

STEGOMASTODON PRIMITIVUS (PROBOSCIDEA: GOMPHOTHERIIDAE) RECORDS (LATEST HEMPHILLIAN-EARLY BLANCAN) FROM THE SAN MIGUEL ALLENDE BASIN, CENTRAL MEXICO

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Abstract—In the San Miguel de Allende basin, Guanajuato State, Mexico, two mandibles of gomphotheriids were collected, and by their diagnostic characters have been assigned to *Stegomastodon primitivus*. The jaws correspond to different ontogenetic and stratigraphic ages. In the Rancho El Ocote fauna, in the upper part of the Hemphillian stratigraphic sequence, the mandible of a young individual and isolated upper and lower molars were collected together with the mandible from the Blanco layer, which has been assigned a latest Hemphillian (Hh4) age. The molars have characters considered more primitive than those described for *Stegomastodon primitivus* (= *Stegomastodon rexroadensis*), characteristic of an early Blancan age in North American faunas. The jaw from the Blanco layer has a very short anterior symphysis, straight and ending in a narrow structure that forms the lingual canal. It has no evidence of tusks. The isolated molars present the most primitive characters referred to a *Stegomastodon* individual: The trefoil and entotrefoil cusps are simple without folds (ptychodonty) or accessory enamel tubercles (choerodont). The isolated M3/m3 has with four lophes/lophids and two large cusps posterior to the fourth lophes/lophids. The m2 has three lophids and two small conids behind the tritriolophid, that, in advanced states of wear, form a posterior half lophid more evident in molars with greater wear. There are no stratigraphic indexes of a late Hemphillian or early Blancan age in the Blanco Layer. Throughout the Blanco Layer only *Dinohippus mexicanus* is present. Zircons separated from ash in the same layer where the *Stegomastodon primitivus* mandible was collected yielded a 4.85 ± 0.17 Ma U-Pb age, which corresponds to the latest Hemphillian (Hh4). This Rancho El Ocote record is the oldest known among North American faunas. This result assumed that the possible diversification of gomphotheriids in faunas of central Mexico happened before that expected by Savage (1955) in his probable phyletic dispersal pattern of the North American gomphotheriids.

A mandible of an old adult gomphothere was collected in the Arroyo Earth Watch, in Los Galvanes area. The fossil was found in sediments assigned to the early Blancan. The jaw is complete without distortion, and it only retains the m3 in an advanced state of wear. This tooth only has five lophids that differentiate it from the m3s of Cuchillo Negro Creek and Elephant Butte Lake *Stegomastodon* of the early Blancan of New Mexico, that have 5+ to six lophids.

The zircons analyzed by the U / Pb method gave an age of 2.9 ± 0.07 Ma for the *Stegomastodon* jaw from Los Galvanes, consistent with the early Blancan. This record correlates with specimens from New Mexico's Cuchillo Negro Creek and Elephant Butte Lake faunas, that have a radiometric age of 3.1 ± 0.3 Ma, early Blancan. The similarity of these radiometric ages suggests that *Stegomastodon primitivus* had a wide geographic distribution in the early Blancan.

Resumen—En la cuenca de San Miguel de Allende, estado de Guanajuato se colectaron dos mandíbulas de gonfoteridos que se han determinado a *Stegomastodon primitivus* que corresponden a edades ontogenéticas y estratigráficas diferentes.

En la fauna de Rancho El Ocote, en la parte superior de la secuencia estratigráfica, se colectó la mandíbula de un individuo adulto-joven y molares superiores e inferiores aislados en el estrato Blanco (se nombra así por su contenido de arena fina de color blanco que confiere este aspecto al estrato), que corresponde a la edad de lo más tardío del Hemfiliano tardío Hh4. Los molares tienen caracteres considerados más primitivos que los descritos para *Stegomastodon primitivus* (= *Stegomastodon rexroadensis*), referido a la edad de Blancano temprano en faunas de Norte América. La mandíbula tiene la sínfisis muy recortada anteriormente y es recta, termina en una estructura angosta que forma el canal lingual. No tiene evidencias de colmillos. Los molares presentan los caracteres más primitivos referidos a *Stegomastodon*: Las cúspides trefoils y entotrefoils son simples sin pliegues ni tubérculos de esmalte accesorias. Los molares M3/m3 con cuatro lofos bien definidos y dos cúspides grandes posteriores al cuarto lofo/lofid que se considera un incipiente quinto lofo/lófid. El m2 con tres lófidos, en estados avanzados de desgaste forman un medio lófid posterior más evidente en molares con mayor desgaste. En el estrato Blanco, no se encuentran índices estratigráficos del Hemfiliano tardío tampoco del Blancano temprano, solo *Dinohippus mexicanus* está presente en todo el estrato Blanco. El resultado del análisis por el método U/Pb, de la ceniza colectada en el mismo sitio donde se colectó la mandíbula dio una edad de 4.85 ± 0.17 Ma, que confirma la edad de Hemfiliano más tardío (Hh4), y refiere a *Stegomastodon primitivus* de Rancho El Ocote, como el más registro más antiguo que se conoce en las faunas de Norte América. Se establece la hipótesis de su posible diversificación en las faunas del Centro de México, antes de lo sugerido por Savage (1955) en su patrón de dispersión de los gonfoteridos de Norte América.

En el área de Los Galvanes, se colectó en el Arroyo Earth Watch la mandíbula de un adulto viejo, en depósitos referidos al Blancano temprano. La mandíbula está completa sin distorsión, solo conserva

el m3 en avanzado estado de desgaste, con solo cinco lófidos que lo diferencian del m3 de Cuchillo Negro Creek y Elephant Butte Lake del Blancano temprano de Nuevo México, los cuales tienen 5+ y hasta seis lófidos. El resultado del análisis por el método de U/Pb de materiales donde se colectó la mandíbula del Arroyo Earth Watch 2.9 ± 0.07 lo refiere a la edad del Blancano temprano. Este registro se correlaciona con especímenes de faunas de Nuevo México, que tienen la edad radiométrica de 3.1 ± 0.3 Ma, Blancano temprano. La similitud de las edades radiométricas de estos registros sugiere que en el Blancano temprano *Stegomastodon primitivus* tuvo amplia distribución geográfica.

INTRODUCTION

A great diversity of fossil mammals has been collected in the sedimentary basins of central Mexico during the past 40 years. These fossils have contributed to the understanding of: 1) geological events that occurred during the formation of these basins, and 2) biological events of continental relevance, such as the Great American Biotic Interchange (GABI), as these faunas contribute important information on the first stages of this phenomenon, which was initiated prior to the final establishment of a long-lasting land connection between the Americas (Montellano-Ballesteros and Carranza-Castañeda, 1981, 1986; Carranza-Castañeda and Miller, 2004; Gillette et al., 2015; McDonald and Carranza-Castañeda, 2018). The Mexican fossils also provide data on the migration routes followed by neotropical immigrants in their journey to reach the southern USA. The fossil faunas also contribute to the understanding of the diversification of an important group of artiodactyls, the Camelidae; the transition of *Dinohippus* to *Equus*; and the recently discussed faunal exchange between central Mexico and North America, such as the displacement of antilocaprids from the Great Plains and central Mexico during the late Hemphillian (Carranza-Castañeda et al., 2013). This exchange probably occurred as these animals searched for refuge, better feeding conditions due to ecological changes, and/or competition triggered by the arrival in North America of new immigrants from Eurasia. Some elements of these Clarendonian-age mammal assemblages were considered extinct in the latest Hemphillian-early Blancan faunas of North America. However, recent collections of fossils in deposits of early Hemphillian age in Zacatecas state in central Mexico (Fig. 1) indicate that they were not extinct, as previously thought, but they migrated southward to Mexico where ecological conditions were probably better or where they did not have competition from the new Eurasian immigrants. These hypotheses require a review as they have important implications for concepts of extinction, geographical distribution, and the stratigraphic ranges of mammals in North America (e.g., Wang and Carranza-Castañeda, 2008; Jiménez-Hidalgo and Carranza-Castañeda, 2010; Carranza-Castañeda et al., 2013; Carranza-Castañeda, 2019).

Another relevant aspect of this research, the description of gomphotheriids from central Mexico, confirms that Central America was not a center of diversification of proboscideans. In addition to increased knowledge about the gomphotheriids that inhabited the basins of central Mexico, these include the earlier reports of the first *Gomphotherium hondurensis* described outside the Honduran faunas are also reviewed. These fossils were found in late Miocene age (NALMA: early- late Hemphillian) sedimentary deposits at Juchipila, Zacatecas, Landa de Matamoros, Querétaro and the (late Hemphillian) Tecolotlán basin in Jalisco (Carranza-Castañeda, 2018). These localities are in central Mexico (Fig. 1). Another gomphotheriid was also known, based on a cast of a jaw collected in the state of Tlaxcala (Fig. 1). This specimen is kept in the Geneva Museum in Switzerland. Falconer (1868) studied the specimen during his stay in that Museum and established that it belongs to the genus *Rhynchotherium*, without designating it to a species. The same specimen was referred years later to a new species, *Rhynchotherium tlascae*, by Osborn (1918, 1921).

Recently, skulls and jaws of two individuals of *Rhynchotherium falconeri* were collected in Pliocene (early Blancan) deposits at the La Goleta locality, in the state of Michoacán (Fig. 1); in addition, the first record of *Rhynchotherium browni* known outside of San Jose de Pimas, Sonora, was collected in early Blancan deposits from the San Miguel de Allende basin. These specimens display characters that allow their assignment to different species (Carranza-Castañeda, 2022).

GOMPHOTHERIIDAE RECORDS IN MEXICO

Arroyo-Cabrales et al. (2007) mentioned the occurrence of four genera of Gomphotheriidae in Mesoamerica with two longirostrine (*Gomphotherium*, *Rhynchotherium*) and two brevirostrine (*Cuvieronius*, *Stegomastodon*) forms. A *Gomphotherium* that has been recently described from the basins in central Mexico is referred to *Gomphotherium hondurensis* (Carranza-Castañeda, 2018). A specimen of *Rhynchotherium* found in early Blancan deposits of the state of Michoacán was referred to *Rhynchotherium falconeri*. Likewise, a fossil from early Blancan deposits of the San Miguel Allende (SMA) basin was classed as *Rhynchotherium browni* (Carranza-Castañeda, 2022).

Brevirostrine forms in Mexico have been mentioned from several localities in the state of Puebla (Fig. 1), where *Cuvieronius* fossils have been collected and described by Montellano-Ballesteros (2002). Other records (Fig. 1) come mainly from Pleistocene deposits in the state of Chihuahua (Álvarez 1965) and Sonora (Lucas et al., 1997).

Other *Stegomastodon* remains have been reported from central Mexico. However, most specimens are molar fragments, which are housed in the Universidad Nacional Autónoma de México (UNAM) or in the Instituto Nacional de Antropología e Historia (INAH) collections. A major drawback of these specimens is that they lack reliable information on location, stratigraphy, and/ or anatomical description to support the designation (Alberdi and Corona-M., 2005).

Undoubtedly, the most complete *Stegomastodon* specimen with diagnostic material found in Mexico, that has been described, is the fossil collected at Santa Cruz de la Soledad, collected near Chapala Lake in the state of Jalisco (Fig. 1). This fossil is a partial skeleton with part of the skull, jaw and postcranial elements and it is referred to *Stegomastodon primitivus*, early Blancan age (Lucas, 2003; Lucas et al., 2011a). The same specimen was described (Alberdi et al., 2002, 2009), and its age was referred to late Pleistocene. *Stegomastodon* remains have also been mentioned as part of the Yepomera fauna by (Lindsay, 1984, Lindsay et al., 2006).

