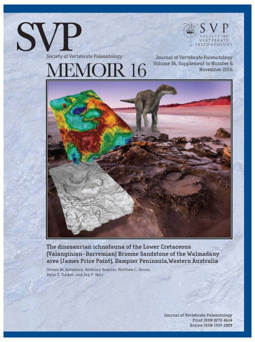

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ARTICLE

A NEW GENUS OF MEGALONYCHID GROUND SLOTH (MAMMALIA, XENARTHRA) FROM THE LATE PLEISTOCENE OF QUINTANA ROO, MEXICO

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ABSTRACT—A new genus and species of late Pleistocene megalonychid sloth, *Nohochichak xibalbahkah*, gen. et sp. nov., is described from Hoyo Negro, a chamber in the Sac Actun cave system, Quintana Roo, Mexico. Phylogenetic analysis indicates that this new sloth is most closely related to *Meizonyx salvadorensis* from the middle Pleistocene of El Salvador, and that these two genera in turn are the sister clade to *Megistonyx* and *Ahytherium* in South America and not the other North American megalonychids, *Pliometanastes* and *Megalonyx*. This new sloth indicates that the number of sloth taxa involved in the Great American Biotic Interchange is greater than previously understood, and that a significant part of the Interchange biodiversity, as represented by taxa confined to the semitropical and tropical portions of Central and North America, remains to be discovered.

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INTRODUCTION

Compared with northern regions of North America, encompassing the northern parts of Mexico, the United States, and Canada, the Cenozoic faunas in general, and Pleistocene faunas in particular, of southern Mexico and Central America are poorly known. Whereas late Pleistocene faunas or records of individual taxa have been described from this region (e.g., Webb and Perrigo, 1984; Lucas et al., 1997; Cisneros, 2005; Ferrusquía-Villafranca et al., 2010), the relative scarcity of documented sites from southern Mexico to Panama limits our understanding of the region's historical biodiversity, its role in the Great American Biotic Interchange (GABI), and patterns of extinction at the Pleistocene-Holocene transition. The discovery of a diverse late Pleistocene fauna along with early human remains in Hoyo Negro, a chamber of the Sac Actun cave system, Quintana Roo, Mexico (Nava-Blank, 2011), not only provides a better understanding of the late Pleistocene fauna in general from this part of Mexico, but also preserves the remains of a previously unknown genus and species of extinct megalonychid ground sloth. This new sloth is not only phylogenetically close to another Central American genus, *Meizonyx*, but these two taxa are in turn more closely related to South American taxa than to the well-known and geographically closer North American genera, *Pliometanastes* and *Megalonyx*. This new taxon is described here, and the implications of its discovery for our understanding of the GABI are considered.

Locality Description

Hoyo Negro is a 62-m-diameter, subterranean, bell-shaped, collapsed dissolution chamber connected to three passages that join Hoyo Negro to the surface in the Sac Actun cave system, eastern Yucatan Peninsula, Quintana Roo, Mexico (Fig. 1). Floors of the submerged passages are ~12 m below sea level (mbsl), and the pit drops to a maximum depth of 55 mbsl. The skeletal material lies at the base of the pit, 600 m from the nearest entrance when it was a dry cave.

Twelve sediment cores from the floor of the chamber were used to reconstruct the Holocene flooding history of the now-phreatic cave passages and cenotes (Ich Balam, Oasis) of the cave system that connect to Hoyo Negro (Collins et al., 2015). Basal accelerator mass spectrometry (AMS) radiocarbon ages on bat guano and seeds combined with cave profiles determined the history of flooding in Hoyo Negro, and when access became restricted for animal and human entry. The bottom of Hoyo Negro was flooded by at least 9850 calibrated years (cal yr) BP, but likely earlier, and the pit containing the faunal remains became inaccessible at ~8100 cal yr BP. Hoyo Negro is now accessible only by technical dive teams. Information collected to date has been derived primarily through videography, photography, minimal sampling, and three-dimensional modeling utilizing remote imaging. Because of the technical difficulties in recovering bones and safely transporting them to the surface, recovery of the skeleton of the sloth has thus far been restricted to major representative parts that would permit taxonomic analysis. Other parts of the skeleton remain in situ.

The faunal assemblage identified to date at the bottom of Hoyo Negro is composed of extinct taxa, including sabertooth cat (*Smilodon* cf. *fatalis*), the extinct tremarctine bear *Arctotherium* (Schubert et al., 2016), highland gomphothere (*Cuvieronius* cf. *tropicus*), Shasta ground sloth (*Nothrotheriops shastensis*), and the megalonychid ground sloth described in this paper, along with extant species, including puma, bobcat, coyote, Baird's tapir, peccary, and white-nosed coati (Chatters et al., 2014). Animal bones are concentrated on the south side

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*Corresponding author.

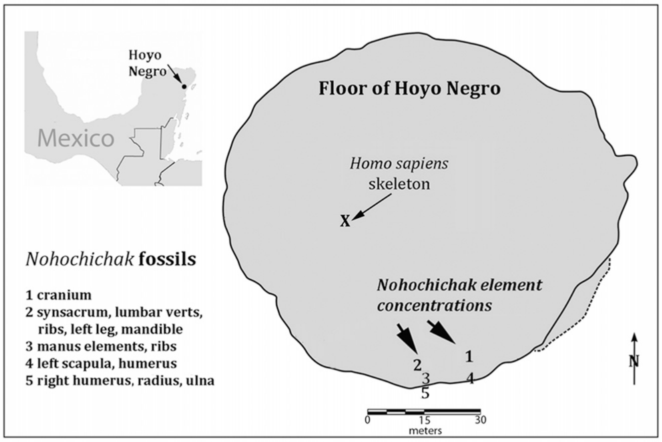

FIGURE 1. Map showing location of Hoyo Negro, Quintana Roo, Mexico, and location of parts of the skeleton of *Nohochichak xibalbahkah*, gen. et sp. nov., within Hoyo Negro.

of the floor and on wall projections or sloping boulders between 40 and 49 mbsl (28–37 m below the pit rim). Bones generally occur as clusters representing single individuals and display varying degrees of disarticulation and scattering. Occasionally, more than one animal may be found in close proximity. Curvilinear fractures (green break) of limb bones are sometimes present, having occurred when an animal fell into the pit and was killed. The observed distribution and condition of skeletal elements is probably explained by the decomposition of the carcasses in a shallow pool present during short-lived episodes of local water table rise, during which remains were transported and scattered toward the walls of the room. Subaerial conditions existed in this room above 42 mbsl before postglacial inundation above the shallow pool.

The megalonychid sloth described here was found on the wall and floor in the southwestern portion of Hoyo Negro, below and between the entrances to the southeastern and southwestern tunnels (Fig. 1). Forelimb elements (Fig. 2) and some ribs are perched on the cave wall as shallow as 40.5 mbsl, with the skull, synsacrum, and lower limb elements on the floor to as deep as 48.2 mbsl (Fig. 3). The distribution of these elements is also indicative of decomposition in a shallow pool on the cave floor, the depth of which stood at approximately 40 mbsl at the time. Elements on the wall and the rostrum portion of the cranium are largely free of sediment and colored a reddish brown by iron compounds, whereas the mandible, synsacrum, articulated leg, and vertebral elements are partially buried in bat guano and stained nearly black. A large stick, which was collected, lay on the mandible. AMS radiocarbon dating of this wood provides a minimum age for its deposition of 9807 ± 38 radiocarbon years (rcy; 11,264–11,183 cal yr BP).

Direct dating of the associated faunal assemblage is challenging because the long submergence of the bone does not favor bone collagen preservation. Attempts to extract collagen from bone and tooth specimens for AMS radiocarbon (^{14}C) dating have thus far been unsuccessful. However, multiple lines of evidence, such as the multiple species of Pleistocene megafauna (sabertooth cat, gomphothere, and Shasta ground sloth) that were largely extinct in North America by 13 ka (Graham, 2001;

FIGURE 2. Right humerus (**1**) and scapula (**2**) of *Nochochichak xibalbahkah*, gen. et sp. nov., as discovered on the floor of Hoyo Negro.

