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First record of the collared peccary *Dicotyles tajacu* (Artiodactyla, Tayassuidae), in the Gliptodonte locality, Villaflores municipality, Chiapas

Primer registro del pecarí de collar Dicotyles tajacu (Artiodactyla, Tayassuidae), en la localidad de Gliptodonte, municipio de Villaflores, Chiapas.

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Abstract

Tayassuidae (peccaries) is a family of artiodactyls exclusively of America, that was widely distributed in North America during the Pleistocene. Nevertheless, records of this family are scarce in Mexico. The only valid species reported from the Late Pleistocene in Mexico were *Platygonus compressus* and *Dicotyles tajacu*, based on a few specimens. In this study, we report a new peccary specimen from the Gliptodonte locality (Late Pleistocene, Rancholabrean NALMA), Villaflores municipality, in the southern State of Chiapas. The new specimen consists of a distal part of the left humerus, which shows morphological differences from other North American Pleistocene and recent peccaries (*Mylohyus*, *Platygonus*, and *Tayassu*), allowing positive identification of the collared peccary *D. tajacu*. Thus, a new record of the species for the State of Chiapas and the first record of the Gliptodonte locality in the municipality of Villaflores is added, expanding the distribution range of the species during the Late Pleistocene in Mexico.

Keywords: collared peccary, Pleistocene mammals, Rancholabrean NALMA, southern Mexico.

Resumen

Tayassuidae (pecaríes) es una familia de artiodáctilos exclusiva de América, que se distribuyó ampliamente en América del Norte durante el Pleistoceno. Sin embargo, los registros de esta familia son escasos en México. Las únicas especies válidas reportadas para el Pleistoceno Tardío de México son Platygonus compressus y Dicotyles tajacu, con base en muy pocos especímenes. En este estudio reportamos un nuevo ejemplar de pecarí de la localidad Gliptodonte (Pleistoceno Tardío, NALMA Rancholabreano), municipio de Villaflores, en el sureño Estado de Chiapas. El nuevo espécimen consiste en la parte distal del húmero izquierdo, que muestra diferencias morfológicas con otros pecaríes del Pleistoceno y del Reciente de América del Norte (Mylohyus, Platygonus y Tayassu), lo que permitió la identificación del pecarí de collar D. tajacu. Se suma así un nuevo registro de la especie para el Estado de Chiapas y el primer registro de la localidad Gliptodonte en el municipio de Villaflores, ampliando el rango de distribución de la especie durante el Pleistoceno Tardío en México.

Palabras clave: *Mamíferos pleistocénicos, NALMA Rancholabreano, pecarí de collar, sureste de México.*

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1. Introduction

Tayassuidae Palmer, 1897, is a New World family of artiodactyls that diverged in the Eocene from a common Asian ancestor with the family Suidae, but has radiated successfully in North America, with a chronological range from the late Eocene to the present (Harris and Li-Ping, 2007; Prothero, 2009, 2021). This family was one of the first to cross South America during the Great American Biotic Interchange in the middle Pliocene (GABI 1; Woodburne, 2010).