The largest collection of *Stegomastodon* remains in Mexico was collected with the early Blancan Miñaca fauna in the state of Chihuahua (Fig. 1). These fossils are housed in the Los Angeles County Museum (LACM) collections and are a large set of upper and lower molars and partial jaws, all referred to *Stegomastodon primitivus* (Savage 1955, Woodburne 1961). Also, in the same LACM collection, there is a set of upper and lower molars of *Stegomastodon* found associated with *Teleoceras* and *Desmathyus* fossils. These fossils were collected by E.L. Furlong in 1929 from sedimentary deposits of Santa Maria Amajac, state of Hidalgo (Fig. 1). They are labeled (L.

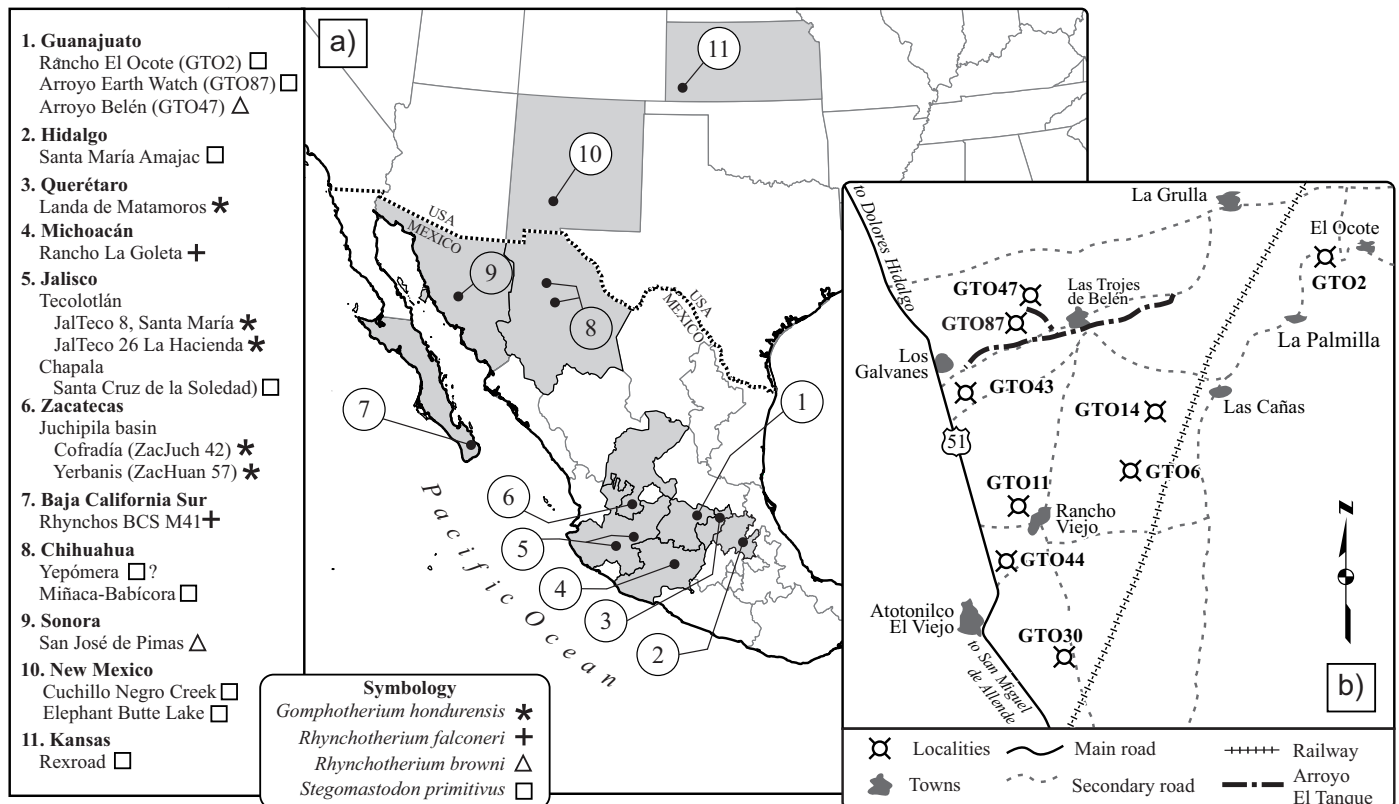


FIGURE 1. Map showing the states and sites where the gomphotheriid fossils were collected: *Gomphotherium hondurensis* *; *Rhynchotherium falconeri* +; *Rhynchotherium browni* △; *Stegomastodon primitivus* □.

Dingus) as *Stegomastodon primitivus*.

The long-term, still active, field research in the San Miguel de Allende basin (Fig. 1) has yielded important results, as several gomphotheriids have been recovered. A jaw of a young individual was collected recently in the sandy Blanco layer (Hh4) at the Rancho El Ocote locality. Another jaw specimen, from an old individual, was collected in the Los Galvanes area, also from early Blancan deposits.

In this work, we follow the criteria of Lambert and Shoshani (1998), which only recognizes two species, *Stegomastodon primitivus* Osborn 1936, restricted to the early Blancan, and *Stegomastodon mirificus* (Leidy, 1858), late Blancan-early Irvingtonian age.

MATERIALS AND METHODS

The *Stegomastodon* records that are mentioned in this work were collected by traditional methods and prepared in the laboratory of Centro de Geociencias (UNAM). They are cataloged and housed in the Paleontology collection in the same institution, Campus Juriquilla, Querétaro. Comparisons were made with jaws and molars from the fauna of Miñaca, Chihuahua, Mexico, housed in the Los Angeles County Museum (LACM), as well as fossils housed at the Jackson Museum of Earth History, University of Texas at Austin (TxVP) and New Mexico Museum of Natural History (NMMNH), Albuquerque. In addition, they were compared with illustrations in the works cited in this article. In this paper, the term cusp is used for large structures that form the half loph/lophids of the molars. Conid refers to small accessory cusps or enamel tubercles at the bases of the loph/lophids. Molar index = width/length.

The measurements are in millimeters (mm). The width of loph/lophids were measured across the main cusp from the base of enamel, and the molars were measured from the outer edges of the enamel.

The analysis of the volcanic ash was by $^{206}\text{Pb}/^{238}\text{U}$ laser ablation inductively coupled plasma mass spectrometry (LA-

ICPMS), and was conducted in the Laboratorio de Estudios Isotópicos of the Centro de Geociencias, UNAM.

GTO 2B Blanco Layer, U-Pb Age Methodology

About 3 kg of ash fall tuff (sample GTO 2B) was collected to obtain heavy minerals by standard techniques of crushing, sieving and panning. Zircons were selected by handpicking and were analyzed with the Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICPMS) technique at Laboratorio de Estudios Isotópicos (LEI), Universidad Nacional Autónoma de México. The detailed methodology has been described by Solari et al. (2010) and Ortega-Obregón et al. (2014). A spot diameter of 32 μm was used with an energy distribution (fluence) of $\sim 6 \text{ J}\cdot\text{cm}^{-2}$ and a repetition rate of 5 Hz of laser pulses. Corrected isotope ratios, ages and errors were calculated using Iolite software (Paton et al., 2011) and the Visual Age data reduction scheme of Petrus and Kamber (2012). Concordia plots and mean ages were calculated using Isoplot R (Vermeesch, 2018).

As shown in Figure 2, a lower intercept age of $4.86 \pm 0.13 \text{ Ma}$ (MSWD = 1.9) that corresponds with the latest Hemphillian North American Land-Mammal “age” (NALMA) was estimated from the youngest zircon analyses ($n=14$) from this sample GTO 2 and is interpreted here as its crystallization and depositional age.

ABBREVIATIONS

Ap, Anteroposterior; R, Right; L, Left; Tr, Transverse; km, Kilometers; mm, millimeters; ~, approximately; Ma, Millions of years; L.F., Local Fauna; NALMA, North American Land-Mammal “age”; BCS M, Baja California Sur, Miraflores; JALTECO Jalisco, Tecolotlán; SMA, San Miguel de Allende; ZAC JUCH, Zacatecas, Juchipila; ZAC HUAN, Zacatecas, Huanusco; GTO, Guanajuato; “GTO 87”, Locality number; UNAM, Universidad Nacional Autónoma de México; CGEO, Centro de Geociencias; LA-ICPMS, laser ablation inductively coupled plasma mass spectrometry; INAH, Instituto Nacional

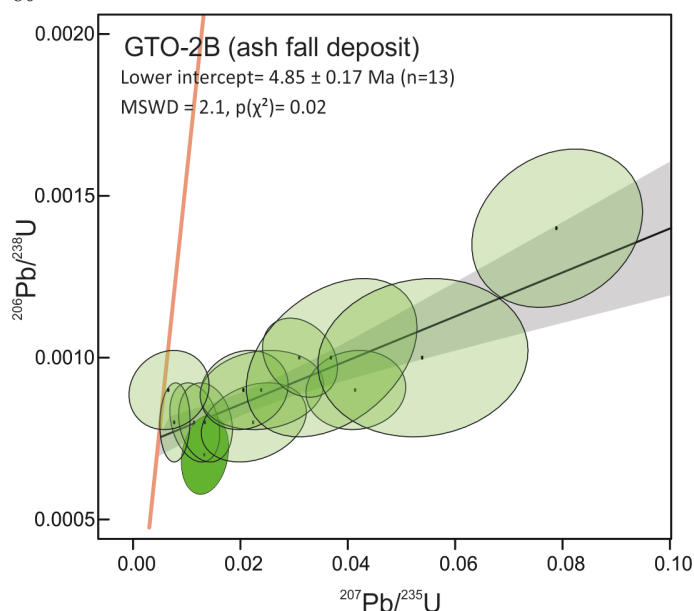


FIGURE 2. Pb/U concordia plots showing the age of the GTO 2B locality from the San Miguel de Allende basin.

Antropología e Historia Mexico; **KUMNH**, University of Kansas Museum Natural History; **LACMNH**, Los Angeles County Natural History Museum, California; **NMMNH**, New Mexico Museum of Natural History; **MPGJ**, Museo de Paleontología; Geociencias Juriquilla; **TxVP**, Texas Vertebrate Paleontology Collections, Jackson Museum of Earth History, The University of Texas; **UMMP**, University of Michigan Museum of Paleontology.

GEOLOGICAL OUTLINE OF THE SMA BASIN

The SMA basin is located immediately north of the Trans-Mexican Volcanic Belt. It occupies an area of 20 x 15 km. The eastern boundary of the basin is a N-S-trending normal fault exposed at the Rancho Viejo hills, and to the west the basin is bounded by a fault that crosses the Tequisquiapan and Rancho Viejo hills. This fault-bound basin controls the current location of the Río Laja in the region. On both sides of the basin are exposed 30.5 ± 1.2 Ma old andesitic lavas, dated by the K/Ar method (Pérez-Venzor et al., 1997). In Palo Colorado village are exposed andesitic lavas that were dated by K-Ar ages of 12.5 ± 0.9 Ma and 10.7 ± 0.7 Ma (Carranza-Castañeda et al., 1994), suggesting a history of volcanism at least 20 million years (Kowallis et al., 1999; Adams et al., 2006). These ages of intra-basinal volcanic rocks reflect in part the time when sedimentation was active within the basin. It is important to mention that the oldest vertebrate-fossil-bearing sediments documented up to now in the region occur at the Soria quarry, municipality of Comonfort, where equid molars were collected from Clarendonian-age sediments. These are the only fossils of this age known in central Mexico faunas, confirmed by radiometric ages obtained by K/Ar analysis of an andesite that is 12.2 ± 0.4 Ma old (Cerca-Martínez et al., 2000; Robles-Rivera, 2015) (Fig. 1).

