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Q1 Two new megalonychid sloths (Mammalia: Xenarthra) from the Urumaco Formation (late Miocene), and their phylogenetic affinities

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Here we describe two new megalonychid sloths from the late Miocene of the Urumaco Formation (Falcón State, Venezuela), *Urumacocnus urbanii* gen. et. sp. nov. and *Pattersonocnus diazgameroi* gen. et sp. nov. The recovery of these distinct taxa greatly improves our understanding of sloth diversity in the late Miocene of northern South America. A phylogenetic analysis based on the combination of cranial and postcranial elements (particularly the femur) partially supports previous interpretations of the relationships of genera within the Megalonychidae, but also suggests the existence of a more complex set of subclades within the family in South America, North America and the Antilles.

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Keywords: Megalonychidae; *Urumacocnus*; *Pattersonocnus*; Miocene; Urumaco Formation; Venezuela

Introduction

The Xenarthra, comprising sloths, anteaters, armadillos, pampatheres and glyptodonts, is a native group of South American mammals, some of which later dispersed into Central and North America and the Antillean Islands. Within Xenarthra the sloths (Folivora = Pilosa) diversified during the Oligocene (Deseadan SALMA), based mainly on records from Argentina and Bolivia, and by that time were represented by several distinct lineages (Pujos & De Iuliis 2007; McDonald & De Iuliis 2008; Q2 Shockey & Anaya 2011). One of the early families of sloths in South America, Megalonychidae, is known since the late Oligocene (Deseadan SALMA), based on the presence of *Deseadognathus* in high latitude localities (Carlini & Scillato-Yané 2004; Pujos & De Iullis 2007). Interestingly, indeterminate megalonychid remains have also been reported from the early Oligocene in the Greater Antilles, in the form of the proximal part of a femur recovered from the Juan Diaz Formation of Puerto Rico (MacPhee & Iturralde-Vinent 1995). This discovery reveals that Megalonychidae had reached the Antillean Islands probably through GAARlandia in the early Oligocene, subsequently giving rise in the Antilles to *Imagocnus*, *Acratocnus*, *Neocnus*, *Megalocnus* and *Parocnus* (MacPhee & Iturralde-Vinent 1994; MacPhee *et al*. 2000) and possibly *Paulocnus* in Curacao (Hooijer 1962). During the Neogene, megalonychid sloths (e.g. *Pliometanastes*) also dispersed into North America prior to the final formation of the Panamanian land bridge and loss of the seaway between South and North America during the late Miocene to Pliocene (McDonald 2005; McDonald & Naples 2007).

The wide geographical distribution of megalonychids during the late Palaeogene reflects the intriguing early pattern of dispersal between South America and the Greater Antilles. Clues about the dispersal pattern should be present in northern South America, but the fossil record of megalonychids in this area is sparse and poorly known. Sloths in northern South America are now known from at least the early Miocene with the presence of mylodontoidsh (Rincón *et al*. 2014, 2016), while representatives of Megatheriidae and Megalonychidae first appear in the middle Miocene of Colombia (Hirschfeld 1985). Two indeterminate members of Megalonychidae have been previously reported from the middle Miocene of Colombia, one from La Venta, and another from Coyaima (see Hirschfeld 1985 for details). More recently, a megalonychid considered a new genus and species, but not yet not

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formally described, was reported from the late Pliocene of the Ware Formation in La Guajira, Colombia (Amson Q3 *et al*. 2016a). In Venezuela, indeterminate megalonychid remains considered to be Plio-Pleistocene in age have been reported from El Breal de Orocual (Monagas State), at ORS-16, and of late Pleistocene ORS-20 (Rincón *et al*. 2009; Solórzano *et al*. 2015). In addition, the late Pleistocene megalonychid *Megistonyx orebios* was described from Cueva de los Huesos at Cerro Pintado, Sierra de Perijá, Zulia State, Venezuela (McDonald *et al*. 2013).

Linares (2004) and Sánchez-Villagra *et al*. (2010) reported the presence of putative members of the Megalonychidae, along with *Pronothrotherium* sp. (Nothrotheriidae), from the Urumaco Formation (late Miocene, Falcón State, Venezuela), but did not formally describe any of these remains, although it was suggested they could represent new taxa. To date, five sloths have been reported from the Urumaco Formation: *Urumaquia robusta*, *Urumacotherium garciai*, *Mirandabradys urumaquensis*, *Bolivartherium urumaquensis* and *Eionaletherium tanycnemius* (Bocquentin-Villanueva 1984; Carlini *et al.* Q4 2006a, b; Rincón *et al*. 2015a, b). The sloth assemblages of northern South American localities (La Venta and Urumaco) include very basal sloths as well as clades unknown from southern South America (Hirschfeld 1985; Carlini Q6 Q5 *et al.* 1997; Rincón *et al*. 2015a, b).

Most of the early palaeontological discoveries in the Urumaco area began in 1972 when staff of the Museum of Comparative Zoology, Harvard University (**MCZ**) made the first systematic collection of fossil vertebrates from the Urumaco desert, Falcón State, northern Venezuela (Fig. 1). These expeditions recovered several vertebrate fossils from the late Miocene Urumaco Formation, the most fossiliferous formation in the area (Sánchez-Villagra *et al.* 2010). Dr Bryan Patterson led the expedition which included A. D. Lewis, R. C. Wood, D. C. Fisher, R. W. Repenning and M. F. Stanford. The resulting collection consisted of 176 vertebrate specimens, including a variety of osteichthyan and chondrichthyan fishes, giant caimanines (*Purussaurus* and *Mousasuchus*), gharials (*Ikanogavialis* and *Gryposuchus*), giant turtles (*Stupendemys geographicus* and *Bairdemys*), continental turtles (*Chelus*), giant rodents (*Phoberomys*), toxodonts, machrauchenids, sirenians, and many bones of the sloth families Mylodontidae and Megatheriidae. The specimens collected by the Harvard University team, originally housed in the MCZ collection, were recently transferred to the Museo de Ciencias de Caracas (**MCNC**), Caracas, Venezuela. The xenarthran material included isolated femora of sloths, which have remained undescribed until now. Thus, the main goal of this work is to describe the megalonychid material from the Urumaco Formation housed in the MCNC, and to provide a preliminary determination of their phylogenetic affinities based on the currently available specimens.

