


Article

Late Pleistocene *Paramylodon harlani* (Xenarthra, Mylodontidae) from Térapa, Sonora, Mexico

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Abstract: While the North American mylodont sloth, *Paramylodon harlani*, has been identified in multiple localities in Mexico, most of these records are from the southern part of the country. Consequently, there is a large geographic gap between its distribution in Mexico and the more northern records of the species in the United States. The recovery of the remains of multiple individuals of *Paramylodon harlani*, as part of a late Pleistocene fauna in San Clemente de Térapa, Sonora, Mexico, partially fills this geographic gap and provides a broader understanding of the differences in the species' ecology over a wide latitudinal range. A comparison of the paleoecology of the Térapa site with other sites with *P. harlani* in the fauna to the south and north provides valuable information on how regional topography and different plant communities impact the sloth's distribution and underlying causes for its extinction.

Keywords: *Paramylodon*; late Pleistocene; Mexico; biogeography



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1. Introduction

Mylodont sloths (Xenarthra, Mylodontidae) are a prominent member of the South American mammalian fauna in the Tertiary and Quaternary. Two taxa participated the Great American Biotic Interchange (GABI), entering North America as two separate dispersal events. In the late Miocene (9.00–4.75 Ma; Hemphillian North American Land Mammal Age), *Thinobadistes* entered North America [1,2] and is only known from a few Hemphillian faunas. There was a gap in the records of the family in North America, until a second dispersal event took place in the Blancan LMA (middle Pliocene, 4.75 to 1.80 Ma). Initially considered to be the South American species *Glossotherium chapadmalense* [3], the North American Plio-Pleistocene mylodont is now considered to be a genus distinct from its South American counterpart [4,5]. The North American Blancan mylodont is referred to *Paramylodon garbanii*, while the Pleistocene Irvingtonian NALMA and Rancholabrean NALMA species is *Paramylodon harlani*. See [6] for a review of its nomenclatural history of *P. harlani*.

Knowledge of the early fossil record of *Paramylodon* in Mexico is limited. *Paramylodon garbanii* is known only in the locality of Rancho Viejo, San Miguel de Allende, Guanajuato [7], and the species is restricted to the Blancan. The Irvingtonian record of *Paramylodon* in Mexico is also restricted to a single locality, El Golfo de Santa Clara, Sonora [8]. Consequently, our primary knowledge of *Paramylodon* in Mexico is based on its Rancholabrean record. The most recent review of *Paramylodon* in Mexico by [9] lists 19 records of *P. harlani* from the Rancholabrean and utilized these localities to address the paleoecology and paleobiogeography of the genus in the late Pleistocene. The record of *Paramylodon* from Térapa described here compliments their overview and adds an important record in northern Mexico that fills a geographic gap in its distribution between central and southern Mexico and the extensive record of the species in the United States [9]. The next closest Rancholabrean

The Late Pleistocene sedimentary deposits of Térapa reflect fluvial sediments deposited by the Río Moctezuma and a few side-drainages in a catchment basin formed by an early medial Pleistocene (1.7 million to 300,000-year old) basalt flow within the Moctezuma volcanic field [24,25]. Previously, ref. [13] described the geological context and stratigraphy of the Térapa deposits, and reported a maximum age for the basalt flow, known as the Tonibabi basalt, of 440–130 thousand years. The impoundment created two episodes of a short-lived marsh and open-water environment separated by an intense (possibly rapidly deposited, 3 m thick) overbank flow. Multiple other methods to date sediments on either side of the basalt flow determined that fossil accumulation in the Térapa deposits was short-lived, from 43–40 thousand years ago (Marine Isotope Stage 3; pre-last full glacial) [26].

The strata at Térapa consists of an 11-m-thick sequence of medium grained to fine-grained fossiliferous sediments that overlay and abut the Tonibabi lava flow [14]. The stratigraphy of Térapa is reconstructed from two primary and three secondary sedimentary profiles (Figure 2). The entire sequence of deposition appears in the deepest portion of the basin at the sub-locality Camel Bill (southwestern area of locality). It is already proposed that once the basin was formed by the Tonibabi flow, sediments and fossils began accumulating [14,26]. Rates of sedimentation have yet to be established for this infilling. All the established ages are statistically indistinguishable throughout the section and suggest that complete infilling may have occurred well within 5000 years. Sediments, ostracodes, mollusks, and vertebrate fossils preserved along the Río Moctezuma at Térapa suggest the presence of a wetter and more-tropical riparian corridor around 43–40 thousand years ago during the Late Pleistocene (Rancholabrean). A Rancholabrean age is supported by the presence of *Bison* in the fauna [14]. The inferred paleohabitats include a slow-moving stream, ponded water, marsh, and savanna, or submerged to emergent grassland [14,15]. To this list, ref. [20] added riparian forest as a concurrent habitat type. Stable isotope geochemistry indicates an adjacent woodland or forest and grassland habitat [27]. The Pleistocene fauna from Térapa has been recovered from about 20 fossil sublocalities in an area of approximately 1 by 2 km. The fauna includes taxa associated with both temperate and tropical habitats, as well as extinct taxa such as the sloth, for which the habitat and environmental preferences must be inferred. Among the vertebrate fossils, the remains of a crocodylian, certain birds, and capybaras indicate the more tropical nature of these habitats [14,18,20]. Yet, other members of the paleofauna, such as species of bison, horse, mammoth, and *Camelops*, are more typical of temperate regions and presumed drier grassland or other open habitats farther north in the United States and eastward in northern and central Mexico. These taxa are often found in association with *Paramylodon harlani* [9,28–30]. The Harlan's ground sloth has been recovered from four separate sub-localities (Armadillo, Beto, Camel Bill, and Ramon), each of which represents separate phases of deposition within the basin. In addition to the sloth, two other xenarthrans are present in the Térapa fauna: a glyptodont, *Glyptotherium cylindricum*, and a pampatherium, *Pampatherium cf. mexicanum* [15]. The presence of these two taxa also supports the idea of a mild and moderate climate. Other research groups [25,31–33] have included the Térapa fauna in their reconstruction of the geological and biological changes that occurred in northern Mexico that led to its present-day biota. Based on the presence of two tropical ostracode genera, *Chlamydotheca arcuata* and *Stenocypris* sp., the mean monthly summer temperatures were probably no more than 4 °C to 6 °C cooler than at present [34]. Winter precipitation dominated the hydrologic cycle based on low ostracode $\delta^{18}\text{O}$ values (−6‰ to −8‰ VPDB), while low $\delta^{13}\text{C}$ values (−7‰ to −8‰ VPDB) in the ostracodes suggest that local vegetation was dominated by C3 plants. These values conflict with the tooth enamel-based paleoenvironmental reconstruction at the same site, which favored a summer-dominated or evaporative hydrology and abundant C4 vegetation [27].