Tayassuidae were very diverse at the end of the Neogene and the beginning of the Quaternary, with the Pleistocene being the geological epoch with most genera and species. During this time interval, six genera were recognized in South America and five in North America. The genera *Brasiliochoerus* Rusconi 1930; *Catagonus* Ameghino, 1904; *Parachoerus* Rusconi, 1930; *Dicotyles* Cuvier, 1816; *Platygonus* Le Conte, 1848 and *Tayassu* Fischer, 1814 are present in South America (Gasparini *et al.*, 2013; Parisi Dutra *et al.*, 2017). The genera *Mylohyus* Cope, 1889; *Platygonus*, and *Dicotyles*, have been recognized in the Pleistocene of North America, but *Tayassu* does not have a fossil record until now (Kurtén and Anderson, 1980; Mayer and Wetzel, 1987; Hulbert *et al.*, 2009; Czaplewski, 2012; Prothero, 2021). Recently, a new taxon, *Muknalia minima*, was established based on an almost complete mandibular ramus, recovered from the Muknal cave (Late Pleistocene-early Holocene), which is part of the Ox Bel Ha system, in Quintana Roo, Yucatán (Stinnesbeck *et al.*, 2017). However, *M. minima* were relegated as a junior synonym of *Pecari tajacu* (=*Dicotyles tajacu* [Linnaeus, 1758]) by Schubert *et al.* (2020). Another Pleistocene Mexican record of peccaries is the flat-headed peccary *Platygonus compressus* Le Conte, 1848, documented for El Cedazo, Aguascalientes; Tequixquiac, State of Mexico; Valsequillo, Puebla and the Chapala Basin, Jalisco (Lucas, 2008; Ferrusquía-Villafranca *et al.*, 2010). Other described species from the Pleistocene of Mexico are *P. ticuli* Mones, 1974 from Chapala and Zocoalco, Jalisco (Mones, 1974) and *P. alemanii* Dugès, 1891 from Moroleón, Guanajuato (Dugès, 1891). However, *P. ticuli* has been synonymized with *P. vetus* Leidy, 1882 by Lucas (2008), while *P. alemanii* does not differ from *P. compressus*, so it can be synonymized with this species. The collared peccary *Dicotyles tajacu* has been documented for the Loltún and Actún Spukil caves in Yucatán (Arroyo-Cabrales and Álvarez, 2003), and for the Santa Marta shelter in Ocozocoautla, Chiapas, based on cranial and appendicular material from the layer XVI, corresponding to the Pleistocene (García-Bárcena, 1976; Acosta *et al.*, 2018).

The fossil record of peccaries in Mexico is poorly known. Therefore, the aim of this work is to report for the first time the presence of the collared peccary *Dicotyles tajacu* in the Gliptodonte locality, Villaflores municipality, based on the distal part of a humerus collected from the Late Pleistocene (NALMA Rancholabrean) fluviolacustrine sediments that crop out in that locality. This discovery contributes to the knowledge of the Late Pleistocene fauna in southern Mexico.

2. Study area and geological setting

The Gliptodonte locality (locally named Rancho Argentina) is located in the vicinity of the town Villaflores, at 16°12'55"N and 93°16'20"W (Figure 1). This locality is registered with the code 2PSP00000134 in the National Database of Paleontological Monuments in the Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos of Instituto Nacional de Antropología e Historia (INAH).

The sedimentary sequence is formed by alternating fluvial sediments of 8.0 m thick (Figure 2). The base is 1.6 m thick and is formed by olive silt, thin sand, and brown clay organic. Over the base section, there is a 0.30 m layer of brown silty clay. In this section, fossil remains of the glyptodont *Glyptotherium cylindricum* (Brown, 1912), the ground sloth *Eremotherium laurillardi* (Lund, 1842), the horses *Equus mexicanus* (Hibbard, 1955), *E. conversidens* Owen, 1869, and the with-tailed deer *Odocoileus virginianus* Zimmermann, 1780 have been recovered (Montellano-Ballesteros and Carbot-Chanona, 2010; Gómez-Pérez and Carbot-Chanona, 2012; Jiménez-Hidalgo *et al.*, 2019; Carbot-Chanona *et al.*, 2022). The next section is a 1.0 m layer composed of dark brown clay and brown clay-silt. Above this section, there is a 0.40 m layer of fine sand to silt section without boulders. The next layer is formed by 0.70 m of brown fine clay. Above

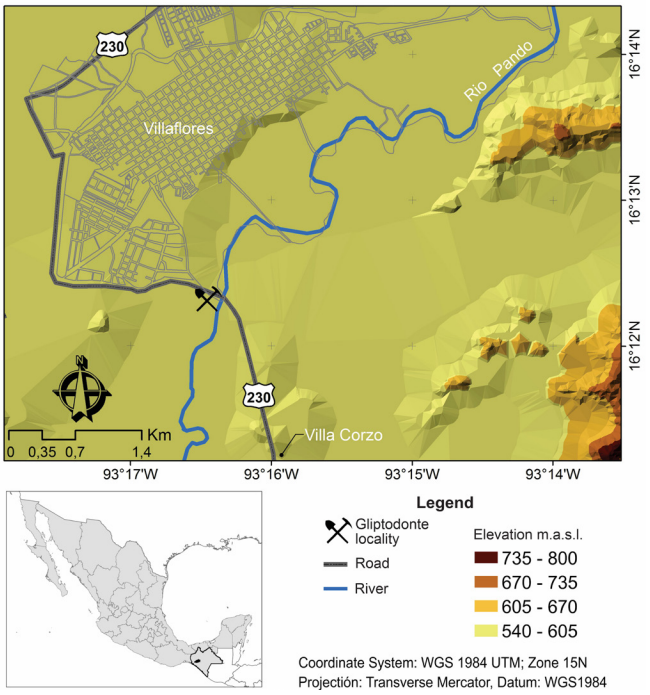

Figure 1. Location of the Gliptodonte locality, in Villaflores, Chiapas, southern Mexico.

