

New record of *Pachyarmatherium* (Cingulata: Pachyarmatheriidae) from the Late Pleistocene in Venezuela

Nuevo registro de *Pachyarmatherium* (Cingulata: Pachyarmatheriidae) para el Pleistoceno tardío de Venezuela

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ABSTRACT

The Falcón state, in northwestern Venezuela, preserves one of the oldest localities documenting human presence on the Americas in association with megafauna remains. One of these localities is the Late Pleistocene Taima-Taima site, which is located in the vicinity of the Caribbean coast. Excavations since the 1960s in the Taima-Taima site, and surroundings, have offered new insights into the faunal assemblages that inhabited this arid coastal savannah region during the Late Pleistocene. Isolated osteoderms collected in recent prospections allow us to report here the presence of the extinct cingulate *Pachyarmatherium* cf. *brasiliense* and *Pachyarmatherium* sp. from the Taima-Taima site, and the new locality Cucuruchú (Las Dunas). The record of these taxa in the Late Pleistocene of the Falcón state increases the known paleodiversity of Cingulata for the region and expands the geographical distribution of the genus, which is poorly known in South America.

Keywords: armadillos, Cenozoic, fossils, northern South America, Taima-Taima, Xenarthra.

RESUMEN

El estado Falcón, en el noroeste de Venezuela, conserva una de las localidades más antiguas que documentan la presencia humana en las Américas en asociación con restos de megafauna. Una de estas localidades es el sitio Taima-Taima del Pleistoceno Tardío, que se encuentra en las inmediaciones de la costa caribeña. Las excavaciones llevadas a cabo desde la década de 1960 en este sitio y sus alrededores han ofrecido nuevos datos sobre los conjuntos faunísticos que habitaban esta región de sabana costera durante el Pleistoceno Tardío. Osteoderms aislados recolectados en prospecciones recientes nos permiten reportar aquí la presencia del extinto cingulado *Pachyarmatherium* cf. *brasiliense* y *Pachyarmatherium* sp. en el sitio Taima-Taima, y la nueva localidad de Cucuruchú (Las Dunas). El registro de estos taxones en el Pleistoceno Tardío del estado Falcón incrementa la paleodiversidad conocida de Cingulata para la región y amplía la distribución geográfica del género, cuyos reportes son escasos en Sudamérica.

Palabras clave: armadillos, Cenozoico, fósiles, norte de América del Sur, Taima-Taima, Xenarthra.

INTRODUCTION

Pachyarmatherium was originally erected by Downing & White (1995) when describing the type species

Pachyarmatherium leiseyi on the basis of numerous osteoderms, cranial and postcranial remains from the Pliocene–Pleistocene in the USA. In South America, the fossil record of *Pachyarmatherium* is restricted mainly to isolated

osteoderms and postcranial remains reported from Brazil, Peru and Venezuela (Rincón & White 2007, Porpino *et al.* 2009, Martínez & Rincón 2010). Rincón & White (2007, figs. 2–3) described the species *Pachyarmatherium tenebris*, based on few isolated osteoderms recovered from Late Pleistocene cave sediments in the eastern Falcón state, western Venezuela (Rincón & White 2007, fig. 1). Porpino *et al.* (2009), based on numerous osteoderms and postcranial remains, described the species *Pachyarmatherium brasiliense*, for the late Pleistocene–Holocene in the Rio Grande do Norte region, northeastern Brazil. Isolated osteoderms assigned to *P. tenebris* from the late Pleistocene of Peru by Martínez & Rincón (2010) have been interpreted as morphologically indistinguishable from those of *P. brasiliense*, leading these authors to consider both species as synonymous.

