GRAVIGRADE XENARTHRANS FROM THE EARLY PLEISTOCENE LEISEY SHELL PIT 1A, HILLSBOROUGH COUNTY, FLORIDA

H. Gregory McDonald[1]

ABSTRACT

Two taxa of ground sloths are present at Leisey Shell Pit 1A, *Nothrotheriops texanus* and *Paramylodon harlani*. The Irvingtonian sample of *Nothrotheriops* is sufficiently distinct morphologically to warrant separation from the Rancholabrean species, *N. shastensis*, and is referred to *Nothrotheriops texanus* (Hay) (new combination). Individuals of the Irvingtonian *P. harlani* average smaller than those of the Rancholabrean and there is a general size increase in the lineage from the Blancan to Rancholabrean with only minor morphological changes. Use of *Paramylodon* instead of *Glossotherium* for the species *P. harlani* is nomenclaturally correct.

RESUMEN

En la fauna local de la Excavación de Conchuelas de Leisey se encuentran dos taxa de perezosos terestres: *Nothrotheriops texanus* y *Paramylodon harlani*. La muestra Irvingtoniana de *Nothrotheriops* es suficientemente diferente en términos morfológicos como para permitir separarla de la bien conocida especie Rancholabreana *N. shastensis* y es referida como *Nothrotheriops texanus* (Hay) (nueva combinación). Los *Paramylodon* del Irvingtoniano son más pequeños que los del Rancholabreaense, existiendo un incremento general de tamaño en el linaje desde Blancano a Rancholabraense, con sólo pequeños cambios morfológicos. El uso del nombre *Paramylodon* en vez de *Glossotherium*, en el caso de la especie *P. harlani*, es correcto en términos de nomenclatura.

---

[1] The author is a Paleontologist at the Hagerman Fossil Beds National Monument, P. O. Box 570, Hagerman, ID 83332-0570, U.S.A.

MCDONALD, H. G. 1995. Gravigrade Xenarthrans from the early Pleistocene Leisey Shell Pit 1A, Hillsborough County, Florida. Bull. Florida Mus. Nat. Hist. 37 Pt. II(11):345-373.

INTRODUCTION

Among the diverse fauna from Leisey 1A are two ground sloths, *Paramylodon harlani* and *Nothrotheriops texanus*. *P. harlani* has long been known as a member of the Pleistocene fauna of Florida. By contrast, the presence of *Nothrotheriops* has only recently been recognized in the state (McDonald 1985). Rancholabrean records of both genera are common, but Irvingtonian age records are rare. Thus the recovery of a large sample of both taxa from the Leisey 1A locality adds significantly to our understanding of the evolution and biogeography of these two animals.

ABBREVIATIONS

The following abbreviations are used: AMNH - American Museum of Natural History, New York, CI - Albertson College of Idaho, Caldwell, FMNH - Field Museum, Chicago, IMNH - Idaho Museum of Natural History, Pocatello, LACM - Natural History Museum of Los Angeles County, Los Angeles, UF - Florida Museum of Natural History, Gainesville, USNM - National Museum of Natural History, Washington D.C., mm - millimeters, cm - centimeters, M - mean, n- number.

ACKNOWLEDGEMENTS

I would like to thank S. David Webb of the Florida Museum of Natural History for the opportunity to study the sloths of the Leisey Shell Pit fauna and for his guidance and help in this and other projects. Gary S. Morgan aided in numerous ways during my visits to the Florida Museum of Natural History. George Jefferson and Chris Shaw have greatly aided my work during my visits to the Page Museum to examine the collections from Rancho La Brea. Larry Barnes and David Whistler have graciously provided access to the collections housed at the Natural History Museum of Los Angeles County. Clayton E. Ray kindly permitted me to study specimens in his care at the Smithsonian. Mary Ellen Ahearn photographed the specimens, and Wendy Zomlefer prepared the illustrations. The efforts of both are greatly appreciated. Les R. Kleinberg greatly helped by measuring mandibles of *Paramylodon* from Rancho La Brea. Elaine Anderson, Gerry de Iuliis, Richard C. Hulbert, Jr., and Gary S. Morgan kindly reviewed the manuscript. A special word of thanks is extended to C. E. "Bud" Leisey, Jr., and Eric Hunter who generously aided the project in many ways. Excavation of the site was conducted by numerous members of the Tampa Bay Gem and Mineral Society, without whose help this important fauna could not have been saved. JoAnn Norris typed the manuscript. Partial funding for the study of the sloths was provided by a grant from Leisey Shell Pit Inc. to the Florida Museum of Natural History.

SYSTEMATIC PALEONTOLOGY

Order XENARTHRA Cope 1889
Family MEGATHERIIDAE Owen 1843
Subfamily NOTHROTHERINAE Kraglievich 1923
Nothrotheriops texanus (Hay 1916) new combination

Nothrotherium texanum Hay 1916.
Nothrotherium shastense Sinclair 1905. Lull 1929 (in part).
Nothrotheriops shastensis (Sinclair 1905). McDonald 1985 (in part).

Type Specimen.– USNM 8353, incomplete cranium.

Type Locality.– Wheeler County, Texas (see Hay 1916).

Referred Leisey 1A Specimens.– UF 86885, 80108, 84464, 86119, 86120, 86980, 86981, 86982, 86983, crania; 64348, 64349, 86899, 86121, 84626, 80314, 83100, 83594, 83900, 86984, 86985, mandible; 86185, 86987, 86989, 86990, 86991, humerus; 65821, 84463, 86996, 86999, 86997, 87000, ulna; 65821, 86168, 86992, 86993, 86994, 86995, radius; 87003 coossified third and fourth metacarpals; 87010, fifth metacarpal; 81500, 86733, 80038, 64350, 84931, 86355, 80211, 81362, 87012, femur; 67354, 64353, 86973, 87013, 87014, tibia; 87017, patella; 65824, 82938, 84449, 87028, calcaneum; 64335, 86891, 84448, 87026, 87027, astragalus; 86837, 87018 83688 coossified entocuneiform and first metatarsal; 65822, 64367, 81502, 87020, 87019, metatarsal II; 65823, 84287, 87021, 87022, metatarsal III; 87882, 86969, 87023, 87024, 86306, 86882, metatarsal IV; 87025, metatarsal V; 86952, 86870, 67127, 87035 coossified proximal and second phalanx, digit 3 pes.

Emended Diagnosis.– Smaller than *Nothrotheriops shastensis* with more gracile cranium. Alveolar length of maxilla less than predental length of maxilla in contrast to *N. shastensis* in which the alveolar length of the maxilla is equal to or greater than the predental length of the maxilla. Total alveolar length of the jaw is less than 50% of the length of the mandibular spout (measured from the anterior edge of the first cheek tooth to the anterior edge of the spout) in contrast to *N. shastensis* in which total alveolar length is equal to or greater than 50% of the spout length.

Description.– Comparison of both adults and juveniles from Leisey 1A, which contains a minimum number of eight individuals, was made with specimens of late Pleistocene (Rancholabrean) *Nothrotheriops shastensis* from San Josecito Cave, Nuevo Leon, Mexico and Rancho La Brea, California. Since the skeletal anatomy of the Leisey 1A *N. texanus* is essentially the same as *N. shastensis*, the reader is referred to Stock (1925) or Lull (1929) for specific descriptions of bones and to Paula Couto (1974) for the manus. Rather than reiterate their excellent descriptions, references to specific bones will be made only in a general way.

Crania of *Nothrotheriops* from Leisey 1A display only a few differences from those from Rancho La Brea (Fig. 1). Overall length is similar in both species but the relative dimensions of other parts of the skull differ. One difference is the relationship between cheek tooth row length and predental length of the maxilla (Fig. 2). Alveolar length is shorter than the predental length in the Leisey 1A sample (73, 79, 84, and 89%) whereas in the Rancho La Brea sample of *N. shastensis* alveolar length of the maxilla is greater than that of the predental length (100, 119, 128 and 129%). Alveolar length of the maxilla is 91% of predental length in the type of *Nothrotheriops texanus* (USNM 8353).

In length and relative proportions, the skulls of the two samples are closely comparable in most respects. Nevertheless, the Leisey 1A sample is consistently smaller than the Rancholabrean sample in many transverse dimensions. This combination of similar length but smaller transverse dimensions gives the skull of *Nothrotheriops texanus* from Leisey 1A a more gracile appearance. These dimensions in the holotype of *N. texanus* are more similar to those from Rancho La Brea and San Josecito than to Leisey 1A specimens except in the relative proportions of the maxilla discussed above. The intermediate size of the holotype of *N. texanus* suggests that it probably represents a later population than that from Leisey 1A.

Although the length of the predental portion of the maxilla is different in the two species, the width of this portion of the skull remains the same. This gives the anterior part of the skull of *N. shastensis* the appearance of having a shorter and stouter rostrum than *N. texanus*. The relative increase in the total alveolar length of the maxilla from *N. texanus* to *N. shastensis* has no affect on the width of the rostrum.

Comparison of the Leisey 1A *Nothrotheriops* mandibles (Fig. 3A) with those from Rancho La Brea and San Josecito Cave indicate some differences. Specimens from Leisey 1A are smaller (Figs. 4, 5) than those from later deposits. Despite the smaller size, the ratio of total alveolar length to maximum depth of the jaw (usually below the third molariform) is essentially the same (Leisey 1A: 0.96-1.08, M = 1.01, N = 6; Rancho La Brea and San Josecito 0.83-1.06, M = 0.99, N = 8). The relationship between alveolar length and mandibular spout length differs between the two samples (Fig. 5). Three specimens from Leisey 1A had total alveolar lengths of 39, 45 and 46% of the mandibular spout. The combined sample from Rancho La Brea and San Josecito Cave (N = 7) had an alveolar length from 52 to 59% (M = 55%) of the length of the mandibular spout. This relative increase in the total alveolar length compared to the mandibular spout length parallels the relative increase in the total alveolar length of the maxilla compared to its predental length.

