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A new Megatheriinae skull (*Xenarthra*, Tardigrada) from the Pliocene of Northern Venezuela – implications for a giant sloth dispersal to Central and North America

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ABSTRACT

A skull of a ground sloth from the Pliocene San Gregorio Formation documents a northern neotropical occurrence of a megatheriine that addresses issues on intraspecific variation and biogeography. The new specimen is broadly similar in size and morphology to that of *Proremotherium eljebe* from the underlying Codore Formation in the Urumaco Sequence, differing in several features such as a longer basicranial area and a more posteriorly projected basioccipital between the condyles. The living sloths species of *Bradypus* and *Choloepus* do not have unequivocal anatomical features that indicate sexual dimorphism. Nevertheless, fossil sloths may have shown such dimorphism, and speculations on this subject are part of the considerations that can be made when allocating fragmentary fossils (e.g., in the new skull the presence of a long sagittal crest could indicate a male individual and the absence of an extended crest in *Proremotherium eljebe* a female one). We speculate that as early as the late middle Miocene, two main lines of Megatheriinae had clearly separated in two geographic areas, one in the rising Andean area and one at low latitudes on the lowlands of central and northern South America.

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INTRODUCTION

The Urumaco sequence, together with several geological formations in northwestern Venezuela, provides an almost continuous paleontological record for the last 20 million years (Sánchez-Villagra et al., 2010; Carrillo et al., 2015). This sequence includes the San Gregorio Formation (Pliocene), which has been in recent years prospected for fossil vertebrates, with the first fossil mammals described from it including rodents, carnivorans, notoungulates and xenarthrans (Vucetich et al., 2010; Castro et al., 2014; Forasiepi et al., 2014; Carrillo et al., 2018). These findings are particularly relevant as they provide the until now rare documentation of northern neotropical fossils from the time of the first phases of the GABI or Great American Biotic Interchange (Woodburne, 2010; Forasiepi et al., 2014; Carrillo et al., 2015; Amson et al., 2016). Here, we report on new skull of a ground sloth from the San Gregorio Formation that expands our knowledge of the northern South America Megatheriinae and its early dispersal to North America.

In Venezuela, Megatheriinae ground sloths are represented by *Urumaquia robusta* Carlini et al., 2006, from the Urumaco Formation (late Miocene); *Proeremotherium eljebe* Carlini et al., 2006, from the Codore Formation (Pliocene); and *Eremotherium* Spillmann, 1948, cf. *E. laurillardii* (Lund, 1842) from several late Pleistocene localities (e.g., Taima Taima, Muaco, Cucuruchú, Cañada Ocañdo, El Breal de Orocuá, see Carlini et al., 2006, 2008a; Solórzano et al., 2015). *Proeremotherium eljebe* is of particular interest given several features that could indicate an ancestral or close relationship with the geographically-widespread megatheriine *Eremotherium laurillardii* (see Carlini et al., 2006). *Eremotherium* comprises three species: *E. eomigrans* De Iuliis and Cartelle, 1999, from the late Pliocene (Blancan) of USA; *E. sefvei* De Iuliis and St-André, 1997, from the Pleistocene of Bolivia, and *E. laurillardii* from several late Pleistocene localities of North America (e.g., southern Mexico and west coast of USA up to South Carolina), Central America and low latitudes of South America (e.g., Brazil, Ecuador, Colombia, Venezuela) (but see Faure et al., 2014). In the study of

Megatheriinae, it is relevant to consider that the upper dental series comprises five teeth with a molar shape, usually called molariforms (see Cartelle and De Iuliis, 2006; Brandoni et al., 2017).