Late Pleistocene deposits in the Falcón state preserve one of the best-recorded paleodiversity records of Cingulata from that time in Venezuela. Such finds are known from archaeological and paleontological excavations, including some specimens collected on the surface in karst systems (see Carrillo-Briceño 2015). Apart from *Pachyarmatherium*, the fossil record of the Falcón state also includes glyptodonts with the genera *Glyptodon* (*e.g.*, Royo y Gómez 1960, Rincón & White 2007, Chávez-Aponte *et al.* 2008a) and *Glyptotherium* (Carlini *et al.* 2008, 2022, Carlini & Zurita 2010), the pampatheres *Holmesina* and *Pampatherium* (Rincón 2004, Aguilera 2006, Chávez-Aponte *et al.* 2008a, Carrillo-Briceño 2015), and the dasyopodid *Propraopus* (Royo y Gómez 1960, Rincón & White 2007). In this contribution, we describe new fossil remains assignable to *Pachyarmatherium cf. brasiliense*, which were collected in the archaeological/paleontological site of Taima-Taima and its surroundings in the Venezuelan state of Falcón. The Taima-Taima site is located in the vicinity of the Caribbean coast (Fig. 1), a region internationally known to contain some of the oldest localities documenting human presence on the American continent (Bryan *et al.* 1978, Carlini *et al.* 2008, 2022, and references therein). Possible evidence of hunting on glyptodonts was reported recently for the Taima-Taima and the Muaco (also in the Falcón state) sites by Carlini *et al.* (2022). The presence of *Pachyarmatherium cf. brasiliense* in the Late Pleistocene of the Falcón state increases the known paleobiodiversity of Cingulata for the region and expands the geographic distribution of the species.

MATERIAL AND METHODS

Four isolated osteoderms, one (MTT-V-320) collected from the surface washed sediments adjacent to the old ex-

cavations in the Taima-Taima site (11° 29' 57" N / 69° 31' 18" W), and the other three (MTT-V-212, -358, -479) from the surroundings of the Taima-Taima park, a locality referred here as Cucuruchú (Las Dunas) site (11° 30' 10" N / 69° 30' 17" W). The later site is located on the coastal area, near the mouth of the Cucuruchú Creek, approximately two kilometers east of the Taima-Taima site (Fig. 1). To avoid the total loss of the specimens, due to the erosion of the outcrops, these were collected by one of the authors (AERC) during a paleontological rescue that took place in 2015 as part of a workshop on protection of paleontological heritage (Zavala & Reyes 2017). Nowadays on the Taima-Taima excavation site there is an *in situ* museum and a park (Fig. 1A–B) that was opened in the year 2000 (see Aguilera 2006, Carrillo-Briceño 2015). The studied remains were compared with published bibliography, and measurements were taken using a digital caliper. Comparative measurements presented in Table 1 were taken from Downing & White (1995; for *P. leiseyi*), Rincón & White (2007; for *P. tenebris*), and Porpino *et al.* (2009; for *P. brasiliense*). The specimens are housed in the paleontological collection of the local Museum of Taratara with the acronym MTT-V- (Museo de Taratara-Vertebrados).

GEOLOGICAL CONTEXT

The study area is located within the Taima-Taima Park polygonal area (Fig. 1A), which covers an extension of approximately 14.8 km². The Taima-Taima site is approximately 18 km NE of the city of Coro, and 3 km NW of the Taratara town. The area is characterized by a continuous exposure of folded strata that constitute La Vela anticline (see Benites-Palomino *et al.* 2021, and references therein). There are no formally defined Pleistocene sedimentary units in this area; most Pleistocene deposits occur on rounded cobble and pebble layers, eroded and deposited from the underlying Miocene limestone layers (Cruxent 1970, Bryan & Gruhn 1979, Carlini *et al.* 2022). Water springs are also common in the area (Bryan *et al.* 1978; Aguilera 2006). Abundant remains of Pleistocene fauna have been reported for the site of Taima-Taima from the successive excavations carried out since the 1960s, and include turtles (Testudinidae), bats (Phyllostomidae), ground sloths (Megatheriidae, Mylodontidae), glyptodonts (Glyptodontidae), native ungulates (Macraucheniiidae, Toxodontidae), artiodactyls (Camelidae, Tayassuidae, Cervidae), perissodactyls (Equidae), carnivore (Felidae, Canidae, Ursidae), and proboscideans (Gomphotheriidae) (Casamiquela 1979; Bocquentin-Villanueva 1982a; Chávez-Aponte *et al.* 2008b; Carrillo-Briceño 2015, Carlini *et al.* 2022; and references therein).

