The oldest known record of a ground sloth (Mammalia, Xenarthra, Folivora) from Hispaniola: evolutionary and paleobiogeographical implications

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Introduction

Extant sloths are represented by only two arboreal genera, Bradypus Linnaeus, 1758, and Choloepus Illiger, 1811, found in the tropical forest of Central and South America. Although absent from the Greater Antilles today, the region was inhabited by an impressive diversity of megalocnuid sloths (Silva-Taboada et al., 2007)—an endemic clade thought to be sister to all other living and extinct continental members of Folivora, according to recent molecular analyses (Delsuc et al., 2019; Presslee et al., 2019). These molecular analyses further suggest that the ancestors of megalocnuid sloths arrived in the Caribbean by the late Eocene–early Oligocene (Delsuc et al., 2019; Presslee et al., 2019), which is supported by the presence of an unnamed species from the early Oligocene of Puerto Rico (MacPhee and Iturralde-Vinent, 1995). The sloths subsequently evolved into distinct clades that were present on these islands for nearly 35 million years, until their extinction ca. 4 Ma (Iturralde-Vinent and MacPhee, 1999; steadman et al., 2005; MacPhee et al., 2007; Presslee et al., 2019). This radiation includes species with distinctive ecomorphologies that range from large ground sloths, such as Megalocnus rodens Leidy, 1861 (<173 kg), to smaller arboreal species, such as Neocnus toupiti MacPhee, White, and Woods, 2000 (<3 kg) (White, 1993; MacPhee et al., 2000). Although the taxonomy of megalocnuids is still in progress, currently 11 species classified in five genera of Pleistocene–Holocene megalocnids are recognized. Cuba had at least four species (Acratocnus antillensis [Matthew, 1931], Megalocnus rodens, Mesocnus browni Matthew, 1931, and Neocnus gliriformis [Matthew, 1931]), Hispaniola had six species (Acratocnus simorhynchus Rega et al., 2002, A. ye MacPhee, White, and Woods, 2000, N. comes [Miller, 1929], N. dousman MacPhee, White, and Woods, 2000, N. toupiti, and Parocnus serus Miller, 1929), and Puerto Rico had only one species (A. odontrigonus Anthony, 1916) (Silva-Taboada et al., 2007; McAfie and Beery, 2021). The species B and C recorded for Cuba by White and MacPhee (2001) and Delsuc et al. (2019) are referable species already known from the island (Silva-Taboada et al., 2007). Older Cenozoic fossils are very rare: only one proximal epiphysis of a femur is known from the early Oligocene of Puerto Rico (MacPhee and Iturralde-Vinent, 1995), and several elements from the early Miocene of Cuba have been assigned to Imagocnus zazae MacPhee and Iturralde-Vinent, 1994 (MacPhee et al., 2003). The scarcity of pre-Quaternary sloth fossils from the Greater Antilles has greatly

Abstract.—Sloths were among the most diverse groups of land vertebrates that inhabited the Greater Antilles until their extinction in the middle-late Holocene following the arrival of humans to the islands. Although the fossil record of the group is well known from Quaternary deposits in Cuba, Hispaniola, and Puerto Rico, remains from older units are scarce, limiting our understanding of their evolution and biogeographic history. Here we report the oldest known fossil ground sloth from Hispaniola, represented by an unassociated partial tibia and scapula that are recognized as a single taxon from the late Miocene–early Pliocene of the Dominican Republic. The combination of characters observed on the tibia suggests a close relationship with Megalocnus, otherwise only known from the Pleistocene–Holocene of Cuba. These fossils fill a temporal gap between those previously known from the early Miocene of Cuba and those from Pleistocene–Holocene deposits in the region and provide additional support for a continuous presence of the group in the Greater Antilles since the Oligocene.

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limited our understanding of the paleobiogeography and diversity of the group.

