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A new specimen of *Eremotherium laurillardi* (Xenarthra, Megatheriidae) from the Late Pleistocene of Chiapas, and comments about the distribution of the species in Mexico

Un nuevo espécimen de Eremotherium laurillardi (Xenarthra, Megatheriidae) del Pleistoceno tardío de Chiapas, y comentarios sobre la distribución de la especie en México

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ABSTRACT

Eremotherium laurillardi was a common giant ground sloth in the Late Pleistocene of the Americas. A right femur referable to this species was recovered from fluvial sediments in Constitución 27 colony, Socoltenango municipality, in the southern State of Chiapas, Mexico. The femur shows the morphological characteristics of *E. laurillardi*, such as: large size; rectangular shape, it is dorsoventrally flattened; lateral and medial margin rectilinear and parallel, and patellar trochlea transversely elongated with the medial margin in the sagittal plane of the femur. The record from Constitución 27 town, adds a new locality for *E. laurillardi* in Mexico, which adds to the previously known seven localities with remains of this species in Chiapas. In Mexico, *E. laurillardi* is present in 31 localities distributed in 13 states, mainly in the central and southern portion of Mexico, with an altitudinal range between 0-200 up to 2000-2500 meters above sea level, indicating a mostly tropical distribution of this species.

Keywords: giant ground sloth, Folivora, paleobiogeography, Late Pleistocene.

RESUMEN

Eremotherium laurillardi fue un perezoso terrestre gigante común en el Pleistoceno tardío de América. Un fémur derecho completo referible a esta especie fue recuperado de sedimentos fluviales en el municipio de Socoltenango, en el estado de Chiapas, sur de México. El fémur muestra las características morfológicas de *E. laurillardi*, como son: forma rectangular, dorsoventralmente aplanado; margen lateral y medial rectilíneos y paralelos; tróclea patelar transversalmente alargada con el margen medial extendiéndose hacia el plano sagital del fémur. El registro de la colonia Constitución 27, agrega una nueva localidad con restos de *E. laurillardi* en México, la cual se suma a las siete localidades previamente conocidas con restos de esta especie en Chiapas. En México, *E. laurillardi* proviene de 31 localidades distribuidas en 13 estados, principalmente en la parte central y sur de México, en rangos altitudinales entre 0-200 hasta 2000-2500 msnm, lo que denota una distribución preferentemente tropical para esta especie.

Palabras clave: perezoso terrestre gigante, Folivora, paleobiogeografía, Pleistoceno Tardío.

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1. Introduction

The sloths (suborder Folivora) are representatives of a singular group in the Xenarthra that includes eight families: Entelopidae, Bradypodidae, Scelidotheriidae, Mylodontidae, Nothrotheriidae, Megalonychidae and Megatheriidae (Rose *et al.*, 2009). The last Family includes the largest ground sloths that lived at the end of Pleistocene, *Megatherium* and *Eremotherium*.

Eremotherium has three species with morphological differences, timing and distribution: *E. omigraus*, found in Late Pliocene-Early Pleistocene of Florida, USA; *E. sefvei*, restricted to the Pleistocene of Bolivia, and *E. laurillardi*, from the Late Pleistocene from Brazil to USA, being this the most commonly found species in the North and South American continents (Cartelle and De Iuliis, 1995; De Iuliis and St-André, 1997; De Iuliis and Cartelle, 1999).

Eremotherium laurillardi was very common during the Rancholabrean of North America and Lujanian of South America (Cartelle and De Iuliis, 2006). It is believed that this species reached a body mass of 3900 to 5000 kilograms and a length of 6 m including the tail (Cartelle, 2000; McDonald, 2012). Isotopic data indicate that this species was herbivorous, and it fed both herbaceous plants and shrubs (Franca *et al.*, 2014; Pérez-Crespo *et al.*, 2015).