LATE PLEISTOCENE PACHYARMATHERIUM OF VENEZUELA

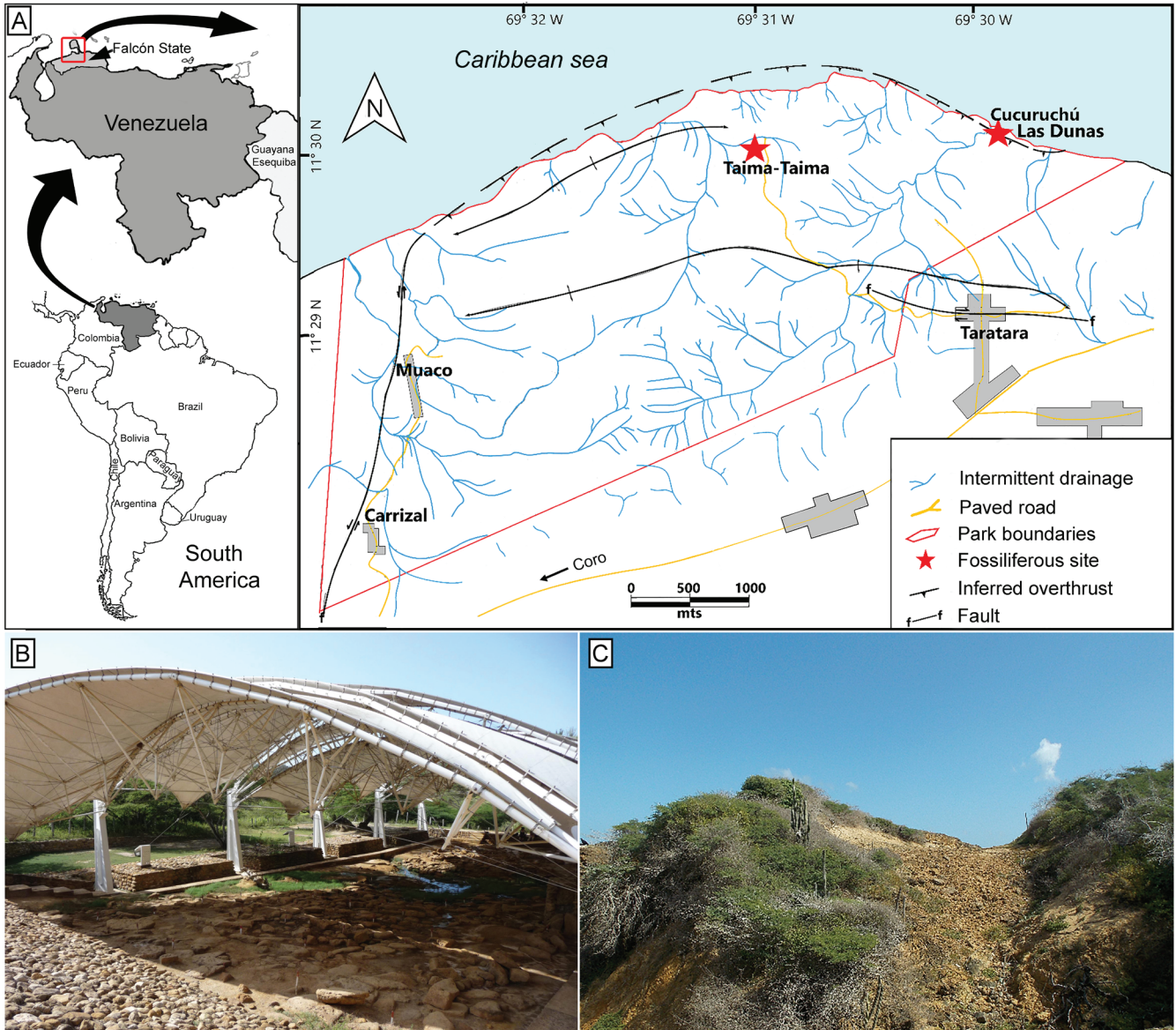


Figure 1. A. Geographical location of the fossiliferous localities and the Taima-Taima Park. B. Taima-Taima *in situ* open museum. C. Cucuruchú (Las Dunas) site.

Table 1. Range of osteoderm measurements of the different species of *Pachyarmatherium* from the literature and measurements of the four specimens discovered at Taima-Taima and the Cucuruchú (Las Dunas) sites. Expressed in millimeters.

Species	Length	Width	Thicknes	Reference
<i>P. leiseyi</i>	-	8.1 – 22.9	5.5 – 13.3	Downing & White 1995
<i>P. tenebris</i>	17.6–32.1	14.8–28.5	6.6–9.8	Rincón & White 2007
<i>P. brasiliense</i>	10.1–26.7	14.5–28	7–18.4	Porpino <i>et al.</i> 2009
MTT-V-320	18.96	17,91	10.36	This paper
MTT-V-212	19.76	16.95	14.72	This paper
MTT-V-358	19.80	17.46	14.29	This paper
MTT-V-479	15.03	13.48	10.26	This paper

Excavations at the Taima-Taima site during the 1960s and 1970s reported lithic artifacts associated with megafaunal remains (e.g., Bryan *et al.* 1978). Possible evidence of hunting on glyptodonts was also reported recently for the Taima-Taima site by Carlini *et al.* (2022). The Taima-Taima assemblage was dated, based on several C14 analyses, to be between $\sim 17,300$ calybp [calibrated years before the present using IntCal20 (Ramsey 2009)] ($14,200 \pm 300$ ybp) and $\sim 15,780$ calybp ($12,980 \pm 85$ ybp) (Bryan & Gruhn 1979; Bryan *et al.