# A SYSTEMATIC REVIEW OF THE <br> MEGATHERIINAE <br> (MAMMALIA: XENARTHRA: MEGATHERIIDAE) 

by

Gerardo De Iuliis

A thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy, Graduate Department of Zoology, in the University of Toronto.
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by<br>Gerardo De Iuliis

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#### Abstract

The subfamily Megatheriinae is known from the Friasian (Late Miocene) through the Lujanian (Late Pleistocene). Megatheriines were generally confined to South America, but Eremotherium laurillardi spread north into the southeastern United States. Most Megatheriinae are large ground sloths; they are morphologically conservative, and less diverse than the megalonychids and mylodontids. A hypothesis of a monophyletic Megatheriinae is corroborated by the following characters: possession of $5 / 4$ molariforms that have squared corners, are functionally similar and equidistantly spaced, and bear mesial and distal transverse crests separated by a V-shaped valley; the ectotympanic is very large with extremely rugose anterior and posterior crura; the olecranon process of the ulna is markedly reduced; and the tibia and fibula are fused proximally. Several taxa contained in the literature are considered invalid. Eremotherium laurillardi is the valid name for the Panamerican, large-sized megatheriine. Various Pleistocene species of Megatherium are synonyms of M. americanum, such as M. gallardoi, M.


parodii, M. Iundi, and M. filholi. The presumed Pliocene (Montehermosan) M. gaudryi is actually Pleistocene in age and a synonym of $M$. americanum. The specific status of three other Pleistocene species of Megatherium (M. medinae, M. tarijense, and M. sundti) is maintained based on wellpreserved and diagnostic remains. Other species of Megatherium (M. elenense, M. istilarti) are provisionally maintained because their remains apparently preserve useful phylogenetic characters, but are too sparse to permit confident taxonomic decisions at present. Pre-Pleistocene megatheriines are generally poorly known, but Pyramiodontherium bergi, Megatheriops rectidens, Megathericulus, and "Plesiomegatherium" halmyronomum may be unambiguously defined, although the generic assignment of the latter is uncertain. The status of other species, such as Plesiomegatherium hansmeyeri, Pliomegatherium lelongi, and Megatherium antiqum, and the genera Eomegatherium and Promegatherium are uncertain.

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## INTRODUCTION

Megatherium americanum, the type species of the subfamily Megatheriinae, has played a significant role in the history and development of paleontology and evolutionary science. Its remains were probably first discovered in 1788 near Lujan, a town some sixty miles west of the city of Buenos Aires, Argentina (Boyd, 1958). This specimen, a nearly complete skeleton of a single individual, was sent for study to the Real Gabinete de Historia Natural, Madrid, Spain. There it was mounted (improperly) and illustrated (crudely) in a life-like position by J.B. Bru y Ramon. This was the first fossil skeleton to be mounted as such (Hoffstetter, 1959a; Simpson, 1984). Although the pose given by Bru (P1. 1) is incorrect, the exhibit has remained nearly unchanged, although it was remounted at least once (A. G. Edmund, pers. comm., 1995).

Bru's illustrations, perhaps by somewhat questionable means, were obtained by Georges Cuvier in Paris, who recognized the scientific importance and correctly established the phylogenetic affinities of the fossil mammal. Cuvier (1796) named it Megatherium americanum in his first of many publications on fossil animals. However, Cuvier, who is generally regarded as the founder of the science of vertebrate paleontology largely by virtue of his (1812, and later editions) "Recherches sur les Ossemens

Fossiles . . ." (Simpson, 1984), considered M. americanum important for other reasons. He reasoned that if analysis of fossil bones by "the powerful new methods of comparative anatomy, could prove that they had belonged to species distinct from any known alive, the reality of extinction would be proved almost beyond dispute"; this conclusion was first suggested to Cuvier by the Megatherium remains (Rudwick, 1985: 107). The importance of extinction to evolutionary theory as understood by modern science was not realized until the publication of Darwin's (1859) "On the Origin of Species . . .". Cuvier claimed that extinction was a reality and opposed the idea that fossil animals had been transformed into living species. The latter theory, particularly favoured by Lamarck, which virtually denied the existence of extinction (Rudwick, 1985). Although Cuvier has thus often been cast in a negative light as being an anti-evolutionist (albeit in a far different sense than in the modern meaning of this term), his work contributed greatly to the proper understanding of fossils as representing forms of life which are no longer in existence.

Remains of M. americanum were among those of the great quadrupeds discovered by Darwin in 1833 at Bahia Blanca (Punta Alta), Argentina, and sent to London for study by Richard Owen, the foremost comparative anatomist and paleontologist of his day. Owen's (1851-60) description and illustration of M. americanum, published as a series over a
number of years due to difficulty in obtaining funding for publication (Desmond, 1982), was among the most extensive and comprehensive studies of a fossil mammal for its time. It became a model for the presentation of information on fossils, and remains the standard text on the skeletal anatomy of M. americanum.

One would think, as Simpson (1980) commented for all sloths, that with such an early start as the object of scientific study and association over the years with the more illustrious and capable scientists of the day, the problems of the history and biology of the Megatheriinae would have been resolved. However, such is not the case. The Megatheriinae have been largely neglected over the past fifty years and studies of their paleontology, biology and phylogenetic relationships have not kept pace with that of other fossil mamal groups. The main reasons for this neglect are 1) until quite recently the remains of Megatheriinae were scarce, fragmentary and scattered, excluding a few notable exceptions, and 2) a lack of a proper appreciation of variation within and among natural populations continued among researchers studying the Megatheriinae well into the 1960 's, which resulted in a nomenclatural maze.

The need for a review of the subfamily became evident through numerous inconsistencies in the literature and lack of a general taxonomic consensus of genera and species. For
example, genera synonymized without explanation by Simpson (1945), consistently reappear in the more recent literature and faunal lists, even though these taxa are poorly defined and understood. Such uncertainty leads to confusion over the paleobiogeography of the group, phylogenetic relationships, and degree of taxonomic diversity.

The present revision undertakes a comprehensive and extensive morphologic and morphometric study of the remains of Megatheriinae to provide as complete and thorough an understanding of their history and biology as is permitted by the available data. These aims are impeded at various levels by the problems that usually hinder paleontological study, such as incomplete stratigraphic and locality information, inadequate samples, and incomplete and imperfect preservation. However, the result of a broad and comprehensive comparative study incorporating nearly all known megatheriine remains, together with consideration of other ground sloths, has produced considerable advances in resolving the taxonomy of megatheriines, and better understanding of their phylogenetic relationships. Thus, a taxonomic framework is now in place that permits the recognition of anatomically definable taxa, and identifies which taxa are of ambiguous status and require further study, and the recovery of more extensive and better preserved samples.

I recognize fewer genera and species than are contained
in the older literature. In fact, only a few of the numerous taxa named in the literature are consistently diagnosable. I recognize the following Pleistocene species as clearly defined morphologically: Eremotherium laurillardi, Megatherium americanum, M. sundti, M. medinae, and M. tarijense. Megathericulus, Pyramiodontherium, Megatheriops, and "Plesiomegatherium" halmyronomum are preRleistocene and distinct morphologically, but knowledge of their biostratigraphic positions is imprecise. There are, in addition, taxa based on material that is too sparse and poorly-preserved to allow them to be unambiguously recognized as valid taxa or synonymized with betterestablished taxa. These include Promegatherium, Eomegatherium, Pliomegatherium, and Megatheridium.

## METEODS AND MATERIALS

The concept of biological species and the recognition of species is and has been somewhat problematic throughout the history of scientific inquiry of organisms (see e.g., Mayr, 1982). The biological species concept and the recognition of species as components of evolutionary lineages, among the more commonly accepted theoretical constructs, are in many cases difficult to implement in practice, particularly so in the attempt to recognize or define species among extinct organisms, in which time is an additional influential factor (Simpson, 1961).

The recognition of individual species in paleontology. with biological information necessarily limited by the vagaries of preservation, is and must be somewhat arbitrary. I have attempted to reduce the degree of subjectivity largely by basing decisions on species recognition, and hence synonomy, on the observed degree of variation in two well-represented popoulations, each from single localities and deposited over relatively restricted time ranges, of the species Eremotherium laurillardi. Thus, for example, many of my decisions on the species limits of Megatherium americanum reflect our knowledge of possible variation as demonstrated by E. laurillardi, although supplemented by morphologic and morphometric evidence of nearly certain conspecific skeletal elements (e.g., the series of astragali
from near Luján, Buenos Aires; vide infra Discussion of $M$. americanum under SYSTEMATIC REVIEW OF THE MEGATHERIINAE). I realize the potential for error based on the possibility that some specimens, particularly those form different localities (which alone does not preclude possible sympatry), may represent sibling or cryptic species. However, it is difficult, if possible at all, to detect such species among extinct organisms. Thus, my decisions are conservative with respect to the more probable or plausible hypotheses that the avalable data may be considered to support.

Such decisions are robust given sufficient remains for a particular taxon, as is the case for M. americanum. For many megatheriine taxa, however, few specimens have been recovered, and for such taxa I have been conservative in taxonomic decisions. Where, for example, two species have been described on dissimilar skeletal elements, I have tended to maintain their taxonomic status, even though I may suspect that they may be conspecific (except in the trivial situation in which the elements were associated), because the taxa cannot be directly compared. On the other hand, if species were described based on homologous elements separated by relatively small distances and from similar geological horizons, and the specimens exhibit minor morphological and morphometric variations, then $I$ have tended to consider them conspecific.

Measurements less than 150 mm were made with Helios Dial Calipers. Measurements greater than 150 mm were made with large calipers (resembling tree calipers and constructed by the maintenance staff of the Department of Zoology, University of Toronto) having 1 mm gradations. All measurements were recorded to the nearest milimetre.

Morphometric data were analyzed using SAS (1988. SAS Institute Inc., Cary, NC 27512-8000). Differences between variables that are normally distributed were tested for significance with Students t-test. Non-normally distributed data were analyzed by appropriate non-parametric tests (e.g., Wilcoxon) on ranked data. Multiple tests of significance were necessary for some skeletal elements. In such cases, the probability of incorrectly rejecting one or more true hypotheses (which is additive) increases with each test performed. Thus, the probability values were adjusted to an overall $\alpha=0.05$ using the Bonferroni method suggested by Rice (1989). Phylogenetic analyses were conducted using PAUP 3.1 (Swofford, 1991) and corroborated with Hennig 86, version 1.5 (Farris, 1988).

Numerous specimens from many museums and academic institutions were studied, described, and measured. Specimens of E. laurillardi and M. americanum that were used in statistical analyses are listed in Appendix 4. The samples of any particular element are defined based on minimum number of individuals (e.g., the sample of astragali
of E. laurillardi remains from Toca das Oncas included only astragali from one side of the body) to minimize bias. Data for taxa represented by only one or two elements (and therefore not used for statistical purposes) are also recorded in Appendix 4.

## ABBREVIATIONS OF MUSEUMS AND ACADEMIC INSTITUTIONS

AMNH - American Museum of Natural History, New York, USA;
ANSP - Academy of Natural Sciences, Philadelphia, USA;
BMNH - British Museum of Natural History (now the Natural History Museum), London, England;

DMAS - Daytona Museum of Arts and Sciences, Daytona Beach, USA;

EPN - Escuela Politécnica Nacional, Quito, Ecuador;
F:AM - Frick Collection, American Museum of Natural History, New York, USA;

FMNH - Field Museum of Natural History, Chicago, USA;
ILSB - Instituto de La Salle, Bogota, Colombia;
MACN - Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina;

MCL - Museu de Ciências Naturais da Pontificia Universiđade Católica de Minas Gerais, Belo Horizonte, Brazil;

MCNA - Museo de Ciencias Naturales y Anthropológicas
"Profesor Antonio Serrano", Paraná, Argentina;
MCPUCRS - Museu de Ciencias, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil. MCS - Museo Civico di Storia Naturale, Milan, Italy.

MGN - Museo Geológico Nacional, Bogota, Colombia;
MLP - Museo de La Plata, La Plata, Argentina;
MMP - Museo Municipal de Ciencias Naturales "Lorenzo

Scaglia", Mar del Plata, Argentina;
MNHN BOL - Museo Nacional de Historia Natural, La Paz, Bolivia;

MNHNM - Museo Nacional de Historia Natural, Madrid, Spain; MNHNP - Muséum National d'Histoire Naturelle, Paris, France.

MNHNU - Museo Nacional de Historia Natural, Montevideo, Uruguay.

MNP - Museo Nacional de Panama, Panama City, Panama;
MNRJ - Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil;

MPCNP - Museo Provincial de Ciencias Naturales, Paraná, Argentina.

MPFLR - Museo Paleontológico "F. Lucas Roselli", Nueva Palmira, Uruguay.

MPCB - Museo Paleontolgía Rodrigo Botet, Valencia, Spain. MUT - Museo Universitario de Tarija, Tarija, Bolivia;

NRM - Swedish Museum of Natural History, Stockholm, Sweden;
PIMUZ - Palaontologisches Institut und Museum der Universitat der Zurich, Switzerland.

PIU - Paleontological Institut of Uppsala, Uppsala, Sweden;
ROM - Royal Ontario Museum, Toronto, Canada;
SGO - Museo Nacional de Historia Natural, Santiago, Chile;
UCMP - University of California Museum of Paleontology, Berkeley, USA.

UF - Florida Museum of Natural History, Gainesville, USA;
USM - Universitá degli Studi di Milano, Milan, Italy.

USNM - National Museum of Natural History, Smithsonian Institution, Washington, USA;

ZMJC - Zoologisk Museum Universitat Copenhagen, Copenhagen, Denmark.

GEOLOGY
Late Tertiary sediments occur extensively in the precordilleran and piedmont regions of Argentina (Marshall and Patterson, 1981). The montane sediments thin out to the east and are deeply buried in the central pampas and in the La Plata River Basin, but outcrop in various places along the margin of the pampas (Simpson, 1940). Recent advances have improved the general understanding of the sequence, stratigraphy and correlation of Late Tertiary mammal-bearing rocks in South America. However, the geochronologic and biostratigraphic relationships of many deposits remain incompletely, or even poorly, understood.

The reasons for the incomplete geological knowledge are: 1) there are few outcrops of extensive sequences of Late Tertiary sediments in South America that yield good mamalian faunae (Marshall and Patterson, 1981); 2) many older collections were made with inadequate or no stratigraphic control; 3) few radiometric dates or magnetostratigraphic correlations are available; and 4) the mammalian remains are in many cases fragmentary and scarce, which impedes biostratigraphic studies. Further, the remains recovered from various localities appear to derive from mixed assemblages, and include some taxa that are redeposited.

Late Tertiary and Quaternary South American Land Mammal

Age usage (and the associated geological formations and faunae) generally follows that of Marshall et al. (1983) for the Tertiary and of Marshall et al. (1984) for the Quaternary, but supplemented by papers on absolute dating, biostratigraphic correlation, and specific locality information (e.g., Marshall and Patterson, 1981; Pascual and Odreman-Rivas, 1973; Cione and Tonni, 1995). The works of Marshall et al. (1983, 1984) are imprecise and tentative in many respects (which reflects their level of understanding, vide supra) but they summarize the current knowledge, and form a useful framework for further study and refinement. The reader is referred to Savage and Russell (1983) and Cione and Tonni (1995) for localities and correlations. Names of land mammal ages are usually given in English. In the text the name is left to stand alone, so that Land Mamal Age (or an abbreviation) is not required. Occasionally, the Spanish name for an age is given. It is worth noting that Cione and Tonni (1995) recently proposed replacing the usage of Land Mammal Ages with stage-ages for South America, mainly because the Ages are represented by chronostratigraphic units rather than patterns in biostratigraphy. They used the Uquian Age as an example of the difficulties that they perceived with the current use of Ages. Their arguments are convincing, but at this stage (as noted by Cione and Tonni, 1995), considerable taxonomic and stratigraphic revisions are required before their
suggestions may be extended to include the remainder of Tertiary and Quaternary South American time.

Friasian Land Mammal Age
All remains of Megatheriinae are post-Santacrucian (early Miocene). The Santacruz Formation is richly fossiliferous and widely exposed in Patagonia, and contains the remains of Planopsinae and other ground sloths. The earliest known certain megatheriine is Megathericulus patagonicus Ameghino, 1904, known initially from the Friasian at Laguna Blanca, Chubut Province, Argentina.

The Friasian (approximately 16 to 12 mya) was discussed in detail by Kraglievich (1930a), who based his review partly on the work of Roth (1898, 1908, 1920), Ameghino (1904), and Rovereto (1914). He recognized three local faunae and three horizons: the colloncurense, friasense and mayoense, from oldest to youngest. These are no longer formally recognized, but the colloncurense and mayoense are believed to represent the early and late, respectively, stages of the Friasian (Bondesio et al., 1980; Marshall et a1., 1983). Marshall et a1. (1977) dated the colloncurense as between 15.4 and 14 mya. The Friasian, however, remains poorly defined (Marshall et al., 1983); even at Rio Frias, the most important locality, the fossils "were found at several different levels and are not all of the same age" (Simpson, 1940:666).

Kraglievich (1930a) reported that the remains of $M$. patagonicus are from the friasense, or miđdle and most extensive part of the Friasian. Additional remains of this species are reported by Scillato-Yané et al. (1993) from near Guenguel, Santa Cruz Province, and Arroyo Pedregoso, Chubut Province, Argentina, and probably correlate with the mayoense stage of the Friasian.
M. primaevus Cabrera, 1939 from Paso Flores, Neuquen Province, Argentina, is possibly, but not certainly a megatheriine. Cabrera (1939) believed the exposures to be Santacrucian, but Pascual et al . (1978) suggest that they are probably equivalent to the colloncurense. Bondesio et al. (1980) considered Megathericulus an index fossil for the Friasian.

Kraglievich (1930a) based other megatheriine species on fragmentary remains from the friasensan: M. friasensis (from the Río Frias 'yacimiento' or horizon), Eomegatherium andium (Rio Huemules horizon), and E. cabrerai (Laguna Blanca and Rio Fenix horizons). Pascual and Odreman-Rivas (1973) list the latter two as taxonomically questionable, and as belonging to Promegatherium, but Bondesio et al. (1980) recorded them as Eomegatherium.

The type fauna and locality of the Friasian occurs along the Alto Rio Cisnes in southern Chile, and is contemporaneous with the Santacrucian (Marshall and Salinas, 1990). These authors therefore replaced the Friasian
(conventionally middle Miocene) with the Colloncuran for the land mammal age between the Santacrucian and Chasicoan (Marshall and Salinas, 1990; Marshall and Sempere, 1991).

## Chasicoan Land Mammal Age

The Chasicoan Age (late Miocene), separated by a hiatus of approximately one million years from the Friasian, is considered to have been from 11 to 9 mya. It is based on the Arroyo Chasicó Formation (southwestern Buenos Aires Province) and is divided into two members by both Fidalgo et al. (1980) and Bondesio et al. (1980). The Las Barrancas Member contains no pansantacrucian taxa and may belong to the Huayquerian Age, and the lower Vivero member contains most of the vertebrates considered as typical Chasicoan. Part of the Chiquimil Formation at Puerta de Corral Quemado and Valle de Santa Maria, Catamarca Province, Argentina (as well as other formations not pertinent here), are referable to the Chasicoan (Marshall et al, 1983).
"Plesiomegatherium" halmyronomum is based on remains from sediments near Laguna Chasico, Department of Villarino (Cabrera, 1928), which are part of the Vivero Member (Marshall et al., 1983).

Huayquerian Land Mamal Age
The Huayquerian Age (late Miocene) is 9 to 5 mya (Marshall et al., 1979). The term was coined by Kraglievich
(1934) from the Huayquerías (=Guayquerías) region of Mendoza Province, Argentina, and was suggested by Simpson (1940) to replace in part the araucanense of Riggs and Patterson (1939). However, Simpson (1974) believed that strata from the Huayquerian Formation in Mendoza were clearly distinct from those of Huayquerian Age in the Valle de Santa Maria. Marshall et al. (1983) considered the Huayquerian Formation of Huayquerian Age. Remains of Megatheriops rectidens (Rovereto, 1914) were recovered from the Huayquerian of Mendoza Province. Cabrera (1928) believed that Megatheriops was possibly synonymous with Pyramiodontherium. The provenance of Pyramiodontherium is unclear; the possibilities are considered below.

Recent stratigraphic studies in northwestern Argentina, from Jujuy Province in the north to Mendoza Province in the south, have advanced our knowledge of the Argentinian Late Tertiary. Megatheriine remains are also reported from the thick sequence at Valle de Santa Maria and Puerta de Corral Quemado, Catamarca Province, but accurate stratigraphic records are available only for specimens recovered during the Field Museum of Natural History's 1926 expedition. The remains are labelled Promegatherium, but listed as "Megatheriinae ind." in Marshall and Patterson (1981:67-71). These are probably the only published records for Tertiary megatheriines with accurate stratigraphic provenance. Other megatheriine remains from these strata have been assigned to

Pyramiodontherium bergi (Moreno and Mercerat, 1891), but their stratigraphic provenance remains unclear.

The thick sequence of Tertiary beds in Catamarca was once commonly geologically and temporally termed Araucanian, araucanaense, or araucano. These terms were confusing because it derived from rock-strata in Río Negro Province, Argentina, and extended to rocks of supposedly similar age elsewhere in Argentina. These Araucanian rocks are discussed in older works as a stratigraphic and faunistic unit (Marshall and Patterson, 1981). It is now realized that the Araucanian of older workers spans considerably more than a single land mamal age.

For convenience, I follow the stratigraphic and faunal sequence proposed by Riggs and Patterson (1939). Marshall and Patterson (1981) subsequently provided radiometric dates and magnetostratigraphic correlations for parts of these sections. It should be noted, however, that the section presented by Riggs and Patterson (1939) is a simplification and their terminology outdated, although it is basically followed by Marshall and Patterson (1981). The geology and stratigraphy of this northwestern region of Argentina are complex and are still being elucidated.

Riggs and Patterson's (1939) sequence comprises three formations, the Chiquimil (with two members, $A$ and B), the Araucanense (more appropriately Andalhualá), and Corral Quemado. The Calchaqui underlies Chiquimil B in the

Chiquimil area, and is approximately equivalent to the Chasicoan (Pascual and Odreman-Rivas, 1973). The Chiquimil contains few fossils, and no megatheriines have been reported.

However, it is still unclear whether Pyramiodontherium derived from the Araucanian or Corral quemado Formation. Rovereto (1914) described the genus as from the Valle de Santa Maria, which he considered the type locality of the araucanense. Cabrera (1929) reported some of the specimens simply as from the Valle de Santa Maria and others from bajo de Andalgualá (= Andalhualá, near Chiquimil in the Valle de Santa Maria). Andalgalá is approximately equidistant from the Valle de Santa Maria and Corral Quemado. Marshall and Patterson (1981) state that no Araucanian beds are known from this area. Thus, possible confusion with Andalgalá is unlikely.

Riggs and Patterson (1939) and Marshall and Patterson (1981) indicate that Pyramiodontherium is from the Corral Quemado Formation. However, Marshall and Patterson (1981:10) state that the "Araucanian faunas from the Valle de Santa Maria on which the basic studies of $C$. Ameghino, $F$. Ameghino, C. Rovereto, L. Kraglievich, and others were based are all without precise stratigraphic data and have no reliable data as to the levels of collection of the vertebrate fossils. They possibly represent a mixture from all the stratigraphic mits recognized by Riggs and

Patterson (1939), but primarily from their Araucanese" (i.e., the whole section, but excluding the Corral Quemado). The precise original localities of these Pyramiodontherium remains is important because authors disagree on the correlation of the Corral Quemado Formation. Pascual and Odreman-Rivas (1973) consider it early Montehermosan, and the Araucanian as Huayquerian. Simpson (1974) believed that a significant difference in age between the Araucanense and Corral Quemado formations had not been demonstrated and provisionally considered both Huayquerian in age. Marshall et al. (1983) refer the Araucanense to the Huayquerian and the Corral Quemado to the Montehermosan.

It would be useful to resolve the taxonomy and systematics of the undetermined Megatheriinae of Riggs and Patterson (1939) recovered from various levels of the Araucanian near Chiquimil in the Valle de Santa Maria, and from the Araucanian and Corral Quemado from Puerta de Corral Quemado.

I follow Pascual and Odreman-Rivas (1973) in assigning the Pyramiodontherium remains to the Araucanian, and hence Huayquerian, as the discussions of Rovereto (1914) and Cabrera (1928) suggest that the remains were likely recovered from the Araucanian strata of the Valle de Santa Maria.

Argentinian Mesopotamia
The fossil mammals recovered from Entre Rios and Corrientes Provinces, comprising Argentinian Mesopotamia (the geographic region between the rivers Uruguay and Paraná), cannot be with certainty assigned to or correlated with other Late Tertiary beds or faunae. These remains had generally been assigned to the mesopotamiense or entrerriense, terms no longer considered valid for either ages or faunal assemblages. Kraglievich (1934) and Simpson (1940:671) explained that Ameghino believed that the mamals from Mesopotamia represented two successive faunae, but was unable to separate the remains objectively, and was thus "obliged to list one supposedly mixed" Entrerrianian fauna.

The precise sources of the individual remains are unknown or unrecorded. Scillato-Yané (1981a, b) described them as a mixed assemblage, with some taxa bearing similarities to those of Huayquerian, some to those of Chasicoan, and others to those of Montehermosan Age. Pascual and Odreman-Rivas (1973) placed all Mesopotamian, Entrerrianian and Rionegrensan mamalian remains in a single faunal list. They stated that, while the remains indicated a predominantly Euayquerian Age, some suggested Chasicoan, Santacrucian (which surely seems in error, at least with respect to megatheriine remains), or Montehermosan Ages.

The question of the age of the beds and their associated mamalian fauna remains unresolved (G. J.

Scillato-Yané, E. P. Tonni, A. L. Cione, pers. comm., 1991). There is a general consensus, however, that the Mesopotamian Eauna is not older than the Araucanian (Huayquerian), as had been believed earlier (e.g., by Kraglievich, 1934; Riggs and Patterson, 1939; Simpson, 1940). The presumed older age £or the Mesopotamian may explain why Kraglievich assigned some scanty remains from the Friasian to Eomegatherium. Marshall et al. (1983) included part of the Mesopotamiense (that north of the city Paraná in Entre Rios) to the Huayquerian and part (that on the east bank of the lower Parana River) to the Montehermosan. The latter assignation is presumably the youngest or most modern limit.

Montehermosan Land Mamal Age
The Montehermosan Age (early and middle Pliocene) is approximately 6 to 2.8 mlya (Marshall, 1985; Marshall et al, 1985b). The type section is the Monte Eermoso Formation exposed between Monte Hermoso and Punta Alta (Buenos Aires Province). Marshall et al. (1979) and Butler et al. (1984) dated the strata of the Corral quemado Formation as between 6.4 and 3.54 mya. The Monte Hermoso Formation probably "Lies within the interval of 3.5 to 2.8 Ma (Marshall, 1985:65). This determination is based largely on the absence in the well-sampled Corral Quemado Formation of North American sigmodontine rodents, which first appear in the Monte Hermoso Formation. Pascual and Odreman-Rivas
(1973) regard the Corral Quemado Formation as older than the Monte Hermoso Formation based on the stage of evolution of the faunae. Cabrera (1928) reported that Megatherium gaudryi as probably derived from the higher horizon or strata from the Monte Hermoso Formation. Indeed, this species was long, and incorrectly, regarded as Montehermosan (vide infra).

Bonaparte (1960) recognized five lithostratigraphic units for the Monte Hermoso Formation, separated by erosional unconformities. He restricted the lowest to the Fermosense Tipico. The Miembro de Limolitas Estratificadas and Miembro de Limnolitas Claras (Bonaparte's second and third units, respectively) have been interpreted as probably intermediate between the typical Montehermosan and Chapadmalalan (Marshall et al., 1983), and may possibly be equivalent to Kraglievich's (1934) Horizonte Irenense. It is not known from which of the units recognized by Bonaparte (1960) M. gaudryi was recovered.

Kraglievich (1934) recognized a horizonte irenense based on the sediments and fauna from the banks of the Rio Quequen Salado between the Atlantic coast and Irene (Buenos Aires Province), which Reig (1955) recognized as the Irene Formation. Most later workers have regarded the Irenense as part of the Montehermosan, probably intermediate between the Montehermosan (from the type locality) and the Chapadmalalan (Marshall et al, 1983). Kraglievich (1934) reported

Megatherium istilarti from the irenense.
Other pertinent strata referable to the Montehermosan are the Corral Quemado Formation (Catamarca Province), the Río Negro Formation (Río Negro Province) at its type Iocality, the Tunuyán Formation (Mendoza Province), and that part of the mesopotamiense (Entre Rios Province) along the east bank of the lower Río Parana (Marshali et al., 1983).

Riggs and Patterson (1939) state that a partial megatheriine mandible from the Corral Quemado agrees very well with the Megatherium gaudryi specimen from Monte Hermoso, and that it differs from the Megatheriops mandible (which Cabrera, 1928, believed was possibly equivalent to Pyramiodontherium). They agreed with Cabrera (1928) and Kraglievich (1934) that this species does not represent Megatherium.

Chapadmalalan Land Mammal Age
The Chapadmalalan (late Pliocene) is approximately from 2.8 to 2.5 mya, or younger (Marshall, 1985), though there is some disagreement to its validity as a land mamal age. It is based on a fauna from the Chapadmalal Formation, exposed along the Atlantic Coast between Miramar and Mar del Plata (Buenos Aires Province). The Chapadmalal Formation may be wholly or partly contemporaneous with the Uquian of Kraglievich (1934).

A chapadmalense fauna was generally recognized by most
previous workers (e.g., Castellanos, 1937; Simpson, 1940, 1974) in this century, mainly following Kraglievich (1934). Simpson (1940:670) stated that "the faunas demonstrate beyond any doubt that the Monte Hermoso beds are older than those of Chapadmalal". However, Pascual et al. $(1965,1966)$ and Pascual and Odreman-Rivas (1973) proposed that the Chapadmalal fauna could be included in the Montehermosan Age, based on reevaluation of the faunae from Monte Hermoso and Chapadmaial; they considered the Chapadmalalan as late Montehermosan. Marshall et al. (1983:39) recognized the Chapadmalalan because it "permits a more precise understanding of late Tertiary faunal changes" and is marked by "the first known record in South America of new mammalian families of North America origin".

