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PRESENTA

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…all those moments will be lost in time, like tears in rain.

Roy Batty (Rutger Hauer)

Blade Runner (1982)

Dedicatoria

A Sofía, Isaí y Ana Laura

A mi madre y a mi padre†

A mis hermanos

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Resumen

En el presente trabajo se identificó taxonómicamente material fósil perteneciente a cérvidos y équidos recolectados en la localidad de Los Hornitos, municipio de Fronteras, Sonora, en el noroeste de México. De igual forma, se determinó el comportamiento dietario de los équidos fósiles para inferir las condiciones paleoambientales del área de estudio. A través de los alcances bioestratigráficos de las especies identificadas se estableció la edad relativa de los sedimentos portadores.

La identificación taxonómica se llevó a cabo a través de un estudio morfológico comparado de los 98 elementos óseos (51 de équidos y 47 de cérvidos) recolectados en el área de estudio con descripciones y figuras de elementos dentales y poscraneales de cérvidos y équidos reportados en trabajos previos. Para conocer el comportamiento dietario de los équidos e inferir sus preferencias de hábitat se implementó un análisis de isótopos estables ($\delta^{13}C$ y $\delta^{18}O$) a partir de muestras del esmalte dental (apatita). Los rangos bioestratigráficos de dichas especies fueron obtenidos en la literatura especializada.

Los restos de équidos fueron referidos a las especies *Nannippus peninsulatus* (Hipparionini) y *Equus simplicidens* (Equini), mientras que el material perteneciente a cérvidos fue asignado a la especie *Odocoileus virginianus*.

Los valores de $\delta^{13}C$ y $\delta^{18}O$ obtenidos del esmalte dental de los équidos indican una dieta mixta C3-C4, lo que sugiere la presencia de una cubierta vegetal variable con bosques (plantas con metabolisto C3 como árboles, arbustos y matorrales) y zonas abiertas (plantas con metabolismo C4 como pastos), probablemente relacionados a condiciones áridas y frías.

De acuerdo con en los alcances biocronológicos documentados de los équidos *Nannippus peninsulatus* y *Equus simplicidens*, así como del cérvido *Odocoileus virginianus*, la edad establecida para la localidad de Los Hornitos fue ubicada entre los ~3.9–2.6 Ma, lo que corresponde al Blancano, de acuerdo con la cronología de mamíferos terrestres de Norteamérica, probablemente al Blancano III o al límite entre la parte tardía del Blancano temprano y la parte temprana del Blancano tardío.

Abstract

In the present work, fossil material belonging to cervids and equids collected in the locality of Los Hornitos, municipality of Fronteras, Sonora, in northwestern Mexico, was taxonomically identified. Also, the dietary behavior of fossil equids was determined in order to infer the paleoenvironmental conditions of the study area. Through the biostratigraphic ranges of the identified species, the relative age of the fossil-bearing sediments was established.

The taxonomic identification was carried out through a comparative morphological study among the of 98 bone elements (51 belongin to equids and 47 belonging to cervids) collected in the study area with descriptions and figures of dental and postcranial elements of cervids and equids reported in previous works. To infer the equids diet and their habitat preferences, a stable isotope analysis ($\delta^{13}C$ and $\delta^{18}O$) was implemented from dental enamel (apatite) samples. In addition, the biostratigraphic ranges of these species were obtained in the specialized literature.

The equid remains were referred to the species *Nannippus peninsulatus* (Hipparionini) and *Equus simplicidens* (Equini), while the material belonging to cervids was assigned to the species *Odocoileus virginianus*.

The values of $\delta^{13}C$ and $\delta^{18}O$ indicate a mixed C3–C4 diet, suggesting the presence of variable cover vegetation, including woodland (C3 plants, such as trees, shrubs, and bushes) and open areas (C4 plants, such as grasses), probably related to cold and arid conditions.

According to the biochronological ranges of the equids *Nannippus peninsulatus* and *Equus simplicidens*, as well as the cervid *Odocoileus virginianus*, the age established for the Los Hornitos locality was about ~3.9–2.6 Ma, which corresponds to the Blancan, according to the chronology of North American Land Mammals Ages, probably to Blancan III or the boundary between late early Blancan and early late Blancan.

Capítulo 1

1. Introducción

En México se conocen una gran cantidad de localidades fosilíferas con fauna cenozoica (Arroyo-Cabrales y Johnson, 2002; Montellano-Ballesteros y Jiménez-Hidalgo, 2006; Carranza-Castañeda y Roldán-Quintana, 2007; Arroyo-Cabrales *et al*., 2008; Pérez-Crespo *et al*., 2018, 2019; Marín-Leyva *et al*., 2016). En el noroeste del país afloran depósitos sedimentarios continentales con abundantes fósiles (Arroyo-Cabrales y Johnson, 2002; Mead *et al*., 2006, 2019; Alberdi *et al*., 2014; Czaplewski *et al.*, 2014) cuya información paleoambiental se basa en mamíferos de talla mediana y grande (Arroyo-Cabrales y Álvarez, 2003), aves (Oswald y Steadman, 2011) y paleosuelos (Cruz-y-Cruz *et al*., 2018).

El Blancano es una edad en la cronología de mamíferos que comprende del Plioceno hasta el Pleistoceno temprano. Esta edad fue propuesta por Wood *et al*. (1941) basándose en la fauna local de Mount Blanco, Crosby County, Texas. Las subdivisiones de esta edad se han definido principalmente en función de la evolución de los roedores arvicolinos (Marshall *et al.*, 1979; Repenning, 1988; Bell, 2000), aunque en México su caracterización se apoya fundamentalmente en asociaciones de mamíferos de gran talla (Jiménez-Hidalgo y Carranza-Castañeda, 2011). El límite inferior de esta edad se ha propuesto entre los 5.2 Ma y los 4.6 Ma, marcado por el arribo de los primeros roedores arvicolinos provenientes del continente asiático hacia el continente americano, mientras que el límite superior se ha ubicado entre los 1.8 Ma y los 1.3 Ma, con la llegada del inmigrante asiático *Mammuthus* (Bell *et al.*, 2004).

En México se emplean los alcances bioestratigráficos de ciertas especies de équidos y la presencia de inmigrantes sudamericanos para proponer el límite entre el Henfiliano y el Blancano (Carranza-Castañeda, 2006). No obstante, determinar en los sedimentos mexicanos las subdivisiones propuestas por Repenning (1988) o Bell *et al*. (2004) resulta muy complicado, ya que, si bien los roedores arvicolinos están ampliamente distribuidos geográfica y estratigráficamente en las Grandes Planicies de Estados Unidos durante el Blancano, en México únicamente se ha descrito a *Pliophenacomys wilsoni* en Chihuahua (Lindsay y Jacobs, 1985).

A pesar de no ser considerado válido por algunos autores (Bell *et al*., 2004), el Blancano II de Repenning (1988) se caracteriza por la presencia de *Ophiomys mcknigthi*, mismo que se considera el ancestro de *O. taylori*, el cual únicamente ha sido documentado en el Blancano III (Bell *et al*., 2004). Este último se distingue por la llegada desde Asia del grupo de las ratas almizcleras del género *Pliopotamys*, además de fauna autóctona como *O. magilli*, *Ogmodontomys poaphagus, Cosomy primus* y *Pliophenacommus antiquus* (Bell, 2000; Bell *et al*., 2004). Por otro lado, el Blancano IV se definió con base en la morfología de los molariformes inferiores de una forma transicional entre *Ophiomys taylori* y *O. parvus* (Bell *et al*., 2004). Por último, el Blancano V se distingue por los primeros registros en América del Norte de los roedores leminos *Mictomys vetus* y *Plioctomys rinkeri*, así como de los arvicolinos *Ondatra idahoensis*, *Ophiomys parvus*, *Pliophenacomys osborni*, *Mictomys vetus* y *Mictomys landesi* (Bell *et al*., 2004).

En su propuesta original, Wood *et al*. (1941) notaron que algunos taxones como los gliptodontes *Megalonyx y Paramylodon*, roedores histricomorfos, así como los géneros *Canis*, *Felis, Camelops*, *Tanupolama, Platygonus, Cervus* y *Odocoileus* aparecen por primera vez en Norteamérica durante el Blancano, pero no estan limitados a esta edad. De igual forma y como referencia para establecer el límite superior del Blancano, estos autores destacan la última aparición de los géneros *Anancus*, *Lutravus*, *Megatylopus* y *Nannippus*. La distribución geográfica de localidades en Norteamérica referidas al Blancano se muestra en la Figura 1.

En Sonora existen pocos registros de mamíferos pliocénicos, lo que contrasta con los múltiples reportes de mamíferos pleistocénicos (White *et al*., 2010). Para el Plioceno se documentan restos de proboscídeos (*Rhynchotherium*) y testudines (*Gopherus*/*Hesperotestudo*) en la parte centro-sur del estado, así como équidos (*Nannippus*) de una localidad desconocida (White *et al*., 2010). Por otro lado, durante el Pleistoceno, los mamíferos se encontraban distribuidos en casi todo el estado y tuvieron una diversidad mayor que la actual, siendo los principales componentes de las faunas fósiles sonorenses conocidas para esa edad (White *et al*., 2010). Los restos que con mayor frecuencia se recuperan pertenecen a proboscídeos (*Mammuthus, Cuvieronius*), équidos (*Equus*) y bóvidos (*Bison*), aunque también se han documentado xenarthros, camélidos y roedores (Mead *et al*., 2006; Carranza-Castañeda y Roldán-Quintana, 2007; White *et al*., 2010; Sánchez *et al*., 2014).

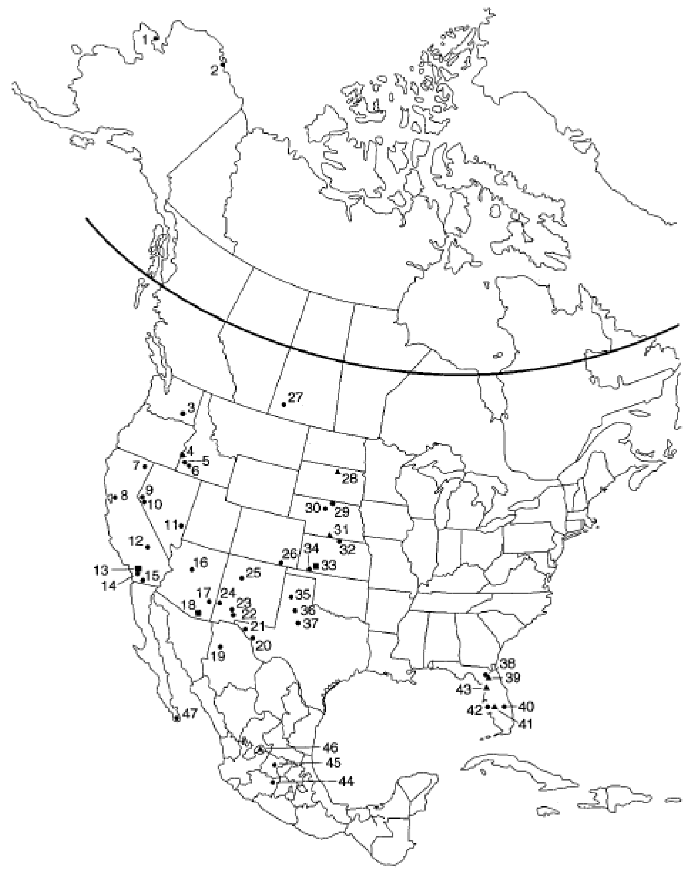

Figura 1. Localidades del Blancano por debajo de los 55° N (línea gruesa). Triángulos = Blancano tardío; cuadrados = Blancano y Blancano tardío: **1**, Cape Deceit, AK; **2**, Fish Creek, AK; **3**, White Bluffs, Blufftop y Taunton, WA; **4,** Froman Ferry Faunal sequence, ID; **5,** Grand View faunas, ID; **6**, Hagerman, ID; **7**, Upper Alturas, CA; **8**, Maxum, CA**; 9**, Buckeye Creek, NV; **10**, Fish Springs Flat y Topaz Lake, NV; **11**, Panaca y Muddy Valley, NV; **12**, Coso Mountains, CA; **13**, San Timoteo Badlands, CA; **14**, Elsinore y Temecula, CA; **15**, Anza-Borrego Desert, CA; **16**, Verde, AZ; **17**, 111 Ranch y Cuencas de Safford y de Duncan, AZ; **18**, San Pedro Valley, AZ; **19**, Concha, Chihuahua, México; **20**, Red Light y Hudspeth, TX; **21**, Hueco Bolson, TX; **22**, Mesilla Basin, NM; **23**, Formación Camp Rice, NM; **24**, Cuenca Mangas (fauna Buckhorn), NM; **25**. Cuencas de Santo Domingo y de Albuquerque, NM; **26**, Donnelly Ranch, CO; **27**, Wellsch Valley, Saskatchewan, Canadá; **28**, Java, SD; **29**, Sand Draw, NB; **30**, Seneca, NB; **31**, Sappa, NB; **32**, White Rock, KS; **33**, Cuenca de Meade, KS; 34, Saw Rock Canyon, KS; 35, Cita Canyon, TX; **36**, Blanco, TX; **37**, Beck Ranch, TX; **38**, Santa Fe River 1, FL; **39**, Haile 15A y Haile 7C, FL; **40**, Kissimmee River, FL; **41**, De Soto Shell Pit, FL; **42**, Macasphalt Shell Pit, FL; **43**, Inglis 1A and Inglis 1C, FL; **44**, La Goleta (en parte), Michoacán, México; **45**, Rancho El Ocote y Rancho Viejo, Guanajuato, México; **46**, Cedazo, Aguascalientes, México; **47**, Las Tunas, Baja California Sur, México. Tomado de Bell *et al*. (2004).

En la localidad de Los Hornitos, noreste del estado de Sonora, se ha recolectado material fósil perteneciente a diferentes grupos de mamíferos, siendo los cérvidos y los équidos los mejor representados. De manera particular, los équidos representan un componente importante de las faunas de mamíferos en Norte América durante el Cenozoico, particularmente desde finales del Neógeno y el Pleistoceno (MacFadden, 1988, 1992; Priego-Vargas *et al*., 2016). El registro fósil de los caballos mexicanos se extiende desde principios del Eoceno al Pleistoceno tardío (Novacek *et al*., 1991; Arroyo-Cabrales *et al*., 2005; Carranza-Castañeda *et al*., 2013; Jiménez-Hidalgo *et al*., 2019). Con base en el registro mexicano conocido, la mayor diversidad de especies se observa durante el Mioceno medio temprano con seis especies (Barstoviano, 15 Ma) y el Mioceno tardío con ocho especies (Hemphilliano, 7 Ma), mientras que es menor durante el Plioceno con dos especies (Blancano, 5 Ma) (Priego-Vargas *et al*., 2016; Bravo-Cuevas y Jiménez-Hidalgo, 2019).

Por su parte, los cérvidos no eran muy abundantes ni estaban muy extendidos en el Plioceno sino hasta principios del Pleistoceno (2-1 Ma), probablemente debido a la diversidad y la gran abundancia de otros animales ungulados de gran talla en ese intervalo de tiempo (Frick 1937; Heffelfinger y Latch, 2023). Durante los periodos glaciales del Pleistoceno, la mayoría de los grandes mamíferos, incluidos los géneros *Mammuthus, Mamut*, *Camelops*, *Glyptotheirum* y *Equus* se extinguieron, pero no *Odocoileus* (Heffelfinger y Latch, 2023). Actualmente, dos especies de este género coexisten en América del Norte, *O. hemionus* y *O. virginianus*, mismas que posiblemente divergieron en algún momento del Plioceno o Pleistoceno temprano, probablemente durante el Blancano (Webb, 1998; Heffelfinger, 2011; Heffelfinger y Latch, 2023).

1.1 Justificación

A pesar de los numerosos estudios paleontológicos que se han llevado a cabo en México, el país aún cuenta con un gran potencial fosilífero. Dicho potencial se debe a los abundantes sedimentos del Cenozoico Tardío de los cuales se ha logrado recolectar una importante cantidad de fósiles, entre los que destacan los pertenecientes a mamíferos. Por ello, llevar a cabo el estudio de fósiles de cérvidos y équidos recuperados de depósitos sedimentarios en el estado de Sonora, noroeste de México, contribuirá al mejor entendimiento de la paleobiología de una parte de la biota que habitó el norte del país durante el Plioceno.

Por otra parte, debido a la importancia que tienen las investigaciones sobre la interpretación de hábitos dietarios utilizando a los mamíferos extintos como objeto de estudio (Wang *et al*., 1994; MacFadden y Cerling, 1996; Cerling y Harris, 1999; Feranec y MacFadden, 2006; Koch *et al*., 2009) es que, mediante un análisis de isótopos estables de carbono y oxígeno en el esmalte dental, se aportará información general acerca de las condiciones ambientales del área de estudio en el Plioceno.

1.2 Objetivos

1.2.1 General

Describir el material fósil de cérvidos y équidos de la localidad Los Hornitos, municipio de Fronteras, noreste de Sonora, mediante un estudio morfológico comparado, para determinar su identidad taxonómica.

1.2.2 Particulares

- Conocer el comportamiento dietario y las condiciones del hábitat de los caballos fósiles del área de estudio por medio del análisis de isótopos estables ($\delta^{13}C$ y $\delta^{18}O$) para realizar inferencias sobre el posible bioma que se desarrolló en el área de estudio.

- Establecer la edad relativa de la secuencia portadora, mediante un análisis bioestratigráfico del registro de cérvidos y équidos, para acotar termporalmente la asociación reconocida.

1.3 Material y método

1.3.1 Área de estudio

El área de estudio de Los Hornitos está ubicada al este del Ejido Esqueda perteneciente al municipio de Fronteras en el noreste de Sonora en México (Figura 2). El polígono del área de estudio, que comprende alrededor de 10.8 km^2, es: 1.- 30° 43’ 19’’ N, 109° 39’ 02’’ W; 2.- 30° 42’ 43’’ N, 109° 41’ 03’’ W; 3.- 30° 41’ 11’’ N, 109° 40’ 56’’ W; 4.- 30° 41’ 09’’ N, 109° 40’ 00’’ W; 5.- 30° 41’ 24’’ N, 109° 38’ 35’’ W; 6.- 30° 41’ 55’’ N, 109° 39’ 05’’ W.

Los depósitos estudiados corresponden a la *Basin and Range*, una provincia fisiográficamente árida, bajo un régimen tectónico extensional (Henry y Aranda-Gomez, 1992). Inicialmente, la secuencia deposicional se describió como una sucesión de arcilla bentonítica con restos de vertebrados, caliche, arcilla diatomítica, arcilla arenosa, limo y arena (Montaño-Jiménez y Fabián- Johnston, 1998).

Para caracterizar el depósito del área de estudio con los restos de vertebrados, se realizaron dos columnas estratigráficas (denominadas I y II) que se sintetizan en la Figura 3. La presencia a lo largo de toda la secuencia de paleosuelos incipientes y calcretas indican la cesión de la sedimentación, mientras que el predominio de limolita y arenisca fina sin estructuras sedimentarias con ocasionales niveles de caliza micrítica con fracturación debida aparentemente por desecación, se interpreta como un ambiente aluvial de tipo planicie de inundación. Este depósito presenta litologías más gruesas hacia el noroeste (sección I) y haciéndose más finas con niveles de tobas de ceniza hacia el sureste (sección II). La sección estratigráfica I, denominada Las Sandías, posee 37 m de espesor y corresponde a un depósito mayoritariamente constituido por limo pardo con intercalación de arenisca de grano fino y suelos incipientes bioturbados, con ocasionales niveles de caliza y calcretas. En la sección estratigráfica II, denominada Los Hornitos, de aproximadamente 21 m de potencia, predominan las lutitas y limolitas con intercalaciones de areniscas finas/medias, esporádicamente calizas y tobas de ceniza. Los niveles bioturbados y de paleosuelos son escasos en esta sección.

Los estratos presentan un rumbo y echado de 136°/10°SW y los fósiles de vertebrados se recuperaron de un estrato de arenisca blanca de grano fino en la sección I que aparentemente pasan a lutitas de manera lateral en la sección II.

A esta secuencia se le asignó una edad del Plioceno por correlación con depósitos similares en la Cuenca de Moctezuma donde se realizó un estudio palinológico (Montaño-Jiménez y Fabián-Johnston, 1998). Esta afirmación no se sustenta debido a que no se ha demostrado que sean depósitos lateralmente equivalentes y porque el estudio palinológico de Los Hornitos continúa inédito (Paz-Moreno, comunicación personal 2019), por lo que el presente trabajo con base en los ejemplares fósiles de équidos y cérvidos de dicha localidad, contribuirá en aclarar la edad de este depósito.