Geological Setting

The Megatheriinae new skull (mentioned as “new Megatheriidae indet.” in Vucetich et al., 2010) comes from a locality in northwestern Venezuela, Falcón State (Figure 1). The outcrops are mostly of neogene deposits, mainly representing a coastal shallow marine environment (Johnson et al., 2009), but continental levels are present (Vucetich et al., 2010). The sediments of San Gregorio Fm. are composed mainly of mudstones and limestones, with intercalations of sandstones and pebbly conglomerates (Quiroz and Jaramillo, 2010; Vucetich et al., 2010), with a total of more than 300 m at the type section (Ministerio de Energía y Minas, 1997). Recent paleontological studies of this formation described invertebrates (e.g., molluscs, crustaceans, foraminiferans) from the overlaying marine Cocuiza Member (Hambalek et al., 1994; Aguilera et al., 2010; Mihaljević et al., 2010). From its basal Vergel Member, crocodylians (*Crocodylus falconensis*, in Scheyer et al., 2013), caviomorph rodents (*Cardiatherium* sp. and cf. *Caviodon*, *Neoepiblema* sp., and *Marisela gregoriana*, in Vucetich et al., 2010), carnivoran procyonids (*Cyonasua* sp., in Forasiepi et al., 2014), toxodonts (Carrillo et al., 2018) and xenarthran cingulates (*Pliodasypus vergelianus*, in Castro et al., 2014) have been described. Also from the same locality of Vergel Member in which we found the specimen reported here are mentioned turtles, osteoderms of a new species of the Glyptodontinae *Boreostemma* (*B.* aff. *codorensis*) and remains of Pampatheriidae tentatively referred to aff. *Holmesina floridanus* (Carlini and Zurita, 2010; Zurita et al., 2011; Scheyer et al., 2013; Castro et al., 2014). The new skull here described is part of the collections of the Museo Paleontológico de Urumaco, Estado Falcón, Venezuela (AMU-CURS).

The age of the San Gregorio Formation is estimated to be late Pliocene / early Pleistocene (Ministerio de Energía y Minas, 1997) by stratigraphical correlation. This estimated age is concor-

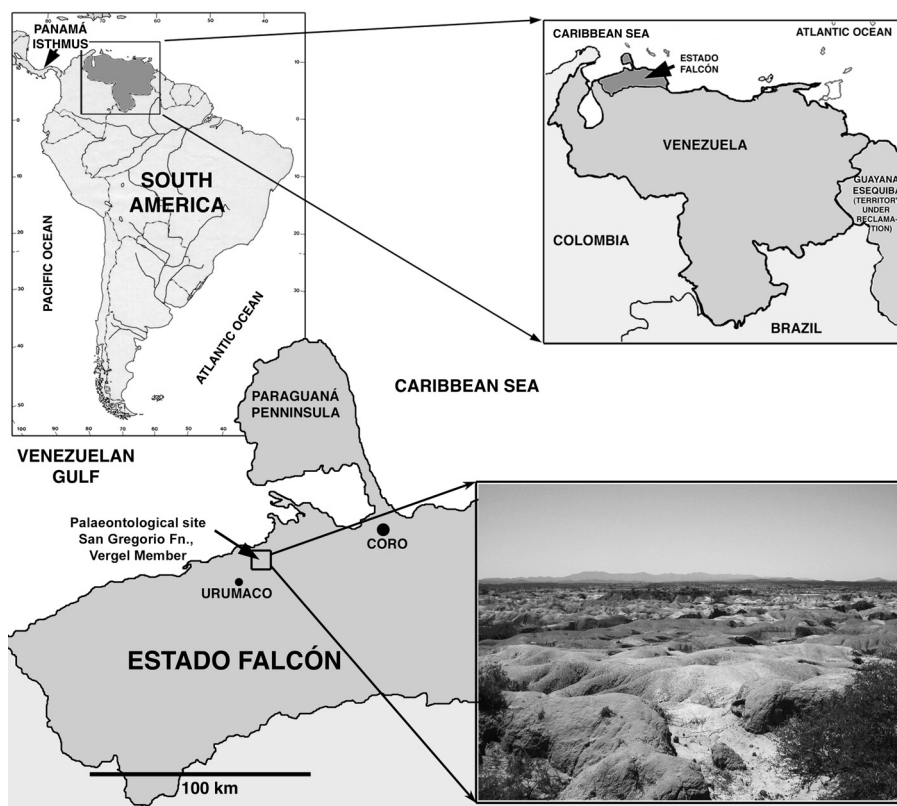


FIGURE 1. Location map showing the locality where the AMU-CURS 184 specimen was recovered from San Gregorio Fm. outcrops.

dant with the biochronologic assessment derived of the tentative assignation of osteoderms of a pam-pathere collected from the lower Vergel member (Carlini and Zurita, 2010), a taxon recorded in the Blancan of USA (4.9 Ma to 1.8 Ma).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

XENARTHRA Cope, 1889

TARDIGRADA Latham and Davies in Forster, 1795

MEGATHERIIDAE Gray, 1821

MEGATHERIINAE Gray, 1821

PROEREMOTHERIUM Carlini, Brandoni and Sánchez, 2006

Type species. *Proeremotherium eljebe* Carlini, Brandoni and Sánchez, 2006.