Material and methods

The material examined in this study includes three femora (MCNC-10-72V, 60-72V and 82-72V) housed at the MCNC. All measurements are in millimetres and were taken with a digital calliper. Skeletal comparisons were based on features mentioned in the literature describing the femur, particularly those referred to megalonychids

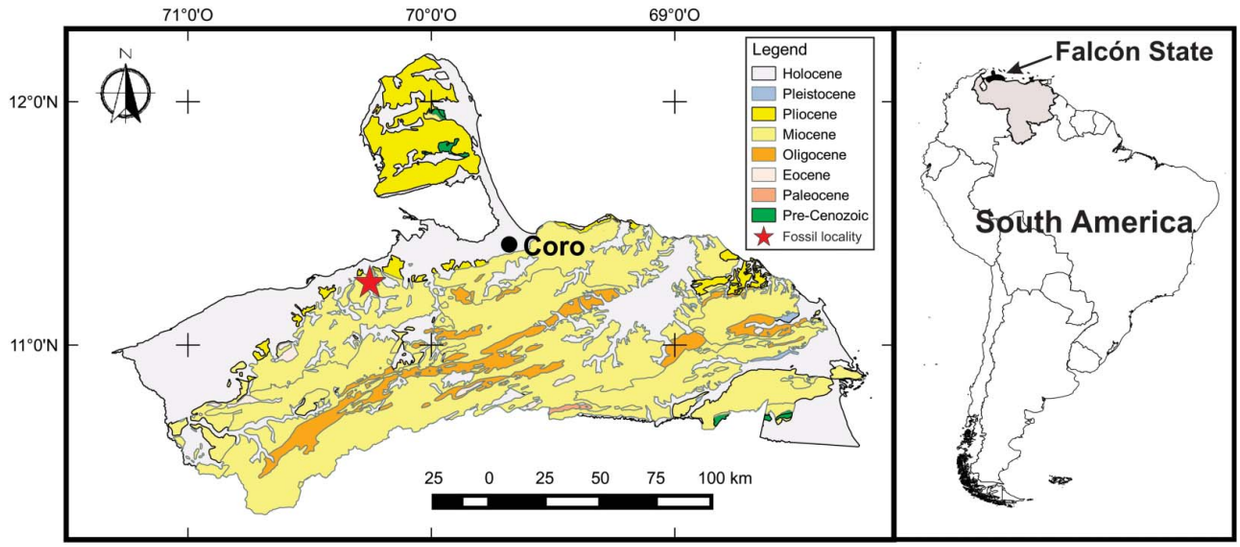

Figure 1. Map of the Venezuelan state of Falcón showing the fossil locality within Miocene deposits of the Urumaco Formation.

from South and North America and the Greater Antilles. See details in the Supplemental material (ESM_1).

In order to provide a first estimate of the broader phylogenetic context of the new sloths described herein, we performed an analysis based on a combination of the original dataset of McDonald *et al.* (2013) and a modified version of those from Rincón *et al*. (2015a, b), dealing with craniodental and postcranial characters, respectively (see Supplemental ESM_2 and ESM_3 for details). It should be emphasized that in view of the limitations of the available material of the new taxa, the goal of the analysis was not to provide a comprehensive review of sloth phylogenetic relationships. Rather, given the combination of the geographical location and age of the new megalonychids, our goal was to determine, in a general way, how they fit into previous studies of the relationships of the other known genera within Megalonychidae. Of equal interest is how the new taxa may relate to subclades within the family identified in previous studies (McDonald *et al.* 2013, 2017; McDonald & Carranza-Castañeda 2017). A similar approach has been employed recently in other studies of the phylogenetic affinities of sloths (e.g. McDonald *et al.* 2013; Haro *et al.* 2016). We emphasize that such a determination should only be considered preliminary given the limited sample currently available, and a more comprehensive analysis will only be possible with the recovery of additional specimens of the new taxa described here.

The original dataset of McDonald *et al.* (2013) included 54 characters, while the modified version of the dataset of Rincón *et al*. (2015a, b) included 25 characters. Thus, the final dataset utilized here contained 79 characters combining craniodental, femur, tibia and astragalus traits (see Supplemental ESM_3). The dataset includes 14 taxa belonging to the Megalonychidae that range from Oligocene to Pleistocene in age, plus *Hapalops*, an early megatherioid sloth as an outgroup (Gaudin 1995, 2004). The character state assignments for the femurs of the 15 taxa used in this study are based on direct observation of specimens and information obtained from the primary literature (Supplemental ESM_1). We codified the morphological characters of the femur of the new Urumaco sloth material, as well as other megalonychids genera included in the dataset of McDonald *et al.* (2013), following the characters described in Supplemental ESM_2 (modified from Rincón *et al*. 2015a, b). For the Urumaco megalonychids for which skull material is unknown, the cranial traits were scored as missing data, as in taxa for which the femur or tibia is unknown (see Supplemental ESM_3). When intraspecific variation was noted for a given character in a taxon, the taxon was coded for all relevant states and treated as polymorphic (see Supplemental ESM_3).

Analysis of the final dataset (Supplemental ESM_3) was performed using TNT 1.5 software (Goloboff & Catalano 2016). Following the original proposal of McDonald *et al.* (2013), 15 characters (related to craniodental traits) were considered as ordered (additive), while the remaining 64 characters were treated as unordered (non-additive; see Supplemental ESM_ 3). Gaps were treated as missing. The characters were analysed using the 'prior weights' and 'implied weight only' methodologies. For the implied weighting method, the default concavity constant value is 3 (k = 3). A heuristic parsimony analysis of 1000 replicates was performed using the 'traditional search option'. The swapping algorithm used was tree bisection reconnection (TBR), with 10 trees saved per replication, collapsing the trees after each search. To measure node stability, we used the absolute frequency and frequency differences (GC) arising from symmetrical re-sampling (Goloboff *et al*. 2008) based on 1000 replicates ($p = 0.33$).

To calculate the body mass of the new taxa, we used the predictive regression equation based on measurements of the femur derived from extant mammals developed by Scott (1990):

$$\mathrm{Log(mass)} = 3.4855 \times \mathrm{Log(Fl)} - 2.9112$$

where Fl is the femur length.

