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CENOTES, CAVES, AND SLOTHS: PLEISTOCENE SLOTH DIVERSITY ON THE YUCATAN PENINSULA, MEXICO AND BELIZE

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ABSTRACT

Exploration of both dry and submerged caves in the Yucatan Peninsula by cave divers has revealed a high diversity of Pleistocene giant ground sloths, representing all four families. Researchers working in the caves of Quintana Roo, Mexico, have identified up to five genera of sloths; a sixth genus is known from Belize. Three of the sloths, *Nohochichak xibalbahka*, *Xibalbaonyx oviceps*, and *X. exenferis* (if valid) are endemic to the peninsula. Preliminary dating indicates the genera were not all sympatric, with *Nothrotheriops* and a mylodontid occurring in the north during the last glacial maximum in what was likely an arid habitat, and with *Eremotherium* in forested central Belize. The northern part of the peninsula supported at least two megalonychids in earlier millennia in what was likely a more forested habitat. Better dating of known specimens is needed, along with stable isotope analyses, to clarify the history and ecology of sloths in the Yucatan.

INTRODUCTION

The recovery of fossil vertebrates from caves raises the question as to whether their presence results from a taphonomic process, such as being left by a predator, being carried in by another animal such as a packrat (*Neotoma* sp.), being transported into the cave after death by water, or falling into a natural trap; or from a behavioral process, including use of the cave as a den, shelter, or roost site. In the case of sloths, the strictly arboreal habits of the two living tree sloths, *Bradypus* and *Choloepus*, precludes caves as part of their ecology, so they cannot serve as a modern analog for the presence of fossil sloths in caves. Likewise, the other extant xenarthrans, anteaters, are not known to utilize caves, and while many armadillos burrow, they are also not commonly found in cave environments. In marked contrast, many different taxa of extinct ground sloths are commonly found preserved in caves in South, Central, and North America (McDonald, 2003). The presence of ground sloths in caves includes skeletal and dental material, and in some dry caves in arid environments there are also preserved large numbers of coprolites, suggesting that the cave served as a common latrine for multiple individuals. To date, all examples of ground sloth dung have been recovered from cave sites (Hunt and Lucas, 2018; Spaulding and Martin, 1979). This suggests that, for at least some ground sloths, caves (when available) played a critical role in their ecology. As caves may be present in many different types of habitats over a wide range of latitudes and different elevations, their role in the ecology of different ground sloth species probably varied considerably. Consequently, each association of a ground sloth with a cave needs to be considered on its own merits and context. The reasons for cave utilization in tropical habitats may differ from its purposes in a temperate zone.

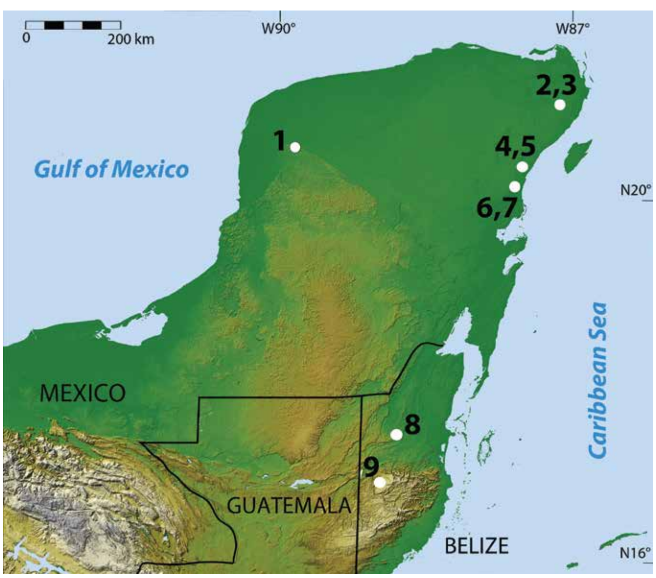

Figure 1. Map of the Yucatan Peninsula showing distribution of caves with sloths listed in Table 2 (white dots). (1) Aktun Spukil. (2) Cenote Zapote. (3) Cenote Tortugas. (4) Sistema Koox Baal. (5) Sistema Sac Actun. (6) Sistema Ox Bel Ha. (7) Sistema Chan Hol. (8) Aktun Lak. (9) Cara Blanca Cenotes.