One right juvenile maxilla (UF 83700) is interesting because of the presence of an atavistic caniniform (Fig. 6). Primitive nothrotheres such as *Hapalops* and

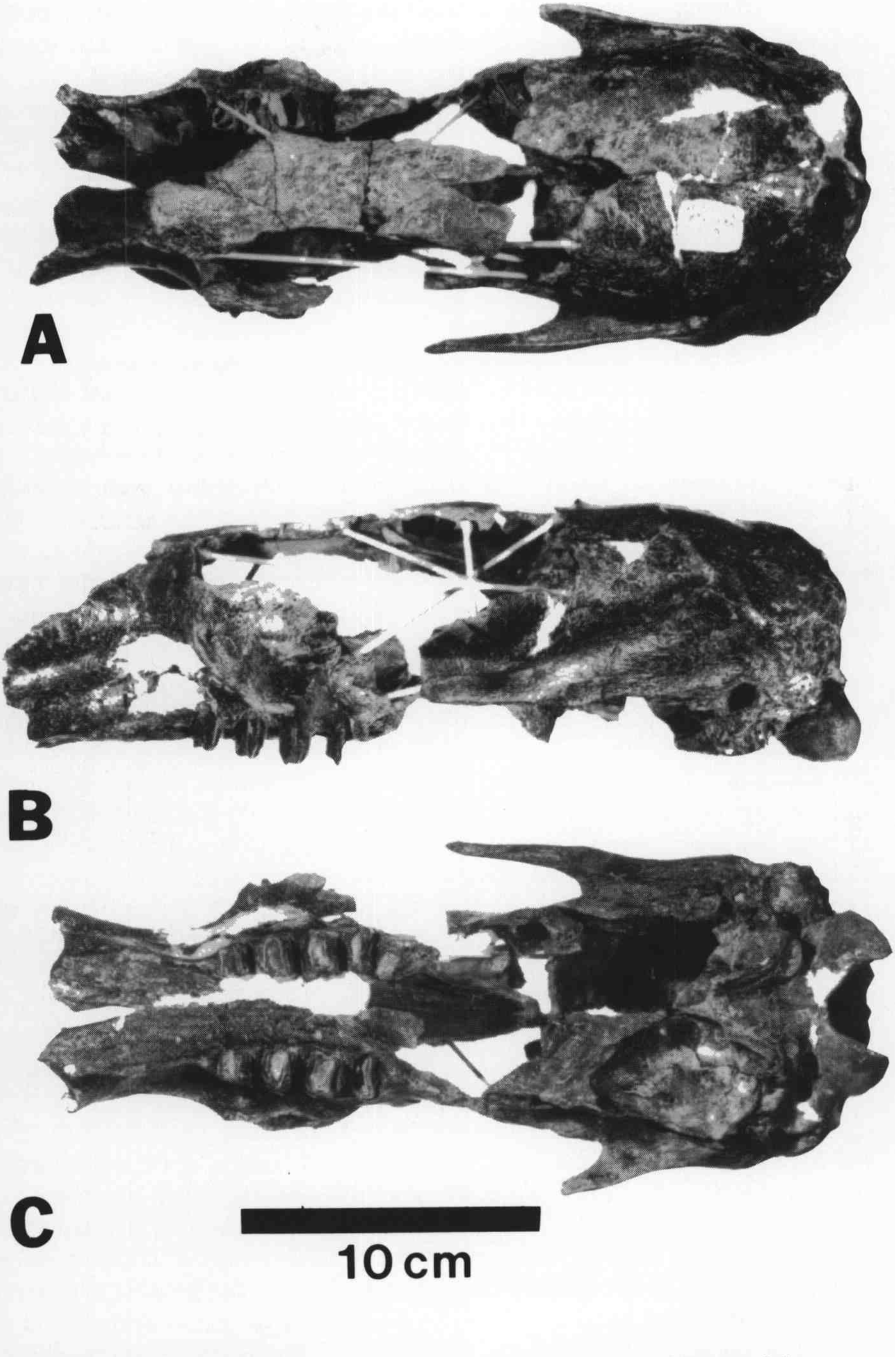

Figure 1. Skull of *Nothrotheriops texanus*, UF 86885, in (A) dorsal, (B) lateral and (C) ventral views.

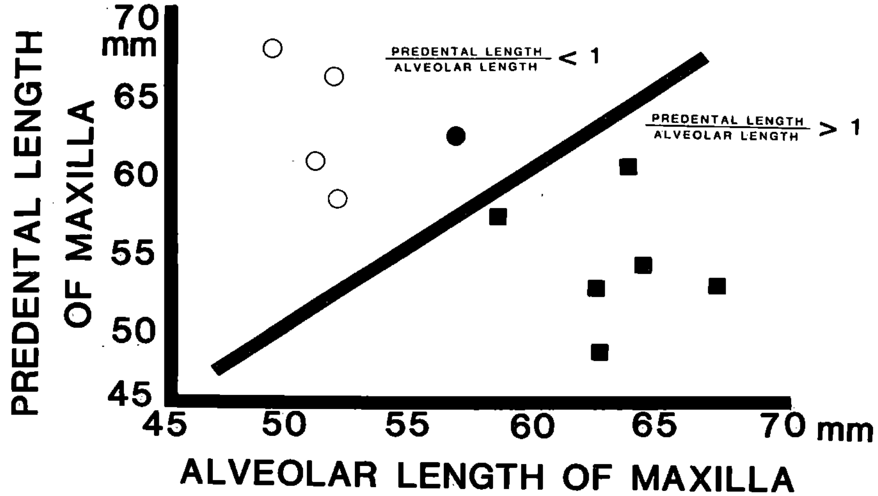

Figure 2. Comparison of predental length of maxilla against total alveolar length of maxilla in *Nothrotheriops texanus* and *Nothrotheriops shastensis*. Open circle = Leisey, solid circle = type *N. texanus*, solid square = *N. shastensis*.

Pronothrotherium, are characterized by the presence of upper and lower caniniforms. Some of the later nothrotheres such as *Nothrotherium* and *Nothrotheriops*, have lost the caniniforms although another Pleistocene genus, *Nothropus*, retained them. The caniniform is separated from the cheek tooth by a diastema and is positioned halfway between the anteriormost cheek tooth and the anterior edge of the maxilla. The caniniform in UF 83700 is strongly curved with its base positioned above the root of the first cheek tooth. The tooth is small measuring only 4.0 by 2.8 mm. Orientation of the long axis is anteroposteriorly. The occlusal surface is broken so it is not possible to tell if there is any wear suggestive of a complimentary lower caniniform. None of the recovered jaws of juveniles have any indication of a lower caniniform.

Coossification of adjacent bones of the manus and pes is a common feature in ground sloths, especially fusion between the entocuneiform and first metatarsal. Stock (1925) described two specimens from Rancho La Brea in which these two bones are fused, and the sample from San Josecito Cave contains 20 left and 8 right examples of this fusion. Three specimens from Leisey 1A (UF 86837, 87018 and 83688), two left and one right, show the coossification of the entocuneiform and first metatarsal. These bones are also fused in the other late Pleistocene nothrothere genus, *Nothrotherium* (Paula Couto 1971), but they are separate in early nothrotheres, such as *Hapalops*. Since *Nothrotheriops* is unknown prior to its appearance in the Irvingtonian of North America, it is not possible to determine when the ungual and proximal phalanx were lost and the entocuneiform and first metatarsal coossified. A mounted skeleton of *Pronothrotherium typicum* of

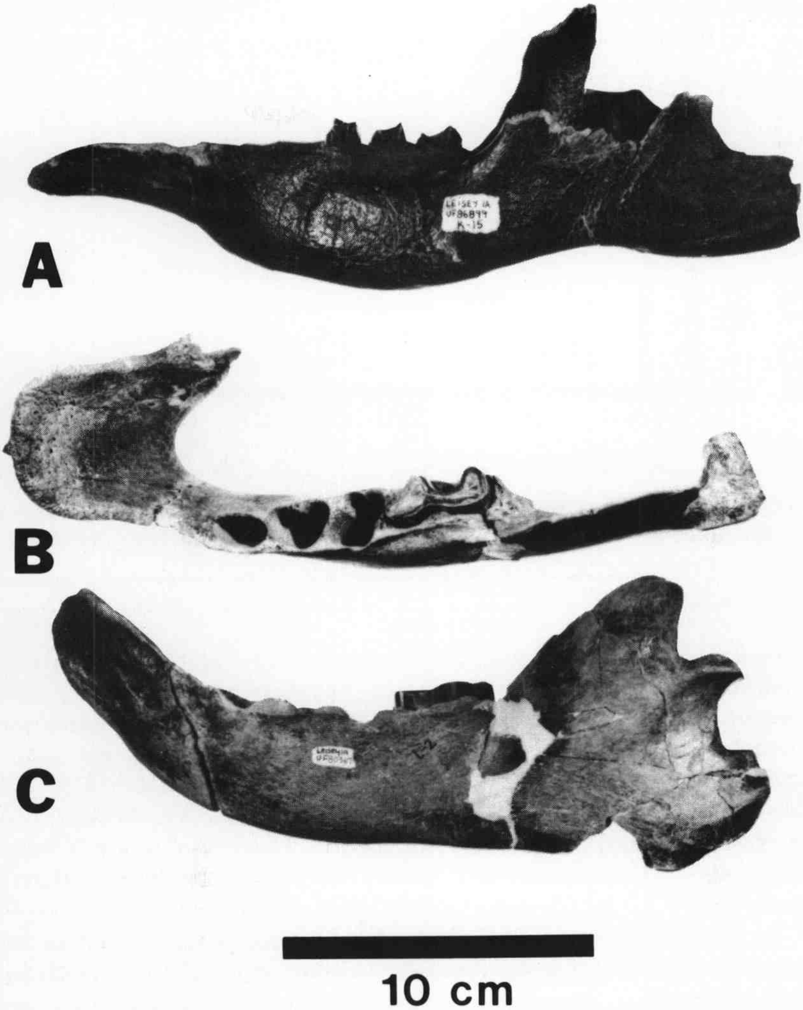

Figure 3. (A) *Nothrotheriops texanus*, UF 86899, lateral view of mandible. *Paramylodon harlani*, UF 80367, (B) occlusal view and (C) lateral view of mandible.

Pliocene age in the Field Museum (FM 14503) has lost the ungual phalanx, but the entocuneiform and vestigial first metatarsal are still unfused.

Another common coossification of two bones is the proximal and middle phalanx of the third digit of the pes. The two phalanges are separate in Miocene *Hapalops*, but are fused in many later sloths. Four specimens from the Leisey 1A locality exhibit the fused condition; UF 86952, 86870, 67127 and 87035. These

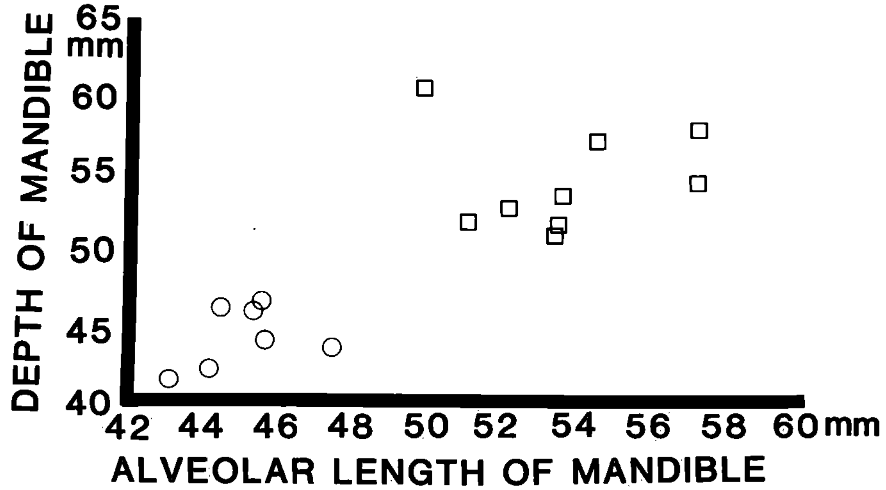

Figure 4. Comparison of total alveolar length of mandible against depth of mandible at third molariform in *Nothrotheriops texanus* from Leisey 1A (open circle) and *Nothrotheriops shastensis* (open square).

two bones are also fused in *Nothrotherium*. This feature seems to have been established early in the nothrotheres as they are already coossified in *Pronothrotherium typicum* (FM 14503) of Huayquerian and Montehermosan (early to middle Pliocene) age. In contrast these two bones do not fuse in the megalonychid, *Megalonyx*, until the late Pleistocene (McDonald 1977).