FIGURE 3. *Nohochichak xibalbahkah*, gen. et sp. nov., mandible (**1**), synsacrum (**2**), left femur (**3**), tibia (**4**), and trunk elements in situ beneath bat guano on the floor of Hoyo Negro. The long branch at left produced a minimum radiocarbon age for the specimen.

Haynes, 2013), indicate that much of the faunal assemblage dates to the latest Pleistocene. The age of the fauna is also constrained by sea-level history after the Last Glacial Maximum (LGM; Milne and Peros, 2013). Both bat guano deposits and subaerially formed calcite ceased accreting after 10 to 9.5 ka (Chatters et al., 2014; Collins et al., 2015), consistent with the timing of inundation expected from global sea-level reconstructions (Bard et al., 2010; Medina-Elizalde, 2013).

Direct dating of the human and one gomphothere by U-Th analysis of overprinted subaerial calcite formations, and ^{14}C ages of the tooth enamel, further supports a terminal Pleistocene age for the assemblage (Chatters et al., 2014). U-Th ages of calcite formations on the pelvis and femur of the gomphothere indicate that it was deposited by at least ~19 ka. Two AMS ^{14}C dates on its tooth enamel suggest an age as early as 41.6 to 36.4 ka, but these teeth are heavily mineralized, so strong dissolved inorganic carbon effects cannot be ruled out. The human skeleton was dated to between 13 and 12 ka by these same methods. These findings support the hypothesis that animals became trapped in Hoyo Negro when the upper horizontal passages were accessible when the sea level of the western Caribbean was below 10 mbsl. The U-Th dates also indicate that Hoyo Negro was largely subaerial and primarily dry above 42 mbsl between 19.0 and 9.5 ka. The radiocarbon age of wood above the sloth mandible corroborates this supposition for that animal.

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope, 1889
Suborder PILOSA Flower, 1883
Family MEGALONYCHIDAE Gervais, 1855
NOHOCHICHAK XIBALBAHKAH, gen. et sp. nov.
(Figs. 4, 5)

Holotype—Instituto Nacional de Antropología e Historia, INAH DP5832. Edentulous rostral portion of skull and complete mandible with bases of caniniforms and complete molariforms on both sides preserved.

Etymology—*Nohochichak*, the generic name, is derived from Mayan *Nohoch* for ‘great’ and *ich’ak* for ‘claw,’ or literally, ‘great claw,’ in reference to its inclusion in the family Megalonychidae, named for the genus *Megalonyx*, or ‘large claw’ in Greek. The specific name *xibalbahkah* is derived from *Xibalba*, the name for the Mayan underworld, associated with death, and *ahkah*, ‘dweller,’ ‘the great claw that dwells in the underworld.’

Type Locality—Hoyo Negro, Sac Actun cave system, Quintana Roo, Mexico 20°18′55″N, 87°25′53″W, elevation ~10 m.

Age—Late Pleistocene.

Diagnosis of Genus—Monotypic genus, see Species Diagnosis.

Species Diagnosis—Large ground sloth similar in size and robustness to *Megalonyx jeffersonii*. Generally resembles *Australonyx aquae* in that the rostrum of the skull anterior to the orbits is narrower than the braincase, with a pronounced slope or angle between the frontals and nasals so the dorsal surface of the rostrum is below that of the braincase; the anterior portion of the rostrum of *Nohochichak* is not expanded laterally as in *Megalonyx jeffersonii, Megistonyx oreobios*, and *Ahytherium aureum*; the area between caniniforms for the attachment of premaxillae is broadly ‘U’-shaped, although not to the same degree as in *Ahytherium aureum* and contrasts with the more ‘V’-shaped space in *Megalonyx jeffersonii*; viewed anteriorly, the nasal opening is ovoid, with middle portion wider than dorsal and ventral margins; infraorbital canal short and positioned between first and second upper molariforms; anterior descending process of the zygomatic short with broadly rounded ventral margin; ascending process of zygomatic elongated, with posterior inclination and of uniform width; upper and lower caniniforms trianguloid in cross-section, with the corners rounded and not sharp as in other megalonychids; mandibular spout is triangular and short and most closely resembles *Megalonyx jeffersonii*; dorsal surface of spout excavated to form a small trough that extends posteriorly to the mandibular symphysis; the anterior midline of the symphysis lacks a keel; posterior margin of mandibular symphysis at anterior margin of the lower first molariform; coronoid process low and broad with a rounded dorsal edge. The presence of a mandibular condyle that is flat in posterior view is a unique, unambiguous autapomorphy of *Nohochichak*, as revealed by phylogenetic analysis. Other unambiguous autapomorphies include an m2 that is rectangular in outline and a ventral internal ridge on the ascending ramus of the mandible. Unique but ambiguous autapomorphies include a caniniform of modest size (neither the largest nor the smallest tooth) and a strong postorbital process of the frontal.

DESCRIPTION

Rostrum

Dorsally, the rostrum has separated from the braincase just posterior to the postorbital process of the frontal (Fig. 4). Breakage through the palatal portion of the rostrum is through the alveolus of the last molariform so that only the anterior margin of the alveolus is preserved. The skull and mandible come from an adult, and virtually all of the cranial sutures are obliterated, so it is not possible to assess the shape and extent of individual bones. The only partially visible sutures are of the nasals, which permits a determination of their contact with the maxillae and frontals.

None of the teeth were retained in the maxillary part of the rostrum, so the relative size and shape of the teeth are inferred from the outlines of the alveoli (Fig. 4D). The close relationship between the size of the teeth and dimensions of the alveoli in sloths allows measurement of the alveoli to serve as a reasonable approximation for tooth size. The rostrum is broken at the anterior margin of the last upper molariform, so although it is possible to estimate the width of the tooth, it is not possible to determine its mesial-distal length or to obtain measurements of the entire tooth row.

Along with the rostrum, the left zygomatic is preserved (Fig. 4A). It is separated from the rostrum, but the broken surfaces of the two bones match, allowing an accurate reconstruction of how the zygomatic was positioned relative to the rest of the skull. The bone is essentially complete except for part of the middle process of the zygomatic (sensu Gaudin, 2004) on the posteroventral margin of the ascending process.

The skulls of megalonychid sloths can be divided into two general groups: (1) taxa in which the rostrum retains the same general width as the braincase, the height of the skull anterior to the orbit is at the same level as the braincase, and the distance from the anterior margin of the orbit to the anterior margin of the maxilla is short (e.g., *Megalonyx, Ahytherium*); and (2) those taxa in which the rostrum anterior to the orbits is narrower than the braincase, with a pronounced slope or angle between the frontals and nasals, so the dorsal surface of the rostrum is below that of the braincase and the distance from the anterior margin of the orbit to the anterior margin of the maxilla is greater (e.g., *Megistonyx, Nohochichak*). The ventral slope of the rostrum in *Nohochichak* starts at the level of the anterior margin of the base of the zygomatic arch, and the rostrum falls into the second group. Thus, *Nohochichak* generally resembles *Australonyx* (De Iuliis et al., 2009), whereas *Megalonyx* (e.g., Leidy, 1855) and *Ahytherium* (Cartelle et al., 2008) have the former morphology. *Megistonyx* is somewhat intermediate between these two groups, because it has a slight ventral slope from the frontal to the nasal but the slope is not as pronounced as in *Nohochichak* and *Australonyx*, and *Megistonyx* more closely

FIGURE 4. *Nohochichak xibalbahkah*, gen. et sp. nov. Anterior part of skull INAH DP5832 in **A**, left lateral view; **B**, dorsal view; **C**, posterior view, showing exposed frontal sinus; and **D**, ventral view.

resembles *Megalonyx* and *Ahytherium* in the dorsal profile of the skull. Although a narrow elongated rostrum is also present in the Caribbean megalonychids *Megalocnus, Parocnus, Neocnus*, and *Acratocnus* (Anthony, 1926; Matthew and Paula Couto, 1959; Paula Couto, 1967; Fischer, 1971; MacPhee et al., 2000), these taxa lack the distinct change in slope between the frontals and nasals present in *Nohochichak* and *Australonyx*.