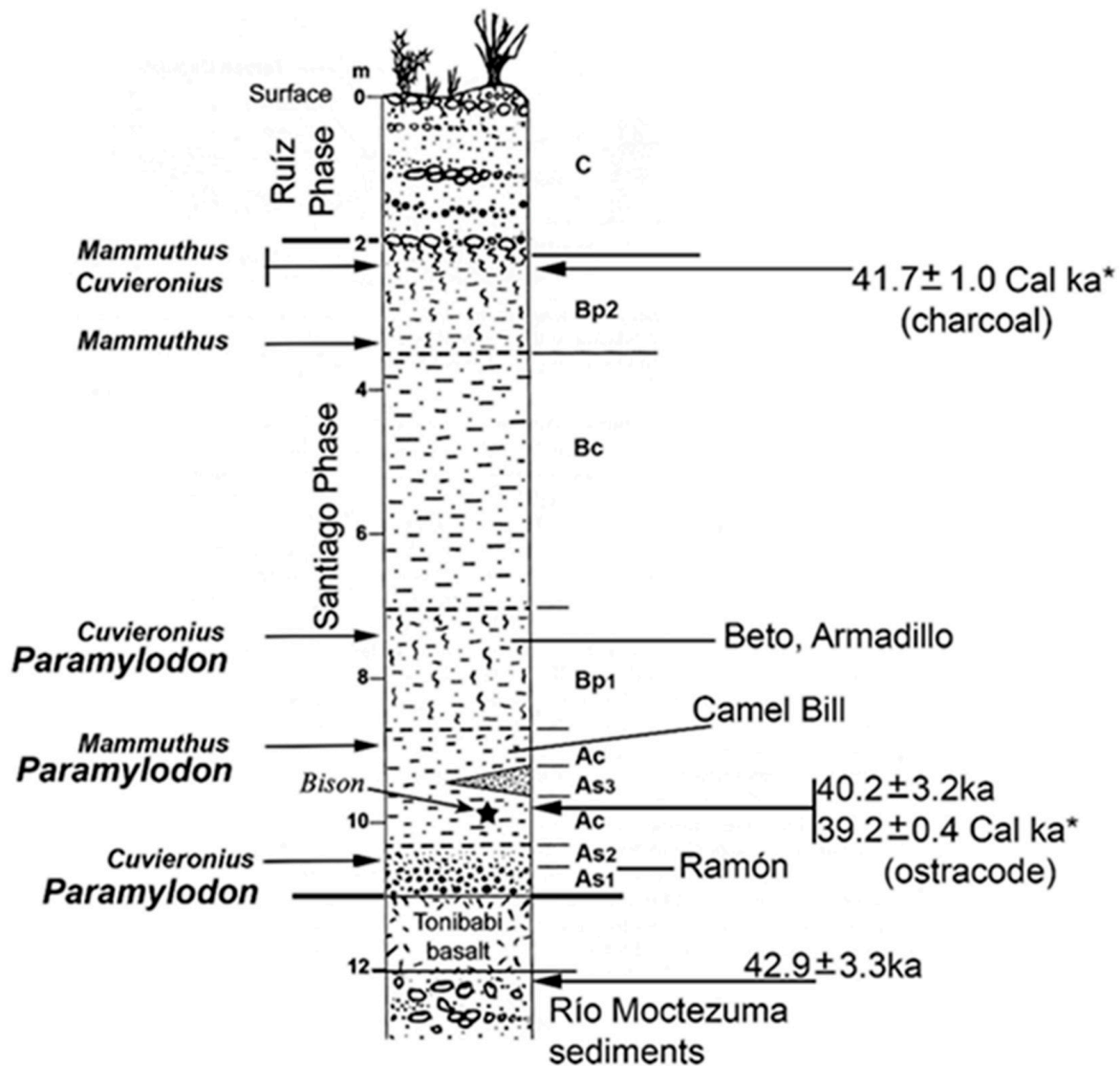


Figure 2. Composite profile of sedimentary deposits at the Térapa local fauna locality, Sonora, México modified from [13]. At base are pre-Tonibabi lava and marsh deposits representing Río Moctezuma fluvial cobbles, gravels, sands, and silts. Chronological analyses using radiocarbon (*, Cal = calibrated date) and infrared stimulated luminescence (see discussion in [25]); years before present. Locations of specimens of *Paramylodon harlani* (left side) and fossil site names (right side) related to stratigraphic section. Abbreviations: Ac, overbank silts of unit A; As3, well-sorted sands; As1,2, sands and gravels; Bp1,2, organic clays of marsh habitat; Bc, overbank silts of unit B; C, return of fluvial deposition of Río Moctezuma; ka = thousands of years.

3. Térapa *Paramylodon*

While 20 sub-localities have been identified at Térapa, only four have included sloth remains. To date, all sloth specimens from Térapa are identified as *Paramylodon harlani* based on the lobate dentition, all skeletal elements, as described below, are morphologically similar to other specimens of *Paramylodon*. *Paramylodon harlani* is currently the only species recognized in the Irvingtonian and Rancholabrean of North America [28]. While there is the potential for the Shasta ground sloth, *Nothrotheriops shastensis*, and, to a lesser degree, Jefferson’s ground sloth, *Megalonyx jeffersonii*, to be present based on their known distributions, both sloth taxa are sufficiently different in their dentition and skeleton to the point whereby they can be readily distinguished from *Paramylodon harlani*.