Since the discovery of fossil sloths in the West Indies in the nineteenth century, researchers have relied on vicariance or overwater dispersal to explain the origin and inter-island distribution of this group (Silva-Taboada et al., 2007). Although current evidence supports an overlap in time between the arrival of sloths to the islands and the existence of a possible landspan between northern South America and the Greater Antilles, known as GAARlandia, little or no consensus has been reached regarding the interisland pattern of distribution of the genera and species (MacPhee et al., 2000; Rega et al., 2002; Davalos, 2004; Silva-Taboada et al., 2007; Philippon et al., 2020; Comnée et al., 2021).

Recent field work in two late Miocene–early Pliocene outcrops in the Dominican Republic led to the discovery of a partial tibia and scapula of a megalocnoid sloth. The tibia is referred to Megalocnidae instead of Megalonychidae based on the characteristic strait shaft, proportionally deeper distal epiphysis, the presence of a discoid facet wider than the odontoid facet, and the most-posterior placement of the fibular facet (MacPhee et al., 2000). The specimen can be further referred to the subfamily Megalocnini on the basis of the presence of a prominent interfacet eminence and the clear distinction between the discoid and odontoid facets.

These remains represent the oldest record of a sloth on the island of Hispaniola and of any mammal described from non-amber-bearing deposits. All previous reports of this family on the islands were from Pleistocene–Holocene deposits (Iturralde-Vinent, 2001; McAfee and Beery, 2021). The new fossils provide fresh insights into the puzzling evolutionary history of Megalocnidae by filling a temporal gap between the early Miocene Imagonax and the well-documented Pleistocene–Holocene taxa. Although the two specimens are not adequate for a formal diagnosis, they likely belong to an undescribed species of megalocnoid sloth, closely related with Megalocnus from the Quaternary of Cuba, with features that suggest they may be related to this genus.

Geological settings

The collecting sites are located along Highway Juan Pablo II (RD-7) in the vicinity of the Parque Nacional Los Haitises (Fig. 1), northeastern Dominican Republic. The Haitises area exposes carbonate-siliciclastic ramp sequences that unconformably overlie and onlap Cretaceous-Paleogene igneous basement (Cordillera Oriental). The ramp system includes nearshore-marine, organic-rich sandstone and shale facies (Yanitguia Formation) that transition laterally to shallow-water carbonate facies of the Los Haitises Formation (Iturralde-Vinent, 2001; Braga et al., 2012; Core, 2015).

The scapula (MNHN SDS FOS 25.1010) was collected at the top-middle section of outcrop the Paleo Pond 1 (18°54'33.07"N, 69°44'36.75"W), whereas the tibia was collected at the top of the section at the outcrop Paleo Pond 2 (18°55'2.16"N, 69°44'6.06"W) (Core, 2015). Both outcrops are ~5 m thick, 140–150 m long, and are located at Kilometer 55 of Highway RD-7 near Sabana Grande de Boya (Fig. 1).

The basal Paleo Pond 1 (PP1) section shows an up to 1-m-thick bioclastic packstone facies capped by a sharp, erosional subaerial exposure surface with local caliche and oxidation. The exposure surface is overlain by a 1.5-m-thick unit composed of clay-rich wackestone facies with abundant vertebrate fossils (e.g., pelomedusoid turtles), large benthic foraminifers (e.g., soritids), and bivalve and gastropod fragments. The clay-rich wackestone facies is overlain by a 30-cm-thick layer consisting of fossiliferous silty sandstone facies with abundant large benthic foraminifers, sandstone pebbles, and vertebrate fossils, including gavialoid crocodilian teeth and fish remains (Core, 2015). The fossiliferous silty sandstone facies is overlain by a 2.2-m-thick, clay-rich wackestone facies with large benthic foraminifers and marine bivalves and gastropods.

The basal Paleo Pond 2 (PP2) section shows a 2.7-m-thick unit compose of bioclastic packstone facies intercalated with bioclastic wackestone facies capped by a sharp, erosional subaerial exposure (SB3) surface that correlates laterally with PP1. The exposure surface is also overlain by a 2.2-m-thick unit composed of clay-rich wackestone facies with abundant vertebrate fossils (e.g., pelomedusoid turtles), large benthic foraminifers (e.g., soritids), bivalves, and gastropod fragments.