Geological setting

The Urumaco Formation is part of a lithostratigraphical unit, around 2000 m thick, composed of a complex intercalation of medium- to fine-grained sandstones, organic-rich mudstone, coal, shale and thick-bedded coquinoidal limestone with abundant mollusc fragments (Linares 2004). Its outcrops are located in the north-western part of Falcón State in north-western Venezuela (Fig. 1). Several geological studies indicate that deposition of the formation occurred along a complex of marginal and near-coastal environments (Díaz de Gamero & Linares 1989; Hambalek *et al*. 1994; Quiroz & Jaramillo 2010). The Urumaco Formation comprises the richest Neogene vertebrate assemblage (including freshwater and marine vertebrates) from Venezuela and the fauna has been described by several authors (e.g. Wood & Patterson 1973; Wood 1976; Gaffney & Wood 2002; Linares 2004; Carlini *et al*. 2006a, b; Sánchez-Villagra *et al*. 2010; Scheyer *et al*. 2013; Rincón *et al*. 2015a, b; Cidade *et al*. 2017). The fauna also documents highly variable environments within the sedimentary sequence. The recovery of several terrestrial mammals from this formation allows its assignment to the middle to late Miocene (Linares 2004). The Urumaco Formation is currently informally divided into three members: lower, middle and upper. As mentioned in Patterson's field notes of 1972, the fossils described here were collected from the upper member of the Urumaco Formation,

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which is usually considered as late Miocene in age (Linares 2004).

Systematic palaeontology

Order **Xenarthra** Cope, 1889
Suborder **Folivora** Delsuc *et al*., 2001
Family **Megalonychidae** Gervais, 1855
Genus ***Urumacocnus*** gen. nov.

Type species. *Urumacocnus urbanii* sp. nov.

Diagnosis. As for type species (monotypic).

Etymology. From Urumaco Formation and *ocnus*, 'delay, slowness' (Latinized Greek); gender of combination is masculine.

Urumacocnus urbanii sp. nov.
(Figs 2, 3)

Material. Holotype: MCNC-10-72V, left femur (Fig. 2). Referred material: MCNC 60-72V, right femur (Fig. 3).

Type locality. Taparito, north-east of Urumaco Town (11°14′00"N; 70°14′55"W), Falcón State, Venezuela. Late Miocene, upper member of the Urumaco Formation.

Diagnosis. A small sized member of Megalonychidae with the following unique character combinations: femur diaphysis transverse shape round to oval, diaphysis straight, but with medial and lateral sides curved; femur head angle with respect to the diaphysis is more than 160°; femur neck well demarcated; valley between the femur head and the greater trochanter shallow; fovea capitis present and larger with respect to the femur head than in other member of the family; proximal end of the femur is broader than the distal end; greater trochanter longer than wide and smaller than the head, and entirely positioned distal to the femur head; lesser trochanter well developed, and caudally and medially directed; the third trochanter does not project from the diaphysis of the femur farther relative to the lateral margin of the greater trochanter, and is positioned close to the middle of the diaphysis; lateral and medial epicondyles small and project only slightly from the shaft; patellar and condylar surfaces separate; patellar surface length and width equal;

Figure 3. Referred material of *Urumacocnus urbanii* gen. et sp. nov. (MCNC-60-72V) from the Urumaco Formation, Venezuela. **A,** anterior; and **B,** posterior views. Scale bar = 10 cm.

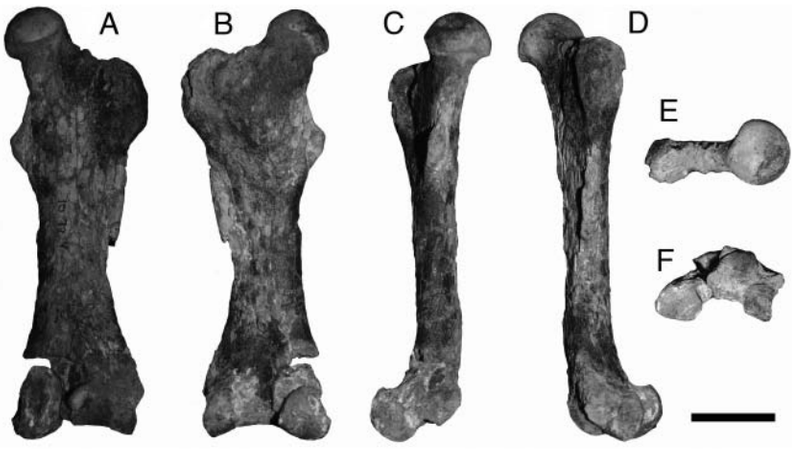

Figure 2. Holotype of *Urumacocnus urbanii* gen. et sp. nov. (MCNC-10-72V) from the Urumaco Formation, Venezuela. **A,** anterior; **B,** posterior; **C,** medial; **D,** lateral; **E,** proximal; and **F,** distal views. Scale bar = 5 cm.

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trochanteric fossa shallow and elongate; medial condyle larger than the lateral.

Etymology. In honour of Franco Urbani, for his important contributions to Venezuelan geology.

Description and comparisons. The proximal end is rotated 75° relative to the long axis of the femur so that the head is positioned strongly anterior to the greater trochanter; however, the diaphysis is straight and does not bend as in the nothrothere *Thalassocnus* (Amson *et al*. 2015, Q8 2016b). The head is perfectly hemispherical, with a large elliptical fovea capitis located posteromedially but within the head. The neck is long and well developed. A shallow notch separates the head and the greater trochanter. In addition, the greater trochanter is strongly developed and completely distal to the head, and is approximately half the size of the diameter of the head of the femur.

In *Urumacocnus* the third trochanter is twice the size of the lesser trochanter, and proximally forms a ridge, which connects to the distal part of the greater trochanter, but its muscular insertion surfaces are distinct and separate from those of the greater trochanter. Also in *Urumacocnus* the third trochanter is connected to the lateral epicondyle by a slender ridge as in *Nothrotheriops* and *Planops*.

The trochanteric fossa is large and shallow. The lesser trochanter is conical, well developed, and projects posteromedially with respect to the diaphysis. It is located about 47 mm distally to the femur head, but is shifted posteriorly and positioned below the most distal part of the muscular insertion surface of the greater trochanter. The muscle scar for the *vastus lateralis* muscle is almost imperceptible; however, a very small ridge is visible on the diaphysis from the shallow notch between the head and greater trochanter and continues distally up to the most proximal part of the third trochanter. There is no visible muscle scar for the *vastus medialis*.