The anterior portion of the rostrum of *Nohochichak* is not expanded laterally as in *Megalonyx, Megistonyx*, and *Ahytherium*, and the caniniform is in the same parasagittal plane as the molariforms. The area between the caniniforms for the attachment of the premaxillae is broadly 'U'-shaped, although not to the same degree as in *Ahytherium*, and contrasts with the more 'V'-shaped space between the caniniforms in *Megalonyx* (Lyon et al., 2015). Viewed anteriorly, the nasal opening is ovoid. The middle portion is wider than the dorsal and ventral portions. The ventral portion is about as wide as the dorsal one and does not become narrow and constricted between the caniniforms as in *Megalonyx* (e.g., Leidy, 1855).

There is just enough visible of the nasal-maxillary suture to determine the outline and extent of the nasals. They extend posteriorly to the base of the rostrum, where their contact with the frontal produces a pronounced change in the slope of the skull, giving the effect of a distinct 'forehead.' Their posterior margin is near the anterior margin of the orbit. The internasal suture is the most visible suture on the rostrum. The nasals are uniform in width throughout their entire length and anteriorly do not subdivide into a medial and a lateral process, like *Megistonyx, Ahytherium*, and several Antillean taxa, and in contrast to *Megalonyx* and the general condition in sloths (Gaudin, 2004; McDonald et al., 2013). The anterior margin of the nasals is slightly rounded, and at their anterior end they are separated by a 'V'-shaped cleft at their medial contact. Because the skull is broken across the frontals, it is possible to see the anterior portion of the enlarged frontal sinuses, which traverse the entire width of the skull in this area. The expansion of the frontal sinuses is also expressed in the inflation of the skull posterodorsal to the orbit.

The palate between the molariforms is straight, horizontal, and does not arch, whereas the diastema has a distinct arch such that the alveolar margin of the caniniform is below the alveolar margin of the molariforms in *Nohochichak*, and this is also the condition in the Antillean taxa, *Hapalops, Eucholoeops, Pliomorphus, Megalonyx, Megistonyx, Ahytherium*, and *Choloepus* (Gaudin, 2004; McDonald et al., 2013). The dorsoventral relationship of the caniniform is similar in *Ahytherium*, but curvature of the diastema positions the caniforms of that genus more ventrally, whereas in *Megalonyx* the ventral shift in the caniniform is not as pronounced. *Nohochichak* is intermediate in the degree to which the caniniform is ventrally positioned. Because of the strong ventral arching of the palate between the molariforms in *Megistonyx*, the alveolar margins of the caniniform and molariforms are at about the same level. The anterior part of the palate of *Nohochichak* is grooved for blood vessels (= anterior palatal foramina and grooves, sensu De Iuliis et al., 2011), and these grooves become pits on the posterior portion of the palate. These grooves are present in all Pilosa (i.e., sloth and anteaters; Gaudin, 2004), although they are lost secondarily in *Megalonychotherium, Acratocnus*, and *Choloepus* (Gaudin, 2004; McDonald et al., 2013).

In ventral view, the lateral margins of the diastema in *Nohochichak* are curved, producing a slight mediolateral narrowing between the caniniforms and molariforms (Fig. 4D). This is similar to *Megalonyx* and unlike *Ahytherium*, in which there is a continuous widening of the diastema between the molariforms and caniniforms and the lateral margin of the diastema is straight. The curvature of the lateral margin of the diastema in *Nohochichak* is broader than in *Megalonyx*, and the buccinator fossa is not as pronounced. The buccinator fossa extends from the posterior margin of the caniniform to below the base of the zygomatic process and then narrows posteriorly, terminating at the anterior margin of the infraorbital canal.

The anterior margin of the infraorbital foramen is located at the anterior margin of the upper first molariform in *Nohochichak*. The bar of bone that forms the floor of the infraorbital canal is short, and the maxillary foramen is at the posterior margin of the upper first molariform. This is similar to *Megistonyx* but differs from *Megalonyx*, in which the infraorbital foramen is at the anterior margin of the second upper molariform and the maxillary foramen is adjacent to the third upper molariform. In *Ahytherium*, the infraorbital canal is short and positioned between the first and second upper molariforms. In this genus, there is a shallow dorsal groove that connects the maxillary foramen to another small foramen in the maxilla.

The lacrimal foramen of *Nohochichak* is a large dorsoventrally elongate opening positioned on the anterior margin of the base of the zygomatic arch. The base of the zygomatic process is separated from the maxilla by a long, narrow groove along its ventral anterior margin. This groove is present in all megalonychids except *Choloepus* (Gaudin, 2004:char. 147). The base of the zygomatic process of the maxillae in *Nohochichak* is mediolaterally flattened.

Nohochichak appears to have had an incomplete zygomatic arch. This is unlike *Megalonyx* and *Ahytherium* in which a distinct secondary articulation has formed between the zygomatic and the zygomatic process of the squamosal. In these genera, the convexly rounded anterior margin of the latter process is in contact with a complementary concave surface on the zygomatic. Despite the presence of a middle zygomatic process in *Nohochichak* at the same position as in *Ahytherium*, there is no indication of an articular contact. A rugose area at the base of the ascending process, on its posterior margin, may have been the point of attachment of the ligament between the zygomatic and the zygomatic process of the squamosal (Naples, 1982).

Unlike *Megalonyx*, in which the anterior descending process of the zygomatic is greatly elongated and tapers ventrally (Lindahl, 1892), this process in *Nohochichak* is short and broadly rounded. In *Ahytherium*, this process is also elongate but with a distinct posterior curvature that extends almost to the plane of the glenoid process and retains a uniform width. Just below the level of the ventral margin of the orbit, at the anterior margin of the zygomatic, there is a rounded muscle scar. A similar-sized muscle scar is present in *Megalonyx* at the same level but on the posterior margin. The lateral side of the descending process of the zygomatic in *Nohochichak* is smooth and lacks the muscle scars for the origins of the subdivisions of the superficial masseter that are present in *Megalonyx* and *Ahytherium*, as well as the two genera of extant sloths and many non-megalonychid sloths (e.g., Naples, 1987). The ascending process of the zygomatic in *Nohochichak* is elongated, has a posterior inclination, and is of uniform width. At its base, at the level of the orbit on the posteroventral margin, is another short, rounded process, the middle process of the zygomatic. The outer margin of this process is broken in the type of *Nohochichak*, but enough is preserved to infer its general outline. A similar process is present in *Ahytherium*, although it is larger, more elongate, and more angular in shape. In *Ahytherium*, this process forms the ventral contact for the zygomatic process of the squamosal, where it articulates with the zygomatic. This process is fused indistinguishably into the zygomatic arch in adult individuals in *Megalonyx*. The zygomatic has not yet been observed for *Megistonyx* or *Australonyx*.

Upper Dentition

Although none of the upper dentition of *Nohochichak* is preserved, the close relationship between the cross-sectional shape of the teeth and the shape of the alveolus in Folivora permits some general observations on tooth shape, proportions, size relative to one another, and size in general.

Although the anterior and lateral margins of the alveoli for both caniniforms are broken, enough is preserved to infer that they were trianguloid in cross-section, an inference supported by the trianguloid shape of the lower caniniforms. The corners of the tooth appear to have been rounded and not sharp like other megalonychids such as *Acratocnus*. This tooth in *Nohochichak* more closely resembles the outline of the caniniform of *Megistonyx*, as similarly inferred from the alveolus, because the type also lacks caniniforms. The alveolus for the caniniform is curved and extends posteriorly to about the level of the midpoint of the diastema.

The alveolus for the first molariform is a rounded equilateral triangle in shape. The longitudinal axis of the alveolus of the first molariform is straight and does not curve, as is the case with the second and third molariforms in most megalonychids.

The second molariform is more trapezoidal in cross-section, with the long axis of the tooth at nearly a right angle to the long axis of the palate. The labial side of the alveolus is shorter than the lingual. This is the largest tooth.

The alveolus for the third molariform is slightly smaller than the second. It is more rectangular in outline, with the long axis at a right angle to the midline of the palate. The lingual and labial sides are subequal in length and shorter than the mesial and distal sides, which are also subequal in length.

The palate is broken just posterior to the anterior margin of the alveolus for the fourth molariform. The labiolingual width of the mesial margin is about the same as that of the third molariform.

Mandible

The mandible is complete, with both sides preserved and missing only the dorsal portion of the left coronoid process (Fig. 5). The dorsal margin of the right coronoid was broken, but the fragments have been reattached, enabling measurements and observation of morphology. The caniniforms are fragmented, so only the bases are preserved. Molariforms on the right side are complete, whereas only the first and second are complete on the left. The occlusal surface of the third is fragmented, but the tooth remains intact below the alveolar margin (Fig. 5C, D).