3.1. Armadillo and Beto Sublocalities

The sediments of the Armadillo and Beto sublocalities consist of organic marsh to palludal sediments of layer Bp1 [14], which contain the highest concentration of vertebrate fossils in the site. Only a single bone of *Paramylodon*, a proximal phalanx DP 9435 (TERA-499), is known in the Armadillo sub-locality. It is associated with the pampathere, *Pampatherium* cf. *mexicanum* [15].

All remains at Beto represent a single individual DP 9436 (TERA-500) from a single area (approximately 1.5 by 2.0 m). Recovered parts of the skeleton include left upper fourth (last) molariform, right ulna, proximal two-thirds of the right radius (Figure 3) and a partial manus represented by the lunar, ulnare, trapezoid, magnum, partial unciform, first, second and third metacarpals, proximal phalanx of digit I, second phalanx and ungual of digits II and III (Figure 4), partial pelvis, and osteoderms. A specimen in which the proximal and ungual phalanges in digit one of the manus of *Paramylodon harlani* are co-ossified was described by [35], but they are distinct bones in the individual from the Beto sub-locality.



Figure 3. Right ulna and radius of *Paramylodon harlani* DP 9436 (TERA-500) from Térapa in lateral view. Scale is 10 cm.

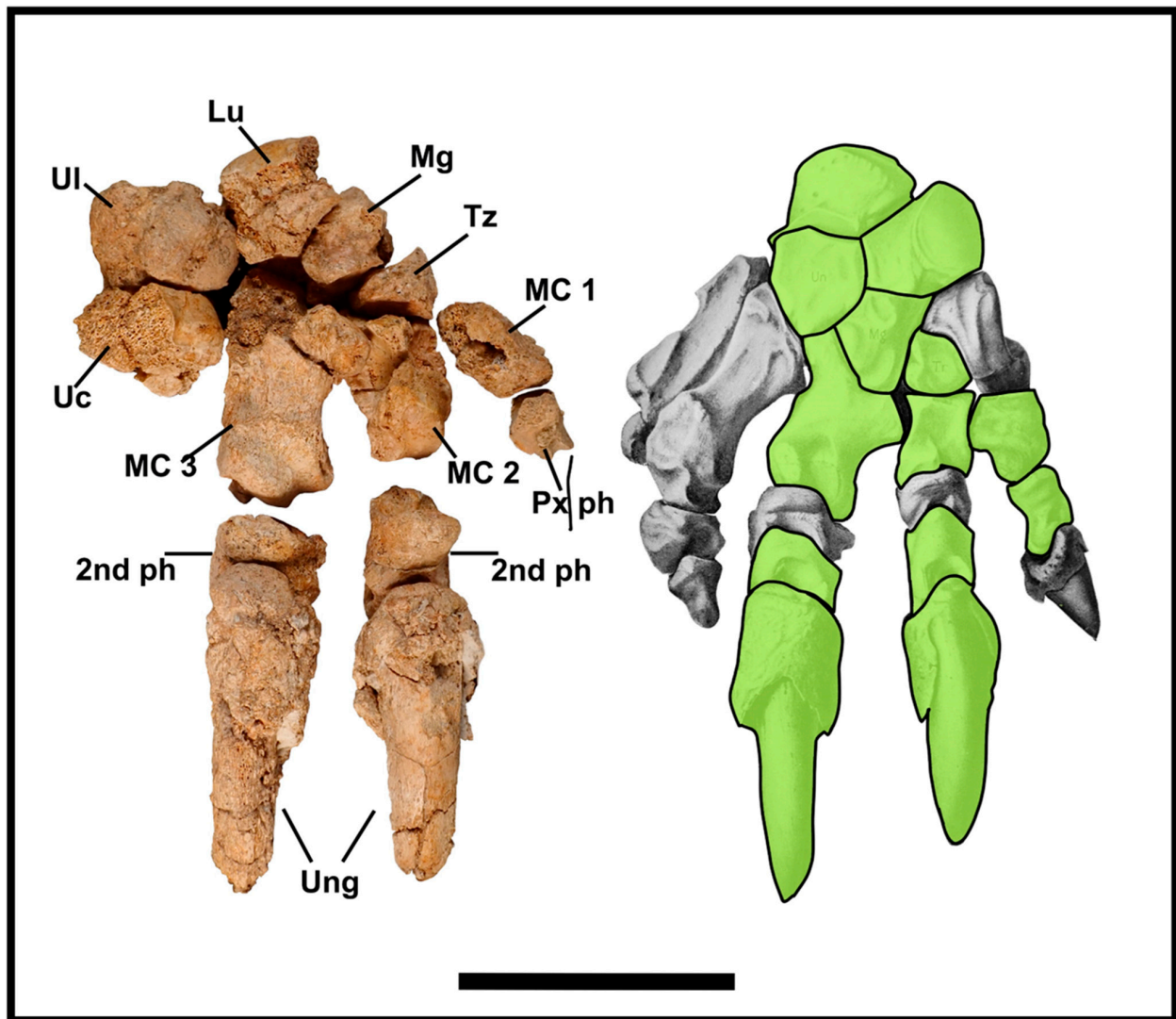


Figure 4. Partial right manus of *Paramylodon harlani* DP 9436 (TERA-500) from Térapa (**left**) compared to complete manus from Rancho La Brea (Stock, 1925 **right**). Abbreviations: Lu—Lunar, MC—Metacarpal, Mg—Magnum, Px Ph—proximal phalanx, TZ—Trapezoid, Uc—unciform, Ul—ulnare, Ung—ungual 2nd ph—Second phalanx. Scale is 10 cm. Colored manus elements on right indicate bones recovered in manus from Térapa.