## Uquian Land Mammal Age

The Uquian is based on the Uquian Formation, with type locality at Esquina Blanca, Jujuy Province. Most of the fossils recovered from the Uquian Formation are from or near this locality, but the stratigraphic provenance of specimens obtained by earlier workers was not recorded (Marshall, 1985). Even so, most authors agree that the remains from the Uquian Formation represent a transitional fauna, which partly fills the paleontological hiatus between the Chapadmalalan and Ensenadan. Remains in earlier collections are possibly from different levels and may represent two
faunal associations. Kraglievich (1934) referred to the earlier fauna as Uquiense and believed it similar to those of Chapadmalalan Age; he considered the younger fauna as Ensenadan in character but did not name it (Marshall, 1985).

The Uquian Formation has been dated at Equina Blanca as between 2.5 and 1.5 mya; Kraglievich's (1934) Uquian is about 2.5 to 2.4 mya (Marshall et al, 1982a). The Uquian represents the lowest level from which fossils have been recorded, the "occurrence of fossils above this level is poorly documented, and it is not known if Uquian age taxa (s.l.) occur throughout" the Uquian Formation (Marshall, 1985:66).

Marshall (1985:66) emphasised that the concept of an Uquian Age as transitional between the Chapadmalalan and Ensenadan is based on the Uquia Formation and its fauna; however, its operational basis is from "the taxonomically diverse faunas of the Barranca de Los Lobos, Vorohue and San Andreas Formations, occurring superjacent to the Chapadmalal Formation" between Miramar and Mar del Plata. J.L. Kraglievich (1952) regarded each as a distinct age, the Uquian (equivalent to the Barranca de Los Lobos), the Vorohuean, and Sanandresian. Though this has not generally been followed (Marshall et al., 1984), there appears to be reason for retaining these distinctions, based on Reig's studies of small mammals (Marshall et al., 1984) and designating them subages of an Uquian Age.

The possible synchronicity of the Chapadmalal Formation and the lower part of the Uquian Formation (i.e., approximately equivalent to uquiense, hence excluding the strata from Buenos Aires Province) suggests two possible interpretations. The Chapadmalal Formation may be included within the Uquian Age, or the Chapadmalalan and Uquian may be recognized as an age distinct from that represented by the strata in Buenos Aires Province (i.e., upper Uquian) (Marshall, 1985). Cione and Tonni (1995) proposed abandoning the Uquian (and its type locality) and replacing it with Marplatan.

Ensenadan Land Mammal Age
The Ensenadan Age (middie Pleistocene) has its type locality in the harbour of Ensenada, a city near Buenos Aires, and is based on the Ensenadan Formation. Ameghino (1889) referred to the strata as piso ensenadense, although he (1880) had previously considered it the pampeano inferior (Marshall et al., 1984). The Ensenadan Formation has been variably subdivided, and its lower levels may be of Uquian Age. The upper parts of the Formation has exposures in various localities in Argentina, and referable "mamalbearing beds in Argentina include the Ensenada and Mirimar Formations, Buenos Aires Province. . . ; capa M of Doering (1882), Cordoba Province; and the lower member of the Yapoi Formation, Corrientes Province" (Marshall et al., 1984:29).

Pascual et al. (1966) assigned Megatherium gallardoi to the Ensenadan.

Ensenadan strata (and faunae) in Argentina have not been dated (Marshall, 1985), but correlation with the evolutionary level of the fauna from the Tarija Formation in southcentral Bolivia permit a reasonable determination of age correlation. MacFadden et al. (1983) dated the Tarija Formation at between 1.0 to 0.7 mya, or possibly younger (see below). The relative evolutionary level the Tarija fauna to the Argentinian fauna suggests a middle or late Ensenadan Age. Thus the Uquian-Ensenadan boundary predates 1.0 mya. Marshall (1985) placed this boundary at 1.5 mya.

The Tarija fauna, including Megatherium, has been recovered from various stratigraphic levels in the basins of Tarija, Concepcion and Padcayu. Rovereto (1914) based his edad tarijense on the fauna and considered it equivalent to the Argentinian puelchense. This is inadmissible because the former is clearly younger than the latter, which is probably of Uquian Age (Pascual et al., 1965). The Tarijan remains traditionally have been considered to represent a single assemblage (e.g., Hoffstetter, 1963), but probably this is an oversimplification (Marshall et al., 1984). The age of the Tarija Formation and its fauna usually have been viewed as Ensenadan or intermediate between the typical

Ensanadan and Lujanian. Kraglievich (1930a, 1934)
emnhasized the post-Ensenadan character of the fauna and
considered it approximately equivalent to the early Lujanian (bonaerensan of Ameghino). MacFadden et al. (1983) assigned the Tarija Formation and its fauna to the Ensenadan, but "it is possible that some fossils from this locality are younger" (Marshall et al., 1984:33).

Lujanian Land Mammal Age
The Lujanian (late Pleistocene) derives its name from exposures along the Río Lujan, near Buenos Aires. Lujanian formations are also well-represented elsewhere in Argentina. MacFadden et al. (1983) and Marshall (1985) place the Ensenadan-Lujanian boundary at 0.5 mya, based on paleomagnetic studies of the Nuapau Formation (southeastern Bolivia), and on the level of evolution of its fauna relative to the fauna the Tarija Formation (vide supra).

The Lujanian has been variably subdivided. Bonaerensan and lujaniensan subages (representing early and late Lujanian time, respectively) have traditionally been recognized. However, the lithologically distinct rock units representing these designations have not been shown to be certainly temporally distinct (Pascual and Fidalgo, 1972; Pascual et al., 1965, 1966; Marshall et al., 1984).

Lujanian mammal-bearing strata are common in Buenos Aires Province but also occur elsewhere in Argentina. Referable strata include the Buenos Aires Formation, the Guerrero (lower) Member of the Lujan Formation (from the
lower Río Salado region), and the Arroyo Seco Formation. Megatheriine remains are common in Lujanian deposits and have been assigned to Megatherium americanum, M. sp., or other species of Megatherium.

The term Pampean or Pampeano was commonly associated with Argentine strata that Ameghino originally considered Pliocene, but it came to be considered nearly synonymous with the Pleistocene; the post-Pampean referred to the Holocene. Neither of these is admissible as either rock or time unit designations and their current use is restricted to an informal sense but understood to mean Pleistocene. The fossils in the older collections were commonly assigned to the Pampeano, or post-Pampeano, and sometimes to the Pampeano inferior or Pampeano superior. The last two are usually understood to be approximately equivalent with Ensenadan and Lujanian, respectively. I recognize these designations but caution that the stratigraphic information in the older collections is not reliable.

Pleistocene megatheriine remains are known from localities in nearly every South and Central American country, and the United States. These remains belong to Megatherium or Eremotherium. Precise stratigraphic locations for many of these remains are poorly documented. The relative or absolute dates of the strata are not clearly understood, but the faunae are sufficiently characteristic to establish a generally Pleistocene age.

The Ulloma Formation, near Ulloma, Bolivia, has yielded Megatherium remains and was considered early Pleistocene by many early workers. More recent evidence suggests, however, that these deposits are probably early Lujanian (Marshall et al., 1984). Megatherium has been reported from strata near Anzaldo (approximately 55 km SE of Cochabamba), Bolivia, from which are clearly Pleistocene (Marshall et al., 1984). Megatheriine remains are reported from many states in Brazil (e.g., Cartelle and Bohórquez, 1982; Lund, 1842; Oliveira and Damasceno, 1987; Paula Couto 1973, 1980; Toledo, 1986, 1989; Simpson and Paula Couto, 1981), and generally are considered of Lujanian or Holocene ages.

Numerous remains have been recovered from limestone caves, including Toca das Onças (near Jacobina, Bahia), which has yielded the largest and most diverse collection of megatheriine remains anywhere. The caves from Minas Gerais are well known and were worked extensively by Lund during the mid-1800's. The remains from Minas Gerais possibly represent a mixture of late Pleistocene or Holocene fossils (Marshall et al., 1984), but those from Toca das Onças appear to be Holocene (Cartelle, 1993). However, Simpson and Paula Couto (1981) stated that the presumed late age of all Eremotherium remains is possibly questionable, based on the apparent middle Pleistocene age of some of the Eremotherium specimens from Acre, Brazil. Toledo (1989) noted that the presence of Eremotherium in the mid-

Pleistocene of North and Central America raises the question of the stratigraphic position of this genus in South America.

Pleistocene Megatherium remains have been recovered from north and central Chile. Casamiquela and Sepulveda (1974) considered the remains from Tarapacá (including those studied by Philippi, 1893) as Pleistocene, but these fossils lack precise stratigraphic information. Frassinetti and Azcarate (1974) and

Marshall and Salinas (1989) reported additional Megatherium specimens from Chile.

Pleistocene deposits yielding mamalian fossils are abundant in Colombia, but most remains lack stratigraphic control (Marshall et al., 1984). Eremotherium is included in faunal assemblages that suggest Iowland habitats, such as Cucuta, Villavieja, El Boqueron, and Fusagasuga (Porta, 1961, 1963; Hoffstetter, 1970; Marshall et al., 1984). These faunae are characterized by the association of Eremotherium and Haplomastodon and, as such, are very similar to faunae found in northern Venezuela, Panama, coastal Ecuador, and northern Peru (Hoffstetter, 1970).

The mamal-bearing deposits of Ecuador may be assigned to the Andean, Coastal and Oriental geographic regions, following Hoffstetter (1957) and Marshall et al. (1984). Megatheriinae specimens are reported from all regions. Those from the Andean and Oriental are scarce and difficult
to assign with certainty, but probably represent Eremotherium (Spillmann, 1949; Hoffstetter, 1970).

The Coastal region is abundantly fossiliferous and has yielded numerous Eremotherium remains. Localities include La Carolina, Engabao de Chanduy (Santa Elena Peninsula), and others on Puna Island, in the vicinity of Rio Daule, and near Punta Surrones. These local faunae have been termed Carolinean (Hoffstetter, 1952), and are apparently of late Pleistocene age, except that the fauna from Punta Surrones may be slightly older than the type fauna La Carolina (Bristow and Hoffstetter, 1972).

Few Paraguayan mamalian fossils have been thoroughly described. Hoffstetter (1978) reported that Megatherium americanum is frequently present in the Pleistocene local mamal faunae from Riacho Negro and General Bruguer (just north and ca. 180 km northwest of Asuncion, respectively), both near the Argentine border. However, "many of the specimens are unlabelled, making locality assignment difficult, if not impossible" (Marshall et al., 1984:51).

The Pleistocene of Peru is known from various localities that may be grouped into Coastal, Andean and Amazonian geographic regions. The localities and faunae of the Amazonian region are not well known, but Eremotherium is reported from beds along the Rios Inuya and Mapuya (Marshall et al. 1984).

Megatheriinae reported from the Andean region are
recovered predominately from caves at 2,500 to $4,000 \mathrm{~m}$ altitude. The presence of undetermined megatheriines is reported from Cajamarca and Celendin in the northern part of this region. The primarily cave localities further south are more richly fossiliferous. These deposits include Huargo, Sanson-Machay, Uchcumachay, Pikimachay, and Casa del Diablo. Little stratigraphic information is available for these localities and faunal successions are not determined (Hoffstetter, 1970). The presence of a true Megatherium (cf. americanum) is indicated by a femur from near Cuzco, and is the most northern record for this genus (Hoffstetter, 1970). Other megatheriine remains, some from caves (e.g., from Cerro de Pasco, Yantac, Tres Ventanas, Cuzco, Llalli), suggest " $£=1$ mas mas modestas (quizas dos tamanos); se trata de un genero inedito, parecido a Eremotherium por la forma de la mandibula $y$ del femur, pero todavia provisto de un dedo II en la mano" (Hoffstetter, 1970:978). The fauna at Pikimachay includes Megatherium, but "generic identifications are used in a broad sense" (Marshall et al.. 1984:55; MacNeish et al., 1975). Various dates have suggested a late Lujanian age for some of the cave deposits. The ages of other megatheriine remains, however, are probably older, as is suggested by sediments from Tres Ventanas dating older than 0.04 mya (Marshall et al., 1984). The coastal strata of Peru have yielded the Talara fauna, one of the best known South American Pleistocene
vertebrate faunas (Lemon and Churcher, 1961; Churcher and van Zyll De Jong, 1965). The most important deposits are the tar seeps in the La Brea-Parinas oil fields. Lemon and Churcher (1961) proposed a Lujanian Age for the Talara fauna. Eremotherium remains, possibly of two species, are common elements of the fauna. Possible Eremotherium remains have also been recovered from near Trujillo (Marshall et al., 1984).

Pleistocene continental deposits occur over large areas of Uruguay, but are generally poorly stratified. Megatherium, ?Eremotherium and Perezfontanatherium have been reported (Marshall et al, 1984).

Megatheriine remains are reported from various Pleistocene localities in Venezuela, principally from the states of Falcon and Lara. The Muaco fauna (Falcón) is probably of Lujanian age and includes Eremotherium (Marshall et al., 1984). Royo y Gomez (1940) reported Megatherium from Muaco, but this seems improbable and taxonomic confirmation is required. Other localities in Falcon that yielded Eremotherium include Cucuruchu (near Cora), and Quebrada Ocando (near Guayabacoa). Elsewhere Eremotherium is known from near Barquisimento (Lara), Lago Valencia (Carabobo), and Cumana (Sucre) (Marshall et al., 1984).

Late Pleistocene vertebrate-bearing deposits are common in many parts of Central America and include remains of Eremotherium. Webb and Perrigo (1984) recorded several of
these from El Salvador (e.g., Horminguero Local Fauna) and Honduras (e.g., Yeroconte and Orillas del Humuya Local Faunae). They reported that the Barranca del Sisimico local fauna from El Salvador, which includes Eremotherium, is probably Irvingtonian, based on the probable early Pleistocene stage of evolution of Megalonyx. They emphasized, however, that further study of this fauna is needed.

Polaco-Ramos (1981) reported Eremotherium remains from Pleistocene cave deposits near Teapa (Tabasco), Mexico. Additional Mexican remains include those recorded by Freudenberg (1922), but without provenance, and Duges (1896) from near Arperos, Guanajuato (originally as Scelidotherium guanajuatensis), and other localities listed by Polaco-Ramos (1981).

## ANATOMICAL DESCRIPTIONS OF MEGATHERIINAE

## SKULI

The skull is the most important unit in diagnoses of genera and species of Megatheriinae, as in most vertebrates. Descriptions have been based on the skulls of Eremotherium laurillardi (= E. "mirabile" and E. "rusconii", vide infra) and Megatherium americanum, as their remains are most wellpreserved and abundant. The skull of $E$. laurillardi was described and diagnosed largely by Hoffstetter (1952), Paula Couto (1954), Gazin (1957), Cartelle and Bohórquez (1982, 1986). Toledo (1989), and Cartelle (1992), and that of $M$. americanum by Owen (1856) and Ameghino and Kraglievich (1921).

The authors who discussed the skulls of these taxa attempted to define the differences between them, but were only partly successful in recognizing the real taxonomic differences in contrast to those caused by interspecific or sexual variation. Differences are readily apparent between the classic specimens described by Owen (1856) for M. americanum, and Hoffstetter (1952) and Gazin (1957) for E. laurillardi. However, not all individuals of these species resemble in detail the classic types, and some are quite different. This is due to normal interspecific variation and postmortem distortion, but also to a high incidence of
pathology in Megatheriinae (see Toledo, 1989).
Interspecific variation among individuals of a species results in changes of proportion and morphology, so that some characteristics in some individuals of one species tend to resemble those of the other. Thus, the diagnoses given in the literature, based on the classic specimens, cannot be applied consistently, and discrimination between species is not always straightforward, particularly with incomplete specimens.

This chapter is divided into three sections. The first, General Morphology of the Skull of Eremotherium laurillardi, focuses on an analysis of the general features of the skull of this species. It addresses the suitability of the characters used to support supposed recognition of more than one large species of Pleistocene Eremotherium. The second section, Anatomical Descriptions of the Skulls of Eremotherium laurillardi and Megatherium americanum, contains detailed descriptions and comparative analyses primarily for these species to each other and to other Megatheriinae and Tardigrada. The third section, Anatomical Descriptions of the Skulls of Other Megatheriinae, describes and compares the skulls of other Megatheriinae to each other, and to those of E. laurillardi and M. americanum.

Various linear dimensions were recorded for megatheriine skulis as estimators of size and to investigate intra- and interspecific differences. These are described
in the appropriate sections, and presented in Appendix 4A. Standard statistics for these variables are presented in Table 1.

General Morphology of the Skull of
Eremotherium laurillardi
The general shape of the megatheriine skull (Pls. 3-11) resembles that of various early Tardigrada such as Planops (Planopsinae), Pseudoprepotherium (Mylodontinae), and Nothrotheriops (Nothrotheriinae sensu stricto). It is approximately cylindrical, but with narrowed cranial and rostral regions, and contrasts sharply with the slender and elongate skull of the Scelidotherinae (e.g., Scelidotherium, Catonyx), the anteriorly truncate skull of most Megalonychidae (e.g., Megalonyx) and the anteriorly widened skull of most Mylodontinae (e.g., Glossotherium, Lestodon) and some Megalonychidae (e.g., Acratocnus). The reader is referred to Hoffstetter (1958) and Paula Couto (1979) for more complete summaries of the general skull form among Tardigrada.

Toledo (1989) and Cartelle (1992) defended the recognition of a single species (including, however, E. elenense, vide infra), but do not provide detailed anatomical comparisons nor consider the large collection from Daytona Beach. It is demonstrated by my research that the variation cannot be used as evidence to support the

TABLE 1. Standard Statistics (mm) for Skulls of Erenotherium laurillardi and Megatherium americanum. Abbreviations: ANIW Width of the rostrum anterior to the anterior zygomatic root; M1OCH, OCH, OPTH as in Figure 3; POCONST - Minimum width of the postorbital constriction; POPW - Width across the postorbital processes; POSTW - Width of the occiput, measured between the lateral margins of the mastoid processes; TRL - Tooth row length.

Eremotherium laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | ---: | :---: | :---: | ---: |
| MIOCH | 7 | 446 | 558 | 509 | 35.1 |
| OCH | 7 | 85 | 124 | 107 | 12.2 |
| OCIH | 7 | 136 | 174 | 156 | 14.3 |
| TRL | 7 | 192 | 214 | 205 | 8.4 |
| ANIW | 7 | 120 | 133 | 127 | 5.1 |
| POPW | 7 | 158 | 202 | 183 | 14.5 |
| POCONST | 7 | 126 | 185 | 155 | 19.2 |
| POSIW | 7 | 226 | 296 | 260 | 23.4 |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | ---: | ---: | ---: | ---: | ---: |
| $-M O C H$ | 10 | 466 | 625 | 547 | 60.5 |
| MIOCH | 10 | 144 | 230 | 201 | 23.5 |
| OCII | 10 | 92 | 150 | 123 | 19.7 |
| TRL | 8 | 200 | 270 | 228 | 21.9 |
| ANIW | 7 | 115 | 177 | 146 | 23.9 |
| POPW | 8 | 160 | 259 | 216 | 29.9 |
| POCONST | 7 | 130 | 172 | 159 | 55.0 |
| POSTW | 8 | 247 | 310 | 275 | 24.9 |

presence of more than one species.
Cartelle and Bohórquez (1982) defended the specific distinction of E. laurillarđi (sensu Cartelle and Bohórquez, 1982 nec Cartelle and De Iuliis, in press; see App. 1) on various characters, which are demonstrated below to be doubtfully valid. Many of their comparisons were apparently based on the skull and mandible of $E$. "rusconii" illustrated by Gazin (1957: fig. 1). Two considerations regarding Gazin's figure must be noted. First, it appears slightly inaccurate and may show the skull (USNM 20872) and mandible (probably USNM 18498) of different individuals. Second, the orientation of the figure (and specimens in general) influences one's perception or recognition of features. The orientation of skulls and mandibles during analysis is an important consideration and one which, in my opinion, usually has been neglected. This situation arises repeatedly in the literature and results in perceived differences among specimens (examples are given below), which are accorded unjustifiable significance.

Cartelle and Bohorquez (1982) stated that the descending process of the jugal projects clearly below the ventral margin of the dentary in E. "rusconii" (if only slightly), whereas in E. laurillardi it ends dorsal to this margin. However, these relative positions are influenced by the orientation of the skull and mandible, and a standard plane of reference is required if the relationships are to
be properly assessed. If Gazin's (1957) figure is rotated a few degrees clockwise such that the occlusal plane is nearly horizontal, the descending process of the jugal ends dorsal to the plane tangential to the most ventral margin of the dentary and parallel to the occlusal plane. Although some variation exists, other Eremotherium specimens do not differ significantly in this regard. Further, the length, width, depth, shape, and robustness of the descending process vary (cf. MCL 1700/01, MCL 1701/01: P1. 3; MCL 1702/01: Toledo, 1989: fig. 3b, Pls. 3, 4), possibly with age and sex (see also Pls. 4, 5).

Cartelle and Bohórquez (1982) stated that the coronoid process lies considerably more posterior to the ascending process of the jugal during occlusion in E. laurillardi (MCL 1701/01) compared to that in E. "rusconii". However, the difference is not as large as implied (compare Gazin, 1957: fig. 3 with Toledo, 1989: fig. 4B). Further, the relative positions of the coronoid and ascending processes often depend on the inclination of the ascending process, which is variable. Indeed, the morphology of the ascending ramus in MCL 1701/01 is very similar to that of the Panamanian specimens. The distinction noted by Cartelle and Bohórquez (1982) is again partly attributable to the inaccuracy of Gazin's (1957) figure (as explained in the following paragraph).

Cartelle and Bohórquez (1982) further stated that
differences existed between these species in the relative positions of the mandibular condyle and angular process. In E. "rusconii" the angular process is shown as lying ventral to the posterior part of the pterygoid blade whereas in $E$. laurillardi it extends nearly to the level of the anterior part of the occipital condyle (see Toledo, 1989: fig. 4B). Again, this relationship in E. "rusconii" is caused by the inaccuracy of Gazin's figure. If it were correctly oriented, the angular process would lie directly ventral to the mandibular condyle, which occurs in no other species of Megatheriinae. The relative position of the angular process and mandibular condyle in dentaries from Panama (USNM 18498; MNP 46) and Mexico (Polaco-Ramos, 1981: fig. 6) is as in all other Eremotherium mandibles. Indeed, close inspection of Gazin's figure 1 reveals that the mandibular condyle is in proper relation to the angular process, but that the condyle is anterior to the mandibular fossa, so that the mandible cannot be in proper articulation with the skull. Thus the coronoid process is also displaced forward. Cartelle and Bohórquez (1982) interpreted the displaced position of the process and its relationship to the ascending ramus of the jugal as a diagnostically important difference (see preceding paragraph).

Cartelle and Bohórquez (1982) suggested that
differences between the mandibles are associated with differences in the occiput and articulation of the mandible
and skull. In E. laurillardi the mandibular fossa lies more dorsal and the occiput is nearly vertical, whereas in $E$. "rusconii" the occiput is inclined anterodorsally. However, there is no evidence to support a more dorsal position for the mandibular fossa; it is located as in all other Eremotherium specimens. The inclination of the occiput varies in the skulls from Toca das Onças (cf. Pls. 3, 4); it inclines anterodorsally in MCL 1702 and MCPUCRS 2364 (see Toledo, 1989: fig. 4a).

Cartelle and Bohórquez (1982) further stated that the posterior width of the skull is considerably greater than the width across the lacrimal tubercles in E. laurillardi, but that the reverse occurs in E. "rusconii". The authors cited additional measurements from Hoffstetter (1952) for $E$. "rusconii" and Paula Couto (1954) for E. laurillardi that appear to agree with their observations based on the Toca das Onças collection, although they noted that the two measurements closely approach each other in some Toca das Onças specimens. However, their conclusion does not hold, because the differences they cite are due to normal interspecific variation, as is shown by the considerably greater posterior width in the skull (USNM 20872) described by Gazin (1957). In fairness to Cartelle and Bohorquez, the measurements for USNM 20872 were not published. Plates 6, 7, and 8 show dorsal views of the skulls of several individuals.

Similarly, their claim that the minimum width between the tooth rows is nearly twice that of the largest molariform in E. laurillardi is incorrect. As in other Eremotherium specimens the minimum width approximately equals that of the largest molariform in the specimens from Toca das Onças (Toledo, 1989).

Numerous other minor differences have been cited to support specific distinctions. For example, Paula Couto (1954) based the species and subgenus $E$.
"(Pseuderemotherium) lundi" on a relatively elongated cranium and large occipital condyles. Porta (1961) based E. "robustum" partly on the robust posterior region of the skull, and $E$. "cucutense" on an occiput that is wider than high and a prominent occipital protuberance. These characters are invalid, and fall within the ranges of variation of the Daytona Beach and Toca das Onças collections.

Toledo (1989) made an important contribution towards recognition and documentation of variation in the skulls of E. Iaurillardi, based largely on the Toca das Onças collection. However, while his work documented and improved our knowledge of variation, some of his interpretations require modification.

Toledo (1989) separated the Toca das Oncas skulls into two morphological groups, each including adults and juveniles, on the form of the dorsal profile (Pls. 3, 4,
13). That of one group is nearly rectilinear (e.g., MCL 1709, 1702/01): in the other it descends anteriorly, so that the rostrum lies more ventrally (e.g., MCL 1703, 3899, MCPUCRS 2364). However, Toledo's description is somewhat inappropriate because the profile of the skull usually descends anteriorly. A more precise description is that the dorsal profile is usually sinuous, convex posteriorly, concave at the junction of the cranium and rostrum, and nearly rectilinear over the rostrum. This pattern is variable in the degrees of convexity and concavity, and in the anteroposterior position of the junction between the cranial and rostral portions. When the variation between the degree of convexity and concavity is great, the dorsal profile is prominently sinuous; when it is small, the profile approaches rectilinearity. There does not appear to be a sharp division between these two extremes, as most other skulls fall between these extremes. The dorsal profiles of skulls recovered from countries other than Brazil (Pls. 2C, 3), and assigned previously to $E$. "rusconii" or E. "mirabile" (e.g., EPN V1508, Engabao de Chanduy; ROM 24240, Santa Elena Peninsula (= Coralito locality of Hoffstetter, 1952), Ecuador; ROM 24239 and ROM 37689, Daytona Beach; FMNH P26970, Honduras) are variable but clearly fall within the range established by the Toca das Onças collection.

Toledo (1989) suggested that increased convexity was
due to differential inflation of the frontal sinuses, and was sexually dimorphic. Further, he stated that a more ventral position of the rostrum was reflected by a greater distance between the alveolar border and occipital condyles; conversely, the planes of the condyles and alveolar border are closer in skulls with nearly rectilinear profiles.

A cursory inspection of the skulls appears to confirm Toledo's (1989) observations, but a more detailed analysis suggests that they are not entirely accurate. It is reasonable that differential inflation of the frontal sinuses would influence the relative positions of the dorsal margins of the cranium and rostrum, but it is unclear why it should affect the relationship between the occipital condyle and the alveolar border.

Three planes (Fig. 1) are used here to analyze the relationships between these areas of the skull. Two of these are longitudinal frontal planes, A, drawn through the alveolar margins and extended posteriorly ventral to the condyles, and $A^{\prime}$. drawn through the centres of the condyles and extended anteriorly, parallel to A. The third plane, B, is perpendicular to $A$ and $A^{\prime}$, and is tangential to the posterior margin of the condyles. These planes allow comparison between the relative positions of the condyles, alveolar borders, and dorsal margin of the skull on a fixed plane of reference, and allow measurement of the height of the condyle above the alveolar border, $A$. The absolute

FIGURE 1.
Diagrammatic Megatheriinae skull in lateral view, with zygomatic arch removed, showing measurements. Abbreviations: A: - Plane passing through the alveolar margins; $A^{2}$ - Plane parallel to plane $A$ and passing through the occipital condyles; $A^{11}$ - Plane parallel to planes $A$ and $A^{1}$, and passing through inion; $B$ - Plane perpendicular to planes $A, A^{1}$, and $A^{11}$, and tangential to the posterior margins of the occipital condyles; OCH - Height of the occipital condyles between planes $A$ and $A^{1}$; OPTH - Height of the occiput between planes $A^{1}$ and $A^{11}$; M1OCL - Length between the mesial surface of M1 and the posterior margin of the occipital condyles (plane B).

height of the occipital condyles, OCH, is measured along plane $B$ as the perpendicular distance between planes $A$ and $A^{\prime}$. The length, M1OCL, is measured on A between the mesial margin of MI and the intersection of planes A and B. A measure of the relationship between OCH and M1OCL is given by the OCH Index (OCHI), obtained by the formula OCHI = OCH/L x 100, and is given as an index figure which is the percentage that $O C H$ represents of MIOCL. The latter is used because it is repeatably measurable and is a consistent estimator of skull length. The region anterior to M1 is often damaged or missing in most megatheriine skulls recovered (vide infra).

In E. laurillardi OCHI varies between approximately 9 and 23, and does not appear to correlate with the dorsal profile of the skull. For example, $\mathrm{OCHI}=21$ in MCL 1700/01 and 20 in MCL 1701/01 (P1. 3). Toledo (1989) considered the latter skull to possess a nearly linear dorsal profile, with which I disagree. In any event, other skulls indicate no particularly close relationship. Indeed, the greatest OCFI (23) is recorded for FMNH P26970 (P1. 5B), in which the dorsal profile is nearly rectilinear (or more precisely, only very shallowly concave at the junction of rostrum and cranium).

In nearly all specimens plane A intersects the dorsal part of the lateral margin of the external choanae. However, it intersects the ventral part of this margin in

MCL 1702/01 (P1. 4A), which also possesses the lowest OCHI value (8). MCL 1702/01 is the only Eremotherium specimen, to my knowledge, in which a concave portion, however subtle, is not present between the facial and cranial portions, and the entire dorsal margin forms a shallow convex arc from rostrum to nuchal crest. It is not clear if this condition is natural, hence due to intraspecific variation, or caused by postmortem deformation. However, as MCL 1702/01 (Pls. 4A, 7A; 10A) otherwise appears well-preserved and some specimens from Toca das Oncas have only a shallow concavity, it is probable that the condition in MCL 1702 forms part of the range of variation for this species. Probably Toledo (1989) was strongly influenced by the relative positions of the condyles and alveolar border, and shape of the dorsal margin of the skull of MCL 1702/01. The other specimens suggest that the inflation of the frontal sinuses has Iittle, if any, bearing on the relative position of the occipital condyles to either the alveolar borders or the rostrum.

Anatomical Descriptions of the Skull of
Eremotherium laurillardi and Megatherium americanum The cranial sutures fused early in megatheriines, and most are imperceptible in adults. A few juvenile specimens of Eremotherium laurillardi and Megatherium americanum preserve many of the sutures and allow descriptions of the
individual bones. The sequence of fusion may be reconstructed for $E$. laurillardi from the fine collection of juveniles from the Toca das Onças sample. The individual bones of the skull are described in detail primarily for $E$. laurillardi, but those for M. americanum are also discussed as available. Comparison of the individual bones of other megatheriine taxa is necessarily limited to more general comments and observations because of paucity of materials.