The recent discovery and description of new taxa of extinct ground sloths from caves in the Yucatan Peninsula (McDonald et al., 2017; Stinnesbeck et al., 2017, 2021) has not only documented the greater diversity of ground sloths along with other Pleistocene taxa (Schubert et al., 2019) in the northern Neotropics, but also raises questions as to how the ecology of Central American ground sloths differed from that of their closest relatives living in more temperate envi-

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ronments. Part of this question revolves around their presence in caves in tropical environments and whether the role played by caves in their natural history was similar to or different from that of ground sloths that lived in in more-temperate environments. For simplicity, all subsequent references to sloths pertain to ground sloths alone.

OVERVIEW OF SLOTHS FROM CAVES IN THE YUCATAN

Knowledge about the fossil record of the tropics is extremely limited, reflecting the high rate of decomposition of organic matter and general rarity of conditions that contribute to its preservation as fossils. One of the primary exceptions to this pattern occurs in tropical karstic regions when vertebrate remains accumulate in caves. An excellent example is the Yucatan Peninsula, which makes up Belize and parts of Guatemala and Mexico (Fig. 1). It is an approximately 181,000 km^2 area of low relief, almost entirely composed of porous limestone. Processes of cave development range from acidic water welling up in a semi-circle around the Chicxulub crater, which outlines the impact of an asteroid at the end of the Cretaceous Period, to primary cave development occurring at the fresh water/saline mixing zone during the elevated sea levels of marine isotope stage (MIS) 5e (Smart et al., 2006). This has resulted in the extensive karst and cave systems seen on the Yucatan Peninsula.

During glacial episodes, as growing ice masses elsewhere confined water on land, the water table of the Yucatan Peninsula was lower. While many of the caves in the Yucatan are flooded, they were air-filled when sea level was lower. Maximum exposure occurred during the last glacial maximum when sea level was 130 m below what it is today (Ludt and Rocha, 2015). This made many of the caves open and accessible to Pleistocene megafauna for most of the last 120,000 years, either as water sources, potential den sites, thermal refugia, or natural traps. With the subsequent decline of the glaciers and rise in sea level, many of these cave systems became flooded (Smart et al., 2006), reaching modern levels by around 5000 cal YBP (Collins et al., 2015). The development of scuba and improvements in technology for cave diving has permitted the exploration of these flooded caves. The discovery of a diversity of Pleistocene fauna has been a welcome byproduct. This includes new species (McDonald et al., 2017; Stinnesbeck et al., 2017, 2021) as well as taxa from South America not previously known to be present in North America (Schubert et al., 2019).

Table 1. Comparison of number of individuals of various taxonomic groups identified from caves in the Yucatan Peninsula documented by PHN and CINDAQ. Remains of humans are not included.

Taxonomic Group	No. of Individuals Identified to at Least the Family Taxon	Total No. of Individuals
Carnivora	36	37
Folivora	17	26
Perissodactyla	11	12
Proboscidea	7	7
Artiodactyla	5	5
Rodentia	2	2
Sirenea	1	1
Reptilia	3	3
Pisces	1	1
TOTAL	83	94

Ongoing exploration of caves and cave systems in the Yucatan consistently results in the discovery of new records of sloths, as well as other Pleistocene taxa. Given the logistical and skill challenges of cave diving and laws regulating fossil recoveries in Mexico, many new finds can only be documented photographically; voucher specimens might not be recovered. Two projects have systematically documented fossil finds within specific cave systems, permitting a quasi-quantitative record of the faunal assemblage. These are Proyecto Arqueológico Subacuatico Hoyo Negro (PHN), a project of the Subdirección de Arqueología Subacuática, Instituto Nacional de Antropología e História (SAS-INAH), and the cave documentation research of El Centro Investigador del Sistema Acuífero de Quintana Roo A.C. (CINDAQ), a non-governmental organization recognized by the 2001 UNESCO Convention on the Protection of Underwater Cultural Heritage. Most of what is reported here comes from those projects, with which we are affiliated and for which we provided some fossil identifications based on scaled, 3D photogrammetric models, and in the case of PHN, collected specimens. Both have addressed caves on the east coast of the peninsula, in the state of Quintana Roo, so most of what is known about ground sloths pertains to that region.