The spout is triangular and short (Fig. 5C), and most closely resembles that of *Megalonyx*. There is a single mental foramen on either side of the base of the spout, oriented so that it opens dorsoanteriorly. The dorsal surface is excavated to form a small trough that extends posteriorly to the posterior margin of the mandibular symphysis. The anterior midline of the symphysis has no keel. The posterior margin of the mandibular symphysis is at the anterior margin of the lower first molariform.

The base of the horizontal ramus is uniformly convex below the molariform series and starts to slope dorsally at the base of the lower first molariform. The horizontal ramus is dorsoventrally deep relative to the size of the mandible. The hypsodonty index (HI) of the mandible for sloths is standardized as depth of the mandible measured at the level of the third molariform tooth, divided by length of the molariform toothrow (Bargo et al., 2006). This value is 1.13 in *Nohochichak* and is similar to that of *Meizonyx*, with a value of 1.12. Fields (2009) reported a mean value of 1.05 for *Megalonyx*.

The diastema is short with a thickened dorsal margin. It occupies 24% of the length from the mesial margin of the caniniform to the distal margin of the lower third molariform. This is similar to *Meizonyx* (29%), *Megalonyx jeffersonii* (23–39% n = 12), and the Caribbean megalonychids (*Neocnus* 29–35%, n = 3; *Acratocnus* 25–32%, n = 4; and *Parocnus* 34%, n = 1). *Ahytherium* has the shortest diastema among Pleistocene megalonychids (10–12%, n = 2).

The coronoid process is low and broad with a rounded dorsal edge. This is unlike *Megalonyx* (Leidy, 1855), *Meizonyx* (Webb and Perrigo, 1985), and *Australonyx* (De Iuliis et al., 2016) in which the coronoid process tapers dorsally to a point (De Iuliis et al., 2016). In *Nohochichak*, the dorsal edge of the coronoid process is only barely above the condyle. In *Meizonyx*, the coronoid process is narrower and more asymmetrical, with the anterior margin inclined more than the posterior margin. It, too, has a rounded dorsal edge, and as in *Nohochichak* the dorsal margin of the coronoid process is at the same level as the condyle.

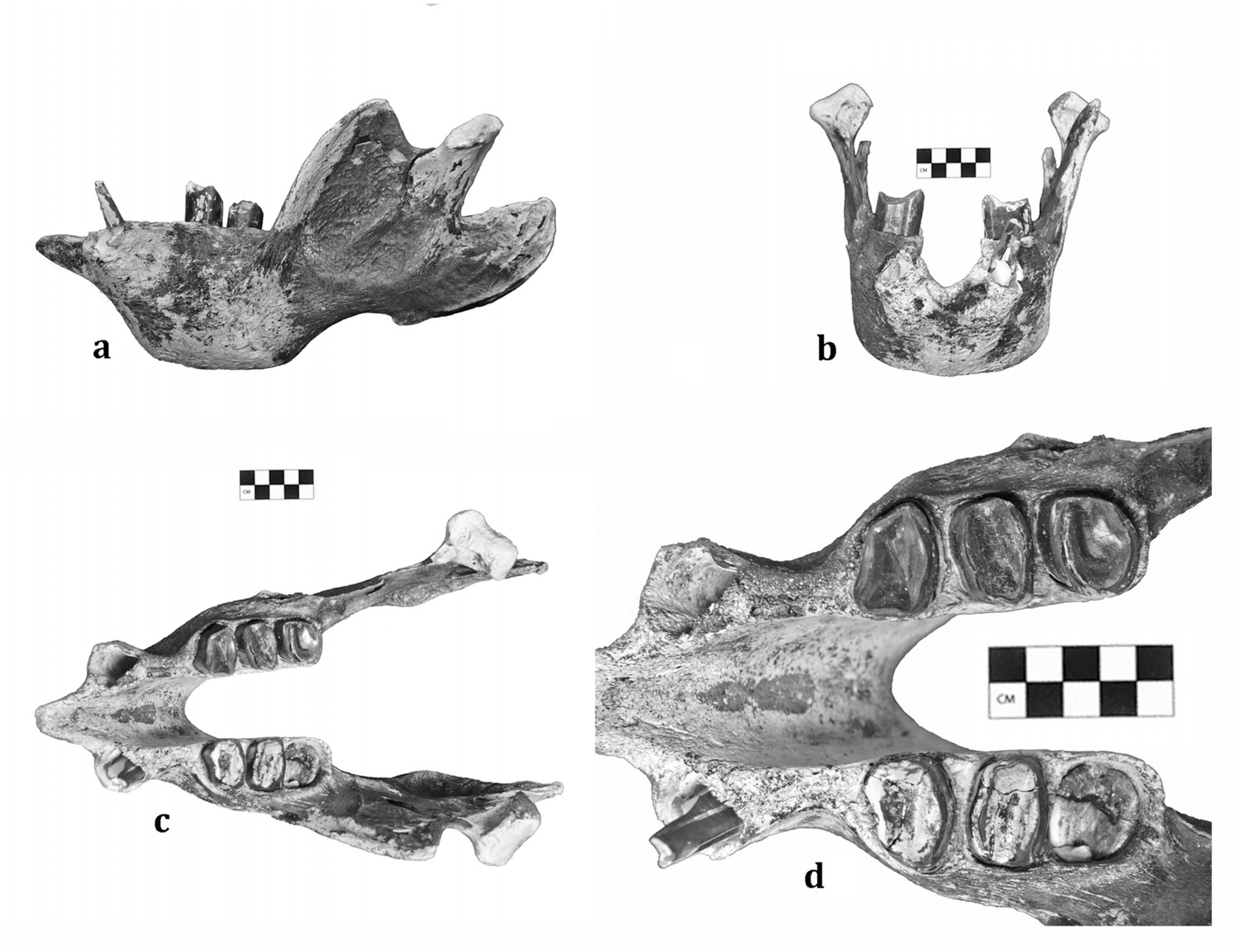

FIGURE 5. *Nohochichak xibalbahkah*, gen. et sp. nov., mandible INAH DP5832 in **A**, left lateral view; **B**, anterior view; **C**, occlusal view; and **D**, close-up of dentition.

TABLE 1. Measurements (in mm) of the rostrum of *Nohochichak xibalbachkah*, gen. et. sp. nov. (INAH DP5832).

Dimension	Measurement (mm)
Length of rostrum anterior to the base of the zygomatic arch	78.3
Width across upper caniniforms	~89.8
Width across upper first molariforms	93.8
Width across upper second molariforms	101.6
Width across upper third molariforms	96.5
Length of palate (to break at anterior margin of upper fourth molariform)	~156
Length of diastema (posterior margin of caniniform to anterior margin of first molariform)	87.6
Width of diastema	58.9
Height of anterior end of rostrum	80.8
Height of anterior narial opening	55.6
Width of anterior narial opening	74.5
Width across base of rostrum	110.1
Width across infraorbital foramina	104.9
Length of nasals	100.2
Labiolingual width of alveolus of caniniform	~14.8
Mesiodistal length of alveolus of caniniform	19.3
Labiolingual width of alveolus of upper first molariform, mesial margin	22.4
Labiolingual width of alveolus of upper first molariform, distal margin	24.1
Mesiodistal length of alveolus of upper first molariform	22.7
Labiolingual width of the alveolus of the upper second molariform	32.3
Mesiodistal length of the alveolus of the upper second molariform	21.0
Labiolingual width of the alveolus of the upper third molariform	28.0
Mesiodistal length of the alveolus of the upper third molariform	18.5

TABLE 2. Measurements (in mm) of the mandible of *Nohochichak xibalbachkah*, gen. et. sp. nov. (INAH DP5832).