* 1978). The osteoderm MTT-V-320 was collected from washed surface sediments accumulated beside the area of the old excavations, which makes the accurate identification of the fossiliferous level from which this specimen comes, highly difficult. However, we do not rule out that the specimen comes from one of the fossiliferous layers reported for the Taima-Taima site (see Carlini *et al.* 2022, fig. 3).

Regarding the Cucuruchú site (Las Dunas), the locality was discovered on the right margin of the mouth of the Cucuruchú Creek, and the Pleistocene deposits are overlaying Miocene rocks (Bocquentin-Villanueva 1982b). The fossiliferous locality is characterized by a conglomerate of alluvial origin with a layer of sand or paleodunes on top (Fig. 1C); both layers yield fossil vertebrates. The age for the Cucuruchú (Las Dunas) site is estimated based on its faunal composition (under study), which corresponds to a typical Late Pleistocene (Lujanian) mammal assemblage.

SYSTEMATIC PALEONTOLOGY

XENARTHRA Cope, 1889

CINGULATA Illiger, 1811

†PACHYARMATHERIIDAE Fernicola *et al.*, 2018

†*Pachyarmatherium* Downing & White, 1995

†*Pachyarmatherium brasiliense* Porpino *et al.*, 2009

†*Pachyarmatherium* cf. *brasiliense*.

(Fig. 2A1–A2)

Referred specimens. MTT-V-320 is a fixed osteoderm from a section of the carapace not corresponding to a movable band.

Locality. Taima-Taima site (Fig. 1).

