CONTRIBUTIONS IN SCIENCE

SEXUAL DIMORPHISM IN THE SKULL OF HARLAN'S GROUND SLOTH

H. GREGORY MCDONALD

Sexual Dimorphism in the Skull of Harlan's Ground Sloth

H. Gregory McDonald[1]

ABSTRACT. Since 1917, two types of skull morphology have been recognized in Harlan's ground sloth from Rancho La Brea. These two morphs have been referred to two separate subspecies: *Paramylodon harlani harlani* (Owen) for more robust, broader skulls and *Paramylodon harlani tenuiceps* (Stock) for more slender, gracile skulls. These observed differences in skull morphology were also used in the diagnosis of *Mylodon garmani* Allen, which has the gracile skull morph. An alternative explanation for the two morphs proposed here is that they indicate sexual dimorphism in a single species and are not of taxonomic value. The two skull morphs are not restricted to Rancho La Brea, but are found in other populations of Harlan's ground sloth where sufficient cranial material is preserved to observe these differences. In addition to differences in proportions of the skull, two distinctive morphs of the caniniform tooth also are present in the species and can be observed in the North American mylodont lineage as early as the Blancan.

INTRODUCTION

Variation within a population arises from many different sources, one of which is sexual dimorphism. In some species this may be expressed by size differences between the sexes, whereas in others its expression may be by distinct structures such as antlers in cervids. The recognition of sexual dimorphism in fossil species can permit inferences of behavior and social structure. Recognition of this phenomenon also has important taxonomic implications since the existence of a fossil species that is sexually dimorphic can potentially result in the incorrect recognition of two distinct species or subspecies rather than a single taxon (Kurtén, 1969). A recent example is the revision of the North American muskox by McDonald and Ray (1989) in which *Symbos* Leidy and *Bootherium* Leidy where determined to be male and female morphs, respectively, of a single species.

Stock (1917) described *Mylodon harlani tenuiceps* (type specimen, LACM HC 642) and distinguished it from other skulls of *Mylodon* Owen (now *Paramylodon* Brown) from Rancho La Brea based on its proportions. His criteria included the more slender shape of the skull, the greater constriction behind the postorbital processes, and the narrower palate posterior to the fifth cheek tooth. These observations were quantified by Lundelius (1972) utilizing specimens from Rancho La Brea and Ingleside, Texas.

DESCRIPTION

The differences observed in the two skull morphs of Harlan's ground sloth are not size dependent

1. Park Museum Management Program, National Park Service, 1201 Oakridge Drive, Suite 150, Fort Collins, Colorado 80525, USA.
Email: greg_mcdonald@nps.gov

(using skull length as the size criterion), but are differences in overall skull proportions as noted by Stock (1917). These two morphs include a robust and a gracile form, which reflect the transverse dimensions of various parts of the skull compared to the skull length, with the robust form having greater transverse dimensions. In addition to the criteria used by Stock, another consistent difference that distinguishes the two skull morphs is the slope of the occiput. In the robust morph the occiput forms a right angle to the basioccipital, whereas in the gracile morph the occiput and basioccipital form an acute angle so that in profile the occiput has a distinct slope. The variation in the slope of the occiput was illustrated by Miller (1971). Related to the slope of the occiput, the occipital condyles appear to project more posteriorly in the gracile morph, whereas in the robust morph they appear to be positioned more closely to the occiput. These two skull morphs are not only found at Rancho La Brea (Fig. 1) and Ingleside, Texas, but also at American Falls Reservoir, Idaho (Fig. 2), and have been recorded from Arizona (McDonald et al., 2004).