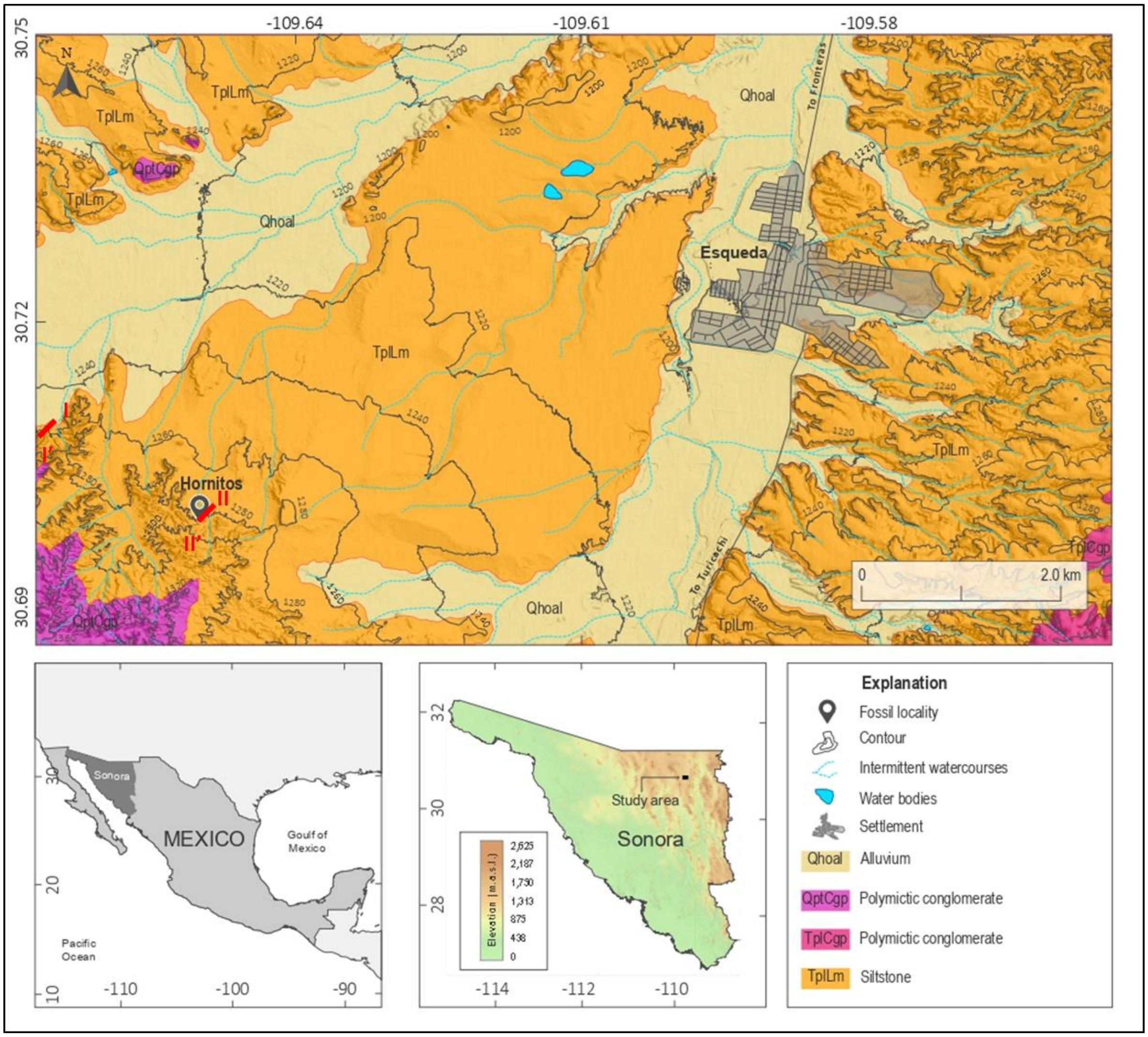

Figura 2. Ubicación geográfica y mapa geológico del área de estudio donde se indican las dos secciones estratigráficas (I, Las Sandías; II, Los Hornitos) que sintetizan el depósito con vertebrados de acuerdo con la carta geológico-minera Esqueda H12-B65 (Montaño-Jiménez y Fabián-Johnston, 1998). I/II se refieren a la base de la sección y I'/II' a la cima (Modificado de Palma-Ramírez *et al*., 2023).

Para establecer la relación espacial y temporal que guardan los fósiles presentes en la localidad se llevó a cabo la descripción litoestratigráfica de la misma, señalando en dos columnas estratigráficas (I y II) los niveles de procedencia de los restos fósiles (Figura 3). Las columnas estratigráficas se realizaron usando el báculo de Jacob, brújula y GPS. La descripción de la litología en campo se realizó usando martillo geológico y lupa de mano (con aumentos de x10 y x20).

La determinación taxonómica de los équidos y los cérvidos se llevó a cabo a través de la comparación con ejemplares fósiles y recientes resguardados en la Colección de Paleontología y la Osteoteca de la UAEH, las colecciones digitales del Peggy Notebaert Nature Museum, Idaho Virtual Museum y la Digital Collection de la Universidad de Michigan, así como con material publicado en literatura especializada (e.g., Gustafson, 2015; Hulbert y Waldrop, 2001; Kurtén y Anderson, 1980; MacFadden, 1984; Morgan *et al*., 2008a, 2008b; Robertson, 1976).

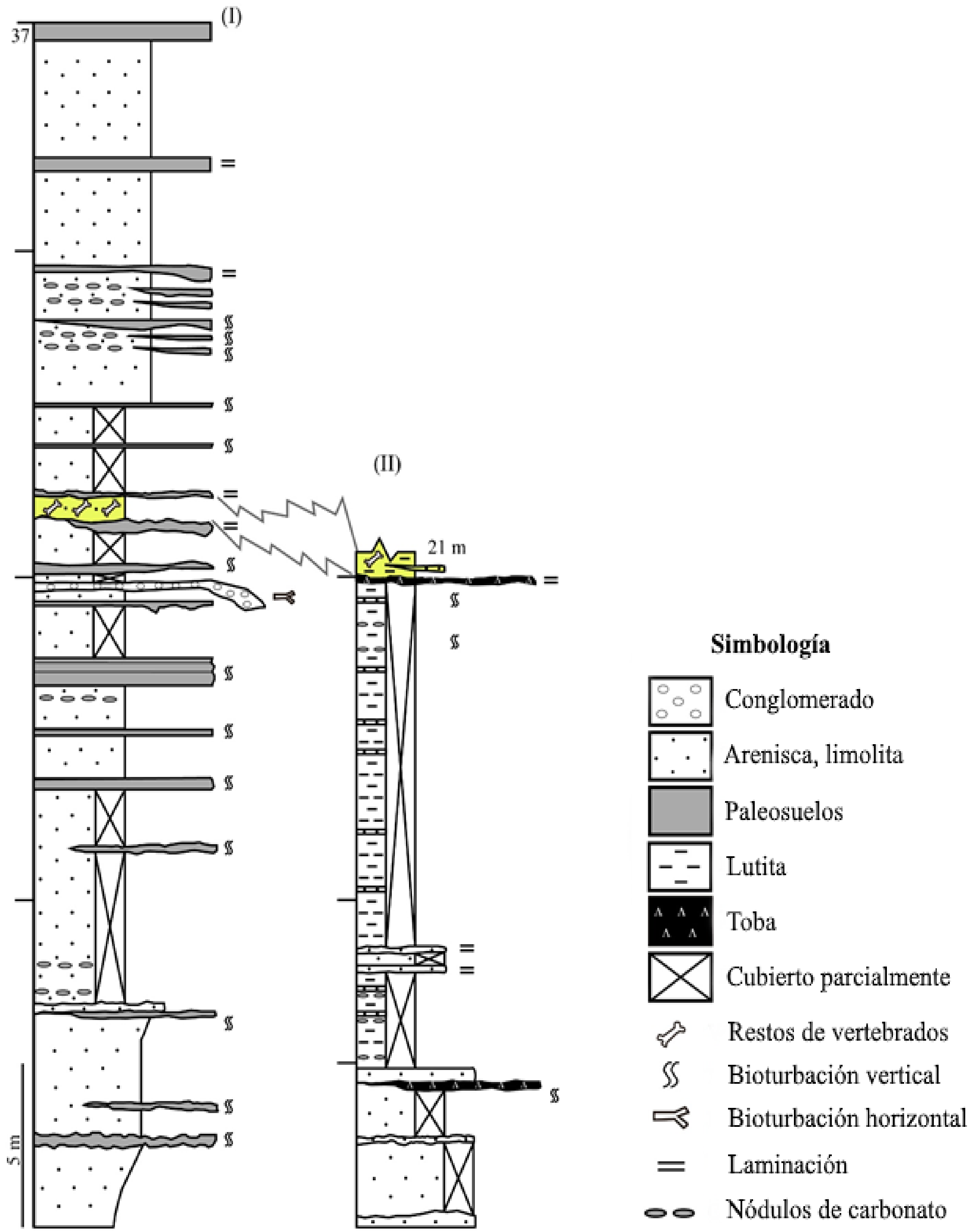

Figura 3. Las dos columnas estratigráficas (I, Las Sandías; II, Los Hornitos) del área de estudio en el Ejido de Esqueda, Municipio de Fronteras, noreste de Sonora, México, que caracterizan el depósito con restos de vertebrados (resaltado en amarillo).

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CAPÍTULO 2

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Systematics, ecology, and biochronology of blancan horses from Sonora, northwestern Mexico

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ABSTRACT

We describe a set of dental and postcranial horse material recovered from the locality Los Hornitos, northeastern Sonora, northwestern Mexico. The fossil-bearing unit consists of brown silt with intercalation of fine-grained sandstone and bioturbated incipient soils, set in an alluvial environment and considered Pliocene in age. The comparative study of the available sample indicates the presence of two species: the small-sized hipparionine *Nannippus peninsulatus* and the medium-sized and primitive equine *Equus simplicidens*. The isotope composition of $\delta^{13}C$ and $\delta^{18}O$ in dental enamel tooth indicates a C3–C4 mixed diet for these species and suggests the presence of woodland and open areas in Los Hornitos during the Pliocene. The less negative $\delta^{13}C$ values observed in *E. simplicidens* are related to a more C4 diet, preferring to roam open habitats. The coexistence and optimal resource partitioning between these species are explained, considering their differences in dietary behavior, body size, home range, and/or vagility. The recognized horse species are typical of the Blancan North American Land Mammal Age, and their biochronological information from the southwestern United States and central Mexico establishes the probable age of the Los Hornitos at about 3.9–2.6 Ma, corresponding to the Blancan III or late early Blancan – early late Blancan.

1. Introduction

Horses were an important component of North American mammalian faunas during the Cenozoic, particularly from the late Neogene and Quaternary geological periods (MacFadden, 1988, 1992; Priego-Vargas et al., 2016). The fossil record of Mexican horses spanned from the early Eocene to the late Pleistocene (Novacek et al., 1991; Arroyo-Cabrales et al., 2005; Carranza-Castañeda et al., 2013; Jiménez-Hidalgo et al., 2019). Based on the known Mexican record, major species diversity is observed during the early middle Miocene (ca. 15 Ma, Barstovian, six species) and the latest Miocene (ca. 7 Ma, Hemphillian, eight species), whereas it is minor during the Pliocene (ca. 5 Ma, Blancan, two species) (Priego-Vargas et al., 2016; Bravo-Cuevas and Jiménez-Hidalgo, 2019).

The small-sized hipparionine *Nannippus peninsulatus* and the medium-sized primitive equine *Equus simplicidens* are typical species of the Mexican Pliocene (Priego-Vargas et al., 2016; Bravo-Cuevas and Jiménez-Hidalgo, 2019). These horses are known by cranial, dental, and postcranial remains recovered from several localities in northern and central Mexico (Lance, 1950; Carranza-Castañeda, 2006; Carranza-Castañeda et al., 2013; Bravo-Cuevas and Jiménez-Hidalgo, 2019). It is worth noting that both species were biochronological elements of the Blancan faunas from the southern United States and Mexico (Lance, 1950; Miller and Carranza-Castañeda, 1984; Carranza-Castañeda and Espinosa-Arrubarena, 1994; Morgan and White, 2005; Morgan et al., 2008, 2011; Morgan and Harris, 2015).

Systematics and phylogeny of *N. peninsulatus* and *E. simplicidens* are known in some detail (cf. MacFadden, 1984; Azzaroli and Voorhies, 1993; Barrón-Ortiz et al., 2019). However, ecological aspects such as

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their dietary characterization and habitat preferences have been explored to a lesser extent (e.g., Wang et al., 1994; Kita, 2011; Plata-Ramírez, 2017). In this regard, the stable isotope analysis in biogeochemical materials (dental tissue and/or collagen of bones) provides important paleoecological and paleoenvironmental information, being the $\delta^{13}C$ and $\delta^{18}O$ the most frequently isotopes used to infer diet and habitat preferences of extinct mammals (MacFadden and Cerling, 1996; Cerling and Harris, 1999; Koch et al., 1994; Koch, 2007; Koch et al., 2009).

Recent paleontological work carried out in northeastern Sonora, Mexico, allowed us to recover from a sedimentary sequence considered Pliocene in age, a set of mammalian remains. The most abundant material includes teeth and bones belonging to horses. The purposes of the present study include the taxonomic identification of the available fossil horse material and the characterization of their dietary behavior and habitat preferences using a stable isotope analysis in dental enamel tissue. Furthermore, we comment on the biochronological significance of the fossil record to know the probable age of the bearing unit.

2. Study area

The studied fossil locality is known as Los Hornitos (30°41′28.2″ Lat N 109°38′57.4″ Long W, 1299 masl), about 6.5 km southwest of the town of Esqueda, Municipality of Fronteras, northeastern Sonora, northwestern Mexico. The studied deposit was formed in an extensional tectonic regime known as Basin and Range Province, which is an arid physiographic province (Henry and Aranda-Gómez, 1992). The Neogene-Quaternary deposits crops out in the study area. Quaternary polymictic conglomerate (QptCgp) and alluvial deposits (Qhoal) unconformably overlie the Pliocene units (Fig. 1). The Pliocene units include a polymictic conglomerate (TplCgp) that laterally varies to a sequence of fine-grained sediments, consisting of siltstone, claystone, and some calcareous strata (TplLm) (Fig. 1). These units are considered Pliocene in age only based on their stratigraphic position

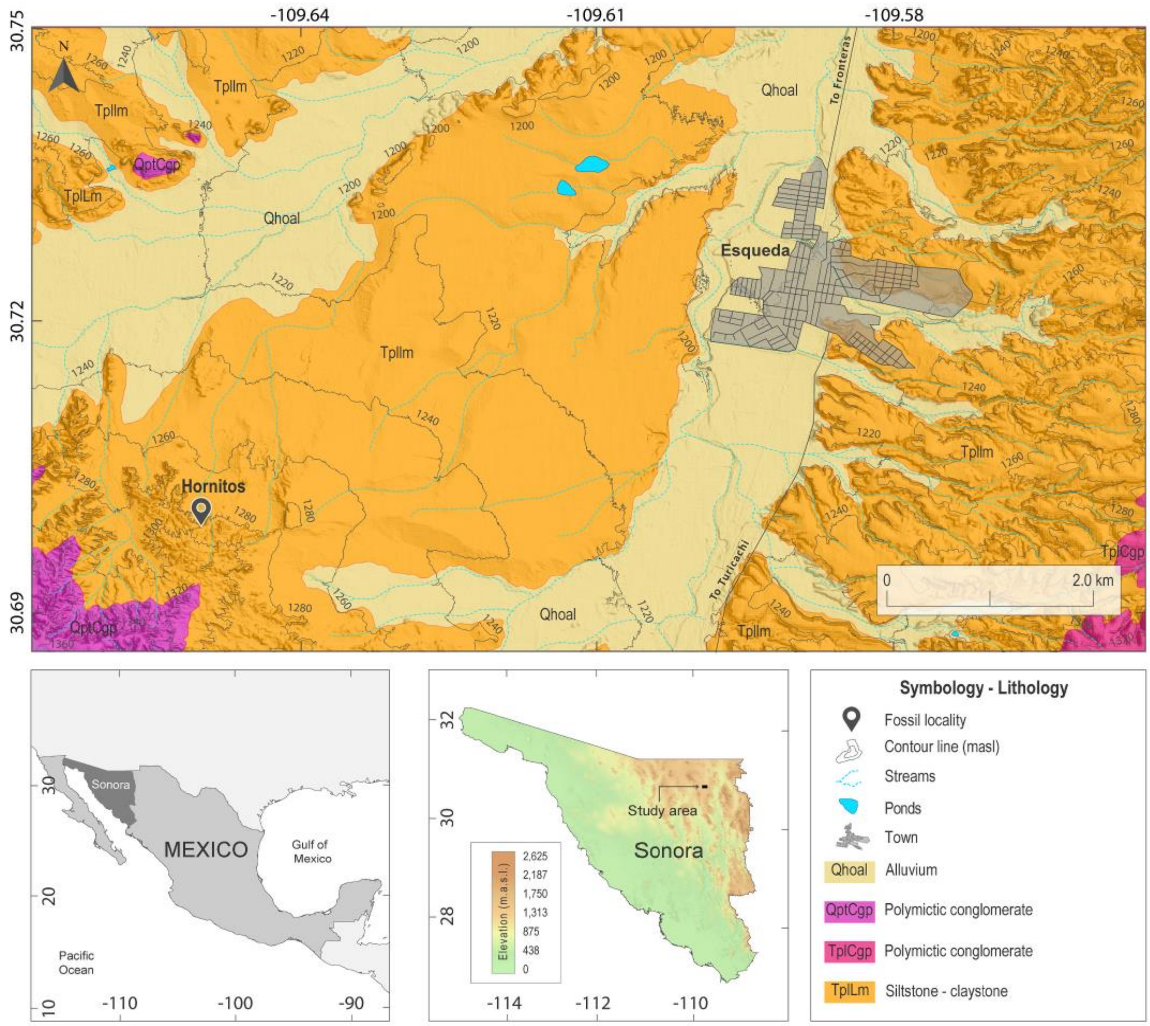

Fig. 1. Index and geologic maps of the study area, municipality of Fronteras, northeastern Sonora, northwestern Mexico. The fossil locality Los Hornitos and the main town Esqueda are indicated.

(Montaño-Jiménez and Fabián-Johnston, 1998) .

The horse-bearing stratum corresponds at least in part to the TplLm unit, consisting of brown silt with intercalation of fine-grained sandstone and bioturbated incipient soils, set in an alluvial environment. The vertebrate fossils are derived from fine-grained white sandstone.

3. Material and methods

The studied material consists of 25 isolated teeth (18 upper molariforms and 7 lower molariforms) and several postcranial remains (3 astragali, one tarsal, 5 metapodials, and 13 phalanges). The studied specimens are housed in the Colección Paleontológica de la Estación Regional del Noroeste (ERNO), Instituto de Geología, UNAM. The fossils are identified with the acronym HO- (Los Hornitos locality), followed by the catalogue number of the specimen.

We evaluate a set of morphological and metric characters of systematic value in fossil horses (MacFadden, 1984; Hulbert, 1989; Hulbert and MacFadden, 1991; Kelly, 1995, 1998). The dental nomenclature is from MacFadden (1984, Fig. 4, p. 17) and dental measurements on the occlusal surface are from Hulbert (1988, p. 226, 228). The wear stage of each molariform was established following Kelly (1998, p. 1–2). Some dental features are sensitive to wear, thus we compare teeth at similar wear stage.

The terminology of the postcranial remains is from Sisson and Grossman (1982). We measured (if was able) the total length and proximal/distal widths of the postcranial elements. The dental and postcranial measurements were taken using a digital caliper with a measuring range of 0–150 mm and a minimum indication of 0.01 mm. All measurements are in mm.

The taxonomic identity of the fossil specimens was assessed by comparing them with descriptions and figures of dental and postcranial material of *Nannippus* and *Equus* reported in previous studies (Gazin, 1936; Howe, 1970; Akersten, 1972; Robertson, 1976; MacFadden, 1984; Morgan et al., 2008, 2011; Morgan and Harris, 2015). We made bivariate plots of APL and TW of P3/P4 and M1/M2 to observe variation in dental size of the studied material with dental samples of selected species of *Nannippus* and *Equus*.

The diet and habitat preferences of horses from the Los Hornitos locality were characterized based on the carbon and oxygen isotope composition in tooth enamel apatite. Eight permanent molariforms were selected for bulk isotopic analysis. Tooth enamel flakes were extracted from the ectoloph using a DREMEL® rotatory tool and then pulverized with an agate mortar and pestle. Enamel powders of about 100 mg were chemically treated following the protocol of MacFadden and Cerling (1996). The samples were analyzed at the Beta Analytic Testing Laboratory, Florida, United States. Detection of CO_2 was via Gas Chromatography (GC) with ISODAT control. Isotopic values are expressed in δ-notation and reported relative to the V-PDB standard (Vienna Pee Dee Belemnite) (after Craig, 1957).

An average ^{13}C enrichment of 14.1 ± 0.5‰ from plant material to tooth enamel (after Cerling and Harris, 1999) is considered the fractionation value of this isotope for extant mammalian herbivores and commonly used in paleodietary reconstructions (Wang and Badgley, 2022). Mammals with a pure C3 diet will have $\delta^{13}C$ values ranging from −20.9‰ to −7.9‰, whereas those with a pure C4 diet will have $\delta^{13}C$ values of about 0.0‰ (Feranec and MacFadden, 2006).

Following Kita (2011), the predicted cutoffs for tooth enamel from different habitats in the Blancan were corrected considering a difference of about 1.3‰ in atmospheric $\delta^{13}C$ values and enrichment between diet and tooth enamel of 14‰. Based on this, values of $\delta^{13}C < -8‰$ would be related to a diet mainly consisting of C3 plants (= browsers and high latitude/altitude grazers), whereas values of $\delta^{13}C > 0‰$ indicate a diet mainly consisting of C4 plants (= grazers). Intermediate values between 0‰ and −8‰ indicate a diet of C3 and C4 plants (= mixed feeders).

The oxygen isotope composition is influenced by several factors, including the composition of ingested water (meteoric water and water contained in plant resources), the metabolism of an organism (respiration, waste disposal by urine, sweat, and feces) (Luz et al., 1984; Luz and Kolodny, 1985; Koch et al., 1994), and the climate (temperature, precipitation, altitude) (Koch, 2007). It is observed that $\delta^{18}O$ values are higher in warm conditions and lower in cool conditions (Rozanski et al., 1992), whereas leaves have an important enrichment of ^{18}O in warm and arid conditions (Ometto et al., 2005). Therefore, animals that occupy open habitats should be expected to ingest more positive $\delta^{18}O$ values compared to those that occupy closed habitats (Feranec and MacFadden, 2006; Feranec et al., 2010). In general, more positive $\delta^{18}O$ values are suggestive of open habitats (e.g. grasslands and savannas), whereas more negative $\delta^{18}O$ values are suggestive of closed habitats (e.g. woodlands and forests) (Feranec and MacFadden, 2006).

Previous studies on extant and extinct ungulates have shown that pure C3 feeders, commonly inhabitants of closed habitats, have $\delta^{13}C$ values more negative of – 8‰ (MacFadden and Cerling, 1996; Cerling and Harris, 1999). Feranec and MacFadden (2006) observed differences in the $\delta^{13}C$ values of animals that inhabited open habitats (values > – 8‰) regarding those that lived in closed habitats (values < – 8‰ to – 13‰) and in the canopy (values – 13‰ to – 21‰), which in turn is related to more positive and more negative $\delta^{18}O$ values respectively. In this study, we followed this model to characterize the potential habitat preferences of the Sonoran horses.

We performed t-student tests to recognize statistical differences in the carbon and oxygen composition between the dental samples of *N. peninsulatus* and *E. simplicidens* from Los Hornitos. Furthermore, the isotope composition of the sample from Los Hornitos was compared with reported data of *Nannippus*, *N. aztecus*, *N. peninsulatus*, *Equus*, and *E. simplicidens* from the following localities: U Bone Valley, Santa Fe 1, Leisey 1 A, and Moss Acres, Florida (Gulf Coast); Broadwater and Big Spring, Nebraska (Great Plains); Yepómera, Chihuahua (northern Mexico); Uruétaro and Misión del Valle, Michoacán (west-central Mexico), and El Ocote, Guanajuato (central Mexico) (Wang et al., 1994; MacFadden and Cerling, 1996; Kita, 2011; Plata-Ramírez, 2017; Hannold, 2019) (Supplementary data). Statistical differences in the average isotope composition among and between selected samples were compared by ANOVA and post-hoc Tukey's procedure.

The bivariate plots and statistical analyses were performed using Past 3.20 (Hammer et al., 2001).