The protracted fluvial sedimentation and concurrent deposition of airborne volcanic ash partially filled the SMA basin. These sediments contain the most important fossil faunas in central Mexico, as they display the greatest diversity of late Neogene mammals described up to now. The abundance of ash beds within the volcano-sedimentary succession has facilitated the radiometric dating of the most complete stratigraphic succession with early-late Hemphillian and early Blancan fossil faunas (Miocene-Pliocene: Kowallis et al., 1999, 2017; Cerca-Martínez et al., 2000; Flynn et al., 2005; Carranza-Castañeda,

2018).

The unconsolidated fluvial and lacustrine sediments as well as pyroclastic deposits that partially filled the tectonic basin have an estimated thickness of at least 100 m. However, only a 30–40 m interval is exposed and contains the fossil material. These sediments are best exposed around the Rancho Viejo village (Fig. 1). This succession has been informally divided and referred as the Upper and lower Rancho Viejo Beds (Carranza-Castañeda et al., 1994).

Lower Rancho Viejo Beds: Late Hemphillian Localities

Paleontological research in the SMA basin has led to the discovery of several sites that have a great diversity of fossil mammals with ages as old as early-late Hemphillian. At least one locality is known with Clarendonian fauna in the region, but fossils are scant. The occurrence of *Calippus hondurensis* at (GTO 44) in the La Presa locality (Fig. 1) supports an early-late Hemphillian age for part of the basin fill-sediments. Fossil fauna was found at the Rinconada (GTO 43) site, where there is a great abundance of equids and carnivores, all of them considered late Hemphillian stratigraphic indexes. This site also has yielded the youngest records of the camel *Alforjas* and antilocaprid *Texoceros* in North America. The Coecillos site (GTO 30) (Fig. 1), contains abundant equid material, especially *Dinohippus* with occlusal teeth features that suggest a transition to *Equus*, and the hog-nosed skunk *Conepatus sanmiguelensis*, which was one of the first carnivores to arrive in South America (Carranza-Castañeda, 1992; Carranza-Castañeda and Espinosa-Arrubarena, 1994; Wang and Carranza-Castañeda, 2008; Carranza-Castañeda, 2019).

However, the most important late Hemphillian age locality in central Mexico is Rancho El Ocote (GTO 2). This is because of its great mammal diversity, which includes the stratigraphic indexes of late Hemphillian mammals, the early records of South American immigrants, and fossils that document several mammalian extinctions at the Hemphillian-Blancan boundary (Carranza-Castañeda and Espinosa-Arrubarena, 1994; Wang and Carranza-Castañeda, 2008; Jiménez-Hidalgo and Carranza-Castañeda, 2010; Carranza-Castañeda et al., 2013; Carranza-Castañeda, 2019).

An almost complete juvenile jaw of *Stegomastodon*, here referred to the latest Hemphillian, was recovered at Rancho El Ocote, in the upper sandy Blanco layer (named by the distinctive white color of the sediments). The detailed description of this record is part of the objectives pursued in this paper.

Upper Rancho Viejo Beds: Early Blancan Localities

Blancan deposits are widespread in the SMA basin, with broad exposures of sediments that unconformably rest atop late Hemphillian-age deposits exposed at the Arroyo Tepalcates GTO 52, Rancho San Martín GTO 42, and Coecillos GTO 30 localities. The most important early Blancan locality south of the USA-Mexico border is found at the GTO 6 (Fig. 1), also known as the Arrastracaballos locality, in the Rancho Viejo area. This locality is pertinent because of the diversity and abundance of fossils present. Other important Blancan localities in the SMA basin are Cuesta Blanca GTO 14 and Garbani's site GTO 11, where the oldest records of *Nechoerus cordobae* were discovered (Carranza-Castañeda and Miller, 1988; Carranza-Castañeda, 2016).

The base of the lower Rancho Viejo beds is exposed at the late Hemphillian Rinconada site (GTO 43), which is near Los Galvanes village, located ~8 km north of Rancho Viejo. That site is important because of its carnivore fossil diversity, and the presence of equids, specifically *Dinohippus mexicanus*, *Neohipparion eurystyle* and *Astrohippus stockii*, as well as the occurrence of artiodactyls such as *Hemiauchenia* and *Megatylopus* (Carranza-Castañeda 1992).

The sediments exposed at Rinconada are unconformably

overlain by an important biostratigraphic succession that contains an early Blancan age fauna. Arroyo El Tanque and its tributaries, such as Arroyo Belén (GTO 47), contain the most important localities of early Blancan age where a large diversity of neotropical immigrants has been collected and described (Montellano-Ballesteros and Carranza-Castañeda, 1986; Carranza-Castañeda and Miller, 1988; Gillette et al., 2015). In addition it has the only record of *Rhynchotherium browni* known outside of Sonora (Carranza-Castañeda, 2022) (Fig. 1).

The long-term field research at Arroyo El Tanque and its tributaries has yielded new specimens of fossils found and described for the first time in central Mexico, which complements the biostratigraphy of the region. Recent discoveries include a *Stegomastodon* mandible in early Blancan deposits at the Arroyo EarthWatch (GTO 87) locality, which is one of the topics discussed in this paper.

Rancho El Ocote GTO 2B

The Rancho El Ocote Local Fauna is the most important in central Mexico. Research has shown the abundance and diversity of fossil mammals, including evidence of the arrival of the first neotropical immigrants in North America. The fauna also includes the last appearance of mammals considered fossil indexes of the late Hemphillian faunas in North America. The taphonomy, magnetostratigraphy and radiometric ages have shown that the stratigraphic sequence could be divided into three different age levels, each one with a distinctive mammalian fauna.

Previous Work

The first fossil mammal list from Rancho El Ocote was published by Arellano (1951). Years later, several papers were published describing parts of the fauna, especially equids (Mooser, 1958, 1960, 1965, 1968, 1973a and 1973b). Unfortunately, the material described in these early papers did not have any stratigraphic control, and the age is broadly referred to as “Hemphillian, slightly younger than the Yepómera fauna from Chihuahua” by Dalquest and Mooser (1980). Subsequent investigations were carried out by Universidad Nacional Autónoma de México along the Arroyo La Carreta, a local name for a water-carved gully near Rancho El Ocote. This fieldwork yielded new records of fossil mammals and the first stratigraphic description of the sediments in the SMA basin (Carranza-Castañeda and Ferrusquía-Villafranca, 1978; Carranza-Castañeda, 1989, 2006; Carranza-Castañeda et al., 2013).

The stratigraphy exposed along Arroyo La Carreta displays a set of fluvial paleochannels with intervening discontinuous, fine-grained layers with variable proportions of clay and fine sand. The exposed succession also shows gravel deposits with variable clast sizes within the channels. In the area are exposed several volcanic ash layers. Outcrops of these deposits have variable thicknesses. The best exposed outcrop is in the southern wall of a dry stream named locality GTO 2. However, other aspects of the local stratigraphy are well displayed in a north-south trending tributary of Arroyo La Carreta, which was named the GTO 2B locality by Carranza-Castañeda (1989).

Rhino Layer Hh3

Rhino layer is an informal biostratigraphic name used to refer to the lowermost stratum. Its name is related to the fact that all the *Teleoceras* remains found at the locality were discovered at this level. The dominant lithology of the layer is clay, locally with different proportions of sand, some sandy-gravel channels and lenses of volcanic ash. Thickness of the Rhino layer is highly variable in each one of the known collection sites. Fossil materials recovered from this level are always fractured and display sharp edges, a characteristic related to the presence of expansive clay at the site. Fracturing of the fossil remains is attributed to the

expansion and contraction of the clay during the yearly wet and dry seasons. The most representative mammals of this layer are late Hemphillian (Hh3) in age and include *Nannippus aztecus*, *Neohipparion eurystyle*, *Astrohippus stockii* and *Dinohippus mexicanus*, horses which occur together with carnivores such as *Borophagus secundus*, *Machairodus* cf. *M. coloradensis*, *Pseudaelurus? intrepidus*, and *Agriotherium schneideri*, as well as the artiodactyls *Hemiauchenia*, *Megatylopus*, *Alforjas*, *Kyptoceras*, *Texoceros*, the tayassuid *Catagonus brachydontus* and the ground sloth *Megalonyx* sp. Almost all the equids, except *Dinohippus* and the carnivores, represent the last appearances in late Hemphillian Mexican faunas. Fission-track dating of zircons separated by the ash at the top of the sequence yielded an age of 4.89 ± 0.2 Ma (Kowallis et al., 1999; Flynn et al., 2005).

Blanco Layer Hh4

The Blanco layer rests above of the Rhino layer over an eroded surface. The sandy Blanco layer is composed of fine sand strata interlayered with sandy-clay with a remarkable white color (hence the name, “Blanco”). Clayey layers are compact and fissile. The total thickness of the succession is ~3 m. Small, isolated shallow channels filled with medium-grained sand and gravel occur in the succession. Layers with abundant volcanic ash are also present. The horse fauna found in the sandy Blanco layer is composed of only a few remains of *Astrohippus stockii*, which are present immediately above the contact with the underlying Rhino layer. *Dinohippus mexicanus* is present throughout the sandy Blanco layer, associated with the artiodactyls *Megatylopus*, *Alforjas*, and *Hexobelomeryx* and the first records of *Paramylodon garbanii*. This faunal assemblage, and the absence of the late Hemphillian index fossils, are consistent with a latest Hemphillian (Hh4) age. This biochronological age has been confirmed with radiometric ages of volcanic ash collected in the uppermost part of the sandy Blanco layer. The succession is buried under a thin (8 cm) layer of caliche, which has been interpreted as an unconformity that separates the early Blancan age deposits from Hemphillian sediments (Carranza-Castañeda, 1989; Kowallis et al., 1999; Carranza-Castañeda, 2006, 2019; Carranza-Castañeda et al., 2013).

SYSTEMATIC PALEONTOLOGY

Order Proboscidea Illinger, 1811

Gomphotheriidae Cabrera, 1929

Stegomastodon Pohling, 1912

Stegomastodon primitivus Osborn, 1936

Figures 3 and 4

Referred material. State of Guanajuato: GTO 2B, Blanco layer (Hh4), Rancho El Ocote Locality, SMA basin, specimen MPGJ 3525, associated right and left dentaries of a single young individual. The left dentary with complete m1, and partially erupted m2, only the protolophid and metalophid are completely erupted on m2. Isolated teeth were also found at the same site: MPGJ 5340 left M3, MPGJ 3529 fragment of M3, MPGJ 3527 left m3, MPGJ 1983 right m2, MPGJ 3528 right m2, MPGJ 5341 fragment of m3.

Description of the Jaw. The jaw MPGJ 3525 is nearly complete. The symphysis is of brevirostrine type and slightly elongated, and the maximum length of the pre-tooth area in the left dentary measured from the middle-anterior part of the protolophid is 213 mm. The distance from the same point to the lingual suture in the symphysis is 164 mm, with no evidence of alveoli for premolars. The jaw lacks tusks or evidence of alveoli that could have had them.