The medial epicondyle is broken, and the lateral epicondyle is eroded anteriorly (MCNC-10-72V), but enough is preserved to determine that the lateral epicondyle is not well developed. The femoral trochlea is broken medially at the level of the medial epicondyle; however, enough is preserved to determine that the medial and lateral condyles have articular surfaces separate from the patellar surface. The medial condyle is slightly longer and wider than the lateral. The intercondylar notch is wide and deep and the lateral and medial trochlear ridges are not well developed.

The femur of *Urumacocnus* shares many characters with other megalonychids. These include: the diaphysis is straight; the third trochanter projects laterally; the greater trochanter is longer than wide and smaller than the head; the lateral epicondyle and medial epicondyle are small and only project slightly from the diaphysis; the fovea capitis is present; the femur neck is well demarcated; the angle of the head of the femur head with respect to the diaphysis is more than 160°; the trochanteric fossa is shallow and relatively long; and the medial distal condyle is larger than the lateral.

The valley between the femur head and the greater trochanter is shallow, as in *Acratocnus* and *Eucholoeops*, but differs from *Torcellia*, *Ahytherium Pliometanastes*, *Pattersonocnus* gen. nov. and *Megalonyx* where it is absent, and from *Megalocnus*, *Acratocnus ye* and *Neocnus* where it is deeper. The lesser trochanter is well developed, and caudally and medially directed, as in *Torcellia*, *Acratocnus*, and *Neocnus*, but unlike *Pattersonocnus* gen. nov., *Megalocnus* and *Eucholoeops*, where it is well developed, and positioned slightly caudally but more medially directed; in *Ahytherium* and *Pliometanastes* it is poorly developed, and aligned with the diaphysis.

The position of the third trochanter in *Urumacocnus* is proximal to the middle of the diaphysis, as in *Acratocnus*, and differs from the rest of Megalonychidae studied where it is located at the middle of the diaphysis, except in *Megalocnus* where it is distal to the middle of the diaphysis and continuous with the ectepicondylar process.

The proximal end of the femur at greater trochanter level is broader than the distal end, as in *Torcellia*, *Neocnus*, *Acratocnus odontrigonus*, *Megalocnus* and *Eucholoeops*, but differs in *Acratocnus ye*, *Pattersonocnus* gen. nov. and *Megalonyx* where it is of the same width as the distal end; and in *Ahytherium* and *Pliometanastes* in which it is narrower than the distal end.

In the Antillean megalonychids the patellar and condylar surfaces are connected, but in *Urumacocnus* and the rest of the South American megalonychids they are separated except in *Pattersonocnus* gen. nov. where the surface of the medial condyle is continuous with the patellar surface but the lateral is separate.

The position of the greater trochanter is distal to the femur head as in the other South American megalonychids studied here, and differs from *Megalocnus* where is proximal to the femur head. The transverse shape in cross-section of the diaphysis of the femur in *Urumacocnus* is cylindrical to oval, so is generally similar to the Antillean megalonychids. It differs from the South American genera, *Megalonyx* in North America and the Antillean *Neocnus dousman* in which the femur shaft is anteroposteriorly flattened. The outline shape of the patellar surface is similar to *Neocnus*, and *Pattersonocnus* gen. nov., and differs from other members of the family in which the patellar groove is shorter than wide. Lateral and medial sides of the femur are curved as in *Torcellia*, *Ahytherium*, *Pliometanastes*, *Megalocnus*, and *Acratocnus odontrigonus*, and differ from *Eucholoeops*, *Acratocnus ye*, *Neocnus*, *Pattersonocnus* gen. nov. and *Megalonyx* in which medial side of the femur is curved and lateral side convex.

Genus ***Pattersonocnus*** gen. nov.

Type species. *Pattersonocnus diazgameroi* sp. nov.

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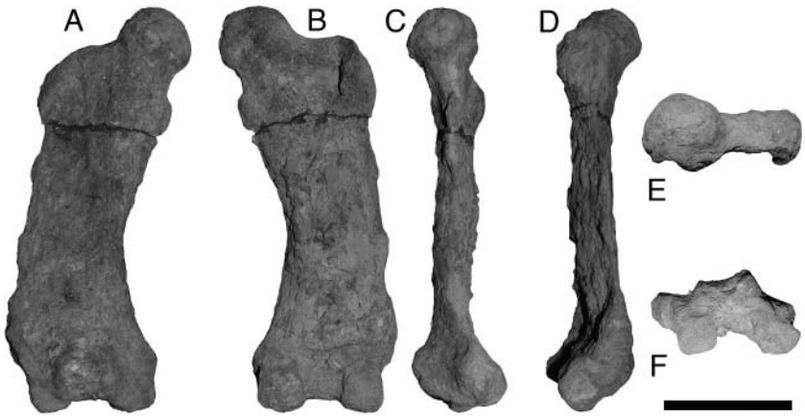

Figure 4. Holotype of *Pattersonocnus diazgameroi* gen. et sp. nov. (MCNC-82-72V) from the Urumaco Formation, Venezuela. **A,** anterior; **B,** posterior; **C,** medial; **D,** lateral; **E,** proximal; and **F,** distal views. Scale bar = 10 cm.

Diagnosis. As for type species (monotypic).

Etymology. In honour of Bryan Patterson, for his contributions to Venezuelan vertebrate palaeontology, and *ocnus*, 'delay, slowness' (Latinized Greek); gender of combination is masculine.

Pattersonocnus diazgameroi sp. nov.
(Fig. 4)

Material. Holotype: MCNC-82-72V, right femur.

Type locality. 0.5 km west of Quebrada Picacho, 50 m east of the Chiguaje fault (14°15′22"N; 72°13′38"W), Falcón State, Venezuela. Late Miocene, upper member of Urumaco Formation.

Diagnosis. Small megalonychid with the following character combination: femur diaphysis anteroposteriorly flattened in transverse shape, and with medial side concave and lateral side convex; femur neck slightly demarcated; femur head angled more than 160° with respect to long axis of diaphysis; greater trochanter almost at same level as the femur head; cranial view of the patellar surface square in outline condyles equal in size and the medial condyle connected with the patellar surface and lateral condyle separated.

Etymology. In honour of María Lourdes Díaz de Gamero for her contributions to our understanding of the geology and palaeontology of the Urumaco Formation.

Description and comparisons. As in many megalonychids, the femur diaphysis is straight; the third trochanter does not project from the diaphysis of the femur relative to the same plane as the lateral margin of the greater trochanter; the greater trochanter is longer than wide and smaller than the head; the lateral and medial epicondyle are small and only project slightly from the shaft; the fovea capitis is present; the femur head angle with respect to the diaphysis is more than 160°; the trochanteric fossa is shallower and relatively long.

