NEOGENE SLOTH ASSEMBLAGES (MAMMALIA, PILOSA) OF THE COCINETAS BASIN (LA GUAJIRA, COLOMBIA): IMPLICATIONS FOR THE GREAT AMERICAN BIOTIC INTERCHANGE

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Abstract: We describe sloth assemblages from the Cocinetas Basin (La Guajira peninsula, Colombia), found in the Neogene Castilletes and Ware formations, located in northernmost South America, documenting otherwise poorly known biotas. The tentative referral of a specimen to a small megatherioid sloth, Hyperleptus?, from the early-middle Miocene Castilletes Formation, suggests affinities of this fauna with the distant Santa Cruz Formation and documents a large latitudinal distribution for this taxon. The late Pliocene Ware Formation is much more diverse, with five distinct taxa representing every family of ‘ground sloths’. This diversity is also remarkable at the ecological level, with sloths spanning over two orders of magnitude of body mass and probably having different feeding strategies. Being only a few hundred kilometres away from the Isthmus of Panama, and a few hundred thousand years older than the classically recognized first main pulse of the Great American Biotic interchange (GABI 1), the Ware Formation furthermore documents an important fauna for the understanding of this major event in Neogene palaeobiogeography. The sloths for which unambiguous affinities were recovered are not closely related to the early immigrants found in North America before GABI 1.

Key words: Cocinetas Basin, Great American Biotic Interchange, Neotropics, palaeobiodiversity, Pilosa, sloth.

Sloths (Tardigrada) are represented today by two genera that are ecologically restricted to a peculiar suspensory mode of life, and geographically restricted to the Neotropical region (Nowak & Paradiso 1983). However, this modern distribution is depauperate when compared to the recent past, as their fossil record includes a wide range of body sizes (up to several metric tones; Fariña et al. 1998; Raj Pant et al. 2014), various feeding ecologies (Bargo & Vizcaíno 2008), and a broad distribution from Alaska (Stock 1942) to southernmost South America (and possibly Antarctica; Carlini et al. 1990; Gelfo et al. 2015 and references therein). Their geographical distribution was particularly broad during the Pleistocene, which is partly the result of a major event in Neogene palaeobiogeography: the Great American Biotic Interchange (GABI; Wallace 1876). As South and North America were isolated during most of the Cenozoic, very distinct faunas populated the two landmasses (Simpson 1980). This isolation was ruptured by the northward migration of South American taxa and southward migration of North American taxa (Webb 1985; Cione et al. 2015). In the classical understanding, this process started with single-taxon dispersals (Woodburne 2010), involving the herald taxa sensu Webb (2006) as early as 20.9 Ma (Bloch et al. 2016). This was followed by the main phases of the GABI (or pulses, GABI 1–4; sensu Woodburne 2010), occurring from 2.6–2.4 Ma, and involving the legion taxa sensu Webb (2006). These migrations have mostly been assumed to have been driven by the closure of the Central American Seaway and the formation of the Isthmus of Panama, the most likely route of migration. However, habitat and climatic changes probably played a much more important role in mammal migration patterns (Bacon et al. 2016). Indeed, the timing of the formation of the Isthmus is nowadays challenged by new geological data (Montes et al. 2015) and the onset of GABI by palaeontological (Bloch et al. 2016) and molecular data (Bacon et al. 2015), that suggest a complex process that started at the Oligocene–Miocene transition.
All four families of ‘ground sloths’ took part in all key steps of the interchange, pre- and post-GABI 1 sensu Woodburne (2010). The earliest immigrants are Thionobadistes (Mylodontidae) and Pliometanastes (Megalonychidae), which are present as herald taxa in North America by c. 9 Ma (Webb 1989). Two other herald taxa, Megalonyx (Megalonychidae) and ‘Glossotherium chapadmalense’ (Mylodontidae; and the subsequent Paramylodon; see McAfee 2009) are in North America by c. 7 and 5 Ma respectively (Woodburne 2010). Finally, subsequent sloths are involved in the main phase of GABI, including Eremotherium (Megatheriidae) and Nothrotheriops (Nothrotheriidae).

Intensive fieldwork recently undertaken in the Cocinetas Basin of the La Guajira peninsula of Colombia (the northernmost continental region of South America) resulted in the collection of thousands of specimens from the Jimol, Castilletes and Ware formations (Moreno et al. 2015). At latitude 12°S, the Cocinetas Basin stands out in delivering rich tropical South American palaeobiotas (Jaramillo et al. 2015) in the most biodiverse region of the world (Wallace 1876), otherwise characterized by a poor fossil record. Moreover, the Ware Formation in particular is critical for the understanding of the GABI (Jaramillo et al. 2015). Firstly, it is geographically near to the Isthmus of Panama (only 700 km away). Secondly, it is just slightly older (c. 2.8 Ma) than GABI 1 (2.6–2.4 Ma). The Ware Formation and its tardigradan assemblage have therefore the potential to improve our understanding of the dynamics of GABI in the Neotropics.

GEOLOGICAL SETTING

The Neogene stratigraphy of the Cocinetas Basin, including the Jimol, Castilletes and Ware formations, was recently revised (Moreno et al. 2015). Of those formations, only the Castilletes and Ware formations contain mammalian assemblages. Both crop out along the West coast of the La Guajira peninsula (Colombia) at various localities, of which one from the Castilletes Formation and several from the Ware Formation delivered specimens ascribed to sloths (Fig. 1). The environment of deposition of the Castilletes Formation ranges from shallow marine to fluvio-deltaic, and it has been dated as 16.7–14.2 Ma (late early Miocene to early middle Miocene, upper Burdigalian–Langhian, SALMA Santacrucian/Colloncuran; Hendy et al. 2015; Moreno et al. 2015). The base of the Ware Formation is dominated by fluvio-deltaic environment deposits, while the top is dominated by open-ocean shoreface and nearshore deposits. Its age ranges from 3.40 to 2.78 Ma, late Pliocene (Piacenzian, SALMA Chapadmalalan/Marplatan; Hendy et al. 2015; Moreno et al. 2015).

MATERIAL AND METHOD

We follow the recommendations on open nomenclature of Bengston (1988). For dental terminology, we follow Gaudin (2004), that is, the mesialmost tooth is designated as the caniniform (C1 and c1 for the upper and lower respectively) even if its shape departs from that of a canine-like tooth. The following (more distal) teeth are designated as molariforms (M1–4 and m1–3 for the upper four and three lower molariforms respectively). Standard measurements were taken with digital calipers when lower than 15 cm and with a tape measure otherwise. In addition to standard digital photographs, stereophotographs were taken using a custom-built seesaw.

