EXOTICS AND ENDEMICS: SLOTHS IN THE NORTH AMERICAN PLEISTOCENE MAMMALIAN FAUNA

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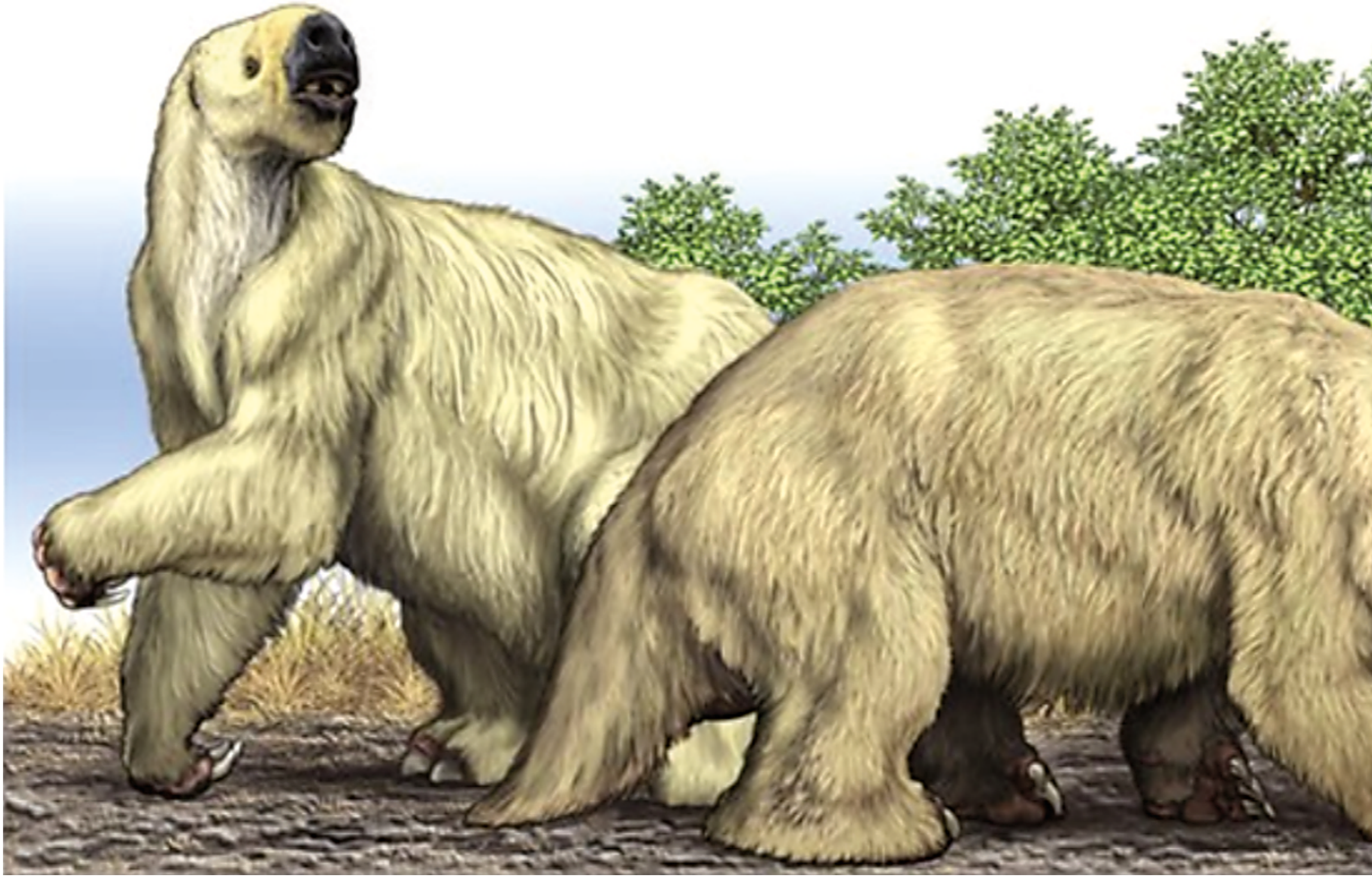
Samenvatting