These marine invertebrate assemblages combined with the abundance of vertebrate fossils, including an undescribed rodent, a gavialoid, and pelomedusoid turtles, suggest an estuarine environment (0–10 m water depth) that was developed during relative sea-level rise and initial transgression after subaerial exposure (Core, 2015). Sr isotope-derived mean ages from marine bivalves (Kuphus incrassatus Gabb, 1873) located stratigraphically below and above the units of interest in this study indicate a late Miocene to early Pliocene age (ca. 7.15–5.57 Ma, Messinian–Zanclean) for the described units (Core, 2015; Ortega-Ariza et al., 2015).

Materials and methods

Specimens examined.—Acratocnus antillensis, left tibia (UCLVP-66, CWS-309); Acratocnus ye (UF 170185, 170333) and right tibia (UF 170335, 315688); Bradypus tridactylus Linnaeus, 1758, partial skeleton (UF 8123); Megalocnus rodens, associated mandible, right and left humeri, left ulna, radius, femur, and tibia (CZACC 26.296), right (ARQC-159, 172), and right scapulae (ARQC-160), left (ARQC-135, 140, 141, 155) and right tibiae (ARQC-137, 168); Megalonyx leptostomus Cope, 1893, right tibia (UF 223808, 274300), M. jeffersoni Desmarest, 1822, right tibia (23569); M. wheateyi Cope, 1871, left tibia (UF 21345); Mesocnus browni, left (CWS-1023) and right tibiae (CLV-1125); Neocnus comes, associated right and left tibiae, right fibula, right and left astragali, and right calcaneus (UF 170440), left (UF-170323, 170444) and right tibiae (UF-170324, 170446); N. dousman, left tibia (UF 170404); N. gliriformis, left (CWS-901E) and right tibiae (ARQC-108); Parocnus serus, right (UF 23863) and left tibiae (UF-170080, 169953); Pliometaanastes protistus Hirschfeld and Webb, 1968, left tibia (UF 95400).

Measurements.—All measurement were made with a Mitutoyo caliper with a 0.01 mm resolution (Absolute Solar Digimatic) and followed the measurements used by Silva-Taboada et al. (2007).
Repositories and institutional abbreviations.—ARQC, collection of the former Arqueocentro, housed at Universidad Central de las Villas, Villa Clara, Cuba; CLV, field number from Lazaro Vinola, Cuba; CWS, Colección William Suarez, housed at Museo Nacional de Historia Natural de Cuba, La Havana, Cuba; CZACC, Instituto de Ecología y Sistemática, La Havana, Cuba; MNHNCu Museo Nacional de Historia Natural de Cuba, La Havana, Cuba; MNHNSD FOS, Vertebrate Paleontology Collection of Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic; UCLVP, Universidad Central de las Villas, Villa Clara, Cuba; UF, Vertebrate Paleontology Collection, Florida Museum of Natural History, Gainesville, Florida, USA.

Systematic paleontology

Superorder Xenarthra Cope, 1889
Suborder Folivora Delsuc et al., 2001
Oder Pilosa Flower, 1883
Family Megalocnidae Kraglievich, 1923
Subfamily Megalocninae Kraglievich, 1923
Megalocninae Kraglievich, 1923
Megalocninae gen. et sp. indet.

Figures 2–4.1

Occurrence.—The specimens come from two outcrops separated by 3.5 km, both located along the Juan Pablo II (RD7) highway on Sabana Grande de Boya, Dominican Republic (Fig. 1). The scapula was collected at locality PP1 (18°54′33.0768″N, 69°44′36.7578″W), whereas the tibia comes from locality PP2 (18°56′15.118″N, 69°44′27.842″W). Both outcrops belong to the upper section of the Yanigua-Los Haitises Formation.