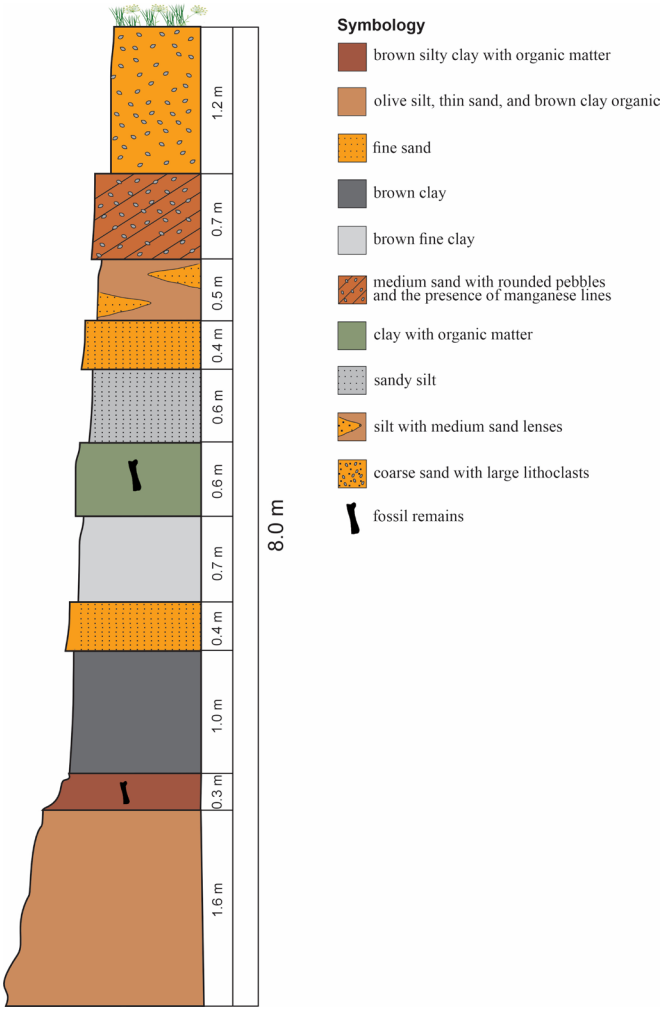

Figure 2. Generalized stratigraphic section of the Gliptodonte locality, Villaflores, Chiapas, southern Mexico

this section is a 0.6 m of clay with organic matter; in this section there are *G. cylindricum*, *E. conversidens*, and *O. virginianus* fossil remains (Gómez-Pérez and Carbot-Chanona, 2012; Jiménez-Hidalgo *et al.*, 2019). The next layer is formed by 0.60 m of sandy silt. Above there is a 0.40 m of fine-grained sand. Over this section, there is a 0.50 m layer of silt with medium sand lenses. The next layer is formed by 0.70 m medium sand with rounded pebbles and the presence of manganese lines. Finally, the upper part of the sequence consists of 1.2 m coarse sand with large lithoclasts.

The faunal association present in the locality has been referred to Rancholabrean NALMA (Gómez-Pérez and Carbot-Chanona, 2012).

3. Material and methods

The specimen described here consists of the distal half of a completely permineralized left humerus that presents a median state of conservation and was recovered from horizontal fluvial sediments that crop out in the Gliptodonte locality in the municipality of Villaflores, Chiapas.

The anatomical terminology used in this study is based on Schmid (1972) and Bortolami and Callegari (1995). The measurements were obtained with a digital caliper with an error range of 0.1 mm and were taken as shown in Figure 3. This study follows the proposal of Acosta *et al.* (2020), who argue that the valid binomina for the collared peccary is *Dicotyles tajacu*, and not *Pecary tajacu*, *Tayassu tajacu*, or *Dicotyles crassus*.

