambiente preferido de este bóvido y pudo habitar en otros tipos de ecosistema, como el inferido para San Dionisio Ocotepec.

6. Conclusiones

Los sedimentos de San Dionisio Ocotepec datan del Pleistoceno tardío, específicamente a la NALMA del Rancholabreano y consta de al menos tres taxones a nivel específico: *Mammuthus columbi*, *Equus* cf. *E. conversidens* y *Bison latifrons*. La presencia del mamut columbino y del onagro mexicano durante el Rancholabreano en México es relativamente común. La presencia de estas especies da conectividad a localidades de la región noroeste de Oaxaca con aquellas de Chiapas. Por otra parte, en este estudio corroboramos la presencia de *Bison latifrons* en los Valles Centrales del estado de Oaxaca, lo que marca la distribución más austral de la especie en el continente, extendiendo en más de 447 km su rango de distribución geográfica conocida.

La información estratigráfica sugiere que el ambiente sedimentario predominante en San Dionisio fue fluvial, con aporte principal de terrígenos y de forma secundaria, tobas, brechas y conglomerados. Considerando la evidencia de la topografía, la estratigrafía y de los restos fósiles, sugerimos que las partes planas de San Dionisio Ocotepec fueron ocupadas por pastizales.

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