The right dentary preserves the complete m1 with thick enamel and no evidence of ptychodonty. The alveolus in the left side is complete, but two posterior cusps are preserved in the corresponding molar. Two mental foramina are in the lingual



FIGURE 3. MPGJ 3525, *Stegomastodon primitivus* GTO2B locality, Rancho El Ocote Fauna. **A**, Lateral view, m1 is complete, the m2 only the protolophid and metalophid are observed. Symphysis elongated without evidence of tusks and the mental foramen is below the protolophid. **B**, Occlusal view, the internal part of the symphysis is rounded and wide, with a long premental area. All measurements in Tables 1 and 2.

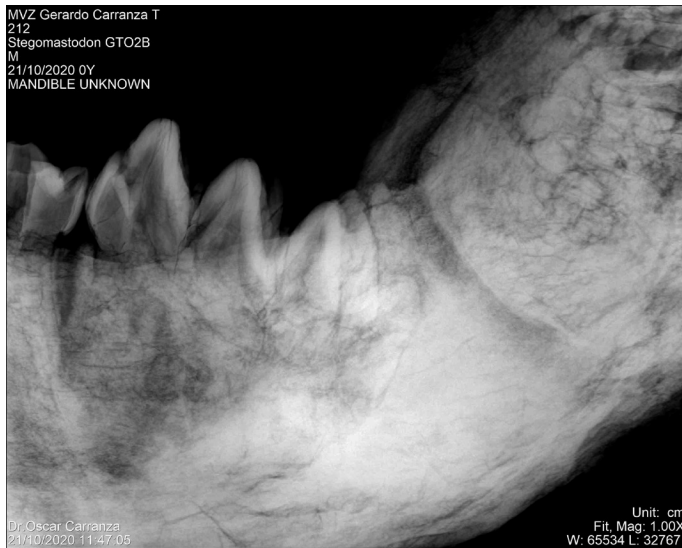


FIGURE 4. MPGJ 3525 *Stegomastodon primitivus*, GTO 2B, Rancho El Ocote Fauna. X Ray of m2; the third lophid is emerging into the alveolus, no accessory cusps are behind the tritolophid, and m3 is developing in the ascending rami.

side of the symphysis; the smallest is posterior, and 57 mm below the protolophid of m1, and the largest is 84 mm in front of the protolophid and 35 mm below the alveolar border. At this point, the horizontal ramus is 104 mm deep, and the foramina are 38 mm apart.

There is no evidence of tusks in the specimen. The depth of the horizontal ramus under the protolophid of m1 is 127 mm, and the breadth posterior to the tritolophid of m1 is 107 mm; the depth of the horizontal ramus below the posterior part of the metalophid is 148 mm, and its breadth 115 mm.

The mandibular angle begins at this point with a pronounced

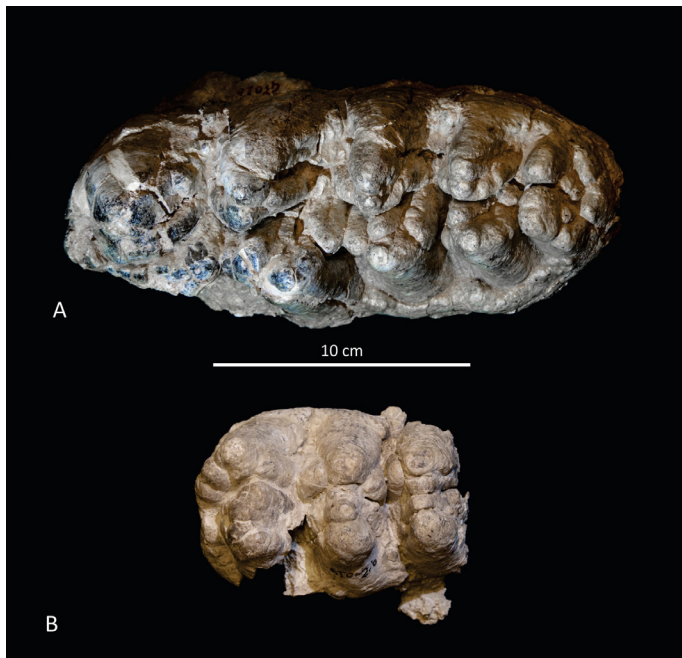


FIGURE 5. *Stegomastodon primitivus* GTO 2B locality, Rancho El Ocote Fauna, A, MPGJ 5340, left M3, The molar corresponds to a mature animal, with almost five developed lophs and a half loph behind the tetraloph are present. B, MPGJ 3529, fragment of M3. Trito and tetraloph are complete and a half loph is behind rounded by tubercles of enamel (choerodont).



FIGURE 6. MPGJ 3527 *Stegomastodon primitivus* GTO 2A Locality, Rancho El Ocote Fauna. left m3. Only the protolophid has slight wear on the cusps, the tooth belongs to a young mature individual, with four well-defined lophids and two posterior cusps considered a half lophid.

curvature up to the level of the occlusal surface, where the posterior border of the ascending ramus becomes straight and ends in the condyle, which is almost complete in the specimen. The height of the condyle measured from the occlusal line is 193 mm, and it is 380 mm measured from the ventral border. The transverse measurement of the ascending ramus is 198 mm.

The coronoid processes in both rami are broken. The lower part at the root of the ascending ramus is preserved. The occlusal line in its intersection with the anterior border of the ascending ramus forms a 110° angle (Fig. 3). The measurements are summarized in Tables 1 and 2.

The left mandible is better preserved than the right one, however it only preserves part of the m1. The protolophid and metalophid are broken. The tritolophid retains a simple, complete entotrefoil. The labial cusp is broken. Two small cusps are behind the middle part of the tritolophid, which forms a transverse ridge structure.

All the teeth have thick and simple enamel. The right dentary has the complete m1, and is tritolophid, with two posterior cusps that form a transverse structure with minimum wear. The protolophid has a simple labial trefoil. The entotrefoil is worn down enough to display its shape. The metalophid has a well-defined labial trefoil, and the entotrefoil has the enamel slightly folded. The tritolophid in the labial cusp is a simple trefoil and the entotrefoil without accessory cusps. Two small cusps are found in the middle of the axis that form a transverse ridge in the back of the tritolophid, which shows medium wear. The Ap length is 118 mm, and the transverse width is 68 mm, with a 57 index (width/length). A short cingulum is observed in the anterior part of the protolophid cusp, and it ends at the base of the anterior part of the entotrefoil. Depth of the horizontal ramus below the protolophid is 135 mm.

As shown in Figure 4, the m2 is not wholly erupted, and only the protolophid and metalophid are complete. The tritolophid is still in the alveolus, and its cusps have no evidence of wear. In the protolophid, the labial cusp has a simple trefoil, the anterior border forms a small cingulum, and the lingual cusp is 68 mm high. The metalophid has a simple trefoil, and the entotrefoil lacks the accessory cusps. In the X-ray, the labial side of the mandible shows that the tritolophid cusps were still developing; a wide cusp can be observed that with time would become the trefoil. In the ascending rami, the m3s can be observed in development.

Isolated upper tooth. MPGJ 5340 M3 left (GTO2 A locality): the molar belongs to a mature animal, has two anterior roots, and its enamel is thicker, 5–6 mm. The molar has five lophs, the anterior fourth lophs are well-defined. The fifth loph is reduced in size in comparison the others. It is formed by a labial

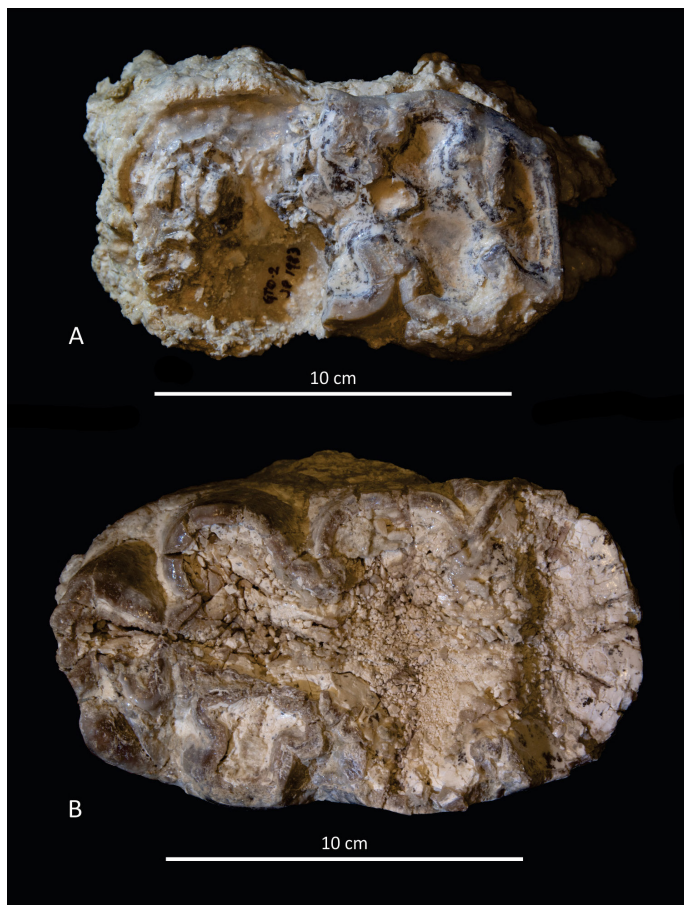


FIGURE 7. **A**, MPGJ 1983 *Stegomastodon primitivus* GTO 2B locality, Rancho El Ocote Fauna. Right m2. Belongs to an old individual, it is tritophid, and only the tritophid is preserved, the trefoil and entotrefoil are simple without folds, and behind the tritophid a well-defined tabular half lophid is observed. **B**, MPGJ 3518 right m2, corresponds to a mature-old animal, the tritophid with simple trefoil and no folds, and a middle lophid formed by several cusps lies posterior to the tritophid.

and lingual cusp separated by a narrow fissure that is more than half the width of the fourth loph. The dentine is slightly exposed in the protoloph. The lingual cusps have slight evidence of wear. The tooth shows enamel protuberances (i.e. choerodont), between its valleys.

The lingual cusp is broken on the protoloph. The entotrefoil has simple cusps that show evidence of wear, and small conids are observed at its base. The metaloph has a simple trefoil cusp, and the entotrefoil displays two small accessory conids. The tritophid has a trefoil lingual cusp, and the entotrefoil has two small accessory conids. On the tetraloph, the trefoil is columnar, and the entotrefoil is wide at the base with small enamel protuberances on the edges of the cusps. The anteroposterior length of the tooth is 213 mm, the metaloph width is 89 mm, and its index is 4.1 (Fig. 5A).

MPGJ 3529, a fragment of M3 (GTO 2B locality), belongs to a mature animal (Fig. 5B). The protoloph is complete, and the trefoil is wide with some additional conids. The entotrefoil has several conids. On the metaloph and tritophid the trefoil has additional enamel tubercles, and the entotrefoil also has accessory conids. The fragment certainly shows evidence of choerodonty.