In Mexico *E. laurillardi* has been mainly reported from localities in the central and southern part of the country (Polaco-Ramos, 1981; McDonald, 2002). However, despite the numerous records, only a little of this material has been formally described, so that the intraspecific variations in individuals found in Mexico are unknown. Another problem is that since the work of McDonald (2002), there has been no updated compilation of new localities for this genus in Mexico and

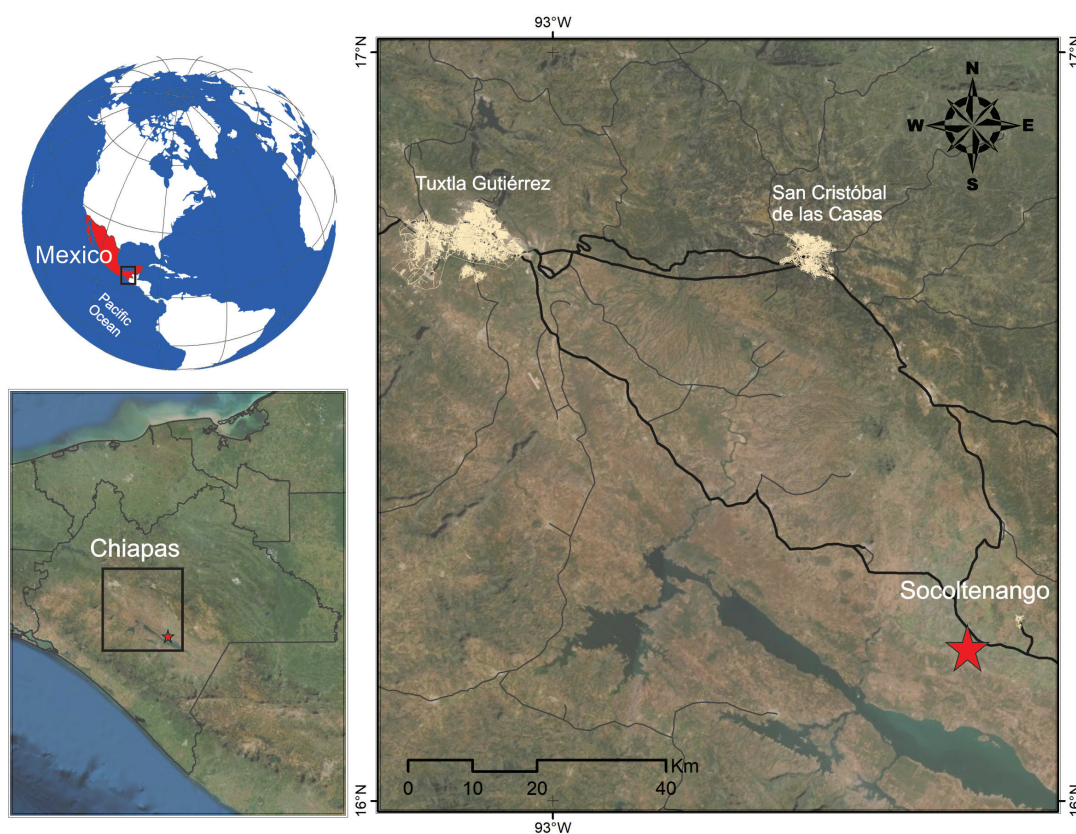


Figure 1 Location of the Constitución 27 (red star), in the Socoltenango municipality, Chiapas, southeastern Mexico.

therefore the paleobiogeographic history of the species has gaps.

Herein, we describe a femur referred to *E. laurillardi* collected from undifferentiated fluvial sediments (sand and gravel) that crop out at the edge of a natural irrigation channel near Constitución 27 town, in the Socoltenango municipality, State of Chiapas, southern Mexico (Figure 1). In addition, an extensive review of the records of *E. laurillardi* in Mexico is presented, adding new locations to the list of McDonald (2002). Finally, the distribution and paleobiogeography of this species in Mexico is discussed.

Institutional abbreviations: *IHNFG*, Instituto de Historia Natural, Fósil Geográfico, historically is the acronym used for the Paleontological Collection of the Secretaría de Medio Ambiente e Historia Natural of Chiapas, Chiapas, Mexico; *FMNH*, Field Museum of Natural History, Chicago, USA; *MCL*, Museu de Ciências Naturais da Pontificia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; *MNP*, Museo Nacional de Panama, Panama City, Panama; *MNRJ*, Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; *ROM*, Royal Ontario Museum, Toronto, Canada; *UCMP*, University of California Museum of Paleontology, Berkeley, USA; *USNM*, National Museum of Natural History, Smithsonian Institution, Washington, USA; *ZMUC*, Zoologisk Museum Universitat Copenhagen, Copenhagen.