Dimension	Measurement (mm)
Length from the anterior margin of the spout to the posterior margin of the angular process	316.7
Length from the anterior margin of the caniniform to the posterior margin of the angular process	283.1
Length from the anterior margin of spout to posterior margin of condyle	294
Length from anterior margin of caniniform to posterior margin of lower fourth molariform	131.8
Length of spout	45.8
Length of diastema from posterior margin of caniniform to anterior margin of lower first molariform	31.3
Mediolateral width of diastema	12.6
Width across lower caniniforms	65.1
Width across both diastema	65.1
Length of mandibular symphysis	111.6
Height of mandibular symphysis	98.6
Length of molariform tooth row	77.9
Depth of mandible below the lower first molariform	91.5
Depth of mandible below the lower third molariform	87.7
Height of coronoid process	124.4
Depth of angular process	54.3
Caniniform mesiodistal length	26.7
Caniniform labiolingual width	25.8
Lower first molariform mesiodistal length	20.5
Lower first molariform labiolingual width	29.3
Lower second molariform mesiodistal length	20.6
Lower second molariform labiolingual width	30.2
Lower third molariform mesiodistal length	28.7
Lower third molariform labiolingual width	26.7

The posterior external opening of the mandibular canal in *Nohochichak* is located on the medial side of the base of the coronoid process, whereas in *Meizonyx* this large foramen opens laterally at the base of the coronoid process (Webb and Perrigo, 1985) and in *Megalonyx* it is positioned on the horizontal ramus anterior and ventral to the base of the coronoid process.

The mandibular foramen in *Nohochichak* is located midway between the lower third molariform and the condyle. The lateral side of the coronoid process has a large fossa that extends ventrally to the notch between the condylar and angular processes. This fossa is divided by a low oblique crest that extends anteroventrally to posterodorsally and terminates at the notch between the coronoid and condyloid processes. Based on Naples (1987: fig. 5-I), the dorsal fossa would have served as the site of insertion for the zygomaticomandibularis muscle, whereas the ventral fossa would have accommodated the insertion of the deep masseter.

The long axis of the mandibular condyle is at an angle to the long axis of the mandible and is oriented anterolaterally to posteromedially in dorsal view (Fig. 3). There is a large rugose fossa on the anterior margin of the condyle. The articular surface of the condyle slopes laterally so that the medial margin is more dorsal. The condyle is divided into medial and lateral facets. The medial facet occupies about one-third of the condyle and lies at a slight angle to the lateral facet.

The angular process is well developed and with a large fossa on the medial side for the insertion of the medial pterygoid muscle. The lateral side has two prominent ridges oriented at an oblique angle, paralleling the posteroventral edge of the process.

Mandibular Dentition

The lower caniniform is trianguloid, having a distally positioned apex and rounded vertices (Fig. 6). The axis of the tooth is inclined at about a 45° angle relative to the long axis of the molariforms and parallels the ventral margin of the anterior mandibular body. Because of this angle, occlusion with the upper caniniform produced an occlusal surface at an oblique angle to the axis of the tooth on the mesial side of the lower caniniform. As with the skull, the caniniform is in the same parasagittal plane as the molariforms.

FIGURE 6. *Nohochichak xibalbahkah*, gen. et sp. nov. (INAH DP5832). Close-up of base of right lower caniniform. Anterior is to the right and medial is up. Base of tooth that surrounds pulp cavity still present in the alveolus.

The lower first molariform is trapezoidal in outline, with the mesial edge narrower than the distal. The labial edge of the tooth is shorter than the lingual. Occlusion has produced ‘cusps’ on the mesiolingual and distolabial corners of the tooth. The second and third molariforms are about equal in size and slightly larger than the first, respectively.

The lower second molariform is rectangular, with rounded corners. The lingual side is shorter than the labial and has a low crest, whereas the excavated middle of the occlusal surface opens on the lingual side.

The lower third molariform is rounded and equidimensional mesiodistally and labiolingually. The center of the tooth is excavated and lower than the edges and opens lingually. There is a single raised ‘cusp’ on the mesiolingual corner of the tooth.

PHYLOGENETIC ANALYSIS

Methods

An analysis of the phylogenetic position of *Nohochichak* was conducted using PAUP (version 4.0a150 for Macintosh; Swofford, 2002). The analysis was based largely on that of McDonald et al. (2013), but because the new taxon is represented by both the skull proper and mandible (in contrast to *Megistonyx*, the subject of the McDonald et al., 2013, study), 26 mandibular characters were added from Gaudin (2004) and scored in the taxa from McDonald et al. (2013), where possible (the mandible is unknown in *Megistonyx*, as just noted, as well as in *Megalonychotherium* and *Pliomorphus*; Scott, 1903–1904; Kraglievich, 1923; Gaudin, 2004). These new mandibular characters are described in Appendix 2, because in many instances the characters had to be modified from their original versions. Because of the presence of mandibular characters, it was possible to include the Central American taxon *Meizonyx* in the phylogeny. *Meizonyx* was discovered in El Salvador and is known from a single, isolated left mandible (Webb and Perrigo, 1985).

A total of 80 cranial and mandibular features were scored via direct observations of the specimens listed in Gaudin (2004), McDonald et al. (2013), and Appendix 1. A data matrix was generated for the 15 taxa included in this study (13 taxa from McDonald et al., 2013, plus *Nohochichak* and *Meizonyx*; Appendix 3). Analyses were conducted using PAUP’s branch and bound option to ensure that a globally parsimonious solution would be obtained. Characters were optimized using PAUP’s DELTRAN option in all analyses (see Gaudin, 1995, for justification), and all character-state changes were weighted equally. Characters were polarized via comparison with a single monophyletic outgroup, *Hapalops*, an early, relatively plesiomorphic megatherioid sloth (following Gaudin, 1995, 2004; Carlini and Scillato-Yané, 2004; Pujos et al., 2007; McDonald et al., 2013). Any intraspecific variation was treated as polymorphic in the PAUP analyses. Of the 80 characters, 32 were multistate, and 22 of these were ordered along numerical, positional, or structural morphoclines (Appendix 2). Several characters proved to be parsimony uninformative in the final analyses, but all values reported for consistency index exclude uninformative characters. A bootstrap analysis (random-addition sequence, 1000 bootstrap replicates) was also used to evaluate the relative support for various groupings (Hillis and Bull, 1993), and Bremer support was calculated for each node following the procedure outlined in Gaudin (2004). The PAUP settings for the bootstrap and Bremer support analysis were identical to those described above.

Results

The PAUP analysis yielded three most parsimonious trees (MPTs; tree length [TL] = 303, consistency index [CI] = 0.563, retention index [RI] = 0.496). The topologies of these trees differ only in their positioning of *Pliomorphus* from the Pliocene of South America, and their arrangement of the extant two-toed sloth *Choloepus* and two small-bodied extinct Antillean genera, *Neocnus* and *Acratocnus*. Regarding the former, two of three MPTs place *Pliomorphus* as the sister taxon to a large clade including subclades from Central America, the South American Pleistocene, and the Pleistocene/Holocene of the West Indies plus the extant *Choloepus*. The third MPT moves *Pliomorphus* within this large clade, as the sister taxon to only the subclade containing the West Indian taxa plus *Choloepus*. Just as in McDonald et al. (2013), two of three MPTs result in a monophyletic Choloepodinae (sensu White and MacPhee, 2001) in the present study, with *Neocnus* as the sister taxon to *Choloepus* and *Acratocnus*. In the third MPT, *Choloepus, Acratocnus*, and *Neocnus* form successive sister taxa to a pair of extinct, large-bodied extinct Antillean taxa, *Parocnus* and *Megalocnus* (= Megalocninae of White and MacPhee, 2001), again as in McDonald et al. (2013). The tree shown in Figure 7 (majority rule consensus tree) is both a 67% majority rule consensus tree and one of the three MPTs resulting from the present phylogenetic analysis. An