Isolated lower teeth. MPGJ 3527, left m3 (GTO 2A



FIGURE 8. MPGJ 5341 *Stegomastodon primitivus* GTO 2A Locality, Rancho El Ocote Fauna. Fragment of m3. The tetralophid is complete, the trefoil is like a weak double trefoil (ptychodontid), some enamel conids are present, the entotrefoil is larger but simple. A set of round enamel conids and two larger cusps form a half lophid. This fragment presents some tubercles (choerodont) on the occlusal surface, more than any other record from the Rancho El Ocote collection.

locality). It has four lophids and two posterior cusps of different size. Due to the slight wear on the protolophid the dentine is exposed, and the labial cusp of the metalophid display minor attrition, allowing referral to a young-mature animal. The enamel is thick. A weakly developed cingulum is present on the labial side. The protolophid has a well-defined simple trefoil, an accessory cusp is located at the base of the anterior trefoil cusp, and the entotrefoil is simple, with two cusps, and an extra small posterior cusp is present at its base. The metalophid, tritophid and tetralophid show the same pattern: a simple trefoil and entotrefoil cusps. Two cusps are behind the tetralophid, and they are smaller than the lophid cusps. The labial cusp has a columnar shape with small protuberances at the base, and the entotrefoil is a simple conical cusp with small enamel protuberances around the base. These cusps are regarded here as a half lophid.

The Ap length of m3 is 212 mm, the metalophid lingual cusp has a height of 73 mm height and the transverse width of the lophid is 83 mm. It has an index of 39 (Fig. 6).

MPGJ 1983 right m2 (GTO 2B locality). Its preservation is poor, and it is tritophid. The protolophid and metalophid are worn down, although the whole tooth retains its shape and size without evident deformation. The tritophid is complete with a labial trefoil. The entotrefoil is wide but simple, and extremely worn. The dentine is exposed across the whole occlusal surface of the tooth. Two very worn cusps posterior to the tritophid form a wide transverse structure that is interpreted as a half lophid. The Ap length is 122 mm, and the transverse width of the tritophid is 79 mm. It has a 64 index (Fig. 7A).

MPGJ 3518 right m2 (GTO 2A). The protolophid and metalophid are worn down, so the dentine is displayed over the entire occlusal surface. The tritophid has a complete labial trefoil. The entotrefoil is broad and rounded as a consequence of wear. The tritophid has a transverse crest formed by two cusps of different sizes. The central cusp-like trefoil is larger, and the dentine covers its surface. The entotrefoil is small, and minor enamel protuberances are present on the labial side. These cusps form a wide ridge that here is considered a half lophid. The Ap length of m2 is 150 mm, the metalophid transverse width is 82 mm and its index is 54 (Fig. 7B).

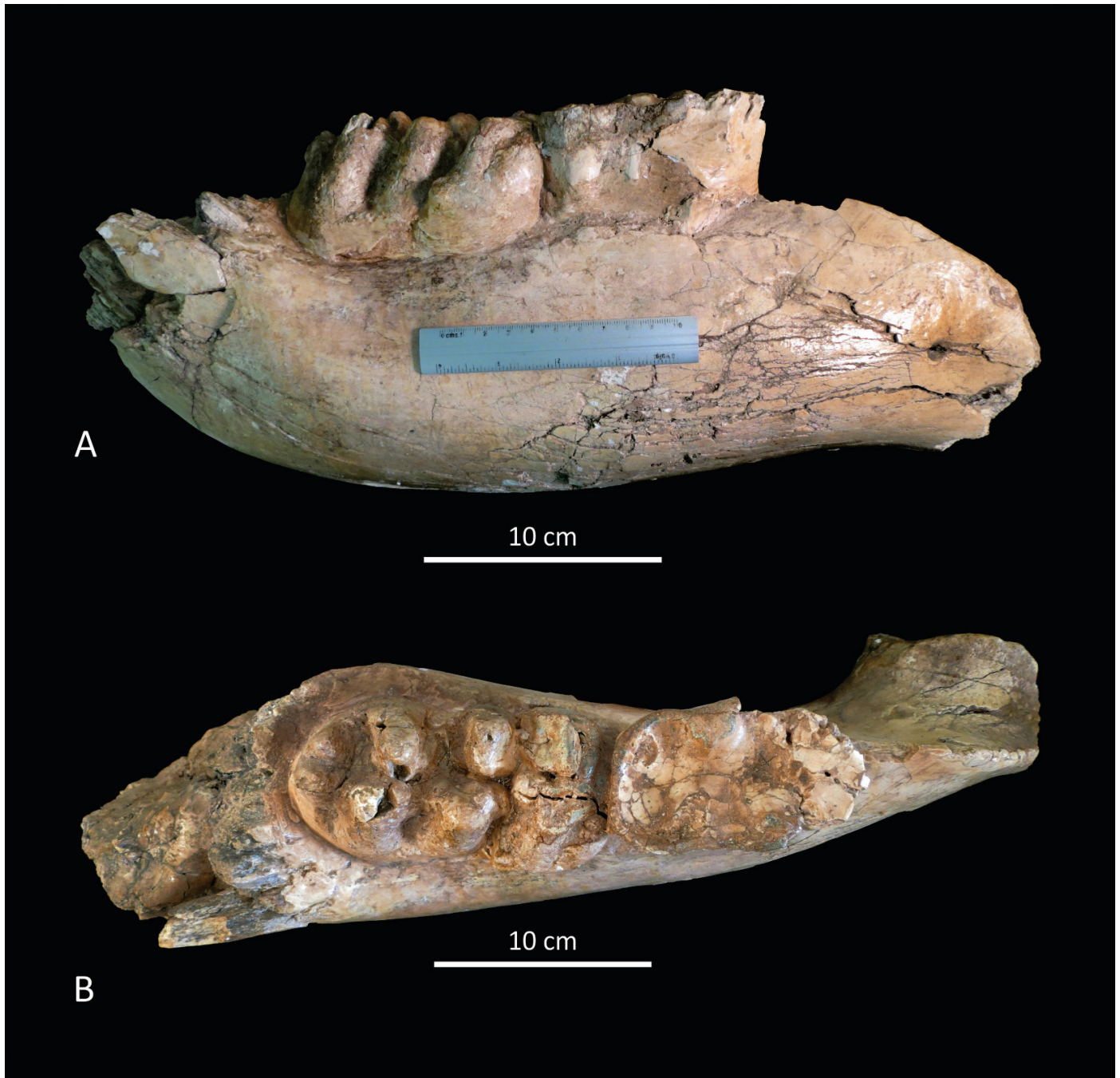


FIGURE 9. **A**, TxVP 41685-11251 *Stegomastodon primitivus* Rancho El Ocote fauna, indeterminate locality and stratum. Lateral view of jaw fragment with m1-m2, short symphysis, no downward inclination, with long predental space, no evidence of tusks, and two mental foramina under m1. **B**, Occlusal view, note the wide and straight lingual canal, long predental border without evidence of tusks. m1 worn, the wide posterior transverse ridge inferred as a half lophid. m2 trilophid, the trefoil is simple without evidence of folding (ptychodont), only a small cusp posterior to the trilophid, and m3 is broken within the alveolus.

MPGJ 5341 fragment of an m3 (GTO 2 A). It only retains the tetralophid, which is complete with a simple and well-defined trefoil. Two small, extremely worn cusps are present in the middle valley, the entotrefoil is large, the dentin is exposed, and the enamel edges are slightly folded. Behind the tetralophid is a ridge formed by cusps, the labial as a trefoil, with two small conids in the middle. The entotrefoil is a simple larger and open cusp, with several posterior conids. This structure suggests it is a half lophid. A cingulum is present on the lingual side (Fig. 8).

Discussion of Previous Proboscidean Finds in the SMA Basin

Dalquest and Mooser (1980) described a fragment of jaw of a juvenile proboscidean referred to *Rhynchotherium* (TxVP 41685-123) from Rancho El Ocote fauna, indeterminate location and layer. According to these authors, this specimen was collected at Rancho El Ocote, but they do not mention the stratigraphic level or a precise locality where it was found. This specimen is housed in the collections of University of Texas at



FIGURE 10. CIT 160 P. 300 57-35 *Stegomastodon primitivus* from the Miñaca Fauna, state of Chihuahua, indeterminate locality and stratum. A, Right and left dentaries of the same young individual. The left m2 has two cusps posterior to the tritolophid that form a transverse ridge that is inferred as a half lophid. The m3 has five well-defined lophids, and simple trefoils, with no sign of enamel tubercles. B, CIT 155 P-300-57-35 *Stegomastodon primitivus*, Miñaca Fauna, Chihuahua state, right m3, belongs to a mature individual, is pentalophid, the trefoils are simple no accessories tubercles. The entotrefoil folded along the midline forming an incipient double entotrefoil (ptychodont).

Austin. A study of this jaw showed that the specimen does not have *Rhynchotherium* features, such as symphysis deflection, or evidence of tusks; instead, the horizontal ramus is straight, elongated, and the pre-tooth area in front of m1 is about 80 mm. There is no evidence of alveoli for possible premolars or lower tusks (Fig. 9A).

The m1 is tritolophid. Its cusps have been worn-down, and the dentine covers the occlusal surface. The outline is evident, and the back of the tritolophid is wider than the previous lophids. The posterior part of the tritolophid shows a wide surface because of the excessive wear.

The m2 is tritolophid with simple trefoils and entotrefails, including two small cusps behind the tritolophid, like those illustrated by Woodburne (1961) for KUMNH 4637 *Stegomastodon primitivus* (= *S. rexroadensis*) and those present in the left m2 of *Stegomastodon primitivus* of the Miñaca specimens CIT 155- P-300-57-35 and CIT 160 P. 300. 57-35, which are housed in the LACM collections.

The preservation of the mandible housed in the University of Texas University at Austin suggests it was collected from the Blanco layer (Hh4), because the fossil material recovered at the base of the stratigraphic sequence (Rhino layer Hh3) always shows multiple fractures and angular edges (Carranza-Castañeda et al., 2013).

Based on these comparisons, it is important to point out that the jaw described by Dalquest and Mooser (1980) as *Rhynchotherium* does not have the diagnostic characters of this genus (Miller, 1990; Pasenko, 2007, 2012; Lucas and Morgan, 2008). It does share characters with the mandible referred here to *Stegomastodon primitivus*, collected at the locality GTO 2B, sandy Blanco layer (Hh4), housed in the Centro de Geociencias, UNAM. Based on these observations, the jaw described by Dalquest and Mooser (1980) should be referred to *Stegomastodon* (Fig. 9A-9B).

Comparisons with Other *Stegomastodon* Records

Jaw Comparison

The mandible MPGJ 3525, collected in the sandy Blanco layer of Rancho El Ocote, belongs to a young individual and it is here referred to *Stegomastodon primitivus* as the jaw symphysis is not deflected. Thus, the pre-tooth area it is straight and elongated; the maximum length measured from the middle-anterior part of the protolophid is 213 mm. The distance from the same reference point to the lingual suture in the symphysis is 164 mm. The symphysis is slightly longer than that documented for *S. rexroadensis* from Kansas (Woodburne, 1961).

Two mental foramina are present in the lateral part of the symphysis. The smaller is posterior and it measures 57 mm below the protolophid of m1. The larger foramen is 84 mm in front of the protolophid and 32 mm below the alveolar border. The foramina are 38 mm apart. This foramen arrangement does not differ substantially from that described for *Stegomastodon rexroadensis* (Woodburne 1961).

The enamel in m1 and m2 is thick and very simple with no folds (ptychodont) and it lacks accessory cusps (choerodont). Enamel in the isolated teeth from the SMA localities described in this work is always simple, without folding, and lacks accessory cusps. The trefoils and entotrefail are simple with no evidence of double trefoils (Fig. 3A-3B; measurements in Table 1).