A pathological coossification of the right third and fourth metacarpals (UF 87003) is represented in the Leisey 1A sample. The area of fusion is restricted to the proximal end and excess bone tissue is present on the dorsal surface of both bones.

A single fifth metacarpal (UF 87010) was recovered. It differs from late Pleistocene forms in being more gracile. A similarly gracile fifth metacarpal was described from the Irvingtonian age Pool Branch, Florida locality by McDonald (1985).

Postcranially the skeleton of the Leisey 1A *Nothrotheriops* and other Irvingtonian specimens tend to be smaller than those from the Rancholabrean. This is shown by various plots for the humerus (Fig. 7). This separation does not hold as well for the femur (Fig. 8). A major impediment to a more accurate analysis of size trends in the post-cranial skeleton is the absence of the same bone from the various localities, so comparable samples are small. In many of the localities listed in Table 1, *Nothrotheriops* is represented by a single bone. However, based on the sample available from Leisey 1A, it does not appear that the size increase of *Nothrotheriops* from the Irvingtonian to Rancholabrean was as great as in *Paramylodon harlani* over the same period of time.

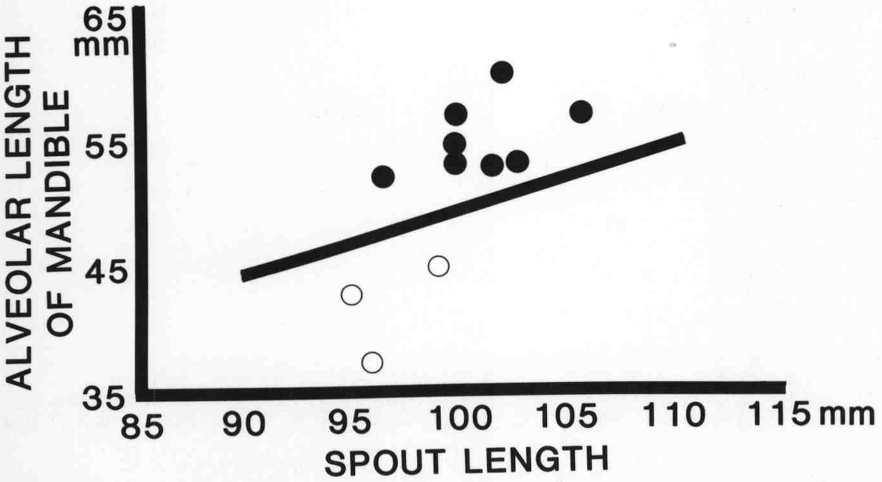

Figure 5. **Comparison of length of mandibular spout anterior to first molariform against total alveolar length of mandible in *Nothrotheriops texanus* (open circle) and *Nothrotheriops shastensis* (solid circle). Line represents ratio of 2:1 for spout length against alveolar length.**

Figure 6. ***Nothrotheriops texanus*** **right maxilla of juvenile, UF 83700, showing atavistic presence of caniniform (indicated by arrow). Scale bar 20 mm in length.**

Discussion.-- Hay (1916) based *Nothrotherium texanum* on an incomplete cranium (USNM 8353) recovered from a well in Wheeler County, Texas. He distinguished it from *Nothrotherium graciliceps* (= *N. shastense*) (Stock 1913), also based on a skull, on a number of morphological features. No comparison was made with *N. shastense* Sinclair (1905), since it was based on an edentulous mandible and 14 isolated teeth. Stock (1925) made *N. graciliceps* a subspecies of *N. shastense*. Lull (1929) reviewed the genus in his study of a mummified specimen from New Mexico and considered *Nothrotherium texanum* to be

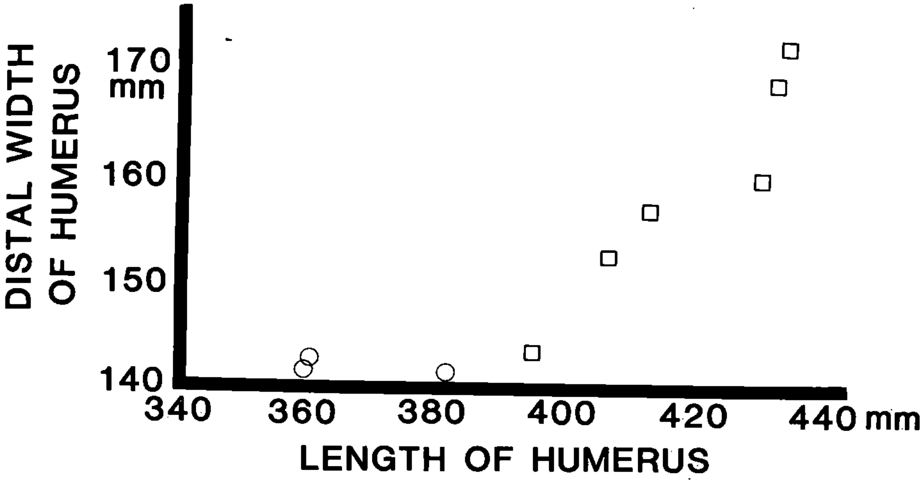

Figure 7. Comparison of humerus length against distal width across epicondyles in *Nothrotheriops texanus* (circle) and *Nothrotheriops shastensis* (square).

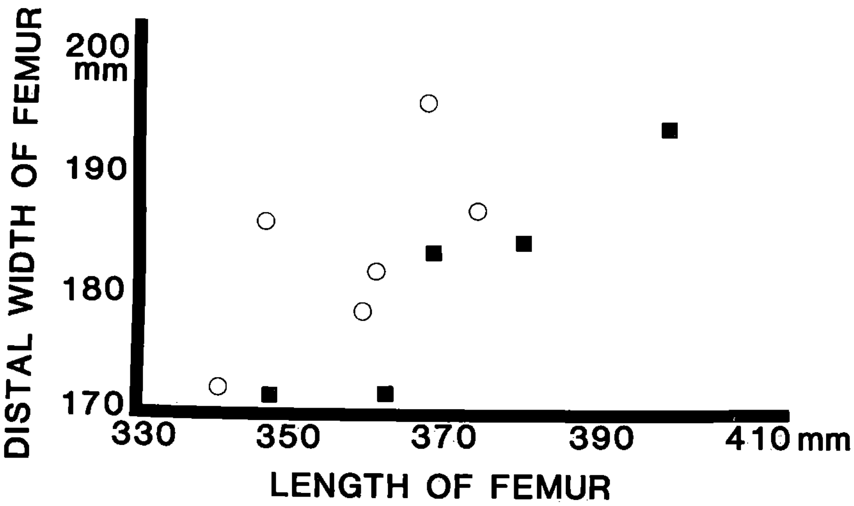

Figure 8. Comparison of femur length against mediolateral width of proximal end in *Nothrotheriops texanus* (circle) and *Nothrotheriops shastensis* (square).

synonymous with *N. shastense*. Since Lull's work it has generally been accepted that there is a single North American species, *N. shastense*. Hoffstetter (1954) proposed that the North American nothrothere was subgenerically distinct from the South American species and established the subgenus *Nothrotheriops*. Paula

Table 1. Irvingtonian records of *Paramylodon harlani* and *Nothrotheriops texanus*. Unpublished specimens are in the following collections: CI = College of Idaho; IMNH = Idaho Museum of Natural History; LACM = Los Angeles County Museum; UF = Florida Museum of Natural History; USNM = United States National Museum. Numbers in front of each locality refer to the localities on the map in Figure 15.

Locality	*Paramylodon harlani*	*Nothrotheriops texanus*	Reference
California			
1. Irvington Alameda Co	X	X	Savage 1951
2. Vallecito Creek San Diego Co.	X	X	Downs and White 1968
Florida			
3. Haile 16A Alachua Co.	X		UF
4. Inglis 1A Citrus Co.	X		Webb 1974
5. Leisey 1A Hillsborough Co.	X	X	This paper
6. Pool Branch Polk Co.		X	McDonald 1985
Idaho			
7. Oreana Owyhee Co.	X		CI
Kansas			
8. Adams Meade Co.		X	Hibbard and Taylor 1960
9. Courtland Canal Jewell Co.	X		Eshelman and Hager 1984
10. Kanopolis Ellsworth Co.	X		Hibbard et al. 1978
11. Sandahl McPherson Co.	X		Semken 1966
Nebraska			
12. Angus Nuckolls Co.	X		Schultz and Martin 1970
13. Gordon Sheridan Co.	X		Schultz and Stout 1948
14. Hay Springs Sheridan Co. (Type Locality for *Paramylodon nebrascensis* and *Mylodon garmani*)	X		Allen 1913; Brown 1903
Oklahoma			
15. Curtis Woodward Co.	X	X	Akersten and McDonald 1991
16. Holloman Tillman Co.	X		Dalquest 1977
Oregon			
17. Rome Malheur Co.	X		IMNH
Pennsylvania			
18. Port Kennedy Cave Montgomery Co.	X		Cope 1899

Table 1 Continued.

Locality	*Paramylodon harlani*	*Nothrotheriops texanus*	Reference
Texas			
19. Gilliland Baylor and Knox Cos.		X	Hibbard and Dalquest 1966
20. Rock Creek Briscoe Co.	X		Lull 1915
21. Wheeler Co. (Type Locality *Nothrotheriops texanus*)		X	Hay 1916
Washington			
22. Delight Adams Co.	X		Matthew 1902
Mexico			
23. El Golfo State of Sonora		X	Shaw 1981
Canada			
24. Medicine Hat Fauna 9 Province of Alberta	X		Harington 1978

Couto (1971) reviewed the North and South American forms and raised *Nothrotheriops* to generic status.

There does not seem to be any reason to believe that there is more than a single lineage of North American nothrothere. They appear in the early Pleistocene (Irvingtonian) and culminate in the Rancholabrean species *Nothrotheriops shastensis*. The question then arises as to the value of subdividing this lineage and formally recognizing an earlier evolutionary stage as a separate species.

In the continuum of an evolving lineage, it is difficult and somewhat arbitrary to demarcate the boundaries distinguishing two species. Smaller samples may show a marked separation in size or proportions which disappear as the sample size increases. Three of the criteria used here to distinguish *N. texanus* from *N. shastensis*; size, ratio of alveolar to predental length of maxilla, and ratio of alveolar length to length of mandibular spout--may blend as intermediate populations are found. However, since these criteria serve clearly to distinguish the two forms, use of a distinct binomen serves the practical purpose of identifying the earlier evolutionary stage of the lineage and thus aiding in the identification of the age of the fauna with which it is associated. The type of *Nothrotheriops texanus* is distinguishable from *N. shastensis* and falls easily within the range of the Leisey 1A sample. Other Irvingtonian samples are also referred to *N. texanus* based primarily on their smaller size. At this time all referred material of *N. texanus* occurs in the Irvingtonian and *N. shastensis* is exclusively Rancholabrean. The timing of the transition of *N. texanus* to *N. shastensis* is currently unknown and must await the recovery of intermediate cranial or mandibular material from known age faunas.