The specimen from the Beto sub-locality is the only place where a significant portion of the skeleton of a single individual was recovered. The presence of a large number of osteoderms in association with the skeleton indicates the carcass was probably buried in situ while still covered with the skin. Both the recovered right ulna and radius were capable of articulation, but the ulna is missing a small part of the distal end and the radius also lacks the distal end. The length of the ulna is approximately 300.5 mm; length of the olecranon is about 199 mm height at the coronoid process is 128.3 mm and mediolateral width across the humeral articular surface is 90.4 mm; anteroposterior length of the proximal radius is 60.2 mm and mediolateral width 44.3 mm. The anteroposterior dimension of the proximal radius is 61.0 mm, and the mediolateral width is 41.4 mm. The epiphysis of the proximal end of the radius is fully fused to the diaphysis, as are the distal epiphyses of the metacarpals. All indications of the preserved bones signal that this is a fully growth, but it is a small individual compared to other members of the species based on the dimensions of the proximal end of the radius (Figure 5). The ungual phalanges (Figure 6) have a semi-circular cross-section, which is a characteristic of mylodontid sloths.

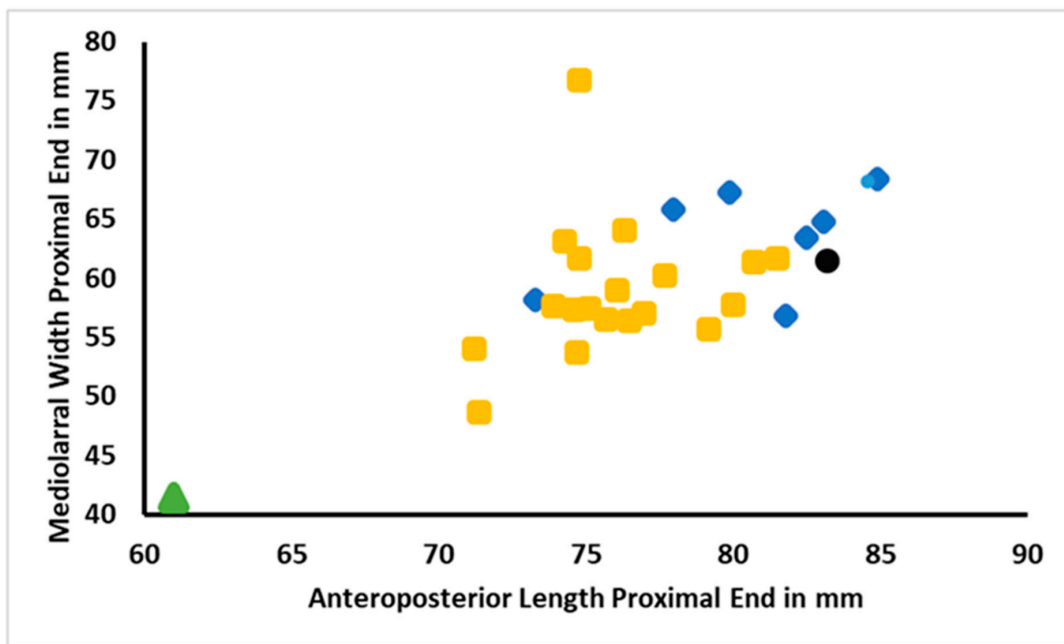


Figure 5. Scatter diagram comparing the anteroposterior length and mediolateral width of the proximal end of radius of *Paramylodon harlani* from Térapa (green triangle lower left) with other individuals of the species. Square—Rancho La Brea, California; Diamond—American Falls Reservoir, Idaho; Circle—Big Bone Lick, Kentucky.

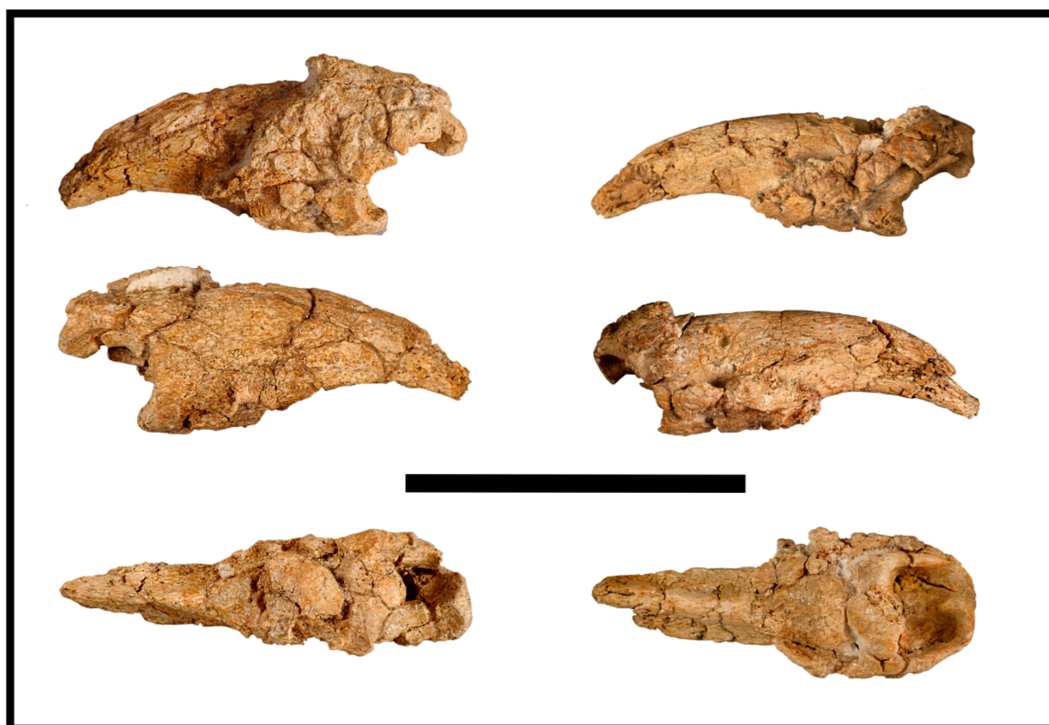


Figure 6. Unguals of *Paramylodon harlani* DP 9436 (TERA-500) in lateral and ventral views. Scale is 10 cm.