The valley between the femur head and the greater trochanter is absent, as in *Torcellia*, *Ahytherium*, *Pliometanastes* and *Megalonyx*, whereas in *Urumacocnus*, *Acratocnus odontrigonus* and *Eucholoeops* the valley is shallow, and in *Megalocnus*, *Neocnus* and *Acratocnus ye* it is deep.

The lesser trochanter is well developed, and positioned slightly caudally but is medially directed as in *Megalonyx* and *Eucholoeops*. The third trochanter is at the middle of the diaphysis as in many megalonychids here compared, except *Urumacocnus* and *Acratocnus*, where it is proximal to the middle of the diaphysis, and *Megalocnus* where it is distal to the middle of the diaphysis.

The proximal end of the femur is of the same width as the distal end, as in *Megalonyx* and *Acratocnus ye.* The medial condyle is continuous with the patellar surface, while the lateral condyle is separated, a unique character not seen in any other megalonychids. In *Urumacocnus*, *Torcellia*, *Pliometanastes*, *Ahytherium*, *Pattersonocnus* and *Megalonyx* both condyles are separated from the patellar surface, while in *Acratocnus* and *Neocnus* they are both connected. In *Pliomorphus* the lateral condyle is connected with the patellar surface.

The femoral neck is slightly demarcated, as in *Ahytherium* and *Eucholoeops*, while in other megalonychids the neck is well demarcated. The greater trochanter is below the femur head, as in *Torcellia*, *Pliometanastes*, *Ahytherium*, *Pattersonocnus*, *Megalonyx* and *Eucholoeops*, while in the rest of the clade it is almost at the same level as the femur head.

The femur diaphysis is anteroposteriorly flattened, as in *Torcellia*, *Pliometanastes*, *Ahytherium*, *Pattersonocnus* and *Megalonyx*, except *Urumacocnus* where the transverse cross section of the diaphysis is cylindrical to oval

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in shape. The patellar surface is square in outline, as in *Urumacocnus* and *Neocnus*, while in the other taxa it is shorter than wide. The condyles of the femur are equal in size, as in *Acratocnus.* The femur has the medial edge of the shaft curved (concave) and lateral side convex, as in *Megalonyx*, *Neocnus*, *Eucholoeops* and *Acratocnus*; in the other megalonychids the lateral and medial sides are curved (concave).

Phylogenetic affinities of the new taxa

The TNT results from the final dataset varied little as a function of the weighting method used (see Supplemental ESM_4) and in general the recovered clades have low support after the symmetrical re-sampling (Supplemental Figs S2, S4). With either weighting method, the two new taxa are grouped as shown in Figure 5, with *Pattersonocus* showing a closer relationship to the North American *Megalonyx*, and *Urumacocnus* being more closely related to the Antillean megalonychids. The 'implied weight' methodology results in a single most parsimonious tree (MPT) (Fig. 5), with a TBR score of 23.75, consistency index (CI) of 0.467 and retention index (RI) of 0.482. In general, the topology recovered resembles those of McDonald *et al.* (2013), with the Santacrucian SALMA sloths *Megalonychotherium* and *Eucholoeops* as successive sister taxa to all other megalonychids (Fig. 5). Minor differences are discussed below in more detail.

The North American *Pliometanastes* and *Megalonyx*, and the South American *Megistonyx*, *Ahytherium* and *Pattersonocnus* form a separate clade. While this clade has very weak support (Supplemental Fig. S4), it can be diagnosed by the same two same unique unambiguous synapomorphies (Fig. 5) (see McDonald *et al.* 2013). *Pliometanastes* appears as the sister taxon of the South American Pleistocene *Megistonyx* and *Ahytherium*; a grouping also with low support (Supplemental Fig. S4) but diagnosed by three unambiguous synapomorphies (Fig. 5), two of which are based on femoral traits: lesser trochanter poorly developed, and aligned with the diaphysis [57(2)] and proximal end of the femur narrower than the distal end [60(2)]. The new Urumaco sloth, *Pattersonocnus*, and the North American *Megalonyx* form a