Since artiodactyl taxa of similar sizes existed in the Late Pleistocene of North America, such as deer (Cervidae Gray, 1821), antilocaprids (Antilocapridae Gray, 1866), and peccaries (Tayassuidae), a first comparison was conducted with recent specimens of these groups to assign the material studied here to a particular family. For this purpose, osteological material of the withe-tailed deer *Odocoileus virginianus* (specimens IHNCR-001 and IHNCR-007), the pronghorn *Antilocapra americana* Ord, 1815 (DP 1555), the with-lipped peccary *Tayassu pecari* (Link, 1975) (IHNCR-042) and the collared peccary *Dicotyles tajacu* (specimens DP 638, DP 5099, DP 7779 and IHNCR-048) was used. Subsequently, the fossil material was compared in detail morphologically and meristically with the tayasuid species present in the North American Rancholabrean NALMA, *Mylohyus fossilis* (Leidy, 1860) and *P. compressus*, and with the living *T. pecari* and *D. tajacu* (Figures 5 and 6, Table 1).

3.1. Institutional abbreviations

DP, Osteological Collection, Laboratorio de Arqueozoología "M. en C. Ticul Álvarez Solórzano" (historically Departamento de Prehistoria), Instituto Nacional de Antropología e Historia, Ciudad de México, México. **IHNFG**, Instituto de Historia Natural, Fósil Geográfico (acronym historically used for the paleontological collection now housed at Secretaría de Medio Ambiente e Historia Natural), Tuxtla Gutiérrez, Chiapas, México. **IHNCR**, Instituto de Historia Natural, Reference Collection, Museo de Paleontología "Eliseo Palacios Aguilera", Secretaría de Medio Ambiente e Historia Natural, Tuxtla Gutiérrez, Chiapas, México.

3.2. Morphological abbreviations

afc, articulation of the flexor complex; **lc**, lateral condyle; **mc**, medial condyle; **le**, lateral epicondyle; **me**, medial epicondyle; **of**, olecranon fossa; **rf**, radial fossa; **stf**, supratrochlear foramen, **tr**, trochlea.

3.3. General abbreviations

NALMA, North American Land Mammal Age.

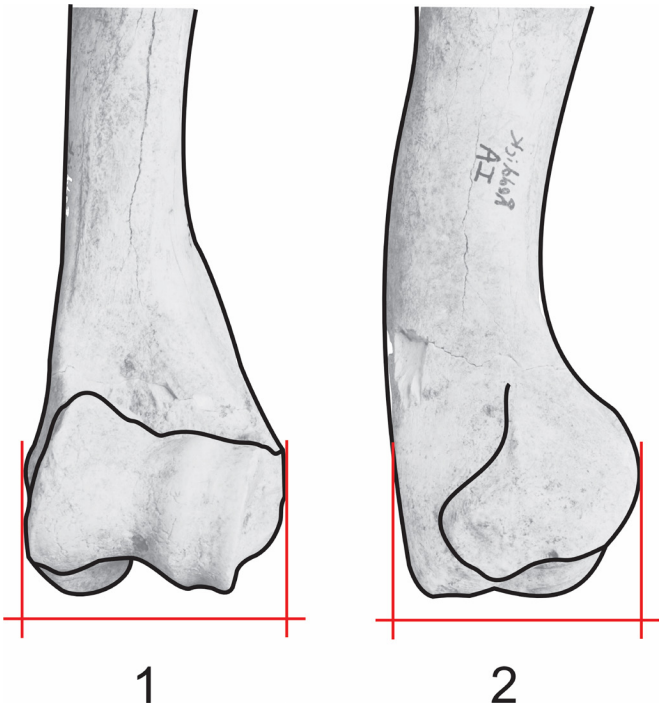

Figure 3. Schematic drawing of the humerus showing the measurements taken. 1) Lateral-medial length through the epicondyles, and 2) anteroposterior width.