Family MYLODONTIDAE Gill 1872

Genus *Paramylodon* Brown 1903

Type Species.– *P. nebrascensis* Brown 1903 (= *Mylodon harlani* Owen 1840).

Discussion.– There has been a common trend in the recent literature to refer the North American species *harlani* to the genus *Glossotherium* (Kurtén and Anderson 1980). I have not followed this usage but rather have retained the older binomen, *Paramylodon harlani*. A short synopsis of the history of these names will demonstrate the nomenclatural problems involved.

Owen (1840) described *Mylodon darwinii* based on a complete mandible and *Glossotherium* based on a left temporal. *Glossotherium* originally was not used in a binomen. Owen (1842) described a second species of *Mylodon*, *M. robustus*. In a footnote in this same publication, Owen (1842:154) considered *Glossotherium* to be the same as *Mylodon darwinii*, the type species for *Mylodon*. Harlan (1831) described and figured a mandible from Big Bone Lick, Kentucky which he referred to his previously described *Megalonyx laqueatus*. This paper was later republished by Harlan (1835). The mandible was that of a mylodont, not a megalonychid, and Owen (1840; 1843) recognizing its affinities, proposed the species *harlani* which he placed in his genus *Mylodon*. This resulted in three species being recognized for the genus *Mylodon* (Leidy 1855). One, and possibly two, of these species represented other genera. Recognizing that more than one genus was represented, Reinhardt (1879) proposed the genus *Grypotherium* to replace *Mylodon* for the binomen *Mylodon darwinii*. Additional confusion arose from considering the species *robustus* to be the type species for *Mylodon* and placing *darwinii* in the genus *Glossotherium* (Ameghino 1889; Lydekker 1894). Kraglievich (1928), assuming that *Glossotherium* had no species attached to it, proposed the name *Glossotherium uruguayense* as the type species for *Glossotherium*, utilizing the temporal described by Owen as the type.

Brown (1903) established the genus *Paramylodon*, with the type species, *P. nebrascensis*. Unfortunately, many workers considered *harlani* to be the type species of *Mylodon* rather than *darwinii* (Stock 1914a, b, 1917, 1925) and felt that there were two North American mylodonts; *Mylodon harlani* and *Paramylodon nebrascensis*. Eventually the convention of recognizing a distinct genus for each species developed; *Mylodon darwinii*, *Glossotherium robustum* and *Paramylodon harlani* (Kraglievich 1928). During this time other species had been described for each of these genera or under a genus proposed as a substitute for an earlier name; for example, *Eumylodon chapadmalensis* (Kraglievich 1925) which later became *Glossotherium chapadmalense* (Kraglievich 1928). Hoffstetter (1952) used

Paramylodon as a subgenus of *Glossotherium*. Cartelle (1980) and Cartelle and Fonseca (1981) resurrected the name *Ocnotherium* Lund 1842 as a subgenus of *Glossotherium*. Given the date of publication of this name, *Ocnotherium* may be the next available name for South American species currently placed in *Glossotherium* should the name *Glossotherium* be considered invalid.

Despite this maze of nomenclatural proposals, there has been very little discussion of the morphological features that distinguish the various genera or the various species grouped within a particular genus. There has certainly been little consideration of evolutionary or phylogenetic relationships of the various taxa and the change in relationships implied by the changing of names. None of the previous studies have demonstrated that *Paramylodon* should be considered a junior synonym of *Glossotherium*. Using the genus *Glossotherium* for the North American species *harlani* is of dubious value (I would even question retaining it as a valid genus). I recommend continued use of the name *Paramylodon harlani* for Irvingtonian and Rancholabrean specimens of North American mylodonts. Use of the genus *Paramylodon* recognizes the geographic isolation and separate evolution of this lineage from the South American mylodonts. In an attempt to avoid further nomenclatural confusion I have followed Robertson (1976) in recognizing the North American Blancan mylodont as "*Glossotherium*" *chapadmalense*. This usage recognizes the ancestor-descendant relationship of the two forms and is with the full realization that further study of the relationships between the North and South American mylodonts is needed.

Paramylodon harlani (Owen 1840)

Mylodon harlani Owen 1840. Owen 1842 1843; Leidy 1855; Stock 1914a, 1914b, 1917, 1925.
Oryctotherium missouriense Harlan 1841. Perkins 1843.
Oryctotherium oregonense Perkins 1843.
Eubradys antiquus Leidy 1853
Megalonyx potens Leidy 1853
Mylodon sodalis Cope 1878
Mylodon renidens Cope 1895
Mylodon sulcidens Cope 1895
Paramylodon nebrascensis Brown 1903
Mylodon garmani Allen 1913
Mylodon tenuceps Stock 1917
Mylodon harlani tenuceps Stock. Stock 1925
Paramylodon harlani (Owen). Kraglievich 1928
Glossotherium (*Paramylodon*) *harlani* (Owen)., Hoffstetter 1952
Glossotherium harlani Kurtén and Anderson 1980

Type Specimen.— Partial right mandible, New York Lyceum, now missing.

Type Locality.– Big Bone Lick, Boone County, Kentucky (see Harlan 1831).

Referred Specimens.– **Leisey 1A:** UF 83769, 64400, 64373, crania; 87039-87042, 67426, 80215, 80911, 83791, 83983, 84077, 86158, 80215, isolated upper caniniform; 87051, 87070, 87058, 67427, 86379, 86739, 86738, 83337, 80778, 80779, M2; 80367, 83335, 87048, 87047, 87037, 84750, 64357, 87046, 87038, 87045, 87044, 87043, 80912, 84848, 80214, mandibles; 67436, 87054, 67437, 80895, 80531, 81216, 87063, 86767, 87065, 95880, isolated lower first molariform; 86846, 87045, 87044, 87043, 80912, 82004, 67446, isolated lower fourth molariform; 84136, 82933, 65851, 65855, 65856, 64364, humerus; 65857, ulna; 80163, radius; 65830, 65828, 65829, metacarpal I; 64368, 81791, metacarpal II; 65831, metacarpal III; 87024, metacarpal IV; 82245, metacarpal V; 80109, 81716, 64361, 80776, 63859, 80039, 80164, 87087, femora; 65860, 64365, 65862, 65861, 80176, 86930, tibiae; 64366, 87100, astragali; 65832, 82658, metatarsal II and mesocuneiform; 87105, 83986, metatarsal III; 65833, 83984, metatarsal V.

Description.– The large sample from Leisey 1A, like that from Rancho La Brea, permits an evaluation of the morphological variation that may be encountered in North American mylodonts. When compared with the Rancho La Brea and other samples, it permits the evaluation of evolutionary trends.

Except for its smaller size and a few minor differences, the skeletal anatomy of *P. harlani* from Leisey 1A resembles that of the sample from Rancho La Brea, which is well described in Stock's (1925) classic monograph. Discussion of the sample from Leisey 1A is restricted here to variation and evolutionary trends.

One evolutionary trend in *Paramylodon harlani* is the tendency to reduce or lose the anterior tooth of the upper dentition (= caniniform). Loss of this tooth parallels a similar loss in *Mylodon darwinii*. Loss of the upper caniniform was used by Brown (1903) in the diagnosis of the genus *Paramylodon*. Stock (1925) noted that in a sample of 45 skulls from Rancho La Brea, 21 had the first tooth on both sides, 14 had the tooth absent on both sides, 7 had the tooth on either the right or left side and 3 were doubtful regarding the condition.

The Leisey 1A sample has six specimens which preserve the anterior portion of the palate where this tooth is located (Fig. 9). Some have the tooth in place, and others have an open alveolus. Twelve isolated upper caniniforms were recovered. Unlike the Rancho La Brea sample all of these caniniforms are large with well developed occlusal surfaces. Based on the Leisey 1A sample it appears that the caniniforms had not experienced any reduction in the early Pleistocene. This observation is confirmed in several other early Pleistocene samples.

Prominent caniniforms are also present in *Paramylodon harlani* from the earlier Inglis 1A and Haile 16A faunas of Florida. Unfortunately, neither of these samples is as large as that from Leisey 1A. Specimens from Irvingtonian localities outside of Florida, such as Rock Creek, Texas (Lull 1915), and Hay Springs,

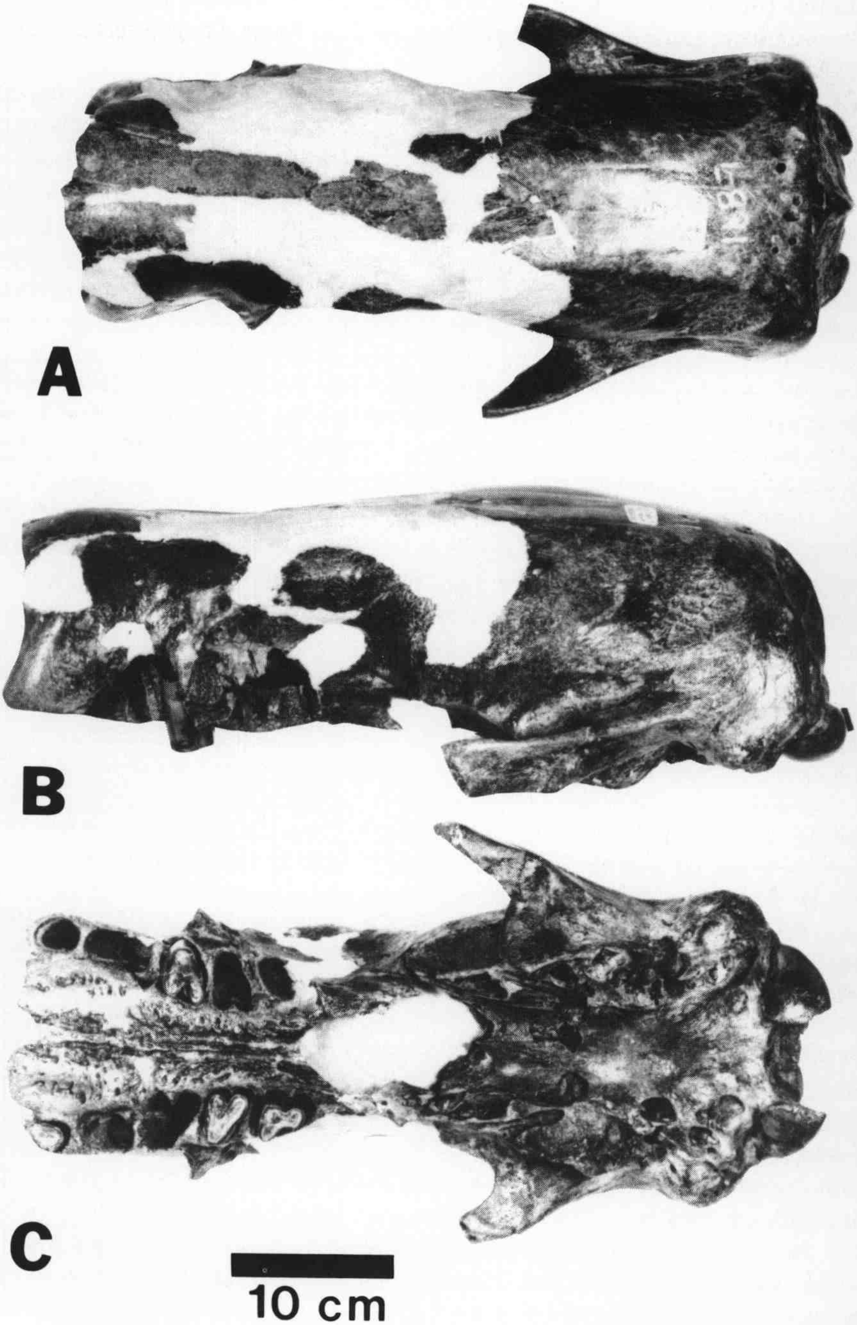

Figure 9. Skull of *Paramylodon harlani*, UF 83769, in (A) dorsal, (B) lateral and (C) ventral views.