Contexts for these finds of fossil sloths vary considerably. Finds are usually of single, isolated individuals or genera, or of co-mingled, gnawed bones from more than one species found in what appear to be the dens of predatory or scavenging species. However, Hoyo Negro, an intensively studied site containing multiple sloth species, is a natural trap inside the Sac Actun Cave System. At Hoyo Negro, 20 species of medium-to-large mammals have been found, showing no sign of carnivore mediation. Included are the extinct sabertooth cat (*Smilodon fatalis*), a gomphothere (*Cuvieronius tropicus*), a short-faced bear (*Arctotherium wingei),* a canid (*Protocyon trogolodytes*), and sloths from three different families (Chatters et al.,

Figure 2. Photograph of a synsacrum and associated bones of *Nothrotheriops shastensis* partially covered with bat guano at 49 m BSL on the floor of Hoyo Negro, Sac Actun system, Quintana Roo, Mexico. Scale rod is colored in 10 cm intervals.

2014; Schubert et al., 2019). Sloths are represented by the Nothrotheriidae (*Nothrotheriops shastensis*), the Megalonychidae (*Nohochichak xibalbahkah*), cf. *Xibalbaonyx* sp., and the Mylodontidae. Extant species are also well-represented, including puma (*Puma concolor*), ocelot (*Leopardus pardalis*), collared peccary (*Pecari tajacu*), and white-nosed coati (*Nasua narica*).

When logistically feasible and if the discovery is of a rare, unique, or possibly new taxon, time and effort have been expended to obtain permits and recover diagnostic parts of a skeleton or even (on extremely rare occasions) the entire skeleton of an individual. That has been accomplished for Hoyo Negro, where voucher specimens of all taxa have been obtained, and for other cenotes where holotypes of two reported species of *Xibalbaonyx* have been obtained. In other cases, identifications are solely based on photographs or digital models. The list of taxa in Table 1 provides only a preliminary comparison of the relative frequency of the different taxa observed by the systematic work of CINDAQ and PHN. Thus, the accuracy of the identifications is limited depending on the skeletal element(s) observed, the degree of completeness, and the degree of exposure in the cave sediments. In many cases identification may be only to order or family rather than species or even genus. As shown in Table 1, sloths (listed there as Folivora) are more likely to be encountered in cave systems in the eastern Yucatan than any order other than carnivorans, but the record may be biased in two ways. First, many of the small carnivorans were found during the painstaking search of the Hoyo Negro site. They are rarely documented by divers in other settings, where an observer may traverse a passage more swiftly. If these are removed from consideration, sloths become the most common large animals recorded. Conversely, ground sloths are larger and more readily seen than all but the proboscideans and some perissodactyls. This, combined with a unique skeletal anatomy compared to other mammals in their size range, greatly facilitates their identification to at least order.

Table 2. List of caves and cenotes on the Yucatan Peninsula from which sloth remains have been published or documented by PHN and CINDAQ.

Taxon	Cave System or Cenote	No. Individuals	Reference or Project
Eremotherium laurillardi	Cara Blanca, Belize	1+	Larmon et al., 2019
Nothrotheriops shastensis	Aktun Lak, Belize	1	De Iuliis et al., 2015
Nothrotheriops shastensis	Chan Hol, Mexico	1	CINDAQ
Nothrotheriops shastensis	Ox Bel Ha, Mexico	2	CINDAQ
Nothrotheriops shastensis	Sac Aktun, Mexico	3	PHN
Nohochichak xibalbahka[h]a	Sac Aktun, Mexico	2	McDonald et al., 2017; PHN
Xibalbaonyx oviceps[a]	Cenote Zapoté, Mexico	1	Stinnesbeck et al., 2017
Xibalbaonyx exinferis[b]	Cenote Tortugas, Mexico	1	Stinnesbeck et al., 2021
cf. Xibalbaonyx[c]	Koox Baal, Mexico	2	Motyčka et al., 2013; CINDAQ
cf. Xibalbaonyx[c]	Sac Aktun, Mexico	3	PHN, CINDAQ
Miezonyx salvadorensis	Koox Baal, Mexico	1	CINDAQ
Mylodontidae sp.	Ox Bel Ha, Mexico	1	CINDAQ
Mylodontidae sp.	Sac Aktun, Mexico	1	PHN
cf. *Paramylodon*	Aktun Spukil, Mexico	1	Hatt, 1953; Mercer, 1896