2. Material and Methods

The material reported here consists of a right femur with excellent preservation, collected by Mario Roberto Pérez Moreno, a local resident of the Constitución 27 town. The specimen is housed in the paleontological collection of the Museo de Paleontología “Eliseo Palacios Aguilera”, Paleontology Department, Secretaría de Medio Ambiente e Historia Natural of Chiapas, under the catalog number IHNFG-5324. The bone showed signs of dragging on the medial and lateral edges in both proximal and distal ends. The measurements were

taken with a tape measure following to De Iuliis (1996) and are shown in figure 2. The photographs were taken with a digital camera and processed in Corel Photo-Paint X8.

Eremotherium laurillardi records from Mexico were compiled based on the compilations of Polaco-Ramos (1981) and McDonald (2002), complemented with the recent reports published in scientific journals, books chapter and academic meeting's abstracts. With this data, we produced an updated distribution map of *E. laurillardi* in Mexico, using the hypsometric range map available at the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.

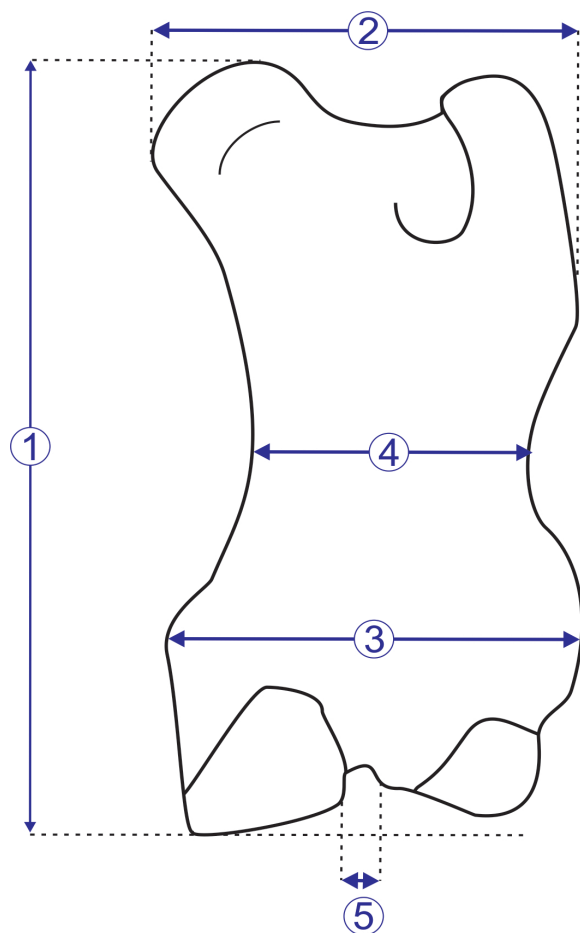


Figure 2 Schematic drawing of the femur showing the measurements taken. 1) Greatest proximodistal length, 2) greatest proximal transverse width, 3) greatest distal transverse width, 4) minimum width at midshaft, 5) distance between the distal articular facets.

3. Results

3.1. SYSTEMATIC PALEONTOLOGY

Superorder Xenarthra Cope, 1889

Order Pilosa Flower, 1883

Suborder Folivora Delsuc, Catzefflis, Stanhope,
and Douzery, 2001

Family Megatheriidae Gray, 1821

Subfamily Megatheriinae Gill, 1872

Genus *Eremotherium* Spillmann, 1948

***Eremotherium laurillardii* (Lund, 1842)**

Type specimen: ZMUC 1130, isolated molariform tooth of a juvenile specimen from the Pleistocene of Lagoa Santa, Minas Gerais, Brazil (Cartelle and De Iuliis, 1995).

Synonymy. *Megatherium americanum* (Palacios, 1950); *Eremotherium mirabile* (Polaco-Ramos, 1981); *E. quanajuatense* (Dugès, 1896); *E. quanajuatense*

(Monés, 1973); *E. rusconii* (Polaco-Ramos, 1981); *E. carolinense* (Hoffstetter, 1952); *E. elenense* (Hoffstetter, 1952).