The only possible comparison with specimens of other faunas is the m1. This tooth in the Rancho El Ocote fossils has a simple trefoil and entotrefails cusps, two small cusps behind the tritolophid that form a narrow transverse crest posterior to the tritolophid and could be considered as a half lophid, and is narrower than the anterior lophids (Fig. 3B). When compared with KUMNH 4637 m1, *Stegomastodon primitivus* (= *Stegomastodon rexroadensis*) from Kansas, where m1 is heavily worn, the dentine covers the occlusal surface, and according to the description, the m1 enamel is simple with no folds and with two cusps behind the tritolophid.

When the m1 from El Ocote is compared with NMMNH 45892, the m1 of *Stegomastodon primitivus* from the Hot Spring Landing site in the Elephant Butte Lake Fauna from New Mexico, it is more similar as it has three lophids, and two posterior cusps joined in the middle by a medial sulcus and some smaller accessory conids on the labial margin (Morgan and Lucas, 2011). It could be assumed that with advanced wear this structure would acquire a shape comparable to the m1 of Rancho El Ocote, a developing half lophid.

The studied m1 from Rancho El Ocote differs from the KUMNH 4637 Rm1, which lacks a transverse ridge posterior to the tritolophid, although this difference could be a result of the fact that the Kansas specimen is very worn (Woodburne 1961, plate IV). The m1 and m2 from Rancho El Ocote show that this ridge it is always wider as a function of wear, and the m1 from Kansas is in the last stages of wear (Fig. 3B).

In M3, m2 and m3 from El Ocote, the enamel is always thick without evidence of accessory conids (choerodonty). The trefoils are simple, although in extreme stages of wear, and some choerodont surface is evident in the half lophid in the very late stages of wear as is observed in MPGJ 5341, a very old m3 (Fig. 8).

The most important feature in the m2, from an adult individual (e.g. MPGJ 3518), is found behind the middle part of the tritolophid. A large, cusp-like an incipient trefoil and other smaller cusps form a transverse ridge smaller and narrower than the anterior lophid. This structure is considered as a half lophid. These features were also observed in the m2 MPGJ 1983, and although it belonged to an older individual, it is noted that this tooth shares similar characters with the MPGJ 3518 specimen. (Fig. 7A-B).

In comparison with the holotype, (UMMP 41207) m2 from Kansas, the holotype is heavily worn with no evidence of a transverse ridge (plate III), although in plate II the m2 retains some evidence of this feature. In the specimens UMMP 29996 and KUMNH 4637, which belonged to young individuals, the m2s have two cusps behind the tritolophid with no evidence of wear.

When comparing these molars (m2) from Rancho El Ocote, with the specimen CIT 160 P. 300.57.35 m2, *Stegomastodon primitivus* from the Miñaca fauna, Chihuahua, Mexico, some similarities are observed. The left m2 is tritolophid, has two cusps in the posterior part that form a broad transverse ridge that is partially worn and the dentine is exposed, interpreted as a half lophid. In the right m2 in the same jaw, the dentine occupies a large part of the surface, and the cusps are located posterior to the tritolophid and form a wider structure because of wear. This probably implies that in the jaw, the same structure in the dentaries may differ due to natural wear (Fig. 10).

This variability can be observed also in UMMP 29996, in which the m2 lacks the posterior cusps, and in KUMNH 4637 in which the m2 is in the early stages of wear and retains two separate cusps.

The ridge size behind the tritolophid is related to the wear of the molar. The m2 of young individuals (age inferred by the state of wear) displays only two different-sized cusps. The m2 cusps from older individuals are worn, and the transverse ridge becomes more evident. This ridge is interpreted here as a half lophid, as mentioned in the description of m2 from Rancho El Ocote (Fig. 7A-B).

An isolated M3 (MPGJ 5340), which belongs to a mature individual, has five developed lophs. In the posterior part of the fifth loph, there are several small conids (choerodont). It is possible that with greater wear the molar would have an arrangement similar to the *Stegomastodon primitivus* from Jalisco. However, the M3 of *S. primitivus* from El Ocote has significant differences from the M3 of *S. rexroadensis*. This specimen has five and half lophs and the likelihood the protoloph and metaloph can form a double trefoil, which is not possible in the El Ocote specimen, which has only four and half lophids and no evidence of the presence of a double trefoil (Woodburne, 1961; Morgan and Lucas, 2011) (Fig. 5A-B).

The most obvious difference between the m3s of *Stegomastodon primitivus* (MPGJ 3527) from México and *S. rexroadensis* UMMP 41207 (Woodburne 1961, table IV), is found in the development of the fifth lophid. In *S. rexroadensis* the Rm3 has 5+ and the Lm3 has 5 1/2 lophids. However, in the specimen from Rancho El Ocote the molar only has four complete well developed lophids and, behind the tetralophid, two cusps with a trefoil and entotrefoil shape considered a half lophid. However, the wear of the protolophid with exposed dentin suggests that the molar corresponds to a young individual, in which the four lophids have the definitive shape and size. The two posterior cusps suggest an incipient half lophid. Based on this the m3 (MPGJ 3527) indicates a primitive form of *Stegomastodon* with distinctive characters, different from those described for *Stegomastodon primitivus*.

Comparisons between the m3 of *Stegomastodon primitivus* from Rancho El Ocote, which has four and half lophids, with specimens from the Miñaca-Babícora early Blancan faunas

of Chihuahua, Mexico, reveal that in the specimen CIT 155 P300.57.35 from Miñaca that belongs to an adult individual, the right m3 has 5 lophids that are partially worn, and the dentine is exposed on all the cusps. The fifth lophid has a simple, well-defined lingual trefoil with some wear but it lacks the posterior cusps that here are suggested as a half lophid. The entotrefails show some folding in the midline that forms an incipient double trefoil (Fig. 10B).

Another specimen from the Miñaca fauna, CIT 160 P-300.57-35, consists of right and left dentaries with m2-m3 of a young adult individual. The m3 has five well-defined lophids and simple trefoils and entotrefails. There is no evidence of possible double trefoils, even in those samples with advanced stages of wear.

In the two dentaries of the same individual from Miñaca specimen 160 P-300, 57-35, m3 has five lophids and lacks posterior cusps. When these fossils are compared with UMMP 41207, the type specimen of *Stegomastodon rexroadensis* (= *S. primitivus*), it is noted that all the teeth have the same shape without enamel wrinkles. The greatest difference among these specimens is observed behind the fifth lophid. The type specimen has a Lm3 with 5.5 and Rm3 with 5+ lophs (Woodburne 1961, table IV). This feature is not present in the Miñaca specimens. However, dentaries from Miñaca differ from the specimen NMMNH 46496, an m3 of *Stegomastodon primitivus* from the Elephant Butte Lake fauna (New Mexico), that has 5.5- 6 lophids. The left m3 behind the fifth lophid presents two cusps separated by a medial sulcus that form a sixth lophid, and the right m3 has only one transverse cusp, which forms the six lophid.

Another specimen, NMMNH 57406, from Cuchillo Negro Creek has six lophids and a simple trefoil. This feature differentiates the *Stegomastodon primitivus* from New Mexico from those described from Miñaca and Jalisco, but also distinguishes them from the more advanced gomphothere species *Stegomastodon mirificus* (Savage, 1955; Woodburne, 1961; Morgan and Lucas, 2011).

An additional important differences between the m3 of Rancho El Ocote and m3 of specimens from the Miñaca fauna (not formally described), and the record described by Woodburne (1961), the holotype of *Stegomastodon rexroadensis* (= *S. primitivus*), is that specimen MPGJ 3527, an m3 of *S. primitivus* assigned a latest Hemphillian age, has only four well developed lophids and two cusps behind the tetralophid, which suggest the existence of an additional half lophid. It is not possible to predict the advanced state of wear in older specimens, so this m3 could have the same shape and structure found in the Miñaca specimens or other fossils from Jalisco, Mexico (Lucas et al., 2011 a) (Fig. 6).

Based on these observations, the most important differences in the taxonomy of *Stegomastodon primitivus* from Rancho El Ocote, assigned a latest Hemphillian age, are found in the M3/ m3, where all the specimens have four well developed lophs/ lophids and an additional half lophid in different stages of development according to wear. The Mexican specimens, from Jalisco, have five lophids, like the m3 from the Miñaca-Babícora faunas previously mentioned, which have been assigned to the early Blancan (Repenning, 1962; Berta, 1981; Lucas et al., 2011 b). All Mexican specimens differ from the *Stegomastodon rexroadensis* (= *Stegomastodon primitivus*) holotype (UMMP 41207), which has five + lophids, and from the specimens NMMNH 46496 from the Elephant Butte Lake Fauna, and NMMNH 57406 from Cuchillo Negro Creek, from New Mexico, which also have five and half or six lophids (Woodburne, 1961; Morgan and Lucas, 2011).

Age of *Stegomastodon primitivus* from Blanco Layer

The age of the *Stegomastodon primitivus* jaw recovered

from the upper part of the Blanco layer has been determined based on the associated fauna and isotopic ages of zircons obtained from the ashes collected in the same place where the jacket was made. The zircons were dated by the U-Pb method at 4.85 ± 0.17 Ma. (Fig. 2, lower intercept, $n = 13$, MDWD = 2.1). This result implies that the *Stegomastodon primitivus* from the Blanco layer at Rancho El Ocote is the oldest record of this species in the Mexican and US faunas. Records from the Miñaca and Babicora faunas in Chihuahua have been assigned to the early Blancan, the same age as the records from Nebraska, Kansas, and New Mexico (Repenning, 1962; Flynn et al., 2005; Lucas et al., 2011b).

The associated fauna from the Blanco layer has been assigned a latest Hemphillian Hh4 age; only *Dinohippus mexicanus* is found in the entire layer, associated with the artiodactyls *Megatylopus*, *Hexobelomeryx*, *Alforjas* and the earliest record in North America of the ground sloth *Paramylodon garbanii*. No early Blancan species have been recovered (Carranza-Castañeda, 1989, 2019; Carranza-Castañeda et al., 2013).

There are additional records of *Stegomastodon primitivus* in Mexican faunas. The senior author found a lower m3 collected at Santa María Amajac in Hemphillian deposits and housed in the University of Hidalgo (Fig. 1). In the collections of LACM are housed jaws and isolated teeth referred to *Stegomastodon primitivus* from the Miñaca-Babicora faunas (collected by E.L. Furlong in 1929). From this collection, the specimen CIT 2008 is a m2 of an old individual, and associated with an M1 of *Teleoceras*, CIT 163/LACM 76746 and jaw fragments of *Teleoceras* with two molars, CIT 163/LACM 76752. This association also contains a jaw fragment of *Catagonus brachydontus*. Although there still no are radiometric ages of these deposits, the association of *Teleoceras-Catagonus* has been also found in the Rancho El Ocote Rhino layer and in other late Hemphillian Mexican faunas from the Tecolotlán basin in Jalisco, which have been dated by $^{40}\text{Ar}/^{39}\text{Ar}$ at 4.95 ± 0.02 Ma (Carranza-Castañeda, 1989; Carranza-Castañeda, 2006; Kowallis et al., 2017; McDonald and Carranza-Castañeda, 2017) (Fig. 1).

The Miñaca fauna (Fig. 1) contains the largest number of *Stegomastodon* fossils so far known in Mexico. The age of this fauna, based on the occurrence of premolars of the carnivore *Chasmaporthestes*, is middle Blancan (Berta, 1981). However, Repenning (1962) referred it to early Blancan based on the presence of the giant ground squirrel *Paenemarmota*. However, it is here stressed that either of these ages is younger than those of the Rancho El Ocote and Santa María Amajac records.