In addition to the two skull morphs, there are differences in the development of the occlusal surface of the first upper tooth (caniniform). The dimorphism in this tooth was observed by McDonald (1995) based on isolated caniniforms of *Paramylodon harlani* from the Irvingtonian Leisey site in Florida. Skulls retaining the caniniform indicate that in the robust skull morph the occlusal surface of the caniniform develops nearly parallel to the long axis of the tooth, resulting in what can be considered oblique wear resulting in a pointed end (Fig. 3A). In gracile skull morphs, the occlusal surface forms perpendicular to the axis of the tooth, resulting in a blunt end (Fig. 3B). The shape of the occlusal surface develops early and is distinctive even in young individuals, as indicated in the maxilla of
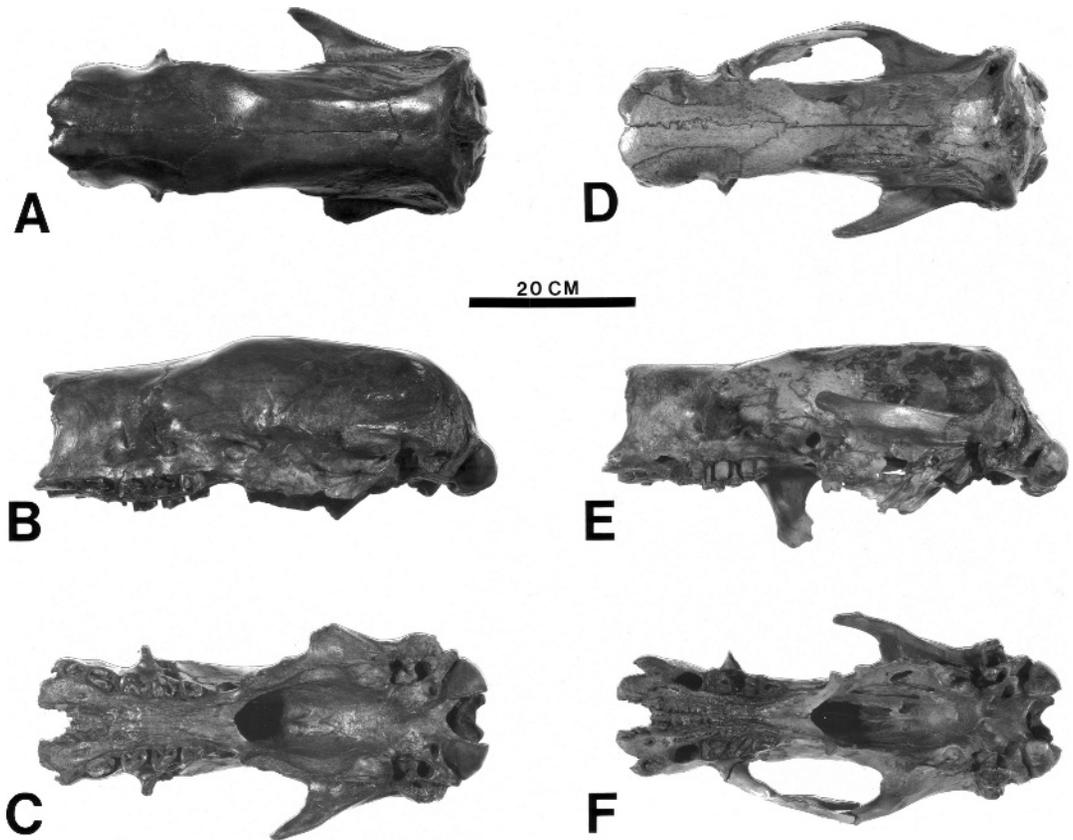
Figure 1 Skulls of *Paramylodon harlani* from Rancho La Brea, California, in dorsal, lateral, and ventral view. **A–C**, robust skull morph, LACM HC 832; **D–F**, gracile skull morph, LACM HC 692

a juvenile (LACM HC 1717-35) (Fig. 3C) with an oblique occlusal surface. Unlike many mammals in which the sex is indeterminate in juveniles, the early development of these distinctive wear patterns in the caniniform makes possible the determination of the sex even in relatively young individuals of *P. harlani*. In assemblages with multiple caniniforms both tooth morphs are consistently present and can be observed in samples as old as the Blancan.

The skull of the type specimen of *Mylodon garmani* (Allen, 1913) is of the gracile morph and in his diagnosis Allen noted the narrowness of the skull and braincase. While Stock (1917) noted the similarities between *M. garmani* and his *M. harlani tenuiceps*, he maintained the distinction of the two forms based on differences in the width of the palate. The type of *M. garmani* retains the caniniforms and the occlusal surface is of the perpendicular type.

DISCUSSION

An objective assignment of sex to each skull morph is difficult. While generally in mammals the skulls of males are more robust than those of females, it may be assumed, but is not conclusive, that the robust morph is male and the gracile morph is female. An independent check on this would be an examination of skulls associated with the pelvis to determine if a particular morph is associated with a pelvis that would be indicative of the sex of the individual. Since there is an overlap in size between the two morphs (based on skull length) (Fig. 4), size as another criteria cannot be used to suggest assignment to sex. Size differences alone may not be sufficient to assign sex to a skull since, while there is a general trend for males to be larger in mammals, this is not always the case since as Ralls (1977) pointed out, there are numerous groups of mammals in which the female is larger and there are several strong selective factors for large females, including a larger neonate and the potential for larger litters.