Description. The osteoderm is hexagonal, with a similar size to *P. brasiliense*, larger and thicker than *P. tenebris* (Fig. 2A1–A2, Table 1). The dorsal surface is well ornamented and almost flat as in *P. brasiliense* (Porpino *et al.* 2009, fig. 2; Oliveira *et al.* 2013, fig. 2), and different from *P. leiseyi* and *P. tenebris* where the dorsal surface is convex (Downing & White 1995, figs. 1–2; Rincón & White 2007, figs. 2–3). MTT-V-320 has four periph-

eral antero-lateral figures slightly higher than the central one; the two proximal are larger than the lateral figures, which reduce in size until disappearing on the margin as a sharp tip pointing backwards; the central figure is larger, rounded to subrounded, similar to *P. brasiliense* (Porpino *et al.* 2009, fig. 2; Oliveira *et al.* 2013, fig. 2), and different from *P. leiseyi* and *P. tenebris* (Downing & White 1995, figs. 1–2; Rincón & White 2007, figs. 2–3) whose shape is mostly polygonal, covering a little more than half of the total exposed surface and posteriorly displaced to reach the posterior border. This figure is surrounded by a main sulcus that is shallow and wide, a feature that differentiates it from *P. leiseyi* and *P. tenebris* (Downing & White 1995, figs. 1–2; Rincón & White 2007, figs. 2–3). The radial sulci are short, deep and as wide as the one that limits the central figure; it has a foramen at the interception between the main and radial sulci in the anterior region, a common feature in osteoderms of Pachyarmatheriidae and Glyptatelinae. Numerous small but well-marked foramina are located on the main sulcus and on the surface of the central figure (Fig. 2). The later shows six small and well-marked foramina, aligned longitudinally in two parallel rows of three each, a feature not reported in any of the species of *Pachyarmatherium* described so far. The internal surface is flat, as in *P. brasiliense* (Oliveira *et al.* 2013, fig. 2) and unlike *P. leiseyi* and *P. tenebris* where it is somewhat concave, and has four large and well-marked vascular foramina.

†*Pachyarmatherium* sp.
(Fig. 2B1–D2)

Referred specimens. Three isolated fixed osteoderms from the part of the carapace not corresponding to a movable band. (MTT-V-212, -358, -479).

Locality. Cucuruchú (Las Dunas) site (Fig. 1).

Description. Osteoderms are hexagonal to heptagonal (e.g., MTT-V-212), very thick in the anterior portion and reducing its thickness to the distal portion, but thicker than the described osteoderms in *P. leiseyi*, *P. tenebris* and *P. brasiliense* in the later part (Downing & White 1995, Rincón & White 2007; Porpino *et al.* 2009); slightly longer than wide, including a rough and convex external surface with the central figure forming the highest relief as in *P. tenebris* (Rincón & White 2007, figs. 2–3) and less pronounced than in *P. leiseyi* (Downing & White 1995, figs. 1–2). There are four to six peripheral figures, which are larger on the anterior margin, reducing significantly in size distally; the central figure is rounded or polygonal as in *P. leiseyi* and *P. tenebris* (Downing & White 1995, figs. 1–2; Rincón & White 2007, figs. 2–3), defined by