The following abbreviations are used in the text and tables. *General*: **AR**, Arizona; **CHI**, Chihuahua; **FL**, Florida; **GTO**, Guanajuato; **ID**, identification number; **L**, left; **MICH**, Michoacán; **NALMA**, North American Land Mammal Age; **NM**, New Mexico; **R**, right; **SON**, Sonora; **TX**, Texas. *Institutional*: **AMNH**, Department of Vertebrate Paleontology, American Museum of Natural History; **NMMNH**, New Mexico Museum of Natural History; **UF**, Vertebrate Paleontology Collection, Florida Museum of Natural History, Gainesville; **UTEP**, University of Texas El Paso. *Statistical*: **OR**, observed range; **SD**, standard deviation; $\overline{X}$, average. *Dental*: **APL/apl**, anteroposterior length upper/lower molariforms; **CH**, crown height; **lmt-lmts**, metaconid-metastylid length; **M/m**, upper/lower molar; **mcch**, metaconid crown height; **MSCH**, mesostyle crown height; **P/p**, upper/lower premolar; **PrL**, protocone length; **PrW**, protocone width; **TW/tw**, transverse width upper/lower molariforms; **WS**, wear stage. *Postcranial*: **Dd**, distal depth; **Dw**, distal width; **Pd**, proximal depth; **Pw**, proximal width; **TL**, transverse length.

4. Systematic paleontology

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Tribe Hipparionini Quinn, 1955
Genus *Nannippus* Matthew, 1926
Nannippus peninsulatus Cope, 1885

4.1. Referred material

Los Hornitos: HO–5B–C, LP3; HO–7C, RM1; HO-221, RM3; HO-230, RP3; HO-329, LM1/M2; HO-333, RM1/M2; HO-422, RM2; HO-423, RM1; HO-424, LP3/P4; HO-525, LM3; HO-0335, HO-444, deciduous premolars; HO-494, Lm3; HO-472, right astragalus; HO-546, left astragalus; HO-544; proximal end of a right third metatarsal; HO-078, distal end of a right metapodial; HO-551, distal end of a left metapodial; HO-131, HO-351, HO-476, HO-477, HO-478, HO-504, HO-547, medial phalanges.

4.2. Distribution and age

Late Blancan of Nebraska, Arizona, Texas, Florida (MacFadden, 1984), and New Mexico, United States (Morgan et al., 2008). In Mexico, this species is reported from Blancan localities in Chihuahua, Guanajuato, Hidalgo, Jalisco, and Michoacán (Arellano and Azcon, 1949; Lance, 1950; Miller and Carranza-Castañeda, 1984; Carranza-Castañeda and Espinosa-Arrubarrena, 1994; Carranza-Castañeda and Miller, 1998; Carranza-Castañeda, 2006; MacFadden, 2006).

5. Description

5.1. Upper cheek teeth

The upper cheek teeth are very hypsodont (HI ≈ 3.0), high-crowned teeth (MSCH ca. 50 mm), and slightly curved in the transverse plane. A moderate layer of cement is present (ca. 1.5 mm) on the cheek teeth. The parastyle and mesostyle are well developed, whereas the metastyle is reduced. The protocone is isolated from the protoloph near the base of the crown; it is oval (PrL/PrW = 1.68) with the lingual border straight and the labial border convex. Pli protoloph and pli hypostyle single and persistent at early moderate wear. The internal fossette borders are moderately plicated (4–5 plications). The pliprotoconule is well developed. The plicaballin is simple, well developed at early wear stages, and persistent at moderate wear. The hypoconal groove is shallow and persistent at late moderate wear (Fig. 2A-J).

5.2. Lower cheek teeth

The specimens HO-335 and HO-444 are deciduous premolars, which have a moderate layer of cement, the metaconid and metastylid are well separated, the linguaflexid is deep and V-shaped, and the ectoflexid is shallow in HO-335 and moderately deep in HO-444. In HO-335, the protoconid is smaller than the hypoconid; the entoconid is rounded and well differentiated. The specimen HO-494 is an unworn left third molar whose occlusal pattern is not discernible; the estimated crown height (along the metaconid) of this tooth is about 30 mm (Fig. 2K-M).

5.3. Astragalus

The astragali are small with maximum length of 32.88 mm and maximum width of 29.44 mm. The medial trochlea is higher than the lateral, and the trochlear ridges are oblique; the intertrochlear groove is deep. In the medial view, the proximal and distal tuberosities are prominent. The plantar surface has four articular facets for the calcaneus

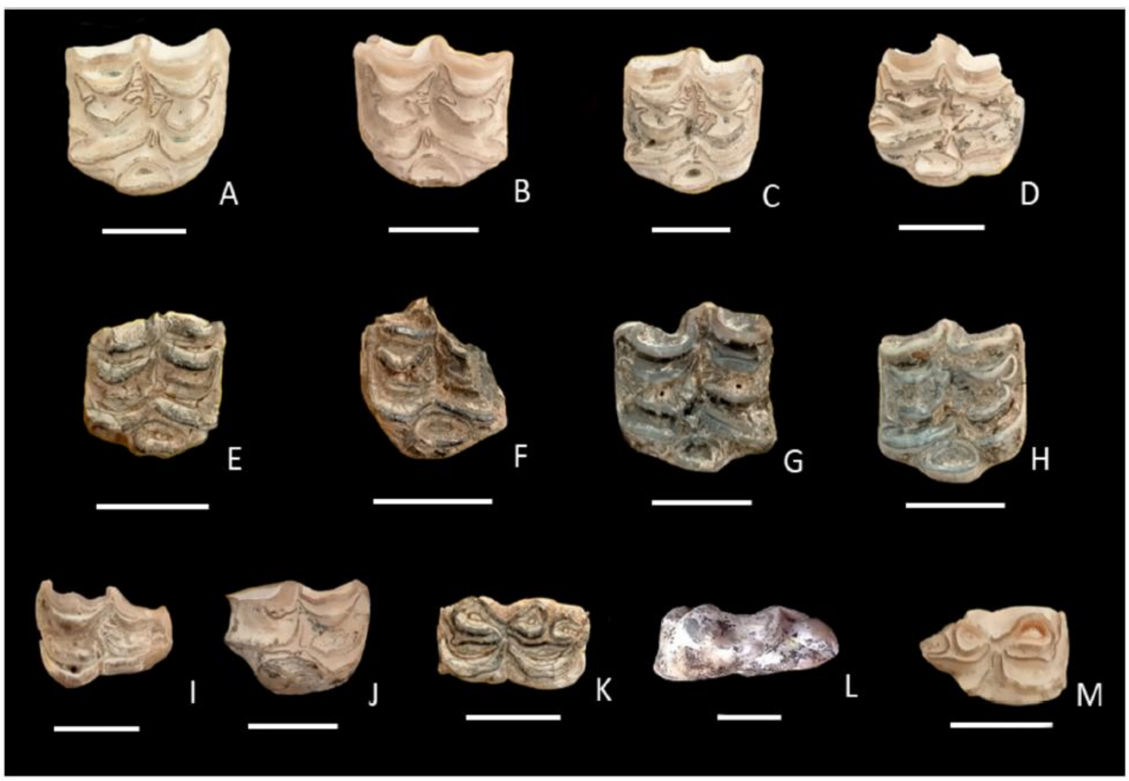

Fig. 2. *Nannippus peninsulatus* cheek teeth from Los Hornitos, northeastern Sonora. **A**, HO-422, RM2; **B**, HO-424, LP3/P4; **C**, HO-423, RM1; **D**, **E**, HO-333, RM1/M2; **F**, HO-329, LM1/M2; **G**, HO–5B–C, LP3; **H** HO–7C, RM1; **I**, HO-525, LM3; **J**, HO-221, RM3; **K**, HO-494, Lm3; **L**, HO-494, Lm3; **M**, HO-444. All scales are 1 cm.

as in *Equus*. The distal surface is somewhat flattened, consisting of the articular facet for the central tarsal bone; laterally located is a small and trapezoidal-like articular facet for the fourth tarsal bone (Fig. 3A and B).

5.4. Metapodials

The specimen HO-544 is the proximal end of a third metatarsal, which is about half of the total length of the element. The shaft is slender; the dorsal surface is strongly convex, whereas the ventral surface is flattened and the articular surfaces for the second and fourth metatarsals are evident. In the proximal view, the anterior articular surface for the third tarsal bone is moon-shaped and the posterior one is rectangular, the articular surface for the second metatarsal is small and rounded, whereas the articular surface for the fourth metatarsal is larger and subovoidal, ventrolaterally there is a deep groove, and the central depression is excavated (Fig. 3C).

In the specimens HO-078 and HO-551 the medial condyle is slightly larger than the medial one, and the sagittal crest is prominent (Fig. 3D–E). The specimen HO-078 includes part of the shaft, which is slender and cylindrical, whereas in cross-section is rounded.

5.5. Medial **phalanges**

These elements are somewhat quadrangular in shape. In the proximal view, the surfaces of the articular foveae are somewhat ovoidal. In the dorsal view, the extensor process is evident and the surfaces for attachment of collateral ligaments are rounded to ovoidal. In the ventral view, the surface for attachment of the middle scutum is wide (Fig. 3F–L).

6. Taxonomic assessment

The studied upper molariforms show an isolated protocone to the protoloph throughout the crown, indicating the typical hipparionine condition (MacFadden, 1984). Among the hipparionines, the Sonoran specimens share with *Nannippus* the following diagnostic combination of dental and postcranial features: hypsodont teeth, commonly oval protocone, moderate enamel plications on fossette borders, single plicaballin moderately to well-developed, slender metapodials, and small body size (MacFadden, 1984).

The genus *Nannippus* includes the species *N. aztecus* (= *N. minor*), *N. westoni*, *N. morgani*, *N. ingenuus*, *N. beckensis*, and *N. peninsulatus* (senior synonym of *N. phlegon*) (MacFadden, 1984, 1985; Hulbert, 1993). *N. aztecus*, the most primitive species of the genus (late Clarendonian – early Blancan), differs from the studied dental specimens in its smaller occlusal surface of the cheek teeth, shorter crown heights of less than 50 mm, and most rounded protocone (MacFadden and Waldrop, 1980; MacFadden, 1984). *N. westoni* (latest Clarendonian – very early Hemphillian) is distinguished from the studied dental sample by having low crowned teeth (MSCH ca. 40 mm), the presence of protoconal spur on the premolars, and simple fossette plications (Hulbert, 1993: Fig. 1, p. 352). *N. morgani* (late early Hemphillian) is the smallest species of the genus (MSCH commonly less than 40 mm), characterized by having elongate-oval protocone and deep hypoconal groove (Hulbert, 1993). The species *N. ingenuus* (Hemphillian) has similar crown heights to the studied specimens, although it differs in having less well-developed styles, fossettes commonly simple plicated (2–3 enamel plications in the inner borders of the fossettes), and the enamel lingual border of the protocone is somewhat oblique (MacFadden, 1984: Figs. 98–99, p. 129–130). The crown height and occlusal pattern of the upper cheek teeth of *N. beckensis* (early Blancan) are comparable to the Sonoran specimens; nevertheless, this species differs in having rudimentary or absent single plicaballin (MacFadden, 1984).

The upper cheek teeth from Los Hornitos share with *N. peninsulatus* the crown height, the complexity of fossette plications, as the protocone and plicaballin configuration (MacFadden, 1984). The dental measurements of the Sonoran upper cheek teeth (P3/P4 and M1/M2) (Table 1) are comparable to those of *N. peninsulatus* from Pearson Mesa, late Blancan of New Mexico – Arizona (Morgan et al., 2008), although the M1/M2's from Pearson Mesa are somewhat larger (Table 2). We observed that the dental morphology of HO-422 (RM2) is closely comparable to the *N. peninsulatus* specimens UF22611 (RM2) from Santa Fe River, late Blancan of Florida (Hulbert and Waldrop, 2001: Fig. 14.18C, p. 293) and AMNH 8345 (holotype R?M2) from Tehuichila, Pliocene of Hidalgo, central Mexico (MacFadden, 1984: Fig. 106, p. 137). In general, the bivariate plots of the APL and TW of P3/P4 and M1/M2 indicate that the teeth from Los Hornitos have a smaller dental size than the other samples of *Nannippus* used in the comparison, although some Sonoran molariforms are near of *Nannippus beckensis* from Beck Ranch Locality, Blancan of Texas (Fig. 4).

The associated postcranial material is correlative in size to the dental elements, indicating a small-sized horse. The specimen HO-78 has the typical slender and elongate condition observed in the metapodials of *Nannippus peninsulatus* (MacFadden, 1984). Furthermore, its midshaft width and distal width (Mdsw = 15.61 mm, Dw = 20.03 mm) are comparable to the metapodials NMMNH 55023 (Mdsw = 17.1 mm, Dw = 21.5 mm) and NMMNH 58262 (Mdsw = 17.0 mm) of *N. peninsulatus* from Pearson Mesa and Williamsburg respectively, late Blancan of New Mexico (Morgan et al., 2008, 2011). The size of medial phalanges from Los Hornitos is comparable to the *N. peninsulatus* specimens NMMNH 33179 and NMMNH 33228 from Pearson Mesa, late Blancan of New Mexico (Morgan et al., 2008) (Table 3).

Tribe Equini Quinn, 1955
Genus *Equus* Linnaeus, 1758
Equus simplicidens Cope, 1892

6.1. Referred material

Los Hornitos: HO-35D2, fossette fragment of an upper cheek tooth; HO–71K1, Lp3/p4; HO-327, Rp3/p4; HO-344, Lp3/p4; HO-526, RM2; HO-527, LP4/M1; HO-528, RP2; HO-529, RM3; HO-530, LP4/M1; HO-531, Lm1/m2; HO-532, L?P3; HO-548, R?P3; HO-73, LP2; HO-256, right astragalus; HO-50D3, right central tarsal; HO-436, HO-491, distal end of left third metacarpals; HO-508, proximal end of a left metatarsal III; HO-79, HO-435, proximal phalanges; HO-0260, HO-549, medial phalanges; HO-80, distal phalanx.

6.2. Distribution and age

Blancan of Idaho (Gidley, 1930) and Nebraska (Hibbard, 1972), late Blancan of California (Downs and Miller, 1994), Arizona (Morgan and White, 2005), New Mexico (Morgan et al., 2008), and Texas (Dalquest, 1975); Blancan of Baja California Sur (Miller, 1980), Michoacán (Arellano and Azcon, 1949; Miller and Carranza-Castañeda, 1984), Guanajuato (Carranza-Castañeda, 1989), and Hidalgo (Castillo-Cerón et al., 1996).

7. Description

7.1. Upper **cheek** teeth

The upper cheek teeth are very hypsodont (IH = 2.88), with high-crowned teeth (MSCH ca. 70 mm) covered by a thick layer of cement (>1.5 mm thick). The parastyle and mesostyle are prominent and the metastyle is reduced; in the specimen HO-526, the mesostyle is bifurcated. The protocone is short, broad, and rounded (PrL/PrW ≈ 1.2), connected to the protoloph from the onset of wear to near the base of the crown. The pli protoloph and the pli hypostyle are simple and nonpersistent. The internal borders of the fossettes are simple plicated, showing 1 to 2 plications on each side. In the specimen HO-530, it is observed four small plications in the inner border of the prefossette and a well-developed pli protoconule. The plicaballin is single and persistent at

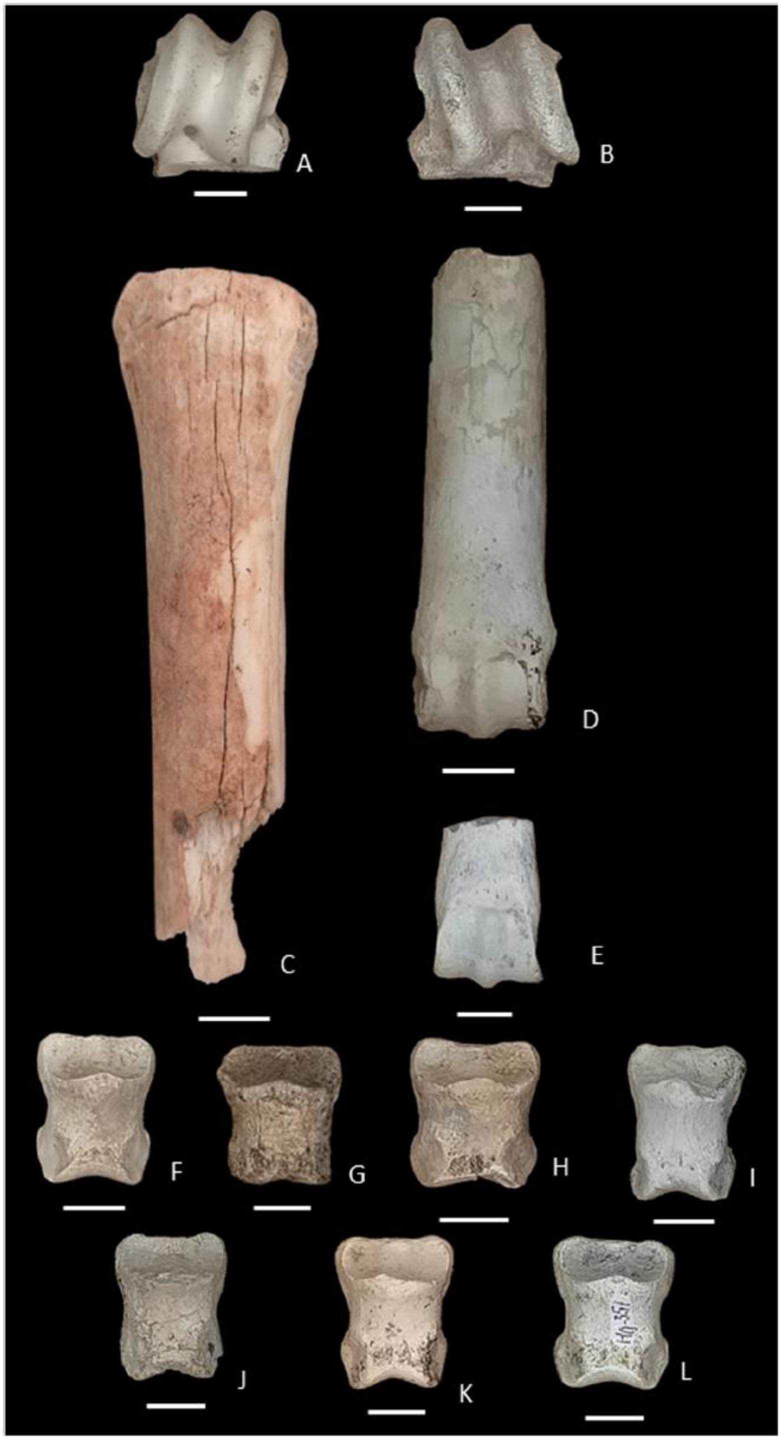

Fig. 3. *Nannippus peninsulatus* postcranial bones from Los Hornitos, northeastern Sonora (All views are anterior views). **A-B**, HO-472, right astragalus; HO-546, left astragalus; **C**, HO-544, proximal end of metatarsal III; **D**, HO-078, distal end of a right metapodial; **E**, HO-551, distal end of left metapodial III; **F-L**, HO-131, HO-351, HO-476, HO-477, HO-478, HO-504, HO-547, medial phalanges. All scales are 1 cm.

Table 1
Measurements (in mm) of the upper cheek teeth of *Nannippus peninsulatus* from Los Hornitos, Sonora.

ID	Position	WS	MSCH	APL	TW	PrL	PrW
HO-230	RP3	Early moderate	37.54e	17	16.1	6.18	3.29
HO–5B–C	LP3	Early moderate	29.57	15.51	16.09	5.68	4.53
HO-424	LP3/P4	Early	39.33e	15.9	13.79	6.12	3.14
HO-329	LM1/M2	Early late	16.86	14.16e	13.99	6.72	3.96
HO-423	RM1	Very early	43.90	14.99	14.58	5.38	3.58
HO–7C	RM1	Early moderate	33.86	14.73	14.56	5.83	3.61
HO-422	RM2	Very early	51.16	15.81	13.87	6.22	3.28
HO-333	RM2	Early late	16.73	14.5	14	5.94	3.71
HO-221	RM3	Very early	44.24	13.47	10	6.9	3.72
HO-525	LM3	Very early	43.40	12.48	8.86	–	–

Table 2
Univariate statistics of selected measurements (in mm) of *Nannippus peninsulatus* from Los Hornitos, Sonora, northern Mexico, and Pearson Mesa, New Mexico – Arizona (Morgan et al., 2008: Table 4, p. 162). Teeth at late wear stage were excluded.

Locality	MSCH	APL	TW	MSCH M1/M2	APL	TW
	P3/P4	P3/P4	P3/P4		M1/M2	M1/M2
Los Hornitos						
$\bar{x}$	35.48	16.13	15.32	42.97	15.17	14.33
SD	5.19	0.77	1.33	8.68	0.56	0.40
OR	29.57–39.33	15.51–17	13.79–16.1	33.86–51.16	14.73–15.81	13.87–14.58
Sample size	3	3	3	3	3	3
Pearson Mesa						
$\bar{x}$	33.2	16.7	17.3	53.4	17.4	16.2
SD						
OR	22.1–44.3	16.7	16.6–17.9	24.6–68.4	16.2–20.1	15.0–17.4
Sample size	2	2	2	11	11	9

the moderate wear stage. The hypoconal groove is deep, persistent at late wear, and it is open near the base of the crown (Fig. 5A–F).

7.2. Lower cheek teeth

The specimen HO–71K1 is the less worn tooth, with a crown height (along the metaconid) of about 60 mm. A thick layer of cement (>2 mm) is present on the lower cheek teeth. The protoconid is rounded and smaller than the hypoconid. In the specimens HO–71K1 and HO-531 an incipient plicaballinid is observed. In the specimens HO-327 and HO-531, both moderately worn, a faint protostylid is observed. The metaconid and metastylid are rounded to oval and are well separated from one another, being the metaconid larger than the metastylid and more lingually located; in HO–71K1 the metaconid and metastylid are subequal in size. The metaconid and metastylid complex is expanded and elongated (i.e., lmt-lmts is greater than 50% of the apl). The ectoflexid is shallow in the premolars, whereas it is deep in the one molar available (HO-531). The linguaflexid is shallow and V-shaped. In the specimens HO–71K1 and HO-531, the entoconid is rounded and well differentiated from the hypoconulid that is trapezoidal (Fig. 5G–I).

7.3. Astragalus

The trochlea of HO-256 consists of two oblique ridges; the internal trochlea is broken. The intertrochlear groove is deep, and spirals dorsally, distally, and laterally at an angle of approximately 60° to the sagittal plane. The distal surface is convex dorsoventrally, with a lateral oblique facet. The plantar surface is oblique and irregular, with four articular facets separated by rough grooves (Fig. 6A).