The sequence of sutural closure for $E$. laurillardi was reconstructed by Toledo (1989), who recognized six developmental stages. Stage 0, probably a neonatal or foetal stage, is represented only by the mandible. Stage $V$ represents the adult stage. I follow with Toledo's (1989) stages, but add the following observations (Pls. 13-16).

The closure of the squamoso-ectotympanic suture, and of the medioventral part of the ectotympanico-entotympanic suture occurred early, and apparently were the first sutures to fuse (Pls. 14; 15A, B). Probably these occurred in Stage II or between Stages II and III. The ventral basioccipitoexoccipital suture (i.e., between the foramen magnum and condyloid foramen) closed early, but probably after the ectotympanic to the squamosal and entotympanic, and approximately at the same time as the supraoccipito-parietal fusion (cf. Pls. 15A, B and 15C, D, 16A, B). These fusions probably occurred early in Stage III.

The skull of M. americanum is apparently larger and
more robust than that of E. laurillardi (Tab. 1), but this is not corroborated by statistical analyses of linear variables. For example, M1OCL is larger in M. americanum, but the difference is not significant ( $t=1.50$, d.f. $=15$, $\mathrm{p}=0.154$ ). Toothrow length (TRL) is significantly larger ( $\mathrm{t}=2.76$, d.f. $=9.2, \mathrm{p}=0.022$ ) in M. americanum only prior to Bonferroni adjustment.

This is also true of the following variables used to assess widths: Anterior width (ANIW; $t=2.01, d f=6.5$, $\mathrm{p}=0.088$ ), the distance across the rostrum just anterior to the M1s; Postorbital Processes Width (POPW; t=2.62, df=13, $\mathrm{p}=0.021$, the distance across the postorbital process; Postorbital Constriction Width (POCONST; $\chi^{2}$ approximation $=0.10$, $d f=1, p=0.749$ ), the minimum width at the postorbital constriction: Posterior Width (POSTW; t=1.17, $\mathrm{df}=13, \mathrm{p}=0.265$ ), the distance across the occiput. A cursory inspection of their values and standard statistics (App. 4A and Tab. 1, respectively) indicates that these differ relatively and absolutely between M. americanum and $E$. laurillardi. For example, ANTW is apparently narrower and relatively smaller compared to POCONST in E. laurillardi. It is unclear if lack of sigaificant differences in these variables is due to the effects of small samples, or reflects their near equivalency in $M$. americanum and $E$. laurillardi. I suspect that the small samples are largely responsible because the skulls of these species are usually
and readily distinguished qualitatively based on many of these variables.

Premaxilla
Premaxillae are known only for E. laurillardi, M. americanum, and $M$. tarijense, but are among the more diagnostic elements in these taxa. The general form of the premaxilla has been described by Cartelle and Bohórquez (1986) for E. laurillardi, and by Owen (1856) and Ameghino and Kraglievich (1921) for M. americanum, but its variations have not. De Iuliis (1994; App. 2) compared the premaxillae of these species, and considered their phylogenetic histories.

In Eremotherium the premaxillae are approximately triangular, V-shaped plates, with an anterior apex, and lack elongated anterior processes. The general triangularity of the premaxillae is shared by various sloths, and is probably plesiomorphic (De Iuliis, 1994: figs. 2B, C). The lateral ramus is greatly expanded and projects considerably beyond the level of a narrower medial ramus. In some specimens the medial ramus is reduced to a nubbin, as in MCL 3001/01 (Toca das Onças, Bahia, Brazil; Cartelle and Bohórquez, 1986: fig. 5) and ROM 28941 (Daytona Beach Bonebed, Florida, USA). The premaxillae thus open medially as well as posteriorly for the palatine fissure. In other specimens of Eremotherium the medial ramus is well developed, as in ROM 11641 (De

Iuliis, 1994: Fig. 2C) and ROM 35813 (Santa Elena Peninsula, Ecuador). In ROM 28944 (Daytona Beach) the medial ramus is broken at the level of its junction with the lateral ramus; the size of the break suggests that the medial ramus was probably as large as in the Ecuadorian specimens. The premaxillae are loosely articulated to the maxilla, have never been found attached to the skull, and thus are seldom recovered. Generally they do not fuse. The anteriorly apices of the premaxillae form an acute angle, and present a triangular outline when viewed in occlusal plan. A protuberance, possibly for the attachment of nasal cartilage, projects laterally from the lateral margin.

In $M$. americanum the premaxillae (Pls. 17-24) bear anterior
processes, and are considerably stouter and more elongate. They are quadrangular, rather than V- or Y-shaped (as in the Nothrotheriinae), and with age firmly fuse to each other and the maxillae (De Iuliis, 1994: Fig. 2D). Therefore, in M. americanum the premaxillae are often preserved with the skull. They are largely missing, however, in some specimens, possibly due to age or damage to the anterior part of the rostrum (e.g., ZMUC 212, MACN 13021). The shape and length of the premaxillae vary considerably. They are particularly long in MLP 42-VI-24-2 (PI. 17C; the premaxillae are omitted in the dorsal view of this skull, Pl. 20C) and MACN 5002 (Pl. 23). They may be
dorsoventrally and uniformly slender (e.g., MACN 64; MLP 42-VI-24-2, Pl. 17C; BMNH 19953, Pl. 18A, B), considerably more robust and variable in dorsoventral height (e.g., MACN 1000 and 5002, FMNH 14293), or somewhat between these extremes (e.g., MNHNP PAM-276, the type of "Essonodontherium gervaisi"). The anterior processes also vary in mediolateral thickness. The ventral margin of each premaxilla is generally and variably sinuous, and concave posteriorly (e.g., BMNH 19953, FMNH P14293), but may also be nearly linear, as in MLP 42-VI-24-2, MLP 2-64. The long axis of the premaxilla is usually inclined slightly anteroventrally in relation to the premolariform part of the maxilla, but may be nearly parallel to it. The marked anteroventral inclination in MHNHM 6 (Pls. 1, 17A, the type specimen) is probably due to distortion or preparation. Each premaxilla bears a prominent lateral protuberance anteriorly, possibly for the attachment of nasal cartilage, as in Eremotherium. The palatine fissures lead to short, narrow canals that pass posterodorsally into the nasal cavity.

The premaxillae in the juvenile specimen of $M$. americanum (MACN 2830; Pls. 25-27) resemble those of Eremotherium. However, they bear anterior processes, which are not as stout as those in adults and impart a general, though superficial, similarity to the Y-shaped premaxillae of nothrotheres. A lateral protuberance is not present.

The medial ramus is clearly discernable. The palatine fissures open posteriorly as in E. laurillardi. However, the medial and lateral rami project posteriorly to approximately the same level. The premaxillae are not fused to each other or the maxilla, and are attached to the skull with plaster or glue. The lateral ramus is slender in lateral view, with sinuous ventral margin, and is somewhat higher posteriorly. The premaxillae in MACN 2831 (Pl. 28A) are slender and elongated. This individual had attained a large size, but was probably not yet mature, as the premaxillae are not firmly fused to the maxillae (the dorsal parts of its skull are largely reconstructed, but the mandible and the rest of the skull are real).

The premaxiliae in M. tarijense (FMNH P14216; Pl. 29) resemble those of juvenile M. americanum, but are clearly quadrangular rather than $Y$-shaped. They are shorter anteroposteriorly than in the adult M. americanum. The anterior processes diverge anteriorly, but this is possibly due to distortion, and a small lateral protuberance is present. In lateral view the height of the lateral ramus tapers anteriorly and the ventral margin is sinuous. The premaxillae are fused to each other at the midline posterior to the diverging anterior processes, but apparently are only weakly articulated to the maxillae, and are held in place by plaster. The palatine fissures do not form ducts, but are instead very short canals that penetrate dorsally through
the premaxillae into the nasal cavity.

> Maxilla
> The maxilla (e.g., Pls. 13A, $B$ and $16 A, B$ ) is approximately trapezoidal in lateral outline, with a nearly straight ventral margin forming the alveolar border. Anterior to the alveolus of M1 the ventral margin slopes gently and variably anterodorsally. The relative length of this edentulous part, from M1 to the maxillo-premaxillary contact, is important in distinguishing between $E$. laurillardi and M. americanum, and is longer in the former (cf. Pis. 9A, 10A and 21, 22C). The Pre-Molariform Maxillary Length (PMML) is the length measured ventrally from the mesial margin of M1 or its alveolus to the apex of the $V$-shaped maxillo-premaxillary contact in M. americanum (in which the premaxilla and maxilla are fused), and $V$ shaped notch in E. laurillardi (in which the bones do not fuse). This part of the maxilla is often preserved and allows comparison between many specimens. The relative length of the premolariform part of the maxilla is designated as the PMML Index (PMMLI), and is obtained by the formula PMMII $=$ PMML/MTRL $\times 100$, where MXTRL is the Maxillary Tooth Row Length. PMMLI is given as an index figure which is the percentage that PMML represents of MXTRL. It ranges between 22 to 27 in $E$. laurillardi, and 9 to 16 in $M$. americanum. The anteroventral margin of the
maxilla is rugose, and is notched for the premaxilla. In lateral view the maxillo-premaxillary suture is oriented at approximately $30^{\circ}$ to the palate of $E$. laurillardi, and approximately $45^{\circ}$ in M. americanum.

The anterior margins of the maxillae form part of the free lateral margins of the external choanae. Their form varies, but is similar in both taxa: the ventral half slopes posterodorsally from the maxilio-premaxillary suture; its dorsal half tends to be more vertical. The position of the margin, however, differs in $E$. laurillardi and $M$. americanum, even though the position varies within either species. In $E$. laurillardi the margin tends to lie more anteriorly, and contributes to the elongated appearance of its rostrum (e.g., Pls. 9, 10). In M. americanum it tends to be nearer the level of the mesial edge of M1 (e.g., Pls. 18A, $B$ and 19B).

The dorsal margin of the maxilla contacts the nasal near the dorsal profile of the rostrum (Pls. 7A, B and 16A, C). In lateral view this suture slopes gently dorsally as it passes posteriorly at similar angles in both species. In dorsal view it is oriented posteromedially and reaches approximately midway between the anterior margin of the anterior zygomatic buttress and postorbital process of the frontal. Here the maxilla turns sharply posterolaterally to accomodate the expansion of the posterior part of the nasal, and finally meets the frontal.

Dorsally the maxillo-frontal suture begins medially on the skull at about the level of the postorbital process (Pl. 16A, C). It passes anterolaterally towards and posterior to the lacrimal (hence anterior zygomatic buttress, vide infra). The posterior portion of the dorsal margin of the maxilla is approximately at the level of the dorsal margin of the lacrimal, and is nearly parallel to the alveolar border. This margin and the triangular surface ventral to it form a squamous suture with the frontal, and is therefore normally hidden from lateral view, but is visible in Plate 13B. The superficial maxillo-frontal contact laterally on the skull is oriented posteroventrally toward the distal alveolar border of M5.

The central area of the lateral surface of the maxilla lies dorsal to M1 to M3, and is extended laterally as the zygomatic process of the maxilia. It bears a very rugose, approximately oval surface for articulation with the lacrimal dorsally and the jugal ventrally (P1. 13A-D). The zygomatic process tends to be more prominent and anterolaterally directed in M. americanum.

Although the position of the zygomatic process relative to the cheek teeth varies somewhat in $E$. laurillardi and M. americanum, the process is consistently further anterior in E. laurillardi. In juvenile and adult individuals of $E$. laurillardi the zygomatic process extends approximately from the middle of M1 to the mesial part of M3 (Pls. 9A, 10, 11).

However, the position of its anterior margin varies and may be more posterior, as in FMNH 226970 (PI. 11B) where the anterior margin begins nearly lateral to the septum between M1 and M2. The position of the anterior root shown in Plate $9 B$ is distorted by the angle of the photograph, and therefore appears to lie more posteriorly than it actually does.

In M. americanum the anterior margin of the zygomatic process is apparently more variable. It lies nearly lateral to the mesial part of M2 or the septum between M1 and M2 in BMNH 19953 and ZMUC 212 (Pl. 21A, B, respectively) and MACN 5002 (P1. 23C), the middle of M2 in FMNH 14293 (PI. 22C), and near the distal part of M2 in MACN 13021 (P1. 24C). The posterior margin lies approximately lateral to the distal part of M3 or the septum between M3 and M4, except in the juvenile MACN 2786 where it lies lateral to the middle of M3.

The infraorbital canal extends anterodorsally through the ventral part of the zygomatic process of the maxilla. Anteriorly the canal is often divided into two or three smaller canals, which may differ between the right and left sides.

In ventral view the maxilla forms most of the hard palate (Pls. 16B, D and 27A, B). Anteriorly it bears a posteriorly directed, nearly V-shaped notch in both species. Posteriorly the maxilla contacts the palatine. The most
anterior part of this suture in E. laurillardi (MCL 1702/01; MCL 7239) and M. americanum (MACN 2830; MACN 2786) runs approximately 20 mm laterally from the midine at the level of the alveolar septum between M3 and M4. It then turns posteriorly, following the gentle, lingually convex curve of the toothrow in $E$. laurillardi. The maxilla tapers posteriorly and extends past M5 a distance approximately equal to twice the mesiodistal length of this molariform. Details of this suture are unclear in any known specimen of M. americanum.

The different arrangements of the toothrows readily allow distinction between adults of Eremotherium and Megatherium (cf. 9-12B, C; 16B, D, and 21, 22C, 23C). In the latter the molariforms in each toothrow are arranged so that a nearly straight line passes through the bucco-lingual midpoints of each molariform. The toothrows are nearly parallel, diverging only slightly posteriorly due to the smaller M4 and, in particular, M5. The buccal margins of the toothrows describe a buccally concave, though shallow, curve, due the placement of the teeth in a nearly rectilinear arrangement. In E. laurillardi a line passing through the bucco-lingual midline of each molariform is convex lingually, and the buccal margin of each toothrow between M1 and M4 is nearly rectilinear; it may be slightly lingually convex mesially, due to the buccal displacement of MI. The Iingually convex arrangement of the toothrows
occurs in adult individuals of E. laurillardi and is a retention of the juvenile condition. In M. americanum the toothrow is convex in juveniles ( Pl . 22A, B), but not in adults.

The maximum distance between the toothrows is between the smallest molariforms, the M5s. The minimum distance occurs between the M2s in M. americanum, and the M2s or M3s in E. laurillardi. However, the minimum distance differs between the two species, and distinguishes between them. In M. americanum this distance is less that the bucco-Iingual width of M2, whereas in $E$. laurillardi it is nearly equal to or greater than the width of M2. These distinctions are also present among juveniles, contrary to Toledo (1989).

A third major difference between these taxa is that the palate arches anterodorsally in E. laurillardi, which lends an ascending aspect to the toothrow, and contributes to the tapered rostum. In M. americanum the palate is nearly flat anteroposteriorly, and the rostrum is deeper.

In both species the palate is slightly dorsally concave in the transverse plane, though it tends to be less so in M. americanum. An anterior palatine foramen lies lingual to each M1 in both taxa (App. 2: Fig. 2B, D), and two may be present, arranged anteroposteriorly. A posterior palatine foramen lies on either side of the midventral line in the maxillo-palatine suture. The palate of both is rugose and pitted with vascular foramina, considerably more so in $M$.
americanum, particularly on the ventral surface of the palatine (cf. Pls. 10C, 11B, C, 12C, and 21A, 23C).

## Lacrimal

In lateral view the lacrimal of E. laurillardi is approximately oval, with long axis oriented nearly anteroposteriorly (Pl. 13B, C). It occupies the dorsal half (MCL 7239) to two-thirds (MCL 7238; MCL 1702/01) of the irregular surface on the zygomatic process of the maxilla. In M. americanum the lacrimal occupies a similar position, but is not as elongate anteroposteriorly (Pls. 18A, B and 19B). Ventrally the lacrimal articulates with the maxillary process of the jugal.

The lacrimal canal emerges anterodorsally, is large in E. laurillardi ( $30 \times 17 \mathrm{~mm}$ in $1700 / 01$ ) and usually oval, with long axis variably oriented (e.g., Pls. 3A, B and 5B). The canal passes posteromedially through the lacrimal and turns medially to pierce the maxilla, where its section is usually circular and considerably reduced ( $10 \times 10 \mathrm{~mm}$ ). The canal continues medially a short distance through the maxilla and then turns anteriorly along the medial wall.

In $M$. americanum the external opening of the canal is relatively smaller (Pl. 18B). Its course was not probed, but may be as in E. laurillardi. A portion of the right lacrimal's lateral surface in M. americanum MACN 14293 is broken and reveals two narrow canals. The lacrimal usually
fuses to the maxilla, but generally its sutural margins are visible even in aged individuals of $E$. laurillardi. In M. americanum the contacts are visible in some adults, but are less prominent.

Jugal
The jugal is similar in all megatheriine taxa for which it is known. It consists of an approximately quadrangular body with five processes. Complete jugals are shown in lateral view on Plates 3B, C for E. laurillardi, 17B, C, 22A, 23A, 24A for $M$. americanum, and 29A for M. tarijense. The maxillary process is expanded dorsally at its articulations with the maxilla and lacrimal. Its elongate narrow body extends posteroventrally and curves laterally to form the medial and ventral margins of the lower orbit (Owen, 1856). The descending process extends posteroventrally from the junction of the body and maxillary process. It is robust, thicker anteroposteriorly than mediolaterally, and the ventral portion turns posteriorly. The orbital process is a short, blunt and approximately triangular protuberance, with the apex oriented anterodorsally. Its anterior margin is continuous with the body, and with it forms the lateral margin of the lower orbit. Its dorsal margin extends into the elongated, approximately feather-shaped and anterodorsally oriented, ascending process. The orbital process is less prominent in

Megatheriops rectidens, and is absent in other Tardigrada. The zygomatic process may be elongated or blunt and approximately triangular or quadrangular. It lies ventral to the anterior end of jugular process of the squamosal. The jugular process fits into the posteriorly open V-shaped notch between the zygomatic process and body of the jugal. These last two make contact, unlike the condition in many other sloths, but usually do not fuse, except in some aged individuals. The orientations of the ascending and descending processes vary. The ascending process may incline posterodorsally so that its posterior margin touches the anterodorsal margin of the jugular process.

Postorbital and zygomatic arch ligaments, as reconstructed for Nothrotheriops shastense by Naples (1987) and based largely on Bradypus (Naples, 1982), are postulated for megatheriines, except that a portion of the postorbital ligament inserted onto the orbital process, where it is scarred laterally. The surface of the maxillary process is smooth except for a small roughened patch dorsally near its articulation with the lacrimal; this region may have served for ligaments reinforcing the contact of the jugal with the lacrimal and maxilla. The articulations between these three bones remain visible in some aged individuals.

The surfaces of the descending process are scarred, except for a small anterolateral portion, by the origin of the superficial masseter muscle. A small tuberosity lies
dorsally on the anteromedial margin. Scarring is more prominent ventrally, and particularly on the region along the ventral margin of the descending process and the anteroventral part of the jugular process. The lateral surface of the descending process bears ridges oriented ventrally and slightly posteriorly, and is variably developed. The superficial masseter was probably a complex muscle, divided into parts, and the ridges may represent the margins of the divisions. Naples (1987) reconstructed five divisions for the superficial masseter in Nothrotheriops shastense, and based on living tree sloths. The body of the jugal and the jugular process of the squamosal are also scarred. Probably the deep masseter and zygomaticomandibular muscles originated from these regions. Naples (1987) reconstructed the deep masseter as originating partly from the medial surface of the ascending process of the jugal and the ligaments between the jugal and the zygomatic process. This is a reasonable assumption and increases the area of origin. However, the ascending process in megatheriines is notably scarred only along its anterior edge.

The prominent lower orbit is a characteristic feature of many sloths, although its function is not understood. It is a deep, full, and rounded notch, opening dorsally in the orbit proper, and facing anteriorly and somewhat laterally in megatheriines (e.g., Pls. 3B, C, 4C, and 5A). Its depth
is variable among sloths. It is not particularly prominent in Choloepus didactylus (Naples, 1982: fig. 2b) and Acratocnus odontrigonus (Anthony, 1926: fig. 59).

The position of the ventral margin of the lower orbit is significant in distinguishing between Eremotherium laurillardi and Megatherium americanum. In the former the margin is ventral to the level of the alveolar border, and reaches approximately to the occlusal surface of the upper molariforms. Thus, the molariforms may be seen through the lower orbit from the lateral position, but in M. americanum the margin lies dorsal to the level of the alveolar border (cf. Pls. 5A and 17B, C). This distinction has been noted by various authors, including Cartelle (1993), Gazin (1957), and Toledo (1989). It is unclear which of these states is plesiomorphic. It is reasonable to assume that the position ventral to the alveolar margin may be plesiomorphic, as this is the condition in many Santacrucian genera, e.g.,

Hapalops. However, an ancestrally and morphologically central position for these forms is not established. The distribution states among other Tardigrada is variable. For example, the margin lies nearly in the plane of the alveolar border in Nothrotheriops, Glossotherium (Stock, 1925: pl.4, fig. 1, and pl. 24, respectively), and Megalocnus (Matthew and Paula Couto, 1959: fig. 1). The margin is ventral to the border in Thinobadistes (Webb, 1989: fig. 4: UF 21509; however, in fig. 5a: $\mathrm{F}: \mathrm{AM} 102658$ the margin is reconstructed
as corsal to the border, but the zygomatic arch of this specimen appears to have been distorted), and dorsal to the border in Choloepus (Naples, 1982: fig. 2b) and Bradypus (Fig. 2A). In Megatheriops rectidens the margin lies somewhat dorsal to the level of the alveolar border.

The exaggerated ventral position of the lower orbit has led various authors to suggest that the eye in Eremotherium laurillardi occupied a more ventral position, nearly directly posterior to the mouth, than is usual among mamals, as restored by Paula Couto (1979: fig. 223). This is based on the assumption that the lower orbit lodged the eyeball. The eye is restored in a more usual position for Megatherium americanum (Paula Couto, 1979: fig. 217), although tine lower orbit lies nearly as ventrally as in $E$. laurillardi. Paula Couto (1979: fig. 231) restored the position of the eye for Nothrotheriops shastense more dorsally than Naples (1987: fig. 8); the position of the lower orbit is approximately intermediate between those of E. laurillardi and M. americanum. However, it is unlikely that the lower orbit lodged the eyeball and that the eye occupied such a low position in E. Laurillardi and N. shastense. There is no evidence to suggest that the eye could not occupy the more usual position within the orbit, approximately posterior to the lacrimal. Further, a position of the eyeball within the lower orbit would require a very unusual posterodorsal course of the optic nerve to

FIGURE 2.
A) Lateral and B) ventral views of the skull of Bradypus tridactylus. Abbreviations: as - alisphenoid; bo - basioccipital; bs - basisphenoid; cf - condyloid foramen; e - entotympanic; et - opening for Eustachian tube; f - frontal; fm - foramen magnum; fo - foramen ovale; fr - foramen rotundum; ic - foramen for internal carotid artery; if - infraorbital foramen; j -jugal; l - lacrimal; If - lacrimal foramen; m - maxilla; n nasal; o - occipital; of - confluent optic canal + orbital fissure; p - parietal; pa - palatine; plf posterior lacerate foramen; pm - premaxillae; pt pterygoid; so - supraoccipital; spf - sphenopalatine and posterior palatine foramina; sq - squamosal; t ectotympanic; v - vomer (modified from Naples, 1982; Gaudin, 1993). Scale bar represents 50 mm.

the optic canal. Possibly the lower orbit lodged some fat, usually present below the eyeball in most mammals. A second possibility is that an enlarged zygomatic gland (and possibly other glands), present in this approximate position in many mammals though covered by the zygomatic arch, occupied the lower orbit in most sloths. This is a reasonable assumption, given the importance of the tongue apparatus in sloths (see Naples, 1987) and a presumed requirement for increased salivation.

## Nasal

The posterior naso-frontal contact lies approximately between the postorbital processes dorsally on the skull, and is oriented variably anterolaterally (Pis. 7A and 16A, C). The lateral margin of the nasal is constricted medially at the level of the lacrimal or just posterior to it (Pls. 16A, C, and 26). The nasal expands gently laterally as it extends forward, and is wider anteriorly than posteriorly (P1. 17A). The nasals form the dorsal margin of the external nares, overlap the lateral surfaces of the maxillae, and extend anteriorly to approximately the level of the maxillo-premaxillary suture (Pls. 4A; 7A).

The constriction of the nasals in megatheriines is similar to that in many tardigrades, such as scelidotheres (McDonald, 1987), and Glossotherium (Stock, 1925). In these, however, the constriction is more prominent, the
anterior expansion begins further anteriorly, and the nasal is relatively wider posteriorly. Some sloths (e.g., Nothrotheriops) have a nearly transverse naso-frontal contact, and the nasal is not constricted.

The anterior margin of the nasal bears an anterolateral process in M. americanum, and extends beyond the level of the maxillo-premaxillary suture (Pls. 18A, 20A). A medial process, as reported for scelidotheres (McDonald, 1987), is absent.

Palatine
The sutures between the palatine and maxilla are clear in some individuals, and are described above. However, the margins of the lateral and ventrolateral exposures of the palatine are not as certainly determinable in the specimens of E. laurillardi examined, but those in M. americanum (juvenile specimens MACN 2830 and MMP 430) are reasonably clear.

The palatine has a short exposure, in palatal view, between the pterygoid and maxilla (Pl. 27A, C). In lateral view it is approximately triangular, with ventral apex, and contributes to the ventral orbital wall and anterodorsal part of the pterygoid blade (P1. 25). The dorsal margin is approximately level with the contact between the maxilla and the zygomatic process of the jugal.

The palatine is present between the pterygoid and
maxilla, and extends further dorsally in the ventral part of the orbital wall in E. laurillardi (MCL 1702/01, 7240: Pl. 4A, B, respectively, and MCL 7230: Pl. 13C), but the palatine's margins are not easily determined. The bony region between pterygoid and maxilla is completely preserved only in MCL 7240, but only the maxillo-palatine suture is visible. In MCL 1702/01 and 7238 the sutures with the palatine are present on the maxilla anteriorly and pterygoid posteriorly, but the palatine is missing. These specimens demonstrate a relatively greater exposure ventrally for the palatine between the pterygoid and maxillae than in $M$. americanum. It is probable, then, that the palatine also formed a larger portion of the pterygoid blade in $E$. laurillardi. A nearly dorsoventral rugose ridge, which resembles a sutural contact, is present on the anterior part of the blade of some individuals, and probably marks the contact between the palatine and pterygoid.

The ventral orbital wall, to my knowledge, has not been adequately described for fossil sloths, largely because the bone forming this region is delicate and usually incomplete, distorted, or obscured by matrix. This region is wellpreserved in MCL 1702/01 and, particularly, 1701/01, although the sutures of the palatine with surrounding bones cannot be determined. However, analogies may be drawn with the regions of Nothrotherium (MCL 1020/01), described here, Glossotherium and Mylodon (figured but not described by

Stock [1925] and Guth [1961], respectively), and Bradypus and Choloepus.

In $E$. laurillardi the palatine included the posterior palatine foramen and probably some of the sphenopalatine foramina. These foramina are contained within a shallow, nearly triangular depression or pit in the ventral orbital wall, dorsal to the anterior part of the pterygoid blade (Fig. 3A). The pit is deepest posteriorly, and a sharp crest hangs over its posterior and dorsal margins.

The pit may be divided into ventral, central and dorsal portions. The ventral portion is smallest and forms the apex of the triangular pit. Its floor is pierced by the posterior palatine foramen, which lies at a level just posterior and dorsal to M5. The foramen is nearly oval, with its long axis oriented anterodorsally and about 10 mm long. Various palatine foramina may be followed back to the posterior palatine foramen.

The central portion of the palatine is nearly rectangular, with its long axis anterodorsal. Its floor, particularly posteriorly, is exceedingly thin and delicate, and in many specimens is incomplete or collapsed by postmortem compression of the skull. Three sphenopalatine foramina, of which only one is complete, are present in MCL 1701/01. They are short canals piercing the thin bony wall. The complete foramen lies about 15 mu dorsal to the posterior palatine foramen. It is nearly oval, with its

## FIGURE 3.

Lateral views of the left lateral walls of the orbital region and cranium, with zygomatic arch removed, of A. Eremotherium laurillardi, MCI 1701/01; scale bar represents 20 mm ; and B. Nothrotherium maquinense, MCL 1020/01; scale bar represent 10 mm . Abbreviations: as - alisphenoid; et - ectotympanic; f- frontal; fo foramen ovale; m - maxilla; M4 - molariform 4; M5 molariform 5; oc - optic canal; ofr - orbital fissure + foramen rotundum; os - orbitosphenoid; p - pterygoid; pl - palatine; pp - posterior palatine foramen; pr parietal; ps - pterygoid sirus (hashed lines represent broken edge of pterygoid); s - squamosal; sp - sphenopalatine foramen; szy - sectioned edges of zygomatic arch.

long axis anteroposterior, and 10 mm in length. The second and third foramina are indicated by parts of their margins. One of these lies directly posterior to the complete foramen, and lacks its posteroventral margin. The other incomplete foramen lies ventral to and between the two other formina, and lacks its posterior margin. The incomplete foramina are oval, with the long axis of the first anterodorsal and of the second anteroposterior. They appear to have been larger than the complete foramen, perhaps 15 mm in diameter. These have been described as separate foramina, but the second and third may have been confluent. It cannot be determined which of these states occurred because the posterior floor of the pit is missing. Nevertheless, the number and arrangement of the foramina in this region probably varied, as their only function is to provide access to the nasopharynx.

The floor of the dorsal portion of the pit is thicker and forms an anterodorsally oriented groove, possibly for the course of the optic nerve. A probable suture coincides with the ventral margin of the groove, and marks the contact between the frontal dorsally and the palatine, alisphenoid, or both, in anteroposterior sequence ventrally. The groove leads posteriorly into an ample canal, undivided in MCL 1701/01, which enters the braincase. This canal probably represents a confluence of the optic canal, orbital fissure, and foramen rotundum. Usually the passages for these canals
are divided by a bony septum into two passages for all or part of their lengths. When completely separated these two canals emerge from the braincase adjacent to one another, the medial canal usually being smaller and somewhat dorsal to the lateral canal. When partially separated the septum occurs in the posterior half of the canal's length. The medial canal is interpreted as the optic canal, because it is smaller; the lateral as the confluence of the orbital fissure and foramen rotundum. The optic canal leaves the braincase slightly dorsal and medial to the orbital fissure + foramen rotundum.