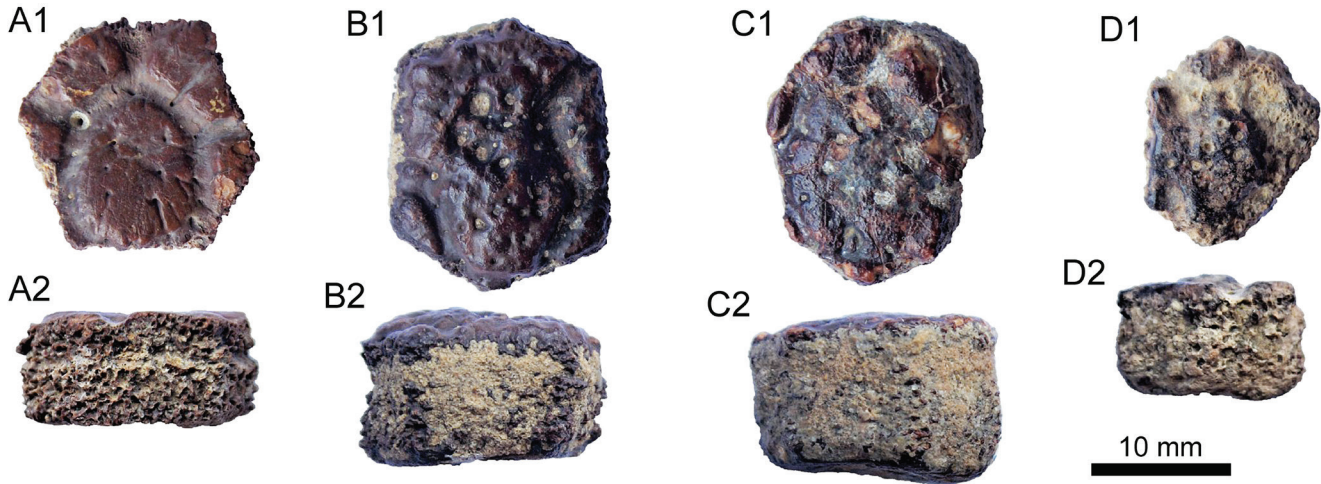


Figure 2. A1-D2. *Pachyarmatherium* osteoderms. A1-A2. *Pachyarmatherium* cf. *brasiliense* (MTT-V-320) from the Taima-Taima site. B1-D2. *Pachyarmatherium* sp. (B1-B2: MTT-V-358, C1-C2: MTT-V-212, D1-D2: MTT-V-479) from the Cucuruchú (Las Dunas) site. Views: dorsal (A1, B1, C1, D1) and lateral (A2, B2, C2, D2). Comparison with images in Downing & White (1995, figs. 1–2), Rincón & White (2007, figs. 2–3), Porpino *et al.* (2009, fig. 2), and Oliveira *et al.* (2013, fig. 2).

a deep and well-marked main sulcus. The central figure is large, encompassing most of the external surface of the osteoderm and posteriorly displaced. The radial sulci are deep, short and well-defined (except in MTT-V-212). The piliferous foramina are at the intersection between the main/central sulcus and the peripheral sulci (Fig. 2B1, C1, D1), being large and well-marked. Specimen MTT-V-358 has a large foramen on the central figure and a series of medium to small-sized foramina scattered throughout this area, giving it a rough and stippled appearance. The internal surface is flat and somewhat concave, as in *P. leiseyi* (Downing & White 1995, fig. 1), and exhibits three to five vascular foramina.

DISCUSSION

Despite the abundant cingulates remains recovered from the Taima-Taima and Cucuruchú sites since the first excavations in the locality in the early 1960s, these have been identified exclusively as glyptodontids (Casamiquela 1979, Ochsenius 1980, Bocquentin-Villanueva 1982a, b, Aguilera 2006). Primarily on the basis of dorsal carapace osteoderms, these materials have been reported as belonging to the genus *Glyptodon* (Bocquentin-Villanueva 1982a, Aguilera 2006). Nevertheless, detailed studies of these specimens, including skulls, postcranial skeletons, dorsal carapaces and caudal rings, from the Taima-Taima and Cucuruchú sites, as well as other Late Pleistocene sites in the surroundings (*e.g.*, Muaco and Quebrada Ocando), indicates that all of them are in fact assignable to *Glyptotherium* and morphologically similar to *G. cylindricum*

(Carlini *et al.* 2008, 2022). The pampatheres *Holmesina* and *Pampatherium*, as well as the dasypodid *Propaopus* have been reported from other fossiliferous localities in the Falcon state (Rincón 2004, Aguilera 2006, Chávez-Aponte *et al.* 2008a, Carrillo-Briceño 2015). The presence of *Pachyarmatherium* in the Taima-Taima and Cucuruchú (Las Dunas) increases the known paleobiodiversity of cingulates for these sites and the geographic distribution of the genus in the region, whose previous record included only the presence of *P. tenebris* in eastern Falcón state (Rincón & White 2007).