The presence of dermal ossicles (osteoderms) (Figure 7) with the skeleton is indicative that it is member of the mylodontini [35–37]. It appears that, with the death of the animal, the dried skin was preserved in place on the skeleton when it was buried. While the ossicles were recovered within the context of other bones of the skeleton, the exact context could not be determined. All of the osteoderms reported here come from a single layer

below the *Paramylodon* skeletal from the Beto sub-locality. Figure 7A shows how many of the osteoderms were incased in a pedogenic caliche. No other taxon was encountered in the immediate area of the osteoderms and *Paramylodon* skeletal remains. There is a great diversity of shapes and measurements to the osteoderms (Figure 7B). The general form of a typical osteoderm includes the following: The shape is elongated, with the length being noticeably greater than the width, and includes two pointed extremes with a keel-like ridge oriented along this length (Figure 7A,B), often with a high-point that may be observed as an apex or a broad high-point swelling. The width is perpendicular to the length. The length and width of an osteoderm are inferred to be positioned parallel within the orientation of the dermis. The depth of the osteoderm is oriented with the apex being toward the surface of the dermis and the opposite side towards the basal aspect of the dermis—transverse to the length and width. The basal surface of the osteoderm typically has a flattened surface and/or rugosity to the surface (Figure 7C). Measurements were taken for the length, width, and depth as described above. Of the 780 recovered osteoderms, 186 were measured, with a selection of the osteoderms being measured based on diversity of size and shape (Figure 8). A similar variation in the osteoderms of South American Pleistocene mylodontini sloths has also been documented [35,36]. Occasionally, multiple osteoderms are fused together—these were not used in the measurements (Figure 7C). The sample includes many examples of individual osteoderms much smaller than previously reported, e.g., [37–39]. Associated osteoderms may not be reported simply because they are dismissed as pebbles or rock fragments, but the lack of recovery of the very small specimens can also be caused by passing through larger mesh screens, even when sediments are collected for microvertebrates.

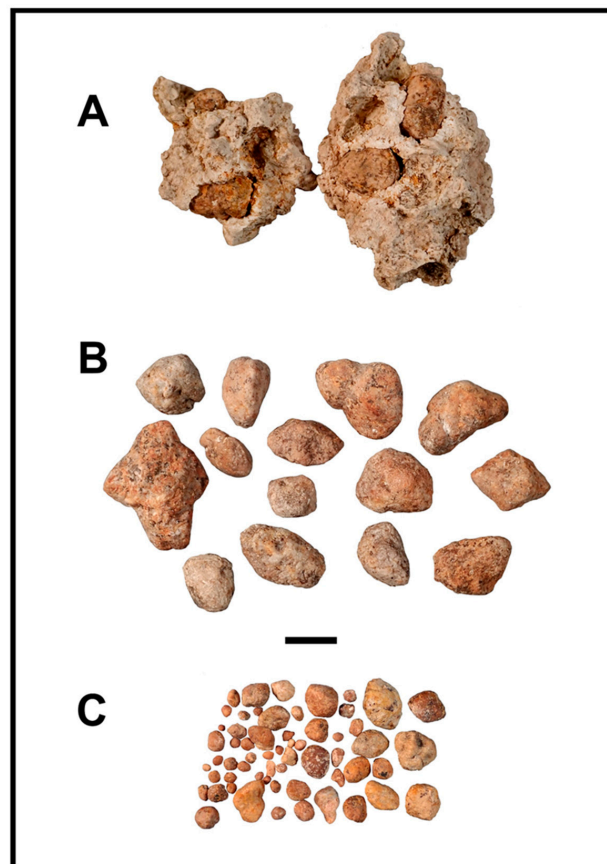


Figure 7. Osteoderms of *Paramylodon harlani* DP 9436 (TERA-500) from a single layer at the Beto locality at Térapa, Sonora, Mexico. Scale is 10 mm. (A) Osteoderms in pedogenic carbonate matrix at locality, (B) Assortment of osteoderms illustrating largest sizes and variety of shapes including those that have grown together, (C) Assortment of smallest osteoderms.

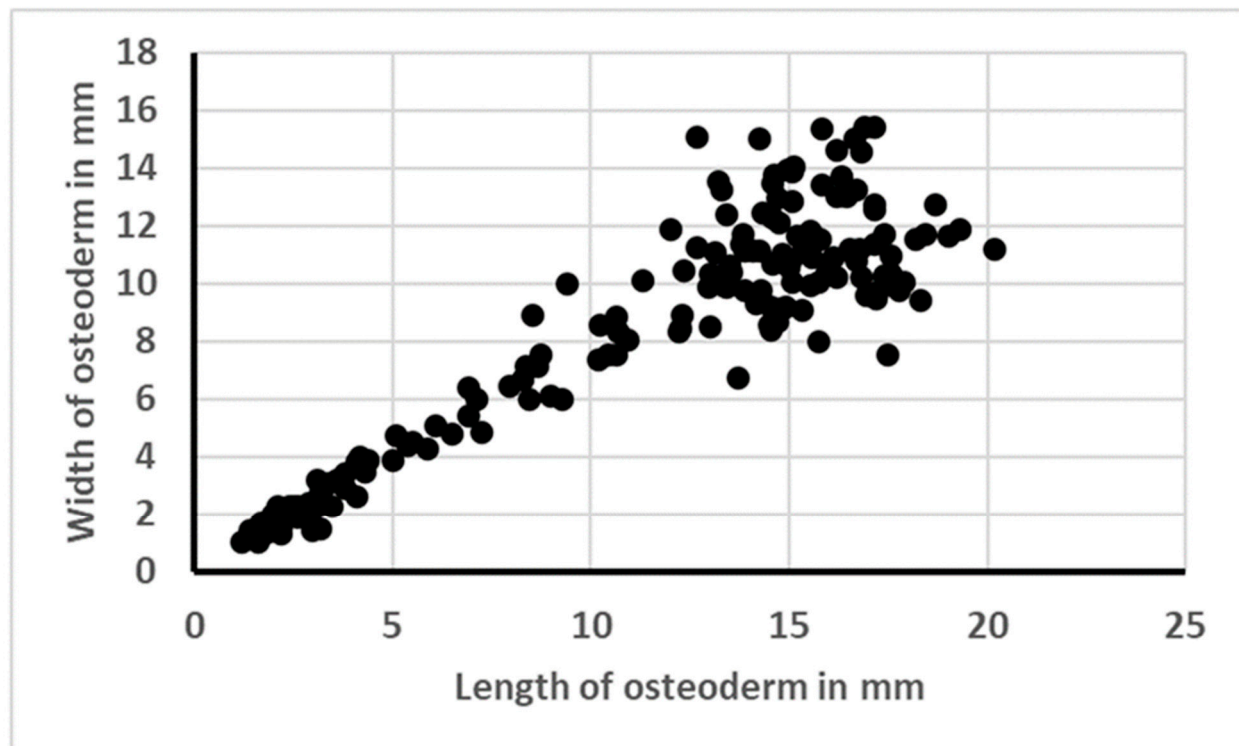


Figure 8. Scatter diagram on the size distribution of osteoderms of Térapa *Paramylodon harlani* based on greatest length and width.