7.4. Central tarsal

The shape of HO-50D3 is an irregular quadrilateral anteroposteriorly flattened. The proximal surface is concave with a non-articular depression cutting its lateral part. The dorsal surface and medial border are continuous, convex, and rough (Fig. 6B).

7.5. Metapodials

The specimens HO-436 and HO-491 include the distal end of the third metacarpal, preserving approximately one third of the bone. In these specimens, the body is semi-cylindrical; the dorsal surface is smooth and convex, whereas the ventral surface is flattened longitudinally and rough. The lateral and medial edges are slightly rounded. The distal end is wider and flattened in comparison to the preserved shaft, consisting of two condyles separated by a sagittal relief, which articulate with the proximal phalanx (Fig. 6C and D).

The specimen HO-508 is the proximal end of a third metatarsal. The body is cylindrical and almost circular, the proximal articular surface is somewhat concave and has a central non-articular depression. In the proximal portion of the lateral surface is observed an oblique groove, distally and ventrally, which is conformed by a channel where the lateral metatarsal is articulated (Fig. 6E).

7.6. Proximal phalanges

In the specimens HO-79 and HO-435, the body is broader and more robust in the proximal portion than the distal portion. The dorsal surface is convex and smooth, whereas the ventral surface is flattened and has a roughly triangular area bounded by ridges that begin at the proximal tuberosities and converge distally. The proximal surface consists of two articular foveae separated by a groove. The distal surface consists of two articular condyles for the middle phalanx, being the medial one slightly larger (Fig. 6F and G).

7.7. Medial phalanges

The specimens HO-260, and HO-549 are characterized by a dorso-ventrally compressed body, which is wider than long, giving a sub-rectangular shape. The proximal surface presents two depressions for the articulation with the proximal phalanx, separated by a smooth ridge. The distal surface is somewhat smaller than the proximal one, consisting of two articular condyles separated by a sagittal groove. The dorsal

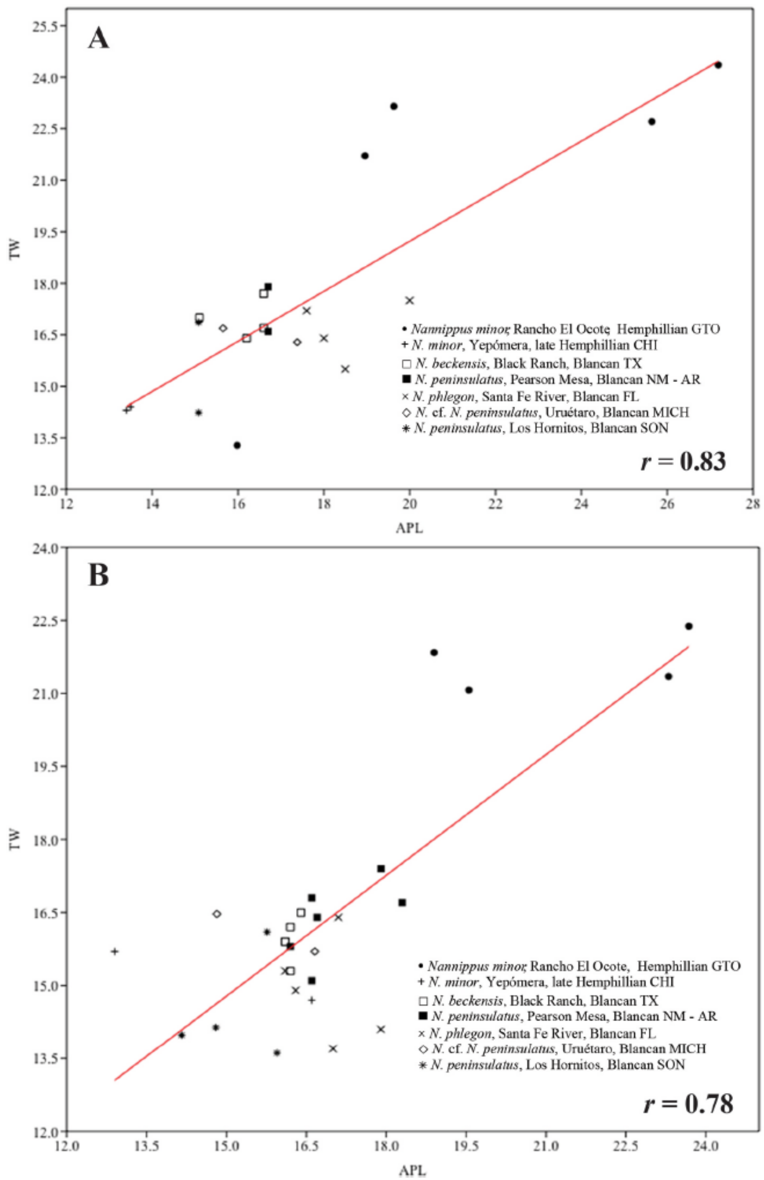

Fig. 4. Bivariate plots of APL and TW of P3/P4 (A) and M1/M2 (B) of selected dental samples of *Nannippus* from Hemphillian and Blancan faunas of the United States and Mexico and *Nannippus peninsulatus* from Los Hornitos, Pliocene of Sonora.

surface is convex, with a rough depression that ends in a tuberosity on either side of the distal part. The ventral surface is smooth and flattened, with concave margins separating it from the dorsal surface (Fig. 6H–J).

7.8. Distal phalanx

The specimen HO-80 comprises the parietal surface of a distal phalanx. The solar surface is arched and divided in two by the semilunar line. The sole is smooth, concave, and crescent-shaped (Fig. 6K).

8. Taxonomic assessment

In the studied specimens, the presence of a thick layer of cement (>1.5 mm thick), very hypsodont (HI > 2), and high-crowned teeth (MSCH ≥60 mm) are distinctive features of *Equus* (Dalquest, 1975; MacFadden, 1988; Kelly, 1998). The genus *Equus* diversified into several lineages during the Plio-Pleistocene (e.g., *E. stenonis*, *E. shoshonensis*, and *E. scotti*), being *E. simplicidens* one of the most primitive species (Kurtén and Anderson, 1980; Hulbert and Waldrop, 2001; Prothero and Schoch, 2002). The sample from Los Hornitos shares with *E. simplicidens* the following combination of features: rounded protocone (PrL/PrW ≈ 1.2),

Table 3
Medial phalanges measurements (in mm) and univariate statistics of *Nannippus peninsulatus* from Los Hornitos, Sonora, northern Mexico, and Pearson Mesa, New Mexico – Arizona (Morgan et al., 2008: Table 5, p. 164).

Locality and ID	TL	Pw	Pd	Dw	Dd
Los Hornitos					
HO 131	25.69	20.41	16.59	18.34	11.45
HO 351	26.15	21.04	15.30	20.27	11.29
HO 476	25.14	20.46	15.66	18.14	10.99
HO 477	25.21	19.80	16.74	19.68	11.67
HO 478	25.27	19.80	16.15	19.92	11.24
HO 504	25.88	21.24	16.73	18.65	11.65
HO 547	27.23	22.84	18.25	18.58	12.94
$\bar{x}$	*25.79*	*20.79*	*16.48*	*19.08*	*11.60*
SD	*0.73*	*1.05*	*0.95*	*0.85*	*0.63*
OR	*25.14–27.23*	*19.8–22.84*	*15.3–18.25*	*18.14 – 20.27*	*10.99–12.94*
Sample size	*7*	*7*	*7*	*7*	*7*
Pearson Mesa					
NMMNH 33179	27.2	23.8	17.9	20.8	14.2
NMMNH 33228	27.5	23.4	18	22.9	14.4
$\bar{x}$	*27.35*	*23.6*	*17.95*	*21.85*	*14.3*
SD	*0.21*	*0.28*	*0.07*	*1.48*	*0.14*
OR	*27.2–27.5*	*23.4–23.8*	*17.9–18*	*20.8–22.9*	*14.2–14.4*
Sample size	*2*	*2*	*2*	*2*	*2*

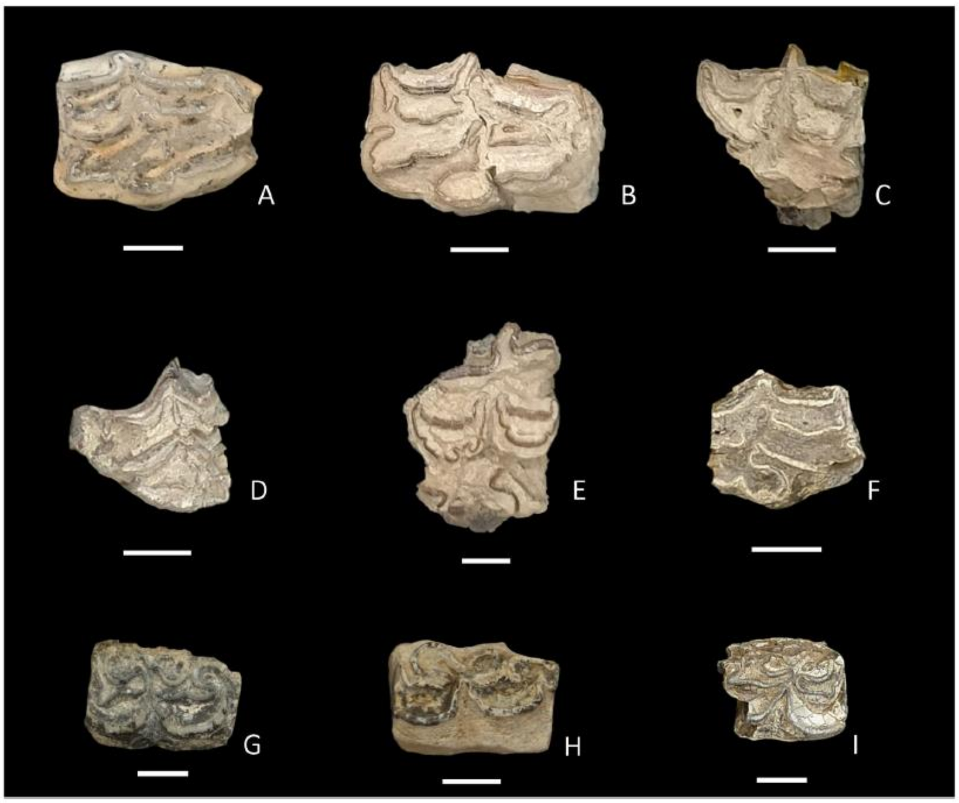

Fig. 5. *Equus simplicidens* cheek teeth from Los Hornitos, Sonora. **A**, HO-526, RM2; **B**, HO-528, RP2; **C**, HO-530, LP4/M1; **D**, HO-529, RM3; **E**, HO-532, L?P3; **F**, HO-73, LP2; **G**, HO–71K1, Lp3/p4; **H**, HO-80, **I**, HO-344, Lp3/p4. All scales are 1 cm.

rounded to oval metaconid and metastylid, simple enamel fossette plications, V-shaped linguaflexid, deep ectoflexid in the molars, and stout metapodials (Dalquest, 1975; Winans, 1989; Downs and Miller, 1994; Scott, 2006; Morgan et al., 2011).

The species *"Dinohippus" mexicanus*, considered the sister species of primitive *Equus*, differs from the Sonoran dental specimens in having somewhat less high-crowned teeth, upper cheek teeth moderately to strongly curved, elongated protocone, and moderate enamel fossette plications (MacFadden, 1984; Kelly, 1998; MacFadden and Carranza-Castañeda, 2002; Carranza-Castañeda, 2019).

Fig. 6. *Equus simplicidens* postcranial bones from Los Hornitos, northeastern Sonora (All views are anterior). A, HO-256, right astragalus; B, HO-50D3, right central tarsal; C-D, HO-491 and HO-436, distal end of left metacarpals III; E, HO-508, proximal end of left metatarsal III; F-G, HO-79 and HO-435, proximal phalanges; H-J, HO-0259, HO-260, and HO-549, medial phalanges; K, HO-80, distal phalanx. All scales are 1 cm.

The species *Equus scotti* is known from numerous Blancan and Irvingtonian localities in the southern United States (Robertson, 1976; Morgan et al., 1997, 2008, 2011), being distinguished from the Sonoran specimens by having larger size, progressive hypsodonty, narrow and elongated protocone with strong lingual indentation, well-developed plicaballin, moderately complex fossette plications, and shallow ectoflexid in the lower molars (Morgan et al., 2011; Morgan and Harris, 2015). Other Pleistocene *Equus* species from Mexico, such as *E. mexicanus, E. conversidens, E. excelsus, E. francisci*, and *E. cedralensis*, differ in having ovoidal to elongated protocone, moderate to complex fossette plications, and variable U- to V-shaped linguaflexid (Bravo-Cuevas et al., 2011; Priego-Vargas et al., 2016).

The MSCH of HO-529 (≈70 mm) is comparable to that observed in unworn/early worn upper cheek teeth of *E. simplicidens* and smaller than that of *E. scotti* (≈90 mm) from the Blancan and Irvingtonian of New Mexico (Morgan et al., 2011; Morgan and Harris, 2015).

The dental measurements of the Sonoran upper molariforms (P3/P4 and M1/M2) (Table 4) are comparable to those of *E. simplicidens* from Sierra County, late Blancan of New Mexico (Morgan et al., 2011: Table 9, p. 697), *Equus* sp. from Pearson Mesa, late Blancan of New Mexico – Arizona (Morgan et al., 2008: Table 6, p. 166), and *Equus* (*Dolichohippus*) *simplicidens* from Haile XV A, late Blancan of Florida (Robertson, 1976: table 15, p. 162), although the molariforms from Truth or Consequences and Palomas Creek, Sierra County, are somewhat wider (Table 5).

Table 4
Measurements (in mm) of the upper cheek teeth of *Equus simplicidens* from Los Hornitos, Sonora.

ID	Position	MSCH	WS	APL	TW	PrL	PrW
HO-550	LP2	36.85	Moderate	–	22.95	7.54	7.26
HO-526	RP2	46.41	Moderate	34.89	26.6	8.49	6.74
HO-527	LP4/M1	47.01	Moderate	25.83	24.15	–	–
HO-528	RP2	58.16	Early	36.72	26.61	9.72	7.31
HO-529	RM3	72.56	Very early	25.19	20.39	–	–
HO-530	LP4/M1	46.13	Moderate	25.83	23.1	–	–
HO-532	L?P3	40.90e	Moderate	28.93e	34.92	–	–
HO-548	R?P3	54.69	Early	24.40	18.46	–	–

Based on the bivariate plots of P3/P4 and M1/M2, we observed that the dental size of the Sonoran specimens is between *Equus* (*Dolichohippus*) *simplicidens* from Haile XV A, late Blancan of Florida, and *Plesippus simplicidens* from Meade, Blancan of Kansas, although near of *E.* cf. *E. simplicidens* from the Blancan of Michoacán. On the other hand, the upper molariforms of *Equus scotti* from the Red Light, Blancan of Texas have a larger dental size (Fig. 7).

The msch of the specimen HO–71K1 (≈60 mm) is somewhat smaller (ca. 15%) than that of *Equus simplicidens* and smaller (ca. 30%) than that of *Equus* sp. from Pearson Mesa, New Mexico – Arizona. The anteroposterior length of the Sonoran lower molariforms is similar to that observed in the *Equus* samples from this locality (Tables 6 and 7).

The size and proportions of the studied postcranial remains are suggestive of a medium-sized horse with stout metapodials. The average distal width of the metacarpals from Los Hornitos (Dw = 46.32 mm) is similar to that of metacarpals referable to *Equus* (*Plesippus*) *simplicidens* (Dw = 44.0 mm) from Broadwater Quarry, Nebraska (Howe, 1970: Table 5, p. 967). On the other hand, the proximal width of the specimen HO-508 (Pw = 44.8 mm) is comparable to the average width of metatarsals (Pw = 48.5 mm) referable to *E.* (*Dolichohippus*) *simplicidens* from Blancan Haile XV A, Florida (Robertson, 1976: table 16 p. 162), although these metapodials are smaller than the specimens TMM 40664–292 (Pw = 54.6 mm), TMM 40891–2 (Pw = 59.9 mm), UMMP V39375 (Pw = 54.5 mm), and UMMP V39376 (Pw = 52.8 mm) of *E. scotti* from Red Light local fauna, Texas (Akersten, 1972: table 12, p. 40). The average total lengths of proximal (TL = 76.65 mm) and medial phalanges (TL = 43.26 mm) from los Hornitos are somewhat comparable to those of *E.* (*Dolichohippus*) *simplicidens* (TL = 78.5 mm, TL = 45.5 mm respectively) from Haile XV A, Alachua County, Florida (Robertson, 1976: table 16, p. 162) and *E.* (*Plesippus*) cf. *simplicidens* (TL = 80.6 mm, TL = 43.8 mm respectively) from Red Light Local Fauna, Hudspeth County, Texas (Akersten, 1972: table 13, p. 41) (Table 8).

9. $\delta^{13}C$ and $\delta^{18}O$ isotope composition of horses from Los Hornitos

The $\delta^{13}C$ isotope values of *Nannippus peninsulatus* from Los Hornitos range from −4.14‰ to – 3.16‰, with an average value of – 3.64‰ (SD ± 0.49), whereas $\delta^{18}O$ isotope values range from – 4.94‰ to – 3.68‰, with an average value of – 4.45‰ (SD ± 0.67) (Table 9). The $\delta^{13}C$ isotope values of *Equus simplicidens* range from – 2.96‰ to −2.29‰, with an average value of – 2.67‰ (SD ± 0.28), whereas $\delta^{18}O$ isotope values range from – 5.75‰ to – 3.51‰, with an average value of – 4.59‰ (SD ± 0.90) (Fig. 8, Table 9).

The species *N. peninsulatus* and *E. simplicidens* from Los Hornitos show statistical differences in their average $\delta^{13}C$ values ($t = 3.6312$, $p = 0.0109$), although they do not show statistical differences in their average $\delta^{18}O$ values ($t = 0.2299$, $p = 0.8257$). The $\delta^{13}C$ isotope values of *N. peninsulatus* are more negative than those of *E. simplicidens* (Fig. 8).

There are statistical differences in the $\delta^{13}C$ values of *N. peninsulatus* from Los Hornitos and the selected samples of *Nannippus* from Florida,

Table 5
Univariate statistics of selected measurements (in mm) of *Equus simplicidens* from Los Hornitos, Sonora, northwestern Mexico, *Equus simplicidens* from Sierra County (SC), New Mexico (Morgan et al., 2011: Table 9, p. 697), *Equus* sp. from Pearson Mesa, New Mexico – Arizona (Morgan et al., 2008: Table 6, p. 166), and *Equus* (*Dolichohippus*) *simplicidens* from Haile XV A, Florida (Robertson, 1976: table 15, p. 162). Teeth at late wear stage were excluded.

Locality	P3/P4			M1/M2		
Los Hornitos	MSCH	APL	TW	MSCH	APL	TW
$\bar{x}$	47.79	26.66	26.69	46.57	25.83	23.65
SD	9.75	3.2	11.63	0.62	0	0.74
OR	40.9–54.69	24.4–28.93	18.46–34.92	46.13–47.01	25.83	23.1–24.15
Sample size	2	2	2	2	2	2
Equus simplicidens						
Elephant Butte Lake (SC)						
$\bar{x}$	–	27.2	32.8	–	25.8	27.6
SD	–	–	–	–	–	–
OR	–	27.2	32.8	–	25.6–26	27.6
Sample size	–	1	1	0	2	1
Cuchillo Negro Creek (SC)						
$\bar{x}$	68.1	29.2	27.6	72.3	28.2	28.3
SD	–	–	–	–	–	–
OR	68.1	29.2	27.6	72.3	28.2	28.3
Sample size	1	1	1	1	1	1
Truth or Consequences (SC)						
$\bar{x}$	19.6	27.3	31.4	22.5	25.1	30.6
SD	2.68	1.41	1.69	6.92	1.13	0.282
OR	17.7–21.5	26.3–28.3	30.2–32.6	17.6–27.4	24.3–25.9	30.4–30.8
Sample size	2	2	2	2	2	2
Palomas Creek (SC)						
$\bar{x}$	–	27.36	30.733	–	25.91	29.6
SD	–	0.75	1.88	–	2.23	0.675
OR	–	26.6–27.4	30.3–32.8	–	22.6–29.1	29–30.6
Sample size	–	3	3	–	6	6
Equus sp.						
Pearson Mesa						
$\bar{x}$	41.82	28.85	30.28	46.77	28.4	24.95
SD	17.63	1.98	0.44	18.75	0.6	1.93
OR	17–61.9	26.6–29.7	29.5–30.8	22.9–61.8	27.7–28.9	22.3–26.9
Sample size	7	7	7	4	5	6
E. (*Dolichohippus*) *simplicidens*						
Haile XV A						
$\bar{x}$	–	23.325	25.125	–	22.625	23.95
SD	–	1.014	0.805	–	0.801	1.19
OR	–	21.9–24.1	24.3–26.2	–	22–23.8	22.6–25.5
Sample size	–	4	4	–	4	4

Table 6
Measurements (in mm) of the lower cheek teeth of *Equus simplicidens* from Los Hornitos, Sonora.

ID	Position	mcch	WS	apl	tw	mml
HO-71K1	Lp3/p4	59.06e	Very early	28.54	16.89	16.99
HO-327	Rp3/p4	33.97e	Moderate	24.55	16.29	14.44
HO-344	Lp3/p4	–	–	24.15	15.39	13.63
HO-531	Lm1/m2	35.21	Moderate	27.81	15.26	15.02

Chihuahua, Michoacán, and Guanajuato ($F = 4.17$, $p = 0.008$). The pairwise comparison indicates that the average $\delta^{13}C$ isotope composition of the studied sample is statistical similar to that of the *Nannippus* cf. *N. peninsulatus* samples from Michoacán (Uruétaro and Misión del Valle localities). By contrast, statistical differences are observed between the *Nannippus* samples from Florida (Moss Acres and U Bone Valley localities) and *N. aztecus* from Yepómera, Chihuahua (Table 10).

There are statistical differences in the $\delta^{13}C$ values of *Equus simplicidens* from Los Hornitos and the samples of *Equus* from Nebraska, Florida, and Michoacán ($F = 5.24$, $p = 0.001$). The pairwise comparison indicates that the average $\delta^{13}C$ isotope composition of the sample from Los Hornitos is statistically similar to the *Equus* sample from Leisey 1 A, Florida. By contrast, statistically significant differences are observed between the *E.* cf. *E. simplicidens* samples from Michoacán (Uruétaro and Misión del Valle localities) and *E. simplicidens* from Nebraska (Broadwater and Big Spring localities) (Table 11).