3.2. DESCRIPTION

IHNFG-5324 is a complete right femur (Figure 3). Its total length is 780 mm (see table 1). Its contour is rectangular in cranial and caudal view (Figures 3A and 3B), with the proximal and distal ends parasagittally aligned. The shaft is thin in the anteroposterior view and laterally it has a small twist that gives it a sigmodial appearance (Figure 3C). The proximal and distal epiphyseal sutures are fused. The medial edge of the femur is almost straight, while the lateral edge is slightly concave. The head of the femur is robust and is proximomedially oriented with an inclination of 40° in relation to the longitudinal central axis. The base of the articular condyle is short and wide, so

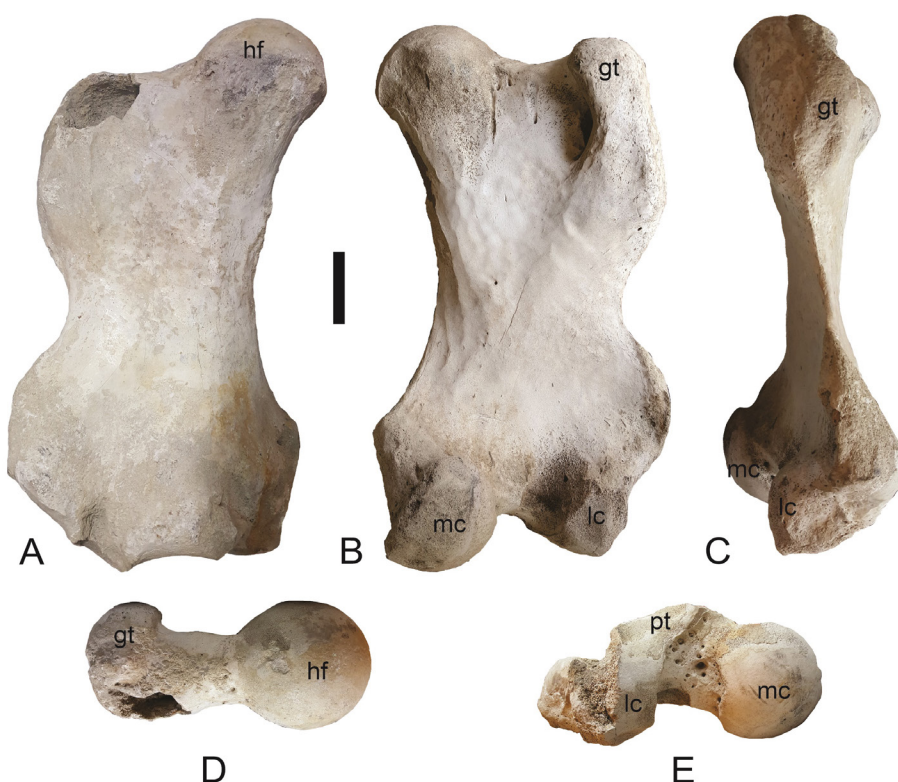


Figure 3 Right femur of specimen IHNFG-5324 from Constitución 27 town, in A) anterior, B) posterior, C) lateral, D) proximal and E) distal view. Abbreviations: gt, great trochanter; hf, head of femur; lc, lateral condyle; mc, medial condyle; pt, patellar trochlea. Bar scale equals 10 cm.

Table 1. Measurements (in mm) of IHNFG-5324 and selected specimens of *E. laurillardii*. Specimens marked with asterisk (*) taken from De Iuliis (1996).

	IHNFG-5324	MCL 9524*	MNRJ 3866*	ROM 19788*	FMNH F26970*	USNM 11650*	MNP 45*	UCMP V4201*
1. Greatest proximodistal length	780	826	714	723	684	816	828	895
2. Greatest proximal transverse width	404	447	365	385	360	416	420	447
3. Greatest distal transverse width	412	432	359	405	356	445	455	476
4. Minimum width at midshaft	260	320	275	280	258	300	255	330
5. Distance between the distal articular facets	44	44	14	38	26	40	26	32

it hardly differs from the rest of the femur. The greater trochanter is not as prominent and does not reach the level of the head of the femur, as in *M. americanum*. At the distal end, the medial condyle and the lateral condyle are present, which have large joint surfaces. The medial condyle is larger than the lateral condyle, the latter being more convex. The patellar trochlea extends transversely to the medial edge of the lateral condyle (Figure 3E).