Nebraska (the type locality for *Mylodon garmani* [= *P. harlani*] [Allen 1913] also have prominent caniniforms. A partial palate from Rome, Oregon has alveoli for both caniniforms.

The holotype of *Paramylodon nebrascensis* (AMNH 2780) is one possible exception to the pattern that all Irvingtonian *Paramylodon* have both upper caniniforms. Brown's (1903) diagnosis of *Paramylodon* was based partially on the absence of the first upper tooth (=caniniform). However, the holotype was actually found near Hay Springs. Thus, it may not be part of the Hay Springs fauna proper, but from younger deposits.

Supporting evidence for the presence of a caniniform in all the individuals of *Paramylodon* from the Leisey 1A fauna is provided by the first lower cheek tooth. All specimens (12), both isolated and those still in the mandible, display a double wear surface reflecting occlusion against the upper caniniform anteriorly and the first upper molariform posteriorly. Specimens lacking the upper caniniform, such as the holotype of *P. nebrascensis*, have a lower first molariform with a wear surface only on the posterior side of the tooth.

There are two morphs of the upper caniniform represented in the sample from Leisey 1A (Fig. 10). The first form develops an occlusal surface at an angle oblique to the long axis of the tooth. The occlusal surface of the second morph develops perpendicular to the long axis of the tooth, so that the occlusal end of the tooth appears truncated. In the second morph the occlusal surface reflects the shape of the tooth's cross-section. The radius of curvature of the two morphs is the same, but the dimensions of the tooth anteroposteriorly and mediolaterally are larger in the first morph (Fig. 11). The occlusal surface of both morphs bear prominent dorsoventral striae and less prominent mediolateral striae. Caniniforms from Inglis 1A (3 specimens) and Haile 16A (1 specimen) include only the larger morph with the obliquely worn occlusal surface. The type of *Mylodon garmani* has upper caniniforms that are worn nearly perpendicular to the long axis of the tooth and has a smaller cross-sectional area.

Both morphs are present in the sample from Rancho La Brea, with nine specimens showing oblique wear and five perpendicular wear. Mean size for the Rancho La Brea population is smaller than that of the Leisey 1A population for both morphs (Fig. 11). There does not appear to be any significant difference in the dimensions of the two morphs from Rancho La Brea but the size difference in the Leisey sample is more noticeable. Those with oblique wear from Rancho La Brea have an anteroposterior (AP) length of 17.3 ± 3.2 mm and mediolateral dimension (ML) of 14.3 ± 1.1 mm, N = 8; while the caniniform with perpendicular wear has an AP dimension of 17.2 ± 3.1 and an ML width of 14.6 ± 1.0 mm, N = 5. In the Leisey 1A sample the values are 23.8 ± 3.1 mm for AP and 15.5 ± 2.2 mm for ML for caniniforms with oblique wear, N = 6; and 19.2 ± 1.6 for AP length and 13.9 ± 0.47 mm for ML width, N = 5, for caniniforms with perpendicular wear.

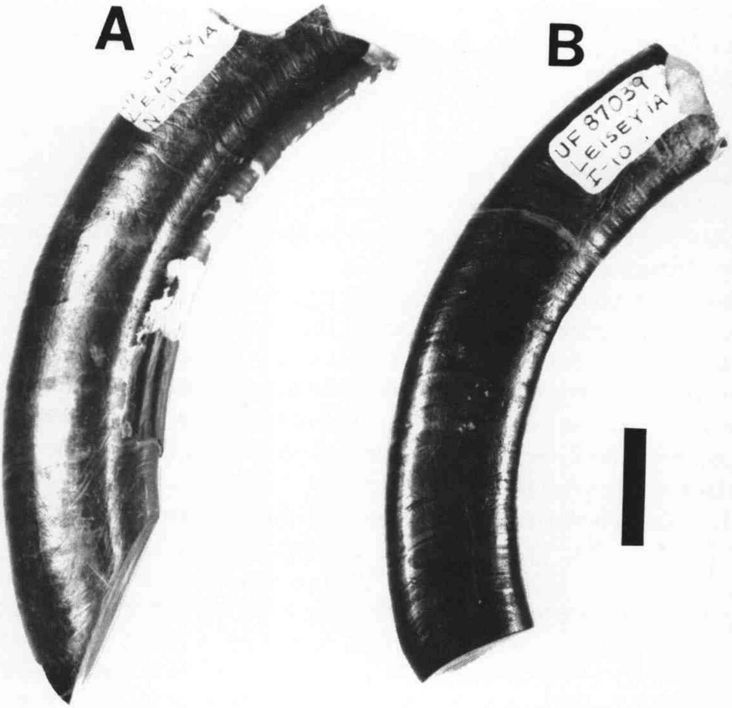

Figure 10. **Lateral view of upper caniniforms of *Paramylodon harlani* showing (A) oblique (UF 87042) and (B) perpendicular (UF 87039) occlusal wear morphologies. Scale bar 10 mm in length.**

Stock (1925, fig. 66) illustrated a series of right lower fourth molariforms showing variation in the shape of the occlusal surface. In the Leisey 1A sample, 14 lower fourth molariforms of both juveniles and adults are preserved. Since sloths lack deciduous teeth, both juveniles and adults can be compared since size is the only difference. A variation in the lower fourth molariform present in the Leisey 1A sample not illustrated by Stock is the presence of an accessory lobe on the lateral side of the isthmus connecting the anterior and posterior lobes of the tooth. This lobe is absent in three specimens, slightly developed in five individuals, prominent in five and in one specimen, UF 82004, there are two lobes (Fig. 12). Another individual, UF 87038, lacks the lobe on the isthmus but has an additional lobe on the posterolateral corner of the anterior lobe of the tooth. The presence of a prominent lobe is reflected in the outline of the alveolus so that even mandibles which have lost the fourth molariform will indicate its occurrence.

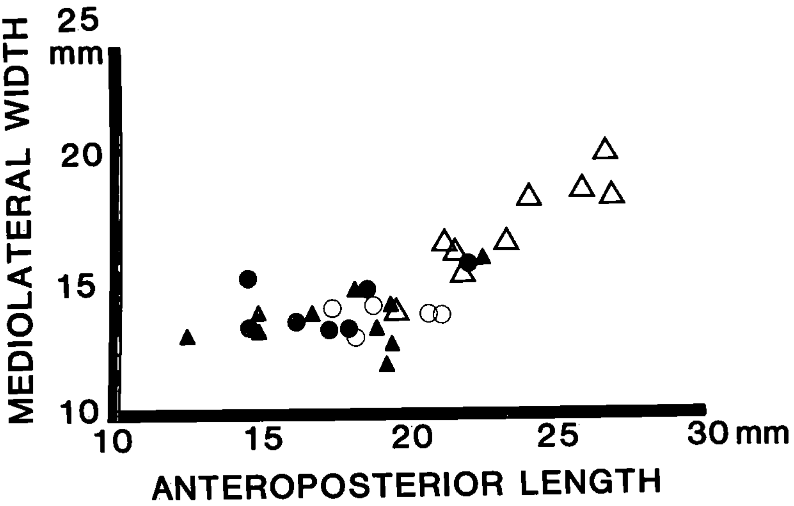

Figure 11. Comparison of anteroposterior and mediolateral dimensions of upper caniniforms of Irvingtonian (open symbols) and Rancholabrean (closed symbols) *Paramylodon harlani*. Triangle indicates oblique wear, circle indicates perpendicular wear.

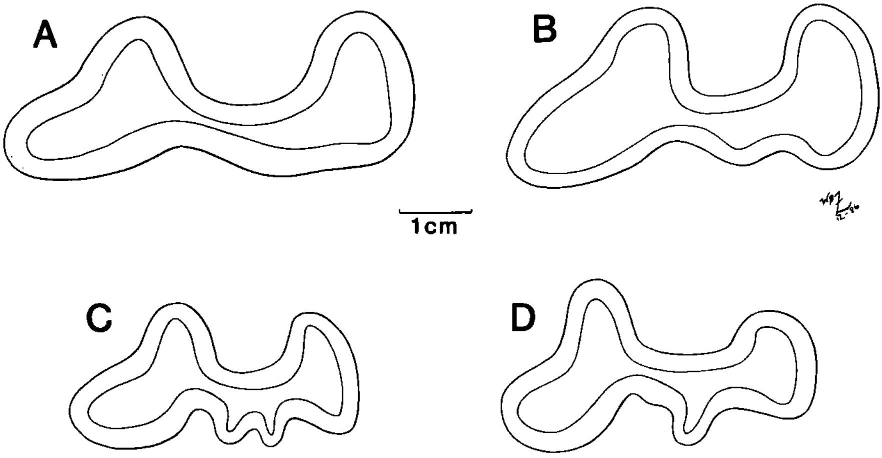

Figure 12. Outline drawings of occlusal surface of lower fourth molariform of *Paramylodon harlani* showing variation in presence of extra columns. (A) UF 80367, (B) UF 67446, (C) UF 82004, (D) UF 83335.

As the cheek teeth of ground sloths lack a distinct crown, and are rootless and grow continuously, it is difficult to directly determine the degree of hypsodonty by the usual methods (Janis 1988; Janis and Fortelius 1988). However, the maximum depth of the mandible below the last cheek tooth relative to the alveolar length of the tooth row of the mandible can be used to establish an "index of hypsodonty" for ground sloths, which reflects a relative greater increase in tooth height relative to an overall increase in size. As the height of the cheek teeth in ground sloths increases, the depth of the jaw increases, but the overall length of the tooth row does not change. Therefore, the depth of the jaw is less than the length of the tooth row in sloths with less hypsodont teeth whereas the depth of the jaw (as measured below the last cheek tooth) becomes greater than length of the tooth row in sloths with more hypsodont teeth. Examination of changes in this index in which the depth of the mandible increases without any change in overall body size can thus be used to possibly identify changes in diet from less to more abrasive foods, or, as was suggested by Janis (1988), a possible shift in habitat preference from closed to more open habitat.