A somewhat analogous condition occurs in Mylodon listai (BMNH 8722: Guth, 1961: fig. 92) in that a pit containing foramina is present in the ventral orbital wall. The pit lies within the palatine, is oval, with long axis anteroposterior, and contains only two foramina. A smaller foramen lies in the palatine, posterior and slightly ventral to the pit. These foramina, which Guth (1961) did not label, lie directly anterior to, apparently, a single large opening probably bounded by the orbitosphenoid, alisphenoid, and, possibly, palatine. Guth (1961:101) termed this foramen the "fente spheno-orbitaire", which, presumably, represents the confluence of the optic canal, orbital fissure, and foramen rotundum. The margins of the foramen ovale are formed from the alisphenoid and pterygoid.

In Glossotherium the four foramina are represented by
two openings externally. Guth (1961: fig. 25) termed the posterior foramen the foramen ovale; Stock (1925: fig. 58) considered it to represent the combined foramen rotundum and foramen ovale. It is formed from the alisphenoid, squamosal, and pterygoid. The anterior opening lies posteriorly in a depression, more shallow than in E. laurillardi and Mylodon, of the ventral orbital wall, and is termed the combined optic canal and orbital fissure (the latter was termed the "anterior lacerate foramen" by Stock, 1958: 123: fig. 58). It is formed from the frontal, alisphenoid, palatine, and orbitosphenoid (though Stock, 1958, stated that its sutures are unclear). Two foramina lie in the anterior part of the depression (only the more dorsal is visible in lateral view in Stock, 1925: fig. 58). The canal from the dorsal foramen passes through the palatine (Stock, 1925), and the opening thus presumably represents the sphenopalatine foramen. The other is the "entrance to the canal that traverses the palate" (Stock, 1925:125), and is probably the posterior palatine foramen.

As stated above, the sutural relationships of the bones that usually converge on this region of the skull (frontal, palatine, alisphenoid, and orbitosphenoid) cannot be determined in known specimens of E. laurillardi. In Nothrotherium (Fig. 3B) the usual series of four foramina, including the optic canal, orbital fissure, foramen rotundum, and foramen ovale, are represented by three well-
separated foramina, probably representing the optic canal, confluent orbital fissure and foramen rotundum, and foramen ovale. The orbitosphenoid makes a minor contribution to the orbital wall and forms most, and possibly all, of the external margins of the optic canal. The alisphenoid contacts the orbitosphenoid, frontal, palatine, squamosal, pterygoid, and parietal. The margins of the foramen ovale are formed from the alisphenoid and pterygoid, the squamosal apparently being excluded, or at most making a very minor contribution. A single sphenopalatine foramen is represented, formed largely by the palatine, but with contributions from the frontal and maxilla. The postpalatine foramen lies entirely within the palatine.

A series of three foramina is present in Bradypus (Fig. 2A) and Choloepus, of which the most anterior is largest. Guth (1961) recognized these as the confluent optic canal and orbital fissure, foramen rotundum, and foramen ovale. The margins of the first of these is formed from the frontal, palatine, alisphenoid and orbitosphenoid in Choloepus didactylus; principally from the orbitosphenoid, with contributions from the alisphenoid and palatine in Bradypus tridactylus; and the orbitosphenoid in B. torquatus. In the same taxonomic order, the foramen rotundum lies between the palatine and alisphenoid; palatine, alisphenoid, and pterygoid; and within the alisphenoid. The foramen ovale lies between the squamosal,
alisphenoid, and pterygoid in all three species.
Three foramina of nearly equal size open externally in Acratocnus (AMNH 17722). The most dorsal is formed from the frontal, orbitosphenoid, and probably alisphenoid. It is divided within deeply by a nearly vertical septum into a small, nearly circular and medial foramen, and a larger, lateral, and oval foramen, with long axis dorsoventral. These are interpreted as the optic canal and orbital fissure, respectively. The foramen rotundum lies posteriorly and ventrally, its margins formed from the alisphenoid and possibly the pterygoid. The foramen ovale, formed from the alisphenoid and squamosal, lies posterior and slightly ventral to the foramen rotundum.

A deep and well-defined pit lies anterior to the foramen rotundum and ventral to the confluent optic canal and orbital fissure. Various foramina emerge from the perimeter of the floor of the pit. A large posterior palatine foramen, divided distally, lies anteroventrally. Its branches pass through the palatine and emerge on the hard palate. Two smaller, though still prominent, foramina lie anterodorsally and posterodorsally, and probably represent anterior and posterior sphenopalatines, respectively. The anterior foramen passes obliquely anteriorly through the maxilla and palatine to the choanae. The posterior passes posteriorly and emerges medially near the
junction of the palatine and pterygoid blade. Smaller foramina are present in the perimeter of the floor of the pit.

Pterygoid
The pterygoid in $E$. laurillardi forms a broad thin blade between the palatine and auditory region, as is cormon in sloths. MCL 1700/01 and 1701/01, which preserve the pterygoids completely, demonstrate that the form of these bones is variable (P1. 3). The pterygoid is more prominent and extends further ventrally, with anterior edge descending more steeply, in MCL 1701/01, which is a smaller individual than MCL 1700/01. The pterygoid blade is nearly parasagittal, but its lateral surface is marked by shallow depressions, and bears many prominent crests, particularly ventrally, for the origin of the masseteric musculature. The medial surface is slightly concave and bears crests for the pterygoid musculature.

In $M$. americanum the pterygoid is prominent. It varies in shape and size, but does not descend as far ventrally below the alveolar border (Pls. 17C, 22A, 23A). The anterior margin is generally considerably smaller than the posterior. In E. laurillardi these margins are more nearly equal, and the blade resembles more that of Glossotherium. The shape and the angle of inclination of the blade's posterior margin in $M$. americanum vary considerably. It may
be nearly linear (e.g., MLP 2-64), smoothly convex posteriorly (e.g., MLP 42-VI-24-2), or smoothly concave posteriorly (e.g., MACN 5002). The angle of the blade to the alveolar border ranges from approximately $110^{\circ}$ (MACN 264; MLP 42-VI-24-2) to nearly $130^{\circ}$ (FMNH 14293; MACN 5002).

In E. laurillardi and M. americanum the pterygoid contributes to the foramen ovale. Posterior to the foramen the pterygoid has a nearly horizontal contact with the squamosal, and continues posterodorsally past the mandibular fossa as a thin and tapering wedge, approximately triangular in section, between the squamosal and entotympanic. The wedge passes far dorsally, and may be observed through the auditory meatus. The entotympanic and squamosal meet dorsal to the wedge, where they contribute to the epitympanic meatus.

Frontal and Parietal
The elongated frontals contribute siguificantly to the roof and orbital wall of the skull in E. laurillardi (Pls. 15C; 16A, C) and M. americanum (PIs. 25A, B; 26A, B). They are elongated in both species, but appear to be relatively longer in E. laurillardi.

The fronto-parietal suture lies relatively far posterior on the skull roof, more so than in most other sloths, and approximately as in Glossotherium. Presumably the posterior position of the suture is plesiomorphic among
sloths, as the feature is shared by Myrmecophagidae, the sister group to the Tardigrada. The suture is approximately sigmoidal in dorsal view, with dorsal half anteriorly convex (Pls. 16A, $C ; 26$ ). The ventral half is anteriorly concave, due largely to an anterodorsal extension of the parietal. The extension is present in many sloths, and usually is more prominent than in Eremotherium and Megatherium. For example, it extends to the level of the anterior part of the squamosal in Glossotherium (Stock, 1925) and Mylodon (Guth, 1961), and to the anterior margin of the squamosal in Nothrotherium (MCL 1020/01) where it makes a short contact with the alisphenoid. In scelidotheres the fronto-parietal suture passes nearly linearly from the midline to the squamosal, except in Catonyx chiliensis, where an anteroventral extension is present (McDonald, 1987).

The squamoso-parietal suture is clear in Eremotherium laurillardi (MCL 7230: Pls. 15A, B; 16A). It extends horizontally toward the occiput, and curves ventrally around the posterior zygomatic root. The parietal forms a short contact with the mastoid. The parieto-supraoccipital suture lies on the occiput. It is approximately sigmoidal and runs dorsomedially toward the midline of the skull roof. A similar arrangement is present in Megatherium americanum (MACN 2830, MMP 430: Pls. 25A, C, respectively). The occipital position of the parietal contrasts to that in Nothrotheriops and Glossotherium (Stock, 1925: figs. 7. 58,
respectively), in which the supraoccipital contributes to the posterodorsal part of the skull in lateral view.

In the juvenile E. laurillardi (MCL 7230) the dorsal portions of the nuchal crests, borne entirely on the occipitals, form the perimeter of the occiput in posterior view (Pl. 15B). The crests are smooth, approximately sigmoidal in dorsal view, and nearly parallel to the frontoparietal suture. In posterior view the parietosupraoccipital suture is nearly parallel to the margins of the occiput, except laterally, where the crest intersects the suture, and dorsomedially, where the supraoccipital sends a triangular wedge between the parietals. The surface of the parietal posterior to the crest slants posteroventrally. MACN 2830 (PI. 25A) suggests that the nuchal crests were also borne by the parietals in $M$. americanum. The parieto-supraoccipital suture closed very early in ontogeny in E. laurillardi and M. americanum. For example, these bones are firmly fused in MCL 7238 (PI. 15D) and MMP 430, but the sutures between the supraoccipital and the exoccipital and mastoid are open. As individuals aged, the nuchal crests were raised and became rugose (e.g., MCL 7239), as did the parietal surface posterior to them, and in adults projected beyond the surface of the occiput.

Anteriorly the frontal contacts the posterodorsal margin of the lacrimal, and passes posteroventrally in $E$. laurillardi and M. americanum (Pls. 4A, 13B, C, 16C, 25B).

In young individuals the margin of the frontal closely approaches the level of the posterior margin of the maxillojugular suture, but the gap increases with age and posterior growth of the maxilla. The frontal descends ventrally to a level just past the infraorbital foramen, lateral to the root of M5, forming a large part of the orbital wall and presumably contacting the palatine. Its margin then is nearly horizontal, presumably contacting the orbitosphenoid and alisphenoid. More posteriorly it forms a suture, oriented posterodorsally, with the squamosal.

The sutures between the bones that contribute to the orbital wall are closed in adults. This region is often too incomplete or damaged to permit recognition of the bones in available juvenile specimens of E. laurillardi. The frontopalatine suture of M. americanum (MMP 430) is described above. However, the orbitosphenoid and anterior part of the alisphenoid cannot confidently be recognized.

In dorsal view the lateral walls of the skull, between the anterior and posterior zygomatic buttresses, are nearly parallel in very young individuals of $E$. laurillardi (e.g., MCL 7230, 7238: Pl. 16A, C, respectively) but widen slightly posteriorly. The postorbital processes are poorly developed in these specimens, still relatively low in MCL 1702/01 (P1. 7A) and 7239, and more prominent in MCL 7240 (P1. 7B). As ontogeny progressed, however, the postorbital processes and the anterolateral parts of the frontals
increased in size, and a postorbital constriction was formed. A similar condition occurs in M. americanum, but the anterior parts of the frontals are relatively wider. In a very young individual (MACN 2830: Pl. 26A) the postorbital processes are barely present, but the walls of the frontals are already very slightly concave. These differences are more pronounced in adults, and contribute to the relatively tubular appearance of the skull of $E$. laurillardi, as compared to the flared and anteriorly widened skull of $M$. americanum (cf. Pls. 6 and 20).

The roof of the skull is smooth in young juveniles and lines and crests limiting the temporal muscle are not yet developed. Their limits, however, are indicated by the junction of the inflated region of the frontals anteriorly and the median, depressed area between them. In progressively older individuals the temporal lines are barely indicated (MCL 7239), and clearly distinct, though not prominent (MCL 7240). In adults, they are raised and prominent (cf. Pl. 7A, B, and 7C).

Two patterns of the temporal lines are represented among both adults and juveniles. These have been described by Cartelle and Bohórquez (1982), and were among the reasons that these authors postulated the existence of a striking degree of sexual dimorphism in E. laurillardi. The patterns are described here because they are present in M. americanum.

In the hypothesized male skull of $E$. laurillardi ( $P$. 6A), the low, rugose frontal lines converge in a gentle curve toward the midline and are raised into a prominent sagittal crest near the middle of the anteroposterior length of the frontals. The sagittal crest marks the margin of the temporal fossa very near the midline of the skull roof. Posteriorly the crest extends approximately to the parietofrontal suture and then diverges into two crests. Each passes posterolaterally and then ventrally, in close apposition to the nuchal crest, and turns anteriorly to become confluent with the dorsal margin of the zygomatic arch.

In the hypothesized female skuil the crest is similar to
that of the male, but is low and less distinct, and diverges posteriorly (Pl. 6B). A band of rugose bone, with irregular lateral margins, marks the dorsal edge of the temporal fossa, which lies a short distance from the midline of the skull. The band arises posteriorly from the margin of the diverging posterior part of the crest, and extends obliquely to the sagittal line. The right and left bands in MCL 1701/01 differ in width, and, therefore, are not
symmetrical. Both pass into the frontal lines, which extend to the postorbital processes. The sagittal crest in the female skull may thus be described as flattened into an elongate, anteroposteriorly oriented shelf or ledge along
the middle of the skull roof. A crest is absent in Glossotherium, but similar shelf, although considerably flatter, is present, and its width varies among individuals (Stock, 1925: pl. 42).

Cartelle and Bohórquez (1982) associated the position of the postorbital processes and the dorsal profile of the skull with these patterns. The profile is more nearly linear in the male skull, whereas in the female the cranial region is concave or domed, and the profile descends more strongly into the facial region. The postorbital processes are approximately directly dorsal to M 3 in the male, and to M4 in the female (Cartelle and Bohórquez reverse these positions, probably transposed). These authors cite an analogous arrangement of the sagittal crest and postorbital processes in Bradypus tridactylus to support the claim of sexual dimorphism in Eremotherium laurillardi, but it is worth noting that the comparison was based on only four Bradypus individuals.

Some specimens conform largely to these patterns. MCL 7240 (Pl. 7B), nearly an adult, conforms largely to the female pattern; MCL 1702/01 (P1. 7A), an older juvenile, and MNRJ 422 V to the male. However, MCL 7240 and other specimens demonstrate that the distribution of these features is not as rigidly constrained as implied by Cartelle and Bohórquez (1982), and thus that skulls do not always conform neatly to male or female patterns. The
postorbital processes in MCL 7240 (Pl. 4B) appear to lie dorsal to M3. MCL 7230 (PI. 16A), a young individual, has a descending dorsal profile, and the crests, though not yet fully developed, appear to be as in MCL 1701/01, but the postorbital processes lie approximately between M3 and M4 (Pl. 13C). The skull profile is nearly linear, the shelf absent, and the postorbital processes lie above M3 in FMNH 26970, but the frontal crests do not converge to form a single and prominent sagittal crest (Pl. 8B). Rather, they lie on either side of the midline for most of their length and are in close apposition only near the fronto-parietal suture. In USNM 20967 the sagittal crest, though not particularly prominent, lies at the midline, a shelf is absent, and the postorbital process lies above M3, but the profile descends strongly. In USNM 20867 (PI. 12A) the frontal lines do not converge at the midline into a prominent sagittal crest, a weakly-developed shelf is present posteriorly on the right side only, and the profile descends as in USNM 20967. In UCV 1178 the frontal lines do not lead into a median sagittal crest, but remain separate along the median skull roof and are well-developed. A shelf is present on the left side, and the profile descends.

These examples are not provided in opposition to the claim of sexual dimorphism in E. laurillardi, because two general patterns may be usually recognized: 1) a more elongated skull with a more nearly linear dorsal profile and
a prominent, median sagittal crest; and 2) a relatively shorter skull with a descending dorsal profile, in which the frontal lines do not lead into a prominent and distinct sagittal crest. It is not clear that these patterns are correctly attributed to male and female individuals, but the assumptions that a larger skull and a more prominent sagittal crests are male features seem reasonable.

More importantly, perhaps, for sloth systematics is that the degree of intraspecific variation in size and morphology demonstrated by skulls of $E$. laurillardi suggests that the possibility of such variation must be considered in analyzing the remains assigned to other species. As with E. laurillardi, many species were erected for Megatherium on the basis of differences which are probably better reinterpreted as due to intraspecific variation.

For example, Ameghino and Kraglievich (1921) and Parodi (1930) cited various characters to distinguish Megatherium gallarđoi (MACN 5002: Pl. 23A-C) and M. australis (MACN 13021: P1. 24A-C), respectively, from M. americanum. However, the differences discussed by these authors may be more reasonably regarded as intraspecific variation, based on the variation in E. laurillardi, and M. americanum specimens not seen by these authors. Among the characters cited by Ameghino and Kraglievich (1921) is the nearly Iinear dorsal profile of the skull of MACN 5002. In the classic specimens of M. americanum the dorsal profile
usually descends steeply, somewhat more so than in $E$. laurillardi. The rostrum thus appears lower in $M$. americanum than in M. gallardoi. However, as such variation in the dorsal profile is entirely within the range of variation of E. laurillardi, it is reasonable to suppose that such variation also exists in M. americanum, and that MACN 5002 cannot be considered distinct on the basis of a nearly linear dorsal profile. Indeed, FMNH 14293 (Pl. 22AC), a M. americanum specimen not examined by Ameghino and Kraglievich (1921), has a dorsal profile intermediate between MACN 5002 and the classic specimens. The difference in profiles in these $M$. americanum individuals may be due to inflation of the frontals, as in E. laurillardi, but also to variation in relative height of the rostrum.

Another character cited by Ameghino and Kraglievich (1921) is the less prominent postorbital processes in MACN 5002. The processes are smaller than in other M. americanum specimens, especially those of Owen's specimen (BMNH 19953), but there is variation in their size, as occurs also in E. laurillardi. It is worth noting that various sutures of MACN 5002 are not closed, suggesting that the individual, while large, was still a young adult. As the postorbital processes increase with age in E. laurillardi and M. americanum, the smaller size of the processes of MACN 5002 do not necessarily indicate specific distinction.

Parodi (1930) cited the presence of a double sagittal
crest in M. australis. However, a single or double crest occurs in E. laurillardi. A feature not noted by Parodi (1930) is the relatively elongated and convex cranial portion of the dorsal skull profile in MACN 13021. Again as in E. Iaurillardi, variation in the position of the junction of the cranial and rostral portions of the skull profile is normal, and not diagnostic. Further, the profile of MACN 13021 strongly resembles that of M. americanum ZMUC 212, from the Pampean of Buenos Aires Province. Parodi (1930) stated that the postorbital processes lie considerably more dorsal, high above the level of the nasals, in M. australis, than in $M$. americanum, in which they lie well below the nasals. However, this is incorrect. The position of the processes varies from approximately between the level of the nasals to somewhat below the nasals in most specimens of $M$. americanum. Those of M. australis are slightly above the nasals, approximately as in ZMUC 212. Interestingly, Parodi (1930) noted that many of the features of $M$. australis were intermediate between those of $M$. americanum and $M$. gallardoi, or resembled more one of these species or the other.

It is worth noting here two features of the skull of the type of M. americanum, MNHNM 6 (Pls. 1, 17A), because they are due to improper reconstruction. Various museums (e.g., BMNH, MLP) have a cast of the type skull, and researchers have probably based observations on such casts,
as I too had done. The features were very puzzling until I had opportunity to examine the original. The dorsal skull profile of the type is distinct from that of other specimens of $M$. americanum. It is markedly angular, and formed essentially from rectilinear cranial and rostral profiles. These meet dorsally approximately at the level of the fronto-nasal contact, and the profile here is prominently raised. However, probing of this region with a dissecting needle demonstrated that the raised region of MNHMM 6 is reconstructed in cork. The extent of reconstruction could not be determined precisely because the skull is mounted and difficult to study in detail. Further, once satisfied that the feature was inaccurate, I did not wish to cause damage to the mount due to its historical significance.

The second feature is the presence of two conical spikes, with apical end ventral, on the ventral surface of the skull. Part of the left side spike is visible in Plate 17A, and lies posterior to the posterior margin of the ascending ramus and ventral to the zygomatic arch. I had first assumed, based on the casts, that these perhaps represented the proximal remnants of the hyoid apparatus. However, the structures are clearly well-anterior to the tympanohyal fossae in the original specimen, and just posterior to the mandibular fossae. It is unclear what the reconstructions, also from cork, were intended to represent. Perhaps they are based on remnants of the posterior parts of
the pterygoid blades.

Occiput
The occiput is generally oriented at right angles to the dorsal plane of the cranial roof in E. laurillardi (PI. 3). Variations include a slight anteroventral inclination (MCL 7240: Pl. 4B), and slight (FMNE 26970: Pl. 5B) to marked posteroventral inclinations (MCL 1702: PI. 4B). The occiput may lie at nearly right angles in M. americanum, as in BMNH 19953 (PI. 18A, B) and MLP 42-IV-24-2 (Pl. 17C). It may also incline moderately (e.g.g., MNHN 6, MACN 1000: PI. 17A, B, respectively) or markedly (e.g., ZMUC 212: PL. 18C) posteroventrally.

OCH is significantly larger in M. americanum ( $\chi^{2}$ approximation=11.68, $\mathrm{df}=1, \mathrm{p}=0.0006$ ). OCHI ranges in this species between 27 (MACN 5002) and 45 (MUT 422V). The height of the occiput dorsal to the condyles, OPTH (Fig. 1), is also significantly greater in M. americanum (t=3.79, df=15, $p=0.0018$ ), and is measured (Fig. 1) as the distance on $B$ between $A^{\prime}$, the centre of the occipital condyles, and A"', a horizontal plane that passes through the dorsal extremity of the inion (junction of the nuchal and sagittal crests). The OPTH Index (OPTHI) is obtained by the formula OPTHI $=$ OPTH/MIOCL $\times 100 \mathrm{~A}$ ) and is given as an index figure which that OPTH represents of M1OCL. OPTHI generally ranges from 25 to 35 in E. laurillardi, and 15 to 27 in $M$.
americanum. Figures 4 and 5 represent graphically the relationships between M1OCL and OCH and OPTH, respectively. Although there are few juvenile individuals, their distributions suggest that they follow the pattern among adults of their species.

The size and projection of the occipital condyles vary, apparently uncorrelated with the inclination of the occiput. The condyles are large and project posteriorly in MCL 1701/01, in which the occiput is nearly perpendicular to the cranial roof. They are large and project somewhat posteroventrally in MCL 1702/01, in which the occiput inclines prominently posteroventrally, and FMNH P26970, in which the inclination is slightly posteroventral. The condyles are smaller in MCL 1700/01 and project posteroventrally, although the occiput is nearly perpendicular. In MCL 7240, where the occiput inclines slightly anteroventrally, the condyles are considerably smaller and project nearly ventrally.

The occiput is formed by the fusion of the four centres of ossification, the supraoccipital, paired exoccipitais, and basioccipital. The supraoccipital is formed from a large central portion and with laterally projecting wings. It contacts the parietal dorsally and dorsolaterally, the mastoid laterally, and exoccipitals ventrally (Pl. 15A-D). Shapes and proportions may vary in E. laurillardi and M. americanum. The ratio between width and height in the of M.

## FIGURE 4.

Bivariate plot (mm) of Height of the occipital condyles (OCH) against Length between the mesial surface of M1 and the posterior margins of the occipital condyles (M1OCL) of Megatheriinae (cf. Fig. 1).


## FIGURE 5.

Bivariate plot (mm) of Height of the occiput (OPTH) against against Length between the mesial surface of M1 and the posterior margins of the occipital condyles (MIOCL) of Megatheriinae (cf. Fig. 1).

americanum (MACN 2830, MMP 430) are apparently less than in E. laurillardi juveniles (MCL 7230, 7238), and partly may explain the more ventral position of the condyles in the Iatter.

An interparietal process tapers anterodorsally between the parietals (PI. 15B). In adults the process becomes thickened and rugose, and forms the occipital protuberance. The external crest, of variable thickness and height, excends ventrally from the protuberance, and divides the occiput into two broad and shallow lateral areas. Each area is bounded dorsally by a thick ridge which is formed along the parieto-supraoccipital sutures (Cf. Pl. 15B and D) and arches dorsolaterally from the occipital protuberance to the nuchal crest; and laterally by a vertical ridge which extends between the nuchal crest and the paraoccipital process. Smaller areas lie between these ridges and the nuchal crest. The occiput is rugose and extensively scarred, particularly dorsal and lateral to the exoccipitosupraoccipital suture, for the insertions of the various epaxial cervical musculature which supports and extends the head. The occipital protuberance possibly represents the insertion of the ligamentum nuchae, as in other large mamals (e.g., Equus, Giraffa). The paired m. semispinatus capitis (m. complexus) inserted chiefly on the small oval regions on either side of the occipital protuberance. The large areas on either side of the external crest served for
the insertion of the $m$. rectus capitis dorsalis major and minor. The $m$. obliquus capitis cranialis inserted laterally on the nuchal crest and vertical ridge, and may have extended onto the paraoccipital process.

## Basicranium

The basicranium, including the auditory region, is complex anatomically and functionally, and contains important diagnostic characters. Its bony elements include the basioccipital and basisphenoid, and the paired exoccipital, mastoid, entotypmanic, ectotympanic, petrosal, and tympanohyal (Fig. 2B). These bones are discussed together under this heading because they are intimately associated, particularly in the auditory region. The discussion below encompasses general descriptions and diagnostic differences, and inconsistencies in the literature are reported and, where possible, clarified. More detailed descriptions of the basicranial and auditory regions are given by Ameghino and Kraglievich (1921), Van der Klaauw (1930), Guth (1961), Patterson et al. (1992), and Cartelle (1992).

The sutures between the basioccipital and exoccipital bones fused early during ontogeny, and indeed appear to be the first sutures of the skull to have fused. The suture is partially fused in MACN 2830 (M. americanum) and represented by a faint line in MCI 7238/01 (E. laurillardi: Pl. 14D).

In both specimens the suture passes posteromedially from the posteromedial margin of the condyloid foramen to the ventromedial margin of the foramen magnum. The more dorsal contact between these bones is preserved along the roof of the condyloid canal in MCL 7238. It runs nearly parallel to the ventral contact from the posteromedial margin of the posterior lacerate foramen.

The basioccipital meets the basisphenoid anteriorly along a transverse suture approximately at the level of the carotid foramen (Pls. 14B, C, D, 15D, 27A). In adult individuals of Eremotherium and Megatherium prominent, rugose, nearly circular and raised basilar tubercles, for insertion of the $m$. longus capitis, are borne principally by the anterolateral corner of the basioccipitals (e.g., Pls. 9A, 10C). A very small anterior portion of the tubercle may be present on the posterolateral corner of the basisphenoid. Tubercles are not present in juveniles but the region is raised.

The condyloid foramen is large, well-defined, and easily recognizable, but often the region between it and the posterior lacerate foramen is poorly preserved. A considerably smaller region of raised, rugose bone lies medial to the condyloid foramen in Eremotherium. In Megatherium this region is better developed, and in some specimens (e.g., BMNH 19953: Pl. 21A; MACN 5002: P1. 23C) a ridge is oriented anteromedially toward the midline from the
condyloid foramen. Probably this region served for the insertion of the $m$. rectis capitis ventralis. The prominence of this region in Megatherium has altered the arrangement and position of the condyloid foramen. In Eremotherium, as in most sloths, the foramen is wide and large, with a semicircular posterior margin, located posteromedial to the posterior lacerate foramen. This condition occurs in a specimen of $M$. americanum reported by Ameghino and Kraglievich (1921), which could not be located for examination. In other Megatherium specimens the lateral development of the ridge toward the exoccipital has displaced the medial margin of the condyloid foramen, to form a narrow elongated fossa posteromedial to the posterior lacerate foramen. The form and position of the condyloid foramen are modified, so that it is divided (probably by a flange of the basioccipital) into small anterior and posterior foramina which emerge from the fossa. Although variation exists, due to age or poor preservation, the anterior foramen is almost medial and adjacent to the posterior part of the posterior lacerate foramen; the posterior foramen lies posterior to the anterior. This condition is described by Ameghino and Kraglievich (1921), who also point out that Owen's (1856:pl. 24) designation of the jugular and condyloid (precondyloid of Owen) foramina is reversed. My description is the proper distinction between the condyloid foramina of Eremotherium and Megatherium,
rather than that offered by Patterson et al. (1992).
The posterior lacerate foramen (or petrobasilar fissure) is a broad, deep, and elongated cleft, between the jugular foramen and the carotid foramen (technically the posterior carotid foramen) in the basicranium, and is formed in the petro-occipital suture. It is continued ventrally in part by the entotympanic and basisphenoid. There is some confusion in the Iiterature as to the elements that contribute to the posterior lacerate foramen and what anatomical feature the name designates. Van der Klaauw (1930) apparently termed the posterior part of the cleft the posterior lacerate foramen, which is technically the jugular foramen, and the anterior part the anterior lacerate foramen for the passage of the internal carotid artery, which is incorrect. The anterior lacerate foramen is a synonym for the orbital (or sphenorbital) Eissure on the orbital wall of the skull. Van der Klaauw (1930) is referring to the median lacerate foramen, the anterior opening of the carotid canal through which the internal carotid artery enters the cranial cavity. As stated above, the posterior lacerate foramen is the cleft between the posterior carotid foramen (through which the internal carotid artery enters the carotid canal) and the jugular foramen (through which the jugular vein emerges from the cranial cavity). Thus the entotympanic forms the anterior margin and the anterior part of the medial margin of the posterior lacerate foramen, contrary to

Patterson et al. (1992), who stated that the entotympanic forms only the anterior wall. The posterior half of the medial margin and approximately the medial half of the posterior margin is formed by the exoccipital; the basioccipital forms the lateral half of the posterior margin and lateral margin.

The entotympanic is an irregular, anteroposteriorly oriented plate of bone principally between the ectotympanic and posterior lacerate foramen. It contacts the pterygoid and basisphenoid anteriorly, and is wedged between the mastoid and exoccipital posteriorly, and the tympanohyal posterolaterally (Patterson et al., 1992). The entotympanic is inclined dorsolaterally to ventromedially in juveniles, but tends to be more nearly vertical in adults due ventral and lateral expansion of the basioccipital and basisphenoid.