A phylogenetic analysis was conducted to suggest a hypothesis regarding the affinities of one specimen (MUN STRI 36643). The data matrix of Gaudin (2004) was used, pruning all non-mylodontid taxa except Bradypus and Megalonyx, which are used in the present analysis as outgroups. Along with MUN STRI 36643, another additional terminal taxon, Kiyumylodon, was included. This recently described mylodontine was coded based on Rinderknecht et al. (2007). The initial ordination of the characters of Gaudin (2004) were kept. The edited data matrix is available in the Dryad Digital Repository (Amson et al. 2016a). The algorithm employed was the exhaustive search (Branch and bound) of PAUP 4.0b10 (Swofford 2002).

All specimens have STRI catalogue numbers and are associated with a locality number and stratigraphic data.
These are accessible through the STRI PaleoDatabase (http://biogeodb.stri.si.edu/jaramillo/fossildb). Specimens are deposited at the palaeontological collections of MAPUKA (MUN), Universidad del Norte, Barranquilla, Colombia.

In order to estimate body mass of several specimens, we used the published regression equations of Janis (1990) (in Farina et al. 1998). One of these equations involves the occlusal area of first lower molariform (herein designated as c1 for Plionegatherium lelongi, see below). This area was measured on a photograph (with scale) of the specimen with the program Fiji (Schindelin et al. 2012).

Institutional abbreviations. F:AM, Frick Collection of the American Museum of Natural History, New York, USA; MCL, Museu de Ciencias Naturais da Pontificia, Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MMP, Museo Municipal de Ciencias Naturales ‘Lorenzo Scaglia’, Mar del Plata, Argentina; MUN, Mapuka Museum, Universidad del Norte, Barranquilla, Colombia; MUT, Museo Universitario, Tarija, Bolivia; STRI, Smithsonian Tropical Research Institute, ciudad de Panamá, Panamá.

Other abbreviations. AP, anteroposterior; CC, craniocaudal; DV, dorsoventral; GABI, Great American Biotic Interchange; LL, labiolingual; MD, mesiodistal; ML, mediolateral; PD, proximodistal. Teeth: C1/c1, upper/lower caniniform; M1–4/m1–3, upper four/lower three teeth distal to the caniniform; ‘A’ preceding one of the former, the corresponding alveolus.

SYSTEMATIC PALAEONTOLOGY

MAMMALIA Linnaeus, 1758
XENARTHRA Cope, 1889
TARDIGRADA Latham & Davies, 1795
[= PHYLLOPHAGA Owen, 1842; = FOLIVORA Delsuc et al., 2001]
Gen. et sp. indet.
Figure 2

Referred material. MUN STRI 20108, locality 390022, Ware Formation.

Description. MUN STRI 20108 consists of a left patella (maximum PD length = 66.7 mm; maximum ML width = 53.8 mm; AP depth at centre of articular facet = 22.8 mm; apex PD length (taken from distal border of articular facet) = 26.9 mm; facet ML width = 52.7 mm). It represents a small-sized sloth, approaching the dimensions of Nothrotherium for instance. The articular surface is strongly convex mediolaterally (Fig. 2C). This indicates a strongly developed medial trochlear ridge of the femur. The medial portion of the articular surface is much smaller than the lateral one, which is reminiscent of Hapalops (Fig. 2B). The proximal side bears two grooves (Fig. 2C), as in

Fig. 2. Tardigrada gen. et sp. indet. from the Ware Formation, left patella (MUN STRI 20108). A, anterior view (proximal towards top). B, posterior view (proximal towards top). C, proximal view (anterior towards top). Scale bar represents 2 cm. Colour online.
subcircular. The m3 is bilobate, and the relative size of the lobes is hard to assess due to their preservation. Such a disposition is typically found in mylodontids. It is noteworthy that geologically older forms of uncertain status, such as Orophodon, also feature such a disposition (Pujos & De Iuliis 2007).

The coronoid process is small and rounded dorsally (Fig. 3A). The condyloid process has a short neck and a ventral position, roughly at the level of the tooth row (diagnostic of the Mylodontidae; Saint-André et al. 2010). The posteromedial opening of the mandibular canal is located ventral to the anterior edge of the horizontal ramus of the dentary. Although eroded, the angular process appears regularly rounded, differing from the posteriorly pointed process usually seen in mylodontids.

Remarks. We will conservatively not consider MUN STRI 38047 to represent a taxon of its own in the diversity count, as the possibility that it represents a juvenile individual of the Lestodontini recognized below cannot be excluded.

**MYLODONTINAE Gill, 1872**

**LESTODONTINI** Ameghino, 1889 *sensu* Gaudin (2004)

*Gen. et sp. nov.*

**Figure 4**

**Referred material.** MUN STRI 36643, locality 470060, and tentatively MUN STRI 20424, locality 390023 and MUN STRI 34353, locality 470060 (see remarks below), all Ware Formation.
Based on width at proximal end, it is 81% as large as *Thinobadistes segnis* (mean of four specimens measured by Webb (1989)).

In proximal view (Fig. 4D), the relative size of the condyles and their shape are reminiscent of *Glossotherium robustum* (Owen 1842) and *Paramylodon harlani* (Stock 1925). As in the latter two taxa, the medial condyle is not circular but oval, and its long axis is directed anterolaterally to posteromedially. A similar condition is found in *Megalonyx jeffersonii* (Leidy 1855). In *Thinobadistes segnis* and *Lestodon armatus*, the medial condyle is not as elongate. In *Catonyx cuvieri* and *Valgipes bucklandi*, the long axis of the medial condyle is directed anteroposteriorly, and the condyle is relatively smaller. The intercondylar space is narrower, especially posteriorly, than in most sloths. However, rather close medial and lateral condyles are found in *Thinobadistes segnis* and ‘a bridge of bone connecting the posterior margin of the two facets’ is described in *Pseudoprepotherium confusum* (Hirschfeld 1985). In proximal view, the tibial tuberosity barely protrudes anteriorly from the level of the medial condyle. A similar condition is found in *Lestodon armatus*, and differs from *Thinobadistes segnis* (and most other sloths) in which the tuberosity is more developed anteriorly at the level of lateral condyle.