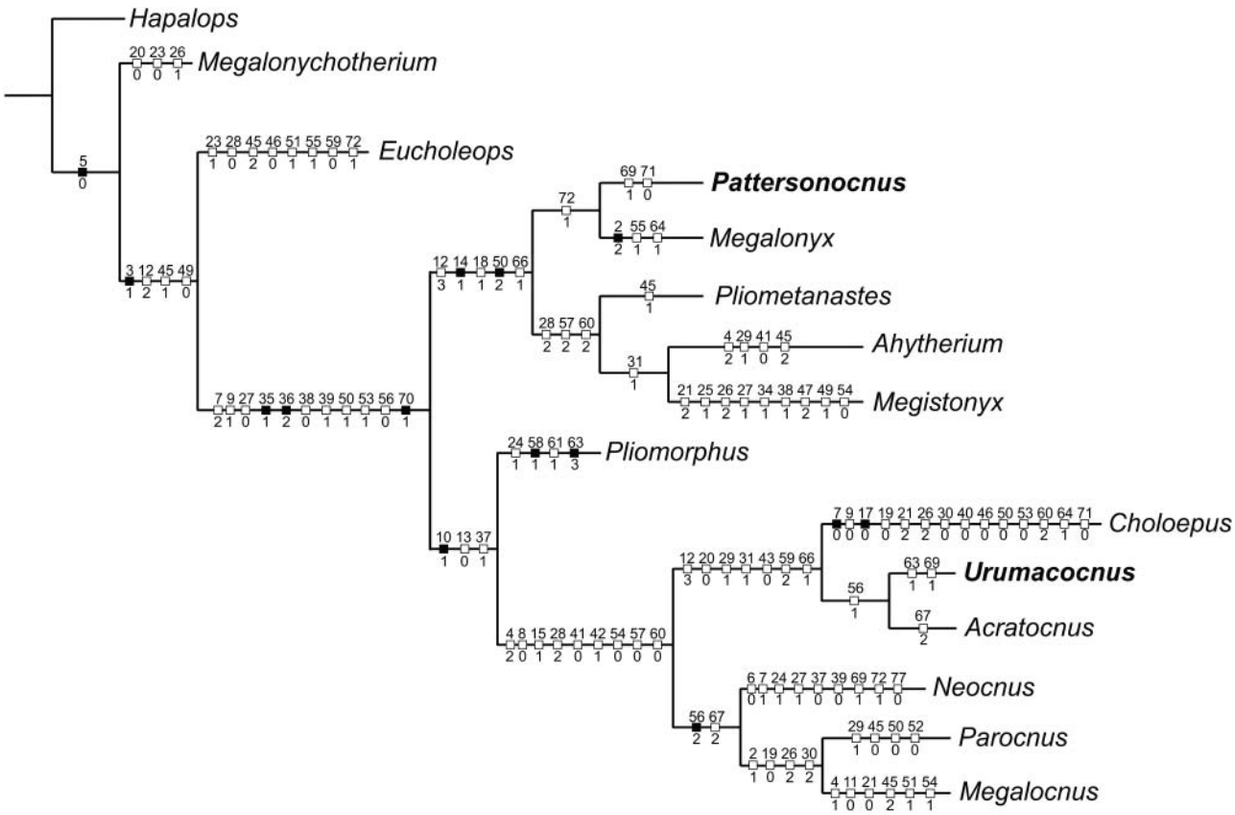

Figure 5. Single most parsimonious tree using the implied weights (k = 3) methodology. tree bisection reconnection (TBR) score = 23.75, consistency index (CI) = 0.467 and retention index (RI) = 0.482. Character/taxon matrix modified after Rincón *et al.* (2015a, b) and McDonald *et al.* (2013). See Material and methods and Supplemental material for details. The two new Urumaco taxa are in bold.

separate clade, also with very weak support (Supplemental Fig. S4) and diagnosed by one unambiguous synapomorphy: femur borders with medial side curved and lateral side convex [72(1)].

The other major clade groups the extant two-toed *Choloepus*, *Pliomorphus* (Pliocene of South America), the Pleistocene Antillean sloths (*Acratocnus*, *Neocnus*, *Megalocnus*, *Parocnus*), and the second Urumaco megalonychid, *Urumacocnus*. This clade is diagnosed by three unambiguous synapomorphies; one based on the cranium is unique: snout orientated downturned anteroventrally in lateral view [10(1)]. *Pliomorphus* is positioned at the base of this clade and is the sister taxon of the two groups of remaining sloths (Fig. 5).

Urumacocnus and *Acratocnus* form a separate clade, supported by only one unambiguous synapomorphy: shallow valley between the femur head and the greater trochanter [56(1)]. The two taxa, together with *Choloepus*, form a clade diagnosed by seven unambiguous synapomorphies, including two based on femoral characters: third trochanter positioned proximal to the middle of the diaphysis [59(2)], and the angle of the femur head with respect to the diaphysis is greater than 160° [66(1)]. The Antillean sloths *Neocnus*, *Megalocnus* and *Parocnus* are closely related and form a clade diagnosed by two unambiguous synapomorphies: greater trochanter positioned almost at same level as the femur head [67(2)], and deep valley between the femur head and the greater trochanter [56(2)]. The last of these traits is a unique synapomorphy (Fig. 5). Thus, the topology of the single MPT recovered (Fig. 5) does not support a monophyletic Choloepodinae, including *Neocnus*, *Acratocnus*, and *Choloepus*, as proposed by White & MacPhee (2001). However, the present analysis found the relative close relationship between the latter two taxa, as noted by McDonald *et al.* (2013).

The hypothesis presented here, based on in the combination of characters of cranial and some postcranial elements, cannot be considered to represent a comprehensive phylogenetic study that refines our understanding of the phylogeny of the megalonychid sloths. It does, however, serve as a useful tool to illustrate the broader relationships of the two new taxa from Urumaco to other known megalonychid taxa until additional material such as the skull and dentition is recovered, which will then permit a refinement of this first approximation of their relationships (Rincón *et al*. 2015a, b).

Body mass of the new taxa

The femur of both new taxa appears to represent those of adult individuals. Since the femur is also preserved for other sloths from the Urumaco Formation, this allows us to estimate the body mass of each taxon based on the same skeletal element (Rincón *et al.* 2015a, b). The result shows that *Urumacocnus* and *Pattersonocnus* were of medium to small size, reaching a body mass of 126 kg and 185 kg, respectively, with *Urumacocnus* being the smallest sloth from the Urumaco Formation (see Supplemental ESM_5).

Discussion

In mammalian taxonomy and phylogenetic reconstructions, the focus is often on cranial and dental morphology, sometimes supplemented by the post-cranial skeleton. While this is equally true for the four recognized families of sloths – Megatheriidae, Megalonychidae, Nothrotheriidae and Mylodontidae – there are also many features of the post-cranial skeleton that distinguish members of these four families. This has permitted us to recognize that the femora of the two new taxa described here are members of Megalonychidae. Also of specific relevance to this paper are that characters of the femur can complement studies based on the skull and dentition, or as in the case here, be used independently to make at least preliminary inferences on the relationships of taxa for which the skull and dentition are not yet known.

There is significant variation in sloth femur morphology that provides both phylogenetic as well as functional information (de Toledo 1998). Consequently, the diagnoses of taxa, including families, using the femur may often be based on a combination of characters and are hence polythetic (Sneath 1962) rather than based strictly on a single apomorphic feature. Serrat *et al*. (2007) noted that in some mammals the femoral head and greater trochanter emerge as separate centres of ossification within a common chondroepiphysis and remain separate throughout ontogeny. In other taxa, including all members of the Xenarthra, these centres coalesce within the chondroepiphysis to form a single osseous epiphysis much like the proximal humerus. In the Xenarthra the connection between them is thin and easily broken during fossilization so can be overlooked as initially having been a single continuous epiphysis. It can, however, be seen on the diaphysis where the complementary area for articulation is continuous with only a slight ridge demarcating their respective areas of contact with the diaphysis.

Proximally, the femur head tends to be large in sloths, but the angle at which it projects from the diaphysis varies. Both the presence and location of the fovea capitis femoris on the femur head will vary, even within a genus. For example, in the late Pleistocene species *Megalonyx jeffersonii*, the fovea is absent, but it is present in all of the older species of the genus (McDonald 1977). In some cases, the fovea is represented by a notch on the margin of the femur head. The greater trochanter tends to be massive and lower than the femur head in the majority of sloth taxa. An intertrochanter fossa may or may not be present.