3.3. RECORDS IN MEXICO

Eremotherium laurillardii is the most widespread ground sloth in Mexico with 31 localities distributed in 13 states (Figure 4, Table 2). Until now, the northernmost record came from El Cedral, San Luis Potosí (Polaco-Ramos, 1981), followed by Arperos, Guanajuato (Dugès, 1896). Chiapas and Jalisco are the states with most localities with *E. laurillardii* remains, eight and seven, respectively. In Chiapas all the localities are distributed in the Central Basin, and are: El Baji6n locality, Suchiapa municipality; Nandachuqu6, Chiapa de Corzo municipality; Ignacio Zaragoza, La Concordia municipality; Road to Monterrey town and La Simpat6a localities, Villa Corzo municipality; Gliptodonte and El Sabino localities, Villaflores municipality, and recently Constituci6n 27, Socoltenango municipality (Palacios, 1950; Santamar6a *et al.*,

1983; Than-Marchese, 2009; Than-Marchese *et al.*, 2012; G6mez-P6rez and Carbot-Chanona, 2012). In Jalisco state, the localities are Zacoalco, Venustiano Carranza, Chapala lake, El Lim6n, El Grullo, Tonaya, and Rancho El Aguacate, Amacueca (Polaco-Ramos, 1981; McDonald, 2002; Viramontes, 2015; Aguilar *et al.*, 2015). Other localities in western Mexico are Arteaga, Aguacate and Hihuitl6n, Michoac6n; and Cerro Guayabilla, Colima (Polaco-Ramos, 1981; McDonald, 2002). Chimalacatl6n, Morelos (Torres-Mart6nez, 2004), Tlatlaya, Estado de M6xico (Polaco-Ramos, 1981), and San Mateo Huexoyuc6n, Tlaxcala (S6nchez *et al.*, 2016), are localities located in the south-central region. In eastern Mexico the localities are Atoyac and Veracruz, Veracruz (Pe6a-Serrano and Carbot-Chanona, 2010; Alvarado-Mendoza *et al.*, 2013), although remains of the genus are known from at least four more locations in Veracruz state, but they have not been formally reported (Pe6a-Serrano, 2016, com. pers.). Besides those from Chiapas, other locations in southern Mexico are Puerto Escondido; Etila, and Barranca del Muerto (Santiago Chazumba), in Oaxaca state (Polaco-Ramos, 1981; Guerrero-Arenas *et al.*, 2016; Vi6as-Vallverd6 *et al.*, 2017); and Apaxtla, Guerrero (Torres, 1981). In southeastern Mexico there is a unique locality in Teapa, Tabasco (Polaco-Ramos, 1981; McDonald, 2002).

Table 2. Localities with records of *Eremotherium laurillardii* in Mexico.

ID locality	Locality	State	NALMA/Age	Reference
1	Etla	Oaxaca	Pleistocene	Polaco-Ramos, 1981
2	Puerto Escondido	Oaxaca	Late Pleistocene	Guerrero-Arenas <i>et al.</i> , 2016
3	Barranca del Muerto, Santiago Chazumba	Oaxaca	Rancholabrean/Late Pleistocene	Viñas-Vallverdú <i>et al.</i> , 2017
4	Chimalacatlán	Morelos	Late Pleistocene	Torres, 2004
5	Apaxtla	Guerrero	Pleistocene	Torres, 1981
6	Tlatlaya	Estado de México	Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
7	Arteaga	Michoacán	Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
8	Hihuitlán	Michoacán	Pleistocene	Polaco-Ramos, 1981
9	Aguanato	Michoacán	Pleistocene	Polaco-Ramos, 1981
10	Cerro Guayabilla	Colima	Pleistocene	Polaco-Ramos, 1981
11	Venustiano Carranza	Jalisco	Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
12	El Limón	Jalisco	Pleistocene	Viramontes, 2015
13	El Grullo	Jalisco	Pleistocene	Viramontes, 2015
14	Tonaya	Jalisco	Pleistocene	Viramontes, 2015
15	Rancho El Aguacate, Amacueca	Jalisco	-----	Aguilar <i>et al.</i> , 2015
16	Zacoalco	Jalisco	Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
17	Chapala lake	Jalisco	Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
18	El Cedral	San Luis Potosí	Late Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
19	Arperos	Guanajuato	----	Dugès, 1896
20	San Mateo Huexoyucán	Tlaxcala	Rancholabrean/Late Pleistocene	Sánchez <i>et al.</i> (2016)
21	Atoyac	Veracruz	Late Pleistocene	Peña-Serrano and Carbot-Chanona, 2010
22	Buenavista, Veracruz,	Veracruz	Late Pleistocene	Alvarado-Mendoza <i>et al.</i> , 2013
23	Teapa	Tabasco	Late Pleistocene	Polaco-Ramos, 1981; McDonald, 2002
24	El Bajián, Suchiapa	Chiapas	Late Pleistocene	Than-Marchese <i>et al.</i> , 2012
25	Nandachuquí, Chiapa de Corzo	Chiapas	Late Pleistocene	this work
26	Socoltenango	Chiapas	Late Pleistocene	this work
27	Ignacio Zaragoza, La Concordia	Chiapas	Late Pleistocene	Than-Marchese, 2009
28	Road to Monterrey town, Villa Corzo	Chiapas	Late Pleistocene	Santamaría <i>et al.</i> , 1982
29	La Simpatía locality, Villa Corzo	Chiapas	Rancholabrean/Late Pleistocene	this work
30	Gliptodonte locality, Villaflores	Chiapas	Rancholabrean/Late Pleistocene	Gómez-Pérez and Carbot-Chanona, 2012
31	El Sabino, Villaflores	Chiapas	Late Pleistocene	Palacios, 1950