The first report of *Stegomastodon primitivus* in North American faunas was a palate found at the *Stegomastodon* Quarry in Nebraska (Osborn, 1936), which is a site included within the late-early Blancan Sand Draw local fauna (Savage, 1955, Skinner and Hibbard, 1972). The type specimen of *Stegomastodon rexroadensis* (= *S. primitivus*) from Rexroad, Kansas has also been assigned to the early Blancan.

The Cuchillo Negro local fauna from the Palomas Formation in New Mexico includes *Equus* cf. *E. scotti*, *Equus simplicidens*, *Borophagus hilli*, *Blancocamelus meadei*, *Hemiauchenia blancoensis*, and *Stegomastodon primitivus*. All these fossils are referred to the late-early Blancan (Morgan and Lucas, 2011; Lucas et al., 2011b). Additional arguments also used to support this inferred age are: 1) the absence of South American immigrants in this southern USA fauna; 2) the presence of *Camelops*; and 3) the stratigraphic relationship, as the fossil bearing succession lies under the 3.1 Ma Mud Spring Pumice. Therefore, the Cuchillo Negro Creek local fauna has an age range between ~ 3.1 and 3.6 Ma (Morgan and Lucas, 2011).

The Elephant Butte Lake fauna, with its co-occurrence of *Equus scotti* and *Stegomastodon primitivus*, has also been assigned to a late-early Blancan age, late Pliocene ~ 3.1–3.6

Ma (Morgan and Lucas 2011). The absence of South American immigrants confirms a pre-late Blancan age. Lucas et al. (2011b) determined that all records of *Stegomastodon primitivus* in North America faunas, including the Rexroad, Kansas, fauna, which includes the type specimen *Stegomastodon rexroadensis*, must be assigned an early Blancan age (Morgan and Lucas, 2011).

It is remarkable that two Mexican faunas, Rancho El Ocote, Guanajuato, and Santa María Amajac, Hidalgo state, of latest Hemphillian age, contain records of *Stegomastodon primitivus*, which implies that these are the oldest records of this species and genus in North American faunas (Savage, 1955; Repenning, 1962; Flynn et al., 2005; Kowallis et al., 1999; Lucas et al., 2011a,b; Morgan and Lucas 2011; Carranza-Castañeda et al., 2013).

DISCUSSION

1. The jaw collected in the Blanco layer at Rancho El Ocote corresponds to a young individual. It is here referred to *Stegomastodon primitivus*, as the mandible is straight and not deflected downwards, and it also has an elongated symphysis with a premental space that lacks evidence of premolars. Furthermore, the horizontal rami are straight and have no evidence of tusks.

2. The mandible has a complete m1 that is trilophid, with two cusps behind the tritophid that are interpreted as a half lophid. The m2 only has the first two complete lophids, and the trefoils and entotrefoids are simple without folding or accessory cusps. The tritophid of m2 is included in the alveolus. The X ray's analysis shows there are no additional developing cusps behind.

3. The isolated m2 records studied in this paper also show that the trefoil and entotrefoids are simple without folds (ptychodont) or accessory cusps (choerodont). In those m2s from old individuals (inferred from wear), the cusps that lie behind the tritophid form a wide transverse ridge, which is most noticeable in heavily worn molars. This structure is here interpreted as a half lophid that is always present in mature and old individuals.

4. M3 has four well developed lophs and two reduced cusps at the back of the tetraloph, which are here considered as an incipient fifth loph. The m3 has four well-defined lophids, with two tall cusps behind the tetralophid considered a half lophids. These characteristics differentiate the SMA *Stegomastodon* records from those described from the Miñaca-Babicora faunas, which always have five lophs/lophids. Furthermore, the m3 of *Stegomastodon primitivus* from Rexroad Kansas (= *S. rexroadensis*) has five and half lophids, and records from the Cuchillo Negro Creek and Elephant Butte Lake Faunas from New Mexico all have 5+ to six lophids.

5. The Rancho el Ocote jaw was recovered from the sandy Blanco layer, which is latest Hemphillian age (Hh4). $^{207}\text{Pb}/^{235}\text{U}$ zircon analysis of ashes recovered in the same site where the jaw was discovered yielded a date of 4.85 ± 0.13 Ma, which is the isotopic age of the fauna at the site, and confirms the latest Hemphillian age.

According to published isotopic ages (Kowallis et al., 1999), and magnetostratigraphic data (Flynn et al., 2005), the Hemphillian-Blancan (NALMA) boundary at SMA is bracketed between 4.89 ± 0.16 and 4.74 ± 0.14 Ma. The new radiometric date of the Blanco layer of 4.85 ± 0.17 Ma agrees with the latest Hemphillian age of *Stegomastodon primitivus* from Rancho El Ocote, and as the oldest record of this species in North American faunas (Kowallis et al., 1999; Flynn et al., 2005; Lucas et al., a, b; Morgan and Lucas, 2011).

Stegomastodon Pohling, 1912 *Stegomastodon primitivus* Osborn, 1936

Long-term field research at Arroyo El Tanque and tributaries has produced new fossil specimens found and described



FIGURE 11. MPGJ 3699 *Stegomastodon primitivus* GTO 87 Arroyo EarthWatch locality, Rancho Viejo Fauna. **A**, Right lateral view of lower jaw with only m3, short symphysis without premental space nor evidence of i2. Comparison with NMMNH 46496 from Elephant Butte Lake and NMMNH 57406 from Cuchillo Negro Creek, both faunas from New Mexico (Morgan and Lucas, 2011). The measurements are in Table 3. **B**, MPGJ 3699, *Stegomastodon primitivus*, anteroposterior view. The measurements and length of different structures of the jaw are displayed. Measurements are shown in Table 4. **C**, MPGJ 3699, jaw in occlusal view. The different measurements and lengths of the structures of the mandible are observed. Measurements are shown in Table 5.

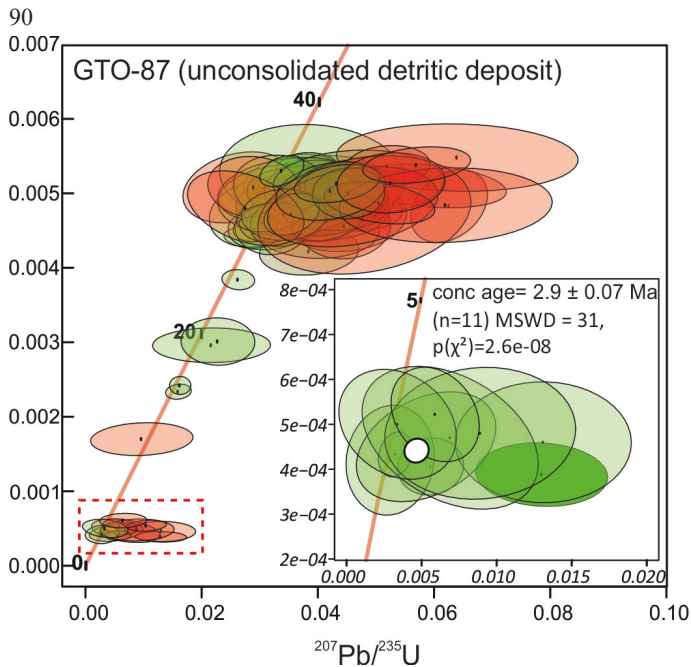


FIGURE 12. Pb/U concordia plots showing the age of the GTO 87 locality from the San Miguel de Allende basin.

for the first time in central Mexico, that complements the biostratigraphy of early Blancan deposits from central Mexico. The last discovery is the first known record of *Rhynchotherium browni* known outside the type locality, San José de Pimas, Sonora state, recovered from the GTO 47 Arroyo Belén locality (Carranza-Castañeda, 2022). The most recent discovery is the mandible of *Stegomastodon primitivus* at GTO 87 Arroyo EarthWatch, collected in deposits from the early Blancan age. The associated fauna from Arroyo El Tanque and its tributaries is characterized by the diversity of South American immigrants discovered in the stratigraphic sequence that has been mentioned in different publications (Montellano-Ballesteros and Carranza-Castañeda, 1981, 1986; Carranza-Castañeda and Miller, 2004; Gillette et al., 2015; Carranza-Castañeda, 2016; McDonald and Carranza-Castañeda, 2017).

Locality GTO 87 Arroyo Earth Watch. This site is ~3 km east of Los Galvanes village (Fig. 1). The site is a small tributary of Arroyo El Tanque. The stratigraphic succession exposed in the area has a thickness of 6–8 m, and it has a uniform, fine-grained lithology. A layer ~3 m thick of clay with abundant irregular concretions of variable sizes is exposed at the base. Resting atop this stratum, there is an alternating succession of clay and fine sand layers where small, rounded concretions are present, sandy strata occur near the top. This succession is covered by a 1-m-thick layer of caliche. A *Stegomastodon* jaw was collected associated with *Nannippus peninsulatus* remains including: a lower molar, a phalanx, a metacarpal fragment and a pelvis fragment, in addition to a complete radius; all of which were inside the jacket in which where the jaw was collected.

Referred material. MPGJ 3699, almost complete jaw that belonged to an old age individual, retaining the m3 on both sides (Fig. 11).

Description. The mandible is complete and displays a brevisrostrine condition. No evidence of tusks is observed. The articular condyles on both sides, and the coronoid processes, are partially missing. The symphysis is decidedly abbreviated in front and ends in a spout-like shape. A large and rounded mental foramen is in the anterior part of the horizontal ramus, 54 mm below the protolophid of m3. A second smaller foramen is 72 mm closer to the edge of the lingual canal and 81 mm away from the m3 protolophid. The foramina are 71 mm apart.

The mandibular angle is pronounced, approximately 50°, considering the line of the occlusal surface from the posterior part of m3 to the lower edge of the gonion. The Ap length of the horizontal rami from the gonion to the most anterior part of the symphysis is 590 mm. The ascending ramus is wide, and the anterior border measured from the coronoid process to the intersection with the alveolar line forms a 110° angle.

In anteroposterior view, the jaw displays strong and deep mandibular rami, and the maximum depth of the horizontal ramus is located under the protolophid of m3. The symphysis is narrow anteriorly, and the length of the lingual channel is 168 mm measured from the protolophid of m3 to the symphysis tip. The lingual channel is bounded by thick edges, and is 58 mm in width. The breadth of the ascending rami is 225 mm. Measurements are illustrated in Fig. 11 and Table 3.

Dentition. The mandible only preserves the two m3s. The molars have five heavily worn lophids because of advanced wear. The right m3 retains small enamel tubercles with no evidence of wear (choerodont) (Fig. 10C and Tables 4 and 5).

Comparison

The specimens of *Stegomastodon* from the San Miguel Allende basin are not easily comparable because they correspond to different stratigraphic ages. Furthermore, MPGJ 3525 from latest Hemphillian age of Rancho El Ocote is a very young individual and MPGJ 3699 belongs to an old adult individual collected in early Blancan deposits; the differences are remarkable and significant.

The specimens MPGJ 3699 and NMMNH 46496 from the Elephant Butte Lake Fauna are similar in the spout-like shape of the symphysis. The depth of the horizontal rami is similar, and, also, the mental foramen is located under the protolophid of m3. In MPGJ 3699 the depth of the horizontal branch from this point is 106 mm. The mandible of NMMNH 46496 is slightly larger than that of MPGJ 3699. The Ap length of m3 in MPGJ 3699 is 204 mm and the Tr 79 mm length in the tritolophid; the index is 38 in NMMNH 46496 specimen Ap is 191 mm and Tr 83 mm with index of 43. The comparison was established using Morgan and Lucas's (2011) measurements (see Table 2).