3.2. Camel Bill Sub-Locality

An upper-left second or third molariform DP 9434 (TERA-160) found at the Camel Bill Site is from Ac sediments, which are silts deposited as overbank deposits [14].

The single tooth from the Camel Bill sub-locality, the two teeth recovered from the Ramon locality, and the left last upper (fourth) molariform from the Beto sub-locality all have the lobate structure characteristic of mylodont sloths [37]. The length of the fourth molariform is 30 mm, labiolingual width of the anterior lobe 18.6 mm, and labiolingual width of the posterior lobe 12.7 mm. It is generally more elongated than other upper last molariforms in *Paramylodon harlani*, but its overall size and measurements fall within the range of the species [37].

3.3. Ramon Sub-Locality

At this sub-locality, the sloth is represented by an upper-right second or third molariform DP 9437 (TERA-501), and the anterior part of a lower-right molariform DP-9438 (TERA-502).

The Ramon site represents the base of the basin created by the Tonibabi lava flow, the initial phase of infilling with water, sediments, and faunal remains. The sloth was found with the gomphothere, *Cuvieronius*. They were preserved in the As2 sediments, which consist of sands and gravels and are some of the earliest deposits in the basin.

4. *Paramylodon* in Mexico

4.1. *Paramylodon* Anatomy and Physiology

Based on a body mass of 1000 kg for *Mylodon darwini*, which is closely related to *Paramylodon*, its estimated lower limit of thermoneutrality would have been 6 °C [40]. Given the slightly larger estimated body size of *Paramylodon* in the Rancholabrean of about 1400 kg and assuming it had a similar fur coat, *Paramylodon* should have been similar in its tolerance to seasonally cold temperatures, especially at lower latitudes than those of Cueva del Milodon at 50.5° S. As discussed below, the estimated temperatures allowing

glaciers to move to lower elevations would have been very close to the lower limits of thermal neutrality for the sloth, even given its large body mass and potential thermal inertia. It seems reasonable to infer that the sloth would have shifted its range to lower and presumably warmer elevations during colder intervals. As the age of Térapa is between 40–43 ka, or to mid Oxygen Isotope Stage (OIS) 3 [26], the sloth and associated fauna were living during a mild climatic interval between the two cold maxima of the last glaciation.

As temperature decreases with increasing elevation and latitude, there is a similar decrease in temperature with each 1° increase in latitude or by an increase in elevation of 107 m [41]. The International Civil Aviation Organization (ICAO) defines an international standard atmosphere (ISA) with a temperature lapse rate of 6.50 °C/km (3.56 °F or 1.98 °C/305 m) from sea level to 11 km (36,090 ft or 6.8 mi, Manual of the ICAO Standard Atmosphere (extended to 80 kilometres (Third ed.). International Civil Aviation Organization. 1993. ISBN 978-92-9194-004-2. Doc 7488-CD, Figure 2). Since approximately the same effective decrease in temperature of 0.35 °C is obtained by 1° of latitude or 107 m in elevation, a comparison of the highest site in *Paramylodon* at Tajo de Tequixquiac, State of Mexico (20° N, 4490 m elevation) and Térapa, State of Sonora (29.7°, 605 m elevation) highlighted that the difference in latitude and elevation between the two sites produces a difference of 8.6 °C (5.2° due to elevational difference and 3.4° due to the latitudinal difference), in addition to the mean seasonal temperatures of the two sites. This assumes the two sites are roughly contemporaneous, and this estimate can be refined when a more precise chronology is available.

Comparing the distribution of *Paramylodon* in Mexico and the United States, the highest elevations it reached are similar despite the difference in latitude (Figure 9), suggesting that lower temperatures due to higher elevations may not have been a significant limiting factor in its distribution. The site with the highest elevation for *Paramylodon* in Mexico (2375 m at 19.6°) is only slightly greater than the highest elevation it reaches in the United States (2330 m at 38.1°). Today, at 40° N, tree line elevations vary between 2100 and 3700 m [42], and, during colder climatic intervals in the Pleistocene, would have been much lower in elevation. By determining the shift in elevation in the tree line through time, it is reasonable to extrapolate that the elevational transitions between the vegetation zones below the tree line would have been comparable in magnitude. In Colorado, during the late Bølling–Allerød (13.6–12.9 ka), the alpine timberline migrated upslope to near-modern elevations, which was followed in the Younger Dryas (12.9–11.7 ka) by a downslope displacement of 60–120 m of the alpine timberline ecotone [43]. This elevational shift indicates a cooling of summer temperature by ~0.4–0.9 °C. The baseline difference in temperature between the high elevation sites for *Paramylodon* in the United States and Mexico is based on differences in latitude and elevation is 6.51 °C, with only 0.01 °C due to the difference in elevation and 6.5 °C due to the difference in latitude. The highest elevation in Mexico is in Pico de Orizaba (Citlaltépetl), on the border of Puebla and Veracruz, with an elevation of 5610 m. The mean elevation of Mexico is 1111 m, while the mean elevation of the United States is 760 m, with the highest elevation in the coterminous United States being Mount Whitney (4401 m). Consequently, while the mean elevation of the United States is less than in Mexico, it does have a significantly greater percentage of its higher elevation land surface available for *Paramylodon* to potentially inhabit, assuming the presence of a grassland habitat.