There is a well-developed crest joining the lateral condyle to the shaft, which forms a deep fossa on the posteriolateral side distal to the proximal facet for fibula (Fig. 4E). This is also found in mylodontines, such as *Glossotherium robustum*, but not in scelidotheriines such as *Catonyx cuvieri* or *Valgipes bucklandi*.
The proximal facet for the fibula faces posterodistally. It faces slightly more laterally in *Glossotherium robustum* and, conversely, it faces slightly more distally in *Catonyx cuvieri*. There is a well-developed facet for the cyamo-fabella as in other sloths, such as mylodontids and megatheriids. In MUN STRI 20424, this facet faces posteriorly and has a triangular outline.

On the anterior side of the bone, there is a crest issuing from the tibial tuberosity that is directed mediiodistally (Fig. 4C). A similar crest is found in *Glossotherium robustum* (Owen 1842). In *Lestodon armatus*, it is more distally directed (Gervais 1873).

MUN STRI 34353 consists of a bilobate tooth formed by concentric layers of orthodentine (Fig. 4F, G; MD length = 17.3 mm; Max LL width of mesial lobe = 13.7 mm; Max LL width of distal lobe = 6.5 mm). The inner nucleus of vasodentine is almost entirely missing (Fig. 4F). Only patches of cementum are preserved at various heights along the tooth. The larger mesial lobe is compressed mostly mesiodistally, but with a diagonal direction as well, giving the tooth an asymmetrical shape in both the labial-lingual and mesiodistal directions. The smaller distal lobe is strongly compressed labiolingually. Well-marked labial and lingual sulci at the level of junction between the lobes are found along the whole length of the tooth (Fig. 4G). The resulting morphology is reminiscent of the right M4 of *Pleurolestodon dalenzae* (Saint-André et al. 2010). The long and constricted distal lobe of M4 is a diagnostic feature of this species, as the other valid species of the genus, *P. acutidens* (Saint-André et al. 2010), lacks the strong labiolingually compression of the distal lobe (Rovereto 1914). However, the distal lobe is longer and less constricted in *P. dalenzae* than in MUN STRI 34353, forming a ‘secondary’ rounded nucleus. The labial side of the mesial lobe forms a somewhat more acute curve in *P. dalenzae* (MNHN-BOL V 3348) is larger (mesiodistal length 1.27 times greater).

It is noteworthy that an approaching morphology is featured by the most distal lower molariform (m3) of *Pseudoprepothereium confusum* (Hirschfeld 1985), but the latter bears a mesiolabially directed facet on its mesial lobe. Moreover, the whole vasodentine nucleus is relatively smaller in the m4 of *P. confusum*.

The occlusal surface is not planar, the lingual part of the mesial lobe being a bit less worn down than the rest of the tooth. The lingual part of the mesial lobe bears a minute wear facet that mostly faces occluso-lingually.

**Remarks.** We performed a phylogenetic analysis including as the ingroup MUN STRI 36643 coded as a terminal taxon and the mylodontids included in Gaudin (2004). Three equally parsimionous trees were recovered. Their topology is the same as the one recovered by Gaudin (2004), as their difference lies in the position of MUN STRI 36643. The latter is indeed either sister-group of *Lestodon*, or *Thinobadistes*, or of the clade formed by the two latter genera (= Lestodontini), as shown by the polytomy of the strict consensus of these three trees (Fig. 5). In a second analysis we included the mylodontine *Kiyumylodon*, also known from an isolated mandible.

A total of 18 equally parsimionous trees were obtained. Their consensus is much less resolved than the first analysis, with the Mylodontinae, except for *Pseudoprepothereium*, forming a polytomy. The only relationship that is resolved within the latter polytomy is the Lestodontini, recovered as in the previous analysis comprising MUN STRI 36643. As a result, MUN STRI 36643 should be considered as a Lestodontini sensu Gaudin (2004). Differing from *Lestodon* and *Thinobadistes*, MUN STRI 36643 most likely represents an undescribed taxon, nov. gen et sp. but we refrain from formally erecting a new taxon, pending the discovery of more complete material.

MUN STRI 20424 and MUN STRI 34353 can only be safely ascribed to a medium-sized Mylodontinae gen. et sp. indet. We tentatively ascribe them to the same taxon as MUN STRI 36643, as no features appear be incompatible.
**Description.** MUN STRI 16535 consists of a complete left ulna (see 3D model in Amson et al. 2016b). The specimen is from an adult, as shown by the epiphyseal closure (PD length = 280 mm; AP depth at coronoid process = 93.3 mm). MUN STRI 16535 is shorter than all scelidotheriines measured by McDonald (1987), which span from 313 to 476 mm. The four specimens of *Scelidotherium leptocephalum* measured by Miño-Boilini et al. (2014) are also longer, the smaller measuring 370 mm. It is however longer than that of *Pseudoprepotherium confusum* (c. 20 cm; Hirschfeld 1985).

In lateral view (Fig. 6C), the posterior end of the olecranon process does not reach the level of the anterior end proximally, which is reminiscent of *Glossotherium robustum* (Owen 1842) and *Scelidotherium leptocephalum* (Miño-Boilini et al. 2014) and differs from those of *Catonyx tarijensis* (McDonald 1987), *Catonyx cuvieri*, *Valgipes bucklandi* (Cartelle et al. 2009) and *Paramylodon harlani* (Stock 1925). The most reminiscent olecranon process is found in *Scelidotherium leptocephalum*, which also features a characteristic pointed proximal end.

The anconeal process is very slightly broken, but is obviously weakly developed (Fig. 6C), which differs from *Glossotherium robustum*, *Catonyx cuvieri* and *Valgipes bucklandi* (Cartelle et al. 2009), and is reminiscent of *Scelidotherium leptocephalum*, *Paramylodon harlani* and *Catonyx tarijensis*.

The radial facet is restricted to a small area continuous with the most lateral part of the humeral facet (Fig. 6A).

The ulna is more elongate (depth at coronoid process/proximodistal length = 0.33) when compared to *Glossotherium robustum* (0.45; Owen 1842) and *Paramylodon harlani* (0.41; Stock 1925), and slightly stouter than *Valgipes bucklandi* (0.26; MCL 22464) and *Pseudoprepotherium confusum* (0.26; Hirschfeld 1985), its proportions being more reminiscent of those of *Scelidotherium leptocephalum* and *Scelidodon chiliense* (both 0.32; MMP 549S and MUT 1510 respectively; McDonald 1987).

A generic attribution is precluded by the paucity of postcrania data for Neogene taxa (Miño-Boilini et al. 2011).