4. Results

4.1. Systematic Paleontology

Class Mammalia Linnaeus, 1758
Order Artiodactyla Owen, 1848
Suborder Suiformes Jaekel, 1911
Family Tayassuidae Palmer, 1897
Genus *Dicotyles* Cuvier, 1816

Dicotyles tajacu (Linnaeus, 1758)
Figures 4 (3D model), 5, and 6, Table 1

4.2. Referred material

IHNFG-2718, distal half of left humerus (Figure 4), collected by Valente Villanueva in 2003 and later donated to the Museo de Paleontología "Eliseo Palacios Aguilera". The specimen is housed in the paleontological collection of the Secretaría de Medio Ambiente e Historia Natural, State of Chiapas, southern Mexico.

4.3. Location and horizon

Gliptodonte locality, Villaflores, Chiapas, southeastern Mexico. Late Pleistocene, Rancholabrean NALMA.

4.4. Description

The IHNFG-2718 specimen corresponds to the distal half of the left humerus (Figure 4). The diaphysis-epiphysis suture was completely ossified, indicating that it was an adult specimen. The lateral and medial borders of the articular end as well as the borders of the articular condyles were rounded, indicating that the material underwent a process of dragging after fossilization. In the anterior view, it can be seen that the medial condyle is slightly wider than the lateral condyle. The medial epicondyle projected slightly medially, whereas the lateral epicondyle extended laterally. The articulating surface of the flexor complex lies distally on the medial epicondyle and is projected distally. In the medial view, the flexor complex joint extends from the posterior part of the medial epicondyle to the medial part of the epicondyle. The olecranon fossa is wide and shallow, and the supratrochlear foramen is located inside. In the posterior view, the lateral supracondylar crest was observed to be incipiently protruding.

5. Discussion

5.1. Comparison of IHNFG-2718 with medium-sized artiodactyls

Medium-sized artiodactyls of the families Antilocapridae (*Stockoceros conklingi* Stock, 1930), Cervidae (*Odocoileus virginianus* and *Navahoceros fricki* Schultz and Howard, 1935), and Tayassuidae (*Platygonus compressus*, *Mylohyus fossilis*, and *Dicotyles tajacu*) inhabited North America during the Rancholabrean (Kurtén and Anderson 1980). Therefore, a first comparison was made between IHNFG-2718 and living representatives of these families, to include the specimen in one of them.

IHNFG-2718 is an adult specimen because the epiphysis-diaphysis suture was completely ossified. Its dimensions are smaller than those of the humeri of *Antilocapra americana* (DP 1555) and *Odocoileus virginianus* (IHNCR-001 and IHNCR-007). Both *A. americana* and *O. virginianus* were approximately 15% larger than IHNFG-2718. In contrast, the dimensions of IHNFG-2718 were comparable to those of an adult specimen of *T. pecari* and *D. tajacu* (Table 1).

Detailed morphological comparisons between IHNFG-2718, *O. virginianus*, *A. americana*, and *T. pecari* revealed distinctive features in the humerus of these species. In anterior view, the medial condyle and the lateral condyle in IHNFG-2718 were of similar proportions, as observed in the humerus of *T. pecari* and *D.*

Figure 4. 3D model of the IHNFG-2718 left humerus. To see the model with better resolution, access in https://sketchfab.com/3d-models/humero-fosil-de-pecari-de-collar-40207bbe0d3d46b4a45550ea2aca46bf

tajacu, whereas in the humerus of *O. virginianus* and *A. americana*, the medial condyle was wider laterally-medially than the lateral condyle (Figure 5). In the posterior view, IHNFG-2718 presents the supratrochlear foramen in the olecranon fossa, which is present in *T. pecari* and *D. tajacu*, but not in *O. virginianus* or *A. americana*. Additionally, the inner lower border of the olecranon fossa in *T. pecari* and *D. tajacu* was almost horizontal, a feature observed in IHNFG-2718. In contrast, in *O. virginianus* and *A. americana*, the border was lateromedially inclined (Figure 5). Another striking feature is that the articulating surface of the flexor complex is more distally prominent in *T. pecari*, *D. tajacu*, and IHNFG-2718 than in *O. virginianus* and *A. americana*. Additionally, the olecranon fossa is wider and deeper in IHNFG-2718 than in *O. virginianus* and *A. americana*, but is similar to the olecranon fossa of *T. pecari* and *D. tajacu*.

All the morphological and meristic features of IHNFG-2718 indicate that it is a tayasuid, similar to *T. pecari* and *D. tajacu*.