There are only a few records of mylodontinae sloths in Central America, including in Guatemala [44,45], Costa Rica [46], and Panama [47]. Generally, most records are reported simply as a mylodontid, but some specimens have been identified specifically as *Paramylodon*. Given the limited documentation and study of the Central American mylodonts, we withhold judgment with regards to the presence of *Paramylodon* in the south of Mexico, pending better records and the much-needed review of the family for this region.

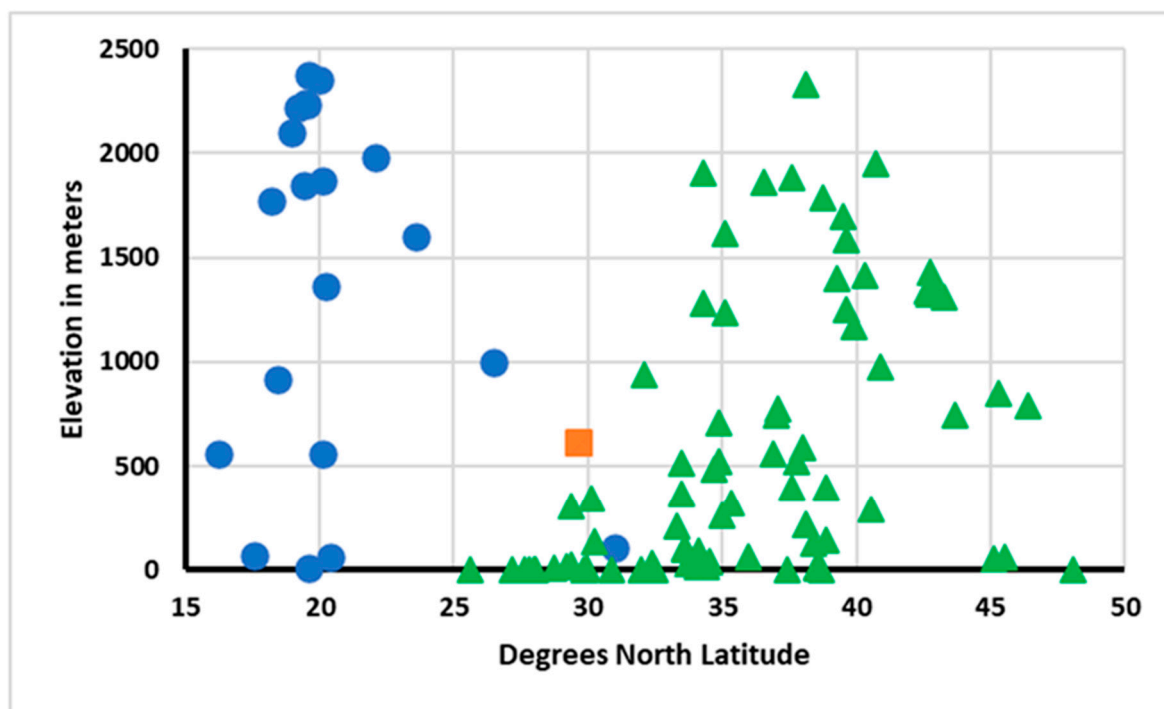


Figure 9. Graph showing relationship of latitude and elevation in distribution of *Paramylodon harlani* in Mexico (circles), Térapa (orange square), and United States (triangle).

In Mexico, the distribution of *Paramylodon harlani* reaches higher elevations at lower latitudes (Figure 9). Térapa falls on this line, suggesting the sloth was at the maximum elevation for this latitude. One caveat to this general pattern is the lack of an absolute chronology for most of the localities with *Paramylodon*, so it is not possible to determine if the sloth was only present at higher elevations during interglacials or interstadials but at lower elevations during colder glacial intervals when mountain glaciers formed in the Sierra Madre Mountains. Glaciers in Mexico formed moraines during MIS 6, between 21–17.5, 17–14, 14–13, 12–10, and 8.3–7 ka BP. Equilibrium line altitudes (ELA) for these five advances were 1030, 930, 730, 550, and 250 m, respectively. The estimated decrease in temperature of 5–9 °C indicates there was a marked cooling over tropical land and oceans during the last glacial maximum [48]. Other examples of ELA at lower elevations during past substages of glaciation include Iztaccíhuatl (1370 m below present ELA during the Tomicoxco Substage), 100 m lower (Diamantes First Advance), 910 m lower (Diamantes Second Advance), about 720 m lower (Alcalican I), about 630 m lower (Alcalican II), and 245 m lower (Ayolotepito Stade). The estimated amount of cooling to accomplish these glaciations was about 8 °C during probable Bull Lake equivalents, about 6°, 5°, and 4 °C during Pinedale equivalents [49].

As the preferred habitat of *Paramylodon* is inferred to have been open grassland habitat based on associated fauna, stable isotopes, and associated vegetation, one potential limit to its distribution at higher elevations would have been the presence of closed forest. The climatic tree line represents an obvious land cover demarcation, and its relation to temperature makes it an ideal reference line for other bioclimatic zones [50], as a tree species' cold range limits are predominantly set by low-temperature extremes [51]. This not only determines the tree line at different latitudes [51] but also how forest habitat may shift to lower elevations during cold climatic intervals. Such shifts in vegetation to lower or higher elevations during interglacials or glacials has been documented on the flanks of the Andes in western Amazonia [52], elsewhere in tropical zones [53], and at temperate latitudes [54].

Tree line is therefore an important global bioclimatic reference line, against which other bioclimatic zones and the associated biomes can be defined [42]. Consequently, changes

in tree line during glacial intervals provide a reference point for the degree of impact to other vegetative biomes in terms of elevational shifts. A forested zone between the lower elevation grasslands and glaciers at higher elevations would suggest that the slope of the line showing the upper limits of the sloth's distribution based on latitude and elevation would also mark the boundary of the grasslands that Harlan's ground sloth could have inhabited. Such a plot may be equally applicable to other grassland taxa, such as bison. One of the results of changes in the temperature is the size of the global potential of forested areas [50]. Consequently, a downslope shift of forest habitat would subsequently reduce the open grassland habitat preferred by *Paramylodon*, and in mountainous habitats, may have resulted in small isolated relict populations of the sloth and other fauna in intermontane basins, such as the Valle de Bravo in Mexico State, the Central Depression in Chiapas, and the Chapala Basin in Jalisco. Therefore, colder temperatures may have limited its distribution not only physiologically but also may have reduced the area of its preferred habitat via shifts of forest habitat to lower elevations.