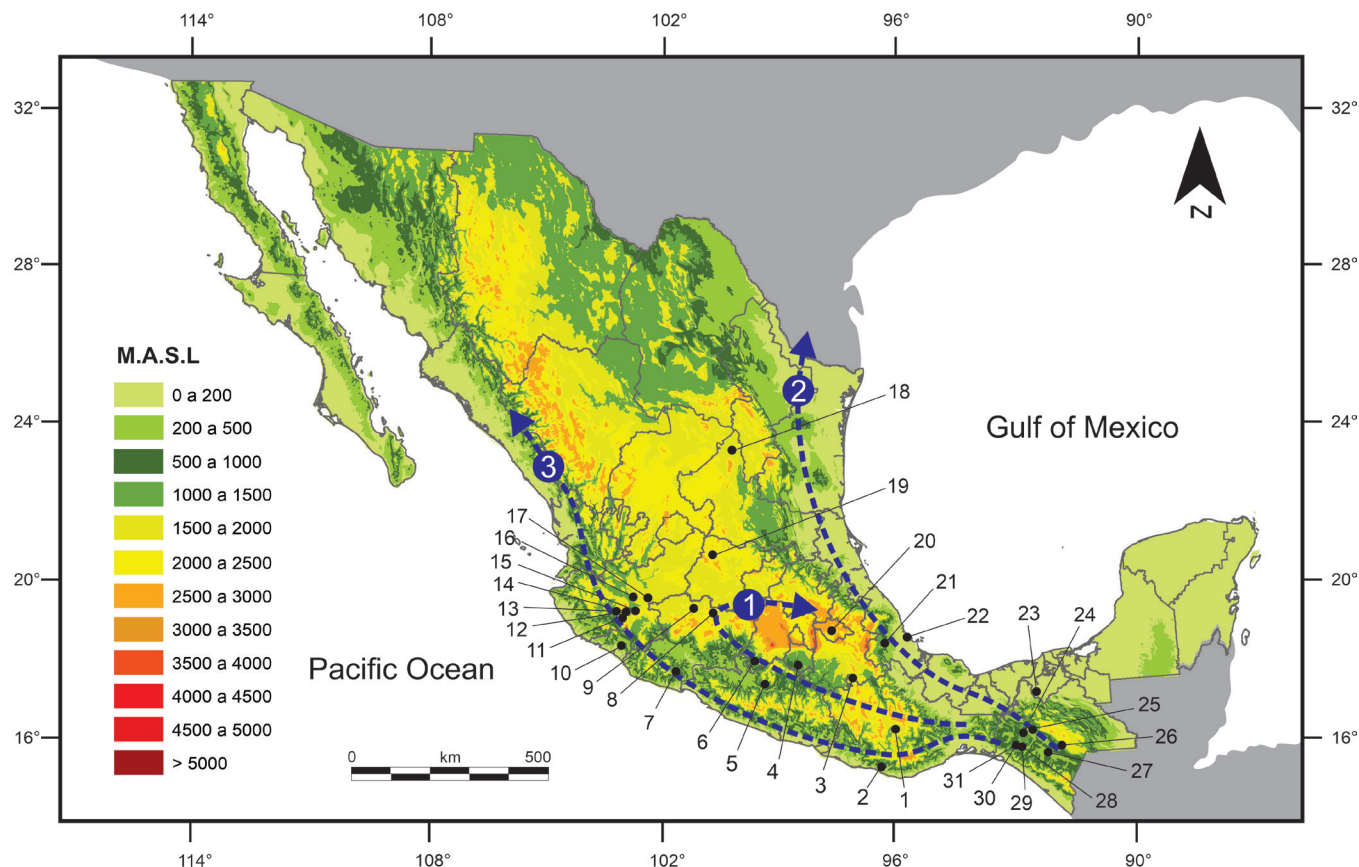


Figure 4 Localities with *Eremotherium laurillardi* in Mexico. For references of the localities see table 2. The arrows show the biological corridors *sensu* Ceballos *et al.* (2010): temperate corridor Transvolcanic Belt - Sierra Madre del Sur (1), and the tropical corridors Tamaulipas - Central America Gulf Lowlands (2), and Sonora - Central America Pacific lowlands (3).

4. Discussion

4.1. TAXONOMIC ASSIGNMENT

Among Pleistocene ground sloths, the femora of Megatheriidae are the only rectangular shaped bones (De Iuliis, 1996). The specimen IHNFG-5324 has the typical rectangular shape, which indicates that it is a Megatheriinae. Two species of Megatheriinae ground sloths are known from the Late Pleistocene, *Megatherium americanum*, restricted to Brazil and Argentina, and *Eremotherium laurillardi*, which had a distribution from the southeastern of the United States of America to Brazil (Cartelle and De Iuliis, 1995). According to De Iuliis and St-André (1997), the femur of *M. americanum* and *E. laurillardi* can be differentiated

by the following features: 1) The greater proximal and distal transverse widths relative to the midshaft width in *M. americanum*; 2) lateral and medial margins are more medially convex in *M. americanum*, whereas in *E. laurillardi* are more rectilinear and parallel; 3) patellar trochlea in *E. laurillardi* is transversely elongated, and the medial anterior margin extends substantially towards the sagittal plane of the femur, while the trochlea of *M. americanum* is reduced essentially to an anterodorsal tibial facet lateral extension. The patellar trochlea is a less variable character in the femur of