5.2. Comparison of IHNFG-2718 to another North American tayasuids

The genera of tayasuids present in the Rancholabrean of North America, *Platygonus*, and *Mylohyus*, and the living *Tayassu* and *Dicotyles*, differ from each other mainly by craniomandibular features and size (see Prothero, 2021). Of the four taxa, *Mylohyus* is the largest, a trait that is reflected in the postcranial bones, which are slightly larger than those of *Platygonus*, *Tayassu*, and *Dicotyles* (Figure 5, Table 1). In addition to size, there were morphological differences between the humeri of the four genera. The humerus in *Mylohyus*, *Tayassu*, and *Dicotyles* is similar in general morphology and proportion and is slenderer than the humerus of *Platygonus* (Lundelius, 1960). In *Mylohyus*, the crest on the lateral border of the olecranon fossa is farther from the fossa and lies on the lateral surface of the humerus (Lundelius, 1960). This feature is similar in *Tayassu* and *Dicotyles*, while in *Platygonus* the crest is located on the back of the humerus (Lundelius, 1960). Additionally, the medial border of the olecranon fossa is narrower and more angular in *Mylohyus* than in *Platygonus*, a feature that is similar in *Tayassu* and *Dicotyles* (Lundelius, 1960). In the specimen IHNFG-2718, the morphological characteristics present in *Tayassu* and *Dicotyles* are observed, in addition to the fact that its measurements fall within the size range of these two genera (Table 1), so it is ruled out that it belongs to *Mylohyus* or *Platygonus*.

Although there are differences in size between the extant species of peccaries, *Tayassu pecari* (total length= 905-1,390 mm; height at shoulders= 400-530 mm; body mass= 25-40 kg; Mayer and Wetzel, 1987) and *Dicotyles tajacu* (total length= 870-940 mm; height at shoulders= 400-480 mm; body mass= 18-27 kg; Hall, 1981), these differences in size are not noticeable in the dimensions of the humeri compared in this study (Figure 6, Table 1). However, a detailed comparison between the humeri of these species allowed us to identify some morphological differences.

In the posterior view, the humerus of *T. pecari* presents a slight elevation on the internal lateral border of the olecranon fossa, which extends distally to the middle part of the lateral epicondyle, forming a small "ridge" (Figure 6). In contrast, in the *D. tajacu* humerus, the medial lateral border of the olecranon fossa, this "ridge" is not present. In the specimen IHNFG-2718, the "ridge" of *T. pecari* humerus was not observed either, but the internal lateral edge of the olecranon fossa was similar to that of *D. tajacu* (Figure 6). Based on this morphological characteristic, the specimen IHNFG-2718 is assigned to *Dicotyles tajacu*, thereby adding a new record of the species for the state of Chiapas and the first record for the Gliptodonte locality, in the municipality of Villaflores, thus expanding the distribution range of the species during the Late Pleistocene in Mexico.

5.3. Paleoenvironmental significance

Today, *D. tajacu* inhabits deserts, arid woodlands, oak woodlands, and tropical areas from the southern U.S.A. through to northern Argentina (Grubb and Groves, 1993). This species has unusual climatic tolerance, because it occurs in forests where average temperatures are around 27 °C, but some populations have also been found in desert areas where temperatures reach 45 °C (Bodmer and Sowls, 1993). The distribution of *D. tajacu* is clearly tropical and semi-tropical, and agrees with the presence of neotropical mammals in the Gliptodonte locality, such as *E. laurillardi* and *G. cylindricum* (Gómez-Pérez and Cabot-Chanona, 2012; Carbot-Chanona *et al.*, 2022), and with the palynological fossil record, that includes Compositae, Mimosoideae, Gramineae, Solanaceae, and Pinaceae (Carbot-Chanona *et al.*, 2008), indicating that this was the main type of environment in Chiapas during the final Pleistocene.