In occlusal view, the maximum width of the mandibular ramus is in the posterior part of m3, which is like NMMNH 46496 from Elephant Butte Lake and NMMNH 57406 from Cuchillo Negro Creek. The only difference that can be mentioned is in the faint divergence in the protolophids of the m3 specimen from Arroyo EarthWatch, which is not observed in the New Mexican teeth. The measurements are summarized in Table 5 and illustrated in Fig. 11C.

The m3 of the Guanajuato specimen MPGJ 3699 has five extremely worn lophids. In the Rm3 the posterior part of the fourth lophid has two cusps separated by a medial sulcus. This structure is like an elongated transverse crest that could be considered a half lophid, narrower than the other lophids of the tooth. The NMMNH 57406 mandible from Cuchillo Negro Creek is similar to the Arroyo Earth Watch specimen but has five + lophids and some enamel tubercles (choerodont).

The differences in dimensions between the m3 from GTO 87 Arroyo Earth Watch and the New Mexico specimens are not considered significant. The similarities indicate that the species *Stegomastodon primitivus* had a wide geographic distribution.

Age of the Arroyo EarthWatch Locality

In the same jacket in which the jaw was collected are remains of *Nannippus peninsulatus*, which is widely distributed in the upper Rancho Viejo Beds of San Miguel de Allende, associated in other localities with early Blancan index fossils such as *Borophagus diversidens*, *Felis studei*, *Equus simplicidens*, *Rhynchotherium browni*, and *Hemiauchenia blancoensis*, in addition to the South American immigrants *Glyptotherium*

texanum and *Nechoerus cordobae*. This associated fauna is assigned an early Blancan age (Carranza-Castañeda and Miller, 1988; Carranza-Castañeda and Espinosa-Arrubarena, 1994; Gillette et al., 2015; Carranza-Castañeda, 2016, 2019).

Radiometric Age

An isotopic U-Pb age obtained from zircons separated from an ash bed interstratified with the fossil-bearing sediments where the mandible was collected yielded a date of 2.9 ± 0.07 Ma (Fig. 12, $n=11$, MSWD=31), consistent with the inferred early Blancan age for the mandible and associated fauna.

This result allows us to correlate the MPGJ 3699 specimen with *Stegomastodon primitivus* from the Cuchillo Negro L.F. and Elephant Butte Lake fauna of the Palomas Formation, New Mexico, assigned to late early Blancan according to Morgan and Lucas (2011). These results allow correlation of the two faunas chronologically (Lucas and Oakes, 1986; Morgan and Lucas, 2003, 2011).

Correlation

The stratigraphic sequence of Arroyo EarthWatch GTO 87 is chronologically correlated with the sedimentary sequence of Arroyo Belén GTO 47, where the skull and mandible of *Rhynchotherium browni* were collected. The U-Pb zircon age at that site is 2.96 ± 0.17 Ma, which is undistinguishable from the age obtained by the same method from the ashes from the EarthWatch GTO 87 site. Both ravines are only 500 m apart (Carranza-Castañeda, 2022).

CONCLUSIONS

1. We follow Lambert and Shoshani's (1998) criteria in this work, which only recognizes two species for the *Stegomastodon* genus, *S. primitivus* Osborn 1936, restricted to the early Blancan, and *S. mirificus* (Leidy, 1858), of late Blancan-early Irvingtonian age.

2. Based on the m3 and m2 characters, it has been considered that *Stegomastodon primitivus* (= *S. rexroadensis*) presents the simplest features of the genus; m2 is trilophid and m3 has five and half lophids (Woodburne, 1961, table IV). However, we note that the isolated MPGJ 5340 M3 specimen collected from the Blanco layer has five lophids (fifth loph is reduced).

3. MPGJ 3527 m3 with four lophids and two posterior accessory cusps, is interpreted as a half lophid. Furthermore, all m2 are trilophid, but in mature individuals it has an additional half lophid as is observed in MPGJ 1983 and MPGJ 3518.

4. All m3s from the Miñaca fauna have five lophids, without accessory cusps, and New Mexico records have five-six lophids. It is noteworthy that the disposition of lophids / lophids of the molars of these faunas differ from the M3/m3 described from Rancho El Ocote, which present simpler and more primitive characteristics than *Stegomastodon primitivus*.

5. The ~4.85 Ma isotopic age, obtained from zircon crystals separated from an ash sample collected at the site where the MPGJ 3525 jaw was collected, agrees with the latest Hemphillian NALMA inferred age for this specimen. Thus, this is the oldest record of *Stegomastodon* in the North American faunas. The not yet formally described *Stegomastodon primitivus* specimens from Santa Maria Amajac, Hidalgo, are associated with *Teleoceras*, which is a late Hemphillian index fossil, is also in accordance with the MPGJ 3525 inferred age.

6. All the evidence discussed in this paper is consistent with the hypothesis that the *Stegomastodon primitivus* radiation could have occurred in the central region of Mexico, before the diversification of *Stegomastodon* (Rexroad, Miñaca), as suggested by Savage (1955), in his tentative phyletic and dispersal pattern of the gomphotheriids in the Northern Hemisphere.

7. It is important to note that in the sedimentary basins

of central Mexico, gomphotheriids have been described in the early-late Hemphillian: *Gomphotherium hondurensis* (Juchipila Basin, Zacatecas, 6.53 Ma; Landa de Matamoros, Querétaro and late Hemphillian Cuenca de Tecolotlán, Jalisco, 4.89 Ma). Early Blancan *Rhynchotherium falconeri* from Rancho La Goleta (3.6 Ma), state of Michoacán and *Rhynchotherium browni*, early Blancan from Arroyo Belén, SMA (2.9 Ma). *Stegomastodon primitivus* from early Blancan from Arroyo EarthWatch 2.91 Ma) and the oldest 4.86 Ma latest Hemphillian from Rancho El Ocote, Guanajuato. Besides, all these Mexican records have isotopic ages.

8. Based on these comments, it is remarkable that gomphotheriids had a wide geographic distribution and representatives during the Hemphillian-Blancan (NALMA), ages in basins of central Mexico.

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APPENDIX

TABLE 1. MPGJ 3525, measurements (in mm) of the left dentary of *Stegomastodon primitivus*, from Rancho El Ocote.

1.	Maximum ventral length from the symphysis to the gonion	625
2.	Width of ascendant ramus from the occlusal Surface line	198
3.	High of the condyle since the occlusal surface	193
4.	Depth of the horizontal ramus under the metalophid of m2	148
5.	Depth of the horizontal ramus under the metalophid of m1	132
6.	Angle of ascendant ramus and the occlusal surface	110°

TABLE 2. MPGJ 3525, jaw, measurements (in mm) of *Stegomastodon primitivus* from Rancho El Ocote,

1.	Distance of mental foramen to enamel of protolophid	84
2.	Lingual length from anterior part of m1 to internal border of symphysis	164
3.	Width of horizontal ramus across the root of ascendant ramus	122
4.	Width of horizontal ramus across m1-m2	88
5.	Width of the protolophid of m1	72
6.	Width of the metalophid of m2	88
7.	Anteroposterior length of m1	119
8.	Width of metalophid of m1	69
9.	m1 index	5.7
10.	Distance from the tip to the anterior border of the posterior mentonian foramen	180

TABLE 3. MPGJ 3699, Measurements (in mm) of *Stegomastodon primitivus*, GTO 87 Arroyo EarthWatch anterior view.

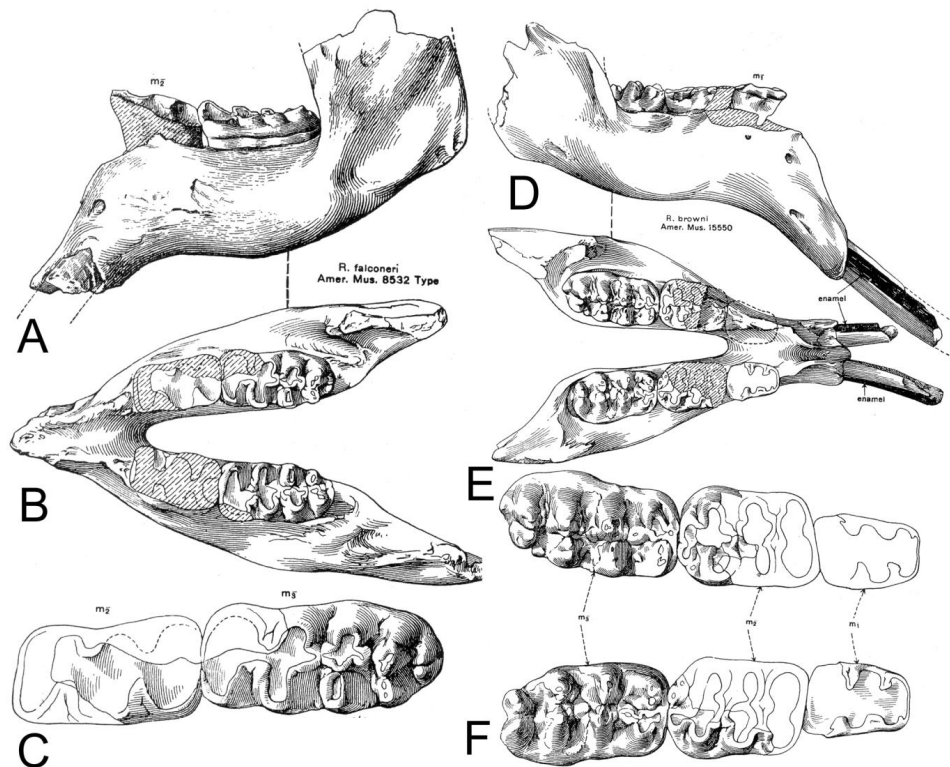
1.	Maximum length between the condyle	436
2.	Lingual width between the protolophid of m3	104
3.	Wide lingual channel	52
4.	Distance between mental foramina	238
5.	Length between the roots of ascendant rami	225
6.	Distance from the tip of symphysis protolophid of m3	168

TABLE 4. MPGJ 3699, Measurements (in mm) of *Stegomastodon primitivus*, GTO 87 Arroyo EarthWatch, jaw lateral view Early Blancan.

1.	Maximum length from the Gonion to the tip of symphysis	590
2.	Maximum length from the Gonion to condyle	240
3.	Depth between gonion and coronoid process	290
4.	Maximum width between the condyle and coronoid process	225
5.	Depth horizontal ramus in posterior part of m3	156
6.	Depth Horizontal ramus below mental foramen	106
7.	Depth horizontal ramus below protolophid of m3	159
8.	Maximum anteroposterior length of m3	204
9.	Distance between the protolophid of m3 and the tip of the symphysis	175
10.	Length from tip of the symphysis to mental foramen	182
11.	Anteroposterior length of ascending ramus	244
12.	Height of coronoid process from the horizontal rami	310

TABLE 5. MPGJ 3699, Measurements (in mm) of *Stegomastodon primitivus*, GTO 87 Arroyo EarthWatch, occlusal view.

1.	Transverse width at the root of the ascending branch	124
2.	Width of the jaw through the roots the ascending rami posterior m3	336
3.	Anteroposterior length of m3	204
4.	Transverse width of m3 (at 3rd lophid)	79
5.	Maximum length between condyles	423
6.	Maximum distance between the condyles and the tip of the symphysis	593
7.	Jaw maximum breadth across middle of m3	345
	index of m3	3.8



Representative lower jaws of *Rhynchotherium* (from Osborn, 1936). (From Lucas, this volume).