a type locality for genus and species.
b type locality for species in existing genus.
c Similar to Xibalbaonyx, but these are adults whereas type specimens of both Xibalbonyx species are juveniles.
PHN: Proyecto Arqueológico Subacuático Hoyo Negro.
CINDAQ: El Centro Investigador del Sistema Aquífero de Quintana Roo A.C.

As well as being the most common group of large mammals identified in the caves in terms of individuals, the ground sloths are the most taxonomically diverse, with multiple genera and species documented to date by CINDAQ, PHN, and in publications (Table 2). Four genera, three of them represented by multiple individuals, have been found in Outland Cave of the Sac Actun system alone. Two skeletons are in the primary, submerged passages about 9–12 m below sea level, and six are in the trap of Hoyo Negro, a 60 m diameter circular collapse chamber that drops to depths up to 50 m below modern sea level (BSL).

Sloths in the shallow tunnels throughout the region usually are represented as articulated, yet often deteriorated, skeletons. In Hoyo Negro, most exhibit patterns indicative of disarticulation through decomposition in water and are in better condition, and lack evidence of carnivore consumption (Chatters et al., 2021). This demonstrates that most of the sloths had entered the caves on their own power, and the remains were not brought in by carnivores. We have, however, seen cases in the Ox Bel Ha and Koox Baal Cave Systems where sloth remains are commingled with those of other species and have marks characteristic of carnivore gnawing. These may have been the dens of carnivores.

Overall, sloth remains from the Yucatan include representatives of four families: Megalonychidae, Nothrotheriidae, Mylodontidae, and Megatheriidae. The megalonychid genus *Xibalbaonyx* and the nothrotheriid *Nothrotheriops* (Fig. 2) are the most common in the number of individuals. Notably, two megalonychid genera, *Nohochichak* and *Xibalbaonyx*, are relatively new to science, with *Nohochichak* (Fig. 3) thus far only known from the Yucatan (McDonald et al., 2017), while *Xibalbaonyx* is known from two species in the Yucatan and a third species from Jalisco, Mexico (Stinnesbeck et al., 2017, 2018, 2021). The megalonychid *Meizonyx*, formerly known only from the Irvingtonian land mammal age of El Salvador, has also been recently found from the terminal Pleistocene of Oaxaca, Mexico (McDonald et al., 2020). One specimen of this genus has also been provisionally recognized by us in a Quintana Roo cave.

Figure 3. Photograph of an articulated forearm of *Nohochichak xibalbahkah* on a wall of Hoyo Negro, 44 m below the water surface. Scale is in centimeters.

Nothrotheriops is best known from dry caves in the southwestern United States, so its presence in the tropics was not expected. *Nothrotheriops* are numerous in Quintana Roo, and there is a single record from a cave in Belize (De Iuliis et al., 2015) indicating that its range extended even farther south into the tropics. Based on recent finds referred to the genus, it may even have ranged as far south as Argentina (Brandoni and Vezzosi, 2019), but to date, the only nothrotheriid known from cave sites in South America, specifically Brazil, is *Nothrotherium* (Pujos, 2001).

A single mylodontid sloth is known from a shallow tunnel of Outland Cave. Although *Paramylodon*, which is well known from other sites in Mexico and the United States, has been previously reported from Actun Spukil, a cave in the northern part of the Yucatan Peninsula, the specimens are not diagnostic (Hatt, 1953; Mercer, 1896). Because a comprehensive study of that material has not been completed, identification of the mylodontid in this region as *Paramylodon* remains unsubstantiated.