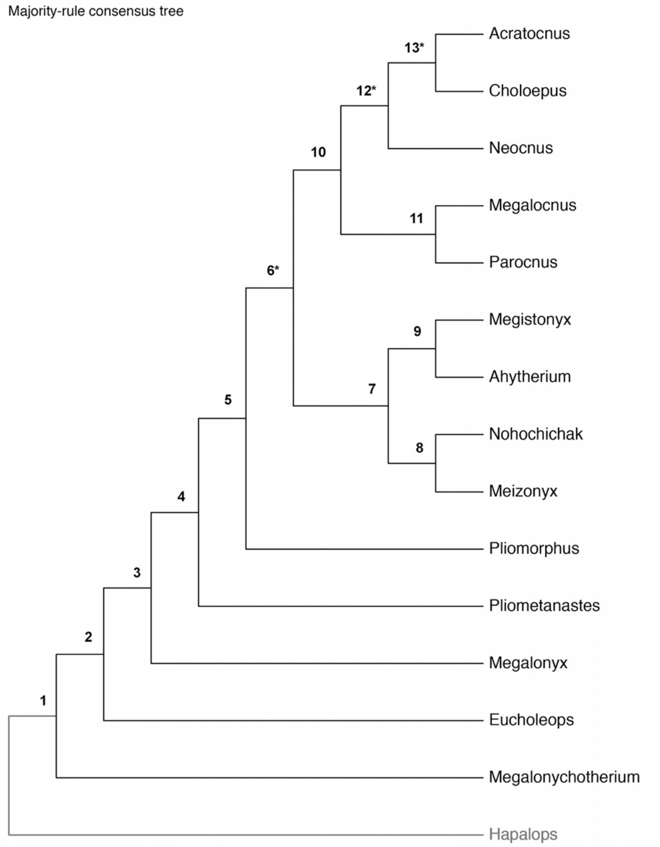

FIGURE 7. One of three most parsimonious majority rule consensus trees (MPTs; TL = 305, CI = 0.566, RI = 0.496) resulting from a phylogenetic analysis of the sloth family Megalonychidae, to assess the position of the new taxon *Nohochichak xibalbahkah*. Nodes marked with an asterisk (*) are those that do not appear in the strict consensus tree. Results based on PAUP analysis of 80 cranial features in 14 ingroup taxa, including 11 extinct sloths and the extant two-toed sloth *Choloepus*. Characters are polarized via comparison with a single monophyletic outgroup, the early Miocene megatherioid sloth *Hapalops*. This tree also represents a 67% majority rule consensus tree of the three MPTs resulting from the same analysis. A list of apomorphies for each of the numbered nodes is provided in Appendix 4. Data drawn mostly from McDonald et al. (2013) and Gaudin (2004).

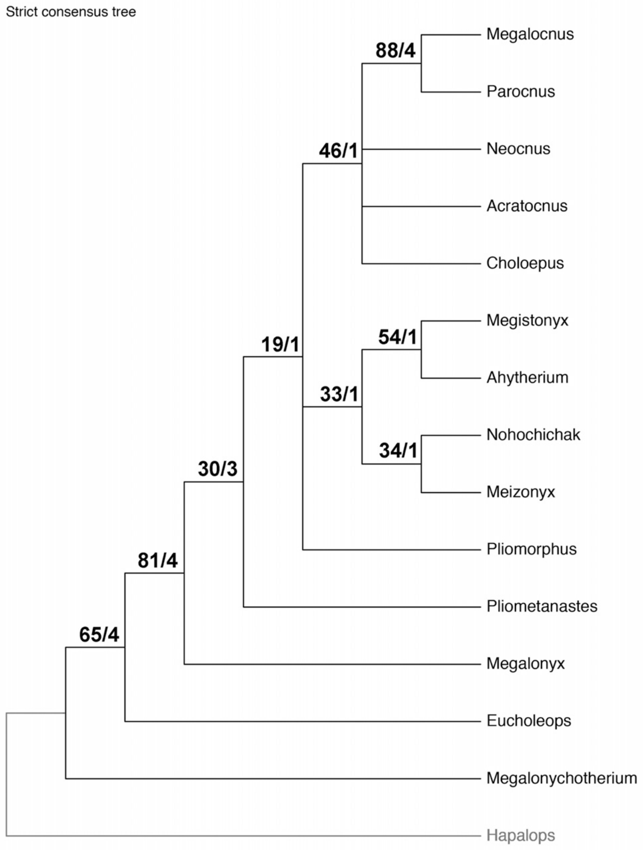

FIGURE 8. Strict consensus tree of the three MPTs produced by the phylogenetic analysis of the sloth family Megalonychidae, to assess the position of the new taxon *Nohochichak xibalbahkah*. The tree is based on PAUP analysis of 80 cranial and mandibular features in 14 ingroup taxa, including 13 extinct sloths and the extant two-toed sloth *Choloepus*. The first number associated with each node represents a bootstrap value, the second a Bremer support value. The calculation of these values is described in the Phylogenetic Analysis section. Data drawn mostly from McDonald et al. (2013) and Gaudin (2004).

apomorphy list for each node in this tree is provided in Appendix 4. A strict consensus tree (Fig. 8) was also generated for the three MPTs, following the methods of McDonald et al. (2013). It is not completely resolved, in contrast to the tree illustrated in Figure 7, but, as McDonald et al. (2013) note, this makes it a more conservative, and therefore probably more reliable, assessment of megalonychid phylogeny, and the position of *Nohochichak*.

DISCUSSION

Given the similarity of the results of the present study to those of McDonald et al. (2013), this discussion will focus on those aspects of the consensus tree (Fig. 7) that differ from the consensus tree of McDonald et al. (2013). The most important result for the purposes of the present study relates to the position of the new taxon described here, *Nohochichak*. It is allied with its fellow Central American form *Meizonyx* into a clade in both the strict and majority rule consensus trees (Figs. 7, 8). This clade in turn forms a sister taxon to a second clade, composed of two taxa from the late Pleistocene of northern South America, *Megistonyx* and *Ahytherium*. The clade that includes these four taxa, although present in both the strict consensus and majority rule consensus trees, receives only weak bootstrap and Bremer support, although it is diagnosed by five unambiguous synapomorphies and two more ambiguous features (see Appendix 4). The subclade of *Nohochichak* and *Meizonyx* is even more weakly supported, with low Bremer support and bootstrap values, and only two unambiguous synapomorphies from the lower jaw (Appendix 4; note the skull of *Meizonyx* is unknown). The subclade including *Megistonyx* and *Ahytherium*, which was also recovered in McDonald et al. (2013), receives more robust support in the bootstrap analysis than either of the other two nodes in this grouping. However, its Bremer support is equally low. It is diagnosed by three unambiguous and three ambiguous synapomorphies (Appendix 4), including only two of the synapomorphies (11[2] and 31[1]; only 11 is unambiguous) recognized by McDonald et al. (2013).

In McDonald et al. (2013), the extinct continental North American megalonychid genera *Pliometanastes* and *Megalonyx* are united to the *Megistonyx/Ahytherium* clade in the strict consensus tree and form a clade with one another in the majority rule consensus tree. Neither of these patterns is recovered in the present analysis. Instead, *Pliometanastes* and *Megalonyx* are progressively more basal taxa (with the younger *Megalonyx* basal to *Pliometanastes*) within the clade including all late Miocene to Recent megalonychids. The present analysis does not recognize the characters uniting the two North American forms in McDonald et al. (2013: characters 18[1] and 47[0]) as being synapomorphies or even derived convergences between the two, nor does it identify other derived convergences among their optimized autapomorphies. The clade uniting *Pliometanastes* to the crown clade, to the exclusion of *Megalonyx*, receives only weak bootstrap support but has a relatively robust Bremer support of 3 (Fig. 7) and is diagnosed by five unambiguous synapomorphies, all derived from the mandibular characters added to the present study (Appendix 4).

The final difference between the results of the present study and those of McDonald et al. (2013) relates to the affinities of a megalonychid from the late Miocene of Argentina, *Pliomorphus*. In the strict consensus tree of McDonald et al. (2013), *Pliomorphus* is the sister taxon to a clade including all the Antillean megalonychids plus the extant megalonychid *Choloepus*. In the results of the present study, the position of *Pliomorphus* is unresolved in the strict consensus tree (Fig. 6). In one of the MPTs, it occupies the same phylogenetic position as it does in McDonald et al. (2013). However, in our majority rule consensus tree (Fig. 7), it is the sister taxon to a larger clade, including not just the Antillean forms and *Choloepus*, but also the Central and South American clade that includes *Nohochichak*. The node linking *Pliomorphus* to the larger clade is the weakest node on the entire consensus tree, with a bootstrap value of 19 and a Bremer support of 1. It is diagnosed by three unambiguous and three ambiguous synapomorphies (Appendix 4).