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The position of the lesser trochanter may vary in its spatial relationship to the head. In many sloths, there is a torsion of the shaft so that the proximal end of the femur is not in the same plane as the distal end but rather the head is rotated to be anterior to the distal medial condyle.

One of the common distinguishing features in most sloths is the anteroposterior flattening of the diaphysis, the mediolateral width being generally much greater than the anteroposterior dimension, resulting in a distinctive ellipsoid shape to the diaphysis in cross section. As with many characters, there are exceptions and this is not seen in either of the two modern genera of tree sloths, *Bradypus* and *Choloepus*, in which these two dimensions are subequal, while in some of the older taxa the cross section is more ovoidal, with the width only slightly greater than the depth. The anterior surface of the diaphysis typically has two prominent parallel muscle scars for the *vastus lateralis* and *medialis*, but their relative development varies in some taxa, as does the presence of these scars: both or either, or in some cases neither, may be well developed or present. Their degree of development may also reflect the ontogenetic stage of the individuals, as they tend to be more rugose and prominent in older individuals. The third trochanter may or may not be present and its position may be more proximally or distally located in different taxa. In some taxa, it may be continuous either with the greater trochanter or with the distal lateral epicondyle.

Distally the medial condyle tends to be significantly larger than the lateral, especially in larger taxa. Among the more variable characters that may distinguish taxa, although not consistent at the family level, is the relationship of the articular surface for the patella and the articular surfaces of the distal condyles. The three areas may be either separate and distinct, continuous between the patellar surface and both condyles, or only a continuous surface between the patellar facet and the medial condyle. The medial and lateral margins of the patellar groove may be equal in height, or the medial side may be substantially more elevated anteriorly than the medial. White (1993) used this difference in height to infer differences in locomotion between different sloth taxa, so it may not be phylogenetically informative.

While the femur of later Pleistocene members of Megatheriidae are readily distinguished by their large size, this simple criterion is not applicable to older and smaller members of the family. Viewed anteriorly, the general shape of the megathere femur appears to be short and stout with the proximal and distal width about half the total length of the bone. The width across the distal epicondyles is greater than the greatest mediolateral width of the diaphysis. There is no development of a third trochanter. Distally the articular surface for the patella is continuous with the articular surface of the medial condyle, while that of the lateral condyle is a distinct separate structure.

The general proportions of the femur in Megalonychidae when viewed anteriorly give it the appearance of being slender for its length compared to megatheres (Figs 2, 3). The mediolateral width of the proximal and distal ends is about one-third of the maximum length of the femur. All members of Megalonychidae have a third trochanter (Figs 2, 3). Generally, its position is at the middle of the diaphysis, but it is located more proximally or distally in some genera. In the Antillean genera *Megalocnus* and *Parocnus*, it may be continuous with the greater trochanter to form an elongate crest. Within Megalonychidae there is variation in whether the patellar articular surface connects with the articular surfaces of the distal condyles. In *Megalonyx*, each is a distinct area, while in the Caribbean megalonychids *Megalocnus*, *Parocnus*, *Neocnus* and *Acratocnus* these articular surfaces are contiguous, a feature that distinguishes this clade from the continental clades. All these traits are noted in the Urumaco material described here (Figs 2, 3).

Diagnosis of the characters of the femur that distinguish Nothrotheriidae is more difficult. The proportions of the femur of this family vary more than in members of Megalonychidae. *Nothrotherium* has a longer and more slender appearance, while the femur of *Nothrotheriops* appears to be relatively stout and wide for its length. While all nothrotheres have a third trochanter, it may be a distinct structure positioned at midshaft as in *Nothrotherium*, or be shifted distally to form a continuous structure with the distal epicondyle in *Nothrotheriops*. The articular surface of the patella is separated from those of the distal condyles in the Pleistocene genera *Nothrotherium* and *Nothrotheriops* and the earlier *Pronothrotherium* from the Huayquerian. In contrast, in *Mionothropus* the lateral condyle is separated from the patellar surface but the medial condyle is continuous with the patellar surface (De Iuliis *et al*. 2011).

Diagnosis for the family Mylodontidae based only on the femur is also challenging, as it is quite distinct between the two subfamilies Mylodontinae and Scelidotheriinae, so can be readily used to distinguish these two subfamilies, while the femur in Urumacotheriinae more closely resembles those of Mylodontinae. Viewed anteriorly the femur in Mylodontinae tapers distally as the proximal end is wider than the distal, while in the scelidotheres the width of the femur is essentially the same for the entire length of the bone, and in Urumacotheriinae the diaphysis is narrower than both the proximal and distal ends, which have similar widths. Both mylodontines and scelidotheres lack a third trochanter but it is present in Urumacotheriinae. In mylodontines and scelidotheres the greater trochanter is lower than the head but in urumacotheres, as represented by *Pseudoprepotherium*, the greater trochanter extends above the head (Hirschfeld 1985). In all three subfamilies the area for the attachment of the teres ligament is a notch on the posteromedial side of the head, and

the patellar surface is broadly continuous with the articular surfaces of the distal condyles.

The MPT tree in our analysis (Fig. 5) is in general agreement with the hypothesis proposed by McDonald *et al*. (2013), with some biogeographical grouping, although *Acratocnus* and *Neocnus* do not form a monophyletic group within the Antillean sloths as in other studies, and the grouping of *Neocnus* with *Megalocnus* and *Parocnus* in this analysis has not been previously observed. As noted above, based on the work of White (1993) this may reflect functional and not phylogenetic similarity. *Pliomorphus* appears to be basal to the Antillean clade of Megalonychidae, but it should be noted that it is geologically much younger than the oldest record of a megalonychid in the Antilles. In McDonald *et al*. (2013) the consensus tree (Fig. 5) recovered *Ahytherium* and *Megistonyx* as a strictly South American clade of Megalonychidae, and *Megalonyx* and *Pliometanastes* as a distinct North American clade of Megalonychidae, so the grouping of the North American *Pliometanastes* with the two South American genera is unexpected.

The result of our phylogenetic analysis (Fig. 5) could indicate complex palaeobiogeographical scenarios. Traditionally, it has been proposed that the Antillean megalonychid sloths could be derived from a South American ancestor (White & MacPhee 2001), which reached these islands by at least the early Oligocene through GAARlandia, via a land bridge connected with north-western South America (MacPhee & Iturralde-Vinent 1995; MacPhee *et al*. 2000). If we agree with this supposition, then *Urumacocnus* represents part of the mainland linage from which the Antillean megalonychids evolved. This is based on the morphological resemblance of the femur of *Urumacocnus* to those of the Antillean megalonychids, and particularly *Acratocnus*.