McDonald (2002) reported 10 localities in Mexico for the megatheriid *Eremotherium*. Since that review, multiple new finds of this species have been described, increasing the number of localities to 19 (e.g. Gómez-Pérez and Carbot-Chanona, 2012; Carbot-Chanona et al., 2022). *Eremotherium* was a widespread taxon with a range extending north to the Atlantic coast of the United States and south into southern Brazil. Despite its wide distribution, it is primarily found in open terrestrial deposits, and while rarely found in caves, occurs frequently in cenotes or sinkholes over much of its range. During the last glacial maximum (26,000–20,000 years ago) when sea level was at its lowest, there was a concurrent lowering of the water table in the karst bedrock of the Yucatan Peninsula. The resulting reduction of surface water would have made cenotes attractive to wildlife, their depth and open surfaces providing access to the lower water table. Such sites would have also potentially served as traps for larger animals, such as *Eremotherium,* that may have been able to climb down to the water in the cenote but not back out. Currently, the only record of this sloth on the Yucatan Peninsula is from two of the Cara Blanca cenotes in Belize (Larmon et al., 2019). In one of these, remains of multiple individuals of *Eremotherium* are present on a ledge 21 m below the current water level. It is not known if this represents

Table 3. Approximate ages of the four taxa of ground sloth in the Hoyo Negro site, Mexico, and *Eremotherium* from Cara Blanca, Belize. All radiocarbon dates are on bioapatite; uranium-thorium date is from flowstone coating bone and is a minimum age. Estimated ages are computed based on an established reservoir effect, as described in the text.

Taxon	Dating Method	Lab and Specimen No.	Sampled Material	Radiometric Age	Age, cal YBP[a]	Estimated Age	MIS
Nothrotheriops 2	U-Th	UNAMQ-HN	flowstone	23,059 ± 134	23,330–22,790	23.3 YBP	2
Nothrotheriops 1	^{14}C	D-AMS 37546	orthodentin	23,355 ± 99	27,760–27,390	24.5 YBPc	2
Mylodontidae	^{14}C	D-AMS 27870	orthodentin	25,837 ± 112	30,500–29,621	26.9 YBPc	2
Eremotherium[b]	^{14}C	A3712	orthodentin	22,640 ± 120	27,300–26,780	27.0 YBPd	2
Nohochichak	^{14}C	D-AMS 25511	orthodentin	33,871 ± 289	39,030–37,370	34.4 YBPc	3
cf *Xibalbaonyx*	^{14}C	D-AMS 31907	bioapatite	38,386 ± 401	43,090–41,950	42.5 YBPc	3

a Calculated using IntCal 20 (Reimer et al., 2020).
b Larmon et al., 2019.
c Computed as median calibrated age minus 3200 (see text).
d No age correction can be applied.
UNAMQ: Universidad Nacional Autónoma de México, Querétaro campus.
D-AMS: DirectAMS, Inc., Seattle.

a time-averaged sample reflecting multiple entrapment events or a herd situation such as is described from other sites (Lindsey et al. 2020).

Accidental entrapment is also recorded for *Xibalbaonyx oviceps* and *X. exinferis*. The holotypes of both species are from cenotes El Zapote and Tortugas in Quintana Roo, Mexico, with openings on the surface connecting via a vertical chimney to an enlarged bell-shaped chamber (Stinnesbeck et al., 2017, 2021). For example, the diameter of the surface opening of cenote El Zapote is 8.5 to 10 m, and its lower chamber has a diameter of 40 m. The top of the debris cone below the opening is 35 m BSL and the bones of the disarticulated sloth were recovered between 50 m and 55 m BSL. In both cases, the animals likely fell through the opening, and even if they survived the fall, there was no means for climbing out. The type specimens of both species are juveniles as indicated by visible sutures of the skull and lack of fused epiphyses of the long bones.

The only two known specimens of *Nohochichak* were also entrapped in a bell-shaped chamber, albeit one located deep inside Outland Cave. This fate also befell other animals in Hoyo Negro (Chatters et al., 2021), including two Shasta sloths and two of what we infer to be adult members of the genus *Xibalbaonyx*.

DISCUSSION

Currently, five and possibly six genera of ground sloths are known from the Yucatan, giving it a greater diversity of Pleistocene sloths, with representatives of all four families, than any other region in North or Central America. Interestingly, two of the species of sloth found in the Yucatan Peninsula appear (for now) to be endemic to the area. *Meizonyx*, having thus far been found only in Oaxaca and Quintana Roo, appears to be endemic to southern Mexico and perhaps Central America. Two genera of sloths that have a greater distribution are *Nothrotheriops shastensis* and *Eremotherium laurillardi*, with ranges that extend north into the southern United States and south into South America. If the observed mylodontid is indeed *Paramylodon*, it has a similarly large range in North America.