Paleobiogeography

McDonald (2005) noted that of all the mammalian lineages of South American origin that entered North America during the Great American Biotic Interchange (GABI), the sloths were the most successful in terms of taxonomic diversity. The recognition of this new genus and species from Mexico increases our knowledge of that overall diversity. The discovery of this new sloth requires a reexamination of McDonald's (2005) observation that at any one time, there appeared to be only one representative of each of the major groups of sloths: megalonychid, nothrothere, megathere, and mylodont, in North America. This observation was biased by the very robust fossil record of xenarthrans from the temperate region of North America, primarily the United States and northern Mexico, in marked contrast to the smaller number of late Cenozoic localities and studies of the fauna from the tropical portion of southern Mexico and Central America (McDonald and Naples, 2008).

Building on the description of *Meizonyx salvadorensis* from the middle Pleistocene of El Salvador by Webb and Perrigo (1985), the recognition of a second genus of megalonychid sloth, *Nohochichak*, in the late Pleistocene clearly demonstrates that the taxonomic diversity of fossil sloths (and very likely additional xenarthrans as well as other groups of South American origin) in the tropical portions of North and Central America is much greater than previously thought. What is interesting is that the diversity is not just at the family level but also occurs at a lower taxonomic level. With the recovery of *Nohochichak* as the sister taxon to *Meizonyx*, and these two genera forming a sister group to the South American taxa *Megistonyx* and *Ahytherium*, we have indications of a second dispersal event north by a South American group of megalonychids. This dispersal represents a distinct clade from the previously known *Pliometanastes-Megalonyx* clade and the clade of Caribbean sloths (McDonald et al., 2013). Whereas the *Pliometanastes-Megalonyx* clade dispersed into more temperate latitudes, the *Nohochichak-Meizonyx* clade appears to be restricted to tropical Central/North America, just as the *Megistonyx-Ahytherium* clade in South America represents a clade confined to tropical habitat. It is possible that the lineage that includes *Meizonyx* and *Nohochichak* then secondarily dispersed back to South America to give rise to *Ahytherium*, but a more robust record is needed to resolve this issue.

This should not be unexpected, given that the greatest taxonomic diversity of extant xenarthrans outside of South America today is in semitropical to tropical Central America and southern Mexico and includes three species of anteaters (*Myrmecophaga tridactyla, Tamandua mexicana*, and *Cyclopes didactylus*), two species of armadillos (*Cabassous centralis* and *Dasypus novemcinctus*—the only taxon with a range that extends into the southern United States), and two species of sloths (*Bradypus variegatus* and *Choloepus hoffmanni*)—the 'camp followers' of McDonald (2005). As discussed by McDonald (2005), the variety of habitats in North America acted as 'nest sieves' that restricted the northern dispersal of xenarthrans. It is clear that the majority of taxa dispersing out of South America were adapted to tropical habitats and hence restricted in how far north their range could extend. Whereas only a small subset, as represented by *Pliometanastes* and *Megalonyx*, was able to disperse into more northern temperate environments for geologically extended periods of time, fluctuating climatic conditions through the Pliocene and Pleistocene did permit some short-term northerly range expansions of other xenarthrans. An example is the giant anteater, *Myrmecophaga tridactyla*, from the middle Pleistocene (Irvingtonian) El Golfo fauna (Shaw and McDonald, 1987). *Nohochichak* and *Meizonyx*, in contrast, are restricted to the tropics and were limited in their northward dispersal by the distribution of this type of habitat.

Megalonychids are generally considered browsers, having a close association with forest habitat, and the presence of *Nohochichak* fits that general pattern. This habitat preference may explain what has been, until fairly recently, the relative rarity of late Pleistocene records of megalonychids, with the exception of *Megalonyx* in North America and the Caribbean megalonychid sloths. Like *Nohochichak, Meizonyx* is currently known only from tropical Central America, and the other three late Pleistocene megalonychids, *Ahytherium aureum* (Cartelle et al., 2008), *Australonyx aquae* (De Iuliis et al., 2009), and *Megistonyx oreobios* (McDonald et al., 2013), are all in areas within what is now tropical South America, between 13°S and 10°N latitudes. As noted by De Iuliis et al. (2009), whereas the region around Poço Azul, Bahia, Brazil (where both *Ahytherium* and *Australonyx* were found), is currently within the Caatinga biome (xeric shrubland and thorn forest), during the final stages of the Pleistocene, the habitat in this area was a mosaic of the Atlantic Forest and Savanna biomes. Except for *Meizonyx, Nohochichak* and these other taxa were recovered from limestone caves, which contributed to their preservation in an environment that is otherwise not conducive to fossilization.

CONCLUSIONS

Previous analyses of the diversity of taxa participating in the GABI have tended to focus on taxa associated with savanna habitats (Webb, 1978). The relative lack of fossil sites within tropical North and Central America as well as South America has limited our knowledge of the diversity of taxa that participated in the Interchange, but whose ecology limited them to tropical or forested habitats. Generally, tropical habitats do not favor the preservation of organic remains, thus biasing our knowledge regarding a significant component of the vertebrate biota that may have participated in the GABI. Caves such as the Sac Actun system (of which Hoyo Negro is a part) can be an exception and provide the opportunity for the preservation of fossil vertebrates in tropical habitats.

The recovery of a new genus of ground sloth, *Nohochichak xibalbahkah*, from Hoyo Negro provides a significant addition to our knowledge of the diversity of xenarthrans that dispersed northward out of South America. Its close relationship with another Central American sloth, *Meizonyx*, and the fact that these two genera are more closely related to a clade formed by the South American genera *Megistonyx* and *Ahytherium* rather than the better known North American genera *Pliometanastes* and *Megalonyx* clearly indicates the existence of multiple separate northward dispersals by members of the Megalonychidae. It was not a single dispersal event with subsequent evolution in North America. What is not currently known is the timing of each of these dispersal events. Because both *Nohochichak* and *Meizonyx* are Pleistocene in age, it is possible that they represent a dispersal event that occurred significantly after the Hemphillian appearance of *Pliometanastes* in North America and, based on current thinking, its evolution into *Megalonyx*. Alternatively, it is possible that the ancestor of *Nohochichak* and *Meizonyx* was part of the same dispersal event as *Pliometanastes*, but, being restricted to the tropics, it simply did not leave as robust a fossil record and its remains have yet to be found.

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APPENDIX 1. List of specimens used and literature consulted to score matrix in phylogenetic analysis, beyond those already used in McDonald et al. (2013) and Gaudin (2004).

Nohochichak: Scored from INAH DP5832
Meizonyx: Scored based on descriptions and illustrations in Webb and Perrigo 1985
Pliometanastes: Lower jaw and teeth scored based on UF 9450, 9480, 9613, 10341, 16161, 16627, 18934, 260560, 260744

APPENDIX 2. List of characters and character states employed in phylogenetic analysis. Characters marked with an (*) are multistate. Those multistate characters that were treated as ordered are so indicated.