In juveniles of E. laurillardi (e.g., MCL 7238/01: PI. 14A, B) the entotympanic is thick mediolaterally. Anteriorly there is a blunt medioventrally directed process, which, in adults (Patterson et al., 1992), is enlarged and extends irregularly over the posterolateral part of the basisphenoid and posteromedial part of the pterygoid. In MCL 7238/01 the anterior part of the entotympanic is pierced by the carotid canal, so that the basioccipital and basisphenoid are excluded from the medial margins of the canal. A short, shallow groove lies on the surface
posterior to the carotid foramen. The entotympanic is thick anteriorly to the canal, resembling the condition in Hapalops elongatus (Van der Klaauw, 1931: fig. 2). The position of that part of the entotympanic medial to the foramen is reminiscent of its presence in other sloths, such as Mylodon darwinii and Megalonyx jeffersonii (Patterson et al., 1992: figs. 1, 6), in which the entotympanic is composed of a lateral plate and a shorter medial plate. These are united anteriorly, posterior to the opening for the Eustachian tube, and dorsally. However, in juvenile E. laurillardi the medial plate is considerably shorter and narrower. The medial plate is retained and clearly visible in ventral view in adults of other sloths, but in $E$. laurillardi and M. americanum only the portion corresponding to the lateral plate is present. Presumably the medial part is submerged by growth of the basioccipital and basisphenoid. The poor preservation of the auditory region in juveniles of $M$. americanum does not permit an accurate description of its early morphology.

Posterolaterally the entotympanic fuses with the tympanohyal, and makes a minor contribution to the medial wall of the large, approximately circular, stylohyal process (Pls. 9B, 14B), which articulates with the hyoid apparatus and which lies lateral to the posterior lacerate foramen. The tympanohyal is as described by Patterson et al.. (1992). except its position may be more medial, to form the
anterior, as well as anterolateral, parts of the stylohyal process. It may also expand ventrally, and is particularly prominent in M. americanum BMNH 19953. The entotympanic fuses with the medial projection of the ectotympanic anterior to the process. The ventral part of the mastoid forms most of the stylohyal process (Pl. 14B), whose ventral surface is concave and usually continuous, although it may be pierced by a foramen. Contrary to Ameghino and Kraglievich (1921), the ectotympanic is apparently excluded from the process.

The ectotympanic is approximately annular and greatly thickened anteroventrally, particularly the triangular medial projection that fuses with the entotympanic. The anterior crus is more prominent than the posterior (Patterson et al., 1992). It is difficult to determine in most specimens whether the ectotympanic is ring-like, as stated by Cartelle (1992), or U-shaped, as described by Patterson et a1. (1992). The auditory region of a juvenile E. laurillardi individual (MCL 7230) shows clearly that the ectotympanic is a closed ring. The portion between the crura is considerably thinner than the rest, and is already fused to the squamosal. The separation between these bones cannot be determined laterally, but fortuitously the bone is broken transversely through the external auditory meatus, revealing a line of separation. In some specimens a series of nutrient foramina is present just dorsal to the meatus,
and the bony surface ventral to the foramina is somewhat thickened. Possibly, the foramina lie on the suture between the squamosal and ectotympanic in older individuals. MCL 7239 provides information on the probable course of development of the dorsal part of the ectotympanic. Apparently, it is formed from posterior and anterior projections of the anterior and posterior crura, respectively. The posterior projection of the anterior crus is thicker and overlaps the narrow anterior projection of the posterior crus.

Ventrally the ectotympanic is irregular and very rugose, considerably more so in E. laurillardi than in $M$. americanum. Indeed, differential development of the ectotympanic is a notable distinction between these taxa, and many other differences between their auditory regions correlate with it (Patterson et al., 1992). The reduction in M. americanum is particularly notable in the posterior crus, posterior to the medial, triangular expansion of the ectotympanic, and is similar to the more regular ectotympanic of most other sloths. The reduced ectotympanic results in a smaller floor to the external auditory meatus, and only a narrow part is visible. In ventral view, a deep and medially directed notch lies lateral to the stylohyal process. In E. laurillardi there is a shallow notch, and the posteroventral part of the ectotympanic forms a robust margin to the floor of the external auditory meatus,
anterolateral to the process. The sinuous groove between the tympanohyal and stylomastoid foramen, described by Patterson et al. (1992), is deeper in E. laurillardi. In Megatherium it is usually lacking, but various specimens possess a shallow groove on one side or the other. In lateral view the stylohyal process projects considerably further ventrally in Megatherium, and the stylomastoid foramen faces more laterally and is better exposed (Patterson et al., 1992).

The posteroventral part of the ectotympanic in juveniles of E. laurillardi (MCL 7230, MCL 7238) is not as rugose as in adults, and thus reminiscent of that in Megatherium, but is still more prominent, particularly in ventral view. The stylohyal process in lateral view is similar to that in adult individuals of $E$. laurillardi.

Patterson et al. (1992) noted the differences in the ectoympanic, but stated that they could not be evaluated properly in the absence of a series of specimens, based on the considerable variation in this element in individuals of similar
ages of Bradypus. However, the specimens of Eremotherium and Megatherium studied here suggest that the differences described are consistent and thus diagnostic. of Other Megatheriinae

Collections from various localities in South America contain specimens of megatheriine taxa that are poorly known or of uncertain taxonomic status. One series of collections is particularly interesting for its taxonomic and biogeographical implications, and includes remains recovered from near Ulloma and Tarija, Bolivia, and the province of Tarapacá, northern Chile.

The skull material from these regions is neither as abundant nor well-preserved as that for Megatherium americanum from Argentina and Eremotherium laurillardi from Brazil and the United States, and is thus somewhat problematic. The exceptions are a well-preserved and nearly complete individual from the Tarija Formation, FMNH P14216, and a less-complete juvenile from Ulloma, PIU M4530. FMNF P14216 is referred to above and clearly represents a distinct species, M. tarijense, which shares various derived features with M. americanum, and is properly included within the same genus. A second skull, NRM M4890, is assigned to M. tarijense; Werdelin (1991) referred it to M. americanum. Two other megatheriine species are probably present in Tarija, as discussed below.

The material from Tarapacá (PIs. 30, 31) has traditionally been allocated to M. medinae, that from Ulloma
(Pls. 32-34) to M. sundti. Casamiquela and Sepulveda (1974), followed by Marshall and Salinas (1991) considered these conspecific, with which I disagree (see FEMUR; SYSTEMATIC REVIEW OF THE MEGATHERIINAE). While I agree with Casamiquela and Sepulveda (1974) that the skull material from Tarapacá and Ulloma demonstrates considerable variation, there are subtle differences, which are correlated with a distinct femoral morphology, that suggest specific distinction.

Among the general similarities cited by Casamiquela and Sepulveda (1974) are the morphology of the skull and its outline in lateral view, width of the rostrum, the length and form of the tooth rows, and the positions of the occipital condyles and anterior zygomatic roots. However, these generalities may be applied to many (though certainly not all) megatheriines. Differences between the Tarapaca and Ulloma skulls are that the rostrum is relatively elongated, slender, and more gracile in M. medinae, and shorter and higher in $M$. sundti. The dorsal profile in the former is more regularly sinuous, with a gentle transition between cranial and rostral portions (the central part of the profile of SGO PV275 [P1. 31A, B] is largely restored), whereas that of $M$. sundti is domed or inflated centrally, just posterior to its anteroposterior midpoint. The outline is concave between the posterior part of the dome and nuchal crest. The absence of a dome in SGO PV273 reflects improper
reconstruction.
In dorsal view the skull of M. medinae (Pls. 30B, 31B) is more elongated, with weak postorbital processes and postorbital constriction, and resembles more that of Eremotherium laurillardi than M. americanum. In M. sundti (PI. 33) the skull is relatively more robust, with a stronger postorbital constriction, and resembles that of $M$. americanum.

Casamiquela and Sepulveda (1974) considered a possible synonymy of their concept of $M$. medinae with $M$. tarijense, but appeared sceptical and deferred to Hoffstetter's (1963) opinion that $M$. tarijense was probably not distinct from $M$. americanum. However, M. tarijense is clearly distinct from M. americanum (see TAXONOMIC REVIEW OF THE MEGATHERIINAE), although its skull (Pl. 29) shares considerable similarities with those of $M$. medinae and M. sundti. The skulls of $M$. medinae, M. sundti, and M. tarijense are similar in size and smaller than in M. americanum and E. lawrillardi. They resemble more that of $M$. americanum in morphology, but they are approximately intermediate between $M$. americanum and E. iaurillardi in proportions. The skull of $M$. tarijense resembles that of $M$. sundti in being raised centrally; however, it is not prominently domed, and the dorsal profile is considerably flatter. In dorsal view the skull of M. tarijense is relatively elongated and narrow, particularly posteriorly, but the postorbital processes are larger and
the postorbital constriction narrower, so that the lateral walls of the skull are markediy concave.

As in M. americanum the maximum width of the palate between the tooth rows is smaller than the width of the largest molariform in SGO PV231 \& 275 ( $M$. medinae from Tarapacá: Pls. 30C. 31C), SGO PV273 \& 278 (M. sundti from Ulloma: PI. 34), and FMNH P14216 (M. tarijense: Pl. 29C). The lingual margin of the tooth rows in the $S G O$ PV specimens is intermediate between those of $M$. americanum and $E$. laurillardi, in being more nearly parallel than in the latter, but diverging slightly anteriorly and posteriorly. A line drawn through the midpoints of the molariforms of each row is nearly rectilinear, as in M. americanum. The degree of divergence varies between and within individuals, and may be largely due to distortion. The width between the molariforms and degree of divergence of the tooth rows is somewhat greater in SGO PV231 (M. medinae), the skull of an immature individual (the midline palatal suture is open). These features are to be expected in juveniles (see discussion of juveniles of $M$. americanum, above). The tooth rows of FMNH P14216 are slightly distorted, but their midpoint lines are nearly linear, with some anterior and posterior divergence. The palatal surface between the tooth rows is similar to that in M. americanum in being nearly flat, but more similar to that in E. laurillardi in being relatively smooth.

The skulls SGO PV, PIU M4530, and FMNH P14216 are nearly identical in linear dimensions. The values for OCHI range from 27 (SGO PV275 and FMNH P 14216) to 32 (SGO PV231), and fall within the low end of the range for $M$. americanum. The values for OPTHI (range =27-30) are similar to the OCHI values. The relationship between OCHI and OPTHI is distinct from that for $M$. americanum, in which OCHI is considerably greater than OPTHI, and E. laurillardi , in which OPTHI is considerably greater than OCHI. PMMLI values range from 19 to 23, approximately intermediate between the values for M. americanum and E. laurillardi.

The position of the anterior zygomatic root is variable, but approximately as in M. americanum. Its anterior margin lies lateral to the middle of or distal half of M2, and the posterior margin lies distal to the mesial part of M3 and M4, respectively. In FMNH P14216 the position of the left and right roots are dissimilar, but fall within the range of the SGO PV specimens.
M. americanum is represented from Tarija by MUT V422, the skull of a large, but imature individual. The midpalatal, and inter- and nasomaxillary sutures of the maxillae are open. The medial margins of the tooth rows still are convex. The premaxillae were not fused to the maxillae, and are missing.

Resemblances to Argentine specimens of $M$. americanum include the relatively narrow postorbital constriction and
concave lateral skull walls between the zygomatic roots (approximately as in MLP 42-V-24-2; the left wall of MUT V422 is exaggeratedly concave due to medial distortion), the prominent and widely spaced postorbital processes (these features are discernable, despite some reconstruction of the processes and the skull roof between them), the minimum width between the molariforms is smaller than the width of the largest molariform, the palate between the tooth rows is rugose and perforated by numerous and large nutrient foramina, and the rostrum is relatively wide. Further, the values for OPTHI (45), OCHI (25), and PMMLI (10) are well within the range for $M$. americanum, as is the relationship between OPMI and OCHI.

MUT V107 (Pl. 35A-C) is a facial fragment preserving the rostrum, palate, and teeth of an apparently adult individual. Most of the maxillae and nasals, and parts of the palatines and frontals are preserved. The left molariforms are complete, except that M5 is broken at the alveolar level; the right molariforms are present but broken at or below the alveolar margins. The wall of the left maxilla is eroded, exposing the basal parts of the molariforms. The individual is considerably smaller than specimens of $M$. americanum and slightly smaller than the specimens SGO PV and FNMN P14216, judging by tooth row length. The specimen, however, is distinct from either of these species. The rostrum is narrow and elongate, and in
lateral view tapers strongly anteriorly, approximately as in Megatheriops and Pyramiodontherium (see below).

In dorsal view the lateral walls of the rostrum of MUT V 107 are nearly parallel, as in the former genus, and in contrast to the anteriorly widened snout of Pyramiodontherium. The rostrum tapers more strongly in MUT V107, but this may be due partly to absence of the anterior parts of the nasals, which in lateral view contribute to the roof of the rostrum. The nasals are elongated, extremely narrow, and widen only slightly posteriorly. PMMLI is 41 , similar to the values for Pyramiodontherium and Megatheriops, but distinct from those for M. americanum, M. tarijense, M. medinae, M. sundti, and E. laurillardi. The molariforms are distinct from those of all preceding taxa, but similar to those of Promegatherium and Megathericulus (see below) in being relatively wide transversely, particularly M2 and M3. The anterior zygomatic root lies lateral to the mesial part of M2 and the middle of M3.

Of the other megatheriine skull remains that are types of species and genera, only two are reasonably complete and well-preserved. These are MACN 2818 (P1. 35D, E), the type of "Megatherium" rectidens Rovereto 1914, which Ameghino (in Ameghino and Kraglievich, 1921) raised to the genus Megatheriops, and MLP 2-66 (P1. 36A-C), that of "Megatherium burmeisteri" Moreno and Mercerat 1891, included by Roth (1911) in his genus Plesiomegatherium, but amended as

Pyramiodontherium bergi (Moreno and Mercerat 1891) by Cabrera (1928).

MACN 2818 represents a young, probably subadult individual. Many of the sutures, such as the maxillofrontal, though fused, remain visible. The right half of the skull is well-preserved, and the form of the skull's posterior end is only slightly distorted. However, the left half, anterior to the posterior zygomatic root, has suffered extensive compression, and the left tooth row is missing. In lateral view the dorsal cranial profile of MACN 2818 (PI. 35D) is somewhat bulbous, rather unlike the dorsal profiles of other megatheriines. The profile drops abruptly at the junction of the cranium and rostrum, in contrast to the gently concave region common in other megatheriines. The rostrum is low, elongated and tapers anteriorly. The nasals are elongated and narrow, but relatively wider than in MUT V107. The long axis of the lacrimal is approximately dorsoventral. The jugal is generally as it is in other megatheriines. The distal part of the orbital process is missing, but the process was possibly less robust than that described for E. laurillardi and Megatherium americanum, judging from its base. The inferior margin of the lower orbit Iies just dorsal to the level of the alveolar border. The ventral part of the descending process does not project posteriorly as strongly as in E. laurillardi and M. americanum. The pterygoid blade is approximately as in

Megatherium, projecting a short distance beyond the alveolar border.

The basicranial and auditory regions are present, but poorly preserved, and therefore demonstrate only a general similarity to those of other megatheriine skulls. The stylohyal fossa is apparently relatively smaller than in $E$. laurillardi and $M$. americanum. The ectotympanic resembles more that of $M$. americanum, but its ventral parts, particularly the posterior crus, are less prominent. The condyloid foramen is a large, approximately semicircular opening, as in E. laurillardi.

All right side molariforms are preserved. A line drawn through the middle of each is nearly rectilinear and parallel to the midine. The tooth rows probably diverged only slightly. The buccal margin of the tooth row is convex, due probably to the large M2 and M3. The lateral walls of the skull are somewhat concave in dorsal view. The anterior zygomatic root lies approximately between the midale of M2 and the distal part of M3.

The skull of MLP 2-66 is low and relatively elongated. The dorsal cranial profile (PI. 36A) is gently convex, but the cranium may be somewhat depressed posteriorly. The rostrum is relatively low and elongated, more so than in Megatheriops rectidens. It tapers anteriorly but not as strongly as in the latter, and its dorsal margin anterior to the level of M1 is nearly parallel to the palatal plane.

The rostrum constricts markedly anterior to M1 and diverges further anteriorly (Pl. 36B, C), but not to the degree in Megathericulus (vide infra). It is remarkably elongated, with PMMLI $=45$. MLP 31-XI-12-25 preserves the palate and rostrum of an adult individual almost certainly conspecific with MLP 2-66. It is approximately as large as MLP 2-66 (tooth row length $=190 \mathrm{~mm}$ in MLP 31-XI-12-25 and 200 mm in MLP 2-66), and shares the proximally constricted and distally divergent, elongated rostrum, with $\mathrm{PMMLI}=46$. In both specimens the tooth rows are nearly linearly aligned, and their lingual margins are nearly parallel to the ventral midline. They diverge posteriorly in MLP 31-XI-12-25, but not in MLP 2-66, due to medial compression of the palate posteriorly. The maximum width between the tooth rows is less than the width of the largest molariform. The buccal margins are strongly convex, particularly on the left side of MLP 2-66. The degree of convexity is possibly due to distortion, as in the right tooth row of SGO PV231. However, the convexity is nearly symmetrical and probably a valid feature of this specimen and species, though somewhat exaggerated in MLP 2-66. The right tooth row of MLP 31-XI-12-25 is convex, but not to the degree of MIP 2-66, while the left tooth row, clearly distorted, is nearly rectilinear.

The anterior zygomatic root lies approximately between the level of the middle of M2 and posterior part of M3 in

MLP 2-66, and the mesial part of M2 and the middle of M3 in MLP 31-XI-12-25. Such variation in the position of the root exists in M. americanum and E. laurillardi, although the position of the root in MLP 2-66 may be inaccurate due to distortion to the anterior part of the tooth row.

Roth (1911) noted various differences between MLP 2-66 and M. americanum. However, these differences are probably largely due to distortion. For example, Roth (1911) stated that the postorbital processes of M4P 2-66 are bulkier and bear two lateral projections, separated by a fossa. The marked depth of the fossa, however, is apparently due to deformation of the anterodorsal part of the lateral orbital wall, as it is present as such only on the right side. The left side resembles more the variable depressions present in the skulls of most other megatheriines. Roth (1911) also stated that the postorbital process is united to the sagittal crest, presumably by the frontal line, which is markedly raised above the surface of the frontal. This description is accurate, but it is worth noting that the middle parts of the skull, between the frontal lines, is depressed by compression and partly reconstructed. In any event, the heights of the frontal lines and sagittal crest in M. americanum and E. laurillardi are variable and probably determined partly by age.

Further, Roth (1911) described the occiput as considerably posterior relative to the occipital condyle,
and the nuchal crest as forming an ample, posterior arch. In contrast, the condyles project posteriorly past the occiput in M. americanum, and the crest passes nearly directly ventrally. However, the relationship between these parts of the skull are clearly due to distortion imposed by shear stresses that have rotated the basicranial region. The right side has been pushed posteriorly; the left is more severely deformed, and has been pushed anteriorly and medially. The damage caused by deformation is best appreciated in ventral view. The left stylohyal fossa lies on the right side of the basicranium, directly anterior to the right occipital condyle. The right fossa lies posterolateral to the left fossa, nearly in proper parasagittal position, but is too far posterior, such that it lies lateral to the anterior half of the occipital condyle.

Cabrera (1928) stated that Pyramiodontherium and Megatheriops were probably congeneric, but preferred to recognize both as valid until each were known from better preserved and more complete remains. The reason for Cabrera's opinion were that the two genera are similar in general form of the skull (which could apply equally well to other megatheriines), position of the anterior zygomatic root (a position that occurs in other genera), PMMLI, and, probably, age the last two are also shared by Plesiomegatherium). He noted the considerable differences
in the rostrum, but considered the differences between the species as nearly equivalent to those between any two species of living genera, and cited Choloepus didactylus and C. hoffmanni as examples. I consider Cabrera's (1928) reasons unconvincing, and believe that he should have noted a greater similarity between the rostrum of Megatheriops and "Plesiomegatherium" halmyronomum (see TAXONOMIC REVIEW OF THE MEGATHERIINAE) . Cabrera (1928) erected the former on remains from near the Arroyo Chasicó, but these do not form the type species of the genus. Further, Cabrera did not note that Megatheriops and Pyramiodontherium differ importantly in OCHI, OPTHI, and the relationship between them. In the latter $O C H I=22, O P T H I=31$, which fall within the ranges for E. laurillardi, whereas in Megatheriops the values for both are 33. OCHI falls within the values for $M$. americanum, but OPTHI for those of $E$. laurillardi. Both values are reasonably close to those for M. tarijense, M. medinae, and M. sundti, as is the relationship between them.

Roth (1911) based Plesiomegatherium on scant left and right maxillary and mandibular remains of different individuals of probably Huayquerian Age. Roth (1911) illustrated the left mandibular and maxillary portions (which I could not locate at MACN) . Cabrera (1928) designated the right maxillary (Pl. 36D) and mandibular fragments of MACN 2895 as the type of the genus and species
P. hansmeyeri. The distinguishing criterion for this genus was the oblique orientation of the transverse crests of the molariforms, which is particularly marked in M2 (the condition in the mandible is discussed below) illustrated by Roth (1911). In other megatheriine taxa the crests are nearly perpendicular to the long axis of the mandibular ramus. However, the crests are nearly as in other megatheriines in MACN 2895. Cabrera (1928) correctly judged the oblique orientations an invalid character. The orientation is caused by deformation, and occurs occasionally in the molariforms of $E$. laurillardi and $M$. americanum. Cabrera (1928) further argued that Roth (1911) considered MACN 2-66 referable to Plesiomegatherium based only on its oblique crests. However, Roth probabiy inferred an oblique orientation based on the paralleliform alveoli of the left M1 and M2, as the molariforms are not preserved. It is worth noting that the right M1, although poorly preserved, and alveolus of M2 are as in other megatheriines. Cabrera (1928) rejected Roth's allocation of MACN 2-66 to Plesiomegatherium, and referred it to Pyramiodontherium. Plesiomegatherium is thus poorly known, and few useful characters are preserved. The tooth rows are arranged nearly linearly. They probably diverged posteriorly, judging by their convex lingual margins. A line drawn through the midpoints of the molariforms is also convex. The relationship between the width between the tooth rows
and width of the largest molariforms is unknown because the palatal midline is absent. M2 and M3 are nearly quadrangular, with transverse width about equal to mesiodistal length. M4 is anteroposteriorly elongated and somewhat lobate, due to its markedly narrower distal transverse crest. The anterior zygomatic root lies lateral to the mesial margin of M2 and the distal part of M3.

Cabrera (1928) erected "Plesiomegatherium" halmyronomum on MLP 26-IV-10-1 (PI. 37A-C), a nearly complete, but poorly preserved, skull. He (1928:350) allocated the species to plesiomegatherium because "los escasos restos que existen de P. Hans-Meyeri se le parecen bastante en el tamano y en otros detalles, $y$, hasta tanto que se disponga de mejor material de uno $y$ otro, me parece innecesario crear un género nuevo, cuyas diferencias con Plesiomegatherium no me sería posible ahora establecer". Cabrera's statement, clearly, refers to general similarities. Further, some of the characters described for the specimen are imprecise. For example, Cabrera (1928) stated that the anterior zygomatic root lies somewhat further posteriorly than in $P$. hansmeyeri and the anterior opening of the infraorbital canal lies lateral to the septum between M2 and M3, rather than near the centre of M2. However, the positions of the right and left sides do not coincide in MLP 26-IV-10-1 (P1. 37C). The left zygomatic root lies nearly lateral to the septum between MI and M2, and the opening of the canal
lateral to the septum between M2 and MB. The right zygomatic root lies lateral to the middle of M2, and the opening about the centre of M2. The original positions of these features are unclear.

The tooth rows of MLP 26-IV-10-1 are neariy linearly arranged, but the lingual margins are convex, so that the rows diverge posteriorly. Only the left M5 is preserved. The distance between the tooth rows is nearly equal to the largest alveolus. Cabrera (1928) stated that the molariforms were relatively small, based on the alveoli, but they are not well-preserved and rounded, and opposite pairs are dissimilar. An important fact is that M4 is quadrangular and non-lobate, in contrast to MACN 2895.

The only certain resemblances between MLP 26-IV-10-1 and MACN 2895 are reduced to similar size, the latter being slightly larger, and perhaps the position of the anterior zygomatic root, which is not clearly distinct from that of various specimens described above. The similarities and dissimilarities between comparable characteristics of these specimens apparently are no more or less than either is to various other specimens. By including MLP 26-IV-10-1 within Plesiomegatherium, Cabrera (1928) repeated Roth's (1911) error of recognizing characteristics of a genus which are absent in the type, and based on a specimen that is not certainly of the same genus and probably of a different age. Despite these criticisms, it is not possible to reject

Cabrera's allocation, because the type of Plesiomegatherium is so incomplete, and MLP 26-IV-10-1 has important differences from other megatheriine skulls.

MLP 26-IV-10-1 preserves various important features. The dorsal skull profile (PI. 37A), though irregular due to crushing, is low and relatively elongated, similarly to that of Pyramiodontherium. The rostrum (Pl. 37B, C) is narrow and tapers anteriorly more strongly than in the latter, and approximately as in Megatheriops, but possibly is due to postmortem compression. The maxilla is relatively elongated anterior to the molariforms (PMMLI is approximately 48), more so than in any other megatheriine, except Megathericulus. I follow Cabrera (1928), though not his motives, in rejecting generic status for MLP 26-IV-10-1. The lateral walls of the rostrm are nearly perpendicular, perhaps converging slightly anteriorly (possibly caused by compression; Cabrera, 1928), as in Megatheriops, and in contrast to Pyramiodontherium and Megathericulus. The postorbital constriction is wider than the rostrum and not prominent. The values for OCHI (22) and OPTHI (32) are nearly identical to those of Megatheriops rectidens.

Ameghino (1904) based Megathericulus patagonicus on a cranial fragment and complete right astragalus of an adult individual from near Laguna Blanca, Chubut Province, Argentina. This specimen is part of the Ameghino Collection at MACN, but has no catalogue number. The cranial fragment
(PI. 37D) preserves the rostrum and palate, but not the molariforms. The alveoli indicate that the molariforms were rectangular and markedly compressed proximodistally, similar to those of "Plesiomegatherium" halmyronomum (see MANDIBLE). The edentulous, anterior part of the palate is remarkably elongated, with PMMLI $=79$. The lateral walls of the rostrum bulge laterally, so that the rostrum diverges anteriorly in dorsal or ventral view, resembling the condition in Plesiomegatherium bergi.

## MANDIBLE

The mandible has a similar form in all megatheriines, and shares characteristics with those of many nonmegatheriine sloths, such as sceliodotheres and other unspecialised mylodonts, Santacrucian and Plio-Pleistocene nothrotheriines, and planopsines. There are three major features which distinguish the megatheriine mandible from that of other sloths: the molariforms form a continuous series, without a diastema, and are functionally similar; the ventral margin forms a prominent mandibular bulge beneath the toothrow; and the posterior lateral opening of the mandibular canal lies dorsally on the surface of the mandibular body, lingual to the anterolateral margin of the coronoid process. These features are discussed below.

The symphysis extends mesially in front of the molariforms to form a transversely narrow and anteroposteriorly elongated symphyseal spout. The lingual surface of the spout forms a trough nearly equal in width to the distance between the tooth rows. Naples (1987) suggested this probably allowed sloths to protrude the tongue with little mandibular depression. Although there is variation in length, an elongated spout is present in many varied sloths, such as the Santacrucian nothrotheriine genera Hapalops, Schismotherium, and Pelecyodon (Scott, 1904), the Plio-Pleistocene nothrotheres (Naples, 1987), the
scelidotheres, including the Santacrucian Nematherium and Analcitherium (McDonald, 1987), and planopsines (Scott, 1904; Hoffstetter, 1961).

The symphysis fused early in ontogeny, as in most ground sloths (McDonald, 1987). The mandible is relatively shallow dorsoventrally at the symphysis, but posteriorly grades into a deep mandibular body. The ventral margin of the body forms a prominent and smoothly convex ventral bulge in megatheriines. The ventral margin is concave in Santacrucian and Plio-Pleistocene nothrotheriines, planopsines, and various other sloths (e.g., the Caribbean Acratocnus; Anthony, 1926), but the bulge is considerably less prominent due to increased apicobasal lengths of the molariforms in megatineriines. In the latter, the bulge projects considerably below a line joining the ventral margins of the symphysis and angular process, whereas in the nothrotheriines and planopsines the mandibular bulge is nearly at the same level as the margin of the angular process. The recognition of a bulge in nothrotheriines and planopsines is due partly to the posteroventral slope of the mandibular body posterior to the spout and its concave margin between the deepest part of the body and the angular process.

Scelidotheres possess a deep mandibular body, but a bulge is not recognizable as such as there is only a slight demarcation between the body and angular process. The
ventral margin below the tooth row is thus nearly rectilinear and parallel to a plane passing through the alveolar margins of the molariforms. Further, the ventral margin of the angular process lies more ventrally, and usually projects below the level of the deepest part of the body.

In more advanced mylodontids, such as MyIodon and Glossotherium, the mandibular body is relatively shallower and there is slight demarcation between the mandibular body and angular process, but the body deepens posteriorly. In Choloepus and Bradypus the body is relatively shallower and the ventral margin nearly linear. The posteroventrai part of the symphysis and the ventral margins of the mandibular body and angular process all lie approximately at the same level.

The coronoid process in megatheriines is prominent, rising considerably above the level of the mandibular condyle, and resembling in this respect more those of Hapalops and Schismotherium than the Plio-Pleistocene nothrotheres. The dorsal part of the process curves posteriorly, but not to the degree observed in sceliodtheres, in which the process overhangs the mandibular condyle. The condyle in megatheriines lies relatively higher above the alveolar marginal plane than in other sloths. The angular process is well-defined. The lateral surface is convex and the medial concave, to produce a
ventrally reflected margin.
The following linear dimensions (Fig. 6; App. 4B) were used as estimators of size and to investigate inter- and intraspecific differences among the dentaries of megatheriines: Mandibular Body Height (MBH), the greatest height of the tooth-bearing ramus; Mandibular Toothrow Length (MTRL); Height of the Mandibular Condyle above the Alveolar Border ( MCABH ); length between the mesial surface of ml and the posterior margin of the angular process (mIAPL). Standard statistics for these variables in $E$. laurillardi and M. americanum are presented in Table 2.

Mandible of Eremotherium laurillardi
As with the skull, Toca das Onças yields a fine series of mandibles representing various stages of growth. Largely adult specimens from other localities supplement the sample and extend the range of mandibular variation. This broadened sample establishes a range of morphological and morphometric variation, and provides a basis for suggesting ranges of variation for mandibles of other megatheriines.

The larger mandibles from Toca das Onças are clearly from adult individuals, based on complete fusion of the symphysis, untapered molariforms, and, for MCL 1700 and 1701, the condition of the cranial sutures. However, the change from tapered to parallel-sided molariforms and the fusion of the dentaries occurred early in development.