Megatheriinae and therefore is useful for differentiating between *E. laurillardi* and *M. americanum* (De Iuliis, 1996). The specimen IHNFG-5324 has all the features known for the *E. laurillardi* femur (Figure 3) and therefore we refer it to this species.

4.2. PALEOBIOGEOGRAPHY

Figure 4 shows that majority of the localities with *E. laurillardi* are distributed in the central and southern portion of Mexico, ranging at heights between 0-200 up to 2000-2500 meters above sea level. Contrarily, in USA, *E. laurillardi* has been found in localities restricted to the Atlantic and Gulf Coastal Plain, south of the Piedmont portion of the Appalachian Highlands and the Balcones escarpment in Texas, where elevation is low (below of 200 meters above sea level) and the relief is minimal (McDonald and Lundelius, 2009). In Central America there are records of *Eremotherium laurillardi* in Guatemala, El Salvador and Honduras (Webb and Perrigo, 1984; Cisneros, 2005; Dávila *et al.*, 2019). In Guatemala this species has been mainly recorded in localities with low elevation, in La Estanzuela (160 m.a.s.l.), Petén (170 m.a.s.l.), and Chiquimula (424 m.a.s.l.); the site with highest elevations is Guatemala City (1500 m.a.s.l.). Similarly, the Río Tomayate locality, San Salvador city, El Salvador, *E. laurillardi* has records in medial elevations (~500 m.a.s.l.). In South America, *E. laurillardi* is recorded mainly in the Atlantic coast of Venezuela and Brazil, whereas in Perú and Ecuador it has a distribution over the Pacific coast (Cartelle and De Iuliis, 1995). Contrarily, in Cundinamarca, Colombia, a record of *E. laurillardi* came from altitudinal range above 3000 m.a.s.l. (De Porta, 1961).