(1–54) See McDonald et al. (2013).
(*55) Gaudin, 2004:char. 14.
(*56) c1 cross-sectional shape: ovate (0); trigonal, apex anteriorly (1); meniscoid (2); ovate with posterior bulge (3); trigonal, apex posteriorly (4) [modified from Gaudin, 2004: char. 30].
(*57) m2 cross-sectional shape: ovate (0); rectangular (1); trapezoidal (2) [modified from Gaudin, 2004:char. 34].
(*58) Depth of mandible: shallow, ≤20% of MML (maximum mandibular length) (0); >20%, ≤22.5% of MML (1); >22.5%, ≤25% of MML (2); >25%, ≤27.5% of MML (3); deep, >27.5% of MML (4) [modified from Gaudin, 2004:char. 37]. Ordered.
(*59) Gaudin, 2004:char. 40.
(60) Relative position of processes of ascending ramus of mandible: condylar and angular processes subequal, both posterior to coronoid process (0); angle posterior to condyle posterior to coronoid process (1) [modified from Gaudin, 2004:char. 41].
(*61) Distance between processes of ascending ramus: condyle closer to angle than coronoid (0); three processes equidistant (1); condyle closer to coronoid (2) [modified from Gaudin, 2004:char. 42]. Ordered.
(62) Gaudin, 2004:char. 43.
(63) Gaudin, 2004:char. 44.
(64) Gaudin, 2004:char. 45.
(*65) Shape of coronoid process: elongate and narrow, ratio of maximum height to anteroposterior length measured at midheight >1.25 (0); roughly equilateral, ratio of height to length ≤1.25, >1.0 (1); short and broad, ratio of height to length ≤1.0 (2) [modified from Gaudin, 2004:char. 47]. Ordered.
(66) Shape of angular process: ratio of maximum length to depth measured at midlength <1.25 (0); elongate and narrow, ratio of length to depth ≥1.25 (1) [modified from Gaudin, 2004:char. 48].
(*67) Gaudin, 2004:char. 51. Ordered.
(68) Shape of mandibular condyle in dorsal view: expanded mediolaterally (0); ovate, slightly wider than long (1) [modified from Gaudin, 2004:char. 54].
(*69) Shape of condyle in posterior view: flat (0); evenly convex (1); convex medially, concave laterally (2) [modified from Gaudin, 2004:char. 55].
(*70) Gaudin, 2004:char. 56. Ordered.
(71) Condylar extensions in dorsal view: extends medially and laterally (0); hooks medially (1) [modified from Gaudin, 2004:char. 57].
(72) Condylar articular surface: forms single smoothly confluent surface (0); with distinct, contiguous medial and lateral surfaces (1) [modified from Gaudin, 2004:char. 58].
(73) Gaudin, 2004:char. 60.
(*74) Length of mandibular symphysis: short, <20% of MML (maximum mandibular length) (0); moderate length, ≥20%, < 27% of MML (1); elongated, ≥27% of MML (2) [modified from Gaudin, 2004:char. 62]. Ordered.
(75) Profile of anterior edge of symphysis in lateral view: straight (0); concave (1) [modified from Gaudin, 2004: char. 65].
(76) Symphysial keel: absent (0); present (on spout) (1) [modified from Gaudin, 2004:char. 66].
(77) Gaudin, 2004 char 71.
(78) Orientation of symphysial spout in lateral view: horizontal (0); inclined anterodorsally (1) [modified from Gaudin, 2004:char. 73].
(*79) Gaudin, 2004:char. 75. Ordered.
(80) Mandible with fossa posterior to c1: weakly developed (0); strongly developed (1) [modified from Gaudin, 2004:char. 76].

APPENDIX 3. Data matrix. ‘?’ represents missing data or characters that are inapplicable to a given taxon. ‘†’ indicates an extinct taxon. The following symbols are used to represent character states in polymorphic taxa: a = {0, 1}; b = {1, 2}; c = {2, 3}; d = {0, 2}; e = {0, 1, 2}.

Hapalops†
01001 01100 0a000 0a101 b121a 01?00 ada10 00100 10110 a2110 a0010 01a0a b101a 21012 101ba 11aaa

Eucholeops†
101b0 11100 1210? 01021 1110? 01001 a20a0 10100 ??102 00100 100?1 1120a b1010 2b011 1001a 11aa1

Megalonychotherium†
1?010 11?00 1110? 11020 11001 111?? 12010 10100 ?0?00 12010 000?? ????? ????? ????? ????? ?????

Pliometanastes†
101?0 ?211? ????? 1?12? 11?0? 0?2?? 0b001 20012 10101 00000 001?1 12320 11002 11012 01?21 01001

Pliomorphus†
a0110 1c111 bb000 11021 11210 0?101 02001 21012 10101 12001 0111? ????? ????? ????? ????? ?????

Megalocnus†
21110 12011 0200? 11?01 002?0 20202 01101 21012 ????2 2?001 11111 22420 10002 020d1 01020 00001

Parocnus†
21120 12?11 1a00? ?1?01 10201 20212 01101 21012 ????0 b2000 00101 22320 10002 02021 01021 10001

Neocnus†
b0120 01011 1b001 11021 10211 11b01 aea01 20001 01101 12001 01101 b1221 20012 11022 01020 ?1001

Acratocnus†
10120 1c011 23001 11020 00200 0a212 12001 2a011 0100b 2d001 01101 11421 10012 12022 01020 10101

Megalonyx†
c21b0 12110 03110 11121 01200 00102 02001 2a012 10101 00002 10111 32421 21110 02111 00a10 10001

Megistonyx†
1?110 02110 23111 ?1?11 21211 21200 11011 20112 10??1 ?2012 0110? ????? ????? ????? ????? ?????

Choloepus
10120 10a01 1300a 10000 21200 20210 1a001 21010 01002 01000 01001 10100 00010 01022 01120 001e0

Ahytherium†
10120 02110 23111 11?01 11210 00210 11001 20012 00102 21002 0111? 12311 11??b 120?0 0??21 ??011

Nohochichak†
0010 0202? 110?1 01001 ?121? ?1320 ????? 2???? ????? ????? ???12 41411 11102 11000 01021 00011

Meizonyx†
????? ????? ????? ????? ????? ????? ????? ????? ????? ????? ????0 42411 21002 20110 10100 00011

APPENDIX 4. Apomorphy list for the tree illustrated in Figure 7 (majority rule consensus). Characters marked by an asterisk (*) represent unambiguous synapomorphy at their respective nodes. Symbol <=> indicates polarity of character states is indeterminate and that derived condition cannot be inferred without reference to more distant outgroups not included in analysis. Italics indicate a character with a distribution that differs from that in McDonald et al. (2013).

Hapalops <=> Node 1: 1(0)* <=> 1(1)*, 4(0)* <=> 4(1)*, 5(1)*<=> 5(0)*, 6(0)* <=> 6(1)*, 11(0)* <=> 11(1)*, 13(0)* <=> 13(1)*, 19(0)*<=>19(2)*, 24(1)*<=>24(0)*, 36(0)*<=>36(1)*, 44(1)* <=> 44(0)* [Missing character 18 from McDonald et al. (2013)]
Node 2: 2(0), 3(1)*, 12(2)*, 30(1), 45(1)*, _47(0)*_, 49(0)*, _55(1), 56(1), 58(2), 70(1), 73(0)_
Node 3, Late Miocene–Recent megalonychids: 7(2)*, 9(1)*, 16(1), 34(0), 35(1)*, 36(2)*, 38(0)*, 39(1)*, 40(2)*, 48(0), 53(1)*, _57(2)*, 58(3)*, 59(2)*, 66(1)*, 71(0)*_ [Missing characters 27, 50 from McDonald et al. (2013)]
Node 4: _64(0)*, 65(2)*, 72(1)*, 74(2)*, 76(0)*_
Node 5: _13(0), 18(0), 46(1)*, 47(2)*, 50(1), 52(1)*_
Node 6: _15(1)*, 28(2), 32(1)*, 77(0)_
Node 7: _6(0)*, 19(0), 24(1), 30(0)*, 59(1)*, 70(0)*, 79(1)*_
Node 8, Central American megalonychids _Nohochichak_ and _Meizonyx_: _56(4)*, 58(4)*_
Node 9, South American Pleistocene megalonychids _Megistonyx_ and _Ahytherium_: 11(2)*, _12(3)*, 13(1)*, 14(1)_, 31(1), _50(2)_ [Missing characters 6, 15, 24, 28, 30, 32, 52 from McDonald et al. (2013)]

Node 10, West Indian megalonychids plus *Choloepus*: *8(0), 10(1)*, 22(0)*, *26(1), 62(0)*, 69(2)** [Missing character 28 from McDonald et al. (2013); characters 8 and 26 unambiguous in McDonald et al. (2013)]

Node 11, Megalocninae: 1(2)*, 2(1)*, *19(0)*, 26(2)*, *27(0)*, 30(2)*, 33(1)*, *37(1), 56(2)*, 60(0)*, 66(0)*, 67(2)** [Missing character 32 from McDonald et al. (2013); character 19 unambiguous in McDonald et al. (2013)]

Node 12, Choloepodinae: 4(2), *40(1)*, 41(0)*, 42(1), 54(0), *57(1)*, 64(1)*, 70(2)** [Missing character 15 from McDonald et al. (2013); character 40 ambiguous, character 41 unambiguous in McDonald et al. (2013)]

Node 13, *Acratocnus* and *Choloepus*: 12(3)*, 20(0)*, *29(1)*, 31(1), 43(0)*, *78(1)** [Character 29 unambiguous in McDonald et al. (2013)]