The morphological characteristics of the Taima-Taima specimen MTT-V-320 *i.e.*, flat external surface, rounded central figure, shallow and wide sulci and flat internal surface (Fig. 2A1–A2) are similar to those of *P. brasiliense*. However, due to the scarcity of material its specific identification is tentative until new material is found and the description can be refined. According to the morphological characteristics of the specimens from the Cucuruchú (Las Dunas) site *i.e.*, thick osteoderms, longer than wide, rough and convex external surface, rounded to polygonal central figure, deep and wide sulci, flat to concave internal surface (Fig. 2B1–D2). These differ from the Taima-Taima osteoderms, as well as from *P. tenebris* and *P. leiseyi*. However, considering that these osteoderms could belong to a non-homologous area of the carapace, only new remains will allow us to have a more precise taxonomic assignment.

The phylogenetic placement of *Pachyarmatherium* has been somewhat problematic, occupying different taxonomic positions, from Dasypodoidea (Downing & White 1995, Rincón & White 2007, Oliveira *et al.* 2013), Glypto-

dontoidea, Glyptatelineae (McKenna & Bell 1997, Vizcaíno *et al.* 2003), Cingulata *incertae sedis* as a sister group of the clade formed by pampatheres and glyptodonts (Porpino *et al.* 2009), to Dasypodinae Dasypodini (Oliveira *et al.* 2013). More recently, Fernicola *et al.* (2018) described *Neoglyptatelus uruguayensis*, based on very complete postcranial materials from the late Miocene of Uruguay, allowing these authors to propose the family Pachyarmatheriidae. This would include the species *Neoglyptatelus originalis* and *Neoglyptatelus sincelejanus* from the Middle and Late Miocene of Colombia (Carlini *et al.* 1997, Villarroel & Clavijo 2005), and the genus *Pachyarmatherium* from the Plio–Pleistocene of North, Central and South America (Downing & White 1995, Porpino *et al.* 2009). They are characterized mainly by a carapace divided into two parts (scapular and pelvic shields) without intermediate dorsal mobile bands, and the central figure of the osteoderms displaced posteriorly. The absence of complete or well-preserved cranial and dental remains has prevented the study to infer on ecological preferences of this family. Downing & White (1995) have suggested myrmecophagous feeding habits for *P. leiseyi*, similar to those of *Dasypus novemcinctus*, based on some mandibular characters and the presence of claws, possibly employed for digging. The paleoenvironmental characteristics inferred for the Leiseyi Shell Pits locality place *P. leiseyi* in a mixed environment such as a coastal mangrove bay in an estuary of a major river, with swampy areas (Rich & Newson 1995, Downing & White 1995). Likewise, Rincón & White (2007) propose that *P. tenebris* inhabited a mixed environment with a predominance of open savannahs with wooded patches. Similar paleoenvironments characterized by dry coastal savannahs with the presence of wooded patches have been suggested for the Taima-Taima area during the Late Pleistocene (Ochsenius & Gruhn 1979, Ochsenius 1980).

CONCLUSION

In the present study, we report the presence of *Pachyarmatherium* cf. *P. brasiliense* and *Pachyarmatherium* sp. from the Taima-Taima and the Cucuruchú (Las Dunas) sites within the area of the Taima-Taima Park, expanding the geographical distribution of the genus in Venezuela during the Late Pleistocene. Although both Taima-Taima and the Cucuruchú (Las Dunas) sites are located closely and could be also chronologically contemporaries, the morphological characteristics of the osteoderms from both sites allow us to differentiate them. Nevertheless, for now the scarcity of the material does not allow identifying them precisely at the species level. Their presence increases the diversity of fossil mammals in these fossiliferous locali-

ties and demonstrates the great paleontological potential for future studies in this region.

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