Geographic and stratigraphic distribution. Estado Falcón, Urumaco; El Jebe Member, Codore Formation and Vergel Member, San Gregorio Formation, Pliocene of Venezuela.

cf. *Proeremotherium*

Referred material. AMU-CURS 184, an almost complete skull lacking mandible, jugals, the pre-

maxillae, the left zygomatic process of the squamosal, vertical lamina of the left pterygoid, anterior part of the nasals, anterior part of the maxillae, lateral and partial anterior wall of the alveoli of right M1 and lateral and anterior wall of the alveoli of left M1, the lateral wall of those of the left tooth row, and teeth (Figure 2).

Geographic and stratigraphic provenance. Twelve Km NNW from Urumaco town; Falcón Basin, Vergel Member, lower levels of San Gregorio Formation, late Pliocene.

Description

The skull AMU-CURS 184 is similar in size and gross morphology to that of *Proeremotherium eljebe* (represented by the type specimen AMU-CURS 126) (Figure 2, Table 1). Similarly to *Proeremotherium eljebe*, *Eremotherium laurillardii* and *E. eomigrans*, AMU-CURS 184 is relatively low (mainly at the anterior third), elongate and “gracile” in comparison with the Pleistocene *Megatherium* Cuvier, 1796, species; with its major width on both the maxillar and the squamosal zygomatic roots (Figure 3). The basicranial area is longer than in *P.*