Description and comparison.—MNHNSD FOS 25.4251 consist of the distal half of a right tibia of a medium-sized sloth with numerous fractures in the diaphysis, partially compressed near the epiphysis, and missing most of the posterior section of the distal articular surface. Although the specimen is somewhat deformed, it is still possible to identify several potentially taxonomically informative characteristics. The fusion of the distal epiphysis with the diaphysis suggests that it belong to an adult individual. The specimen is larger than the tibia of Neocnus and Acratocnus Anthony, 1916, and smaller than that of Megalocnus Leidy, 1868, but falls within the size range of Mesocnus Matthew, 1931, and Parocnus Miller, 1929 (Anthony, 1918; Matthew and Paula-Couto, 1959; Silva-Taboada et al., 2007). In MNHNSD FOS 25.4251, the cross-section of the diaphysis near the midpoint
of the diaphysis are not sharp. The diaphysis of Megalocnus curves medially, unlike that of MNHNSD FOS 25.4251, but some of the differences in the shape of the diaphysis observed between two taxa can be found among species of the same genus in other West Indies sloths (e.g., Neocnus comes vs. N. dousman). The shaft of the tibia in Neocnus Arredondo, 1961, and Acratocnus is similar to that of MNHNSD FOS 25.4251 in being relatively narrow with respect to the distal epiphysis, but in some species of these genera (e.g., Neocnus comes and Acratocnus antilensis) the diaphysis has a D-shaped cross section with sharp posterolateral and posteromedial margin. The width of the shaft of MNHNSD FOS 25.4251 increases steadily towards the distal epiphysis with a slight increment in the slope of the medial plane at about the half point of the specimen. The maximum width of the distal epiphysis is ~42.9 mm, but it may be slightly wider considering that the specimen is partially eroded. The anterolateral surface of MNHNSD FOS 25.4251 is convex, and no evidence of torsion of the diaphysis is present, in contrast with Parocnus where the distal and proximal epiphysis of the tibia are rotated with respect to each other, resulting in a lateral torsion of the diaphysis. The anterior surface near the epiphysis is continuous, lacking the pivot for the articulation of the navicular process of the astragalus, which is present only in the species of Mesocosmus.

The articular surface of the tibia in MNHNSD FOS 25.4251 is partially preserved and possesses a prominent interfacet eminence that separates anteriorly the discoid and odontoid facets. The eminence is broad and high, its long axis is anteroposteriorly oriented, and it is located near the center of the articular surface, towards its anterior margin. The interfacet eminence seems to be associated in some continental sloths, as in Megatheriidae and Nothrotheriidae, with the medial ridge that separates the discoid and odontoid facets, but such a ridge is absent in MNHNSD FOS 25.4251 and other Greater Antilles sloths (Amson et al., 2015; Toledo et al., 2015, 2018). In Megalocnus, the interfacet eminence does not extend posteriorly as in MNHNSD FOS 25.4251. In Mesocosmus and Parocnus, the interfacet eminence is located more medially and internally on the articular surface, whereas in Acratocnus and Neocnus the eminence is extremely reduced. The discoid and odontoid facets in MNHNSD FOS 25.4251 are concave and possess similar depth in anterior view, as in Megalocnus. In distal view, the postero medial region of the discoid facet seems to be more expanded and deeper than that of the anterior portion. The odontoid facet has an oval outline and is oriented anteroposteriorly, but it does not expand as far posteriorly as the discoid facet. In the smaller Caribbean taxa, Neocnus and Acratocnus, the odontoid and discoid facet are also at the same level, but almost undifferentiated. In MNHNSD FOS 25.4251, a smaller eminence separates anteriorly the fibular and discoid facet, but only a reduced section of the former facet is preserved on the specimen. The fibular facet is relatively narrow and longer than wide. Just proximal to the odontoid facet, on the medial side of the specimen, there is a small remnant of the medial malleolus, which is separated from the facet by a wide groove, as in other Caribbean taxa, except in Parocnus in which the medial malleolus and the groove are reduced. Poorly defined grooves in MNHNSD FOS 25.4251, interpreted here as marking the
course of the flexor hallucis longus and the tibialis caudalis, are located on the posteromedial and medial side of the tibia, respectively. The two possible muscle scars are separated by an almost entirely lost medial malleolus, where a groove of the flexor digitorum longus was likely located (Amson et al., 2015; Toledo et al., 2015).