Luiaards zijn in de Noord-Amerikaanse fauna terechtgekomen nadat ze zich meerdere keren hebben verspreid, van het Laat-Mioceen tot in het Vroeg-Pleistoceen. Elke taxonomische groep paste zich op zijn eigen specifieke manier aan aan de ecologie. Daardoor konden luiaards verschillende habitats in Noord- en Centraal-Amerika bezetten, van de tropen tot aan de grens van de continentale gletsjers. Hun verschijning roept vele fundamentele vragen op over hun invloed op de Noord-Amerikaanse ecologie. Concurreerden ze met inheemse herbivoren om voedsel of waren ze een nieuwe prooi voor inheemse vleeseters? Omdat luiaards op een ander continent met afwijkende ecosystemen zijn geëvolueerd, is het ook mogelijk dat ze simpelweg een lege ecologische niche konden bezetten. Om die vragen te beantwoorden, is chronologie een van de belangrijkste bronnen. Het is cruciaal te weten wanneer een specifieke luiaard voor het eerst op het toneel verschijnt en hoe lang daarna een inheemse soort met een mogelijk gelijkwaardige ecologie uitsterft. Om te begrijpen hoe de taxa die overleefden tot in het Pleistoceen zich hebben aangepast, is het dus essentieel om hun gehele geschiedenis te kennen.



Reconstructions of examples of late Pleistocene North American sloths. From left to right: Megalonyx jeffersonii, Paramylodon harlani, Eremotherium laurillardi *(in back) and* Nothrotheriops shastensis *(in front).*

Reconstructietekening van voorbeelden van laat pleistocene Noord-Amerikaanse luiaarden. Van links naar rechts: Megalonyx jeffersonii, Paramylodon harlani, Eremotherium laurillardi *(achterop) and* Nothrotheriops shastensis *(voorop).*

CARL BUELL

The presence of sloths in the North American fauna resulted from multiple dispersal events from the late Miocene (Hemphillian) into the early Pleistocene (Irvingtonian). Their appearance raises many fundamental questions on their impact on North American ecology, whether competing with native herbivores for food resources or serving as a new addition to the prey base of the native mammalian carnivores. Understanding the ecological success of sloths in North and Central America requires understanding their ecology such as their reproductive capacity compared to the native species, the introduction of diseases or parasites to which the native fauna had no immunity and other ways they may have impacted how the North American ecosystem functioned. Different sloths would have competed with different members of the North American fauna, so one taxon may have competed with the native horses or camels while another may have been in ecological competition with mastodons or mammoths. It is possible that, having evolved on another continent with distinctly different ecosystems, sloths may not have been in competition with the native species but were sufficiently different and simply filled an "empty" ecological niche. Not all sloths that dispersed into North America were giants and each taxon had its own distinctive ecological adaptations that allowed them to utilize different habitats in North and Central America, from the tropics to near the margin of the continental glaciers (McDonald, 2021).

Resolving such questions is only possible using multiple approaches and sources of information. Chronology is perhaps one of the most important sources, as it is critical to know when a particular sloth first appears and how long after its appearance a native species with possibly a similar ecology goes extinct. Equally important is whether the sloth and endemic species overlapped in their distribution or whether they are commonly found together in a fauna, thus indicating potential competition. As different sloths entered North America at different times and lived on the continent for different lengths of time prior to their extinction, each sloth would have experienced different climatic events depending on their distribution in time and space. Consequently, to understand the adaptations of the taxa that survived into the Pleistocene, understanding their entire history from their first appearance is critical.

MEGALONYCHIDAE

Representatives of all four major families of ground sloth, Megalonychidae, Mylodontidae, Megatheriidae, and Nothrotheriidae, dispersed into Central and North America. Megalonychids were the first sloths to enter North America prior to the formation of the Panamanian land bridge (Hirschfeld & Webb, 1968) and they successfully colonized multiple islands in the Caribbean (White & MacPhee, 2001). *Megalonyx* has the longest chronology, first appearing in the late Miocene (Hemphillian) and surviving into the Late Pleistocene (Rancholabrean). There was a significant increase in size from the Hemphillian with an estimated body mass of 185 kg to 1090 kg in *M. jeffersonii* (McDonald, 2005). *Megalonyx* has been considered a browser based on morphology and this is supported by associated vegetation at various sites (Schubert et al. 2004) and by stable isotope analysis (France et al. 2007). It had the widest distribution in North America of any of the late Pleistocene sloths, with a range extending from coast to coast and from the Yukon and Alaska south into central Mexico. Its northernmost records occurred during the Sangamon interglacial (MIS 5) and its range extended to higher elevations, such as the Zeigler Reservoir in Colorado at 2667 m (Miller et al. 2014). These adjustments in latitude and elevation indicate a response to changes in temperature as a controlling factor in its distribution.

The youngest radiocarbon date for *Megalonyx jeffersonii* is 11,235 ± 40 ^{14}C yr BP (13,180–13,034 calibrated years Before Present (cal yr BP)) (McDonald et al. 2015). This date overlaps with the earliest age estimate for the Clovis Culture (Waters & Stafford, 2007). It predates the Younger Dryas Stadial (~ 12.8–11.7 cal ka BP) so there is currently no evidence that its extinction was due to this climatic event.