El Cedral, San Luis Potosí, is the northernmost locality in Mexico, and the southernmost localities are Constitución 27 and Ignacio Zaragoza, in the State of Chiapas. Of the 31 localities, only two (Buenavista, Veracruz and Puerto Escondido, Oaxaca) are at sea level. The low occurrence of *E. laurillardi* in sea level sites in Mexico is different to the occurrence seen in USA, where the species seems to have a coastal plain environment preference (McDonald and Lundelius, 2009).

The wide altitudinal distribution of *E. laurillardi* in Mexico suggests that it inhabited diverse types of ecological regions, from coastal plains to open forests. *Eremotherium laurillardi* was distributed

throughout Mexico using the temperate corridor of the Transvolcanic Belt – Sierra Madre del Sur, and the tropical corridors Tamaulipas – Central America Gulf Lowlands, and Sonora – Central America Pacific lowlands (*sensu* Ceballos *et al.*, 2010). This shows that *E. laurillardi* used the same routes and habitat as the Harlan's ground sloth *Paramylodon harlani* (Carbot-Chanona *et al.*, 2021) to move from south to north. The presence of a greater number of localities with *E. laurillardi* remains in Chiapas, compared to other states of Mexico, could be due its geographical position, where the climate was more agreeable for this species, given to its preference for tropical or semitropical areas. The several records in Guatemala (Dávila *et al.* 2019), and the abundant individuals recovered in the Río Tomayate, El Salvador (Cisneros, 2005), areas close to Chiapas, support this idea.

Ferrusquía-Villafranca *et al.* (2010) proposed that migration routes from South America toward North America, in Mexico where: (1) along the Pacific coast, bordering the Sierra Madre de Chiapas; and (2) along the Gulf coast. However, the *E. laurillardi* fossil record in Chiapas, as well as of other megamammals (*e.g.* glyptodonts, capybaras, mammoths, gomphotheres, horses, camels) found in the region (Gómez-Pérez and Carbot-Chanona, 2012; Jiménez-Hidalgo *et al.*, 2019; Carbot-Chanona *et al.*, 2020), indicate that probably the major migratory route from South America was through the Central Basin of Chiapas.

5. Conclusions

The right femur IHNFG-5324 described in this work, documents a new specimen of the giant ground sloth *Eremotherium laurillardi* in the State of Chiapas. The record from Constitución 27 town, adds the eighth locality with remains of this species in Chiapas. Its wide occurrence in Chiapas could be indicative of the tropical or semitropical climate in the region. The presence of *E. laurillardi* and other megamammals in several localities in the Chiapas Central Basin, shows that this area

was the principal migratory route from Central America to the central and northern parts of Mexico, and vice versa, denoting the importance of southern of Mexico in the understanding of the migratory routes of megamammals across the country.

In Mexico, *E. laurillardi* is the Late Pleistocene ground sloth with most records, distributed mainly in the central and southern part of the country. It has been recorded in 31 localities, with altitudinal ranges between 0-200 up to 2000-2500 meters above sea level, suggesting that it inhabited diverse types of ecological regions

that the specimen was placed in the Museum of Paleontology “Eliseo Palacios Aguilera”. Thanks to Eduardo Jiménez-Hidalgo for the comments on the early draft of the manuscript. H. Gregory McDonald, Ana Lucia Valerio and one anonymous reviewer provided useful comments that improved the manuscript.

Conflicts of interest

The authors of this work declare that there is no conflict of interest.

Contributions of authors

This article was prepared by G. Carbot-Chanona (G.C.C.), L. E. Gómez-Pérez (L.E.G.P.) and M. A. Coutiño-José (M.A.C.J.) also, specifically, (1) conceptualization (G.C.C.; L.E.G.P.; M.A.C.J.), (2) analysis or data acquisition (G.C.C.; L.E.G.P.; M.A.C.J.), (3) methodologic-technical development (G.C.C.; L.E.G.P.; M.A.C.J.), (4) writing of the original manuscript (G.C.C.; L.E.G.P.; M.A.C.J.), (5) writing of the corrected and edited manuscript (G.C.C.; L.E.G.P.; M.A.C.J.), (6) graphic design (G.C.C.; L.E.G.P.; M.A.C.J.), (7) fieldwork, (8) interpretation (G.C.C.; L.E.G.P.; M.A.C.J.),

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