The scapula (MNHNSD FOS 25.1010) is fragmentary (Fig. 3), and only part of the glenoid cavity, spine, and lateral border is preserved. The specimen is assigned to a sloth because it is significantly larger than the scapula of any other terrestrial mammals known to occur in younger or older deposits in Hispaniola (e.g., rodents, solenodons, primates). It further differs from rodents, primates, eulipotyphlans, and sirenians by not having a constriction in the scapular neck between the glenoid cavity and the rest of the body of the scapula. Other diagnostic characters are absent, and we can only conclude that it may belong to a sloth of the body size between *Megalocnus* and *Parocnus*.

Materials.—Distal end of right tibia (MNHNSD FOS 25.4251) (Figs. 2, 4.1) and proximal region of left scapula (MNHNSD FOS 25.1010) (Fig. 3) of a medium-sized sloth.

Remarks.—This late Miocene sloth from Hispaniola differs morphologically from all Quaternary genera known from the Greater Antilles, but can be referred to the subfamily Megalocninae because of the presence of a prominent interfacet eminence and the clear distinction between the discoid and odontoid facets. Its morphology further suggests that it may have been closely related with *Megalocnus* from Cuba. On the other hand, the gracility of the diaphysis of MNHNSD FOS 25.4251 resembles that of *Acratocnus*, *Neocnus*, and arboreal species, but the morphology of the distal epiphysis suggests a more terrestrial habitat.

Discussion and conclusions

The morphology of the distal end of the tibia of sloths is regulated by functional and phylogenetic constrains (White and MacPhee, 2001; Silva-Taboada et al., 2007; McDonald, 2012). The wide range of niches occupied by members of the suborder Folivora and their locomotion modes resulted in the evolution of very complex morphologies. In the Greater Antilles, the tibia of *Mesocnus* is among the most peculiar ones. It bears a deep depression for articulation of the astragalus at the middle of the anterodistal surface of the tibia; this feature is absent in other Caribbean sloths. Although *Mesocnus* has been considered a junior synonym of *Parocnus* (MacPhee et al., 2000), the skeletal differences among the Cuban and Hispaniola taxa indicate that they belong to different genera.
In the large sloths from the Greater Antilles, the position and morphology of the navicular facet on the tibia and its articulation with the astragalus probably restricted the eversion and inversion of the pes, but extended range of the flexion. The interfacet eminence, like the medial ridge, limited the lateral and medial displacement between the astragalus and tibia, giving more stability to the pes, which seems to be exacerbated in *Mesocnus*. The robustness of the diaphysis of the tibia, articulation between the tibia and astragalus, and the presence of many other traits in the rest of the postcranial skeleton argue in favor of a more terrestrial locomotion for *Megalocnus*, *Mesocnus*, and *Parocnus* (White and MacPhee, 2001; Silva Taboada et al., 2007; Arredondo Antúnez, 2011). In contrast, the lack of differentiation of the articular facets on the distal epiphysis on the tibia of *Neocnus* and *Acratocnus* is associated with arboreal species. Furthermore, *Acratocnus* and *Neocnus* share a remarkably large groove for the flexor hallucis longus tendon, which is also present in some extinct continental taxa, such as santacrucian genera *Hapalops* Ameghino, 1887, and *Eucholoeops* Ameghino, 1887, and the extant *Bradypus* (Toledo et al., 2015). Other authors have previously noted the similarity among the postcranial skeletons of *Hapalops*, *Eucholoeops*, *Acratocnus*, and *Neocnus* (Anthony, 1916; De Iuliis et al., 2014), suggesting it is possibly related to a shared arboreal or climber ecology (Braga et al., 2012; Toledo, 2016).