While it is not possible at this time to make an objective assignment of each skull morph to a specific sex, the recognition of the two morphs as indicative of sexual dimorphism and not of taxonomic significance may provide some insight regarding the social organization of Harlan's ground sloth. The samples of *P. harlani* from
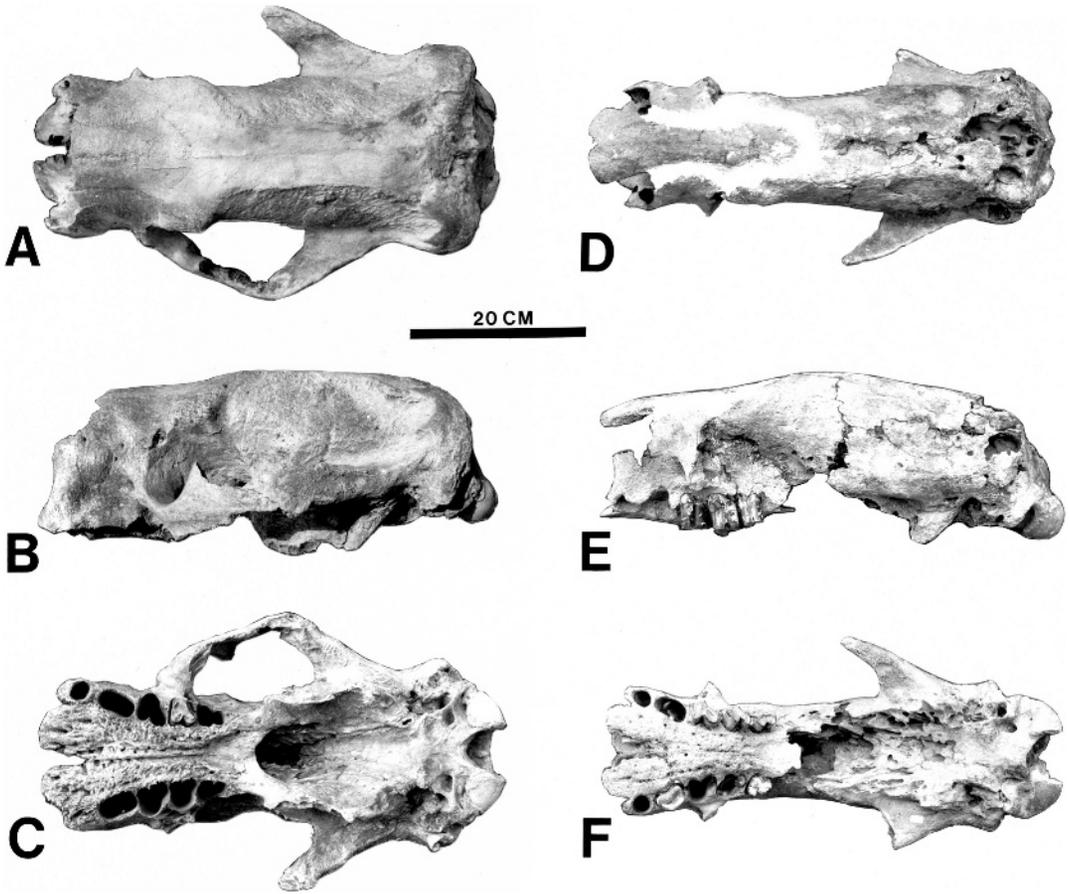
Figure 2 Skulls of *Paramylodon harlani* from American Falls Reservoir, Idaho, in dorsal, lateral, and ventral view. **A–C**, robust skull morph, IMNH 15273; **D–F**, gracile skull morph, IMNH 23246
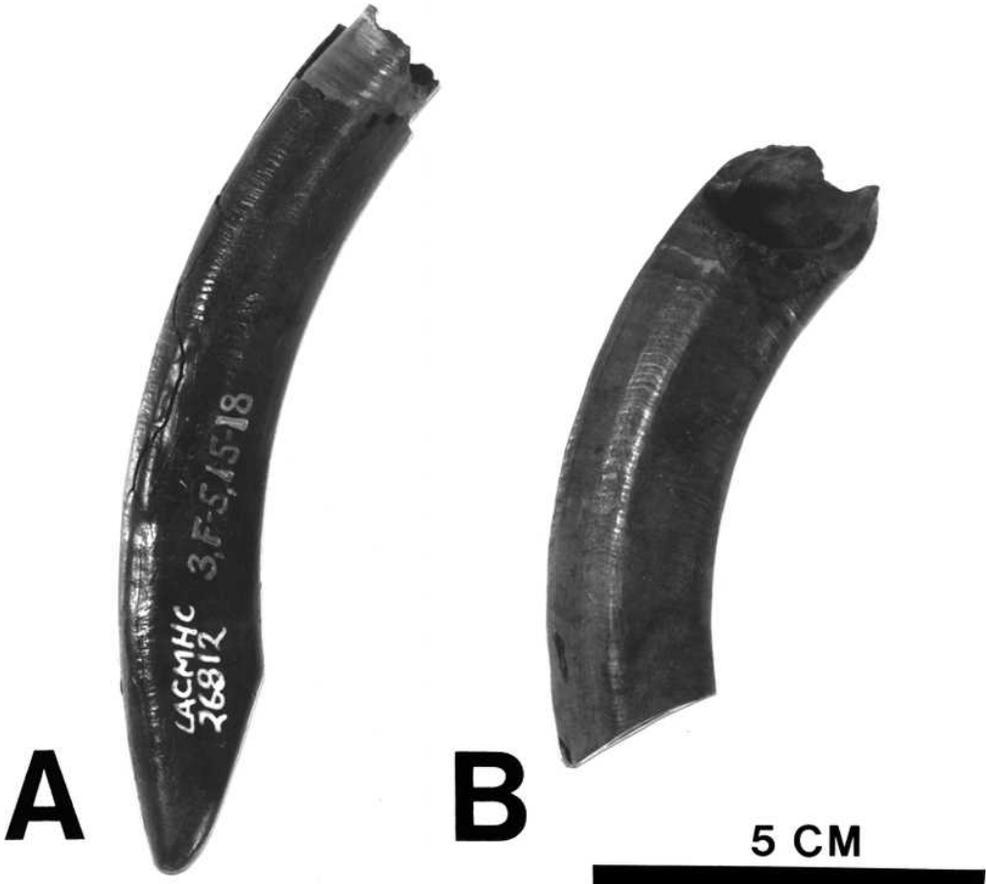
Rancho La Brea, American Falls Reservoir, and Ingleside are time-averaged samples and do not represent a single herd or social group such as that of *Eremotherium* Spillman described by Cartelle and Bohorquez (1982), in which they report sexual dimorphism in the skull of this species. Given the length of time over which individuals of *Paramylodon* at Rancho La Brea accumulated in a particular pit (Marcus and Berger, 1984), it would be expected that there would be equal opportunity of entrapment and preservation of both sexes and the ratio of the two skull morphs should approach 1:1. However, using modern sloths as an analog may not be appropriate since a 1:1 sex ratio is not always present in modern sloth populations. In populations of the extant two-toed sloth, *Choloepus hoffmanni* Peters, females predominate (91.6% to 94.1%), while in the three-toed sloth, *Bradypus variegatus* Schinz, both sexes are present in roughly equal proportions (Meritt, 1985).