**MEGATHERIOIDEA** Gray, 1821

*Hyperleptus?* Ameghino, 1891

Figure 7

**Referred material.** MUN STRI 37413, locality 130024, Castilletes Formation.

**Description.** Bone fragment with three poorly preserved molariforms (M2 MD length = c. 6 mm; M2 LL width = c. 10 mm; M3 MD length = 6.8 mm; M3 LL width = c. 8 mm; M4 MD length = 6.8 mm; M4 LL width = 6.2 mm). The different types of dental tissues are not discernable. There is no diastema (Fig. 7A). On the lingual side of the middle and mesial teeth, there are tooth scars of a relative large size. The root of the molar is conical and the internal structure is not discernable.

**Figure 6.** Scelidotheriinae gen. et sp. indet. from the Ware Formation, left ulna (MUN STRI 16535). A, anterior view (proximal towards top). B, posterior view (proximal towards top). C, lateral view (proximal towards top). Scale bar represents 10 cm. Colour online.
the bone projects medially. Attributable to a small portion of the posterior end of the palate, this indicates that the specimen represents upper teeth and maxilla. The occlusal surface of the teeth does not reach the most ventral level of the bone, possibly suggesting a very immature individual or a very abrasive diet (Fig. 7B). Furthermore, each tooth is surrounded by a large space, which would tend to corroborate the first hypothesis. The M2 is poorly preserved. Its outline and that of M3, although not entirely preserved, are clearly compressed mesiodistally. The M3 preserves mesial and distal ridges, a synapomorphy of megatherioids (Gaudin 2004). Conversely, the outline of M4 (the only one entirely preserved) is subcircular, a singular trait in sloths. The mesial half of its occlusal surface is covered by a labiolingual ridge. Although mostly broken, there was most likely a lower distal ridge as well. Hyperleptus garzonianus is characterized by a rounded M4 and mesiodistally compressed M1–3 (Ameghino 1891). However in Hyperleptus garzonianus the M4 is not as circular as in MUN STRI 37413, being slightly wider labiolingually than long mesiodistally (see measurements of Scott (1903–1904)).

Remarks. A sub-circular outline of M4 seems to be a derived trait found of Hyperleptus garzonianus. As the M4 of MUN STRI 37413 also departs from the plesiomorphic strongly elliptical condition of megatherioids, a close affinity with the latter species is likely. But the fragmentary nature of MUN STRI 37413 and the fact that its M4 seems even more circular than that of Hyperleptus garzonianus preclude a definitive attribution to this species. Hyperleptus is known from the Santa Cruz Formation (Scott 1903–1904), and is one of a number of small megatherioids of uncertain affinity, which also includes Pelecyodon, Schismotherium, Analcimorphus and Hapalops (Gaudin 2004).

MEGALONYCHIDAE Gervais, 1855
Gen. et sp. nov.
Figure 8

Referred material. MUN STRI 16601, locality 390077 and MUN STRI 34226, locality 470060, both Ware Formation.

Description. MUN STRI 16601 consists of a left patella representing a relatively large-sized taxon (Fig. 8D–E; maximum PD length = 112.3 mm; maximum ML width = 92.7 mm; AP depth at centre of articular facet = 32.2 mm; apex PD length (taken from distal border of articular facet) = 47.8 mm; facet ML width = 86.4 mm). It is slightly smaller than the specimen of Megalonyx jeffersonii measured by Leidy (1855), but much larger than Pliomorphus mutilatus, as shown by the width of the patellar trochlea of the femur (Brandoni 2009). The tapered apex gives the patella a teardrop shape in anterior view (Fig. 8D), as commonly seen in sloths. The articular facet is only very weakly convex mediolaterally (Fig. 8E), precluding the attribution to a pedalateral sloth (Mylodontidae or Megatheria) or a glyptodont. Moreover, the lateral half of the facet is shorter proximodistally than the medial half, as in Megalonyx jeffersonii (Leidy 1855). However, in anterior view, the general shape differs from that of Megalonyx jeffersonii, in that both its proximal border and apex are more tapered.

MUN STRI 34226 consists of an ulna preserving the proximal epiphysis and part of the diaphysis (Fig. 8A–C; AP depth at coronoid process = 83.0 mm; PD length from proximal end to level of coronoid process = 62.2 mm). The specimen is from an
adult, as shown by the epiphyseal closure. The most distal part of the preserved diaphysis is anteroposteriorly deep, suggesting that roughly at least a fifth of the diaphysis is missing.

The olecranon process is directed posteroproximally, forming an angle of roughly 45° with the proximodistal axis of the bone (Fig. 8A–C), as in Megalonyx jeffersonii (see for instance Leidy 1855, pls IX, X). However, it differs from the latter genus by lacking the strong medial inflection that affects the whole tuberosity (Fig. 8A). Indeed, the olecranon process only slightly protrudes medially in MUN STRI 34226. The presence of a small tuberosity on the medial side of the tip of the olecranon process is reminiscent of Megalonyx jeffersonii, and Nothrotheriops shastensis as well.

The articular surface for the humeral trochlea is not entirely preserved, but one can observe that it is weakly expanded laterally and posteriorly (Fig. 8A, C), a characteristic feature of Megalonyx jeffersonii, and differing from Nothrotheriops shastensis for instance. As in both latter genera, the anconeal process is weakly developed anteriorly. It appears even narrower mediolaterally than in these two genera. Although fragmentary, it can be discerned that the radial facet is continuous with the humeral facet. Intraspecific variation regarding this trait is described in Megalonyx jeffersonii (McDonald 1977). A large rounded pit is present distal to the radial facet. A strong crest, issued from the process for the radial notch, joins rapidly the anterior edge of the shaft.

The shaft is slightly bent medially (Fig. 8A, B). Its lateral side bears a strong muscular crest issued from the posterior end and directed anterodistally.

Remarks. MUN STRI 16601 and MUN STRI 34226 were found isolated and each can be ascribed to an undescribed Megalonychidae. We conservatively ascribe both specimens to the same Megalonychidae gen. et sp. nov. in order to avoid overestimating the taxonomic diversity of the Ware Formation.

MEGATHERIA sensu Gaudin (2004)
MEGATHERIIDAE Gray, 1821
MEGATHERINAE Gray, 1821
Pliomegatherium lelongi Kraglievich, 1930

Figure 9

Referred material. MUN STRI 36685, locality 390024, and tentatively MUN STRI 19747, locality 390017 and MUN STRI 20446, locality 390026, all Ware Formation.