The ecology of the sloth species that thus far appear to be endemic to the Yucatan and adjacent regions currently remains unknown. Out of all the sloths known from the Yucatan, only two genera that have been identified with certainty include species with a wide distribution and are known from multiple other sites outside of the Yucatan Peninsula. This allows some inference about their paleoecology. The two species are *Eremotherium laurillardi*, with a range that extends north into the United States along the Gulf Coast and eastern coastal plain and south into South America and southern Brazil, and *Nothrotheriops shastensis*, which in the late Pleistocene is primarily known from the southwestern United States. In the United States, the distributions of these two taxa are for the most part mutually exclusive in the late Pleistocene with one exception: the Nueces River fauna, Nueces County, Texas (Sagebiel, 2022). This is the eastern extreme of the range of *Nothrotheriops* and the westernmost record of *Eremotherium*. The fauna was recovered from sand-and-gravel, valley-fill deposits, so it is possible that it represents a time-averaged sample. There are no radiometric dates of either of these taxa from the site to confirm they were contemporaries. Likewise, while both genera are known from multiple sites in Mexico, *Eremotherium* by 19 records and *Nothrotheriops* by 10 records, the only locality where both taxa have been reported is Lago de Chapala, Jalisco, Mexico. The faunal remains reported from this site include taxa of Blancan, Irvingtonian, and Rancholabrean land mammal ages (Lucas, 2008), so again, while both taxa were present in the region, they may not have been contemporaries.

Given the significant differences in the ecology of the two sloths, with *Nothrotheriops* found primarily in desert habitat and with *Eremotherium* in subtropical to tropical forest (McDonald, 2021), it seems unlikely that they overlapped and were contemporaries on the Yucatan Peninsula. This is also indicated by the differences in their relative representation in the area, with multiple records of *Nothrotheriops* from cave sites, while *Eremotherium* is known only from two cenotes near the southern-most margin of the Yucatan Peninsula.

Diversity of the sloth fauna reflects the differences in the ecology of the various species, which allowed niche partitioning within the diverse tropical environment. During the late Pleistocene, the ranges of the various species probably shifted in response to changes in the distribution of the vegetation upon which sloths fed, which in turn, was responding to changes in the climate during the Pleistocene.

Precise radiometric dates on bone collagen are generally lacking from sloths and other fossil animals found in the Yucatan, but our ongoing studies in Hoyo Negro indicate some chronological patterning in the taxonomic composition of the local communities. Analysis of paired dates, matching radiocarbon dates on bone bioapatite, and actual ages of three animals from the site determined by both radiocarbon and uranium-thorium analyses indicates an approximately 3,200year reservoir (or diagenesis) effect, rendering the dates older due to dissolved inorganic carbon (Chatters, 2021). That chronological offset is valid for recomputing actual ages from bioapatite dates only for the approximate 23,000- to 10,000-year range from which it was computed and cannot be extrapolated to older materials with confidence. Subtracting that reservoir effect from bioapatite ages of older specimens can, however, provide approximate ages and enable an enhanced ordinal chronology (Table 3).

We can tentatively compare this chronology with the regional climatic record. *Nothrotheriops* and the mylodontid occupied the region later, likely during marine isotope stage (MIS) 2, whereas the megalonychids *Nohochichak* and cf. *Xibalbaonyx* were likely present earlier, apparently during MIS 3. According to Correa-Metrio et al. (2012), temperatures on the Yucatan Peninsula declined from 2.5 °C–3.5 °C below modern levels 84,000 years ago to 4 °C–5 °C below modern at the last glacial maximum. They infer that declining temperatures would have led to depression of the intertropical convergence zone southward, leading to lower cloud cover on the peninsula and hence dryer conditions. Given that *Nothrotheriops* tends to be found in desert environments and mylodontids in grasslands or open savannah (McDonald, 2021; Naples, 1989), it is likely the habitats of the peninsula were more open later in the late Pleistocene. Most megalonychids appear to have been browsers or at least mixed feeders (McDonald, 2022), so the earlier habitat was probably more forested. The *Eremotherium* from Belize dates approximately between the two groups, suggesting that a tropical forest habitat was available farther south in Central America even when more open vegetation appears to have prevailed in the northeastern Peninsula (Colinvaux, 1997). Central America is now highly diverse ecologically (Wallace, 1997; Janson, 2001), so it is possible, even likely, that several distinct, adjacent animal communities occupied the peninsula during different periods as climates changed. Marked fluctuations in the temperature record as well as precipitation during the late Pleistocene could mean sloth fauna frequently adjusted their geography during the time period the animal skeletons were collecting in regional caves.