Such a change accounts for one of the differences that exists between the Irvingtonian and Rancholabrean samples of *Paramylodon harlani*. Irvingtonian specimens have a relatively shallower mandible relative to the alveolar length than Rancholabrean specimens (Fig. 13). This relatively deeper mandible in Rancholabrean *Paramylodon* is not formed as in *Nothrotheriops* in which the relatively greater depth of the jaw is the result of an allometric change due to an increase in size (Fig. 4) but rather the deepening of the mandible is greater than that expected as resulting from an increase in size. Both the Blancan "*Glossotherium*" *chapadmalense* and Irvingtonian specimens of *P. harlani* have similar proportions of the mandibular depth to alveolar length. Yet Rancholabrean individuals of *P. harlani* have relatively deeper mandibles than individuals of Irvingtonian age with similar length tooth rows. This deepening of the mandible allows the teeth to be taller overall and thus aids in compensating for increased wear caused by feeding on abrasive food, whether or not the abrasion is due to factors intrinsic or extrinsic to the plants consumed. Stock (1925) interpreted *Paramylodon* as a grazer and inhabitant of open country, and it appears that from the Irvingtonian to the Rancholabrean this ground sloth made a shift to greater hypsodonty which allowed it to make better use of this niche or to shift from closed to more open country.

Stock (1925) reported that only 2 out of 20 specimens from Rancho La Brea had the mesocuneiform fused with the second metatarsal. Two specimens from Leisey 1A, UF 65832 and 82658, have this condition. Unfused mesocuneiforms or second metatarsals are not represented in the Leisey 1A sample. Neither element is preserved in the skeleton of "*Glossotherium*" *chapadmalense* (UF 10922) from Haile 15A, so the condition of the Blancan predecessor is unknown. The possibility exists that these two bones were unfused in "*G.*" *chapadmalensis*, and that this digit may have born an ungual, a feature lost in later species such as *P. harlani* and *G. robustum*.

There is a noticeable size difference between "*Glossotherium*" *chapadmalense* in the Blancan and *Paramylodon harlani* in the Rancholabrean. The gap is bridged by a graded series of specimens of *P. harlani* in the Irvingtonian. Samples

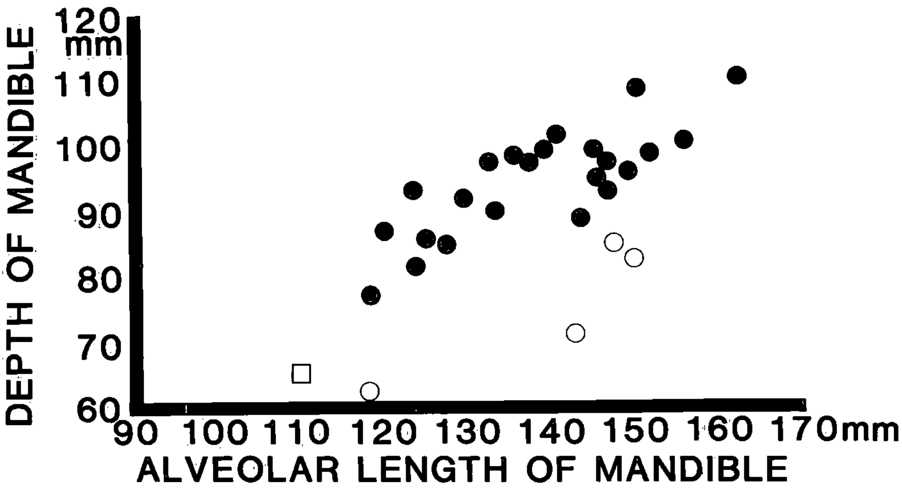

Figure 13. Comparison of alveolar length and depth of mandible in Rancholabrean, Irvingtonian and Blancan mylodonts. Blancan "*Glossotherium*" *chapadmalense* (open square), Irvingtonian *Paramylodon harlani* (open circle), and *Rancholabrean P. harlani* (solid circle).

of Irvingtonian *P. harlani* are not large enough to quantify the size change. It can nevertheless be indicated in a simplistic way for certain abundant elements. A series of astragali (Fig. 14) from different Florida faunas demonstrate the gradual increase in size. The sequence of these faunas was independently determined using the biochronology of other species present (see Morgan and Hulbert this volume). This gradational sequence blurs the distinction between "*G.*" *chapadmalense* and *P. harlani* when based on size alone. A careful reevaluation of the morphological features which distinguish the two taxa is therefore needed. Such a reevaluation, however, must await a larger sample of Blancan and very early Irvingtonian mylodonts.

PALEOECOLOGY

Juvenile Representation.— The samples of both *Nothrotheriops* and *Paramylodon* include juveniles as indicated by limb bones lacking epiphyses, incompletely fused cranial bones, or isolated teeth that are conical. The juvenile characteristics of the *Paramylodon* sample are more strikingly displayed than those of the *Nothrotheriops* sample. This is indicated in *Paramylodon* by the presence of mandibles with conical teeth. Sloth teeth are markedly expanded basally during early stages of their eruption. They generally have become parallel-sided,

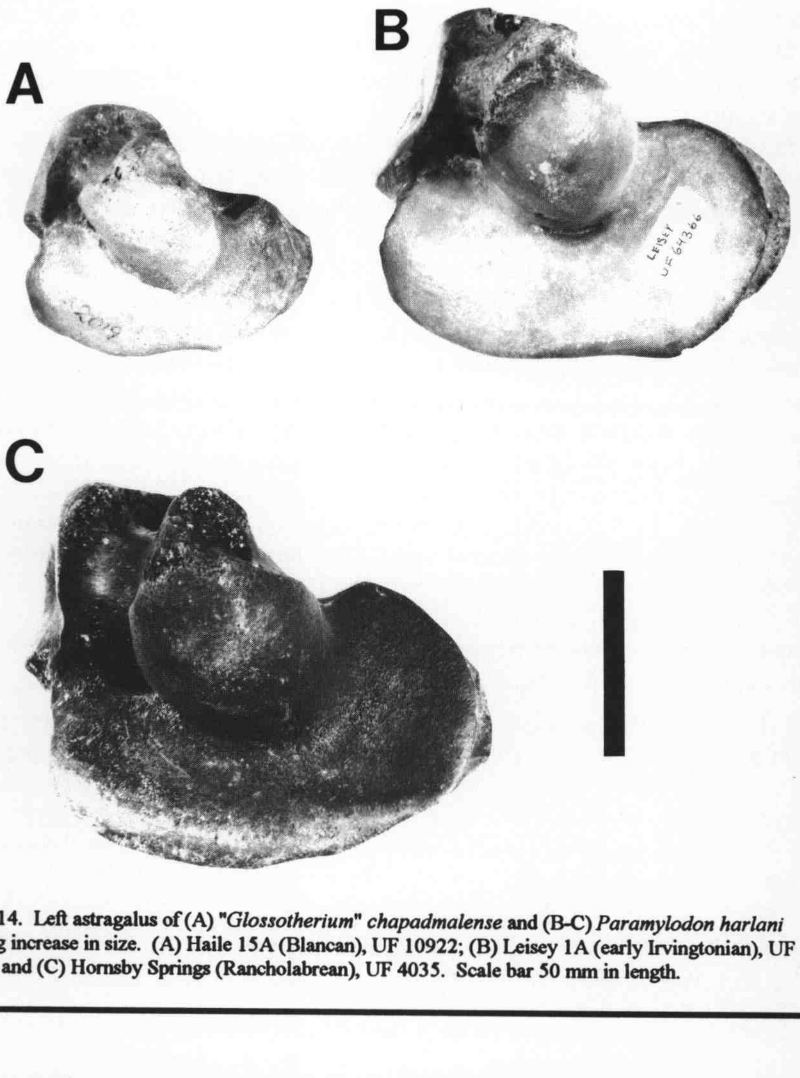

Figure 14. Left astragalus of (A) "*Glossotherium*" *chapadmalense* and (B-C) *Paramylodon harlani* showing increase in size. (A) Haile 15A (Blancan), UF 10922; (B) Leisey 1A (early Irvingtonian), UF 64366; and (C) Hornsby Springs (Rancholabrean), UF 4035. Scale bar 50 mm in length.

however, prior to fusion of the epiphyses of the limbs and the presence of conical teeth indicates an extremely young individual. In the Leisey sample there are a number of juvenile *Paramylodon* jaws with conical teeth. On the other hand, juvenile mandibles of *Nothrotheriops* are recognized on the basis of their smaller size and porous texture of the bone, but all specimens have parallel-sided teeth. It is not clear whether nothrothere teeth progress more rapidly that those of mylodonts, or whether there is some taphonomic bias against younger nothrotheres at the Leisey site.

At the time of deposition of Leisey 1A, four species of ground sloth were present in Florida: *Megalonyx wheatleyi*, *Eremotherium* n. sp., *Nothrotheriops* *texanus* and *Paramylodon harlani*. Yet only the latter two species were recovered from this deposit, and they were quite richly sampled. Their abundance, as well as the absence of *Megalonyx* and *Eremotherium*, reflects the local environment and is not an artifact of small sample size.

Distribution of *Eremotherium* in the United States is restricted to the Gulf and southern Atlantic coastal plains. The few inland records of this species are from riverine deposits, suggesting that the invasion inland was facilitated by the river, but limited to gallery forests. A similar distribution pattern occurs in South America where the genus is found along the coast or lowlying coastal plains. *Eremotherium* has generally been interpreted as a browser. This is confirmed by the recovery from the tar seeps of Peru and Ecuador of cut twigs, whose length matches the distance between the transverse lophs of eremothere teeth (A.G. Edmund pers. comm.). Absence of *Eremotherium* from the deposit cannot be attributed to its antiquity, since the genus is present in the older Inglis 1A, DeSoto Shell Pit, and Haile 7C faunas (Webb 1974; Morgan and Hulbert, this volume). Specimens of *Eremotherium* were collected at the Leisey Shell Pit (but not the Leisey 1A site). In fact, *Eremotherium* was the most common ground sloth from the Leisey Shell Pit 3 quarry, located only 0.5 km north of Leisey 1A.

Megalonyx is the most ubiquitous of the North American ground sloth genera. The Irvingtonian species, *M. wheatleyi* did not range as widely as the Rancholabrean *M. jeffersonii*, but is known from numerous localities in Florida (McDonald 1977). Two of these, Inglis 1A, which is earlier than the Leisey 1A fauna, and the younger McLeod fauna, produced large numbers of individuals of *Megalonyx* indicating that the genus was common in Florida. *Megalonyx*, in fact, can be considered the most common ground sloth in Florida, having been found in deposits ranging in age from late Hemphillian to late Rancholabrean. Like *Eremotherium*, it is hypothesized to be a browser and an inhabitant of forests. Although commonly found in deposits along rivers, unlike *Eremotherium*, it was not restricted to gallery forests. Given its widespread distribution, its absence from the Leisey 1A fauna must reflect local ecological conditions which prevented it from living close to the area of deposition. However, a few specimens of *M. wheatleyi* are known from Leisey Shell Pit 3.