## FIGURE 6.

Diagrammatic Megatheriinae left dentary in lateral view showing measurements. Abbreviations: m1APL - Length between the mesial surface of $m 1$ and the posterior margin of the angular process; MBH - Mandibular body height; MCABH - Height of the mandibular condyle above the alveolar border; MTRL - Mandibular tooth row length.


TABLE 2. Standard Statistics (mm) for the Dentaries of Megatheriinae. Abbreviations as in Figure 4.

Eremotherium laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | ---: |
| MBH | 17 | 127 | 156 | 145 | 7.8 |
| MTRL | 17 | 174 | 200 | 189 | 6.8 |
| MCABH | 11 | 114 | 156 | 137 | 12.2 |
| M1APD | 8 | 387 | 461 | 429 | 22.8 |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | ---: | ---: | ---: | ---: | ---: |
| MBH | 22 | 180 | 254 | 215 | 18.1 |
| MTRL | 22 | 186 | 259 | 212 | 18.1 |
| MCABH | 11 | 136 | 234 | 192 | 28.4 |
| M1APD | 5 | 405 | 511 | 453 | 45.9 |

Megatherium medinae

| Variable | N | Minimm | Maximum | Mean | Std Dev |
| :--- | :--- | :---: | :---: | :---: | :---: |
| MBH | 4 | 116 | 161 | 134 | 21.4 |
| MTRL | 4 | 130 | 172 | 149 | 17.7 |
| MCABH | 1 |  | 168 |  | - |
| MIAPD | 1 |  | 413 |  | - |

Megatherium sundti

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| MBH | 3 | 126 | 146 | 137 | 10.1 |
| MTRL | 3 | 145 | 154 | 149 | 4.5 |
| MCABH | 2 | 122 | 141 | 132 | 13.4 |
| MIAPD | - | - | - | - | - |

Large adult mandibles unassociated with a skull include MCL 7225, 7229, 7233, and MNRJ 3858 and 2225. The Mandibular Tooth Row Length (MTRL) of these is greater than approximately 180 mm , and it is reasonable to assume that any mandible of at least this size belongs to an adult. It is not possible, however, to conversely consider that unassociated mandibles of smaller sizes derive exclusively from juvenile or subadult individuals. The reason is that postcranial evidence suggests that some juveniles attained a greater size than some adults. The MTRL of MCL 1702/02, for example, is nearly 180 mm , but the cranial sutures indicate that the individual was not yet fully grown.

An examination of the series of mandibles reveals trends, in addition to the obvious increase in size, that occurred during ontogeny in $E$. laurillardi. The specimens are listed and described below in order of increasing magnitude of MTRL. Medial or lateral views of most of the following are given in Plates 38 - 41B; occlusal views in Plates 42 - 45C.

MCL 7235 (PI. 38A), MTRL unavailable - The specimen is a partial left dentary, preserving only m3 and m4 (broken at the alveolar borders). Although MTRL is not available, MCL 7235 is clearly the smallest juvenile individual. m 3 is strongly tapered, particularly mesiodistally (MD vs TR = 1.1:1.5, at the alveolar border). A mandibular bulge is
clearly present, but not prominent, as it does not project ventrally below the ventral margin of the angular process. MCL 7234 (Pls. 38B; 42A), MTRL=83 mm - The posterior part of a larger left dentary preserving all molariforms. The teeth taper, but their MD and TR dimensions, measured at the alveolar borders, are nearly equal. The ventral bulge is more prominent.

MCL 7232 (Pls. 38C; 42B), MTRL=85 mm - A right dentary with four tapered molariforms, the posterior part of the spout and symphysis, and roots of the ascending ramus and angular process. The symphysis is unfused. Its posterior margin lies considerably mesial to ml . The ventral bulge is approximately as in MCL 7234, and projects below the ventral margin of the angular process.

MCL 7221 (Pls. 38D, 42C), MTRL=116 mm - A nearly complete mandible preserving all molariforms. The spout is broken anteriorly, but nearly entirely preserved posteriorly. The molariforms are nearly parailel-sided. The symphysis is partially fused (the specimen is reinforced by plaster) and a suture line is clearly evident. The posterior end of the symphysis lies approximately at the level of the mesial third of $m I$.

MCL 7220 (Pls. 38E, 42D), MTRL=124 mm - A nearly complete mandible preserving all molariforms, the right angular process and root of the right ascending ramus. The tip of the spout is missing. The molariforms are nearly parallel-
sided. The symphysis is partially fused and reinforced with plaster. Its posterior end lies approximately level with the mesial third of mI .

MCL 7236/01,02 (Pls. 39A, 43A), MTRL=127 mm - Left and right dentaries, respectively. The left is more complete and preserves $m 1-m 3$, alveolus of $m 4$, mandibular condyle and angular process, and root of the ascending ramus. The tip of the spout is missing. The molariforms are parallelsided. The symphysis is unfused and reaches posteriorly to approximately the level of the distal third of ml . The ventral bulge is prominent, projecting below the angular process, but shallower than in MCL 7221 or MCL 7220. MCL 7246, MTRL=130 ma - Central part of a left dentary, which preserves four parallel-sided molariforms. MCL 7226 (Pls. 39B, 43B), MTRL=134 mem - A right dentary preserving all molariforms (m4 broken at the alveolar border), angular process, and root of ascending ramus. The tip of the spout is missing. The symphysis is largely unfused and reaches posteriorly to approximately the level of the middle and distal thirds of ml. The molariforms are parallel-sided, and the ventral bulge is prominent. MCL 7223/01 (Pls. 39C, 43C), MTRL=135 mm - A right dentary, preserving all molariforms, angular process, and root of the ascending ramus. The tips of the spout and mandibular condyle are missing. The symphysis is largely unfused and reaches posteriorly to approximately the level of the mesial
part of m 1 . The molariforms are parallel-sided, and the ventral bulge is prominent.

MCL 7228 (Pls. 39D, 43D), MTRL=144 mm - A partial mandible preserving a nearly complete right dentary (the tip of the coronoid process, m3, and a small portion of the ventral margin below m4 are missing), and the left symphyseal region. The molariforms are parallel-sided. The symphysis is largely fused, though not yet well-knit, and zones of unfused deep suture are evident; the suture line is clearly evident dorsally and ventrally. The symphysis reaches posteriorly to approximately the level of the middle of ml , and the ventral bulge is prominent.

MCL 7222 ( Pl .44 A ), MTRL=144 mm - An incomplete left dentary preserving all molariforms, which are parallel-sided. The specimen is more robust than MCL 7228 , and the ventral bulge is deeper.

MCL 1702/02 (PIs. 40A, 44B), MTRL=174 mm - A nearly complete mandible preserving all eight, parallel-sided molariforms. The tips of the coronoid processes, left angular process, and spout are missing. The symphysis is largely fused. Its lines of fusion are clearly evident superficially, but some relatively small regions of non-fusion occur deeply posteriorly and ventrally. The symphysis reaches posteriorly to approximately the level of the middle of ml . The associated skull, MCL 1702-01, indicates that this large individual was not yet completely mature, and probably a
subadult. Some sutures, particularly on the dorsal and lateral surfaces of the skull are largely closed, but some on the ventral surface remain partially open. The molariforms are parallel-sided.

MCL 7229 (Pls. 40B, 44C), MTRL=182 mm - A nearly complete mandible, lacking only the right $m 1-m 3$ and the tip of the spout. The molariforms are parallel-sided. The symphysis is solidly fused. Only a trace of the suture line is evident, except for a small open portion ventrally. The symphysis reaches posteriorly to approximately the level of the middle of $m i$.

MCL 1701/02 (Pls. 40C, 44D), MTRL=186 mm. A nearly complete mandible preserving all eight, parallel-sided molariforms, but with major plaster reconstruction to the left angular and right coronoid processes, and minor reconstruction to the tip of the right angular and left coronoid processes. The dorsal margin the right angular process (the left is modelled on the right) is odd, because it tapers posteriorly, rather than extending nearly horizontally. It is the only specimen in which the level of the angular process falls considerably below the level of the alveolar margin. This may be due to individual variation, but the dorsal surface presents some evidence of smooth wear, which suggests that its form is due to postmortem deformation. The tip of the spout is missing. The associated skull, MCL 1701-01, which Cartelle and Bohórquez (1982) identified as a
female, indicates that the individual is an adult. The symphysis reaches posteriorly approximately to the level of the distal surface of ml or of the alveolar septum between ml and m 2 .

MCL 7231 (Pls. 40D, 45A), MTRL=188 mm - The spout of a right dentary, and nearly complete left dentary with all four, parallel-sided molariforms, but missing the angular process. The symphysis is largely fused, though reinforced partially by plaster, and reaches posteriorly to approximately the level between the mesial and middle thirds of ml .

MCL 7225 (Pls. 41A, 45B), MTRL=190 mm - A nearly complete mandible, missing the left angular and coronoid processes and mandibular condyle, and the tips of the symphyseal spout and right coronoid. The molariforms are preserved, except for a small part of the right m 2 , and are parallel-sided. The symphysis reaches posteriorly to approximately the level of the distal surface of $m 1$ or of the alveolar septum between m 1 and m 2 . It is almost solidly fused, with only a trace of a suture line anteriorly.

MCL 7233, MTRL=194 mm - A nearly complete rigit dentary and the left spout. The molariforms are preserved, except for the distal half of m 4 , and are parallel-sided. The angular process is missing. The symphysis is solidly fused and reaches posteriorly to approximately the level of the middle of ml .

MCL 1700/02 (Pls. 41B, 45C), MTRL=196 ma - A nearly complete
mandible with eight parallel-sided molariforms, but with coronoid processes and left mandibular condyle restored, and tip of spout missing. The symphysis is solidly fused, with only a possible trace of the suture line, and reaches posteriorly to approximately the level of the distal surface of ml . The associated skull, MCL 1700-01, was considered a male by Cartelle and Bohórquez (1982). It shows that the individual was undoubtedly adult, as the heavier, prominent crests and muscle scars suggest that it may have been an old adult, though not an aged animal.

The series suggests various trends occurring through development, and reveals variation among individuals. The change between tapered and parallel-sided molariforms is gradual, but is complete by the stage when MTRL $=$ about $110-$ 120 mm , and well before the symphysis is fully fused, which occurred as the individual neared maturity, at about 170-180 mm. A trace of the symphyseal suture may persist in some adults.

A posterior displacement of the posterior end of the symphysis occurred during growth. It lies well anterior to mI in the youngest animal for which its position is known (MCL 7332). In the next largest individual (MCL 7221) the symphysis ends posteriorly within the mesial third of m1 (when the molariforms are already parallel-sided). The symphysis continued a general posterior migration as
animals aged, though some smaller individuals have a more posterior (albeit marginally so) symphysis than some larger individuals. The symphysis reached the level of the distal surface of $m$ or the aiveolar septum between $m 1$ and $m 2$ in the largest individuals from Toca das Onças. However, it reaches the level of the mesial surface of m 2 in the Honduran specimen FMNH P26970. The posterior limit of the symphysis has been considered phylogenetically important among megatheriines, principally by Kraglievich (1930b), and is discussed below.

A further trend that occurred during growth is reduction in thickness of the mandibular body vestibular to m 1 and m 2 . This trend may be noted by comparing dorsal views of mandibles in various stages of growth (cf. Pls. 42B, $C$ and $45 A-C)$. The greater vestibular or buccal thickness of the mandibular body in younger individuals gives the appearance that each tooth row is more nearly aligned with the long axis of the mandibular body. In adults the vestibular margin of ml closely approximates the lateral margin of the mandibular body, and the tooth row appears to be obliquely oriented to the long axis of the body.

The ventral margin of the mandibular body is ventrally convex in the youngest specimen, but lies approximately at the level of the ventral margin of the angular process. In older individuals the ventral bulge is more prominent, and
projects below the level of the angular process, but there is variation in its prominence. For example, the bulge is shallower in MCL 7236/01, 02 than in MCL 7220 and MCE 7221, in which MTRIs are shorter.

The inclination of the anterior edge of the coronoid process is variable. The ascending ramus takes root from the lateral surface of the body ventral to $\mathrm{m4}$. Its anterior edge curves posterodorsally into the anterior edge of the coronoid process. More dorsally, approximately at the level of the mandibular condyle, the process swings posteriorly. The angle of inclination is measured at the point where the curved ventral edge grades into the upright anterior edge (i.e., excluding the dorsal part of the process), based on the alveolar marginal plane. This edge rises nearly perpendicularly to the alveolar borders in most specimens, and apparently is independent of age. However, the inclination cannot be described accurately for some specimens because the anterior edge of the coronoid process is not rectilinear. In some individuals, e.g., MCL 7229, the anterior edge is slightly convex anteriorly, and the leading edge leans slightly anterior to the perpendicular. In other specimens the posterior inclination is slight, approximately $2^{0}-3^{0}$ from the vertical. The process is notably inclined posteriorly in MCL 7223 ( $7^{\circ}$ ) and MCI 7231 (15ㅇ). Similar variation exists among E. laurillardi specimens from other localities.

The form and position of the angular process is important in distinguishing among some megatheriine genera. In Eremotherium n. sp. and E. laurillardi the angular processes lie relatively more ventrally than in Megatherium. The ventral margin of the process lies entirely below the level of the alveolar margins. The ventral margin of the mandible between the angular process and the posterior limit of the ventral bulge is usually parallel to the alveolar plane. The dorsal margin of the angular process usually lies a relatively short distance dorsal to the alveolar plane, but may be nearly coincident with it or marginally below it (the single specimen, MCL 1701/02, in which it lies considerably below it is discussed above). Thus, most of the angular process usualiy lies below the alveolar plane. The size of the ventral bulge is also important in distinguishing among some megatheriine genera. Size is measured both absolutely (MBH), and as the relationship between MBH and MTRL, which is here designated as the Mandibular Bulge Index (MBI). It is obtained by the formala MBI $=$ HMB ${ }^{(M T R I ~} \times 100$ and is given as an index figure which is the percentage that MBH represents of MTRL. MBI is equivalent to the index used by Zetti (1964) for $M$. americanum. Zetti (1964:261), however, did not attribute differences among specimens to individual variation, and viewed them as within species evolutionary stages: "se desprende directamente, que el ejemplar en estudio ha
alcanzado un grado de evolución avanzado respecto de los ejemplares conocidos de la misma especie".

The Toca das Onças series indicates that, as would be expected, absolute depth of the jaw increased during growth, but that the relationship between MBH and MTRI remained constant (within the limits of individual variation). MBI in E. laurillardi, including juveniles, ranges from 66.3 to 83.0. Juveniles rank among the higher and lower values (MCL $7234-80.7$; F:AM 95790-66.3).

The mandibular spout in Eremotherium is dorsoventrally slender, especially anteriorly. The long axis of the spout is inclined anterodorsally with respect to the mandibular body, but not as markedly as in scelidotheres (see McDonald, 1987: fig. 26). The dorsal margin describes an ample arc, and rises variably above the level of the alveolar margin. Anteriorly the dorsal margin passes gently anterodorsally. The length of the spout and symphysis cannot be precisely determined as its tip is never preserved. From the contours of the preserved part of the spout, it is reasonable to assume that the missing tip would have extended the spout's length by approximately 10 to 20 mm in most specimens. The most nearly preserved spout (MCL 7229) is nearly as long as MTRL; were it complete, it probably would have exceeded MTRL. However, it is clear that the spout in most individuals did not reach this length. Estimates of the length of the spout in E. Laurillardi lie approximately
between $80 \%$ and $90 \%$ of MITRL.
The Height of the Mandibular Condyle Above the Alveolar Border (MCABH) is also taxonomically important. The absolute height of the mandibular condyle is considered with respect to MBH and MTRL. The MCABH-MBH Index (MCABH-MBHI) is obtained by the formula $H M C A B / M B H \times 100$ and is given as an index figure which is the percentage that mCABH represents of MBH. The MCABH-MTRL Index (MCABH-MTRLI) = MCABH/MTRL x 100, and is an index figure which represents HMCAB as a percentage of MTRL.

Clearly, the absolute value of the height of the condyle increased as the individual grew. The relative height, as given by MCABH-MBHI, is variable (range $=75.0$ to 115.9), and apparently not correlated with age. Indeed, the lowest value is from the largest adult (FAM 95785). The juvenile individual MCL 7221 yields the second lowest value (88.8). The highest value is from MCL 7223/01, a juvenile or possibly subadult individual.

## Mandible of Megatherium americanum

The mandible of Megatherium americanum is well-known, largely from the descriptions by Owen (1856), but also by Lydekker (1894) and Ameghino and Kraglievich (1921). These authors based their work on relatively complete large adult specimens which closely resembled each other. Specimens displaying slight variations, including size, from this
general form were often considered to represent species distinct from M. americanum. Such practice was extended to variation in postcranial elements as well. However, as with the skull, the mandible of $M$. americanum is variable.

The following descriptions are based largely on nearly complete mandibles of almost certainly adult individuals, except as noted, and include isolated elements, those that are associated with skull and postcranial elements, and those associated with only a few postcranial elements. Precise stratigraphic information is often lacking. Most specimens are noted simply as being from the "Pampean"; others more precisely but possibly less reliably as from the "Inferior" or "Superior Pampean"; a few lack any stratigraphic information. Similarly, the locality of many specimens is available, but imprecise. Usually, a specimen is known to have been recovered from near a town, city, or region of a province. However, the mandibular specimens possess morphological features that identify them as $M$. americanum, or associated with cranial or postcranial elements clearly belonging to this species, and help establish a range of variation for this species. The initial description omits specimens that have been formally assigned as the types of other species. These, and other specimens, probably representing somewhat smaller, younger or juvenile individuals, are discussed once the general characteristics of the mandible are given, and used to
extend the range of variation.
The posterior end of the symphysis lies more posteriorly in
M. americanum than in E. laurillardi. Its position varies from approximately the level of the mesial part of the septum between $m 1$ and $m 2$, and the middle of $m 2$ (Pl. 49A-C). The mandibular bodies approach each other more closely at the symphysis in $M$. americanum, and their union usually forms a more nearly $V$-shaped outline in dorsal view, although in some specimens (e.g., MLP 28-III-16-2) the outline is nearly U-shaped. The large ventral bulge reflects the increased hypsodonty in this species. However, the $V$-shaped arrangement at the symphysis does not, as was supposed by Kraglievich (1931), because the thickness of the bodies is similar to those in E. laurillardi. It is due, rather, to a mandibular construction which places the rami initially closer together, and is demonstrated by the relatively narrower distance between the condyles and the toothrows, and possibly, but less likely, the more posterior position of the symphysis. The distance between the toothrows is clearly less than the transverse width of the molariforms in $M$. americanum, which is the reverse of the condition in E. laurillardi (cf. Pls. 44B-D and 49A, B). The narrower space between the mandibular toothrows thus mirrors the condition of the maxillary toothrows.

The symphyseal spout is more robust, particularly
anteriorly, in M. americanum. Its tip is often preserved and bears a medial notch (P1. 49A, B). Such a notch was probably also present in E. laurillardi. The spout in M. americanum widens slightly anterioriy, whereas that of $E$. laurillardi tapers slightly. The length of the spout varies (cf. Pl. 47A and B) and may be greater than MTRL; it is thus somewhat longer in M. americanum than in E. laurillardi. The spout usually lies somewhat anterodorsal to the alveolar plane, as in E. laurillardi. However, it may lie nearly horizontally, with only a small portion of its dorsal margin projecting above the alveolar plane, as in the type specimen, MNHNM 6 (Pl. 17A). The anterior part of the spout is deflected strongly anteroventrally in MLP 2-56 (PI. 48B). However, this condition is probably pathological. The right dorsal mental foramen is greatly enlarged. A large and irregular exostoseal flange, approximately 40 mm long and protruding about 15 mm , lies dorsal to it. A smaller irregular region lies ventral to the foramen. The dorsal margin of the spout is considerably more rugose than usual. A large and irregular rugose ridge extends from side to side between $30-50 \mathrm{~mm}$ mesial to the ml 's on the spout. These features may have been caused by an infected fracture which healed, but caused a downward displacement (A. G. Edmund, 1991, pers. comm.).

The angular process in M. americanum (e.g.. Pls. 17B; 46A; 47A-D) lies more dorsally than in E. laurillardi. Its
dorsal margin always lies considerably above the level of the alveolar plane. This level usually intersects the process approximately between the middle and ventral fourth of its dorsoventral height, such that most of the process often lies dorsal to the alveoli. The ventral margin of the process inclines posterodorsally, unlike the nearly horizontal margin in E. laurillardi. The ventral margin of the mandibular body between the ventral bulge and angular process is concave, as in E. laurillardi, but is oriented posterodorsally as it passes into the more dorsal angular process. The shape of this region is most useful in distinguishing between the Megatherium and Eremotherium mandibular patterns.

The mandible of $M$. americanum (Pls. 17A, B; 19; 46-49) is easily distinguished from that of $E$. laurillardi by the considerably more prominent ventral bulge and more dorsal positions of the angular process and mandibular condyle. The MBE is relatively (MBI ranges from 92.7, MLP 2-52, to 112.0, MLP 2-54) and absolutely significantly ( $t=16.31$, df=30, $p=0.0001$ ) greater in M. americanum, and projects well below the symphysis and angular process. The MTRL ( $t=5.47$, $d f=28.1, p=0.0002$ ) and MCABH ( $t=5.94, d f=13.6, p=0.0001$ ) are also significantly greater in M. americanum. The relationships between MTRI and MBH and MCABH are presented graphically in Figures 7 and 8, respectively. However, these species do not differ significantly in miAPD ( $t=1.26$,
$\partial f=11, \quad p=0.2350$ ).
These results indicate that $E$. laurillardi and $M$. americanum differ significantly in anatomical regions associated with the dentition. The TRL of the skulls did not differ. Probably, this latter result is therefore indeed due largely to the few skulls available, as suggested above (see SKULL), as MTRL is based on more adequate samples.

The MCABH is absolutely and relatively greater compared to MTRL in M. americanum. However, values for MCABH-MBHI, while variable, are similar to those in E. laurillardi. The anterior margin of the coronoid process is usually more erect, and rarely inclines posteriorly. The central third of the margin is usually convex.

Various of the features characteristic of the mandible of $M$. americanum may be explained in terms of increased hypsodonty in the evolution of this species. Thus, the ventral bulge is greater to accommodate the deeper mandibular alveoli and more hypsodont molariforms. The more hypsodont maxillary molariforms require deeper maxillae (reflected by increased OCH) and thus the ventral margin of the lower orbit lies dorsal to the maxillar alveolar plane. The height of the mandibular condyle is raised to accommodate the more ventrally positioned occlusal plane between the upper and lower molariforms. The angular process and the region between the process and body are
raised so that a dramatic rearrangement of the muscular attachment sites and force vectors might be averted. The greater values for MBI and MCABH-MTRLI in M. americanum reflect these changes. The MCABH-MBHI values, however, are similar to those in E. laurillardi. The similarity reflects the fact that concomitant increase has occurred in depth of the mandibular body and height of the condyle in $M$. americanum. This may be appreciated graphically by superposition of Figure 7 on Figure 8.

Various juvenile and subadult mandibular specimens (PIs. $28,50,51$ ) have been recovered and assigned in the past to either M. americanum or to some other Pleistocene species of this genus thought to have existed within the general areas also inhabited by M. americanum. Unfortunately, few are certainly associated with adult remains of this species. However, as these Pleistocene specimens are from localities near those that have yielded remains undoubtedly referable to $M$. americanum, and considerably fewer species probably existed throughout most of the Argentinian Pleistocene than previously believed, it is likely that many of the juvenile specimens belong to $M$. americanum. At the very least, the specimens may be considered without much reservation to belong to Megatherium, and demonstrate various differences between the ontogenies of species of this genus and E. laurillardi. The ventral bulge is considerably less prominent in

## FIGURE 7.

Bivariate plot (mm) of Mandibular body height (MBH) against Mandibular tooth row length (MTRL) of Megatheriinae (cf. Fig. 6). Equations for regression lines: Eremotherium laurillardi, $y=$ $0.90 x$ - 25.12; Megatherium americanum, $y=0.63 x+$ 81.14 (cf. Fig. 6).


## FIGURE 8.

Bivariate plot (mm) of Height of the mandibular condyle above the alveolar margin (MCABH) against Mandibular tooth row length (MRTL) of Megatheriinae (cf. Fig. 6).

juveniles of Megatherium; its relative (and absolute) depth increases through ontogeny to reach adult proportions. This contrasts with the situation in E. laurillardi, in which the depth of the ventral buige remains approximately constant through ontogeny. Indeed, Figure 7 suggests that juveniles of $M$. americanum resemble more those of $E$. laurillardi than adults of its species. As with toothrow length this contrasts with the variables of the skull such as OCH, for which juveniles of $M$. americanum apparently resemble the ađults (Figure 4).

MACN 10149 (Pl. 28B) preserves nearly completely the right dentary and a small anterior part of the left, partially fused at the symphysis. The posterior two-thirds of the symphyseal surface of the right dentary are exposed, indicating that this individual had not reached maturity. Its relatively long MTRI suggests that it was probably a young subadult. According to records on the MACN label, the specimen was associated with a larger, adult individual clearly recognizable as $M$. americanum. MBI is 92.0, a value near the lower end of the range for the species. MACN 2830 (identified as M. americanum on the museum label) and MACN 2786 preserve nearly completely the skull and mandible, which indicate that the former is older than the latter. These individuals (PI. 50B, C, and 51B, C) are younger than MACN 10149, but present features clearly identifying them as belonging to Megatherium. MBI is 88.7 and 76.0,
respectively.
The mandible of MACN 5002 (Pl. 48C), the type of $M$. gallardoi, is of particular interest. Ameghino and Kraglievich (1921) cited a less prominent ventral bulge as the most important character that distinguishes the mandible of this individual. They also noted that the ventral margins of the mandible anterior and posterior to the bulge were less concave. The latter characteristics, however, are correlated with the less prominent bulge. Further, they stated that the angular process lies more ventrally than that of $M$. americanum, and the posterior margin of the symphysis lies at the level of the alveolar septum between m 2 and m 3 . The last two observations are incorrect. The angular process, though incomplete, lies well within the range for M. americanum. Posteriorly the symphysis lies approximately at the middle of $m 2$, which is normal for $M$. americanum. It is true that the buige is less prominent, but evidence suggests that MACN 5002, though a relatively large indiviđual, was probably still a subadult. Various of the cranial sutures, including the premaxillary, premaxillomaxillary, nasofrontal, nasoparietal, parietofrontal, and posterior part of the maxillopalatal, are incompletely fused. Also, the suture between the diaphysis and head of both the humerus and the femur are clearly evident; the head of the femur may not have been solidly fused at all (it is largely attached with mastic to
the diaphysis). It seems probable therefore that the less prominent ventral bulge on the dentary in MACN 5002 is due to the individual's youth.

The partial dentaries MACN 62 and MACN 855 (Pls. 50A, 51A), respectively the types of Neoracanthus burmeisteri and N. brackenbuschianus, and MLP 2-61 were considered by Lydekker (1894) as juveniles of M. americanum. Cabrera (1928) agreed to the juvenile stage of the mandibles, but assigned them to Megatherium sp. because it was generally believed at that time that numerous Megatherium species existed in Buenos Aires Province during the Pleistocene. These individuals are considerably younger than MACN 2786 or MACN 2830. In responding to Lydekker's (1894) criticism, Ameghino (1895) stated that MLP 2-61 and MLP 2-62 could not represent sequential growth stages, as Lydekker believed. Ameghino assumed that MLP 2-62 belonged to a larger, older individual, and thus should have a more prominent ventral bulge than MLP 2-61. Presumably, Ameghino perceived a less prominent ventral bulge for MLP 2-62, perhaps because the specimen is less complete and well-preserved, but it does, in fact, have a relatively deeper bulge than MLP 2-61 (MBI = 87.2 for MLP 2-62; 83.8 for MLP 2-61). MACN 855 is the smallest of these juvenile mandibles, and MBI $=77.8$. As in E. laurillardi, the thickness of the bone vestibular to m 1 (as is particularly evident in dorsal view) is relatively greater in juveniles (this is not evident in MACN 2786 ,

Plate 51C, due to distortion mesially of its toothrows).
The symphysis reaches posteriorly just mesial to level of the middle of $m 1$ in MLP 2-61, and approximately within the mesial third of ml in MACN 855 (Pl. 51A). The symphysis is too poorly preserved in MLP 2-62 to permit recognition of its posterior end. As in E. laurillardi, retrogression of the posterior limit of the symphysis occurs throughout ontogeny, but it appears to be more advanced in $M$. americanum. For example, MTRL $=85 \mathrm{~mm}$ in $E$. laurillardi MCL 7232, but the symphysis still lies considerably mesial to m1.

The molariforms in the M. americanum juveniles are tapered as in E. laurillardi. In both, they become parallel-sided early in ontogeny, and are nearly so in MLP 2-62. The distance between the toothrows (P1. 51B, C) is equal or greater than the transverse width of the largest molariform in the specimens available, and thus resembles more the condition in adults and juveniles of $E$. laurillardi than aduIts of M. americanum. The angular process in MACN 855 (Pl. 50A), with a nearly horizontal ventral margin, lies largely below the alveolar plane, and so resembles the juvenile and adult conditions of $E$. laurillardi. A more dorsal position, however, is rapidly achieved in adults. It is already evident in MLP 2-61, in which the ventral margin of the body posterior to the bulge slopes more posterodorsally than in E. laurillardi. In MACN 2786 and

MACN 2830 ( $\mathrm{Pl} .50 \mathrm{~B}, \mathrm{C}$ ), the characteristic angular process of the adult condition of $M$. americanum is present, though it is relatively still somewhat ventral.

MLP 2-60, the type of Megatheriun gaudryi (PI. 48D) from Monte Hermoso, includes an incomplete and not particularly well-preserved right dentary, part of the left symphyseal region, and a few postcranial elements. Its somewhat smaller size and supposedly older stratigraphic age have been cited often as distinguishing it from $M$. americanum. However, there are compelling reasons for rejecting this distinction. The material is not of Montehermosan Age, but is Pleistocene (see SYSTEMATIC REVIEW OF THE MEGATHERITNAE). $\operatorname{MBI}=96.8$, nearer the lower end of, but well within, the range for M. americanum. Posteriorly the symphysis reaches approximately the level of the mesial surface of m 2 , again within the expected variation for $M$. americanum. The symphysis is shown by Lydekker (1894: pl. 47, fig. la) as lying approximately at the middle of ml ; however, the occlusal surface of MLP 2-60 as photographed in Lydekker's figure is not in the horizontal plane, and so the symphysis appears to be further forward due to tilted orientation.