In contrast to megatheriid and mylodontid sloths that are only infrequently found in caves, the remains of both megalonychid and nothrotheriid sloths are often found in caves and may be represented by multiple individuals, including adults and juveniles (McDonald, 2003). This suggests that when available, caves played an important role in the ecology for sloths in these families. The presence of juveniles of *Nothrotheriops* in Rampart Cave (Arizona) and San Josecito Cave (Nuevo León, México) (Couto, 1974) supports the idea that this species used caves for birthing or as dens to protect young from potential predators. McDonald (2003, 2022) suggested that, given the low basal metabolism and low body temperature of sloths, caves may have served as thermal refugia during seasonal extremes, particularly low temperatures. While seasonal low temperatures may not have been the issue on the Yucatan Peninsula like they would have been in temperate North America, caves could have provided a relatively cooler environment and prevented overheating during warmer seasons. A computer model of the seasonality temperature addressing the time represented by well-dated records of *Nothrotheriops* from dry caves in the United States does suggest caves may have also served as thermal refugia during summer high temperatures (McDonald, 2022).

While the proposed use of caves in temperate zones by sloths may not be fully applicable to explain the presence of sloths in caves in warmer subtropical to tropical zones, there is one distinctive feature of the Yucatan Peninsula during the late Pleistocene to consider, the availability of water. Given the absence of surface water on the karst platform of the Yucatan Peninsula for extended periods during the late Pleistocene, caves and cenotes may have provided the primary access to fresh water for the fauna. Such a scenario certainly can explain the presence of *Nothrotheriops* on the Yucatan Peninsula, given its close association with arid environments elsewhere in its range, but it raises questions about the ecology of other sloths. Based on other evidence, the megalonychids and megatheriids likely preferred habitats in which water was more abundant, or at least more readily available.

CONCLUSION

Over the last 30,000 years of the late Pleistocene, a high diversity of ground sloths utilized the Yucatan Peninsula. Up to six genera dwelled there in the range of plant communities that changed as temperatures and rainfall fluctuated. The preservation of sloth remains in a tropical environment was possible because of the karst systems of the region. During dry episodes and seasons, these animals were dependent on cenotes for fresh water, and sometimes this involved entry into the sinkholes. When water was at its lowest, freshwater would have been more limited and farther below ground level. Thus, the search for water would lead to entry into cave passages and deeper, more dangerous surface cenotes. The ongoing exploration of the flooded cave systems of the Yucatan and recovery and documentation of not only sloths, but also other Pleistocene vertebrates, remains provide a great opportunity for understanding the composition of mammalian communities and their dynamics as climates rapidly changed at the end of the Pleistocene.

When cave divers find animal remains, leave them undisturbed, and report them to the appropriate authorities of INAH, they are providing information of scientific value that ultimately can enable a better understanding of the reasons why ground sloth and other animal remains are often found in caves, whether intentional, accidental, or incidental, and their relative frequency. Once discoveries have been made, two additional steps are necessary: (1) good photography for 3-D modeling to enable preliminary identifications, and (2) authorized collection of specimens so that research can move forward. In demonstrating the presence of this important record, it is our hope that further support will be granted to collect vouchers of important specimens for museums and research. If this can be accomplished, it may ultimately enable us to understand the ecology of these extinct sloths and their contemporaries and reveal clues to the causes of their extinction.

Figure 4. Photograph of a skeleton of a mylodontid sloth in a 9-meter-deep passageway of Outland Cave, Sac Aktun Cave System, Quintana Roo, Mexico. For scale, the radius (white arrow at left) is 26 cm long and 9.5 cm wide.

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