6. Conclusions

Although the material described here consists only of a distal fragment of the left humerus, an exhaustive morphological comparison with the humeri of various species of living and fossil North American medium-sized artiodactyls allowed us to refer the specimen IHNFG-2718 as belonging to the collared peccary *Dicotyles tajacu*, a species that lives in several regions of the State of Chiapas. With this finding, we document a new record of this species for the Late

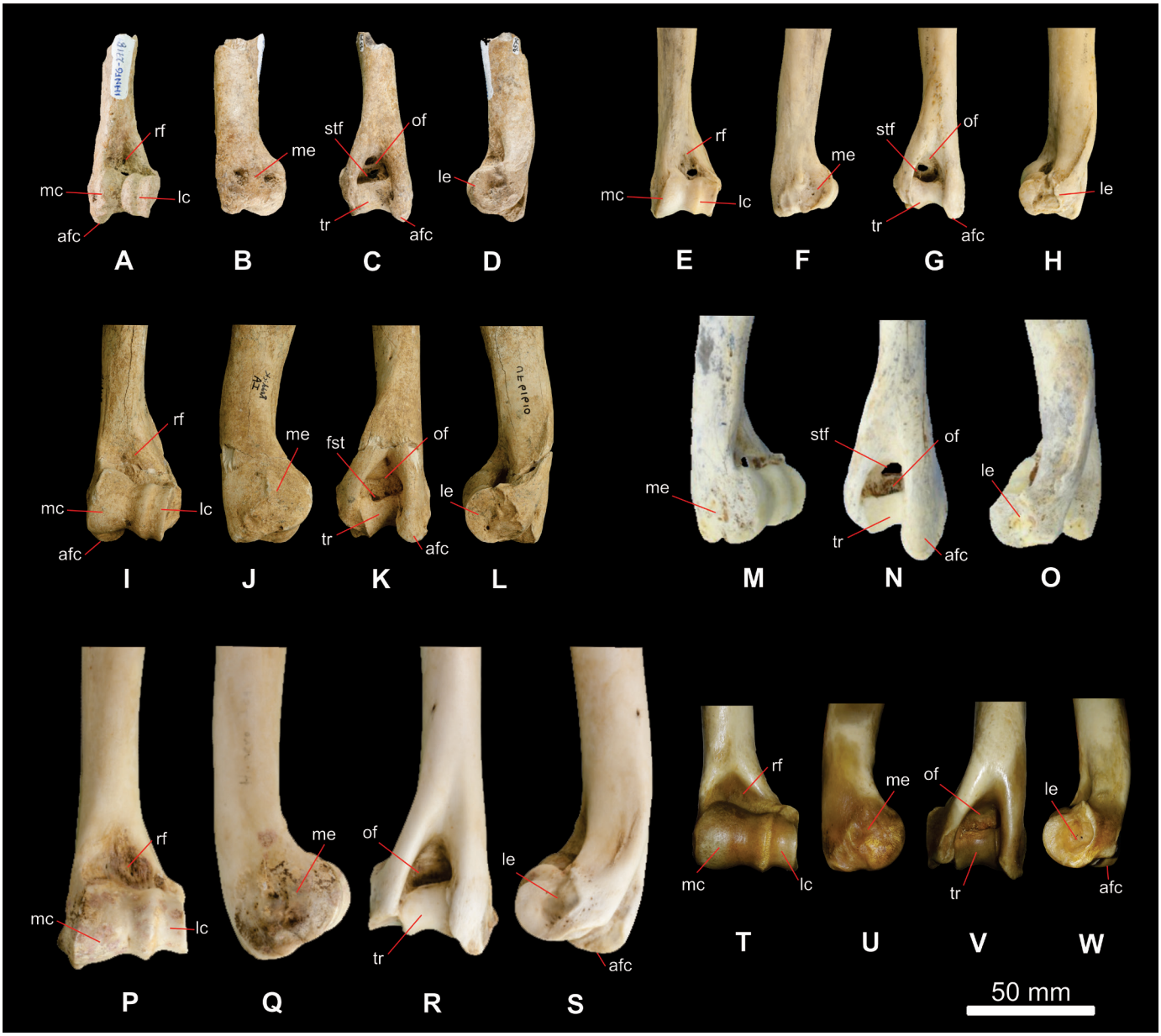

Figure 5. Comparison between North American medium-sized artiodactyls. A–D, left humerus (IHNFG-2718), in anterior (A), medial (B), posterior (C), and lateral (D) view. E–H, left humerus of *Tayassu pecari* (IHNCR-042), in anterior (E), medial (F), posterior (G), and lateral (H) view. I–L, right humerus (flipped images) of *Platygonus compressus* (UF-61610), in anterior (I), medial (J), posterior (K), and lateral (L) view. M–O, right humerus (flipped images) of *Mylohyus fossilis* (RMM 4567), in anteromedial (M), posterior (N), and posterolateral (O) view. P–S, left humerus of *Odocoileus virginianus* (INHCR-001), in anterior (P), medial (Q), posterior (R), and lateral (S) view. T–W, left humerus of *Antilocapra americana* (DP 1555), in anterior (T), medial (U), posterior (V), and lateral (W) view. Scale bar equal 50 mm.