More is known of the ecology and food preferences of *Nothrotheriops shastensis*, the descendent species of *N. texanus* than any other ground sloth, except possibly *Mylodon darwinii*. The preserved dung balls of both *N. shastensis* and *M. darwinii* have been collected and analyzed, although more so for *Nothrotheriops* (Hansen 1978; Martin, Sabels and Shutler 1961). Cave deposits preserving the dung of *N. shastensis* are chronologically and geographically restricted to the late Rancholabrean of the Southwest, so caution must be exercised in extrapolation from these data. Although the primary food resource was desert shrubs (eg. *Sphaeralcea*, *Ephedra*, *Atriplex* and *Acacia*), *N. shastensis* was catholic in its tastes and an opportunistic feeder (Hansen 1978). As pointed out by McDonald (1985) the plant types in Florida available to *Nothrotheriops* are similar enough to their western relatives that they were probably utilized by the genus.

Nothrotheriops and *Megalonyx* in the late Pleistocene seem to be ecologically incompatible. There are a few faunas in the western United States which contain both genera, but there is a marked difference in the number of individuals of each genus. At Rancho La Brea in Los Angeles, numerous individuals of *Nothrotheriops* have been recovered but only parts of a single individual of *Megalonyx* (Stock 1925). Likewise a similar pattern is seen in the fauna from San Josecito Cave--numerous individuals of *Nothrotheriops*, but a single individual of *Megalonyx* (Stock 1943). The only other locality in Florida at which *Nothrotheriops* has been found, Pool Branch, did not include *Megalonyx* (McDonald 1985). This generally consistent pattern of exclusion suggests that the few localities where both genera have been recovered are probably near an ecotone that provided a small area of overlap between their preferred habitats.

Paramylodon harlani is as common as *Nothrotheriops* in the Leisey 1A fauna (9 and 8 individuals respectively). Irvingtonian records of the species are rare, as in the case of *Nothrotheriops* so it is difficult to evaluate the degree of overlap in their habitat preference. Both are known from Rancho La Brea but *P. harlani* is the more abundant. *P. harlani* is similarly abundant at American Falls Reservoir, Idaho in which *Megalonyx* is also common but *Nothrotheriops* is absent. The ecological requirements of *P. harlani* apparently were such that it could co-exist with either *Nothrotheriops* or *Megalonyx* with equal probability. Stock (1925) suggested that *P. harlani* was a grazer, and this interpretation has been followed by most subsequent workers. It could also be argued that the powerful forelimbs, with the expanded distal end of the humerus, short radius, ulna with an enlarged olecranon process and dorsoventrally flattened unguals permitted *Paramylodon* to dig up roots and tubers. Both interpretations permit us to view *Paramylodon* as primarily an inhabitant of scrub or open country habitat.

BIOSTRATIGRAPHY

Compared to other North American ground sloth genera, *Nothrotheriops* along with *Eremotherium*, was a relatively recent addition to the North American fauna. The first ground sloth in North America is the megalonychid, *Pliometanastes*, from the early Hemphillian (Late Miocene) (Hirschfeld and Webb 1968). *Pliometanastes* is replaced by *Megalonyx* in the late Hemphillian. The mylodont lineage also first appears in the early Hemphillian and is represented by the genus *Thinobadistes* (Webb 1989). A second invasion of mylodonts occurred in the Blancan with the appearance of "*Glossotherium*" *chapadmalense* (Robertson 1976). It is presumed, but not yet demonstrated, that *Paramylodon harlani* is derived from "*G.*" *chapadmalense* and does not represent a third immigration of mylodonts into North America.

Webb and Marshall (1982) recognized three phases to the Great American Faunal Interchange, with the third phase subdivided into two parts. The first rance of *Nothrotheriops* is considered to be indicative of Phase 3B, and Leisey 1A appears to be the earliest fauna which includes *Nothrotheriops*. *Eremotherium* is present in four Florida late Blancan sites (Morgan and Hulbert this volume) and thus entered Florida much earlier. The slightly younger El Golfo fauna, State of Sonora, Mexico is the earliest west coast record of *Nothrotheriops*. It is considered to be early Irvingtonian in age (Shaw 1981). A supposed Blancan record of *Nothrotheriops* (Golz, et al. 1974) has since been determined to be a megalonychid, probably *Megalonyx* (Akersten and McDonald 1991).

BIOGEOGRAPHY

The wide coast to coast distribution of *Nothrotheriops* (Fig. 15) at the time of its earliest appearance in North America suggests a fairly rapid dispersal and integration into the North American fauna. This widespread distribution in the Irvingtonian is in marked contrast to its range in the later Rancholabrean in which it is confined to the western United States and northern Mexico (Akersten and McDonald 1991). Assuming that the ecological requirements of *Nothrotheriops* did not change during this time, the observed range reduction may represent the animal's response to changes in available habitat. McDonald (1985) has already suggested that its disappearance from Florida was due to the onset of more mesic conditions in the early Rancholabrean. Whether this pattern holds in other parts of its range can only be determined by the recovery of additional specimens with associated pollen or flora.

Unlike *Nothrotheriops*, there does not appear to be an appreciable difference in the Irvingtonian and Rancholabrean distribution of *Paramylodon*. During the Irvingtonian, the northern edge of its range was at Rome, Oregon; Hay Springs, Nebraska and Port Kennedy Cave, Pennsylvania. Northernmost records of *Paramylodon* in the Rancholabrean include the Olympic Peninsula, Washington; American Falls, Idaho; Tecumseh, Nebraska; and Big Bone Lick, Kentucky. Such differences that do exist more likely reflect the relative paucity of Irvingtonian faunas compared to those of the Rancholabrean.

McNab (1985) suggested that the northern expansion of *Paramylodon* was facilitated by the combination of its large size and long hair. This permitted it to tolerate climates with seasonally cool to cold periods. Another factor which may have contributed to heat retention is its relatively short and compact limbs which would have had a low ratio of surface area to volume. *Nothrotheriops* too was covered with long hair but had a smaller body volume and its limbs were long and slender. Studies of amino acid ratios in the bone indicate that *Nothrotheriops* had a core body temperature lower than expected for an animal of its size (McNab 1985). Northernmost records of *Nothrotheriops* are from southern Oregon, southern Utah, and Oklahoma. Comparison of *Paramylodon* to the similar sized South American genus, *Mylodon*, by McNab showed that *Mylodon* and by

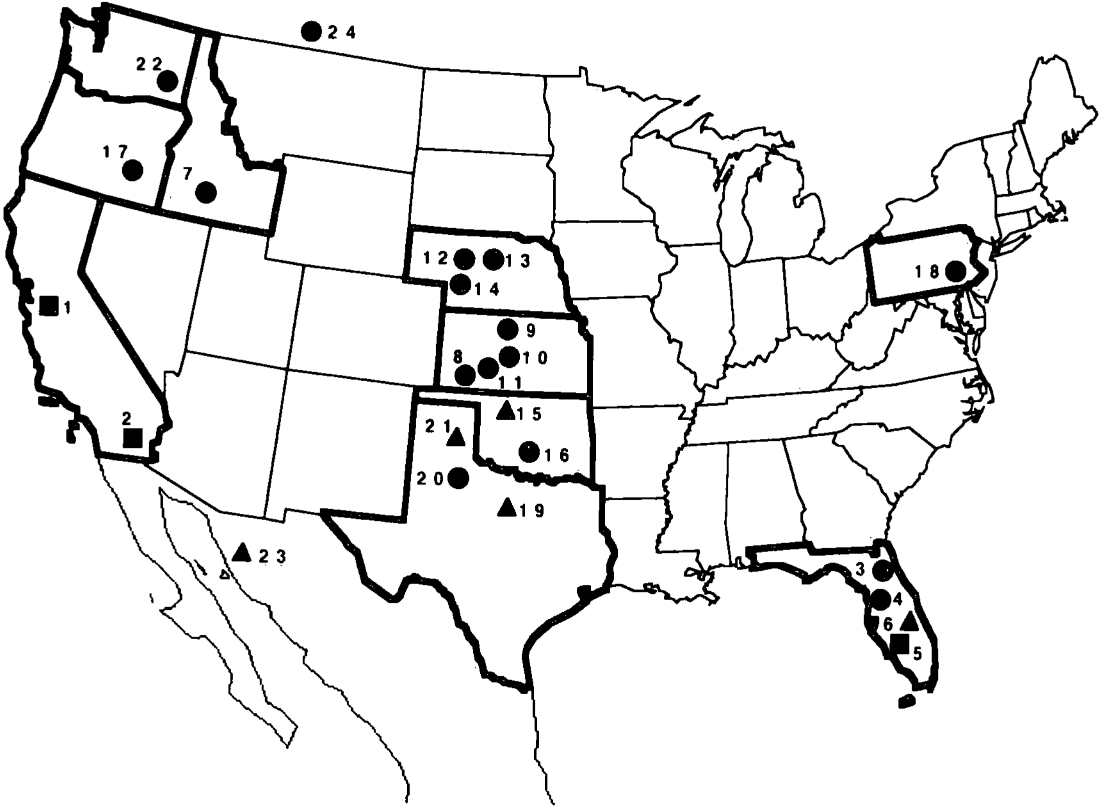

Figure 15. Distribution of *Nothrotheriops texanus* and *Paramylodon harlani* in the Irvingtonian. Symbols are: triangles = localities with only *Nothrotheriops texanus*, circles = localities with only *Paramylodon harlani*, squares = localities with both taxa. Numbers refer to the localities listed in Table 1.

inference *Paramylodon* had a lower thermal conductance than *Nothrotheriops*, thus permitting a greater tolerance to colder environments. As already noted, the Blancan age "*Glossotherium*" *chapadmalense*, the probable ancestor to *Paramylodon harlani*, is a much smaller animal, roughly half the size of the Rancholabrean form. Although the number of faunas containing this species is small, they all tend to be restricted to the southern United States (Arizona, Texas and Florida). The northward expansion of the range of *P. harlani* during the Irvingtonian may have been possible due to improved thermoregulation permitted by the increase in body size, already discussed. The stability of *Paramylodon*'s distribution from the Irvingtonian to the Rancholabrean, in contrast to the reduction of range of *Nothrotheriops*, may reflect this difference in thermal sensitivity rather than being controlled by changes in habitat or food resources.

LITERATURE CITED

Akersten, W. A., and H. G. McDonald. 1991. *Nothrotheriops* from the Pleistocene of Oklahoma and paleogeography of the genus. Southwest Nat. 36(2):178-185.

Allen, G. M. 1913. A new *Mylodon*. Mem. Mus. Comp. Zool. 40(7):319-346.

Ameghino, F. 1889. Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Act. Acad. Nac. de Cienc. Cordoba:661-757.