In contrast to *Megalonyx,* with a primary distribution at northern temperate latitudes during the Pleistocene, the other megalonychids in North America had distributions restricted to lower tropical latitudes. The number of records is limited and reflects the relatively recent discovery of these taxa.

The megalonychid sloth, *Meizonyx salvadorensis*, was first described from a middle Pleistocene deposit in El Salvador (Webb & Perrigo, 1985) and has recently been documented from the Late Pleistocene of Mexico (McDonald et al., 2020). While the genus is only known from these two distant localities, El Salvador at 13.75°N to 18.1°N in southern Mexico indicates the species had both a wide latitudinal and elevational range (ca. 687 meters above sea level (masl) in El Salvador to 1599 masl in Mexico). In Central America and Mexico, vegetation composition changes with elevation resulting in a high diversity of habitats, including thorn scrub, tropical semi-deciduous forest, pine-oak forest, oak forest and cloud forest (Rzedowski, 1978). As these vegetation zones shifted in elevation during the Pleistocene in response to climatic change (Prance, 1982), there would have been similar shifts in the animal's distribution. While *Meizonyx* appears to have had a strictly tropical distribution, its preferred habitat and whether it utilized both tropical dry forest and rainforest or was restricted to one or the other is not known. The bioregion in which it is found in Mexico at 18.1°N places it at the northern edge of the tropics, and today includes tropical moist broadleaf forests, tropical dry broadleaf forests and tropical coniferous forests. At higher elevations in the mountains there are cool-climate montane forests, grasslands and shrublands. The δ ^{13}C stable isotope ratio of 23‰ in *Meizonyx* from Mexico indicates *Meizonyx* was feeding on C3 plants in a reasonably mesic environment.

Recent work using scuba diving gear has provided access to submerged cave systems in the Yucatan Peninsula of Mexico that were accessible during the lower sea levels in the Late Pleistocene. This has resulted in the recovery of a diversity of taxa including multiple sloths (Schubert et al., 2019). Among these is *Nohochichak xibalbahkah* from Hoyo Negro, a chamber in the Sac Actun cave system, Quintana Roo (McDonald et al., 2017). The current cave openings are only about 10 m above sea level, but U-Th dates indicate

Hoyo Negro was largely subaerial and primarily dry above 42 mbsl between 19.0 and 9.5 ka. Currently this monotypic genus is only known from Hoyo Negro and has not yet been identified from any other sites. It may have been limited in its distribution to the tropical lowlands, but this assumption may change with future discoveries. No stable isotope work has been done on this taxon. Leaching of collagen from the bone may limit both stable isotope analysis, as well as obtaining radiocarbon dates.

A second genus of megalonychid sloth from the Yucatan Peninsula is *Xibalbaonyx*. The type species *X. oviceps* is from the Late Pleistocene and was discovered in the Zapote cenote near Puerto Morelos, Quintana Roo (Stinnesbeck et al., 2017). The type specimen is from a juvenile and is large, suggesting that a full-grown adult may have been the largest of the megalonychids in the northern Neotropics. A second species, *Xibalbaonyx exinferis,* was described from cenote Tortugas which is close to the Zapote cenote (Stinnesbeck et al., 2021a). A third species of the genus, *X. microcaninus* was described from Upper Pleistocene sediments of the Zacoalco paleolake in Jalisco, west-central Mexico. Like *Nohochichak*, each species of *Xibalbaonyx* is only known from the type specimen, limiting inferences as to the paleoecology of each species, other than the broader inference of differences between the tropical lowlands of the Yucatán compared to the drier and higher elevations in Jalisco. During the Last Glacial Maximum with sea level approximately 100 m lower, surface water would have been essentially nonexistent on the karst platform of the Yucatán Peninsula (Szabo et al., 1978). Therefore, sloths as well as other taxa would have become concentrated around accessible water sources such as sinkholes or they would have ventured into underground caverns to access water and may have also used them as shelter (Stinnesbeck et al., 2021b). As with *Nohochichak*, no stable isotope work has been done on *Xibalaonyx* that might indicate dietary or habitat preferences.