The ratio of the two morphs in the collective sample at Rancho La Brea is slightly greater than 3:1 (23 and 7 individuals respectively) (Table 1).

In Pit 4 from which the largest sample of skulls (9) was recovered the ratio is 3.5:1 and based on isolated caniniforms the ratio of the two wear morphs is 1.4:1 (7 oblique, 5 perpendicular). At both American Falls Reservoir and Ingleside the sample of skulls is small (3 each) with the ratio of the two skull morphs from American Falls roughly equal (1 robust, 2 gracile) and from the Ingleside fauna all three skulls are of the gracile morph. At Ingleside four of the six isolated caniniforms preserve the occlusal surface and there are two of each morph.

Differences in the relative preservation of male and female skulls of the extinct muskox, *Bootherium*, were recorded by McDonald and Ray (1989) with a male to female ratio of 3:1 (171 and 51 specimens, respectively). Their explanation of this bias was that the more gracile (female) skulls were more vulnerable to destruction. At Rancho La Brea it is also the more gracile skull morph that is underrepresented.

Rather than a preservational bias, the differences in the relative numbers of the two skull morphs in *Paramylodon* at Rancho La Brea
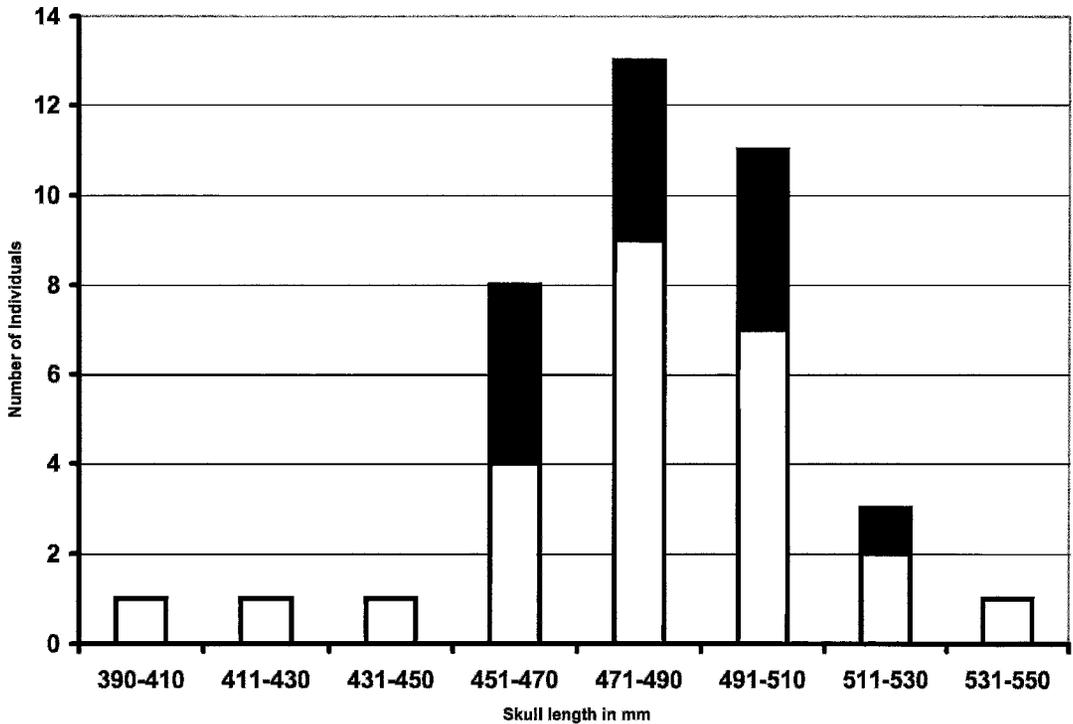
5 CM