Description. MUN STRI 36685 consists of a partial mandible with c1 (mesialmost tooth, molarized in megatherines), eroded below the level of the alveolar plane (Fig. 9A–B; maximum MD length of c1 = 32.3 mm; maximum LL width of c1 = c. 36 mm; LL width at distal end = 33.8 mm; maximum MD length of alveolus of c1 = 37.4 mm). It is an adult

FIG. 8. Megalonychidae gen. et sp. nov. from the Ware Formation. A–C, left ulna (MUN STRI 34226); A, anterior view (proximal towards top); B, posterior view (proximal towards top); C, lateral view (proximal towards top). D–E, left patella (MUN STRI 16601); D, anterior view (proximal towards top); E, posterior view (proximal towards top). Scale bar represents 10 cm. Colour online.
FIG. 9. *Pliomegatherium lelongi* from the Ware Formation. A–B, partial mandible with c1 (MUN STRI 36685): A, photograph and drawing in occlusal view (anterior towards top); B, right lateral view (occlusal towards top). C, partial caudal vertebra (MUN STRI 19747) in dorsal view (cranial towards top). Scale bar represents 5 cm. Colour online.
individual, as indicated by the thorough closure of the symphysis, and the very short distance between the labial side of c1 alveolus and lateral side of horizontal ramus (De Iuliis 1996). Based on the tooth dimensions, it is a medium-sized megatheriine, similar to the holotype of Pliomegatherium lelongi (Brandoni 2006), and smaller than Pyramiodontherium brevisrostrum (Carlini et al. 2002; and, by extension, also smaller than Megatheriops rectidens, see Pujos et al. 2013). The cross-section of c1 is trapezoidal, with the mesial side slightly narrower labiolingually than the distal side (Fig. 9A). This is characteristic of Pliomegatherium lelongi (Brandoni 2006), and differs from the mesiolabially constricted teeth of early megatherelines such as Megathericulus, and square cross-section of the teeth of Megatherium americanum, Eremerotherium aurillardi and Eremerotherium comignans. The dorsal edge of the preserved portion of the spout is not preserved (Fig. 9B), which prevents us from precisely assessing the relative development of the ventral bulge of the dentary (diagnostic within the Megatheriinae subfamily; De Iuliis 1996). The posterior end of the symphysis is preserved (Fig. 9A). It forms a partially closed notch (c. 80°). This is reminiscent of Pliomegatherium lelongi (Brandoni 2006) and Eremerotherium aurillardi, and differs from the more open symphysis of Megathericulus patagonicus, and more closed one of Megatherium americanum. It is located approximately at the level of the mid-mesiodistal length of c1, roughly as in one of Megatherium americanum. The transverse processes are either oriented only laterally or laterocranially (e.g. Glyptotherium texanum, Gillette & Ray 1981). MUN STRI 20446 consists of a centrum of caudal vertebra (CC length of centrum = 57.9 mm; DV height of centrum at cranial side = 56.2 mm; ML of centrum at caudal side = c. 71 mm; maximum ML width (one side doubled) = 170 mm). The cross-section of the centrum is slightly flattened dorsoventrally, indicating proximity to the cranial region of the series. The cranial and caudal facets of the centrum are onl y slightly oblique to each other (i.e. the cranial is set slightly dorsal to the caudal). The four hypophyseal processes and their facets for the haemal arches are well developed.

Remarks. Pliomegatherium lelongi is otherwise recorded in the ‘conglomerado osífero’, Ituzaingó Formation, Entre Ríos Province, Argentina (upper Miocene – Pliocene; Brandoni 2006). Pliomegatherium sp. is also reported in the ‘Barrancas de San Gregorio’, San José member of Raigón Formation (Perea et al. 2013), San José Department, Uruguay (Mones 1988). These localities are at a latitude of c. 32–34°S, and are c. 5000–5500 km from the localities of the Ware Formation. The geographical range of P. lelongi is hence drastically expanded, with specimens being found across the northern two-thirds of South America. The broad geographical distribution seems to be common in the subfamily, as exemplified by the Panamerican Ereutherium aurillardi (Cartelle & De Iuliis 1995). Based on the dimensions of the c1 of MUN STRI 36685, the body mass of this individual is estimated to be between c. 1000 and 4400 kg, with a mean value of 2400 kg (Table 1). This is consistent with the 2500 kg estimate given for another medium-sized megatheriene, Pyramiodontherium scillatoyanei (De Iuliis et al. 2004). MUN STRI 19747 and MUN STRI 20446 can only be safely ascribed to Megatheriinae indet. and Xenarthra indet., respectively. But, given the similar morphology and dimensions of the centra, and the fact that no features appear to be incompatible, we tentatively ascribe them to the same taxon as MUN STRI 36685.
NOTHROTHERIIDAE Ameghino, 1920
NOTHROTHERINAE Ameghino, 1920

cf. Nothrotherium Lydekker, 1889
Figures 10, 11

Referred material. MUN STRI 12924, locality 390024, Ware Formation.

Description. MUN STRI 12924 consists of a fragmentary basicranium, with the posterior portion of the skull roof (Fig. 10; see 3D model in Amson et al. (2016b); ML width at postorbital constriction = 54.5 mm; ML width at mastoid processes = 82.0 mm; ML width at root of zygomatic process of squamosal = 95.1 mm; maximum ML width of occipital condyles = 56.5 mm; occipital height = 53.7 mm; maximum ML width of foramen magnum = 30.0 mm; maximum DV height of foramen magnum = c. 28 mm). Two foramina are present at the posterior edge of the basioccipital, which indicate the incomplete ossification and hence immaturity of the specimen. Moreover, some of the sutures appear thoroughly closed (e.g. interfrontals, interparietals), while others are not (e.g. supraoccipital-exoccipital). A subadult stage is hence

**FIG. 10.** Cf. Nothrotherium from the Ware Formation, partial basicranium (MUN STRI 12924), general views (photograph and drawing). A, dorsal view (right lateral towards top). B, left lateral view (dorsal towards top). C, occipital view (dorsal towards top).

**Abbreviations:** ape., anterior process of entotympanic; coa., canal for the occipital artery; eoc., external occipital crest; exc., exoccipital crest; f., foramen; frag., fragment; nc., nuchal crest; oc., occipital condyle; Occ., occipital bone; p., process; sf., stylomastoid foramen.

Scale bars represent 5 cm. Colour online.
inferred for this specimen. The size of the specimen falls within
the range of the adult specimens of *Nothrotherium maquinense*
measured by Cartelle & Fonseca (1983), and is slightly larger than
*Mionothropus cartellei* (De Iuliis et al. 2011) and *Pronothrotherium*
typicum (Patterson et al. 1992).