We do not observe statistical differences in the average $\delta^{18}O$ isotope composition of *N. peninsulatus* from Los Hornitos and the selected samples of this species from Michoacán and *N. aztecus* from Chihuahua ($F = 3.22$, $p = 0.054$). On the other hand, there are significant statistical differences in the $\delta^{18}O$ values of *Equus simplicidens* and the samples from Michoacán and Nebraska ($F = 33.39$, $p < 0.05$).

10. Discussion

10.1. Diet and habitat of the sonoran horses

Previous stable isotope studies indicate that *Nannippus peninsulatus* from the Blancan of Arizona and Florida had a predominantly grazing diet of C4 plants (Wang et al., 1994; MacFadden et al., 1999). The results in this study indicate that *N. peninsulatus* from Los Hornitos was a mixed-feeder of both C3 and C4 plants, which is comparable to the suggested diet for *N.* cf. *N. peninsulatus* from the Blancan of Michoacán (Plata-Ramírez, 2017) (Tables 9 and 10). Based on this, it seems that the Mexican populations of this species had high dietary flexibility compared to others from the Great Basin and Gulf Coast of Florida, United States.

Stable isotope analyses of samples referable to *E. simplicidens* from the Blancan of Nebraska and Michoacán are indicative of a C3–C4 mixed diet (Kita, 2011; Plata-Ramírez, 2017). Our results are related to a similar dietary behavior for the population from Los Hornitos (Table 11), suggesting that this horse could have been a generalist species able to consume a wide range of plant resources and inhabit a range of habitats.

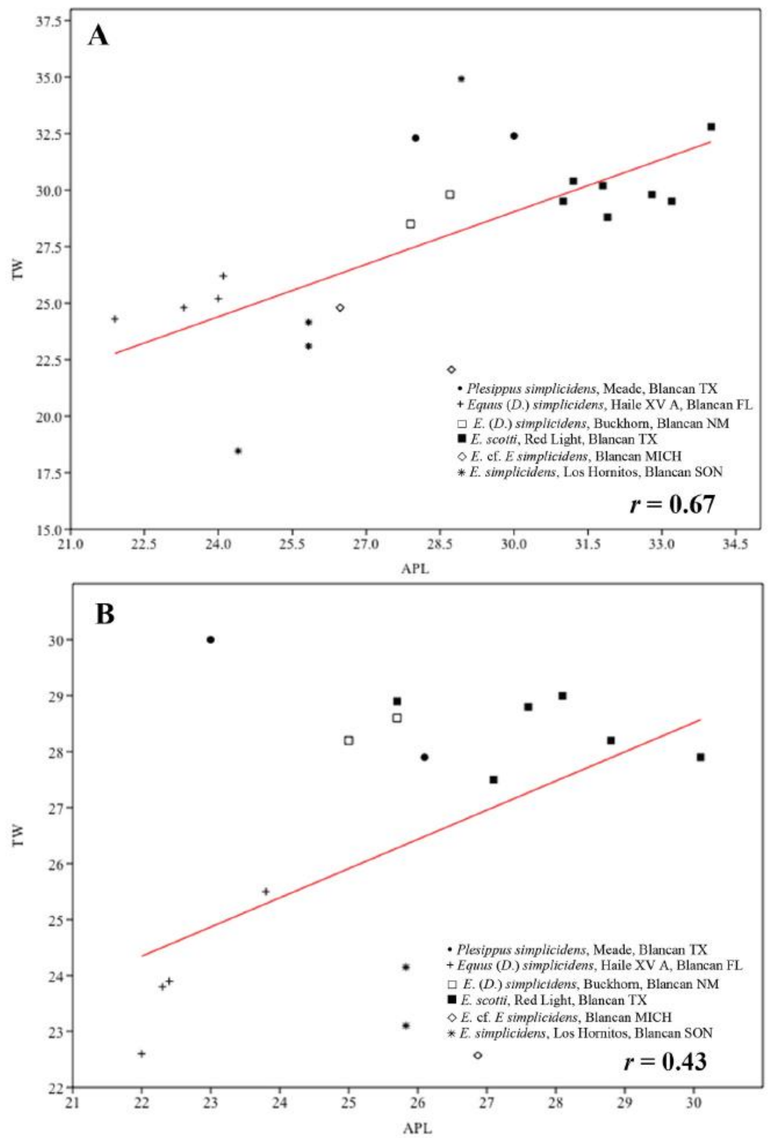

Fig. 7. Bivariate plots of APL and TW of P3/P4 (A) and M1/M2 (B) of selected dental samples of *Equus* from Blancan faunas of the United States and Mexico, and *E. simplicidens* from Los Hornitos, Pliocene of Sonora.

Although our isotope results indicate that both horse species from Los Hornitos may have had a mixed trophic regime, we noted that the $\delta^{13}C$ average value of *E. simplicidens* (– 2.67‰) is less negative than that of *Nannippus peninsulatus* (– 3.64‰), which probable indicates a tendency in the consumption of C4 plants in the former species (Fig. 8, Table 9). The statistical differences ($p < 0.05$) observed in the carbon isotope composition between the Sonoran horses indicate different trophic regimes in these species, supporting the contention mentioned above.

Nannippus peninsulatus was a small-sized horse with a body mass of about 60 kg, whereas *Equus simplicidens* was a large-sized horse with a body mass of about 400 kg (MacFadden, 1986; MacFadden et al., 1999). It is known that large mammals tend to have a large range of home and are more migratory in comparison to small mammals (Eisenberg, 1981; McNab, 1963). Thus, the potential differences observed in the dietary regime, body size, vagility, and home range between these species could explain their coexistence, allowing them optimal resource partitioning and occupied different habitats in the area (MacFadden, 1992).

Based on the model of Feranec and MacFadden (2006), the average $\delta^{13}C$ values (ca. – 4‰) of the Sonoran horses suggest that they inhabited open areas. On the other hand, the observed average carbon composition is in the predicted interval of $\delta^{13}C$ values of C3 and C4 grassland habitats in the Blancan (Kita, 2011: Fig. 4, p. 33). *Nannippus peninsulatus* and *E. simplicidens* have similar average $\delta^{18}O$ values (greater than – 5‰), suggesting that inhabited open or closed habitats, although *E. simplicidens* could have shown a preference for open areas. In this

Table 7
Univariate statistics of selected measurements (in mm) of lower teeth of *Equus simplicidens* from Los Hornitos, Sonora, northwestern Mexico, and *Equus simplicidens* and *Equus* sp. from Pearson Mesa, New Mexico – Arizona (Morgan et al., 2008: Table 6, p. 167). Teeth at late wear stage were excluded.

Locality	p3/p4			m1/m2		
Los Hornitos						
	msch	apl	tw	msch	apl	tw
$\bar{x}$	56.09	25.71	16.19	35.21	24.2	14.82
SD	14.14	2.37	0.75	–	–	–
OR	33.97–59.06	24.15–28.45	14.82–16.94	35.21	24.2	14.82
Sample size	2	3	3	1	1	1
Pearson Mesa						
E. simplicidens						
$\bar{x}$	72.3	33.1	–	68.6	28	–
SD	–	1.41	–	6.92	1.13	–
OR	72.3	32.1–34.1	–	63.7–73.9	27.2–28.8	–
Sample size	1	2	–	2	2	–
Equus sp.						
$\bar{x}$	88.85	29.84	18.42	86.06	27.72	16.78
SD	5.58	3.30	1.26	3.55	2.79	1.74
OR	84.9–92.8	25.7–33.6	16.8–19.8	84.9–92.8	25.7–33.6	16.8–19.8
Sample size	2	5	4	2	5	5

Table 8
Phalanges measurements (in mm) and univariate statistics of *Equus simplicidens* from Los Hornitos, Sonora, northwestern Mexico; *Equus* from Sierra County, New Mexico (Morgan et al., 2011: Table 11, p. 700); *E.* (*Dolichohippus*) *simplicidens* from Haile XV A, Alachua County, Florida (Robertson, 1976: table 16, p. 162); *Plesippus simplicidens* from Hagerman, Idaho (Gazin, 1936: Table 5, p. 320); and *E.* (*P.*) cf. *simplicidens* (Akersten, 1972: table 14, p. 42), from Red Light local fauna, Hudspeth County, Texas. "—" Indicates a missing measurement.

Locality	TL	Pw	Pd	Dw	Dd
Proximal phalanx					
Los Hornitos					
$\bar{x}$	76.65	43.26	30.3	35.4	22.32
SD	7.82	8.11	7.04	5.84	6.45
OR	67.62–81.4	37.3–52.51	24.63–38.19	31.39–42.12	17.89–29.73
Sample size	3	3	3	3	3
Sierra County					
$\bar{x}$	81.53	48.5	34.47	40.8	25.2
SD	1.05	5.71	3.11	4.24	2.35
OR	80.4–82.5	42.1–53.1	31.6–38.6	35.9–43.3	22.5–26.8
Sample size	3	3	4	3	3
Haile XV A					
$\bar{x}$	78.5	43.7	–	36.4	–
SD	3.08	1.02	–	3.39	–
OR	75.8–81.2	42.8–44.5	–	33.7–38.5	–
Sample size	3	2	–	4	–
Red Light					
$\bar{x}$	80.6	48.66	35.33	40.72	–
SD	2.96	3.31	2.01	1.17	–
OR	78–85	45.6–53.7	33.2–37.2	39–42.1	–
Sample size	5	5	3	5	–
Hagerman					
$\bar{x}$	78	52.6	37.6	41.3	–
SD	0	0.28	0.56	0.919	–
OR	78	45.6–53.7	33.2–37.2	39–42.1	–
Sample size	2	2	2	2	–
Medial phalanx					
Los Hornitos					
$\bar{x}$	44.57	19.8	31.465	42.39	30.37
SD	4.03	0	1.11	4.25	0.947
OR	41.72–47.43	19.8	30.68–32.25	39.38–45.4	29.7–31.04
Sample size	2	2	2	2	2
Sierra County					
$\bar{x}$	47.86	48.06	32.5	43.23	29.6
SD	2.27	5.71	0	2.43	0
OR	46.0–50.4	47.1–48.7	32.	40.6–45.4	29.6
Sample size	3	3	1	3	1
Haile XV A					
$\bar{x}$	45.5	40.7	–	40.9	–
SD	2.33	2.89	–	2.82	–
OR	44.1–47.4	39.1–43.26	–	38.8–42.8	–
Sample size	6		–	6	–
Red Light					
$\bar{x}$	43.8	40.4	27.7	37.5	–
SD	2.68	1.13	1.41	0.14	–
OR	41.9–45.7	39.6–41.2	26.7–28.7	37.4–7.6	–
Sample size	2	2	2	2	–

Table 9
$\delta^{13}C$ and $\delta^{18}O$ isotope composition and related diet and habitat preferences of *Nannippus peninsulatus* and *Equus simplicidens* from Los Hornitos, Sonora. Dietary categories: G, grazer; M, mixed-feeder.

Taxon	ID	$\delta^{13}C$ (‰)	$\delta^{18}O$ (‰)	Diet	Category	Habitat
N. peninsulatus	HO-422	−4.14 ± 0.16	−4.94 ± 0.17	C3/C4	M	Open/Close
N. peninsulatus	HO-221	−3.62 ± 0.13	−4.73 ± 0.23	C3/C4	M	Open/Close
N. peninsulatus	HO-7C	−3.16 ± 0.09	−3.68 ± 0.20	C3/C4	M	Open/Close
E. simplicidens	HO-35	−2.66 ± 0.26	−3.51 ± 0.12	C3/C4 – C4	M – G	Mostly open
E. simplicidens	HO-71K1	−2.96 ± 0.06	−3.95 ± 0.08	C3/C4 – C4	M – G	Mostly open
E. simplicidens	HO-73	−2.52 ± 0.07	−5.17 ± 0.20	C3/C4 – C4	M – G	Mostly open
E. simplicidens	HO-529	−2.29 ± 0.15	−4.57 ± 0.13	C3/C4 – C4	M – G	Mostly open
E. simplicidens	HO-530	−2.93 ± 0.15	−5.75 ± 0.20	C3/C4 – C4	M – G	Mostly open

regard, hypsodonty and a thick layer of cement are adaptive traits related to the consumption of abrasive resources (Janis and Fortelius, 1988; MacFadden, 1992), such as the C4 grasses. Both conditions are observed in *Equus simplicidens* from Los Hornitos, which would allow their exploitation. Hence, *N. peninsulatus* would prefer woodland habitats and *E. simplicidens* open habitats.

Temperature decreased across North America during the Pliocene, increasing aridity and promoting the expansion of open vegetation areas (Cerling et al., 1997; MacFadden, 2000). The Pliocene mammalian and floral assemblages from central and northern localities of Mexico are related to temperate forests and grassy habitats in arid conditions (Graham, 1993, 1994; González-Medrano, 1998; Carranza-Castañeda, 2006). The mixed C3–C4 diet observed in the Sonoran horses suggests the presence of variable cover vegetation, including woodland (C3 plants, such as trees, shrubs, and bushes) and open areas (C4 plants, such as grasses), probably related to cold and arid conditions at Los Hornitos. Paleoecological studies in the other mammalian groups present at the area and implementation of other paleoenvironmental proxies (e.g., pollen, paleosols) will lead to supplement this interpretation.

11. Biochronology

The Pliocene encompasses two NALMA's, including the Hemphillian and the Blancan. The Blancan extends from about ~4.9 to 1.9–1.72 Ma, i.e., late early Pliocene to earliest Pleistocene. The division of this NALMA is largely based on the evolutionary history of arvicoline and microtine rodents (Repenning, 1988; Bell et al., 2004). Repenning (1988) considered five intervals for the Blancan, including Blancan I (4.9–4.62 Ma), Blancan II (4.62–4.1 Ma), Blancan III (4.1–3.0 Ma), Blancan IV (3.0–2.5 Ma), and Blancan V (2.5–1.72 Ma). Bell et al. (2004) reviewed the Blancan intervals and concluded that the Blancan II and IV are the continuations of the Blancan I and Blancan III respectively. Morgan and Harris (2015) divided the Blancan vertebrate faunas from New Mexico, as the late early Blancan (~3.6–2.7 Ma), early late Blancan (~2.7–2.2 Ma), and latest Blancan (~2.2–1.6 Ma). Despite the lack of micromammals (so far) from Los Hornitos, the overlapping of the biochronological range of *Nannipus peninsulatus* and *Equus simplicidens* allows a regional correlation of this site with faunas from Arizona, New

Table 10
Statistical differences ($p < 0.05$) in $\delta^{13}C$ values for *Nannippus peninsulatus* from Los Hornitos and selected samples of *Nannippus* from late Neogene localities of United States and Mexico.

	B	C	D	E	F	G
A	0.554	0.738	0.5988	0.539	0.999	1
B		0.999	0.0557	0.024	0.312	0.514
C			0.0759	0.026	0.444	0.695
D				0.999	0.673	0.639
E					0.584	0.593
F						1

(A) *N. peninsulatus* from Los Hornitos, (B) *Nannipus* from Moss Acres, (C) *Nannippus* from U Bone Valley, (D) *Nannippus* sp. from El Ocote, (E) *N. aztecus* from Yepómera, (F) *N.* cf. *N. peninsulatus* from Misión del Valle, and (G) *N.* cf. *N. peninsulatus* from Uruétaro. Bold values indicate significant differences between samples.

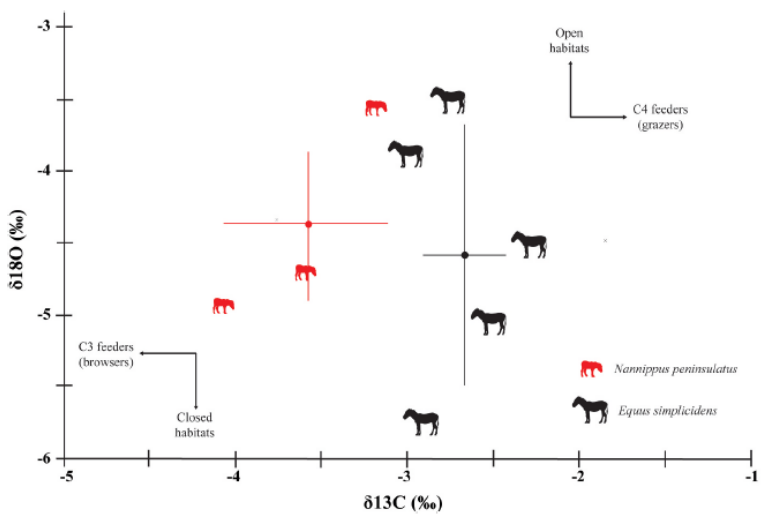

Fig. 8. $\delta^{13}C$ and $\delta^{18}O$ isotope composition of the horse dental sample from Los Hornitos, northeastern Sonora, northwestern Mexico. Average values (dots) and standard deviations (lines) are depicted.

Table 11
Statistical differences ($p < 0.05$) in $\delta^{13}C$ values for *Equus simplicidens* from Los Hornitos and selected samples of *Equus* from late Neogene localities of United States and Mexico.

	B	C	D	E	F	G
A	0.6892	1	0.6018	0.4141	0.3916	0.6655
B		0.7681	0.0986	0.0590	0.9995	0.9995
C			0.8996	0.8237	0.5183	0.8171
D				1	0.0351	0.0322
E					0.0191	0.0108
F						0.9628

(A) *Equus simplicidens* from Los Hornitos, (B) *Equus* from Santa Fe 1, (C) *Equus* from Leisey 1 A, (D) *E.* cf. *E. simplicidens* from Uruétaro, (E) *E.* cf. *E. simplicidens* from Misión del Valle, (F) *E. simplicidens* from Broadwater, and (G) *E. simplicidens* from Big Spring. Bold values indicate significant differences between samples.

Mexico, and Texas, United States and some faunas of central Mexico.

N. peninsulatus is a typical Blancan species (MacFadden, 1984, 1985), whose last appearance datum in western North America is placed at about 2.5 to 2.2 Ma (Blancan V, latest Blancan) (Lindsay, 1984; Morgan et al., 2011), although this species does not survive into the Irvingtonian (early Pleistocene) (Rook et al., 2019). This hipparionine is unknown from Blancan faunas in New Mexico and Arizona with geochronological data younger than the Gauss – Matuyama reversal (~2.58 Ma) (Kurtén and Anderson, 1980; Morgan and Harris, 2015), considered the Pliocene-Pleistocene boundary (Suc et al., 1997).

E. simplicidens appeared of about 3.5 Ma (Blancan III) and occurred throughout most of the Blancan except for the very early and latest Blancan (Morgan et al., 2008). This species is reported from early Blancan and early late Blancan localities in New Mexico, although it became extinct at about 2.6 Ma (Morgan and Harris, 2015; Morgan et al., 2017).

N. peninsulatus and *E. simplicidens* are reported from the Blanco Local Fauna, Texas, dated at about 2.5 Ma, corresponding to the lower Matuyama Chronozone (Lindsay et al., 1976; Morgan and Harris, 2015). In Mexico, these species have been reported from several Blancan localities in northern and central Mexico, including the states of Chihuahua, Michoacán, and Guanajuato (Lindsay, 1984; Carranza-Castañeda, 2006). The chronological information of the majority of these sites is from the biochronological correlation with other North American faunas from the southern United States (Lindsay, 1984; Carranza-Castañeda and Miller, 2004; Carranza-Castañeda et al., 2013). However, there is radiometric information for some localities in San Miguel de Allende, Guanajuato (La Pantera: 3.9 ± 0.3 Ma) and Charo, Michoacán (La Goleta: 3.6 ± 0.3 Ma), whose ages are related to the Blancan III (Carranza-Castañeda, 2006; Ferrusquía-Villafranca and Ruiz-González, 2015).

The age of the Los Hornitos locality could be at ~3.9–2.6 Ma, corresponding to the Blancan III or late early Blancan – early late Blancan, based on the biochronological information of *Nannippus peninsulatus* and *Equus simplicidens*. The application of some direct or indirect dating techniques would conduct to support or modify the proposed age.

12. Conclusions

We formally described a set of dental and postcranial horse remains recovered from the Los Hornitos locality, Pliocene of northeastern Sonora. A comparative study of this material indicates the presence of two species, the small-sized hipparionine *Nannippus peninsulatus* and the medium-sized equine *Equus simplicidens*.

The isotope composition of $\delta^{13}C$ in tooth enamel indicates that *N. peninsulatus* and *E. simplicidens* were C3–C4 mixed feeders, although it is probable that the latter species had an emphasis in the consumption of C4 plants. The optimal resource partitioning between these species is explained by their differences in dietary behavior, body size, vagility, and home range. The dietary and habitat preferences of the Sonoran horses suggest the presence of woodland and open areas in Los Hornitos during the Pliocene.

The age of the Los Hornitos is located at ~3.9–2.6 Ma, corresponding to the Blancan III or late early Blancan – early late Blancan, considering the biochronological information of *N. peninsulatus* and *E. simplicidens* reported from selected Pliocene mammalian faunas from the southwestern United States and central Mexico.

CRediT authorship contribution statement

Arturo Palma-Ramírez: Writing – original draft, Methodology, Formal analysis, Conceptualization. **Victor M. Bravo-Cuevas:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Uxue Villanueva Amadoz:** Writing – review & editing, Resources, Methodology, Conceptualization. **Alexis Pérez-Pérez:** Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

I have inlcuded the data in the article and Supplementary Material

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jsames.2022.104119.

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CAPÍTULO 3

HISTORICAL BIOLOGY
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First record of *Odocoileus virginianus* (Artiodactyla: Cervidae) from the Blancan of Sonora, Northwestern Mexico

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ABSTRACT

Blancan III or late early Blancan–early late Blancan (3.9–2.6 Ma, Pliocene) cervid remains are described from alluvial deposits of the locality Los Hornitos, northeastern Sonora, northwestern Mexico. These remains include antlers, teeth, a mandible fragment, and other several postcranial elements. These Sonoran Blancan fossil cervid elements constitute the second most abundant group of the mammalian assemblage after the equids in the studied area. The morphometric comparative study with Pliocene and Pleistocene cervid material from United States and Mexico together with statistical analyses (bivariate and multivariate), indicate that herein described material correspond to the species *Odocoileus virginianus*. This is the first record of this medium-sized deer from the Blancan of Sonora and the earliest unequivocal record to Mexico.

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Introduction

Cervidae is in the Order Ruminantia, apart from the families Tragulidae, Antilocapridae, Moschidae, Giraffidae, and Bovidae. Cervids comprise about 54 extant species found in all climatic zones and a broad diversity of habitats, including harsh environments of the Arctic tundra (Schilling 2021).