5 CM

Figure 4 Size distribution of skull morphs in *Paramylodon harlani*. White bars = robust morph; black bars = gracile morph. Sample includes specimens from Rancho La Brea, California; American Falls Reservoir, Idaho; Arizona (McDonald et al., 2004); Colorado (Cockrell, 1909); and Nebraska including the types of *Paramylodon nebrascensis* (Brown, 1903) and *Mylodon garmani* (Allen, 1913)

actually may be indicative of differential habitat use by the two sexes. If, as is the case in many mammals, the males had a greater territorial range than females, or there were bachelor males with no fixed territories (transients), then males may have been more frequently entrapped. Additionally, many species of modern herbivores that are sexually dimorphic will form separate social groups and the two sexes may display spatial segregation reflecting sex-related patterns of resource use, with each sex utilizing different parts of the habitat (Gross et al., 1995). Therefore, the two sexes may only co-occur in a social context during the breeding season. If this was the case for Harlan's ground sloth then this could also account for the reduced presence of the females in the vicinity of the Rancho La Brea if they were preferentially utilizing habitat elsewhere.

Biases against one sex or the other due to differences in the habits utilized by the two sexes are even reflected in collections of extant taxa. Ralls and Harvey (1985) noted an unequal representation of the sexes of the extant least weasel, *Mustela nivalis* Linnaeus, in museum collections. These samples in which males predominate reflect differences in habitat preference in the two sexes and the greater susceptibility of males to being trapped. Examples from the fossil record include other taxa from La Brea such as the horse, in which there is an unequal sex ratio. Gust (1991) interpreted the preponderance of subadult males as reflective of the taphonomic factors related to the formation of the deposit. A bias towards the entrapment of young male mammoths, *Mammuthus columbi* (Falconer), at the Mammoth Site in Hot Springs, South Dakota, also has been documented (Agenbroad, 1990). In each of these cases the bias reflects the social organization of the species in which after weaning, young males leave the family group and are either solitary or join bachelor groups.

SIGNIFICANCE OF SEXUAL DIMORPHISM IN EXTINCT SLOTHS: POSSIBLE MODELS

In mammals sexual dimorphism may be restricted to that of size or there may be other secondary sexual characteristics such as coloration or

←
Figure 3 Caniniforms of *Paramylodon harlani* from Rancho La Brea in lateral view showing differences in development of the occlusal surface. **A**, oblique wear, LACM HC 26812; **B**, perpendicular wear, LACM HC 26808; **C**, right maxilla in lateral view of juvenile, LACM HC 1717-35, with caniniform with oblique occlusal surface

Table 1   Distribution of the robust and gracile skull morphs of *Paramylodon harlani* at Rancho La Brea by pit. Number in columns 2 and 4 is LACM HC catalog number.

Pit number	Robust morph	Total number	Gracile morph	Total number	Ratio
3	820	4	644	1	4:1
	830				
	834				
	835				
4	761	7	642—Type of	2	3.5:1
			P. harlani tenuiceps		
	816		646		
	823				
	828				
	829				
	832				
	14551				
13	826	3	695	1	1.5:1
	831		818		
	833				
60	814	1		0	1:0
61	0	0	643	1	0:1
67	1717-7	3		0	3:0
	696				
	819				
77	822	3		0	3:0
	707				
	827				
91	49901	1	63000	1	1:1
Unknown	14537	1	12369	1	
Total		23		7	3.3:1

structures used for display such as horns and antlers. Usually only size and osteological features such horns and antlers are available for interpretation in the fossil record. The difference in the degree of development of these structures reflects differences in the intensity of selection between the two sexes, depending on the social behavior of the species. Based on skull length, dimorphism in size does not occur in *P. harlani* (Fig. 4) and the differences in the skull are merely that of proportion. Since characteristics that contribute to the immediate visual recognition of the sexes are an important aspect of the social structure of many mammals the question is whether the differences observed in the skull and dentition of *P. harlani* would have served this purpose. While these sexually dimorphic features can be observed and contribute to the identification of sex, it is not readily apparent they would have provided any visual clues as to the sex of the individual sloth.

Among mammals only three different orders have been extensively studied with regard to the relationship of sexual dimorphism in the skeleton and social behavior: artiodactyls, carnivores, and primates (Alexander et al., 1979). The question is whether any of these groups would serve as appropriate analogs for interpreting the significance of the sexual dimorphism observed in *P. harlani* or other fossil sloths.

In ungulates, sexual dimorphism can be roughly divided into three categories: high, medium–high, and low (Guthrie, 1990). In species with high sexual dimorphism the two sexes live in separate social groups with the females associated with larger groups than males. Species with low sexual dimorphism form mixed-sex groups and are highly social, staying together throughout the year (Estes, 1974). In carnivores, monogamous species tend to be less sexually dimorphic, whereas the more polygamous species are highly dimorphic. As such, carnivores parallel ungulates in social structure in which highly dimorphic forms only come together during the mating season, whereas minimally dimorphic forms form a stronger social bond.

Since the degree of sexual dimorphism in ungulates is closely related to social structure (Estes, 1974), this relationship has been used to infer the social behavior of extinct species such as the steppe bison, *Bison priscus* (Bojanus) (Guthrie, 1990). However, since ground sloths lack obvious visual structures such as horns or antlers, the ungulate model may not be useful for inferring their possible social organization.