Pleistocene in Mexico, as well as the first record of the species for the Gliptodonte locality.

The presence of *D. tajacu* in Chiapas allows us to know the fauna present in southeastern Mexico during the Late Pleistocene. In future studies, these findings could provide data to understand which taxa managed to prevail over the extinction caused in the Pleistocene-Holocene interval as a consequence of climate change.

Conflicts of interest

The authors declare that they have none.

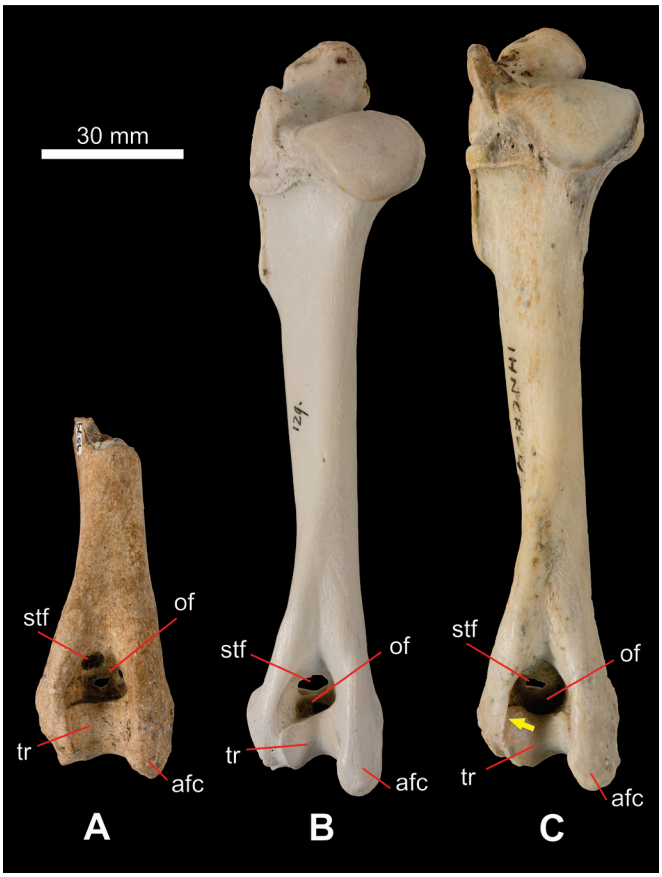

Figure 6. Comparison between (A) IHNFG-2718, (B) *Dicotyles tajacu* (IHNCR-048), and (C) *Tayassu pecari* (IHNCR-042) in posterior view. Scale bar equal 30 mm. The yellow arrow shows the slight elevation on the internal lateral border of the olecranon fossa present in *T. pecari*, but not in *D. tajacu* and IHNFG-2718.

Table 1. Comparative measurements (in mm) of tayassuids during the Late Pleistocene in North America. Data were taken from Finch *et al.* (1970)[a] and Lundelius (1969)[b].

Specimens	Lateral-medial length through the epicondyles	Anteroposterior width
IHNFG-2718	29	26
Tayassu pecari IHNCR-045	27	24
Dicotyles tajacu DP 608	27.5	23
Dicotyles tajacu DP 5099	25.4	22.2
Dicotyles tajacu DP 7779	29	24.8
Dicotyles tajacu IHNCR-048	27	23
[a]*Platygonus compressus* USNM 26098	42	--
[a]*Platygonus compressus* USNM 26100	45	--
[a]*Platygonus compressus* USNM 26102	40.5	--
Platygonus compressus UF 61610	38.6	36.6
Mylohyus nasutus (=*M. fossilis*) RMM 4567	46.7	33
[b]*Mylohyus nasutus* (=*M. fossilis*) TMM 933-3232	42.5	45.6

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