Carbon and oxygen isotopes assessed from tooth enamel carbonate from various mammalian species (*Bison*, *Cuvieronius*, *Equus*, *Mammuthus*, *Nechoerus*, *Odocoileus*, and *Paramylodon*) from Térapa indicate that at least the river valley was cooler with a more equable and less seasonal environment than in the area today [27]. Based on the available data, the reconstruction is that the Late Pleistocene of western and eastern Sonora had a cooler summer climate, one with more winter rains and less summer rains and less summer evaporation. Woodlands and shrub communities were in the upper bajadas and rocky hills (packrat midden data) in western Sonora. The region around Térapa, in one of the lower mountainous regions of eastern Sonora, had a tropical/subtropical marsh, savanna, and riparian forest environment, at least within the river valleys [12,14]. A similar variety of habitats have been proposed, as utilized by *Paramylodon harlani*, elsewhere in its range.

The existence of six primary biogeographic corridors for north–south movements of sloths and other taxa; Western US–Baja California; the Rocky Mountains–Sierra Madre Occidental, Transvolcanic Belt–Sierra Madre del Sur; Eastern US–Sierra Madre Oriental; Sonora–Central America Pacific Lowlands, and the Tamaulipas–Central America Gulf Lowlands has been proposed [6]. Térapa is located just west of the northern portion of the Rocky Mountains–Sierra Madre Occidental dispersal corridor. Physiographically, Térapa is near the latitudinal transition between the present Neotropical and Nearctic biotic zones that extend from the high Sierra Madre Occidental and Madrean Sky Island mountains (Madrean Archipelago of [55,56]) to the low Sonoran Desert at the Sea of Cortez. Even during the latest Pleistocene (Rancholabrean), the short distance from Térapa north to Arizona (183 km, 114 mi) was apparently a critical barrier and transition zone for some members of the fauna of northern México and the arid Southwest of the United States. During the Pleistocene, the presence of a well-developed riparian corridor along the Río Yaqui from the Gulf of California to the mountain-valley setting at Térapa, which would have facilitated the movement of animals with tropical adaptations 350 km inland, has been proposed [14]. The Río Yaqui would also have provided a connection of the inland Térapa site with the coastal Sonora–Central Pacific Lowlands of [6].

4.2. Biogeography of *Paramylodon harlani*

The geographical position and topographic setting of the Térapa locality within the boundary zone between recent biogeographic regions enhances the likelihood that basins and ranges in the Térapa area underwent many ecological and environmental changes during the Pleistocene. Ecogeographically, today, Térapa is in a broad transitional area between the Nearctic and Neotropical biogeographic realms. Térapa is at the northeastern edge of the Sonoran–Sinaloan transition subtropical dry forest. This ecoregion was included in the Nearctic biogeographic realm [57] and within the Mexican phylogenetic zoogeographic region of the Nearctic realm for mammals and other terrestrial vertebrates [58]. The same biotic community has also been called the subtropical Sinaloan thornscrub—included in the

Neotropical realm [59,60]. This ecosystem is now called Matorral Espinoso de Piedemonte (foothill thornscrub) and is considered tropical [61,62].

Today, the “boundary” between Neotropical and Nearctic biogeographic regions is necessarily transitional rather than a hard line (e.g., [41,63–69]). A somewhat arbitrary reference point is the latitude of the Tropic of Cancer ca. 23° (range 22.1 to 24.5°), which forms the northern boundary of the area referred to as the tropics and is north of the subtropics that extend to about 35° north, above which is the North Temperate Zone. At 29.7° N, today’s Térapa is in the Neotropics and well above the northern margin of the Tropics, possessing a climate consisting of hot summers with monsoonal rains and mild, generally frost-free winters.

With regard to the distribution of various mammalian species, the transition in western Mexico is usually drawn along the Pacific Coast between the coastal lowlands and the highlands of the Sierra Madre Occidental to approximately the Río Mayo and Río Fuerte river systems of the Pacific versant of the Sierra Madre Occidental. Farther north, along the coastal lowlands and central Sonora, are parallel ranges and basins, and the region becomes more arid, thus acting as a barrier to humid-adapted tropical species. The deep canyons of the Río Mayo and Río Fuerte drainage basins afford dispersal corridors and filter barriers between the tropical coastal lowlands (in southern Sonora and northern Sinaloa) and the temperate uplands of the Sierras (in Chihuahua). The next major drainage (south of the Río Yaqui), with its tributaries, including the Río Moctezuma (formerly Río Oposura) and Térapa, is the Río Mayo. Given the potential vegetation and floristic changes during the Pleistocene, these drainages might have provided a corridor through the Sierras to the Mexican Central Plateau morphotectonic province. Although *Paramylodon harlani* has a wide distribution in Mexico extending from Baja California and Sonora south to Chiapas and Yucatan, the majority of *Paramylodon* localities are closely associated with the Trans-Mexican Volcanic Belt and occur between 1500 and 2200 m.a.s.l [6]. While [6] proposed that altitude was not a limiting factor to its distribution, we would note that the role of elevation as a controlling factor in distribution also needs to consider latitude as well, since mean average temperatures become lower at both higher latitudes as well as higher elevations, as noted by [41] in his use of Equatorial Equivalents to compare different Pleistocene localities. As previously discussed, temperature may not only control the species distribution due to physiological tolerances, especially to low temperatures, but in a way that is equally important, it also may directly impact the vegetation utilized by a herbivore as well. An analysis of the distribution of the Shasta ground sloth, *Nothrotheriops shastensis*, utilized this approach [70], and as shown here, is applicable to *Paramylodon* as well.

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