In larger species of mammals there is a greater potential for more pronounced sexual dimorphism in size resulting from allometric growth than in smaller species. In species with strong selection for larger size in one sex, skeletal features with a positive allometric relationship to size will become more enhanced with an increase in size. In ground sloths it might be expected that the largest species would have the most pronounced sexual dimorphism and this has been observed in
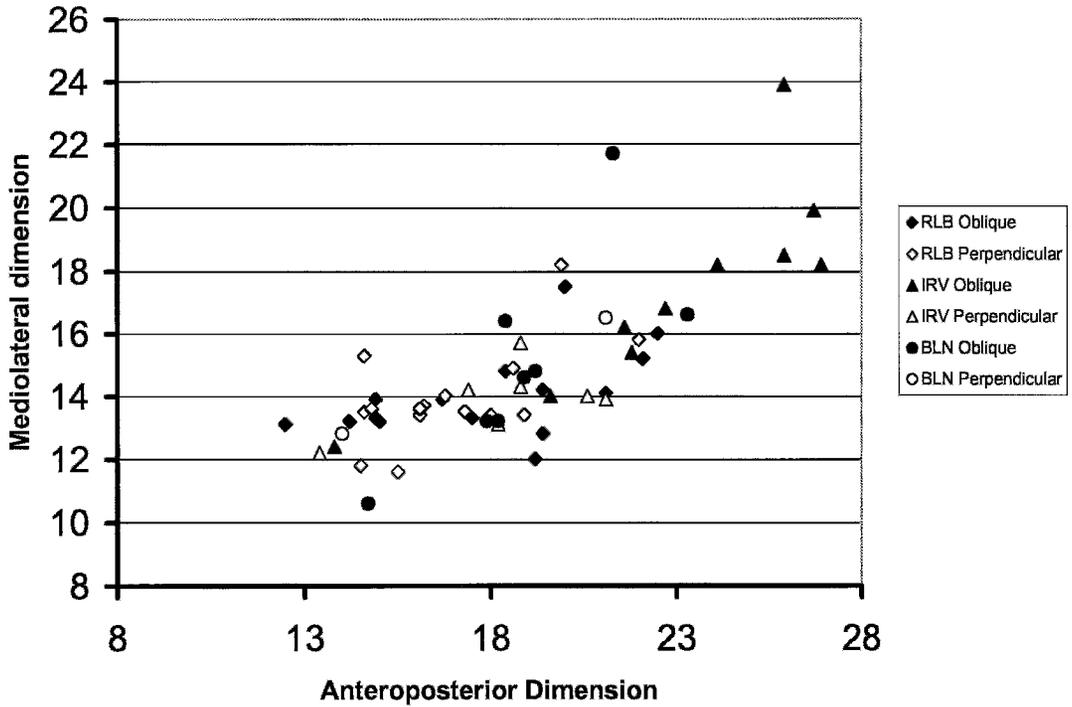
Figure 5 Scatter diagram of anteroposterior and mediolateral dimensions (in mm) of caniniforms of *Paramylodon harlani* and *Glossotherium chapadmalense*. **Abbreviations:** RLB = Rancholabrean; IRV = Irvingtonian; BLN = Blancan

one of the largest sloths, *Eremotherium laurillardi* (Lund) (Cartelle and Bohorquez, 1982). As noted previously, while there is a general trend for males to be larger in mammals, this is not always the case (Ralls, 1977).

Since there is a morphological and to a certain degree size difference in the caniniforms in *P. harlani*, another model that focuses on the canines may be more appropriate. A difference in canine size between the two sexes has been observed in primates (Leutenegger and Kelly, 1975) and carnivores (Kurtén, 1955). This size difference is present in the two morphs in earliest members of the North

American *Paramylodon* lineage, becomes more pronounced, but then becomes less distinct (Fig. 5) (Table 2). The Blancan member of the lineage referred to *Glossotherium chapadmalense* is considered to be an ancestor to *P. harlani*. In the Blancan, Irvingtonian, and Rancholabrean samples the oblique wear morph is larger than the perpendicular morph in both the anteroposterior and mediolateral dimensions. The difference in size is most pronounced in Irvingtonian specimens of *P. harlani*, with the oblique morph 1.25 times larger than the perpendicular morph, whereas in both the Blancan and Rancholabrean forms the ratios of

Table 2 Averages of dimensions of the caniniform tooth and ratio of dimensions in the two morphs of *Glossotherium chapadmalense* from the Blancan and *Paramylodon harlani* from the Irvingtonian and Rancholabrean of North America. **Abbreviations:** AP = anteroposterior; ML = mediolateral; Measurements in mm.

	Number of specimens	Average AP dimension	Average ML dimension	Ratio of oblique/ perpendicular in AP	Ratio of oblique/ perpendicular in ML
Blancan					
Oblique	8	19.0	15.1	1.08	1.03
Perpendicular	2	17.6	14.7		
Irvingtonian					
Oblique	10	22.9	17.4	1.25	1.25
Perpendicular	7	18.3	13.9		
Rancholabrean					
Oblique	16	17.9	14.0	1.06	1.0
Perpendicular	13	16.8	14.0		

these measurements are similar (Table 2) despite the Rancholabrean *Paramylodon* being significantly larger than the Blancan form. The absolute dimensions indicate a relative decrease in the size of the caniniform relative to the overall increase in body size from the Blancan to Rancholabrean. While the two tooth morphs are still present in Rancholabrean *P. harlani*, the size difference between the two is negligible compared to its predecessors in the Irvingtonian, suggesting a reduction in the degree of sexual dimorphism in the species.