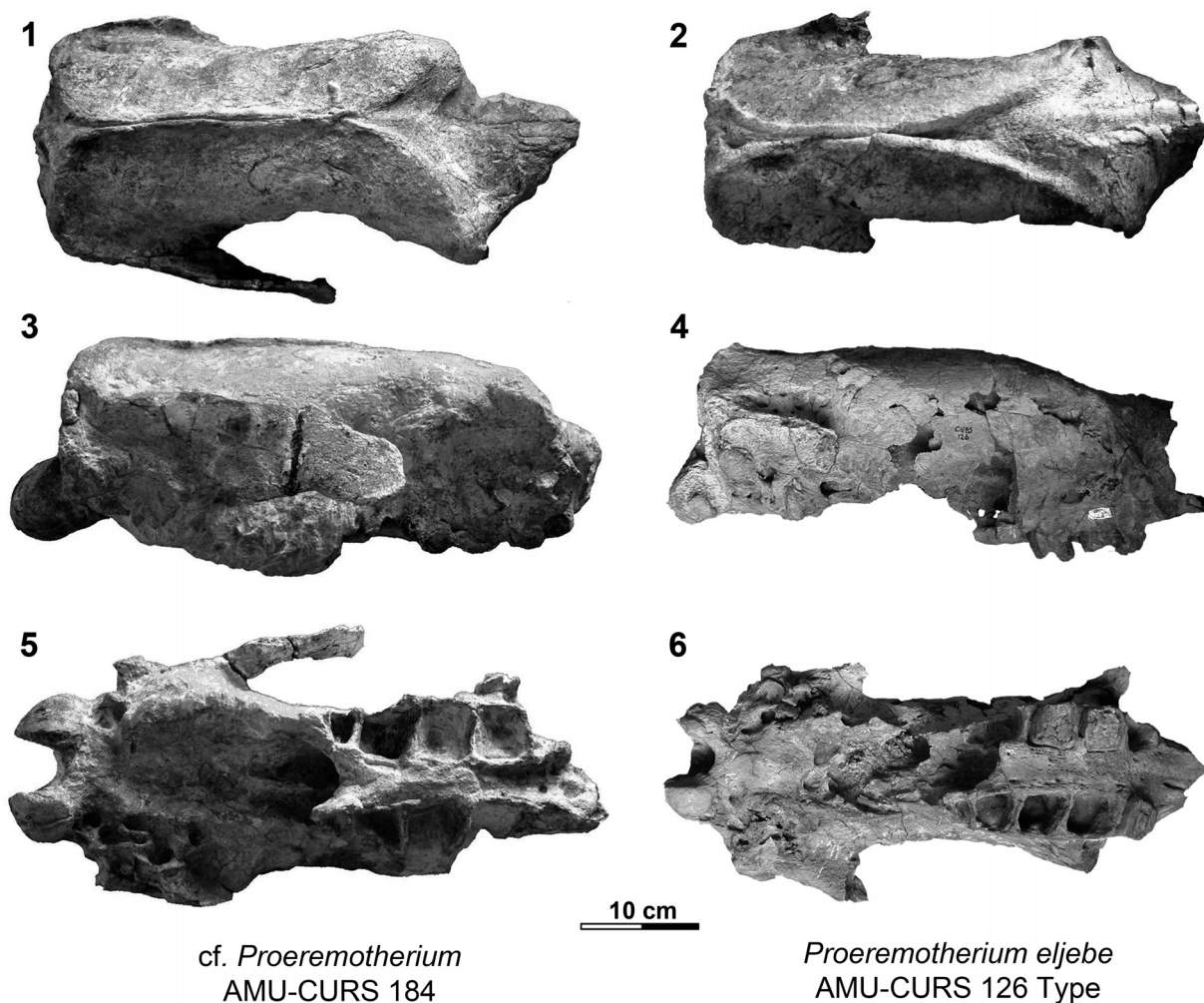


FIGURE 2. Skulls of AMU-CURS 184 and AMU-CURS 126 (*Proeremotherium eljebe* type specimen). AMU-CURS 184 in 1, dorsal; 3, lateral, and 5, palatal views. *Proeremotherium eljebe* in 2, dorsal; 4, lateral, and 6, palatal views.

eljebe, and the basioccipital is more posteriorly projected relative to the condyles. The antero-dorsal and postero-dorsal edges of each temporal fossa are convex both anteriorly and posteriorly,

respectively, and the edge were both fossa converge at midline is straight and form a longer sagittal crest than that of *P. eljebe*. Because of the latter, in AMU-CURS 184 sagittal crest starts just poste-

TABLE 1. Approximate cranial measurements of the type specimen of *Proeremotherium eljebe* and cf. *Proeremotherium* (AMU-CURS 184).

	<i>Proeremotherium eljebe</i> Type AMU-CURS 126	cf. <i>Proeremotherium</i> AMU-CURS 184
Preserved length	460 mm	455 mm
Occipital width	160 mm	168 mm
Bi-condylar width	97 mm	108 mm
Palatal width at M2 tooth	33 mm	30 mm
Alveolus of M2 (w x l)	29 mm x 30 mm	31 mm x 32 mm
Alveolus of M3 (w x l)	30 mm x 32 mm	32 mm x 36 mm
Alveolus of M4 (w x l)	28 mm x 26 mm	31 mm x 29 mm
Alveolus of M5 (w x l)	Not preserved	14 mm x 18 mm