MYLODONTIDAE

The earliest record of a mylodont sloth in North America is *Thinobadistes* which appears after *Pliometanastes* in the middle Hemphillian (Webb, 1989). The genus is only known from the Hemphillian of North America and did not survive into the Blancan. There is a hiatus between *Thinobadistes* and the next appearance of a mylodont sloth in North America. While *Thinobadistes* dispersed into North America when there was still a water barrier between North and South America, the next appearance of a mylodont sloth in North America ca. 3 mya occurred after the formation of the Panamanian land bridge. Originally referred to as *Glossotherium chapadmalense* from Argentina (Robertson, 1976), the North American Blancan mylodont is now referred to as *Paramylodon garbanii* (Montellano-Ballesteros & Carranza-Castañeda, 1986). The Irvingtonian and Rancholabrean species is *P. harlani*. There is a progressive increase in size of *Paramylodon* from the Blancan (311 kg), through the Irvingtonian (915 kg) to the Rancholabrean (1392 kg) (McDonald, 2005). Starting in the Irvingtonian and continuing into the Rancholabrean, *Paramylodon* was widely distributed in North America from coast to coast and from 48.1°N on the Olympic Peninsula, Washington to 17.6°N in Gruta de Cocona, Teapa, Tabasco, Mexico. The more northern records appear to represent an expansion during the Sangamonian interglacial, as the northernmost records during Wisconsinan are farther to the south. Although mylodont remains are known from Central America they have not been studied in detail, so while possibly from *Paramylodon*, they may be a distinct semitropical to tropical taxon.

Unlike the other major sloth groups in North America, which are browsers, the mylodonts are considered grazers or at least mixed feeders (Stock, 1925; Naples, 1989). Stable isotope analysis of teeth of *Paramylodon harlani*, from the Gulf Coast of Texas (Ingleside fauna) which is Sangamonian interglacial, showed $\delta^{13}C$ values of –4‰. This places its diet within the range expected of mixed feeders, but its carbon isotopic composition is close to that of modern grazers (Ruez, 2005). Coltrain et al. (2004) examined 10 specimens of *Paramylodon* from the late Pleistocene Rancho La Brea fauna and obtained a $\delta^{13}C$ values between –19.99 and –21.49, with an average of –20.99. The $\delta^{15}N$ values for *Paramylodon* from Rancho La Brea ranged from 6.44 to 10.12, with an average 7.93. Two individuals of *Paramylodon* from the Willamette Valley, Oregon at 45.5°N had $\delta^{13}C$ values of –20.8 and –21 and $\delta^{15}N$ values of 7.4 and 6.6 indicating they were feeding primarily on C3 vegetation in an open grassland with sparse canopy (Gilmour et al., 2015). The inferred diet of *P. harlani* from Valsequillo, Mexico, ca. 19°N, based on $\delta^{13}C$ indicated this individual was primarily a grazer (Pérez–Crespo et al., 2014). In contrast, two samples from Térapa, Sonora produced quite different δ^{13}*Paramylodon* from different localities suggests dietary flexibility. It also suggests that *Paramylodon* utilized a variety of different open environments, from grasslands to more wooded areas, but not closed–canopy environments.

Tracks attributed to *Paramylodon* have been found in Nevada in shoreline deposits associated with Pleistocene pluvial lakes (LeConte, 1882). Subsequently, trackways of *Paramylodon* were found in gypsum sediments associated with Lake Otero, another pluvial lake in New Mexico. Along with the sloth and other large mammal tracks, human tracks are also present and indicate the sloth was perhaps being hunted (Bustos et al., 2018). The age of the tracks was originally considered to be between 10 and 15.56 ka BP but radiocarbon dating of seeds beneath the tracks indicated the tracks were between ~23,000 and 21,000 calendar years BP (Bennett et al., 2021). There are very few specimens of *Paramylodon* that have been radiocarbon dated and none of the current dates are close in time to the Pleistocene megafaunal extinct event. Consequently, there are no good estimates when *Paramylodon* went extinct.

MEGATHERIIDAE

The other sloth that entered North America during the Blancan after the formation of the isthmus of Panama is *Eremotherium*, the largest ground sloth. The Blancan species is *E. eomigrans* and it continued into the early Irvingtonian (De Iuliis & Cartelle, 1999) when it was succeeded by *E. laurillardi*. Unlike many other sloth taxa that showed an increase in body mass after entering North America, in *Eremotherium* there is only a slight increase in size; from *E. eo-*

migrans at 2584 kg, to late Irvingtonian *E. laurillardi* at 3149 kg to Rancholabrean *E. laurillardi* at 3961 kg.