Previous phylogenetic analyses found some alliance between the two continental North American genera *Pliometanastes* and *Megalonyx* (McDonald *et al*. 2013), consistent with their known biogeographical distributions. But this putative alliance was based on a polytomy. Despite poor bootstrap support, the results here presented show *Pattersonocnus* as closely related to *Megalonyx*, with *Pliometanastes* as the sister taxon of the late Pleistocene South American megalonychids *Ahytherium* + *Megistonyx*. Therefore, the placement of *Pattersonocnus* and *Megalonyx* as sister taxa is interesting and may suggest a different origin for *Megalonyx* than from *Pliometanastes*, as has been previously suggested by McDonald & Naples (2007).

The rich sloth assemblage from the late Miocene of the Urumaco Formation includes four Mylodontidae (*Urumacotherium garciai*, *Mirandabradys urumaquensis*, *Bolivartherium urumaquensis* and *Eionaletherium tanycnemius*: Bocquentin-Villanueva 1984; Carlini *et al*. 2006a; Rincón *et al*. 2015a, b), one Megatheriidae (*Urumaquia robusta*: Carlini *et al*. 2006b), and the two new megalonychids described here (*Pattersonocnus diazgameroi* and *Urumacocnus urbanii*). Linares (2004) indicated the tentative presence of *Pronothrotherium* (a member of Nothrotheriidae *sensu* Gaudin 2004) from the Urumaco Formation (based on a partial left humerus), but did not describe the specimen. This specimen was subsequently placed within Megalonychidae by Sánchez-Villagra *et al*. (2010), but again is neither described nor illustrated. Consequently, the megalonychids described here represent the first unequivocal evidence for the family in this locality, and increase the known taxonomic richness of the sloths from the Urumaco Formation to seven genera. Though the taxonomic diversity of the sloths from the Urumaco Formation is higher than any other locality in northern South America, it is still lower than faunas in the early and late Miocene of Argentina (Brandoni *et al*. 2016). Compared with the chronologically equivalent sedimentary units of the late Miocene of Entre Ríos Province, Argentina (Brandoni 2011, 2014), the megalonychid diversity of the Urumaco Formation is low and the two regions have no sloth taxa in common.

The sloths from the Urumaco Formation appear to be particularly common in the middle and upper members (Linares 2004), but sloth remains are often recovered as single finds which come from multiple stratigraphical levels and locations, and the degree of sympatric occurrence of the different taxa still needs to be determined. The Urumaco sloths include medium- to large-sized forms, ranging from 126 kg to 2100 kg in body mass (see Supplemental EMS_5). Within this size range the megalonychids represent the smallest taxa so far recovered (Supplemental EMS_5). Besides the body mass, additional evidence of the palaeobiological affinities of the Urumaco Formation sloths, similar to those described for the Santacrucian fauna (e.g. Bargo *et al*. 2012; Toledo *et al*. 2012, 2014, 2015; Toledo 2016), are unfortunately difficult to determine due in large part to the poor preservation and fragmentary nature of the remains so far recovered. Here we hypothesize that the Urumaco sloths could have inhabited the same area, and even the same palaeoenvironment, but would have exploited the habitat in dissimilar ways. However, this assumption requires more specimens and detailed study.

A detailed muscular reconstruction and functional morphology of the femur of the new megalonychids is beyond the scope of this paper. However, some features are remarkable in the new taxa described here. The femur of *Pattersonocnus* is massive and wide transversely, while in *Urumacocnus* it is rather gracile. In both taxa, the orientation of the proximal and distal ends relative to each other are in different planes, resulting in a difference in the torsion to the diaphysis, a feature common in megalonychids. Unlike *Pattersonocnus*, the fovea capitis is very

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well developed in *Urumacocnus*, suggesting a robust *teres femoris* ligament (Toledo *et al.* 2015). The general morphology of the femur, as well as the rather low body mass of *Urumacocnus* (~126 kg), allows us to hypothesize that it may have had climbing capabilities and was possibly semiarboreal, constrained in its agility by its size. Similar configurations have been noted for the Santacrucian sloths, although it should be noted that the forelimb bones of sloths provide clearer information about the locomotion and preferred substrate (e.g. Bargo *et al*. 2012; Toledo *et al*. 2012, 2014, 2015; Toledo 2016) and these are not yet known for the two new taxa.

Pattersonocnus was most likely to have been a robust medium-sized megalonychid (similar in size to *Protomegalonyx praecursor*; Supplemental EMS_5), and as for other sloths from the Urumaco Formation, was probably of terrestrial quadrupedal habit (Rincón *et al.* 2015a, b). Future studies describing in more detail the reconstruction of the muscular and functional morphology of the hind limb and especially the forelimb (Bargo *et al*. 2012; Toledo *et al*. 2012, 2014, 2015; Toledo 2016) will add more reliable information about the palaeobiological affinities of the sloths from the Urumaco area.

Conclusions

The recovery of two distinct *megalonychids*, *Urumacocnus urbanii* and *Pattersonocnus diazgameroi*, from the late Miocene of the Urumaco Formation greatly improves our understanding of sloth diversity in the Neogene of northern South America, an area traditionally scarcely sampled compared to higher latitudes. As the phylogenetic relationships of the two new taxa presented here are based only on the femur they will certainly be refined with the discovery of additional parts of the skeleton, especially the skull and mandible. Despite this limitation, our analyses based on the combination of cranial and postcranial elements (particularly the femur) produce generally similar results to previous phylogenetic analyses, and also provide some new information on the relationship of what appears to be distinct clades within Megalonychidae. That the megalonychid sloths in the Antilles and North America would form distinct clades from the South American clade is intuitively obvious based on biogeography, but it also suggests that there are subclades within these larger clades. Such a distinction between *Megalocnus*/*Parocnus* and *Acratocnus*/*Neocnus* was recovered by the analyses of White & MacPhee (2001) and Gaudin (2004). Based on our preliminary analysis, *Urumacocnus* appears to be more closely related to the Antillean taxa, while *Pattersonocnus* groups with the North American *Megalonyx* and *Pliometanastes* and the South American genera *Ahytherium* and *Megistonyx*.

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Supplemental data

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