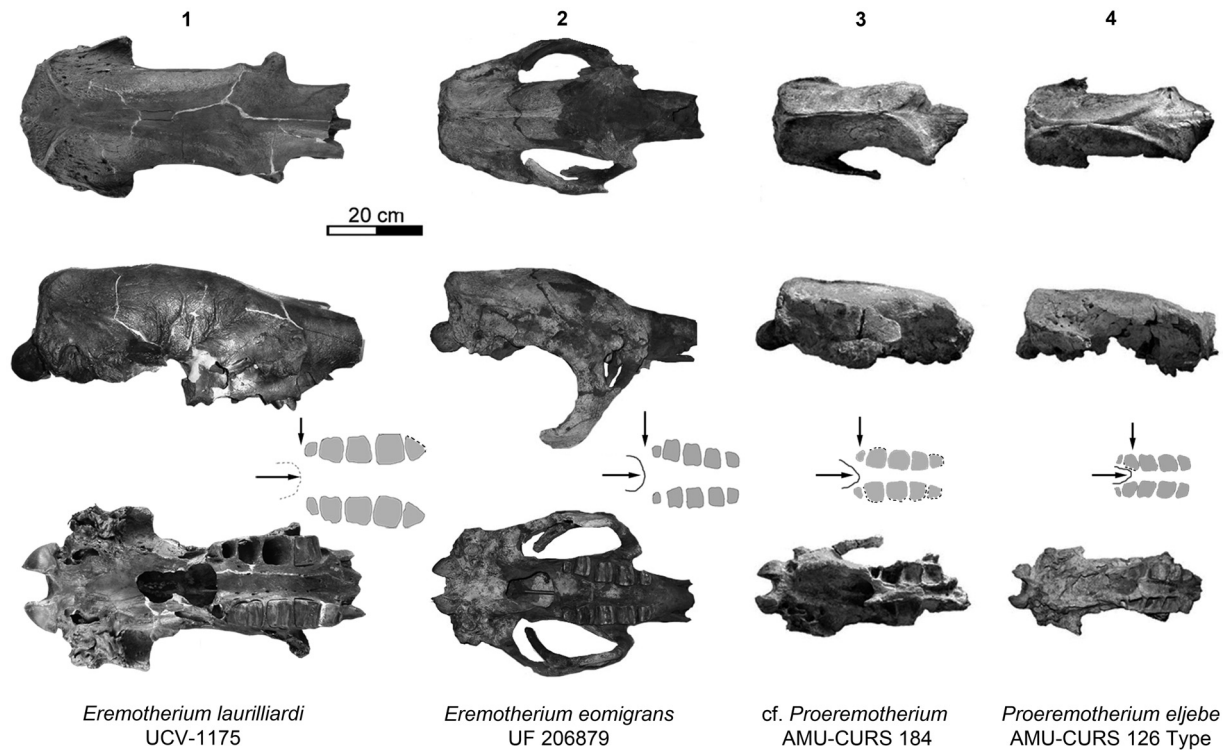


FIGURE 3. Skulls of 1: *Eremotherium laurillardi*, 2: *Eremotherium eomigrans*, 3: AMU-CURS 184, cf. *Proeremotherium* sp., and 4: *Proeremotherium eljebe* (AMU-CURS 126, type), compared in (from top to bottom) dorsal, lateral and palatal views. In light grey are the upper dental series alveoli contours of each skull; black arrows shows the outline and extension of the posterior palatal notch, and up to where it reaches in relation to the dental series (in 1 the dotted line is used because that part of the palatal notch was mechanically broken).

rior to the level of the maxillar zygomatic root (anteriorly to the interorbital constriction), whereas in *Proeremotherium eljebe*, the margins converge posteriorly, at the anterior edge of the squamosal zygomatic root, and consequently form a shorter sagittal crest. The dorsal margin of the skull of AMU-CURS 184 is slightly convex at the middle third, but abruptly descends at the fronto-nasal level, where a sub-triangular concave area is present (with a side parallel to a transverse plane and its opposite angle pointed posteriorly); in *P. eljebe* the triangular area is much more extended and almost convex, and in the species of *Eremotherium* it is almost flat; in *Proeremotherium eljebe* and *Eremotherium laurillardi* the fronto-nasal area descends gradually antero-ventrally. As in *P. eljebe*, *E. laurillardi* and *E. eomigrans*, AMU-CURS 184 has an occiput forming a ca. 90° angle, either with the parietal dorsal plane of the skull roof and the palatal plane (different to the species of *Megatherium* where the angle with the palatal plane is close to 70°). As in *E. laurillardi* and *E. eomigrans*, AMU-CURS 184 has the occipital condyles posteriorly projected, hemispherical in lateral view,

and bigger and with an antero-posterior axis more sub-horizontal than in *P. eljebe*. As in *P. eljebe*, *E. laurillardi*, and *E. eomigrans*, the basilar plane of AMU-CURS 184 is close to the palatal plane, surely related to the low hypsodonty reached (not as in *Megatherium* species where it is higher, as do the hypsodonty, see De Luliis, 1996:154). In AMU-CURS 184, the maxillar zygomatic root is located lateral to M2, whereas in *Proeremotherium eljebe* lies a little more posterior, extending between the mid plane of the M2 and the mid plane of the M3. The infraorbital foramen is at 24 mm above the alveolar plane, whereas it is at 22 mm in *P. eljebe*. The abundant remains of *Eremotherium laurillardi* and *Megatherium americanum* Cuvier, 1796, indicate that both the position of the root and the height of the infraorbital foramen could vary somewhat. In *Eremotherium laurillardi* the root tends to lie more anteriorly, extending from the level of the middle of M1 to that of the middle of M3; whereas in *M. americanum*, the position of the root is more variable than in *Eremotherium laurillardi* (see De Luliis, 1996). In AMU-CURS 184, because the height of the squamosal zygomatic root, it is more

dorsally extended and is higher than in *P. eljebe*. As in other megatheriines, the squamosal part of the zygomatic arch is a laminar vertical bone over the alveolar plane, but its ventral margin is sub-horizontal as in *Proeremotherium eljebe* and *Eremotherium* species (not oblique as in *Megatherium* species), and its anterior end reaches the level of the M4–M5 septum. The preserved palatal pre-molariform extension is concave, as is at the M1–M2 area, but is almost flat at the M3–M4. The posterior palatal notch is U-shaped, and its anterior margin is at the M5 level; whereas in *P. eljebe* it is anteriorly extended reaching the mid M4 level, and in *Eremotherium laurillardi* and *Megatherium americanum*, the position of the posterior palatal notch is variable (see De Luliis, 1996), but always posterior to the M5 level.