Only a dorsal portion of the posterior half of the frontals is pre-
served (Fig. 10A, B). There is no sagittal crest (diagnostic of the
Nothrotheriidae; De Iuliis et al. 2011), but this could be due to
the immaturity of the specimen. The frontoparietal suture is at the
level of the root of the zygomatic process of the squamosal. Part of
the alisphenoid is present on both sides. It contacts the parietal
(diagnostic of the Nothrotheriinae except *Mionothropus cartellei*,
De Iuliis et al. 2011). The temporal line joins the dorsal edge of
the zygomatic process of the squamosal posteriorly, as in
*Mionothropus cartellei*, *Nothrotherium maquinense* and
*Nothrotheriops shastensis*, but not in *Pronothrotherium typicum* (De Iuliis et al. 2011). The parietals are globose and posteriorly depressed
(diagnostic of *Nothrotherium maquinense*, Paula Couto 1971).

The root of the zygoma is directed anteriorly (diagnostic of the
Nothrotheriinae; De Iuliis et al. 2011). Lateral to it, there is
a bulge (diagnostic of the Nothrotheriinae except *Mionothropus*
cartellei, De Iuliis et al. 2011), although it does not appear as
developed as in *Pronothrotherium typicum*, *Nothrotherium*
maquinense and *Nothrotheriops shastensis*.

Anterior to the carotid foramen, and medial to the Glaserian
fissure, the bone has an irregular surface and displays a broken
ridge (Fig. 11). Medial to it, and just anterior to the basioccipital
tuber, the basisphenoid shows a rugose surface. This region
most likely represents the location of the posterior part of the
ossified pterygoid bulla, which presumably would not have been
thoroughly sutured yet to the basiphenoid in this immature
specimen. An ossified pterygoid bulla is present in *Nothrotherium*
maquinense and *Nothrotheriops shastensis*.

The ectotympanic is missing on both sides, except maybe for
a small portion of the anterior crus on the left side. The ento-
tympanic is well preserved on both sides. Anterolateral and pos-
teromedial portions can be distinguished, as described in
*Pronothrotherium typicum* (Patterson et al. 1992) and *Mionothro-
pus cartellei* (De Iuliis et al. 2011). The posteromedial portion is
much smaller than the anterolateral one, differing in that regard
from *Pronothrotherium typicum* (Patterson et al. 1992). A similar
disposition is found in *Nothrotherium maquinense* (MCL 21703),
but in this species the posteromedial portion seems more dorsally
elevated. In MUN STRI 12924, the anterolateral portion forms a

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**FIG. 11.** *Cf. Nothrotherium* from the Ware Formation, partial basicranium (MUN STRI 12924), close-up of the left auditory region in ventral view (anterior towards top). A–B, left and right stereophotographs. C, same view as B but labelled. Abbreviations: ant. cr. fr., anterior crus fragment; ant. p. ent., anterior process of entotympanic; Bo., basioccipital; Bs., basisphenoid; car. f. + mlf., carotid fora-
men and medial lacerate foramen; ent. p. ali., entoglenoid process of alisphenoid; exo. cr., exoccipital crest; f., foramen; gl., Glaserian
fissure; mast. p., mastoid process; pet. fr., petrosal fragment; p., process; post. p. ent., posterior process of entotympanic; th., tympano-
hyoid; sm., superficies meatus; ssp., scar of suture for pterygoid bulla; sth. fos., stylohyal fossa; stylo. f., stylomastoid foramen; su.
int. car. art., sulcus for internal carotid artery. Scale bar represents 2 cm. Colour online.
ventrally expanded crest-like process. It is sigmoidal in ventral view. This process appears to be particularly vertical, not being inclined medially. The posterior end of the entotympanic forms the medial part of the stylohyoid fossa. The junction between the postero medial and anterolateral portions of the entotympanic is marked by a shallow sulcus, presumably accommodating, as in *Mionothropus cartellei*, the internal carotid artery. The jugular foramen (or posterior lacerate foramen) is large, extending posteriorly up to the level of the hypoglossal foramen (diagnostic of the Nothrotheriidae; De Iuliis et al. 2011). Both of these foramina somewhat share the same excavation and are located especially close to one another, which is very reminiscent of *Nothrotherium maquinense* and *Nothrotheriops shastensis*, and differs from the more separate foramina of *Mionothropus cartellei* and *Pronothrotherium typicum*. Postero medial to these foramina, there is a globular paracondylar process, very reminiscent of *Nothrotherium maquinense*, and differing from the more elongate process of *Nothrotheriops shastensis*. The stylo mastoid foramen is found at the dorsal end of a sulcus formed laterally by the mastoid process and medially by a well-developed ridge extending from the nuchal crest (possibly the exoccipital crest *sensu* Gaudin 1995). This sulcus, terminating dorsally by a foramen, may represent a widely exposed canal for the occipital artery, a synapomorphy of the Nothrotheriidae (Gaudin 1995). A groove also leading dorsally to the mastoid foramen is described in *Acrotocnus odontogri gonus* and *Schismotherium fractum* (Patterson et al. 1992). Most of the preserved articular surface of the stylohyoid fossa is formed by the posterodorsal side of the entotympanic. The rest of the preserved articular surface is a narrow strip, presumably formed by the tympanohyoid, as in *Mionothropus cartellei* for instance (De Iuliis et al. 2011).

The occipital condyles are sessile (Fig. 10C; diagnostic of the Nothrotheriidae; De Iuliis et al. 2011). They have a peculiar (abnormal?) morphology, being marked at mid-height by a mediolaterally oriented depression. There is a distinct external occipital crest, developed to an extent very similar to that of a juvenile specimen of *Nothrotherium maquinense* (MCL 1020). The nuchal crest, however, is inconspicuous.

**Remarks.** *Nothrotherium* is represented by the Pleistocene *N. maquinense* and *N. escrivanense*, which are restricted to Brazilian localities. While we provisionally ascribe MUN STRI 12924 to cf. *Nothrotherium* due to the fragmentary nature and immaturity of the specimen, it is likely to represent a closely related new taxon. Based on the occipital height of this specimen, the body mass of the individual is estimated to be c. 41 kg (Table 1). We estimate this specimen to be subadult, and consider it unlikely that this individual would have reached 100 kg at maturity.

**DISCUSSION**

**Mammalian assemblage of the Castilletes Formation**

Although not the main focus of the present contribution, the Castilletes Formation is discussed here because of an important modification to its faunal composition. The specimen previously referred to Megatheriidae (MUN STRI 16777; Moreno et al. 2015), the only sloth formerly recognized in the formation, is actually an astrapothere.