## Mandible of Other Megatheriinae

The samples for other megatheriine species are small, and do not permit the detailed analyses possible for $M$.
americanum and E. laurillardi. The mandibles of most taxa named in the literature demonstrate the pattern in $M$. americanum. The ventral bulge tends to be prominent. The angular process is usually situated dorsally, and the ventral margin of the body posterior to the bulge slopes posterodorsally. The toothrows are narrowly separated.

The mandibles of $M$. medinae (Pls. 52, 53) and M. sundti (Pls. 54, 55) cannot be consistently distinguished. The few specimens assigned to these species are usually incompletely and poorly preserved. Variation exists in shape of the ventral bulge and ventral margins of body anterior and posterior to the ventral bulge, angle of inclination of the spout, position of the posterior end of the symphysis, in size and robustness. Apparently, however, the variation is not particularly greater than occurs in the mandibles of $M$. americanum and E. laurillardi. Cranial differences between M. medinae and M. sundti are subtle, but the species may be distinguished clearly on the morphology of the femur (see FEMUR) .

The mandibles from Ulloma appear relatively more robust or compact, so that the body seems anteroposteriorly compressed. The possibly more anterior position of the anterior margin of the ascending ramus, which covers most or all of $\mathrm{m4}$ laterally, lends to the compressed appearance. Some of the mandibular variation among the species may be due to preservation, but age of the specimens probably
contributes. Oddly, it appears that a high percentage of the megatheriine skulls and mandibles recovered from northern Chile and near Ulloma, Bolivia, are probably of juveniles, subadults or young adults, and it is thus impossible to give a reliable range for the size of adult individuals. It appears that the larger mandibles, however, SGO PV236 (MTRL = 172 mm ), SGO PV286 (165 mm), and SGO PV291 (170 mm) probably belonged to adults. Mandible SGO PV276 (MTRL $=149 \mathrm{~mm}$ ) is associated with skull SGO PV273, in which the sutures appear to be largely closed, and is thus probably adult. These values indicate that M. medinae and M. sundti were smaller than either M. americanum and $E$. laurillardi, an observation corroborated by the skull and postcranial remains. The range of MBI is generally intermediate between those for M. americanum and $E$. laurillardi, but apparently the relationship between these variables resembles more closely that of $E$. laurillardi (see Fig. 7), aIthough there is overlap between the high end of the range for $M$. medinae and $M$. sundti and the lower end of that for M. americanum.

The mandibles from the Tarija Valley, Bolivia, fall into distinct morphological types. In one type, the proportions resemble those of $M$. medinae and M. sundti; in the other those of $M$. americanum. The probable presence of M. americanum in the Tarija Valley has already been discussed. MUT V1082, preserving the molariform-bearing
portion of a right dentary, supports the hypothesis. M. tarijense has also been recovered from Tarija. FMNH P14216 includes the remains of a nearly complete and nearly adult individual. Its mandible (PI. 56A), smaller than that usual for M. americanum, falls within the range for $M$. medinae and M. sundti, but seems more robust. The ventral bulge is prominent, with MBI $=92.5$, but the angular process seems to be more ventral, with its ventral margin only slightly inclined posterodorsally. There appear to be no consistent differences in either absolute or relative dimensions between the mandibles from Tarija, Ulloma, and Chile; or at least none that can be tested for significance.

MUT V1080 is a nearly complete right dentary from a larger individual from Tarija. It largely resembles FMNH P14216, with less prominent ventral bulge, but the ventral margins of the body posterior to the bulge and of the angular process resemble more those of $M$. medinae and $M$. sundti. NRM M4890 is from a considerably larger adult. Its MTRL of 208 mm easily falls within the range of $M$. americanum, but MBI $=82.8$ is considerably lower. The angular process is more dorsal than in FMNH P14216, and approximately as in MUT V1080. FMNH P13655, a partial left dentary from the Tarija area, is approximately as large as NRM M4890. MTRL $=21.0$ and $M B I=89.5$; these values are higier than in NMR M4890, but fall between those for MUT V1080 and FMNH P14216.

Hoffstetter (1952) assigned three dentaries from the Santa Elena Peninsula, Ecuador, to E. elenense, which I consider referable to Megatherium (see SYSTEMATIC REVIEW OF THE MEGATHERIINAE). EPN V978 is the most well-preserved; Hoffstetter (1952: fig. 13D) illustrated it with the mandibular condyle in place, which is missing in Plate 56B and C. A fourth dentary, ROM 3756, from the vicinity of Talara, Peru, was recovered from deposits of the same age as those that yielded Hoffstetter's specimens. All of these specimens belong to immature individuals. Adult specimens of E. laurillardi were also recovered from Talara and Hoffstetter's localities.

The dentaries are within the size range expected for juveniles of $E$. laurillardi, but the morphologies of the mandibular bulge and angular processes are not. The bulge is apparently more prominent, although MBI ranges between 71 (EPN V950) and 76 (EPN V978), probably because the angular process lies further dorsally and resembles that of e.g., M. americanum and $M$. tarijense. This condition occurs in the smallest individual, EFN V980, in which the molariforms taper occlusally. The process is apparently even further dorsal than in MACN 855, a juvenile of $M$. americanum of nearly identical size. This prominence may be due to a probably more advanced ontogenetic age and development of EPN V950: M. elenense was considerably smaller than $E$. laurillardi and M. americanum, based on adult postcranial
remains (see SYSTEMATIC REVIEW OF THE MEGATHERIINAE), and probably similar in size to M. medinae. The dentaries differ from those of the medium-sized Megatherium species in being relatively elongated and gracile, and lack their anteroposteriorly compressed appearance.

The right dentary of Megatheriops rectidens (P1. 57A) is well-preserved, but lacks $m 1-m 3$ and the tips of the spout and coronoid process. The morphology of the mandibular bulge and condyle are intermediate between those of Megatherium americanum and E. laurillardi, but the position of the angular process and the shape of its ventral margin resemble more the condition in E. laurillardi. The MTRL = 165 mm and suggests that Megatheriops rectidens was similar in size to Megatherium medinae, M. sundti, and M. tarijense, but the morphology of its skull, mandible, and humerus distinguish it from these species. MBI is nearly 88, and the symphysis ends posteriorly approximately at the middle of MI. The mandible of Plesiomegatherium hansmeyeri is incompletely known. It is represented by the type specimen MACN 2895 (Pl. 57B, C), which comprises a partial right dentary and maxilla and the proximal and distal portions of a tibia (Cabrera, 1928), and the illustrated left dentary illustrated by Roth (1911: fig. 1). The catalogue number of the latter is uncertain, and the specimen could not be located at MACN. The right dentary preserves m2-m4, the distal surface of the alveolus for $m 1$, and the root of the
ascending ramus; the ventral margin of the bulge is missing. The left preserves m1-m2 and the portion of the mandibular body that contains them. Roth (1911) also illustrated a partial left maxilla (no catalogue number given, and unlocated at MACN), but designated no type for the genus and species. Cabrera (1928) designated MACN 2895 as the type, rather than the illustrated specimen, possibly because the maxilla of MACN 2895 is more complete; the specimen includes some postcranial elements, and the molariforms appear relatively undistorted.

The dentaries of $P$. hansmeyeri demonstrate a closer resemblance to those of Megatherium, with a relatively deep bulge and steeply inclined ventral margin between the buige and angular process. Cabrera's (1928) type dentary is slightly larger than that illustrated by Roth (1911). The toothrow length, including only m2-m4, is 106 mm in the type, and 94 mm in the illustration. From the illustration, the complete MTRL is approximately 124 mm , MBH 116 mm , and MBI $=93.0$, which falls in the lower end of the range in $M$. americanum. The posterior limit of the symphysis cannot be precisely determined, but it probably lay near m1, rather than mesial or distal to it.

Plesiomegatherium hansmeyeri is distinguishable by its smaller size from M. americanum. It is slightly smaller than M. medinae, but the relative depth of the body is similar. The mandible of Promegatherium (MACN 4995; see
below) is larger, but measurements given by Kraglievich (1940a, b) for other mandibles from Paraná are nearly equal in size to those of Plesiomegatherium.

I agree with Cabrera that this genus is distinct from the Catamarca remains reassigned to Pyramiodontherium bergi (Pl. 58A, B), which Roth (1911) had assigned to Plesiomegatherium burmeisteri. The Catamarca species is considerably larger than $P$. hansmeyeri, and the ventral bulge relatively shallower (MBI = 82.8).

Roth (1911) stated that the main distinguishing feature of $P$. hansmeyeri was the parallelogram outline of the molariforms, in which the transverse crests of the teeth are obliquely oriented with respect to long axis of the dentary, rather than the more nearly quadrangular shape of other megatheriines. However, Cabrera (1928) demonstrated that Roth based this on the specimen which he illustrated. The molariforms are nearly quadrangular in MACN 2895 (P1. 57C), with mesiodistal length approximately equal to transverse width. The condition in the illustrated specimen is due to distortion, and occurs occasionally in specimens of M. americanum and E. laurillardi.

MLP 30-XII-10-21 (PI. 58C-F) includes partial left and right dentaries of a small megatheriine, possibly from the same individual. Both preserve all or parts of ml-m4. The left is more complete, preserving the posterior area of symphysis and the root of the ascending ramus. This
specimen was recovered from the Arroyo Chasicó Formation, near the Arroyo Chasicó, Buenos Aires Province, Argentina, and was probably assigned originally to "Plesiomegatherium" halmyronomum by Cabrera (1928), though he did not report a mandible for this species. Pascual et al. (1966)
illustrated MLP 30-XII-10-21 as "P." halmyronomum. Although the mandible is from the same formation and possibly the same locality as the type skull of that species, MLP 26 -IV-10-1, the two are not certainly associated. It is probable, nevertheless, that they belong to the same species, based on provenance and size. It is not clear, however, whether they belong to Plesiomegatherium, or more broadly, to the same genus as P. hansmeyeri. Cabrera (1928) admitted that assignment of the skull to Plesiomegatherium was tenuous and based largely on similar size and that the remains are too sparse to establish a new genus.

MLP $30-$ XII-10-1, with MTRL $=115 \mathrm{~mm}$, is only slightly smaller than the mandibles of $P$. hansmeyeri. The ventral bulge appears shallower, but the MBH (12.4) is marginally greater than the MTRL, so that MBI = 108, a value which falls within the higher end of the range for $M$. americanum. The ventral margin of the mandible between the bulge and angular process is incomplete, but is apparently less steeply inclined than in $M$. americanum and $P$. hansmeyeri, but resembles more the jaw of Megatherium than that of Eremotherium. However, the molariforms of "P. **
halmyronomum, based on MLP 30-XII-10-1, differ strikingly from those of Megatherium, Eremotherium, and P. hansmeyeri in being relatively shorter mesiodistally the molariforms and alveoli of the skull, MLP 26-IV-10-1, are not as wellpreserved, but are apparently somewhat less mesiodistally compressed). This probably results in a shorter toothrow, and explains the high MBHI. The symphysis reaches posteriorly well anterior to ml .

Pliomegatherium is known from Entre Rios, and is based on the type of $P$. Ielongi (MACN 13213: Pl. 59A, B), an edentulous right dentary preserving the ventral part of the angular process. MACN 5269 is the type of $P$. paranense, a less complete right dentary preserving $m 1$ and $m 2$, and the alveoli for $m 3$ and $m 4$, which are broken ventral to the alveolar margins.

Kraglievich (1930a) stated that Pliomegatherium is similar in size to Plesiomegatherium, but is distinguishec by the more anterior position of the symphysis and the curved posterior outline of the symphysis, as opposed to the more angular contact between the mandibular bodies. The symphysis reaches posteriorly near the level of the middle of ml in Pliomegatherium, and the outline of its symphysis is indeed curved, as in Eremotherim, but not in Megatherium.

The location of the posterior end of the symphysis in Plesiomegatherium is not precisely known. Kraglievich
(1930a) based his diagnosis on Roth's (1911) illustration, but the symphyseal region is broken. The body begins to curve medially into the symphysis at the septum between m 1 and m2, but this does not necessarily indicate the midine position of the posterior end of the symphysis.

The two genera are, nevertheless, distinguishable. The mandible of Pliomegatherium strongly resembles the eremothere type, with a relatively shallow ventral bulge, more ventral position of the angular process, and less steeply inclined ventral margin between the bulge and angular process. Measurements given by Kraglievich (1930a) for $P$. Ielongi and $P$. paranense are incorrect. The MBH and MTRL for $P$. lelongi are 103 mm and 144 mm , respectively, and, for $P$. paranense, 106 mm (this value is the actual preserved height, because a small portion of the ventral margin is missing) and 147 mm , respectively. MBI = approximately 72 for $P$. lelongi (an estimated value for $P$. paranense is also 72), which falls within the range for $E$. Iaurillardi.

There is no basis for maintaining specific distinction for MACN 13213 and MACN 5269. They are nearly identical in size. The posterior part of the symphysis is similarly curved, and falls in nearly the same position. The molariforms are of the normal quadrangular megatheriine shape, as in Plesiomegatherium hansmeyeri, Megatherium and Eremotherium. The slight morphological differences between

MACN 13213 and MACN 5269 probably reflect the poorer preservation of MACN 5269.

Promegatherium is based on molariforms from the "Mesopotamian" of Entre Rios Province, Argentina. Various dentaries from this area have been assigned in the Iiterature or by museum staff to this genus, including MACN 4995 (Pl. 59C, D). The latter is an incomplete right dentary missing most of the ascending ramus, the ventral part of the mandibular bulge (thereby exposing the $\mathrm{m} 2-\mathrm{m} 4$ basally), and the part anterior to the septum between $m 1$ and m2. Despite its imperfect preservation, MACN 4995 differs from the type of Pliomegatherium lelongi in size of the bulge and position of the angular process. In these characteristics it more closely resembles the dentaries of, for instance, Megatherium americanum and M. medinae. However, the unsettled taxonomy of Promegatherium is complex and discussion of its status deferred (see SYSTEMATIC REVIEW OF THE MEGATHERIINAE).

Kraglievich (1930) identified MACN 2833 as belonging to Megatheridium annectens. The specimen was recovered from the typical bluish sands of the "rionegrensen" from Rio Negro Territory, which yielded the partial cranial elements (MLP 69) on which Cabrera (1928) erected this genus and species. There is no certain association between MLP 69 and MACN 2833, and whether they are from the same or similar stratigraphic positions or localities is unknown.

MACN 2833 preserves the nearly completely left mandibular body, but is missing m3 and the coronoid and angular processes. The symphysis and symphyseal spout are nearly complete. The right mandibular body is missing posterior to the mesial part of m4. Kraglievich's (1930a: figs. 5d, 6d) illustrations of MACN 2833 are inaccurate. The symphyseal spout extends further anteriorly (to the level of the septum between $m 1$ and $m 2$ ) and neither the right m4 nor its alveolus are complete. Kraglievich (1930a) correctly compared the mandible favourably to the typical megathere type. It is interesting to note that the museum label identifies MACN 2833 as the type of "Megatherium rionegrense. Kragl.". This name was not published formally and thus is invalid, but the label suggests that at some time Kraglievich considered MACN 2833 as inseparable from Megatherium. The ventral bulge is prominent, with MBI nearly 106, well within the range for $M$. americanum. The symphysis reaches posteriorly to the level of the mesial surface of m 2 , forms a narrow and more angular outline, and the intermandibular space is narrow. The main difference from that in M. americanum is its smaller size. $\quad$ MTRL $=149$ mm , which is below values for adults of $M$. americanum. It may be important to note, however, that the ventral symphyseal surface shows signs of incomplete fusion, and may indicate that MACN 2833 had not yet reached adult size.

MACN 2833 falls well within the ranges of morphological and
size variations for M. medinae, M. tarijense and M. sundti), and cannot be separated confidently from these species at the present time based on these variables. However, the high MBI of MACN 2833 is well-above those recorded for then latter species and suggests affinity to $M$. americanum. Conversely, if MACN 2833 represents an immature individual, as its size would suggest, then it is the only such individual in which MBH exceeds MTRL. More complete specimens with better stratigraphic control are prerequisites for more sound conclusions.

Kraglievich (1931) based M. Iundi seijoi on MNHNU 443, from the Pleistocene of Uruguay. The specimen is relatively complete, and lacks all molariforms but the left $m 1$, the symphyseal spout, the angular processes and the dorsal parts of the coronoid processes. The mandible is from a relatively large and apparently adult individual, well within the size range for $M$. americanum. The mandibular bulge is large, with MBI nearly 93, near the low end of the range for $M$. americanum. Among the characteristics noted by Kraglievich (1931), only the position of the posterior end of the symphysis is probably relevant. It lies approximately at the level of the middle of ml , and thus further anteriorly than in the specimens of M. americanum discussed above. Conceivably, this position may be considered within the range of variation for this species, as the character is hignly variable in E. laurillardi.

Conversely, MNHNU 443 may represent a large individual of one of the smaller species, such as M. medinae. I consider M. Iundi invalid for other reasons (see SYSTEMATIC REVIEW OF THE MEGATHERIINAE), but cannot assign MNENU 443 confidently to any taxon. I strongly suspect, based on its morphology, MBH, MTRL, and MCABH (Figs. 7, 8), that it represents M. americanum, and provisionally regard it as such.

Roselli (1976) based Perezfontanatherium fiandrai on an incomplete left dentary, MPFLR 396, from the Pleistocene of Uruguay. It lacks m 3 , the tip of the spout, and most of the ascending ramus; $m 1, m 2$, and $m 4$ are broken at the level of the aIveolar margin.

Roselli (1976) believed that the dentary represented an immature individual, based on the largely unfused symphysis, but considered it nearly adult, based on the parallel walls of the alveolus of $\mathrm{m3}$, and, therefore, untapered molariforms. The dentary of P. fiandrai was distinguished by Roselli (1976) from that of $M$. americanum on its smaller size, less prominent mandibular bulge, convex or bulbous lateral surface, more inclined ascending ramus, more anterior position of the posterior end of the symphysis, and lateral position of the posterior lateral opening of the mandibular canal.

While MPFLR 396 clearly belonged to a young animal, it was probably considerably younger than Roselli (1976) believed. The alveolar walls taper only in the youngest
individuals of $E$. laurillardi. The molariforms may taper slightly occlusally in individuals with MRTL of approximately 120 mm , but the alveolar walls are parallel by this stage (vide supra). This length represents nearly 65\% of that of adult individuals. The symphysis is largely unfused at this stage; and largely, though still incompletely, fused when MTRL is nearly 150 mm . The convex lateral wall of the dentary (Roselli, 1976: fig. 13, 5) is apparently due to the relatively greater thickness of the bone buccal to $m 1-m 2$ in juveniles. Further, the toothrow of MPFLR 396 is more nearly aligned to the longitudinal axis of the tooth-bearing ramus, as occurs in immature $E$. laurillardi, rather than obliquely oriented (vide supra). The more inclined ascending ramus and anterior position of the posterior end of the symphysis are also juvenile characteristics.

The vertebral column is completely known in Eremotherium laurillardi, Megatherium americanum, and M. tarijense. Isolated vertebrae of other taxa are also known. Homologous vertebrae of megatheriines are generally morphologically similar. Diagnostic differences exist, but are usually minor. An appreciable knowledge of size and morphologic variation in E. laurillardi is possible due to the collection from Jacobina, which was described by Cartelle (1992). Although a number of nearly complete vertebral columns of $M$. americanum are preserved, they are usually mounted and inaccessible for detailed study. Therefore, the morphology of the vertebrae are known largely from Owen's (1851) description. Virtually nothing is known of their variation in M. americanum.

The vertebral formula is 7 cervical (CV), 16 thoracic (T), 3 lumbar (L), 5 sacral (S), 17-18 caudal (CD). Cartelle (1992) justifiably questioned the accuracy of the type specimen of $M$. americanum, MNHNM 6 , in which a supernumerary cervical vertebra is apparently present. Those corresponding morphologically to CV 6 and CV 7 are seventh and eighth in the series. The extra vertebra appears to be one of those with a short spinous process, between the axis and CV 6 and thus may have been added erroneously. Other specimens (e.g., BMNH 19953, MPCB 1,

MNHNP 1871-383) have the normal 7 CV . The lumbars are free, as in most ground sloths, and in contrast to Glossotherium, where they are usually fused to the sacrum. The transverse processes of SI-S3 fuse with the ilium and those of S4-S5 fuse with the ischium in most megatheriines. In Pyramiodontherium bergi those of S1-S2 fuse with the ilium, and of $\$ 3-\$ 5$ with the ischium; further, $S 5$ is not fused in the sacrum, in contrast to the five fused sacrals of other megatheriines (Roth, 1911). There are probably 17 or 18 (and possibly more) caudals. MNHPP 1871-383 has 17; most other specimens of M. americanum (e.g.g., BMNH 19953; MPCB 1) and E. Laurillardi (the mounted specimen at DMAS) and Eremotherium n. sp. has 18 caudals, but the terminal elements may have been lost.

The vertebrae are usually not diagnostically useful because of their general similarity among taxa, and the limited knowledge of ranges of variation in M. americanum and M. tarijense. Cartelle (1992) described most of the differences between E. laurillardi and M. americanum. Here, a few of the more significant distinctions are noted.
M. americanum and E. laurillardi differ in the relationships of the facets of the atlanto-axial joint. In M. americanum three separate facets (one for the dens of the axis and two dorsolateral to it) lie posteriorly on the atlas; the anterior surface of the axis bears three corresponding facets. These facets are contiguous in the
atlas and axis of E. Laurillardi and Eremotherium n. sp. Further, these facets are oval, with long axes dorsoventral in M. americanum, but transverse in E. laurillardi (Cartelle, 1992).

Isolation of the facets on the atlas and axis is apparently the more usual condition among extinct tardigrades (Cartelle, 1992), and also occurs in extant sloths. It is also the condition in the non-tardigrade xenarthrans, such as Myrmecophaga (atlas and axis ROM R732); pamapatheres (cf. Holmesina, atlas ROM 3856, axes ROM 3856, ROM 5897, ROM 4923); Dasypus bellus (axis ROM 32767, atlas unavailable): D. novemcinctus (atlas and axis ROM R948); and Glyptodon cf. G. clavipes (atlas and axis ROM 409). Isolated facets in outgroups of the Tardigrada suggests that the contiguous arrangement of $E$. laurillardi is the derived condition. However, it is worth noting that the "large facet for the odontoid process of the axis is continuous with the posterior cotyles" in Hapalops longiceps (Scott, 1903:187), which suggests convergence. Asymmetrical arrangements of the facets may occasionally occur. Cartelle (1992), citing Stock (1925), noted that the facet for the dens is contiguous with the left lateral facet in an atlas of Glossotherium harlani. The facets are isolated on the atlas and axis of an individual of M. medinae (SGO VP 89); in a second individual the facets on the atlas (SGO VP 231) are contiguous on the right side.

In M. tarijense (FMNH P14216) the facets of the atlas are contiguous on the left side, and nearly so on the right. The facets of the axis are contiguous on the left side, but widely separated on the right. The axis of $M$. tarijense is apparently stouter than in M. americanum and E. laurillardi, particularly dorsally. The facets for the axis are separate. The spinous process is elongated and higher, with its dorsal margin nearly horizontal.

The spinous process of CV7 in E. laurillardi bears a smooth articular surface dorsally for a supraspinous sesamoid. Cartelle (1992) confidently identified 4 sesamoids from Jacobina, apparently based on their articular facets (but see also discussion on the cyamellae, TIBIA: Sesamoid Bones). Such sesamoids have not been recovered or recognized in other collections. An articular surface on the spinous process is apparently absent in other sloths, and is probably an autapomorphy of E. laurillardi.

Dorsally, the spinous process of CV7 is compressed transversely in M. tarijense. The spinous process of CV6 is relatively short, slender, and tapers dorsally, as in $E$. laurillardi (mounted specimens in DMAS and USNM). It is more similar to the spinous processes of CV3-CV5, rather than of CV6 of $M$. americanum. The processes of CV3-CV5 of FMNH 14499 are higher and stouter than in M. americanum and M. tarijense. The spinous process of CV6 is approximately as in M. americanum, but that of the axis more as in M.

Possible distinction between E. laurillardi and M. americanum occurs in S4 and S5. The transverse processes of these vertebrae are apparently connected by an osseous lamina in E. laurillardi. Those of $M$. americanum remain distinct, as do those of M. cf. M. tarijense (see PELVIS; cf. PI. 91A and B).

The asymmetry of various of the thoracic vertebrae is discussed by Gazin (1957), Hoffstetter (1959b), McDonald (1977), and Stock, (1925). Hoffstetter (1959b) stated that this condition occurred only among the larger Pleistocene forms, but apparently occurs also in Nothrotheriops (Stock, 1925; McDonald, 1977). Asymmetry occurs because the right pedicle of the neural arch is anteroposteriorly narrower than the left, resulting in a larger right intervertebral foramen. Asymmetry is recorded among T2-T4 in mylodonts (Hoffstetter, 1959b, Stock, 1925), T3-T6 in megatheriines (Hoffstetter, 1959b; Gazin, 1957), and T5-T7 in Megalonyx (McDonald, 1977).

SCAPULA
The scapula is reasonably well-known from complete specimens only for Megatherium americanum and Eremotherium laurillardi. Complete scapulae are known from single individuals in M. tarijense (FMNH P14216) and the unnamed megatheriine from the Toro Negro Formation (MLP 68-III-141).

Cartelle (1992) briefly described the scapula of $E$. laurillardi, and noted some of the differences between it and that of $M$. americanum, described by Owen (1859). Additional characters and differences are recorded here.

The scapula is approximately triangular, with elongate vertebral and posterior margins. In E. laurillardi (e.g. ROM 22117, Pl. 60A,B) the vertebral margin is markedly and regularly convex. In M. americanum it usually tends to be relatively flattened, particularly in its middle length (e.g.. MNHNM 6, Pl. 1; MLP 2-207, Pl. 60C,D), but may curve (e.g.. ZMUC 212, PI. 61A). Anteriorly, however, the margin curves ventrally into the anterior angle. The angle is more prominent in M. americanum, and relatively anteroventral, so that it projects beyond the anterior margin. In $E$. laurillardi the angle is more acute and better-defined.

The anterior margin is more strongly concave in $M$. americanum, although the degree of concavity varies. It is strongly concave in the mount figured by Owen (1855: pl. 17)
and MNHNM 6, and less so in ZMUC 212. The anterior margin is apparently more elongate, and slopes further anteroventrally in $E$. laurillardi. This is reflected by the more acute angle between the anterior margin and scapular spine in E. laurillardi.

The central part of the vertebral margin of $M$. tarijense (FMNH P14216, Pl. 61B) is somewhat more curved than that in $M$. americanum, whereas that of MLP 68-III-14-1 (Pl. 61C, D) is more nearly rectilinear. The anterior angle M. tarijense is approximately as in M. americanum and E. laurillardi, but is less robust in MLP 68-III-14-1. The anterior margin in $M$. tarijense is similar to that in M. americanum; and that of MLP 68-III-14-1 resembles that in $E$. laurillardi. Distally the anterior margins in MLP 68-III-14-1 and $M$. tarijense resemble that in M. americanum.

The posterior angle is rounded in $E$. laurillardi. It is progressively more acute in M. americanum, M. tarijense, and MLP 68-III-14-1. It is coarsely rugose in all taxa, and probably served for the insertion of the posterior part of the rhomboideus musculature. A series of small, roughly pyramidal processes project medially along the length of the medial margin of the vertebral border and suggests that the rhomboideus muscle originated from much of the length of the vertebral border, as occurs in most mamals.

The gienoid fossa is similar in all taxa discussed. It is anteroposteriorly oval, approximately twice as long as
wide. The chord length of the fossa is approximately threefourths and chord width approximately two-thirds that of the head of the humerus. The anteromedial margin is usually slightly indented in E. laurillardi. In M. tarijense and MLP 68-III-14-1 the middle part of the lateral margin is indented.

The scapular spine arises dorsally near the vertebral border just anterior to the level of the posterior angle. Its origin varies in M. americanum and E. laurillardi, and presumably also in M. tarijense and MLP 68-III-14-1. The spine extends toward the articular angle parallel to the posterior margin, and ends in a prominent acromion. The acromion and coracoid process are joined by a bridge of bone, the acromial arch of Stock (1925), as in all sloths. Dorsally, towards the vertebral margin, the spine is low and relatively wide. It rises and narrows distally to a point approximately midway between the dorsal margin and the articular surface. The rest of the spine is strongly raised and thickened, with a broad and coarse lateral surface. The spine narrows just dorsal to the acromion in E. laurillardi. The supraspinous fossa is approximately twice as large as the infraspinous fossa in E. laurillardi (Cartelle, 1992). The supraspinous fossa is relatively larger compared to the infraspinous fossa in M. americanum, M. tarijense, and MLP 68-III-14-1.

The trapezius and omotransversarius muscles (= levator
scapulae ventralis, atlantoscapularis, etc., of others, see Jouffroy, 1971; omotrachelian of Windle and Parsons, 1899) commonly insert on the spine and the deltoid muscles originate from it. The trapezius almost certainly inserted on the spine in Eremotherium and Megatherium, but the presence and insertion of the omotransversarius is variabie in edentates (Windle and Parsons, 1899; Taylor, 1978). The deltoid muscles probably took origin from near the anterior half of the spine. A nearly horizontal ridge which demarcates the acromion from the spine may delineate the division of the deltoid into spinodeltoid and acromiodeltoid muscles in E. laurillaraí.

The presence of a secondary scapular spine in ground sloths was noted by various authors (e.g., Owen, 1859; Stock, 1925). However, it is unclear whether this structure is a proper secondary scapular spine with its concomitant posterior elaboration into a post-scapular fossa from the dorsal part of the posterior margin as occurs in Ursus and Ailuropoda (Davis, 1964), or Tamandua and Dasypus (Taylor, 1978). In the former two the post-scapular fossa increases the insertion area for the subscapularis muscle, which curves from the medial side of the scapula and inserts on the lateral surface of the fossa (Davis, 1964). In Tamandua and Dasypus the post-scapular fossa increases the insertion surface and lever arm of the teres major.

The posterior margin of the scapula in megatherines is
transversely expanded and nearly flat, particularly over its dorsal three-fourths, and faces posteroventrally and slightly laterally. The degree of lateral rotation of this surface, hence its exposure in lateral view, varies. Its medial and lateral borders are thickened into prominent edges, as in most mamals. The edge referred to as the secondary scapular spine is more prominent and faces laterally; the other faces posteromedially. The posterior scapular margin in ground sloths may thus be viewed as similar to that in most manmals, and the exaggerated appearance of the edges may reflect a normal allometric increase in size. The surface between them probably served for muscular attachment.