The upper dental series (M1–M5) has approximately 165 mm in length. Each tooth row is convex on its lingual margin and straight-convex on the labial margin, whereas in *P. eljebe* the margins are much more straight either lingual/labial side (Figure 3). The maximum distance between the alveolus of both tooth rows is between the preserved anterior most margin the M1 (43 mm) and the middle plane of the M5 (49 mm). Despite the fact that the specimen AMU-CURS 184 does not preserve the molariform teeth, judging from the shape of the alveoli, we hypothesize that the M1 is subtrapezoidal, the M2–M4 are sub-squared, and the M5 (the smallest) is mesiodistally compressed (as in other Megatheriinae), and nearly oval in outline.

DISCUSSION

Intraspecific variation has been considered in studies of Tardigrada (e.g., McDonald, 1995; De Luliis, 1996; Esteban, 1996; White and MacPhee, 2001; Brandoni et al., 2010). There are many factors that could lead to variation, including genetic, environmental and dietary factors, ontogenetic stage of the specimen and sexual dimorphism. With regard to sexual dimorphism, studies in living sloths such as *Bradypus torquatus* Illiger, 1811, indicate the existence of sexual dimorphism in body mass (females heavier than males) (see Lara-Ruiz and Chiarello, 2005; Chiarello, 2008). Fossil sloths do not have unequivocal anatomical features that indicate sexual dimorphism, as in living sloth *Bradypus* and *Choloepus* (Figure 4). Nevertheless, some speculations about extinct sloths have been made on the basis of cranial morphology (e.g., Cartelle and Bohórquez, 1982; De Luliis, 1996; McDonald, 1995, 2006; Miño-Boilini and

Zurita, 2015) and postcranial features (Amson et al., 2015a, 2015b). For *Eremotherium laurillardi*, Cartelle and Bohórquez (1982) and De Luliis (1996), considered that variation in the temporal region of the skull could be explained by sexual dimorphism. A consideration of differences in other areas of the skull would also be important to assess this important matter. Although the assignation to a specific sex seems to be difficult (see McDonald and Lundelius, 2009, p. 408), De Luliis (1996) suggested that a larger skull and a more prominent sagittal crest are male features. We agree that it occurs in different groups of mammals, and add that the ontogenetic age of the specimens can also influence the occurrence and size of such crest (e.g., Carnivora). For scelidotheres, Miño-Boilini and Zurita (2015) suggested that specimens with sagittal crest are males, and specimens lacking sagittal crest are females, but again the ontogenetic stage of the specimens is also a factor to consider.

As we stated above, the AMU CURS 184 skull shares some features with *P. eljebe* (e.g., size, general shape of the skull), but differs in others (e.g., anterior palatal notch extension, position and size of the occipital condyles, position and height of the squamosal zygomatic arch, shape of the temporal crests). If sexual dimorphism is present in megatheriines as is sustained by different authors (e.g., Cartelle and Bohórquez, 1982; De Luliis, 1996) and considering their arguments, in AMU-CURS 184 the presence of a long sagittal crest could indicate a male individual, and the absence of an extended crest in *Proeremotherium eljebe* a female one, but given the lack of at least two specimens from the same stratigraphic level, the idea of sexual dimorphism is at this point mere speculation. Should new material justify the erection of a new species to include AMU CURS 184, this discussion would be in part clarified.

The Megatheriinae assemblage of Urumaco sequence. Among the Urumaco tardigrades, the first Megatheriinae from the Cenozoic of Venezuela were described by Carlini et al. (2006), represented by two new genera and species from the late Miocene - Pliocene. For the Urumaco Formation (late Miocene), *Urumaquia robusta* was described based on few but significant remains (see Carlini et al., 2006), that were collected in the Urumaco outcrops in the 1970s; subsequently, Carlini et al. (2008a) improved the knowledge of this taxon by describing and comparing new remains.