However, the Castilletes Formation does contain a tardigrade, as MUN STRI 37413 represents a small megatherioid. Tentatively referred to *Hyperleptus*, this record could be consistent with the geological age of the Formation as it is otherwise known from the Santacrucian fauna. A sparassodont from the Castilletes formation, *Lycopsis padillai* (Suárez et al. 2015), also suggests affinities with the Santacrucian fauna. On the other hand, crocodilian taxa of the Castilletes Formation are otherwise known from Laventan and Huayquerian faunas (Moreno-Bernal et al. 2016). This emphasizes the importance of the detailed description of the rest of the mammalian fauna from the Castilletes Formation.

**Diversity of the tardigradan assemblage of the Ware Formation**

A greater taxonomic diversity in the lower latitudes is a global pattern broadly found today among eukaryotes (Hillebrand 2004), and it is the result of a long and complex history, as shown in particular for the Neotropics (Jaramillo et al. 2006). Recent studies have shown how Neotropical Miocene formations can preserve hyperdiverse vertebrate assemblages (for crocodilians, see Scheyer et al. 2013; Salas-Gismondi et al. 2015). However, taxonomic richness of fossil tropical assemblages is still severely underestimated (Carrillo et al. 2015). The Ware Formation gives an important insight into the otherwise poorly documented diversity at low latitudes during the Pliocene. The conservative diversity count for the tardigradan assemblage of the Ware Formation is of five distinct taxa. Each of the four families of ‘ground sloths’ (Mylodontidae, Megatheriidae, Nothrotheriidae and Megalonychidae) is represented. When compared with assemblages from other Pliocene Neotropical formations (Table 2), the Ware assemblage has a rather diverse tardigradan composition. The San Gregorio Formation is a geographically nearby formation that records a roughly synchronous continental fauna, and yet only one sloth has been reported (Vucetich et al. 2010), most likely due to taphonomic and/or sampling biases. When compared to older formations, the Ware Formation’s tardigradan diversity is equalled by the Urumaco Formation (late Miocene; where the taxa might not have been coeval, Carlini et al. 2006a) and surpassed by the better-known Laventan fauna. An example of an extensively sampled Pliocene formation that is found at higher latitudes is the Monte Hermoso Formation. Although it records five species in three families, only two to three species are...
found in the same facies (Tomassini et al. 2013), making it roughly half as diverse as the Ware Formation. When compared to other temperate Pliocene assemblages (Table 2), a similar conclusion can be drawn, except for the Uquia Formation. The astonishing 22 species of sloth of the Late Miocene Ituzaingó Formation (‘Conglomerado osifero, mesopotamian’) has to be taken with caution, as a recent and unfinished taxonomic revision (every family except the Mylodontidae) has revealed a lower diversity than previously reported (Brandoni 2013).

Another aspect of the diversity of the sloths of the Ware Formation dwells in their ecologies. With a body mass estimated to be c. 2400 kg, *Pliomegatherium lelongi* is a megaherbivore *sensu* Owen-Smith (1987). While the closely related *Megatherium americanum* is reconstructed as a selective feeder (Bargo & Vizcaíno 2008), broad geographical distribution is common in the subfamily, which is usually considered to be indicative of generalist habits. In contrast, the specimen ascribed to *cf. Nothrotherium* is a small-sized sloth weighing roughly 41 kg. Although not much can be argued about the ecology of the latter, the range of two orders of magnitude in body size featured by this tardigradan assemblage suggests that disparate ecological niches were occupied. In addition to intermediate body size, the other sloths recovered feature other feeding ecologies. Based on the morphology of its close relatives, *Lestodon* and *Thinobadistes*, Lestodontini gen. et sp nov. was most likely wide-muzzled. This is argued to correlate with another feeding ecology, namely bulk-feeding (Bargo & Vizcaíno 2008; Czerwonogora et al. 2011). Furthermore, Scelidotheriinae gen. et sp. indet. was most likely as narrow-muzzled as *Scelidotherium leptocephalum*, which has been interpreted as a mixed or selective-feeder with possible uprooting habits (Bargo & Vizcaíno 2008). Similarly, niche partitioning was previously argued to explain the high diversity of Neotropical crocodilian communities (Scheyer et al. 2013; Salas-Gismondi et al. 2015).

### Ware Formation and GABI

Sloths are main elements in the American Biotic Interchange, as they are present in North America as early as c. 9 Ma (Hemphillian; Woodburne 2010), and as they take part in the main pulses of GABI migration. Additionally, it was recently emphasized how the Ware Formation can enlighten our understanding of the GABI, with the example of the carnivoran procyonid *Chapalmalania* sp., found in Ware, which is suggestive that procyonids, North American immigrants, dispersed into South America in two separate events (Forasiepi et al. 2014).

All four families of ‘ground sloths’ that participated in GABI (Mylodontidae, Megatheriidae, Nothrotheriidae, Megalonychidae) were present in the Ware formation. A taxon closely related to Ware’s *Pliomegatherium lelongi* (MUN STRI 36685), the megatheriine *Eremotherium*, is found in North America c. 2.6 Ma (Woodburne, 2010). This taxon is widespread in both South and North America while its sister taxa, *Megatherium*, is restricted to South America. The relationships of *P. lelongi* to both *Megatherium* and *Eremotherium* are unresolved, and therefore, it is not possible to assess whether the *P. lelongi* clade participated in GABI. Megatheriinae are also represented in northern South America by *Proemetherium* and *Urumaquia* (Carlini et al. 2006b, 2008), but the recovered elements of those taxa do not include a mandible or lower teeth that would have allowed a comparison with MUN STRI 36685.

### Table 2. Comparison of the sloth diversity in Neotropical and Temperate Pliocene formations.

<table>
<thead>
<tr>
<th>Epoch</th>
<th>Formation</th>
<th>Latitude (°S)</th>
<th>Environment</th>
<th>Taxonomic diversity Species (families)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Neotropical formations</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Late Pliocene</td>
<td>Ware</td>
<td>11.8</td>
<td>Fluvio-deltaic</td>
<td>5 (1)</td>
<td>Moreno et al. 2015; present study</td>
</tr>
<tr>
<td>Early Pliocene</td>
<td>San Gregorio</td>
<td>11.3</td>
<td>Alluvial fans</td>
<td>1 (1)</td>
<td>Vucetich et al. 2010</td>
</tr>
<tr>
<td></td>
<td>Codore</td>
<td>11.3</td>
<td>Fluvio-deltaic with marine inundation</td>
<td>3 (3)</td>
<td>Carlini et al. 2006a, b</td>
</tr>
<tr>
<td><strong>Temperate formations</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pliocene</td>
<td>Uquia</td>
<td>–23 to –24</td>
<td>Fluvial</td>
<td>5 (3)*</td>
<td>Reguero et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Corral Quemado</td>
<td>–27</td>
<td>–</td>
<td>1 (1)</td>
<td>Reguero et al. 2007</td>
</tr>
<tr>
<td></td>
<td>Inchasi</td>
<td>–19.7</td>
<td>Fluvial</td>
<td>3 (2)</td>
<td>Anaya &amp; MacFadden 1995</td>
</tr>
<tr>
<td></td>
<td>Monte Hermoso</td>
<td>–39</td>
<td>Fluvial</td>
<td>5 (3)*</td>
<td>Tomassini et al. 2013</td>
</tr>
<tr>
<td>Montehermosan/</td>
<td>Andalhualá</td>
<td>–27</td>
<td>–</td>
<td>3 (2)</td>
<td>Reguero &amp; Candela 2011</td>
</tr>
<tr>
<td>Chapadmalalan</td>
<td></td>
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</table>

* Taxa most likely not coeval.