Brown, B. 1903. A new genus of ground sloth from the Pleistocene of Nebraska. Bull. Amer. Mus. Nat. Hist. 14(22):569-583.

Cartelle, C. 1980. Estudo comparativo do Rádio e esqueleto da Mão de *Glossotherium* (*Ocnotherium*) *giganteum* Lund, 1842. An. Acad. brasil. Cienc. 52(2):359-377.

_____, and J.S. Fonseca. 1981. Espécies do gênero *Glossotherium* no Brasil. Anais II Congr. Latino-Americano Paleon., Porto Alegre:805-818.

Cope, E. D. 1899. Vertebrate remains from the Port Kennedy bone deposit. J. Acad. Nat. Sci. Philadelphia 11:193-267.

Dalquest, W. W. 1977. Mammals of the Holloman local fauna, Pleistocene of Oklahoma. Southwest Nat. 22(2):255-268.

Downs, T., and J. A. White. 1968. A vertebrate faunal succession in superposed sediments from late Pliocene to middle Pleistocene in California. Proc. 23rd Internat. Geol. Congr. Prague 10:41-47.

Eshelman, R., and M. Hager. 1984. Two Irvingtonian (Medial Pleistocene) vertebrate faunas from North Central Kansas. Pp. 384 - 404 *in* H.H. Genoways and M.R. Dawson, eds. Contributions in Quaternary Vertebrate Paleontology: A Volume in Memorial to John E. Guilday. Carnegie Mus. Nat. Hist. Spec. Publ. No. 8:1-538.

Golz, D. J., G. T. Jefferson, and M. P. Kennedy. 1974. Late Pliocene vertebrate fossils from the Elsinore Fault Zone, California. J. Paleon. 51(4):864-866.

Hansen, R. M. 1978. Shasta ground sloth food habits, Rampart Cave, Arizona. Paleobiology 4(3):302-319.

Harington, C. R. 1978. Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. Syllogeus No. 15:1-105.

Harlan, R. 1831. Description of the jaws, teeth and clavicle of the *Megalonyx laqueatus*. Monthly Amer. J. Geol. Nat. Sci. 1:74-76.

_____. 1835. Description of the jaws, teeth and clavicle of the *Megalonyx laqueatus*. Medical and Physical Researches:334-336.

Hay, O. P. 1916. Descriptions of two extinct mammals of the Order Xenarthra from the Pleistocene of Texas. Proc. U.S. Nat. Mus. 51(2147):107-123.

Hibbard, C. W., and W. W. Dalquest. 1966. Fossils from the Seymour Formation of Knox and Baylor counties, Texas and their bearing on the Late Kansan climate of that region. Contrib. Mus. Paleontol. Univ. Michigan 21(1):1-66.

Hibbard, C. W., and D. W. Taylor. 1960. Two late Pleistocene faunas from southwestern Kansas. Contrib. Mus. Paleon. Univ. Michigan 16(1):1-223.

Hibbard, C. W., R. J. Zakrzewski, R. E. Eshelman, C. D. Griggs, and C. Griggs. 1978. Mammals from the Kanopolis local fauna, Pleistocene (Yarmouth) of Ellsworth County, Kansas. Contrib. Mus. Paleon. Univ. Michigan 25(2):11-44.

Hirschfeld, S. E., and S. D. Webb. 1968. Plio-Pleistocene megalonychid sloths of North America. Bull. Florida State Mus., Biol. Sci. 12(5):213-296.

Hoffstetter, R. 1952. Les mammifères pléistocenes de la République de L'Équateur. Mem. Soc. Géol. France 66:1-391.

Hoffstetter, R. 1954. Les Gravigrades (Édentés, Xénarthrés) des cavernes de Lagoa Santa (Minas Gerais, Brésil). Ann. Sc. Nat. Zool. 16:741-764.

Janis, C. M. 1988. An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. Pp. 367-387 *in* D. E. Russell, J.-P. Santoro, and D. Sigogneau-Russell, eds. Teeth Revisited: Proc. VIIth Internatl. Symp. Dental Morph., Paris 1986. Mem. Mus. Natl. Hist. Nat., Paris (serie C)53.

Janis, C. M., and M. Fortelius. 1988. On the means whereby mammals achieve increased functional durability of their dentitions, with special reference to limiting factors. Biol. Rev. 63:197-230.

Kraglievich, L. J. 1925. Cuatro nuevos gravigrados de la fauna araucana "chapadmalense". Ann. Mus. Nac. Hist. Nat. 33:215-235.

_____. 1928. "*Mylodon darwinii*" Owen es la especie genotipo de "*Mylodon*" Ow. Rectificacion de la nomenclatura genérica de los milodontes. Physis 9:169-185.

Kurtén, B., and E. Anderson. 1980. Pleistocene Mammals of North America. Columbia Univ. Press. New York:442 pp.

Leidy, J. 1855. A memoir on the extinct sloth tribe of North America. Smithsonian Contrib. Knowl. 7: 1-68.

Lull, R S. 1915. A Pleistocene ground sloth, *Mylodon harlani*, from Rock Creek, Texas. Amer. J. Sci. 39(232):327-385.

_____. 1929. A remarkable ground sloth. Mem. Peabody Mus., Yale Univ. 3(2):1-21.

Lydekker, R. 1894. Contributions to a knowledge of the fossil vertebrates of Argentina. Pt. 2. Extinct edentates of Argentina. Ann. Mus. de La Plata, Paleontologia Argentina Pt. 3:1-103.

Martin, P. S., B. E. Sabels, and D. Shutler Jr. 1961. Rampart Cave, coprolite and ecology of the Shasta Ground Sloth. Amer. J. Sci. 259:102-127.

Matthew, W. D. 1902. List of the Pleistocene fauna from Hay Springs, Nebraska. Bull. Amer. Mus. Nat. Hist. 16(24):317-322.

McDonald, H. G. 1977. Description of the osteology of the extinct gravigrade edentate, *Megalonyx*, with observations on its ontogeny, phylogeny and functional anatomy. M.S. Thesis, Univ. Florida, Gainesville.

_____. 1985. The Shasta Ground Sloth, *Nothrotheriops shastensis* (Xenarthra, Megatheriidae) in the Middle Pleistocene of Florida. Pp. 95-104 *in* G. G. Montgomery, ed. The evolution and ecology of armadillos, sloths and vermilinguas. Smithsonian Inst. Press, Washington, D.C., 451 pp.

McNab, B. K. 1985. Energetics, population biology, and distribution of xenarthrans, living and extinct. Pp. 219 - 232 *in* G. G. Montgomery, ed. The evolution and ecology of armadillos, sloths and vermilinguas. Smithsonian Inst. Press, Washington, D.C., 451 pp.

Owen, R. 1840. The zoology of the voyage of the H.M.S. Beagle, 1832-1836. Pt. 1, Fossil mammals. London:73-99.

_____. 1842. Description of the skeleton of an extinct giant sloth, *Mylodon robustus* Owen, with observations on the osteology, natural affinities, and probable habits of the megatheroid quadrupeds in general. London, 176 pp.

_____. 1843. Letter from Richard Owen, esq., F.R.S., F.G.S., etc. etc., on Dr. Harlan's notice of new fossil mammalia. (Letter dated 1842). Amer. J. Sci. ser. 1 Vol. 44:341-345.

Paula Couto, C. de. 1971. On two small Pleistocene ground sloths. Acad. Brasileira Cienc. Anais 43 suppl.:499-513.

_____. 1974. The Manus of *Nothrotheriops shastensis* (Sinclair 1905). Anais do XXVIII Congresso Brasileiro de Geologia:165-176.

Reinhardt, J. 1879. Beskrivelse af Hovedskallen af et Kaempedovendyr, *Grypotherium darwinii*, fra La Plata-Landesnes pleistocene. Dannelser. Vidensk. Selsk. Skr., 5 Raekke naturvidenskabelig og mathematisk Afd. 12:351-380.

Robertson, J. S., Jr. 1976. Latest Pliocene mammals from Haile XVA, Alachua County, Florida. Bull. Florida State Mus. Biol. Sci. 20(3):111-186.

Savage, D. E. 1951. Late Cenozoic vertebrates of the San Francisco Bay Region. Univ. California Publ. Bull. Dept. Geol. Sci. 28(10):215-314.

Schultz, C. B., and L. D. Martin. 1970. Quaternary mammalian sequence in the central Great Plains. Pp. 341-353 *in* W. Dort, Jr., and J.,K. Jones, eds. Pleistocene and Recent environments of the central Great Plains. Spec Publ. Dept. Geol. Univ. Kans. 3

Schultz, C. B., and T. M. Stout. 1948. Pleistocene mammals and terraces in the Great Plains. Geol. Soc. Amer. Bull. 59(6):553-588.

Semken, H. A., Jr. 1966. Stratigraphy and paleontology of the McPherson *Equus* beds (Sandahl local fauna), McPherson County, Kansas. Contrib. Mus. Paleon. Univ. Michigan 20(6):121-178.

Shaw, C. A. 1981. The Middle Pleistocene El Golfo Local Fauna from northwestern Sonora, Mexico. M.S. Thesis, California State Univ., Long Beach.

Sinclair, W. J. 1905. New Mammalia from the Quaternary caves of California. Univ. California Publ. Bull. Dept. Geol. Sci. 4(7):145-161.

Stock, C. 1913. *Nothrotherium* and *Megalonyx* from the Pleistocene of southern California. Univ. California Publ. Bull. Dept. Geol. Sci. 7(17):341-358.

_____. 1914a. The systematic position of the mylodont sloths from Rancho La Brea. Science n.s. 39(1012):761-763.

_____. 1914b. Skull and dentition of the mylodont sloths of Rancho La Brea. Univ. California Publ. Bull. Dept. Geol. Sci. 8(18):319-334.

_____. 1917. Further observations on the skull structure of mylodont sloths from Rancho La Brea. Univ. California Publ. Bull. Dept. Geol. Sci. 10(11):165-178.

_____. 1925. Cenozoic gravigrade edentates of western North America. Carnegie Inst. Washington Publ. 331:1-206.

_____. 1943. The cave of San Josecito, Mexico. Engineering and Science Monthly, Sept., 6 pp.

Webb, S. D. 1974. Chronology of Florida Pleistocene mammals. Pp. 5-31 *in* S. D. Webb, ed. Pleistocene Mammals of Florida. Univ. Presses Florida, Gainesville. 270 pp.

_____. 1989. Osteology and relationships of *Thinobadistes segnis*, the first mylodont sloth in North America. Pp. 469-532 *in* K. Redford and J. F. Eisenberg, eds. Advances in Neotropical Mammalogy. Sandhill Crane Press, Gainesville, Florida, 614 pp.

_____ and L.G. Marshall. 1982. Historical biogeography of Recent South American land mammals. Pp. 469-352 *in* M. A. Mores and H. H. Genoways, eds. Mammalian Biology in South America. Pymatuning Lab. Ecol., Univ. Pittsburgh, Spec. Publ. Ser. 6, 539 pp.