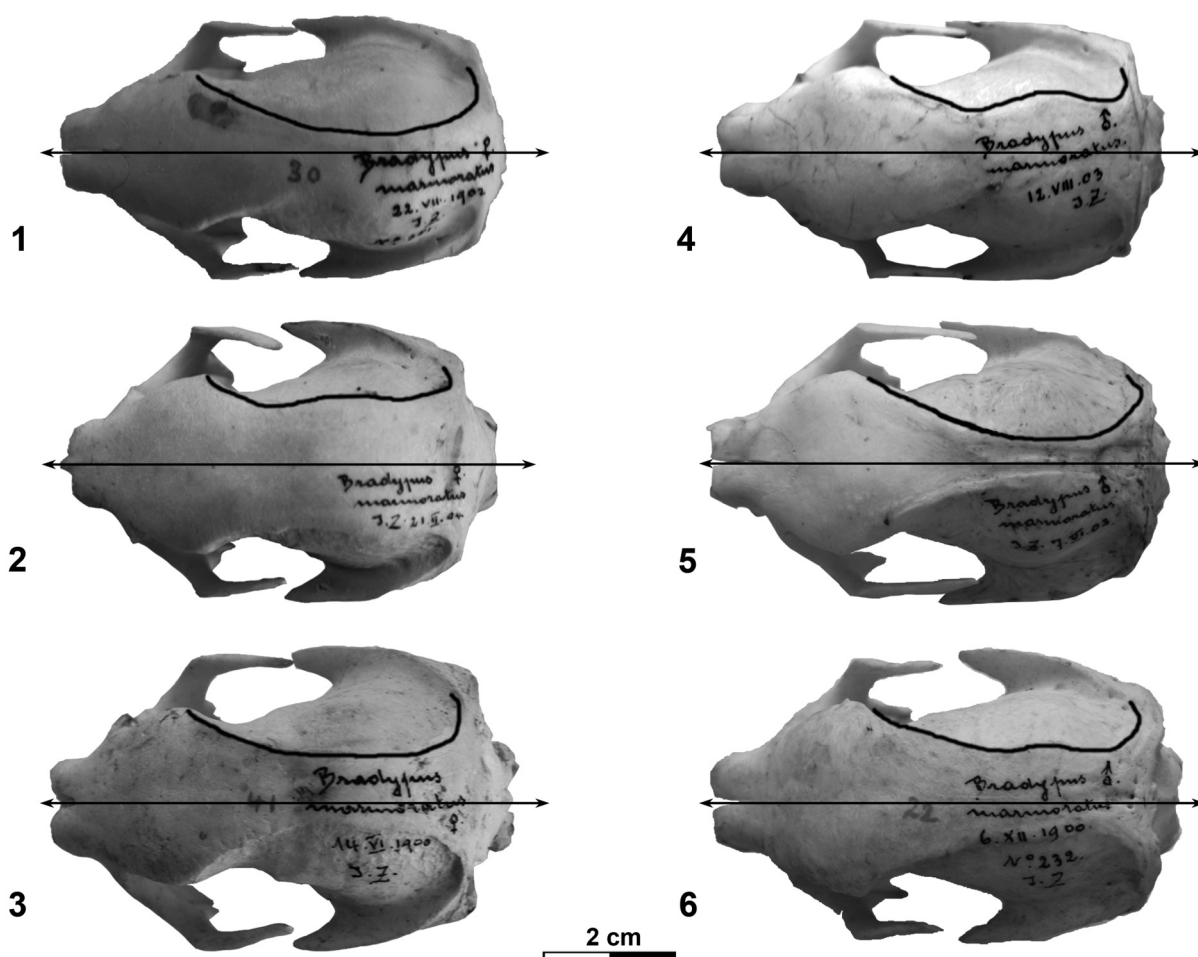


FIGURE 4. Skulls of *Bradypus marmoratus* (sic) of the PIMUZ comparative collection in dorsal view; females on the left and males on the right, in three different sutural ages: 1 and 4, young adults (with most of the posterior sutures opened); 2 and 5, adults (with most of the posterior sutures closed but visible); and, 3 and 6, old adults (with most of the posterior sutures closed and not visible). In all the skulls the right temporal line was marked with a black line showing a great variation among sexes and ages.

For the Codore Fm. (Pliocene) *Proeremotherium eljebe* was described based on an almost complete skull (Figure 2), and was originally interpreted to be phylogenetically close to *Eremotherium* species, because it shows characters (e.g., lower basilar plane, low hypsodonty) (Figure 3) that we could expect in an “ancestral form” or sister group close to *Eremotherium* lineage. A phylogenetic analysis is pending and is not the intention of this contribution.

Eremotherium is mainly a Quaternary megatheriine genus distributed almost exclusively at low latitudes of North America, Central America and South America (Pujos and Salas, 2004; Cartelle and De Iuliis, 2006; Tito, 2008; McDonald and Lundelius, 2009), and is recognizable by its large

size, by the triangular shape of the premental part of its rostrum and by its lower positioned basilar plane and condyles (with respect to the palatal plane) than in the *Megatherium* species. *Eremotherium eomigrans* and *E. laurillardi* were proposed as forming a phyletic sequence (De Iuliis and Cartelle, 1999); this sequence could have begun in the Pliocene of Venezuela with *P. eljebe*. The new remains described in this paper from San Gregorio Fm. (late Pliocene) and that we refer tentatively to *Proeremotherium*, show differences on its basicranial, temporal and dental morphology, and the size and proportions with *P. eljebe* (compare in Figure 2), but share with it the general appearance, the height relation between the palatal and basicranial

planes, profile and low hypsodonty degree (Figures 2 and 3).