References

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Nothrotheriops is recorded in North America during the Pleistocene (c. 1.4 Ma, Woodburne 2010). However, coeval Nothrotherium species, which share diagnostic features with the specimen from Ware, are restricted to Brazil. Therefore, it seems that Ware’s Nothrotherium is a member of the South American Nothrotherium that did not participate in GABI.

Two other sloths of the Formation, Megalonychidae gen. et sp. nov. and Lestodontini gen. et sp. nov. (Mylodontidae), have ambiguous affinities. Megalonychidae represents one of the earliest ‘ground sloth’ families to migrate to North America (c. 9 Ma) and includes the early immigrants Pliometanastes, and subsequently Megalonyx and Meizonyx (Woodburne 2010). The Megalonychidae gen. et sp. nov. of Ware is reminiscent of Megalonyx (and by extension Pliometanastes, of which the postcranium is hardly distinguishable; McDonald & Naples 2007), but also features clear differences. A comparison with Meizonyx is impossible due to the incompatibility of the elements recovered. At this point, it is not possible to assess if the Megalonychidae gen. et sp. nov. of Ware is more closely related to North American or South American megalonychids, as South American large-sized megalonychids are still poorly documented (e.g. Megalonychops primigenius, known by a fragmentary humerus from the Itzañigó Formation, late Miocene of Argentina; Brandoni 2013).

Lestodontini gen. et sp. nov. belongs to Mylodontinae, a subfamily of Mylodontidae that includes Thinobadistes, one of the earliest migrants to North America c. 9 Ma (Woodburne 2010). The subfamily continued taking part in GABI with the late Pliocene – late Pleistocene Paramylodon harlani (and a specimen of ‘Glossotherium chapadmalense’; McAfee 2009). Unfortunately, Ware’s Lestodontini gen. et sp. nov. is not complete enough to provide synapomorphies that could have discriminated between South and North American affinities. As emphasized by the phylogenetic analysis (see above), Lestodontini gen. et sp. nov. is found within a clade with unresolved relationships with both the early immigrant Thinobadistes and Lestodon, known from the Pleistocene of temperate South America. Lestodontinae is also represented in northern South America by Bolivartherium (Urumaco and Codore formations; Carlini et al. 2006a).

A subfamily of Mylodontidae, the Scelidotheriinae, did not take part in GABI (Miño-Boillini et al. 2014) but has been found in Ware. This subfamily had a wide distribution during the Pliocene and Pleistocene being recorded in multiple localities (from 20 to 39°, Paleobiology Database and the related references included therein: Rusconi 1954; MacFadden et al. 1993; Rodríguez-Brizuela & Tauber 2006; Reguero & Candela 2011). The non-migrating scelidotheriine contrasts with other taxa in Ware, whose relatives took part in GABI (Woodburne 2010). The record of Ware, in the vicinity of the Isthmus of Panama, further raises the question of why Scelidotheriinae was not involved in GABI. The specialized niche possibly associated with derived muzzle shape is most likely a contributing factor (McDonald 2005). Scelidotheriines are indeed characterized by long and narrow premaxillae, also acquired, although under other modalities, in non-migrant members of other subfamilies such as Megatherium and Mylodon.

CONCLUSIONS

The Cocinetas Basin comprises two units that record continental Neogene biotas, the Castilletes and Ware formations. Both delivered rich mammalian assemblages including tardigradan taxa. Sloths are represented in the early-middle Miocene Castilletes Formation by one fragmentary specimen. Referred to a small-sized megatherioid, this record could suggest affinities with the distant Santacrucian fauna.

The sloths from the late Pliocene Ware Formation are represented by 12 specimens that belong to 5 taxa from the 4 families of ‘ground sloths’. Their body sizes span over two orders of magnitude, and they most likely featured various feeding strategies, documenting a highly diverse assemblage of sloths from the Neotropics. Although geographically close to the Isthmus of Panama, and temporally preceding GABI 1 by only 0.2–0.4 my, the sloths for which unambiguous affinities were recovered are not closely related to the early immigrants found in North America before the first main pulse of the Great American Biotic interchange.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.57025
Locality and stratigraphical data are available in the Smithsonian Tropical Research Institute PaleoDatabase: http://bioged.db.si.edu/jaramillo/fossildb
3D models are available in MorphoMuseuM: http://dx.doi.org/10.18563/m3.2.1.e3

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REFERENCES


CARRILLO, J. D. and JARAMILLO, C. 2016b. 3D models related to the publication: Neogene sloth assemblages (Mammalia Pilosa) of the Cocinetas Basin (La Guajira, Colombia): implications for the Great American Biotic Interchange. MorphoMuseuM, 2, e3. doi: 10.18563/m3.2.1.e3


BRANDONI, D. and SÁNCHEZ, R. 2006b. First Megatheriines (Xenarthra, Phyllophaga, Megatheriidae) from the Urumaco (Late Miocene) and Codore (Pliocene) Formations, Estado Falcón, Venezuela. Journal of Systematic Palaeontology, 4, 269–278.

2008. Additions to the knowledge of Urumaquia robusta (Xenarthra Phyllophaga, Megatheriidae) from the Urumaco Formation (Late Miocene), Estado Falcón, Venezuela. Paläontologische Zeitschrift, 82, 153–162.


Estratigrafía y mamíferos fósiles de la Formación Toro Negro (Neógeno), Departamento Vichina, noroeste de la provincia de La Rioja, Argentina. Ameghiniana, 43, 257–272.

ROVERETO, C. 1914. Los estratos araucanos y sus fósiles. 
Anales del Museo Nacional de Buenos Aires, 25, 1–249.