Cervids are the second most diverse group among the Ruminantia, widespread in the Americas, Europe, and Asia. This group reached areas of South America, although mainly restricted to the Northern Hemisphere (Webb 1998; Heckeberg 2020). The earliest true deer appeared in Eurasia during the Miocene (Heffelfinger 2006), while *Eocoileus gentryorum* is considered the most primitive deer from the New World, appearing about 5 million years ago during the latest Hemphillian, North American Land Mammal Age (NALMA), early Pliocene (Webb 2000).

Deer were not very abundant or widespread until the early Pleistocene (2–1 Ma), probably due to the diversity and abundance of other large hoofed animals at that time, resulting in an intense resource partitioning among them (Frick 1937; Heffelfinger and Latch 2023). During the Pleistocene Ice Age, most of the large mammals as the genera *Mammuthus, Camelops, Glyptotherium*, and *Equus* went extinct, but not *Odocoileus* (Heffelfinger and Latch 2023). Two species of this genus inhabited North America today, including *O. hemionus* and *O. virginianus*. These species possibly diverged sometime in the Pliocene or early Pleistocene, during the Blancan (Webb 1998; Heffelfinger 2011; Heffelfinger and Latch 2023).

In Mexico, the record of *Odocoileus* is abundant and widespread in the Pleistocene, including *O. halli* (= *Navahoceros* sensu Webb 1992), *O. hemionus*, and *O. virginianus* (Ferrusquía-Villafranca et al. 2010; Montellano-Ballesteros and Carbot-Chanona 2010; Díaz-Sibaja 2013). The Pliocene record of this genus is lesser-known, including *Odocoileus* sp. from the Blancan of Michoacán (Plata-Ramírez 2017) and? *Odocoileus* from the early Blancan of Chihuahua (Lindsay 1984). There are mentions of *Navahoceros fricki* from several late Pleistocene localities, including El Cedazo, Guanajuato (Mooser and Dalquest 1975); San Josecito Cave, Nuevo Leon; Tlapacoya, Basin of Mexico; and San Agustín, Oaxaca (Kurtén 1975; Kurtén and Anderson 1980). This species is considered a *nomen nudum* and should be invalidated and referred to as *Odocoileus lucasi* (sensu Flueck and Smith-Flueck 2013, p. 329).

Palaeontological work carried out in northeastern Sonora, Mexico, allowed us to recover from a sedimentary sequence considered Pliocene in age (Palma-Ramírez et al. 2023), an important sample of fossil material belonging to cervids, including cranial, dental, and postcranial elements. The purpose of this study is to provide the formal taxonomic identification of the available fossil material by a comparative analysis. Furthermore, we comment on the palaeobiological significance of this record.

Study area

The fossil material comes from Los Hornitos locality (30°41'28.2" N 109°38'57.4" W, 1,299 masl), about 6.5 km southwestern the town of Esqueda, Municipality of Fronteras, northeastern Sonora, northwestern Mexico (Figure 1). Neogene and Quaternary units crop out in this area. There is a polymictic conglomerate (TplCgp) and a sequence consisting of siltstone, claystone, and some calcareous strata (TplLm) of Pliocene age. A Quaternary polymictic conglomerate (QptCgp) and alluvial deposits (Qhoal) unconformably overlie the Pliocene units (Montaño-Jiménez and Fabián-Johnston 1998).

The fossil-bearing strata are equivalent (in part) to the TplLm unit, consisting of brown silt, fine-grained sandstone, and bioturbated incipient soils, set in an alluvial environment. The analysis of material belonging to the horses *Nannippus peninsulatus* and *Equus simplicidens* recovered from this sedimentary sequence is related to the Blancan North American Land Mammal Age (Palma-Ramírez et al. 2023).

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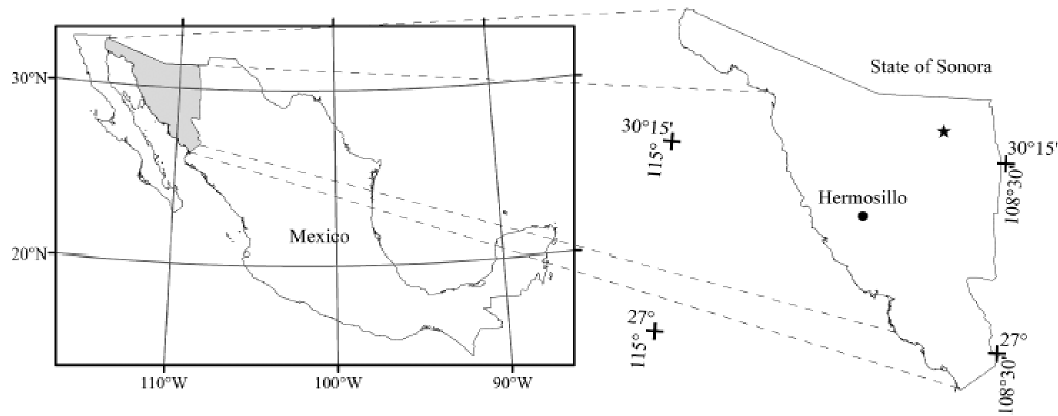

Figure 1. Index map of the study area in northeastern Sonora, northwestern Mexico. The Los Hornitos fossil locality is depicted (star).

Material and methods

The studied material consists of 51 skeletal remains, including antlers, teeth, a mandible fragment, and several postcranial elements. The sample is in the Colección Paleontológica de la Estación Regional del Noroeste (ERNO), Instituto de Geología, UNAM. The fossils are identified with the acronym HO- (Los Hornitos locality), followed by the catalogue number of the specimen.

The terminology of the antlers and dental elements are from Gustafson (2015), while that of postcranial remains is from von den Driesch (1976) and Sisson and Grossman (1982). In the dental elements, the crown height (CH), anteroposterior length (APL), and transverse width (TW) were measured at the occlusal surface. We measured, in some instances, the total length and proximal/distal widths of the postcranial elements. All measurements are in mm and taken using a digital caliper with a measuring range of 0–150 mm and a minimum indication of 0.01 mm.

We assessed the taxonomic identity of the fossil specimens by comparing them with selected antler, dental, and postcranial material of *Odocoileus* reported and figured in previous studies (Oelrich 1953; Strain 1966; Lundelius 1972; Fry and Gustafson 1974; Robertson 1976; Webb and Stehli 1995; Jacobson 2003, 2004; Wheatley and Ruez 2006; Morgan and Rinehart 2007; Morgan et al. 2008a, Morgan et al. 2008b, 2011; Díaz-Sibaja 2013; Jiménez-Hidalgo and Bravo-Cuevas 2015; Gustafson 2015; Plata-Ramírez 2017; Emery-Wetherell and Schilter 2020).

Bivariate plots of anteroposterior length and transverse width of M3, m1, and m3 were conducted to observe variation in the dental size of the studied material with dental samples of selected species of *Odocoileus, Rangifer tarandus*, and *Navahoceros fricki*. This analysis was performed in PAST 4.10 (Hammer et al. 2001).

The astragali and phalanges were analysed using a Canonical Discriminant Analysis (CDA). A set of morphometric characters was used as discriminating variables and the grouping variable were selected samples of *Odocoileus*. The measures considered to perform this analysis were taken following the proposal of von den Driesch (1976), including the greatest length of the lateral half (**GLl**), greatest length of the medial half (**GLm**), depth of the lateral half (**Dl**), depth of the medial half (**Dm**), breadth of the distal end (**Bd**), anteroposterior length (**APL**), transverse width (**TW**), total length (**TL**), proximal width (**Pw**), distal width (**Dw**), smallest breadth of the diaphysis (**Sd**). Wilks' lambda (λ) value was used to measure the similarities or differences between the groups (species), where 1 means total similarity and 0 total difference. This analysis was performed using the software STATISTICA v.7.0 by StatSoft Inc. (2004)and PAST 4.10 (Hammer et al. 2001).

The following abbreviations are used in the text, tables, and figures. *General*: **AGS**, Aguascalientes; **CA**, California; **CHIS**, Chiapas; **CO**, Colorado; **DGO**, Durango; **FL**, Florida; **GRO**, Guerrero; **HGO**, Hidalgo; **ID**, Idaho; **MICH**, Michoacán; **MX**, Mexico; **NAY**, Nayarit; **NL**, Nuevo Leon; **NM**, New Mexico; **OR**, Oregon; **SON**, Sonora; **WA**, Washington; **WI**, Wisconsin; **WY**, Wyoming. *Institutional*: **CPOEI**, Colección Paleontológica, Organización Especial de Investigación de la Piedad de Cabadas, Michoacán; **HAFO**, Hagerman Fossil Beds National Monument, Idaho; **INAH**, Colección Osteológica del Laboratorio de Arqueozoología, Instituto Nacional de Antropología e Historia, México; **NMMNH**, New Mexico Museum of Natural History; **OCMP**, Osteoteca de Comparación, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo; **TMM**, Texas Memorial Museum, The University of Texas at Austin; **UM**, Colección Paleontológica, Laboratorio Paleobiología, Facultad de Biología, Universidad Michoacana de San Nicólas de Hidalgo. *Measurements*: **APL**, anteroposterior length of upper/lower tooth; **CH**, crown height; **DmaxR**, maximum diameter at rosette height; **DmaxP**, maximum diameter at pedicel height; **TW**, transverse width of upper/lower tooth. *Statistical*: $\bar{x}$, average; **SD**, standard deviation; **OR**, observed range.

Systematic palaeontology

Class **Mammalia** Linnaeus 1758
Order **Artiodactyla** Owen 1848

Family **Cervidae** (Rafinesque 1832)
Genus ***Odocoileus*** (Rafinesque 1832)
Odocoileus virginianus (Zimmerman 1780)
(Tables 1–6, Figures 2–9)

Referred material

Antler fragments: HO-0009C, HO-0015, HO-0016C, HO-0018C, HO-0022C, HO-0068 G.2, HO-0070J.2, HO-0077, HO-0091, HO-0104, HO-0111, HO-0119, HO-267, HO-277, HO-512, HO-513, HO-518, HO-519, HO-0024D1, HO-0276, HO-0443, HO-470, HO-520, HO-521; right mandible fragment: HO-537; isolated teeth: HO-

Table 1. Antler measurements (in mm) of *Odocoileus virginianus* from Los Hornitos, Sonora, and selected samples of *Odocoileus* from the United States and Mexico.

Specimen	Species	Locality	State	Country	DmaxP	DmaxR
NMMNH 42,298	*Navahoceros fricki*	Arroyo La Parida	New Mexico	USA	40.3	36.8
UM-O001	*Odocoileus hemionus*	La Cinta-Portalitos	Michoacán	Mexico	55.81	25.2
UM-600	*Odocoileus hemionus*	La Cinta-Portalitos	Michoacán	Mexico	47.55	21.32
UM-604	*Odocoileus hemionus*	La Cinta-Portalitos	Michoacán	Mexico	47.16	42.67
UM-605	*Odocoileus hemionus*	La Cinta-Portalitos	Michoacán	Mexico	46.38	41.3
UM-O002	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	38.87	32.78
UM-O003	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	41.52	38.41
UM-O004	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	41.09	34.73
UM-O005	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	34.9	30.71
UM-O006	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	38.45	31.93
UM-O007	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	39.09	33.94
UM 139	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	31.81	28.41
UM 592	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	36.3	30.95
UM 593	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	38.58	32.52
UM 594	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	40.96	33.97
UM 595	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	32.95	30
UM 596	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	37.22	31.53
UM 597	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	43.88	39.11
UM 598	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	24.15	26.73
UM 599	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	32.6	28.38
UM 601	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	38.47	32.2
UM 602	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	37.74	31.56
UM 603	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	33.99	30.21
UM 606	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	37.14	31.4
UM 607	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	33.59	30.2
UM 608	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	37.12	31.11
UM 609	*Odocoileus virginianus*	La Cinta-Portalitos	Michoacán	Mexico	31.22	28.28
CPOEI-O001	*Odocoileus virginianus*	Piedad-Santa Ana	Michoacán	Mexico	38.73	32.52
HO-0009 C	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	30.48	18.92
HO-0015 C	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	47.45	28.11
HO-0016 C	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	44.7	32.2
HO-0018 C	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	41.3	30.67
HO-0077	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	32.2	24.61
HO-0091	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	48.94	32.74
HO-0111	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	38.41	24.33
HO-0267	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	46.54	30.12
HO-0277	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	31.41	26.44
HO-0512	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	33.04	23.73
HO-0518	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	23.05	19.02
HO-0519	*Odocoileus virginianus*	Los Hornitos	Sonora	Mexico	29.28	21.25
USGSD 40,206	*Odocoileus* sp.	Truth or Consequences	New Mexico	USA	33	24

0144, HO-0148, HO-217, HO-219; cubonavicular: HO-0263; astragali: HO-0053 D3, HO-0122, HO-198, HO-251, HO-350, HO-434, HO-438, HO-439, HO-440, HO-471; proximal phalanges : HO-0112, HO-441, HO-442, HO-473, HO-474; medial phalanges, HO-0162, HO-352, HO-475; distal phalanges: HO-0153, HO-0187, HO-353.

Distribution and age

Blancan to Rancholabrean of Alabama, Arkansas, California, Indiana, New Mexico, Texas, Florida, United States (Kurtén and Anderson 1980). In Mexico, there are records from the Irvingtonian of Sonora and the Rancholabrean of San Luis Potosí, Jalisco, Hidalgo, Chiapas, and Yucatán (Kurtén and Anderson 1980; Montellano-Ballesteros and Carbot-Chanona 2010). Nowadays, this species is widespread from Canada to South America (Montellano-Ballesteros and Carbot-Chanona 2010).

Description

Antlers

None of the antler fragments retain the main branch. The specimens correspond to the burr and isolated antler tines. In cross-section, the beam is nearly circular across its length. Some burrs have an accessory basal tine (brow tine) located close to the base, and their surface is rough and irregular with grooves and ridges, tending to rugosity with small bumps (Figures 2–4).

Upper cheek teeth

The LM3 HO-144 is at a late early wear stage, selenodont, brachydont (CH = 14.50 mm), and four-cusped teeth. The parastyle, mesostyle, and metastyle are prominent, and the paracone rib is more prominent than the metacone rib. The entostyle is evident, and the mesial lobe has a buccally convex V-shaped protocone (Figure 5A).

Lower cheek teeth

The lower cheek teeth HO-148 and HO-217 are brachydont (CH ~ 15 mm), four-cusped, stylids well-developed, with selenodont cusps, particularly the labial one. The mesial lobe has a buccally convex protoconid, V-shaped in HO-148 and somewhat U-shaped in HO-217. Both teeth have a V-shaped hypoconid, with an evident ectostylid in HO-148. The Rm1/m2 HO-219 is at a late wear stage (CH ~ 9 mm), and the protoconid and hypoconid are somewhat rounded and U-shaped, while the ectostylid is obliterated. The specimen HO-217 (Lm3) is trilobate, and the lobes decrease in size from mesial to distal, being the distal lobe the smallest (= hypoconulid) (Figure 5B – 5D).

Mandible fragment

The body of the specimen HO-537 is narrowed from cranial to caudal, in dorsal view is transversely thin, and both labial and

Figure 2. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Antlers of adults: (A) HO-0009C; (B) HO-0015C; (C) HO-0016C; (D) HO-0018C; (E) HO-0022C; (F) HO-0068 G.2; (G) HO-0070J.2; (H) HO-0077; (I) HO-0091; (J) HO-0104; (K) HO-0111; (L) HO-0119; (M) HO-267; (N) HO-277; (O) HO-512; (P) HO-513; (Q) HO-518; (R) HO-519. All scales are 1 cm.

lingual sides are smooth. The preserved portion of the horizontal ramus is slightly curved with a convex ventral border. This specimen contains the p4, m1, and the first lophid of the m2. The p4 is anteroposteriorly elongated, and the anterior lophid is larger than the posterior. The molars are typically selenodont teeth, with styles rounded and well-developed, and a prominent ectostylid is observed (Figure 5E).

Astragali

All the specimens (HO-0053 D3, HO-0122, HO-198, HO-251, HO-350, HO-434, HO-438, HO-439, HO-440, HO-471) have a somewhat rectangular shape with distinctive rounded edges, giving an S-shaped appearance in lateral view. These specimens have a double-trochlear ('double pulley') shape typical of cervids. The trochlea comprises most of the dorsal surface and is distinguishable from the anterior, posterior, and medial views. The head is distinguished from the trochlea by its greater robusticity and shallow midline depression; it comprises the entire ventral surface. The first of two calcaneal articular facets occupies around ¾ of the posterior surface and has a convex shape. The second is semicircular and located along the inferior border of the lateral surface. The lateral malleolar articular facet is along the superior portion of the lateral surface, with an elongated curved shape (Figure 6).

Figure 3. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Antlers of juvenile: (A) HO-0024D1; (B) HO-0276; (C) HO-0443; (D) HO-470; (E) HO-520; (F) HO-521. All scales are 1 cm.

Cubonavicular

The bone is fused, having a thick square shape in ventral and dorsal view. The front rim of the astragalar facet shows two peaks, one central in line with the astragalar trochlea and a second at the lateral corner. The articular surface for the astragalus occupies a great part of the dorsal surface, and the calcaneal articular surface is an elongated slightly convex facet located on the lateral side of the element adjacent to the articular surface for the astragalus (Figure 7).

Proximal phalanges

These phalanges are elongated with few muscular scars. The proximal end is arc-shaped, having a lateral surface higher than the medial. A deep groove with straight lateral and medial borders separates the articular surfaces of the proximal end. The body becomes thinner to the distal end. The trochlea is somewhat expanded and has a straight medial condyle and inclined lateral condyle (Figure 8).

Medial phalanges

The body of these phalanges is smooth, with some muscle scars on the ventral surface; it is laterally compressed, with an expanded base at its proximal end and less expanded at its distal end. The proximal articular surface is concave with a mid-sagittal ridge, while the distal articular surface presents a noticeable oblique groove. The body is reduced gradually to the distal end and is triangular in cross section, with the apex projecting dorsally (Figure 9 A1–A3).

Distal phalanges

These phalanges are laterally compressed, with smooth surfaces, and triangular or pyramidal in shape. Two nutrient foramina are at the base. The dorsal surface is convex, while the ventral surface is flat and concave at the posterior end. The proximal articular surface has a sagittal ridge (Figure 9, B1–B3).

Morphometric comparison

Antlers

Burr antlers are cervid because of their overall shape, surface ornamentation, and thick layer of cortical bone with a small core of spongy bone (Morgan et al. 2022). Despite the absence of complete antlers, we noted that the specimens from Los Hornitos differ from *Bretzia* in lacking highly flattened, broadened, and palmate antlers (Gustafson 1985, 2015). *Navahoceros* antlers have comparable ornamentation of the burr consisting of ridges and knobs but differ in being simple (three-tined) and having a large size (Kurtén and Anderson 1980). The bivariate plot of antlers (DmaxP and DmaxR) shows that the specimens from Los Hornitos have a somewhat smaller antler size than that of *Odocoileus hemionus* from La Cinta-Portalitos, and is in the observed range of *O. virginianus* from La Cinta-Portalitos and La Piedad-Santa Ana, Rancholabrean of Michoacán (Díaz-Sibaja 2013). Some Sonoran specimens have a comparable antler size to *Odocoileus* sp. from the Truth or Consequences locality, Blancan of New Mexico (Morgan et al. 2011) (Table 1, Figure 10).

In the *Odocoileus* antlers, the main beam above the burr is rounded in cross-section, showing a somewhat posterodorsal curvature, ornamentation with ridges and knobs (pearling), and the first tine commonly branches at less than 70 mm from the burr (Morgan et al. 2008a, 2008b). These features are observed in several specimens from Los Hornitos, including HO-0015C, HO-0018C, HO-0077, HO-267, and HO-519. Particularly, *Odocoileus virginianus* has a prominent brow tine and single main beam (Genoways et al. 2008; Murray 2008), as in some specimens from Los Hornitos, which have a conspicuous brown tine base and single beam above the burr (HO-0018C, HO-0077, and HO-519). The species *O. hemionus* differs in having a less prominent brow tine and symmetrically dichotomous branches from the main beam (Murray 2008).

Teeth

The M3 HO-144 has the typical configuration of *Odocoileus* third upper molars, including a posterior loph that is smaller than the anterior loph, buccal and lingual sides of the tooth with two

Figure 4. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Antler tines: (A) HO-0012C, (B) HO-0025D1, (C) HO-0072, (D) HO-0098, (E) HO-0099, (F) HO-0195, (G) HO-0266, (H) HO-0269, (I) HO-0270, (J) HO-0271, (K) HO-0273, (L) HO-0274, (M) HO-0275, (N) HO-0280, (O) HO-425, (P) HO-480, (Q) HO-0481, (R) HO-515, (S) HO-516, (T) HO-517, (U) HO-524. All scales are 1 cm.