Carlini et al. (2006, 2008a) considered the possibility that a species morphologically close to *Proeremotherium eljebe* migrated into North America and gave rise to the early species of *Eremotherium* (i.e., *E. eomigrans* from the Blancan, latest Pliocene- middle Pleistocene). The record of AMUCURS 184 from the San Gregorio Formation is consistent with that hypothesis, because it seems to be morphologically intermediate between *Proeremotherium eljebe* and *Eremotherium eomigrans* (see Figure 3). After the cladogenetic process of *Eremotherium* giving rise to *E. laurillardii* in the Rancho Labrean (late Pleistocene) of North America, *E. laurillardii* migrated to South America and colonized most of the north and central lowlands of South America (Carlini et al., 2008a). This biogeographic scenario proposed for northern megatheriines, i.e., migration from South America during the mid/late Pliocene, dispersion and diversification into North America and re-ingression into South America during the latest Pleistocene, was also proposed for pampatheres (Scillato-Yané et al., 2005), glyptodonts (Carlini et al., 2008b; Carlini and Zurita, 2010; Zurita et al., 2011) and dasypodids (Castro et al., 2014), breaking with the traditional assumption that the GABI for the xenarthrans was a unidirectional process in which they simply dispersed from South America to North America and an ulterior diversification happened there.

Xenarthrans were one of the most successful South American mammals participating in the GABI, given that Tardigrada and Cingulata reached and diversified in North America (McDonald, 2005; Carlini et al., 2008a, 2008c; Carlini and Zurita, 2010). There are records of South American taxa at 4.7 to 3.6 Ma in Mexico (Carranza-Castañeda and Miller, 2004; Flynn et al., 2005). The main phase (in terms of diversity and frequency of findings of xenarthrans) of GABI began ca. 2.7 Ma, as it represents the oldest records of continuous bidirectional flux of land mammals without a marked selectivity.

Concerning the diversity and dispersal paths followed by Megatheriinae, overviews of the megatheriine remains of the late Cenozoic of South America and their geographic and temporal distribution (Carlini et al., 2002, 2006) show that the Cenozoic findings are not frequent at low latitudes. The new megatheriines of the Urumaco sequence not only extended the knowledge of their diversity in South America, but they lead us to

speculate about the moment of differentiation of *Megatherium* and *Eremotherium*, both genera with maximum diversity in the Pleistocene. Concerning *Urumaquia robusta*, of similar size (or even larger in some respects) than the late Miocene-Pliocene Argentinean species of *Pyramiodontherium* Rovereto, 1914, and *Megatheriops* C. Ameghino and Kraglievich, 1921, it is clear that some of its morphological features are derived with respect to those of the taxa from the middle Miocene of Argentina. The taxa recorded in the middle Miocene of La Venta, Colombia, were very likely the smallest and most gracile Megatheriinae at the time (see Hirschfeld, 1985; Carlini et al., 2006) and with a greater number of plesiomorphic characters than those of the fauna from Venezuela. The phylogenetic relationships among these middle to late Miocene megatheriines need to be investigated, but based on the known records we could speculate that as early as the latest middle Miocene, two main lines of Megatheriinae are clearly separated in two geographic areas: one in the rising Andean (on western high to low latitudes, represented by *Megathericulus*, *Eomegatherium*, *Pyramiodontherium*—see Brandoni et al., 2017) and one at low latitudes on the lowlands of central and northern South America, the latter documented in the La Venta and Urumaco deposits of Colombia and Venezuela (represented by *Urumaquia*, *Proeremotherium*, *Eremotherium*—see Carlini et al., 2008a). However, some megatheriines sloths may have had a wide latitudinal distribution across the continent, e.g., *Pliomegatherium lelongi* (see Amson et al., 2016) or even *Eremotherium laurillardii* (Cartelle and De Iuliis, 1995).

The vertebrate faunas coming from the successive Socorro, Urumaco, Codore and San Gregorio Formations are different between each other. However, we can recognize a process of speciation along the different xenarthran lineages recognized (e.g., mylodontoids, megatherioids, glyptodontoids). Notwithstanding, the overlying continental San Gregorio fauna is radically different to all the previous three: the crocodylians include the first and oldest record of a group in that area (Scheyer et al., 2013) and, many groups of mammals are novel, including the first record of North American procyonid immigrants from the northern half of the continent (Forasiepi et al., 2014).

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