In addition to the decrease in their size there is also a trend in the loss of the caniniforms in Rancholabrean specimens, a feature not observed in either the Blancan or Irvingtonian. The loss of the caniniform is not symmetrical and can include both or either side of the skull (Stock, 1925). The diagnosis of *Paramylodon nebrascensis* Brown (1903) included the loss of both caniniforms. The type skull is of the robust morph and in the sample from Rancho La Brea the loss of the caniniforms occurs equally in both skull morphs (sexes).

Based on caniniform size, sexual dimorphism was more prominent in earlier members of the lineage and decreased through time, so that whatever selective advantage was initially provided by the difference in caniniform size in the species declined through time. One possible explanation was the lack of other mylodonts in the fauna, which would require each species to maintain some level of distinctiveness to avoid interbreeding. Consequently it might be expected that in South American faunas with multiple species of closely related sloths, such as mylodonts, sexual dimorphism in the various species might be more pronounced.

Naples (1990) proposed that the smaller North American ground sloth, *Nothrotheriops shastensis* (Sinclair), also found at Rancho La Brea, like modern tree sloths, was not a social, family, group, or herd animal and probably utilized a large home range for feeding. Her interpretation was that its only social interaction was a long dependence of a single young upon the mother, which along with a long gestation period and extended interbirth interval would have limited the interaction between males and females. There is no apparent sexual dimorphism in *Nothrotheriops* either in body size or skeletal structure or if present is more subtle than in the larger *Paramylodon*. If either the carnivore or ungulate model is used to explain ground sloth social behavior, there should be pronounced sexual dimorphism in this species if it was primarily solitary. Based on a carnivore model the low sexual dimorphism seen in *Nothrotheriops* would be indicative of monogamous pairing and some type of continuous social interaction between the male and female.

If *Nothrotheriops*, with a smaller body size than *Paramylodon*, is used as an example of a ground sloth with low sexual dimorphism, then *Paramylodon* would be best described as having medium–high sexual dimorphism at least in the skull. Based on the ungulate model, *Paramylodon* would have been solitary to semisolitary in its habits or would have formed small, single-sex social groups during much of the year. This behavior would fit the pattern of accumulation of individuals in different pits at Rancho La Brea, in which the sample is dominated by the robust and presumed male morph. If a carnivore model is used, then the medium–high sexual dimorphism in *Paramylodon* would suggest a polygamous lifestyle and the absence of any type of fixed herd structure that would also contribute to the pattern resulting from sporadic entrapment at Rancho La Brea.

SUMMARY

At the moment it is not possible to generate a plausible interpretation of the behavior and social structure for ground sloths based on available knowledge of their sexual dimorphism and our limited ability to determine the sex ratio in the few large samples available, such as Rancho La Brea. Likewise, neither an ungulate nor carnivore model for behavior may provide an adequate analog for such an interpretation. Unfortunately, these two orders, along with primates, are the only mammals for which the most information is available regarding the relationship between sexual dimorphism of the skeleton and types of social behavior. Ground sloths, like many other extinct groups, pose their own special problems with regard to understanding their evolution and paleoecology. While it would be easy to restrict ourselves to their modern relatives, the tree sloths, which are solitary animals, the differences in size and anatomy between the living and extinct sloths suggest that the extinct forms probably had a more diverse social repertoire than their extant relatives. It may be that no single modern group can serve as an analog to interpret the social organization of the extinct sloths. Additional and multiple independent sources of information are needed to strengthen any interpretation of their social behavior. The recognition that there exist varying degrees of sexual dimorphism in different taxa of ground sloths should provide a starting point to eventually make such an interpretation possible.

Even if the recognition of sexual dimorphism in ground sloths does not permit inferences as to behavior, social organization, and in turn their paleoecology, recognition of the existence of sexual dimorphism will aid our understanding of the group in other ways. Since it has also been observed in another extinct sloth, *Eremotherium*, sexual dimorphism is not restricted to Harlan's ground sloth and is most likely present in other mylodont sloths as well as other groups of sloths. Some sympatric taxa in South America such as "*Mylodon*" *lettsomi*, "*Mylodon*" *robustus*, and "*Mylodon*" *gracilis* are distinguished by

differences in skull proportion and the degree of robustness of the skull, and Cabrera (1936) utilized skull proportions to distinguish different species of *Glossotherium* Owen. If the differences observed are the result of sexual dimorphism, then its recognition may lead to the resolution of a number of taxonomic questions for the South American taxa, as it has for the North American forms *P. harlani harlani*, *P. harlani tenuiceps*, *Mylodon garmani*, and *P. nebrascensis*.