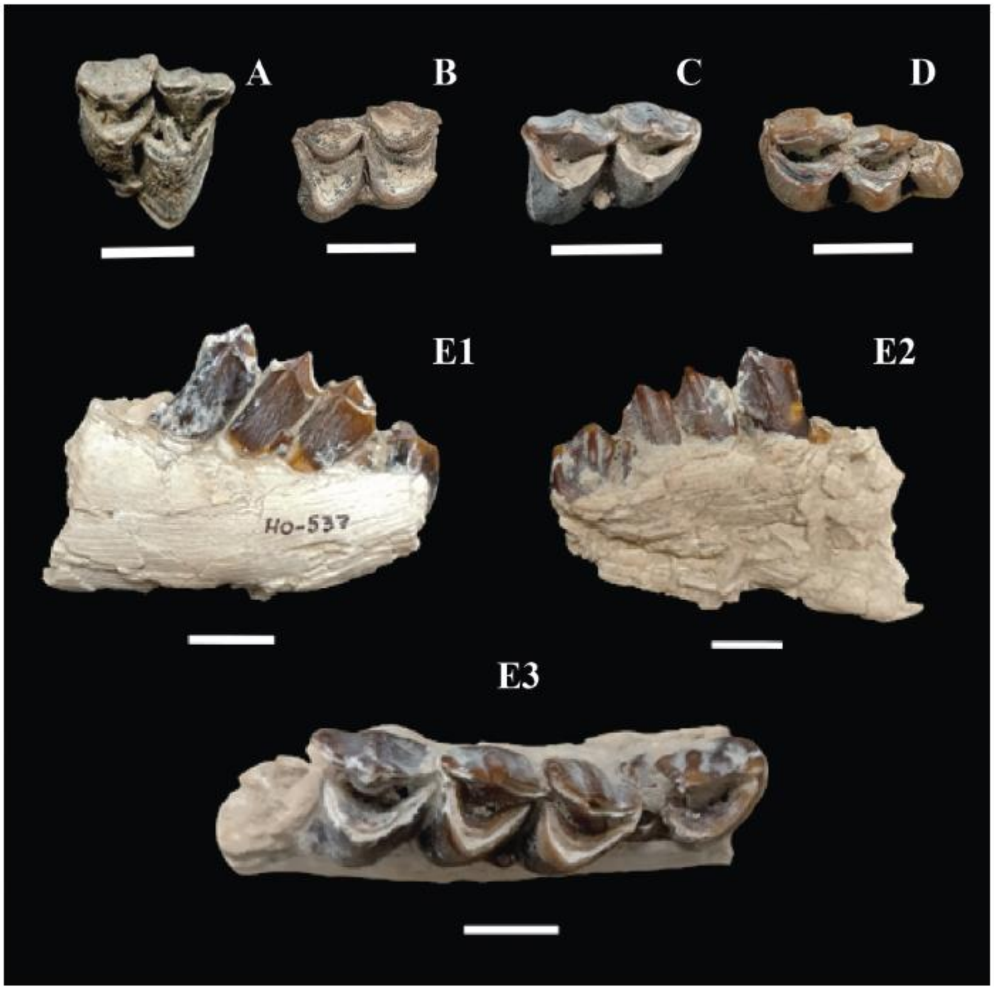

Figure 5. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Isolated teeth (A–D) and mandibular fragment (E1–E3). Occlusal views of (A) HO-144, LM3; (B) HO-219, Rm1/m2; (C) HO-148, Rm1; (D) HO-217, Lm3. Lateral (E1), medial (E2), and occlusal (E3) views of HO-537, right mandible fragment with p4, m1, and anterior lophid of m2. All scales are 1 cm.

crescents, and a pair of buccal and lingual crescents on each loph (Gustafson 2015). The APL and TW of the Sonoran specimen are larger than *O. virginianus* from the Holocene of northern and central-western Mexico and Ingleside from the late Pleistocene of Texas (Table 2). The measurements of HO-144 are comparable to specimens referable to *O. brachydontus* from the Blancan of Texas, *O. hemionus* from the Rancholabrean of New Mexico, and in the observed range of *Odocoileus* sp. from the Rancholabrean of Michoacán (Table 2). In the bivariate plot of M3s, we observed that the dental size of HO-144 is within the observed range of *O. hemionus* from White Mesa, New Mexico; however, the Sonoran specimen is wide (TW ~ 18 mm) as in *Odocoileus* sp. from La Cinta-Portalitos, Michoacán (Figure 11A).

The lower first molars from Los Hornitos share with *Odocoileus* the short-crowned height condition (less than 20 mm) and with *O. virginianus* by having a distinguishable ectostylid (Churcher 1984; Gustafson 2015). The average measurements of the studied lower molars (APL = 16.89, TW = 9.67) are close to *O. virginianus* from the Leisey Pit, Irvingtonian of Florida. The TW of HO-148 and HO-537 is in the observed range of samples belonging to *O. virginianus* from the Rancholabrean of Texas and the Holocene of Wisconsin and Mexico (Table 3). In the bivariate plot of the m1's, the Sonoran specimens are scattered among the selected samples of *Odocoileus virginianus* and have a dental size comparable to individuals from the Holocene of Mexico and smaller than that of *O. hemionus* from the Rancholabrean of New Mexico and *Navahoceros fricki* housed at the INAH collection (Figure 11B).

The specimen HO-217 has the typical configuration of the third lower molars of deer, consisting of three lophids (protoconid, hypoconid, and hypoconulid) with an entoconulid and back fossettid well differentiated (Gustafson 2015). The measurements of the Sonoran specimen are in the observed range of *Odocoileus*

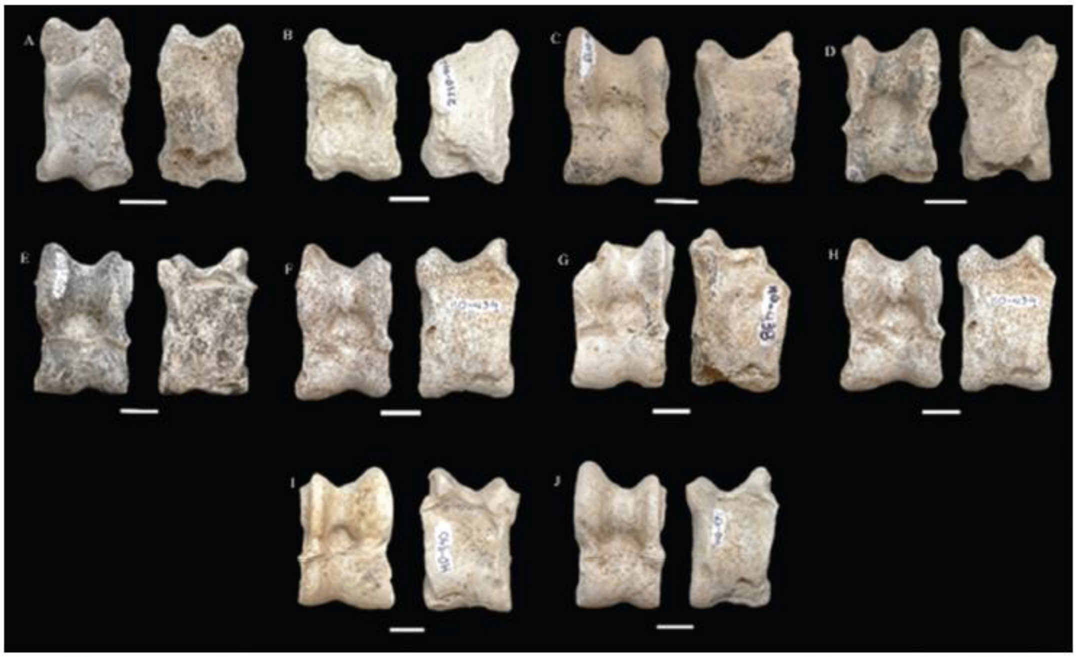

Figure 6. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Astragali anterior and posterior views: (A) HO-0053 D3, (B) HO-0122, (C) HO-198, (D) HO-251, (E) HO-350, (F) HO-434, (G) HO-438, (H) HO-439; (I) HO-440, (J) HO-471. All scales are 1 cm.

Figure 7. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Cubonavicular (HO-0263): (A) proximal, (B) lateral, (C) distal, and (D) medial, views. Scale is 1 cm.

Figure 8. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Proximal phalanges dorsal and ventral views: (A) HO-0112, (B) HO-441, (C) HO-442, (D) HO-473, (E) HO-474. All scales are 1 cm.

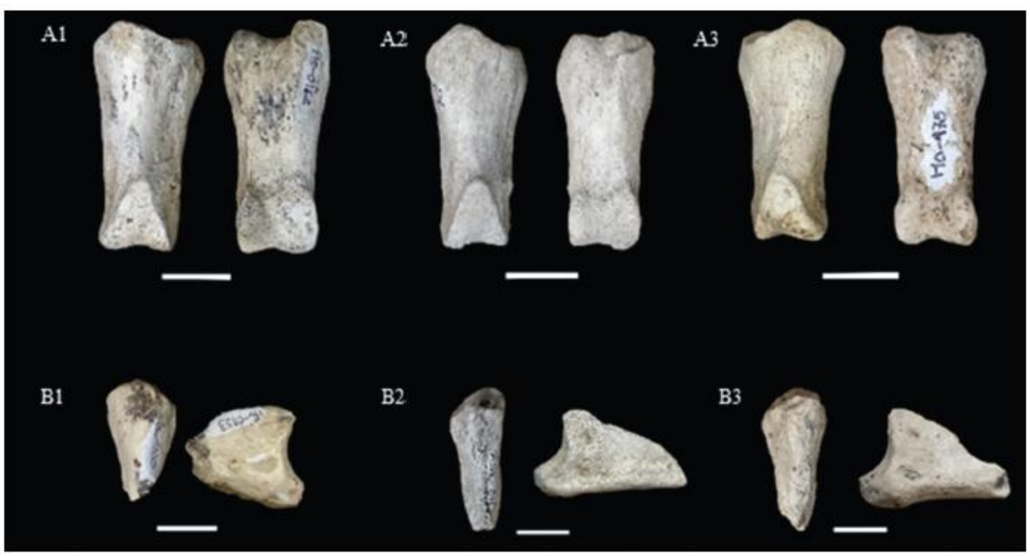

Figure 9. *Odocoileus virginianus*, Los Hornitos, northeastern Sonora. Medial (A1-A3) and distal (B1-B3) phalanges dorsal and ventral views: (A1) HO-0162, (A2) HO-352, (A3) HO-475, (B1) HO-0153, (B2) HO-0187, (B3) HO-353. All scales are 1 cm.

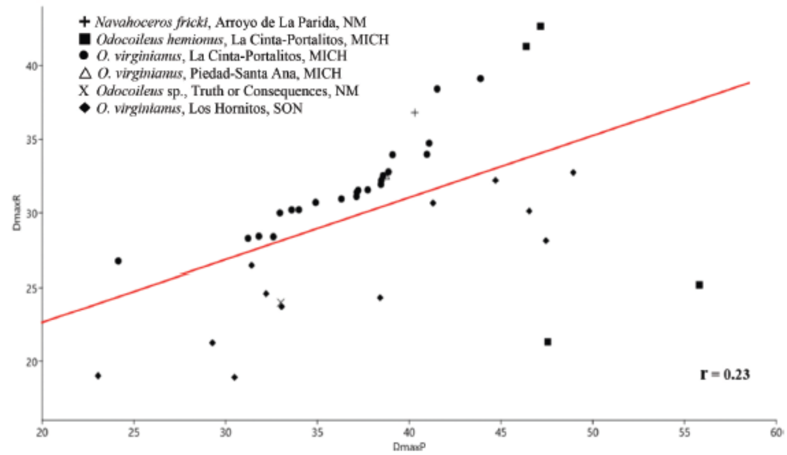

Figure 10. Bivariate plot of DmaxP and DmaxR of antlers (adult individuals) from Los Hornitos and selected samples of cervids from the United States and Mexico.

Table 2. Measurements (in mm) of the M3 HO-144 from Los Hornitos, Blancan of Sonora, and selected samples of *Odocoileus* from the United States and Mexico. The average and observed range (in parenthesis) are indicated when at least two data of the compared samples were available.

Specimen/Sample	Age	APL	TW	Source
HO-144	Blancan	18.67	17.80	This study
Odocoileus virginianus				
Michoacán, MX	Holocene	12.70 (12.47–12.84)	12.91 (12.1–13.8)	Díaz-Sibaja (2013)
Nayarit, MX	Holocene	13.53 (13.03–13.82)	13.11 (12.1–14.11)	Díaz-Sibaja (2013)
Guerrero, MX	Holocene	12.85 (12.25–13.24)	13.03 (12.08–14.07)	Díaz-Sibaja (2013)
Sonora, MX	Holocene	13.43 (13.01–13.66)	12.86 (12.42–13.16)	Díaz-Sibaja (2013)
Ingleside, TX	Rancholabrean	14.25 (13.6–14.9)	14.3 (14.2–14.4)	Lundelius (1972)
Odocoileus brachyodontus				
Rexroad, TX	Blancan			Oelrich (1953)
TMM 30,967–1822		17.1	19	
Odocoileus hemionus				
White Mesa, NM NMMNH-54153	Rancholabrean	19.1	16.2	Morgan and Rinehart (2007)
Hagerman, ID	Blancan			Wheatley and Ruez (2006)
HAFO 5151		15.3	14.8	
Odocoileus sp.				
La Cinta-Portalitos, MICH	Rancholabrean	17.23 (17.19–17.27)	18.07 (17.99–18.15)	Díaz-Sibaja (2013)

virginianus from the Holocene of Mexico and are somewhat smaller compared to the sample of this species from Ingleside, Rancholabrean of Texas (Table 4). The bivariate plot of m3s shows that *O. lucasi* from the Rancholabrean of New Mexico and the Holocene of Idaho and Oregon have large dental size, and that from the Pleistocene of central Mexico is even larger (Table 4, Figure 11C).

Postcranial remains

The morphology of the astragali from Los Hornitos is comparable to that of *Odocoileus* in having a broad trochlear groove, large and deep interarticular fossa, prominent lateral process, a faint posterior extension of the medial tibial articulation, and distal keel on the lateral condyle for the cubonavicular near to the distal trochlea (Gustafson 2015). The astragalus of *Bretzia* is narrow and has a noticeable posterior extension of the medial tibial articulation. The latter condition is also observed in *Mazama*, whereas *Cervus canadensis* lacks this feature (Gustafson 2015). According to Jacobson (2003,2004) is possible to differentiate between the astragalus of *O. hemionus and O. virginianus*, considering that in dorsal view, the latter species possess a defined mid-crest medially to laterally directed, and the medial tibial articulation sloped at a smooth angle; these conditions are observed in the Sonoran specimens. The discriminant analysis for the astragalus shows four groups, including *Cervus elaphus*, *Odocoileus lucasi*, *O. hemionus*, and *Odocoileus* sp. from the Rancholabrean of Michoacán. Some specimens from Los Hornitos fall in the size range of *Odocoileus* sp., and there is a separation among the studied sample with *O.hemionus*, *O. lucasi*, and *C. elaphus* (Wilks' Lambda: 0.016; approx. $F_{25.198} = 15.92$; $p < 0.00$) (Figure 12A).

Table 3. Measurements of first lower molars (in mm) from Los Hornitos, Blancan of Sonora, and selected samples of *Navahoceros* and *Odocoileus* from the United States and Mexico. The average and observed range (in parenthesis) are indicated when at least two data of the compared samples were available.

Specimen/Sample	Age	APL	TW	Source
HO-0219	Blancan	17.36	12.26	This study
HO-148		16.3	7.8	
HO-537		17.01	8.95	
Navahoceros fricki INAH-1082	—	20.3	13.8	Jiménez-Hidalgo and Bravo-Cuevas (2015)
Bretzia pseudalces **White Bluffs, WA** UWBM-92895	Blancan	14.6	11.5	Gustafson (2015)
Odocoileus virginianus **Vilas County, WI**	Holocene	13.95 (13.5–14.4)	8.50 (8.2–8.8)	ArctosDatabase
INAH, MX	Holocene	15.35 (14.3–16.4)	9.10 (8.5–9.7)	Jiménez-Hidalgo and Bravo-Cuevas (2015)
Ingleside, TX	Rancholabrean	12.25 (11.4–13.7)	9.95 (9.9–10)	Lundelius (1972)
Leisey Shell Pit, FL	Irvingtonian	16.7 (14.1–19.3)	9.55 (9.0–10.1)	Webb and Stehli (1995)
Odocoileus hemionus **White Mesa, NM** NMMNH 54,153	Rancholabrean	19.5	11.3	Morgan and Rinehart (2007)
Odocoileus sp. **Uruétaro, MICH** UM-571	Blancan	14.4	6.74	Plata-Ramírez (2017)

Table 4. Measurements (in mm) of the m3 HO-0217 from Los Hornitos, Blancan of Sonora, and selected samples of *Odocoileus* from the United States and Mexico. The average and observed range (in parenthesis) are indicated when at least two data of the compared samples were available.

Specimen/Sample	Age	APL	TW	Source
HO-0217	Blancan	18.1	8.2	This study
Odocoileus virginianus **Aguascalientes, MX**	Holocene	17.75 (17.24–18.06)	10.05 (9.75–10.63)	Díaz-Sibaja (2013)
Chiapas, MX	Holocene	16.83 (16.49–17.33)	8.89 (8.19–9.86)	Díaz-Sibaja (2013)
Durango, MX	Holocene	16.49 (16.21–16.78)	9.58 (9.57–9.59)	Díaz-Sibaja (2013)
Guerrero, MX	Holocene	16.4 (14.58–17.34)	8.67 (7.75–9.36)	Díaz-Sibaja (2013)
Michoacán, MX	Holocene	15.67 (15.5–15.85)	8.95 (8.79–9.11)	Díaz-Sibaja (2013)
Ingleside, TX	Rancholabrean	19.53 (18.8–19.9)	10.2 (9.5–10.9)	Lundelius (1972)
Odocoileus hemionus **White Mesa, NM** NMMNH-54153	Rancholabrean	25.6	10.2	Morgan and Rinehart (2007)
Pocatello, ID IMNH *R*-146	Holocene	21.1	8.7	Idaho Virtual Museum
Oregon, USA	Holocene	21.51 (20.46–22.95)	9.99 (9.86–10.15)	Emery-Wetherell and Schilter (2020)
Odocoileus lucasi **El Cedazo, AGS** FC-663	?Irvingtonian	28.4	12.9	Mooser and Dalquest (1975)
Odocoileus sp. **La Cinta-Portalitos, MICH** UM-172	Rancholabrean	24.9	13.69	Díaz-Sibaja (2013)

The cubonavicular HO-263 shares with *Odocoileus* the presence of a convex calcanear facet that occupies most of the lateral side and a deep peroneal groove that cuts across the lower end of the calcanear facet (Morejohn and Dailey 2004; Gustafson 2015). *Bretzia* differs in having a small calcanear facet and shallow peroneal groove; this latter condition is also observed in *Cervus* (Gustafson 2015).

The proximal phalanges HO-0112, HO-441, HO-442, HO-473, and HO-474 share with *Odocoileus virginianus* a concave proximal articular surface with a deep midsagittal groove, the lateral glenoid cavity shallower than the medial one, and small articular facets at the proximal palmar surface (Rumph, 1975). The proximal phalanges of *O. lucasi* differ in having a posteriorly broad lateral glenoid cavity, a posterolateral bulge, and a pair of perpendicular tubercles at the posterodistal portion (Morejohn and Dailey 2004). The average length and widths of the proximal phalanges from Los Hornitos are close to those of *O. virginianus* from the Blancan and Irvingtonian of Florida and the Rancholabrean of Michoacán. By contrast, the samples of *O. hemionus* from the Rancholabrean of Michoacán and *O. lucasi* from the Plio-Pleistocene from Idaho and California have a larger size (Table 5). The discriminant analysis of the proximal phalanges indicate four groups, including *Odocoileus virginianus*, *O. hemionus*, *O. lucasi*, and the sample from Los Hornitos. The size range of the studied sample is close to *O. virginianus* and separated from

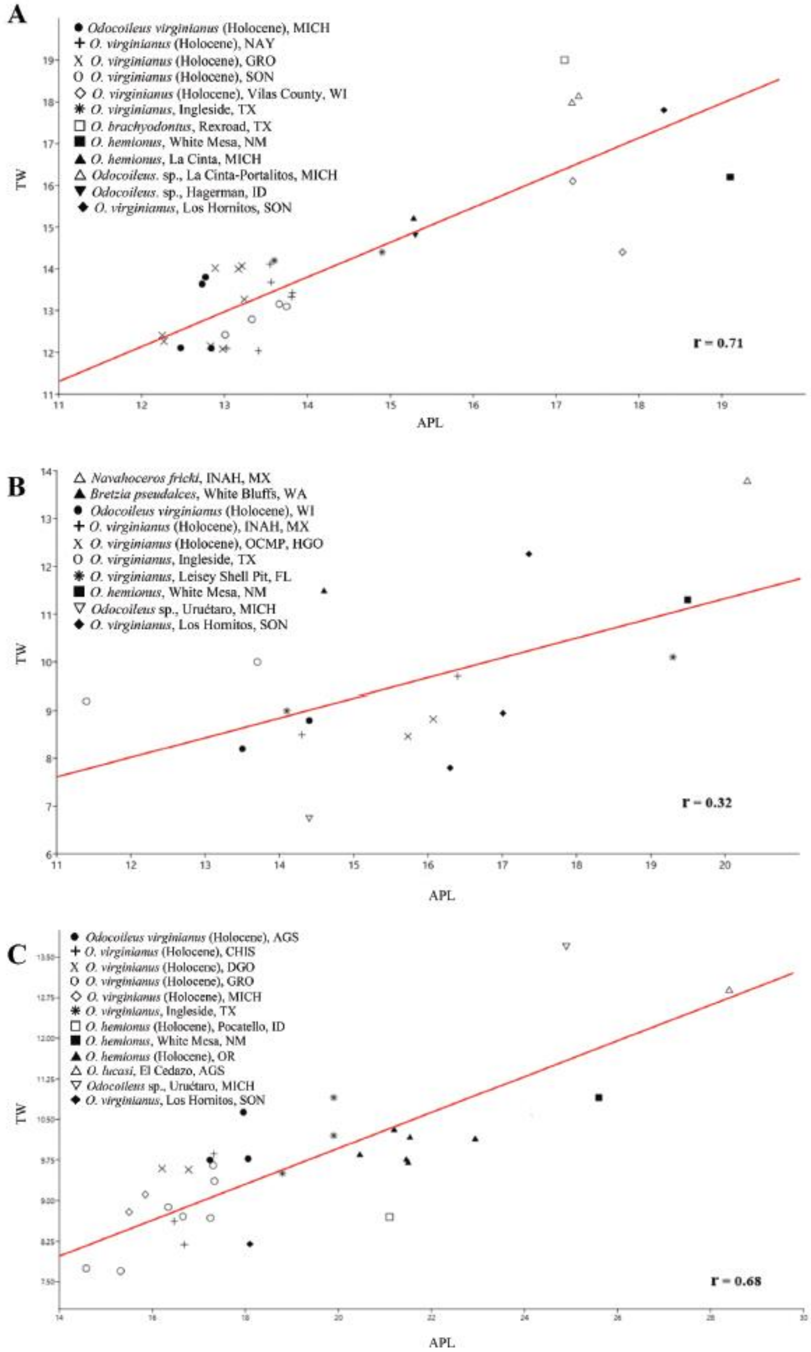

Figure 11. Bivariate plots of APL and TW of (A) M3, (B) m1, and (C) m3 from Los Hornitos and selected samples of extant and extinct cervids from the United States and Mexico.

O. hemionus and *O. lucasi* (Wilks' Lambda: 0.11; approx. $F_{20.143} = 20.06$; $p < 0.00$) (Figure 12B).

The body of medial phalanges HO-0162, HO-352, and HO-475 is similar to that of *Odocoileus virginianus* in the lateromedial compression, tapered distally, and triangular appearance in cross-section with the apex projected dorsally (Rumph, 1975). The medial phalanges of *O. hemionus* are broad and elongated with a rounded distal epiphysis forming a distinctive laterally compressed head in ventral view. In *O. lucasi*, this phalange is short and broad, with large anteroposteriorly compressed distal epiphysis, and incipient osseous hood on the medial side at the dorsoproximal portion (Morejohn and Dailey 2004). The average length and widths of the specimens from Los Hornitos are comparable to those of *O. hemionus* from the Rancholabrean of Michoacán and the Holocene of Mexico. The size of the medial phalanges of *O. virginianus* from the Holocene of Mexico is somewhat smaller, and that of *O. lucasi* from the Plio-Pleistocene of California is larger (Table 6). In the discriminant analysis of the medial phalanges, the size range of the sample from Los Hornitos is between *Odocoileus virginianus* and *O. hemionus*, while *O. lucasi* is separated from these groups (Wilks' Lambda: 0.009; approx. $F16.98 = 54.82$; $p < 0.00$) (Figure 12C).