Eremotherium laurillardi had the greatest distribution of all sloths, extending from Rio Grande do Sul, Brazil ca. 30.5°S to New Jersey, United States ca. 40.3°N, and has been referred to as the Panamerican ground sloth (Cartelle & De Iuliis, 1995). Despite this extensive range of latitude, its distribution was primarily found in subtropical to tropical environments. Marginal records such as that in New Jersey, which is considered Sangamonian in age, are probably short-term range expansions in response to favorable changes in the climate. McDonald and Lundelius (2009) noted that the youngest records of *E. laurillardi* in the United States are Sangamonian with possibly one record in the earliest Wisconsinan. *Eremotherium laurillardi* therefore appears to have disappeared from the northernmost part of its range long before it became extinct in Mexico or farther south in Brazil. Some of the youngest radiocarbon dates from Brazil include Abismo do Fóssil, São Paulo State ca. 25°S with a date of 12,550 ± 60 ^{14}C yr BP (15,130–14,240 cal yr BP) (Hubbe et al., 2013). The youngest radiocarbon date for *E. laurillardi* is from Itaituba, State of Pará, northern Brazil ca. 4.4°S which dated at 11,340 ^{14}C yr BP (~13,000 cal yr BP) (De Fátima Rossetti et al., 2004).

Most stable isotope analysis for *Eremotherium* has been done on specimens from South America. The one North American specimen was recovered from a cenote in Belize. Stable isotope analysis for carbon and oxygen was done for the entire length of the tooth of an individual from the Last Glacial Maximum (26,975 ± 120 cal yr BP). The average δ^{13}*Eremotherium* likely relied more on C4 or CAM vegetation during the wet season, switching to C3 plants during the dry season. The results from the Belize specimen are supported by data from *Eremotherium*, and *Eremotherium* was a generalist species feeding more on C4 plants (pi = 53%) than C3 plants (pi = 47%).

NOTHROTHERIIDAE

The last sloth to enter North America is *Nothrotheriops*. Originally identified as the South American genus, *Nothrotherium*, it was later determined sufficiently different to be placed in its own genus. It is represented by two species. The first, *N. texanus,* appears in the early Irvingtonian, ca. 1.7 ma. *N. shastensis* appears in the latest Irvingtonian and continues into the Rancholabrean until the Pleistocene extinction event. *Nothrotheriops texanus* is only slightly smaller, 323 kg, than *N. shastensis* at 463 kg.

Nothrotheriops was widely distributed across North America from Florida to California in the Irvingtonian, but in the Rancholabrean its range was restricted to the western United States south into Mexico (McDonald & Jefferson, 2008). Recently *Nothrotheriops* was recovered from a cave in Belize, greatly extending the range southward from the previous record in central Mexico (De Iuliss et al., 2015). Initially only known from North America, the genus has recently been reported from the Late Pleistocene of Argentina (Brandoni & Vezzosi, 2019), raising some interesting questions regarding the evolution and dispersal of the genus.

Many of the late Pleistocene sites with *Nothrotheriops* are caves in the arid southwestern United States, that preserve soft tissue such as hair, skin, and keratin on the unguals. Along with the dried body tissues these caves have also preserved the dried dung of the sloth. Analysis of the dung has provided extensive information on the sloth's diet (Hansen, 1978). Many of the taxa present in the dung are restricted to desert environments such as desert globemallow (*Sphaeralcea ambigua*), Nevada Mormon tea (*Ephedra nevadensis*), saltbushes (*Atriplex* spp.), catclaw acacia (*Acacia greggii*), creosote (*Larrea* sp.) and yucca (*Yucca* spp.). Other plants with wider distributions found in other habitats include common reed (*Phragmites communis*), Utah juniper (*Juniperus utahensis*), cattail (*Typha* sp.), three leaf sumac (*Rhus trilobata*) and gray rabbitbrush *(Ericameria nauseosa* = *Chrysothamnus speciosus*). Similar suites of plants have been identified in the dung of *Nothrotheriops* from Rampart Cave, Arizona (Hansen, 1978), Gypsum Cave, Nevada (Laudermilk & Munz, 1934) and Shelter Cave, New Mexico (Thompson et al., 1980).

While *Nothrotheriops* was clearly the most desert adapted of all the sloths in North America, it also has been found in less arid environments. Examples include Rancho La Brea in southern California which is close to the Pacific Ocean. Hawver, Potter Creek and Samwell Caves, between 39 and 41 °N in northern California are in the foothills of the Sierra Nevada Mountains (McDonald & Jefferson, 2008). Its eclectic diet appears to have permitted *Nothrotheriops* to utilize multiple different habitats.

There are more radiocarbon dates for *Nothrotheriops* than for any of the other North American sloths (Steadman et al. 2005). Most dates are from dung from Rampart Cave, Arizona with very few based on skeletal remains of the sloth. The youngest radiocarbon date for *Nothrotheriops* from a dung sample from Rampart Cave is 10,940 ± 60 ^{14}C yr BP (= 11,023-10,759 cal yr BP).

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