ACKNOWLEDGMENTS

LITERATURE CITED

Agenbroad, L.D. 1990. The mammoth population of the Hot Springs site and associated fauna. In *Megafauna and man: Discovery of America's heartland*, ed. L.D. Agenbroad, J.I. Mead, and L.W. Nelson, The Mammoth Site of Hot Springs, South Dakota, Inc., Scientific Papers, vol. 1, 32–39.

Alexander, R.D., J.L. Hoogland, R.D. Howard, K.M. Noonan, and P.W. Sherman. 1979. Sexual dimorphism and breeding systems in pinnipeds, ungulates, primates and humans. In *Evolutionary biology and human social behavior, an anthropological perspective*, ed. N.A. Chagnon and W. Irons, 402–435. North Scituate: Duxbury Press.

Allen, G.M. 1913. A new *Mylodon*. *Memoirs of the Museum of Comparative Zoology* 40:319–346.

Brown, B. 1903. A new genus of ground sloth from the Pleistocene of Nebraska. *Bulletin of the American Museum of Natural History* 19:569–583.

Cabrera, A. 1936. Las especies del género *Glossotherium*. *Notas Museo de La Plata* 1:193–206.

Cartelle, C., and G.A. Bohorquez. 1982. *Eremotherium laurillardi* Lund, 1842. Parte I. Determinação específica e dimorfismo sexual. *Iheringia* 7:45–63.

Cockerell, T.D.A. 1909. A fossil ground-sloth in Colorado. *The University of Colorado Studies* 6:309–312.

Estes, R. 1974. Social organization of the African Bovidae. In *The behavior of ungulates in its relationship to management*, ed. V. Geist and F. Walther. *IUCN Publication new series 24, vol. 1*, 166–205.

Gittleman, J.L. 1984. *The behaviorial ecology of carnivores*. University of Sussex, Sussex, United Kingdom: Thesis.

Gross, J.E., P.U. Alkon, and M.W. Demment. 1995. Grouping patterns and spatial segregation by Nubian ibex. *Journal of Arid Environments* 30:423–439.

Gust, S. 1991. Age and sex distribution of the Rancho La Brea horse based on pelvic characters. *Journal of Vertebrate Paleontology* 11 supplement:33A.

Guthrie, R.D. 1990. *Frozen fauna of the Mammoth Steppe: The story of Blue Babe*. Chicago: The University of Chicago Press, 323 pp.

Kurtén, B. 1955. Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmuller and Heinroth. *Acta Zoological Fennica* 90:1–48.

———. 1969. Sexual dimorphism in fossil mammals. *International Union of Geological Sciences*, Series A, No. 1:226–233.

Leutenegger, W., and J.T. Kelley. 1975. Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *American Journal of Physical Anthropology* 42:314 (abstract).

Lundelius, E.L., Jr. 1972. Fossil vertebrates from the late Pleistocene Ingleside fauna, San Patricio County, Texas. *Bureau of Economic Geology, Report of Investigations* No. 77:1–74.

Marcus, L.F., and R. Berger. 1984. The significance of radiocarbon dates for Rancho La Brea. In *Quaternary extinctions: A prehistoric revolution*, ed. P.S. Martin and R.G. Klein, 159–188. Tucson: University of Arizona Press.

McDonald, H.G. 1995. Gravigrade xenarthrans from the middle Pleistocene Leisey Shell Pit 1A, Hillsborough County, Florida. *Bulletin of the Florida Museum of Natural History, Biological Sciences* 37 Pt. II:345–373.

McDonald, H.G., L.D. Agenbroad, and C. Manganaro Haden. 2004. Late Pleistocene mylodont ground sloth *Paramylodon harlani* (Mammalia: Xenarthra) from Arizona. *The Southwestern Naturalist* 49:229–238.

McDonald, J.N., and C.E. Ray. 1989. The autochthonous North American musk oxen *Bootherium*, *Symbos*, *Gidleya* (Mammalia: Artiodactyla: Bovidae). *Smithsonian Contributions to Paleobiology* 66:1–77.

Meritt, D.A., Jr. 1985. The two-toed Hoffmann's sloth, *Choloepus hoffmanni* Peters. In *The evolution and ecology of armadillos, sloths and vermilinguas*, ed. G.G. Montgomery, 333–341. Washington, D.C.: Smithsonian Institution Press.

Miller, W.E. 1971. Pleistocene vertebrates of the Los Angeles Basin and vicinity (exclusive of Rancho La Brea). *Los Angeles County Museum of Natural History Science Bulletin* 10:1–124.

Naples, V.L. 1990. Morphological changes in the facial region and a model of dental growth and wear pattern development in *Nothrotheriops shastensis*. *Journal of Vertebrate Paleontology* 10:372–389.

Ralls, K. 1977. Sexual dimorphism in mammals: Avian models and unanswered questions. *The American Naturalist* 111:917–938.

Ralls, K., and P.H. Harvey. 1985. Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society* 25:119–167.

Stock, C. 1917. Further observations on the skull structure of mylodont sloths from Rancho La Brea. *University of California Publications, Bulletin of the Department of Geology* 10:165–178.

———. 1925. Cenozoic gravigrade edentates of western North America. *Carnegie Institution of Washington Publications* 331:1–206.