The distal phalanges HO-0153, HO-0187, and HO-353 are comparable to *Odocoileus virginianus* in the pyramidal shape, concave palmar surface, flat and smooth ventral surface, and two large foramina at the posteromedial surface (Rumph, 1975). The distal phalanges of *O. lucasi* are proportionately shorter and broad (Morejohn and Dailey 2004).

Table 5. Measurements (in mm) and univariate statistics of proximal phalanges from Los Hornitos and selected samples of *Odocoileus* from the late Cenozoic of the United States and Mexico.

Locality	Age	TL	Pw	Dw	Sd	Source
Los Hornitos	Blancan	45.55	16.29	13.33	12.2	Present study
x̄		3.53	1.17	0.76	0.79	
SD		41.56–49.38	15.34–17.94	11.99–13.82	10.98–13.21	
OR		5	5	5	5	
Sample size						
Odocoileus virginianus						
Haile XV A, FL	Blancan	41.0	13.4	—	—	Robertson (1976)
x̄		—	—	—	—	
SD		37.7–43.2	12.2–13.9	—	—	
OR		7	7	—	—	
Sample size						
Santa Fe I, FL	Blancan	43.5	13.3	—	—	Robertson (1976)
x̄		—	—	—	—	
SD		39.4–48.9	11.6–15.2	—	—	
OR		10	10	—	—	
Sample size						
Inglis IA, FL	Irvingtonian	46.6	15.4	—	—	Robertson (1976)
x̄		—	—	—	—	
SD		46.6	15.4	—	—	
OR		1	1	—	—	
Sample size						
Coleman IIA, FL	Irvingtonian	43.4	13.0	—	—	Robertson (1976)
x̄		—	—	—	—	
SD		40.3–44.4	12.2–13.8	—	—	
OR		7	7	—	—	
Sample size						
La Cinta-Portalitos, MICH	Rancholabrean	39.00	14.33	13.07	12.17	Díaz-Sibaja (2013)
x̄		3.83	0.48	1.24	0.41	
SD		36.29–41.72	13.99–14.68	12.19–13.95	11.88–12.46	
OR		2	2	2	2	
Sample size						
Odocoileus hemionus						
La Cinta-Portalitos, MICH	Rancholabrean	57.2	21.54	15.79	13.96	Díaz-Sibaja (2013)
x̄		1.35	2.20	1.68	1.34	
SD		56.44–59.24	16.37–19.55	14.3–17.81	12.92–15.85	
OR		4	4	4	4	
Sample size						
Odocoileus lucasi						
Honey Lake, CA	Plio-Pleistocene	64.32	26.22	21.94	19.05	Morejohn and Dailey (2004)
x̄		1.19	0.55	1.31	0.38	
SD		63.1–65.2	25.0–26.3	20.1–23.2	18.21–19.31	
OR		7	7	7	7	
Sample size						
Hand Sollow, ID	Plio-Pleistocene	65	25	22	18.21	Morejohn and Dailey (2004)
x̄		—	—	—	—	
SD		—	—	—	—	
OR		1	1	1	1	
Sample size						
Odocoileus sp.						
Hudspeth, TX	Blancan	48	20	16.8	—	Strain (1966)
x̄		—	—	—	—	
SD		—	—	—	—	
OR		1	1	1	—	
Sample size						

Table 6. Measurements (in mm) and univariate statistics of medial phalanges from Los Hornitos and selected samples of *Odocoileus* from the late Cenozoic of the United States and Mexico.

Locality	Age	TL	Pw	Dw	Sd	Source
Los Hornitos, SON	Blancan	32.43	16.01	11.66	11.67	This study
$\bar{x}$		1.12	0.81	0.50	0.91	
SD		31.37–33.61	14.38–16.01	11.29–12.24	10.88–12.67	
OR		3	3	3	3	
Sample size						
Odocoileus virginianus						
INAH, MX	Holocene	28.19	11.83	9.71	9.61	Díaz-Sibaja (2013)
$\bar{x}$		1.60	0.69	0.39	0.47	
SD		26.02–20.93	10.66–12.93	8.96–10.2	8.9–10.12	
OR		16	16	16	16	
Sample size						
Odocoileus hemionus						
INAH, MX	Holocene	31.84	13.45	11.33	10.63	Díaz-Sibaja (2013)
$\bar{x}$		1.46	0.90	0.44	0.71	
SD		29.91–33.4	12.97–15.02	10.89–11.71	10–11.03	
OR		6	6	6	6	
Sample size						
La Cinta-Portalitos, MICH	Rancholabrean	44.01	16.09	11.46	12.21	Díaz-Sibaja (2013)
$\bar{x}$		0.17	0.78	0.30	0.37	
SD		43.89–44.14	15.54–16.65	11.25–11.68	11.95–12.48	
OR		2	2	2	2	
Sample size						
Odocoileus lucasi						
Honey Lake, CA	Plio-Pleistocene	45.93	25.36	20.98	18.04	Morejohn and Dailey (2004)
$\bar{x}$		1.39	0.70	0.42	0.33	
SD		44.2–48.3	24.7–25.2	20.3–21.3	17.53–18.29	
OR		12	12	12	12	
Sample size						

Discussion

The cervids *Bretzia*, *Navahoceros*, and *Odocoileus* are documented from several Pliocene and Pleistocene faunas of North America (Kurtén and Anderson 1980; Prothero 2002). *Bretzia* is characterised by having palmate and spread laterally antlers similar to moose antlers (Fry and Gustafson 1974; Gustafson 2015). This cervid is from the early Pliocene to the late Pleistocene of the western United States (Fry and Gustafson 1974; Gustafson 1985, 2015).

Navahoceros is a short-legged stocky deer found in the Rocky Mountains, occurring for the first time about 3 Ma and becoming extinct 11,550 years before the present (Heffelfinger 2011). This cervid has three-tined antlers and shares some cranial features with *Rangifer* (Kurtén and Anderson 1980; Webb 1992). This monotypic genus consists of *N. fricki*, although some authors have considered this species as *nomen nudum* and should be referred to as *Odocoileus lucasi* (see Flueck and Smith-Flueck 2013).

Odocoileus is the most abundant and well-known deer from the Pliocene and Pleistocene of North America, which includes the species *O. virginianus* (white-tailed deer) and *O. hemionus* (mule deer) (Webb 1998; Prothero 2002). Some cranial features, such as antlers and lachrymal fossae, are considered reliable to distinguish these species (Smith 1991; Heffelfinger 2011; Heffelfinger and Latch 2023), although some postcranial elements are also suitable in their identification (see Jacobson 2003, 2004). The identity of an *Odocoileus* species is restricted by using solely teeth because these elements are somewhat variable (Wheatley and Ruez 2006; Emery-Wetherell and Davis 2018).

The comparative study indicates that the general morphology of the material from Los Hornitos is that of *Odocoileus*. The bivariate plots and discriminant analyses show that the size of the Sonoran specimens is comparable to *O. virginianus*, although smaller than *O. hemionus*, *O. lucasi*, and *Navahoceros* (Figures 10–12). Furthermore, several morphological features of antlers and post-cranial remains are distinctive of the white-tailed deer, as is stated in the morphometric comparison section.

Paleobiological significance

The earliest occurrences of *Odocoileus* are from localities in Florida, Kansas, and Idaho, dated about four million years ago (middle Pliocene) (Hibbard 1941, Oelrich, 1953; Gustafson 1985, 2015; Webb et al. 2008; Heffelfinger 2011; Heffelfinger and Latch 2023); thus, first known appearances of this deer are indicative of the early Blancan (Morgan and Lucas 2003). There are mentions of *Odocoileus* from several late Blancan localities in the Southwestern United States, such as Cal Tech, California (Lindsay 1984); Curtis Ranch and San Simon, Arizona; and Pearson Mesa and Arroyo La Parida, New Mexico (Morgan and Lucas 2003; Morgan and White 2005). This genus extends throughout the Pliocene and the Pleistocene, with the two extant species *O. virginianus* and *O. hemionus*, which probably derived from the same *Odocoileus* stock during the Pliocene (Heffelfinger 2011; Gustafson 2015). In particular, *O. virginianus* appeared about three million years ago, and probably *O. brachyodontus* (*nomen dubium*) (according to Wheatley and Ruez 2006) from the early Blancan of Idaho is the ancestor species (Smith 1991).

Palma-Ramírez et al. (2023) reported the presence of the typical Blancan horses *Nannippus peninsulatus* and *Equus simplicidens* from Los Hornitos, suggesting that its probable age could be at ~ 3.9–2.6 Ma, related to the Blancan III or late early Blancan–early late Blancan. The analysis of *Odocoileus virginianus* recovered from the same locality adds evidence and is in agreement with this North American Land Mammal Age, indicating that *Odocoileus virginianus*, *Nannipus peninsulatus*, and *Equus simplicidens* were typical components of the Blancan faunas from the Southwestern United States (Lindsay et al. 1975; Goltz et al. 1977; Morgan et al. 2008a, 2008b, 2011), spreading their geographic distribution and coexistence to areas that now are part of northwestern Mexico during the Pliocene.

Previous to this study, the Sonoran record of late Cenozoic cervids are known from seven Pleistocene localities and consists of *Odocoileus virginianus*, *O. hemionus*, *Odocoileus* sp., and cf.

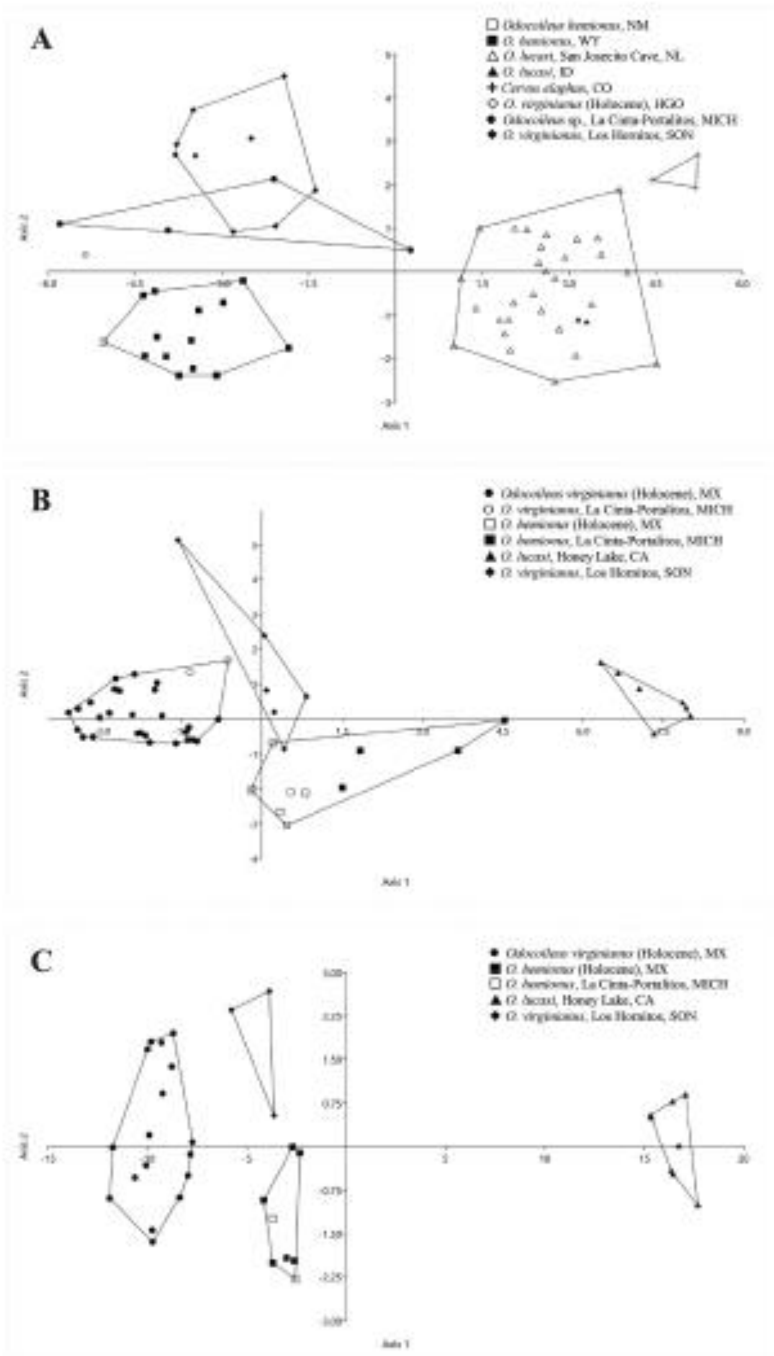

Figure 12. Scatter plots of discriminant analysis of (A) astragali, (B) proximal phalanges, and (C) medial phalanges from Los Hornitos and selected extant and extinct species of cervids from the United States and Mexico.

Table 7. Deer record from the Pliocene and Pleistocene of Sonora, northwestern Mexico.

Species	Locality	NALMA	Source
Odocoileus virginianus	Los Hornitos	Blancan	This study
	El Golfo Santa Clara	Irvingtonian	Croxen et al. (2007)
O. hemionus	Rancho La Brisca	Rancholabrean	White et al. (2010)
Odocoileus sp.	Terapa, Bajimari, La Playa, La Botana, Tesopaco	Rancholabrean	Nunez et al. (2010); White et al. (2010)
cf. *Navahoceros* sp.	El Golfo Santa Clara	Irvingtonian	Croxen et al. (2007)

Navahoceros (Croxen et al. 2007; Nunez et al. 2010; White et al. 2010) (Table 7). Therefore, *Odocoileus virginianus* from Los Hornitos represents (so far) the earliest and first reported occurrence of this species for the Pliocene (Blancan) of Sonora, which is added to that from El Golfo de Santa Clara locality, early Pleistocene (Irvingtonian), northwestern Sonora (Croxen et al. 2007). The white tailed-deer is widespread across the Mexican territory today, and *O. virginianus couesi* is the subspecies whose distribution includes the state of Sonora (Smith 1991; Galindo-Leal and Weber 2014). Given this, it seems that *O. virginianus* has inhabited areas of northwestern Mexico for at least three million years.

Conclusion

We formally described a set of cranial, dental, and postcranial cervid remains recovered from the Los Hornitos, northeastern Sonora. A comparative study and statistical analyses indicate that the studied sample should be referable to the medium-sized deer *Odocoileus virginianus*. This record represents the earliest and first reported occurrence of the white-tailed deer from the Pliocene of Sonora, indicating that has inhabited areas of northwestern Mexico during at least three million years.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Discusión general

Desde los inicios de la clasificación taxonómica, la mayoría de las especies conocidas se han propuesto con base en rasgos morfológicos distintivos (del Castillo-Batista *et al*., 2017). Para el caso de los équidos de Los Hornitos, los rasgos que pemiten asignar al de talla pequeña a la especie *Nannippus peninsulatus,* son los dientes hipsodontos (HI≈3.0), protocono ovalado, la configuración del plicaballín simple, bien desarrollado en las primeras etapas de desgaste y persistente en estado moderado; esmalte moderadamente plegado en el borde de las fosetas, metapodiales gráciles y un tamaño corporal pequeño (MacFadden, 1984).

Nannippus peninsulatus se considera típica del Blancano (MacFadden, 1984, 1985), cuyo último dato de aparición en América del Norte se sitúa alrededor de 2.5 a 2.2 Ma (Blancano V o Blancano tardío) (Lindsay, 1984; Morgan *et al*., 2011), sin llegar a sobrevivir hasta el Irvingtoniano (Pleistoceno temprano) (Rook *et al*., 2019). Hasta el momento, no hay datos de este taxón en faunas blancanas de Nuevo México y Arizona con datos geocronológicos más jóvenes a la inversión de Gauss – Matuyama (~2.58 Ma) (Kurtén y Anderson, 1980; Morgan y Harris, 2015) que establece el límite Plioceno-Pleistoceno (Suc *et al*., 1997).

Por su parte, el équido de talla grande corresponde a *Equus simplicidens* de acuerdo con las siguientes características: una gruesa capa de cemento (>1.5 mm), molares muy hipsodontos (HI > 2), dientes de corona alta (MSCH ≥60 mm), protocono redondeado (PrL/PrW ≈ 1.2), metacónido y metastílido de redondeado a ovalado, pliegues de esmalte simples en las fosetas, linguafléxido con forma de "V", un profundo ectofléxido en los molares, así como metapodiales robustos (Dalquest, 1975; MacFadden, 1988; Winans, 1989; Downs y Miller, 1994; Kelly, 1998; Scott, 2006; Morgan *et al*., 2011).

El dato de primera aparición de *Equus simplicidens* es de hace aproximadamente 3.5 Ma (Blancano III) y estuvo presente a lo largo de la mayor parte del Blancano, exceptuando las partes más temprana y más tardía (Morgan *et al*., 2008). Esta especie se documenta en localidades del Blancano temprano y de la parte más temprana del Blancano tardío, extinguiéndose hace unos 2.6 Ma (Morgan y Harris, 2015; Morgan *et al*., 2017).

Nannippus peninsulatus y *Equus simplicidens* han sido reportados en varias localidades del Blancano tanto en el norte como en el centro de México, incluyendo los estados de Chihuahua, Michoacán y Guanajuato (Lindsay, 1984; Carranza-Castañeda, 2006). La información cronológica de la mayoría de estos sitios es correlacionable con localidades sureñas de Estados Unidos (Lindsay, 1984; Carranza-Castañeda y Miller, 2004; Carranza-Castañeda *et al*., 2013). A su vez, existe información radiométrica para algunas localidades como San Miguel de Allende, Guanajuato (La Pantera: 3.9 ± 0.3 Ma) y Charo, Michoacán (La Goleta: 3.6 ± 0.3 Ma), cuyas edades se relacionan con el Blancano III (Carranza-Castañeda, 2006; Ferrusquía-Villafranca y Ruiz-González, 2015).

Por otro lado, las características distintivas de los elementos de cérvidos referidos a *Odocoileus virginianus* son: para el caso de las astas, el pedícelo y la cornamenta se elevan desde los frontales en un ángulo mucho más pronunciado y en una orientación más vertical que en otros cérvidos, que se eleva en un ángulo muy bajo y tiene una orientación ligeramente posteroventral en relación con el frontal (Morgan *et al*., 2008; Gustafson, 2015). A su vez, los molariformes exhiben un ectostílido bien desarrollado y, además, los molares inferiores presentan columnas accesorias (Tomiati y Abbazzi, 2002).

Adicionalmente en este caso, y dado que los límites entre especies de *Odocoileus* pueden resultar difíciles de establecer (Jacobson, 2004; Heffelfinger y Latch, 2023), el análisis multivariado representó una herramienta útil para delimitar entre ellas. Los valores estadísticos en los diferentes elementos esqueléticos permiten concluir que la muestra de Los Hornitos está más cercana a *O. virginianus*.

El género *Odocoileus* aparece por primera vez durante el Blancano temprano y sus fósiles más antiguos se conocen de Florida, Kansas e Idaho (Oelrich, 1953; Kelly, 1994; Gustafson, 2015; Heffelfinger y Latch, 2023). Es uno de los géneros cuya primera aparición ayuda a definir el comienzo del Blancano (Morgan y Lucas, 2003) y, al igual que *Nannippus peninsulatus* y *Equus simplicidens*, se ha documentado en muchas de las faunas del Blancano tardío del sur de América del Norte, como Cal Tech, Curtis Ranch, La Unión y San Simón Fauna (Lindsay, 1984; Morgan y Lucas, 2003). Además, este género está presente durante el resto del Plioceno y el Pleistoceno, con dos especies aún existentes en América del Norte (Morgan y Harris, 2015; Morgan *et al*., 2022). Tales especies son *O. hemionus* and *O.*

virginianus, las cuales se estima se separaron durante el Plioceno o el Pleistoceno temprano, probablemente durante el Blancano (Webb, 1998; Heffelfinger, 2011; Heffelfinger y Latch, 2023).

Con base en la información biocronológica de *Nannippus peninsulatus*, *Equus simplicidans* y *Odocoileus virginianus*, la edad de la localidad de Los Hornitos se estima que podría ser de ~3.9–2.6 Ma, correspondiente al Blancano III o Blancano temprano tardío – Blancano tardío temprano, lo cual representa el primer registro de esa edad para el área y el segundo en el estado de Sonora.

Con base en el modelo de Feranec y MacFadden (2006), el promedio de los valores de $\delta^{13}C$ (ca. – 4‰) de los équidos sonorenses sugieren que habitaron áreas abiertas. Por otro lado, la composición de carbono promedio observada está en el intervalo de los valores de $\delta^{13}C$ de pastizales y hábitats C3 y C4 en el Blancano (Kita, 2011). *Nannippus peninsulatus* y *Equus simplicidens* tienen valores promedio de $\delta^{18}O$ similares (superiores a – 5‰), sugiriendo que habitaban hábitats abiertos o cerrados, aunque *E. simplicidens* podría haber mostrado preferencia por las áreas abiertas dado su grado de hipsodoncia y la capa gruesa de cemento en los molares, rasgos relacionados con el consumo de recursos abrasivos (Janis y Fortelius, 1988; MacFadden, 1992), como las gramíneas C4. Ambas condiciones son observadas en los ejemplares de *E. simplicidens*. Por lo tanto, *N. peninsulatus* preferiría hábitats boscosos y *E. simplicidens* hábitats abiertos.

Conclusiones generales

El análisis morfológico comparado del material fósil de cérvidos y équidos de la localidad Los Hornitos, noreste de Sonora, permitió establecer la identidad taxonómica a nivel específico de los taxones descritos, siendo para el caso de los cérvidos la especie *Odocoileus virginianus*, mientras que para los équidos las especies *Nannippus peninsulatus* (Hipparionini) y *Equus simplicidens* (Equini).

Por otro lado, la dieta mixta C3-C4 observada en los équidos de la muestra de Sonora sugiere la presencia de una cubierta vegetal variable, la cual incluía bosques (plantas con metabolismo C3 como árboles, arbustos y matorrales) y áreas abiertas (plantas con metabolismo C4 como pastos), que probablemente estuvieron relacionados con condiciones áridas y frías.

Con base en los alcances biocronológicos conocidos de los équidos *Nannippus peninsulatus* y *Equus simplicidens*, así como del cérvido *Odocoileus virginianus*, muy posiblemente la edad de la localidad de Los Hornitos se ubique entre los ~3.9–2.6 Ma, lo que corresponde al Blancano III o al límite entre la parte tardía del Blancano temprano y la parte temprana del Blancano tardío.

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