Recent molecular studies suggest that Greater Antilles sloths are a clade that arrived in the Caribbean by the Eocene-Oligocene boundary, where it evolved and diversified in isolation for more than 35 million years (Delsuc et al., 2019; Presslee et al., 2019). A Paleogene origin agrees with the age proposed for the GAARlandia hypothesis (Iturralde-Vinent and MacPhee, 1999; Philippon et al., 2020), which suggests sloths and other terrestrial elements of the Greater Antilles biota would have colonized the region ca. 35 Ma across a transient aerial exposure of land that connected some islands with northern South America. Additional molecular and paleontological evidence seems consistent with this hypothesis, or at least suggests a synchronous colonization of the region by other terrestrial taxa (Alonso et al., 2012; Vélez-Juarbe et al., 2014; Chamberland et al., 2018; Blackburn et al., 2020; Marivaux et al., 2020). The oldest fossil referable to a sloth in the Greater Antilles is a proximal end of a small femur from the early Oligocene of Puerto Rico (MacPhee and Iturralde-Vinent, 1995) that may belong to the smallest folivoran known. In contrast, the early Miocene *Imagocnus zazae* from Cuba reached a large body size, probably close to or larger than *Megalocnus* (∼270 kg) (MacPhee and Iturralde-Vinent, 1994, 1995). Although a number of other fossils have been referred to *Imagocnus zazae* (MacPhee et al., 2003), a wide range of body sizes, ranging from a humerus about the size of an *Acratocnus*...
humerus to a pelvis comparable with that of *Megalocnus*, suggests that the sample may be composed of more than one taxon, even when taking sexual dimorphism into account. *Imagocnus zazae* has a combination of characters that are also found in *Megalocnus* and/or *Parocnus*, but most of its skeleton is poorly known and its phylogenetic relationships remain poorly resolved. The specimens described here (MNHN SD FOS 25.4251 and MNHSND FOS 25.1010) belong to an undescribed new taxon that inhabited the northern paleoisland of Hispaniola when the Greater Antilles were already separated from each other and fills a temporal gap between *Imagocnus* and the Quaternary species. The fossils of this undescribed species, along with those of *Imagocnus zazae* from Cuba, suggest the presence of multiple lineages of sloths across the Greater Antilles during the Neogene that disappeared before the late Quaternary.

The occurrence of sister taxa on different islands in the Greater Antilles during the late Pleistocene (Fig. 5) has been interpreted either as the result of Quaternary overwater dispersal (Rega et al., 2002; Silva-Taboada et al., 2007) or vicariance during the Neogene (Iturralde-Vinent and MacPhee, 1999; MacPhee et al., 2003). Some authors supporting the former hypothesis argue that separation of populations since the early Miocene or before should have resulted in more than just species level diversification (Simpson, 1956; Rega et al., 2002; Silva-Taboada et al., 2007). In agreement with the molecular results, remains of pre-Quaternary sloths from Puerto Rico, Cuba, and now Hispaniola support the existence of the group starting in the early Oligocene, through the late Holocene (Fig. 5). Whether some of these older forms represent taxa closely related to the Quaternary species or other extinct branches of the megalocnids radiation in the region is still unknown. If the split-up of the Greater Antilles core islands (Puerto Rico-Hispaniola-Cuba) during the Neogene, coupled with extinction of some lineages, caused the distribution patterns observed in the Pleistocene–Holocene, then fossils of the clades shared among islands should be found in Neogene deposits, which does not seem to be the case. On the other hand, if overwater dispersal among Puerto Rico, Cuba, and Hispaniola was prevalent during the Quaternary, we would expect to find them also in the Bahamas, Jamaica, or some of the offshore islands in the Greater Antilles, especially given that good dispersers such as some rodents, frogs, lizards, and snakes did colonize these regions repeatedly (Hedges, 2006). However, intense fossil collecting on those islands has not yielded fossils of sloths from the Quaternary (Silva-Taboada et al., 2007). The current pre-Quaternary fossil record of the group is rather limited and fragmentary, and it is necessary to incorporate more molecular results from recently extinct taxa.

Although efforts aimed at collecting fossils of terrestrial vertebrates in Neogene localities are ongoing (e.g., Rio Guatemale in Puerto Rico; Vélez-Juarbe et al., 2014; Blackburn et al., 2020; Marivaux et al., 2020, 2021), future fieldwork in Hispaniola and across the Greater Antilles is needed. Filling the temporal and geographical gaps in the fossil record between the Eocene–Oligocene and the Quaternary terrestrial fauna would lead to an improved understanding of the origins and evolution of sloths and other components of the Greater Antillean vertebrate fauna. The fossils herein described represent the oldest sloth known from Hispaniola, implying that this group was present in the island at least since the late Miocene–early Pliocene.

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