The lateral edge (or secondary spine) arises as a low ridge just distal to the ventral margin of the posterior angle. It rises gradually to its maximum height approximately midway between the posterior angle and glenoid surface, and forms a prominent, elongate, and coarsely rugose tuberosity approximately 120 man long in $E$. laurillardi. The tuberosity may occur more dorsally in some specimens of E. laurillardi and M. americanum. It is apparently less prominent in MLP 68-III-14-1. The posterior border continues distally from the spine and is relatively narrow. It is rugose, but considerably less so than the tuberosity. The tuberosity probably represents the origin of the long head of the triceps muscle. Probably this
origin also extended onto the dorsal part of the lateral spine, and may have occupied some of the surface between the two spines. The teres minor muscle probably arose more distally from the posterior margin of the scapula.

The medial spine represents the morphological posterior margin. It arises from the posterior angle and lies approximately parallel to the lateral spine in posterior view. The two are separated by a slightly low and transversely convex tract of bone some $50-60 \mathrm{~mm}$ wide. The spines diverge slightly as they extend toward the glenoid fossa. The medial spine forms the dorsal part of the posterior margin of the scapula. It is narrower and less rugose than the lateral spine, and ends abruptly as a distinct structure approximately opposite the tuberosity of the lateral spine. The medial spine and adjacent parts of the posterior angle probably served largely for the origin of the teres major muscle.

The surface of the scapula distal to the medial spine rolls smoothly and gently into the subscapular fossa. The contour of this region suggests that a slip of the subscapularis muscle passed over it to insert on the posterolateral surface of the scapula. As noted above, the posterior margin is continued toward the glenoid fossa by the lateral spine.

The medial surface of the scapula served largely for the origin of the subscapularis. Its posterior three-
fourths are deeply concave and rugose and, as Owen (1859) described for Megatherium, is subdivided into shallow depressions by intermuscular ridges. The serratus ventralis (=serratus ventralis + levator angulae scapulae of Stein [1981] in Didelphidae; + levator scapulae of Davis [1964] in Ursidae; serratus magnus and levator scapulae of Taylor [1978] in Didelphidae and Myrmecophagidae) also originates from the medial surface of the scapula but its origin in ground sloths cannot be confidently determined. In the xenarthran anteaters (Myrmecophagidae) the serratus ventralis and levator scapulae appear to have separate origins. The latter, subdivided into anterior and posterior parts, originates from the medial surface adjacent and posterior to the cranial angle. In megatheriines this area is rougher than the surrounding bone and bears small tuberosities, and possibly represents a distinct origin for the levator scapulae. All or part of the serratus ventralis commonly originates from near the caudal angle in other mammals and may arise from the length of the vertebral border in some. It is reasonable to suppose that it originated at least partly from the posterior angle and adjacent parts of the vertebral and caudal margins in megatheriines.

A large, semicircular, and rugose tuberosity lies distal and adjacent to the anterior half of the lateral margin of the glenoid fossa. A second, smaller, and
approximately circular tuberosity lies slightly anterior to the larger medial tuberosity on the medial surface of the scapula. The position of the medial tuberosity lies almost directly dorsal to the bicipital groove of the humerus, when articulated with the scapula, suggesting that the tuberosity probably served for insertion of the tendon of the biceps.

## CLAVICLE

The clavicle in megatheriines (Pls. 62, 63) follows the general pattern of that of other ground sloths, and has diverged little from the general mamalian pattern. It is variably sigmoid, compressed dorsoventrally, and expanded at its extremities. There is a smooth facet for articulation with the acromial arch of the scapula, as occurs in some ground sloths (e.g., Glossotherium, Stock, 1925: pl. 31, fig. 2; Thinobađistes, Webb, 1989: fig. 11).

The clavicle of Megatherium americanum was properly described and figured by Owen (1855: pl. 26, fig. 7; 1859: pl. 20, fig. 1). The sternal, or medial, end points anteriorly and is more expanded than the posteriorly deflected acromial or lateral end (PI. 63A, B). The ventral surface of the shaft is generally smoother than the dorsal. The dorsal surface bears an obliquely oriented and coarsely rugose ridge near the midpoint of the shaft. The sternal end of this ridge intersects the posterior margin. Owen's figures are somewhat misleading as they apparently depict a groove instead of a ridge. The extremities are usually rounded or condyioid in dorsal view. The articular surfaces are generally somewhat truncated, and coarsely rugose.

The degree of variation in form of the clavicle is poorly known for M. americanum. In MLP 2-207 (PI. 63C) the sternal end extends further anteriorly, is thus less
condyloid, and is relatively larger than the acromial end. In FMNH P13694 (P1. 63D) the sternal end is approximately as in MLP 2-207, though less elongated, but the acromial articular surface is truncated, rather than condyloid, and the acromial half of the shaft narrows.

This spectrum of variation reflects that observed in Eremotherium laurillardi. Its clavicle has been figured by various authors (e.g., Schaub, 1935; Hoffstetter, 1948; Spillmann, 1948; Paula Couto, 1978; Ray, 1979). Cartelle (1992) alluded to the wide range of variation observed in the sample from Toca das Onças.

This clavicle is easily distinguished from that of $M$. americanum by the truncated and nearly flattened articular ends. The sternal end is less prominently deflected and extended anteriorly but it is strongly compressed. The acromial end is generally condyloid and mediolaterally narrow, but may be prominent. An eminence may lie on the posterior surface just medial to the acromial end (UCV 257). The acromial half may be relatively gracile or expanded (MB 236). A variably rugose ridge similar to that in clavicles of $M$. americanum lies on the dorsal surface. In $E$. laurillardi, however, the ridge is more prominent anteriorly, and forms a projection on the anterior margin near or slightly sternal to the midpoint of the shaft.

Ray (1979) speculated that degree of robustness might represent a taxonomic character, based on differences
between clavicles from Georgia (USA) and Panama. However, this conjecture is improbable, as a series of clavicles from Daytona Beach, Florida (P1. 62) demonstrate a variation in robustness and size in $E$. laurillardi that encompasses both degrees considered by Ray.

The clavicle of E. laurillardi varies considerably in length, ranging from 299 mm to 447 mm (MNRJ $3862-\mathrm{V}$ and UCV 257, respectively). Similar variation probably exists in M. americanum, but fewer clavicles are known. Minimum and maximum lengths are 360 mm to 420 mm (FMNH P13964 and ZMUC 212: Kraglievich, 1925a:473, respectively).

The clavicle of M. nazarrei, MACN 7127 (P1. 63E; assigned by Kraglievich, 1925a to Paramegatherium, see SYSTEMATIC REVIEW OF THE MEGATHERIINAE) is sigmoid, with rounded acromial and sternal surfaces, although Kraglievich (1925a) noted that the sternal surface had somewhat deteriorated, and gave the length as 430 mm . Apparently both surfaces are less strongly deflected than in $E$. laurillardi and $M$. americanum. The sternal third of the shaft is broad anteroposteriorly, but becomes gracile laterally toward the acromion (Kraglievich, 1925a). A distinctive feature is that the posterior surface, lateral to the projection of the ridge, lies relatively medially. The posterior surface lateral to the projection is nearly rectilinear and has an abrupt contact with the lateral part of the posterior surface. This produces the appearance of
an elongated acromial and short, stout sternal ends. It is unclear whether this is an important feature of this species or due to individual variation. However, I believe that it is significant due to similarity to the clavicle of $M$. tarijense.

The clavicle of M. tarijense (Pl. 63F) has similar proportion to that of M. nazarrei, though it is more gracile. It is nearly as long ( 415 mm ) as that of $M$. nazarrei and the longer clavicles of E. laurillardi, which is surprising because $M$. tarijense is a considerably smaller animal. The acromial surface is less prominent, and the sternal surface is truncated and is not deflected strongly anteriorly; it thus resembles that in E. laurillardi.

FMNH P13695 (Pl. 63G) includes a right clavicle that lacks its acromial end, and in which the sternal end is deflected markedly anteriorly. Otherwise it closely resembles that of M. tarijense. Probably FMNH P13695 belongs to this species, and the deflection of the sternal end probably reflects individual variation and, possibly, some postmortem deformation.

The clavicle of the unnamed megatheriine from the Toro Negro Formation, MLP 68-III-14-1 (PL. 63H), resembles that of M. americanum in form of the shaft and deflection of the sternal surface, but is considerably shorter ( 226 mm ). The acromial surface is obliquely truncated.

The humerus of megatheriines is simpler, more gracile, and elongated than that of most other ground sloths. It bears fewer and less prominent ridges and crests for muscular attachment than the humerus of, for instance, mylodontids and planopsines. In particular, the prominent and elevated deltoid and pectoral crests in the latter are considerably reduced in some later megatheriines.

The humeral diaphysis is flattened anteroposteriorly, particularly distally, as opposed to the somewhat cylindrical diaphysis of most other ground sloths. Its posterior surface is nearly flat and its anterior raised centrally, so that a cross-section through the middle of the diaphysis is approximately triangular. The distal third of the humerus is laterally expanded and anteroposteriorly compressed, as in most ground sloths, to form large and nearly flat supinator and pronator plates, which support large and elongated extensor and flexor ridges, respectively. The entepicondylar foramen is absent in megatheriines.

As the humeri of Megatherium americanum and Eremotherium laurillardi have been described by Owen (1859) and Hoffstetter (1949, 1952), respectively, detailed descriptions are omitted here. The elements of the front Iimb are longer in E. Iaurillardi than in M. americanum, in
contrast to the generally larger size of the skull and mandible in the latter.

The humerus (Tab. 3; App. 4C) of E. laurillardi (Pls. 64-66B), ranging from 878 mm to 734 mm (MCL 8631 and FMNH P27081, respectively) in length, is significantly longer ( $\mathrm{t}=5.50, \mathrm{df}=24, \mathrm{p}<0.0001$ ) than that of $M$. americanum ( Pl . 66C, D), which varies between 787 mm and 626 mm (MACN 5002 and ZMOC 212). The length of the humerus of M. tarijense (FMNH P14216; Pl. 67A, B) is 527 mm ; of M. sundti 531 mm (P1. 67B) ; of M. nazarrei 800 mm (P1. 67C); and of Megatheriops rectidens 482 and 467 mm (MACN 2818 right and left, respectively; P1. 68A, B).

The caput is separated from the tuberosities by a distinct though short neck. The tuberosities lie further distally and are generally less prominent than in most ground sloths, particularly the greater tuberosity, which is also positioned somewhat more medially (cf. Hapalops, Scott, 1904: pl. 41; Planops, Hoffstetter, 1961: fig. 6; Pseudoprepotherium, Hirschfeld, 1985: fig. 7; scelidotheres, McDonald, 1987: fig. 30; Nothrotheriops and Glossotherium, Stock, 1925: pls. 8 and 32, respectively; and Thinobadistes, Webb, 1989: fig. 12). In E. laurillardi the greater tuberosity consists of a large, transversely elongated, anteroproximally-facing protuberance, and a smaller, nearly oval, and more lateral protuberance. These probably served for the insertions of the supraspinatus and infraspinatus

TABLE 3. Standard Statistics (mm) for the Humeri of Megatheriinae. LENGTH measured as the longest distance between the head and most distal articular surface, parallel to the long axis of the disphysis; Distal Width (DSWIDTH) as the distance between the pronator and supinator plates.

Eremotherium laurillardi

| Variable | M | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 14 | 730 | 870 | 780 | 39.0 |
| DSWIDTH | 14 | 250 | 400 | 330 | 34.0 |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 12 | 590 | 780 | 680 | 50.0 |
| DSWIDTH | 13 | 260 | 360 | 310 | 27.0 |

muscles, respectively. The greater tuberosity projects further laterally in E. laurillardi than in M. americanum, as the protuberances are subequal in the latter (Owen, 1859). The greater tuberosity in Eremotherim n. sp. is similar to that of $E$. laurillardi, but its dorsal margin is concave, so that the neck is more defined. The tuberosities of $M$. tarijense and M. nazarrei resemble those of $M$. americanum.

Owen (1859) described the pectoral ridge as arising from the lesser tubercle and ending in a tuberosity on the proximomedial margin of the humerus. This structure is usually designated as the ridge (or crest) of the lesser tubercle (e.g., Evans, 1993). The tuberosity commonly serves for the insertion of the teres major and latissimus dorsi muscles, when the latter shares an insertion with the teres. The relative arrangements of the latissimus and teres in Eremotherium and Megatherium are at present unknown but it is probable that at least the teres major inserted on the tuberosity.

Hoffstetter (1949, 1952) stated that the medial margin of the humerus is more arched in E. laurillardi than in M. americanum. This description was probably based on three observations: the less abrupt junction of the lesser tuberosity with the diaphysis, a more laterally projecting pronator plate (as is also usual in E. laurillardi), and the relatively weak development of the insertion surface for the
teres major and latissimus dorsi in EPN V151, which is a young, probably subadult individual. However, the size of the insertion is variable, as demonstrated by ROM 22101 (Pl. 64) and ROM 19756 (Pl. 65A, B), both from Daytona Beach, and is particularly well-developed in FMNH P27080. The other features are generally true of $E$. laurillardi, when compared to M. americanum, although variation exists here as well. The boundary between the lesser tuberosity and diaphysis is nearly as abrupt in FMNH P27080 as in M. americanum (cf. Pl. 66A, B and C, D). The proximal part of the pronator plate projects further laterally in $E$. laurillardi. These features contribute to a less parallel diaphysis in $E$. laurillardi.
E. laurillardi and M. americanum do not differ significantly ( $t=1.28, \mathrm{df}=25, \mathrm{p}=0.214$ ) in distal width (measured across the pronator and supinator plates perpendicularly to the long axis of the shaft). This, in combination with the significantly longer humerus of $E$. laurillardi, impart a relatively slender appearance to the latter. The humerus of Eremotherium n. sp. is similar, but its diaphysis is more slender, such that it is a more elongated and relatively gracile element. The medial and lateral margins of the diaphysis are more nearly parallel, and particularly so in M. nazarrei (P1. 67C) and M. tarijense (P1. 67D), which possess relatively stocky humeri, thus resembling that of M. americanum. This
parallel appearance is partly due to a generally weaker development of the middle part of the lateral surface of the humerus, just proximal to the notch (see below). The oval insertional surface usually lies just proximal to the middle of the length of medial surface of the humerus in $E$. laurillardi, M. americanum, and M. nazarrei. It lies near the middle of the length in $M$. tarijense.

The function and homology of the ridges on the anterior and lateral surfaces of the humerus are unclear with respect to those in other ground sloths. The typical condition in most megatheriines is that described by Owen (1859) and Hoffstetter (1949, 1952). Two ridges lie on the anterior surface. These arise proximally a short distance distal to the head, converge distally, and meet in a prominent process or tuberosity, approximately at the distal third of the humeral length. The prominence and proximal origins of the ridges vary among conspecific individuals, perhaps due to age and sexual differences. In some they are barely perceptible, and the lateral and medial margins of the raised region are often smooth, but may be rugose.

The medial ridge usually begins more distally, and its weak origin may be traced to near the medial margin of the greater tuberosity. The lateral ridge arises from near the lateral surface of the greater tuberosity. A short and prominent scarline lies along the proximal part of the lateral ridge in some specimens of E. laurillardi (e.g.,

FMNH P27080; Pl. 66A). The medial and lateral ridges were identified as the inner and outer deltoid ridges by owen (1859) for the insertion of the deltoid musculature.

Hoffstetter's (1949, 1952) descriptions suggest that he considered the positions and functions of these ridges as different from those described by Owen. Hoffstetter (1949) described a prominent and rugose external deltoid crest, for insertion of the deltoid muscles, near the middle of the lateral margin of the humerus. Later, Hoffstetter (1952) designated this as the deltoid crest. It is clear that this crest is not Owen's (1859) outer deltoid ridge, because Hoffstetter (1952) stated that the crest was on the lateral margin of the humerus and continued proximally on to the posterior surface of the humerus, and that Schaub (1935) had compared the crest in $E$. "rusconii" to the femoral third trochanter of Equus.

The deltoid crest continues proximally and medially on the posterior surface of the humerus, and ends near the middle of the posterior margin of the humeral head.

Hoffstetter $(1949,1952)$ stated that this proximal portion served for the insertion of a powerful external anconeus (= anconeus, of Jouffroy, 1971:788) muscle. As far as I can ascertain, however, the anconeus usually arises from the distal part of the humerus in mamals (although its proximal part may sometimes fuse with the distal part of the medial head of the triceps) to insert on the proximal part of the
antebrachium. A large, approximately triangular, rugose, and shallowly concave region lies posterolaterally on the humerus between the proximal part of the crest and lateral margin of the humerus. The lateral head of the triceps probably arose largely from this region, and the teres minor may have inserted proximally. The morphology in $M$. americanum is similar, except that the crest is less rugose and prominent, particularly along the middle of the lateral surface. Hoffstetter $(1949,1952)$ described the distal part of the crest, on the middle of the lateral surface, in $M$. americanum as longer but less prominent, and as more diffuse in M. nazarrei.

Hoffstetter (1949) designated the crest lying approximately medially on the anterior surface of the humerus as the internal deltoid crest (i.e., = Owen's inner and outer deltoid ridges) in E. laurillardi, but as the pectoral crest in 1952. Hoffstetter (1949, 1952) stated that it was weakly developed, as in M. americanum. Hoffstetter's designations suggest that he considered the pectoral musculature to insert approximately centrally on the anterior surface of the humerus (i.e., largely on Owen's inner and outer deltoid ridges), and the deltoid along the middle of the lateral surface of the humerus.

Owen's (1859) interpretation of the insertion for the pectoral musculature is probably incorrect and is discussed above. Cartelle (1992) apparently followed Hoffstetter's
designations in stating that the degree of lateral projection of the deltoid crest varies in E. Iaurillardi. In most individuals of $E$. laurillardi the morphology of the anterior surface of the humerus is similar to that described and figured by Owen (1859). The medial portion is raised proximally. Distally this region becomes progressively higher and narrower. The distal, tapered end of the raised region often bears short, prominent, and proximodistally oriented scarlines. In some specimens (e.g., DMAS 1L, PI. 65C, D), however, a wide, coarsely rugose, and curved muscular attachment lies medially to the sagittal midine of the central third of the diaphysis.

While the morphology of the ridges on the anterior surface of the humerus is relatively straightforward, interpretation of muscular insertions and the homology of the ridges is problematic. There are at least two possibilities. One, the pectoral and deltoid musculature insert, respectively, on Owen's (1859) inner and outer deltoid ridges in M. americanum and E. laurillardi. This interpretation implies that a reduction in size of the crests has occurred in these megatheriines as compared to most other ground sloths. Two, following Hoffstetter (1952), the pectoral musculature inserted along the anterior surface of the humerus, and the deltoid along the middle of the lateral surface of the humerus. This interpretation implies that the crests, which converge distally in most
other ground sloths, have separated during evolution of the megatheriines.

These interpretations have different implications for the positions of other musculature associated with the upper brachium, particularly that for the brachialis. The brachialis usually lies in the musculospiral groove, and passes from the proximoposterior to distoanterior surfaces of the humerus through the notch separating the supinator plate and lateral surface of the humerus. Hoffstetter (1952:64) stated that the notch represented "un vestige de la gouttière de torsion, si marquée chez les Mylodontidés et Dasyodidés; cette reduction . . . indique certainement une diminution $d$ 'importance des faisceaux externes de muscle brachial antérieur*.

Various authors have designated the structure on the anterior surface of the humerus as the deltopectoral ridge (e.g., Stock, 1925, for other ground sloths; Davis, 1964, for Ailuropoda and Ursus; Taylor, 1978, for Dasypus). These ridges are present in other mamals and may parallel the convergence observed in ground sloths (e.g., Carnivora, Choloepus). The ridges may, however, arise close together near the medial margin of the greater tubercle and extend distally and parallel to each other as in Didelphis, in which they appear to form a single structure termed the deltopectoral ridge by Taylor (1978).

In most other sloths, except in living genera, the
anterior surface of the humerus bears a prominent and raised deltopectoral shelf, as in Pseudoprepotherium and Planops (Fig. 9A, B). Hirschfeld (1971) designated the medial crest as the insertion for the pectoralis, the distal part of the lateral crest for the deltoid, and the proximal part for the triceps. The short, medial crest lying distally at the junction of the pectoral and deltoid crests probably served for the brachioradialis or cephalohumeralis. The musculospiral groove, along which the brachialis passes from the proximoposterior surface of the humerus, lies along the posterior surface of the lateral part of the deltopectoral shelf. A similar arrangement for insertions probably applies to most other sloths with a raised deltopectoral plate.

In some scelidotheres, such as Catonyx tarijensis and C. cuvieri (McDonald, 1987: fig. 30), the deltoid crest is deflected strongly posteriorly, and projects laterally. A musculospiral groove is clearly identifiable, but lies largely on the posterior surface of the humerus. An arrangement of muscular insertions similar to that for Pseudoprepotherium is proposed by McDonald (1987). However, he (1987:114) stated that a deltopectoral shelf is present in the earliest species of Proscelidodon, P. gracillimus, but that in $P$. patrius and later scelidotheres "the crests converge, joining at the midline of the shaft to form a tapered distal edge and not a square shelf". This condition

## FIGURE 9.

A. and B. Anterior and posterior views, respectively, of the right humerus of Glossotherium harlani (modified from Stock, 1925: pl. 32); C. and D. Anterior and posterior views, respectively, of the right humerus of Planops martini (modified from Hoffstetter, 1961: fig. 6). Scale bar represents 100 mm . Abbreviations: dp - deltopectoral crest; ms - musculospiral groove.

seems to be closer to that present in megatheriines discussed to this point, in which the central part of the anterior surface of the humerus bears a raised region which tapers distally. In Proscelidodon, however, the central part of the lateral surface of the humerus apparently lacks scarring, and it is reasonable to suppose that the deltoid did not insert along this surface. The condition in $M$. americanum is somewhat similar in that the lateral surface of the humerus is not heavily scarred, and the lateral and medial margins of the raised region on the anterior surface of the humerus (i.e., Hoffstetter's pectoral crest) converge distally toward the midline of the anterior surface of the humerus.

The humerus of Eremotherium differs somewhat. There are well-defined and distally converging lateral and medial margins for the raised region on the anterior surface, in addition to a prominent, rugose, and laterally projecting crest along the middle of the lateral surface. The morphology of the lateral surface resembles the condition in Catonyx (see above). Further, it resembles the condition in Tamandua (Taylor, 1978) and, to a lesser degree, Myrmecophaga (Lessertisseur and Saban, 1967: fig. 527a), in which the laterally projecting part of the lateral surface of the humerus, the deltoid tubercle, serves largely for the insertion of the deltoid musculature, although the homologous surface in Eremotherium is less prominent.

These differences suggest a third possibility for the function of the crests in M. americanum and E. laurillardi that the insertions of the deltoid and pectoral musculatures lie in quite distinct positions: the pectorals and deltoids insert on Owen's inner and outer deltoid crests, respectively, in M. americanum; and the pectorals insert centrally on the anterior surface of the humerus, while the deltoids insert on the middle of the lateral surface of the humerus in E. laurillardi. However, this interpretation is unlikely, because the humeri of these megatheriines largely differ in that the middle part of the lateral surface is not as prominent in $M$. americanum. This probably reflects a reduction in the size of this region in this species, rather than a phylogenetic increase in E. laurillardi.

An analysis and comparison of the humeri of these megatheriines with those of various non-megatheriines, such as Glossotherium, Paramylodon, and Planops, is useful. In these latter forms the lateral, or deltoid, crest continues proximally and medially toward the posterolateral margin of the humeral head. A rugose, shallowly concave, and nearly triangular region lies between the proximal part of the crest and lateral surface of the humerus, essentially on the posterior surface of the greater tuberosity. This condition strongly resembles that described above for E. laurillardi. It would seem probable, on the basis on the non-megatheriine sloths, that the deltoid crest in megatheriines has been
deflected laterally and posteriorly to form both the middle part of the lateral surface of the humerus, and the proximal margin of the notch between the supinator plate and lateral surface of the humerus.

Despite this strong general resemblance, the humeri of various earlier megatheriines suggest that this is not the case. A deltopectoral shelf is present in Megatheriops rectidens (MACN 2818; Pl. 68A, B), an unidentified Pliocene megatheriine humerus (FMNH P14511: Pl. 68C), and the unnamed megatheriine from the Toro Negro Formation (MLP 68-III-14-1; Pl. 68D). It is similar to but not as prominent as the shelf in Planops, Glossotherium, and Pseudoprepotherium. An important distinction, however, is that the middle part of the lateral surface of the humerus already projects laterally in the megatheriines. The proximal margin of the notch, therefore, is not formed from the distolateral part of the deltopectoral shelf, as in non-megatheriine sloths, but by the lateral surface of the humerus. It is not clear whether the musculospiral groove passed proximally around the deltopectoral shelf or the lateral projection of the lateral surface of the humerus. The origin and position of the brachialis would differ depending on which of these courses it actually did take.

The form of the anterior surface of the humerus in these earlier megatheriines strongly suggests that the deltoid crest and lateral projection of the middle part of
the lateral surface of the humerus occurred together, and that the deltoid crest has thus undergone reduction in $M$. americanum and E. laurillardi; it lies on the anterior surface of the humerus and corresponds to Owen's (1859) outer deltoid ridge. The lateral projection of the lateral surface of the humerus may have served to extend distally the origin of the lateral head of the triceps, or proximally the origin of the extensor carpii radialis. Taylor (1978) described a delto-epicondylar ligament, between the distolateral margin of the deltoid tubercle and proximal end of the extensor ridge and closing the notch laterally, to increase the area of origin of the extensor carpii radialis. McDonald (1987) postulated the presence of a similar ligament for scelidotheres. Probably a ligament was present in at least those megatheriines that possess a welldeveloped notch. In some megatheriine specimens a small protuberance projects medially from the proximal margin of the extensor ridge, and probably represents the attachment of the ligament. It is also possible that the deltoid musculature may have had an expanded insertion that included part of the anterior surface of the lateral projection of the humerus. Further, the brachialis may have arisen from the distal part of the anterior surface of the projection, rather than from the posterior surface of the humerus. This conditions occurs in Tamandua (Taylor, 1978), where the middle part of the lateral surface of the humerus is similar
to, but larger than, that of Eremotherium.
The lateral projection of the lateral surface of the humerus is most prominent among megatheriines in $E$. laurillardi. It is less prominent and scarred in $M$. americanum, and homology of the muscular insertions is clear. This reduction in M. americanum lends a more parallel-sided outline to its humerus, and varies. The humerus of $M$. sundti (P1. 68D) resembles that of $M$. americanum. The conditions in M. tarijense (PI. 67A, B) and M. nazarrei ( Pl .67 C ) apparently are derived compared to that of $M$. americanum. In $M$. tarijense the anterior surface of the humerus is not as prominently developed proximally, and the crests are only weakly developed distally. An oblique crest, however, is clearly present along the course of the lateral (i.e., outer deltoid) crest. The middle of the lateral surface of the humerus is somewhat reduced as compared to that in M. americanum, and thus its humerus is more cylindrical and parallel-sided, and the notch is relatively small. The lateral surface in M. nazarrei is even further reduced, with little, if any, scarring present, and the notch is barely present. An apparently single, narrow, and elongated crest lies centrally on the anterior surface of the humerus. The diaphysis is nearly relatively narrower and nearly cylindrical and parallel-sided.

Distally the humerus is as described by Owen (1859) and is similar to that of Tamandua and Myrmecophaga. The
origins of the extensor muscles are not individually recognizable, but probably their distribution pattern followed the comon mamalian arrangement, i.e., extensor carpi radialis, digital extensors and extensor carpi ulnaris (see discussion under RADIUS). The supinator originates anteriorly from the lateral epicondyle adjacent to the capitulum in Tamandua (Taylor, 1978) and may have had a similar origin in the giant ground sloths.

The radius in Megatherinae is relatively elongated and gracile, and generally resembles that of Nothrotheriops and in Planopsinae. In mylodonts the radius is generally relatively short and stocky, deeply impressed by scars for muscular attachment, and widens distally more markedly than in megatheriines. Owen (1859) described the radius of Megatherium americanum, but reversed its anatomical surfaces. The anterior surface of the radius is usually considered that surface facing anteriorly when the antebrachium is fully pronated (i.e., with the palmar surface of the forepaw facing the earth). This orientation is followed here.

Hoffstetter (1952) briefly discussed most of the differences, reviewed here in detail, between $M$. americanum and Eremotherium laurillardi. The radius (Tab. 4; App.4D) of E. laurillardi (Pl. 69) varies in length between 822 mm and 637 mm (MCL 8645 and FMNH P26970, respectively) is significantly longer ( $t=4.14, \mathrm{df}=16.6, \mathrm{p}=0.0007$ ) than that of M. americanum (PI. 70A-C, F), which varies between 645 mm and 531 mm (MACN 10148 and FMNH P13665, respectively).

In articulation, with the corresponding proximal facets for the ulna and radius in nearly full contact, and with the humerus approximately vertical, the radius lies slightly dorsolateral to the ulna. When the antebrachium is extended

# TABLE 4. Standard Statistics (mm) for the Radii of Megatheriinae. LENGTH is measured as the greatest distance parallel to the long axis of the diaphysis; Distal width (DSWIDTH) as the greatest distal transverse distance; Minimum Shaft Constriction (MSCONST) as the minimum width of the diaphysis distal to the tuberosity (see text). 

Eremotherium laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| - LENGTH | 12 | 600 | 820 | 700 | 66.0 |
| DSWIDTH | 12 | 170 | 240 | 200 | 24.0 |
| MSCONST | 9 | 100 | 130 | 110 | 12.0 |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | ---: | ---: | ---: | ---: | ---: |
| LENGTH | 13 | 550 | 670 | 610 | 35.0 |
| DSWIDTH | 13 | 130 | 170 | 160 | 10.0 |
| MSCONST | 11 | 70 | 120 | 90 | 12.0 |

it is oriented so that its broader anterior and posterior surfaces face approximately laterally and medially, respectively, and its medial surface approximately anteriorly. This condition appears to be usual in ground sloths, but is approximately midway between full pronation and supination. McDonald (1987) termed the anatomically anterior and posterior surfaces in scelidotheres the lateral and medial surfaces, respectively.

Webb (1989) stated that the radius of Thinobadistes was capable of extensive rotation on the evidence of the greater extent of the radial facet on the ulna when contrasted to the ulnar facet on the radius. In megatheriines the chord of the radial notch of the ulna and articular circumference of the radius are more nearly equal, suggesting that less rotation of the antebrachium was possible. A small degree of added supination probably occurred through antebrachial flexion, during which the distal end of the ulna rotates slightly laterally.

The head of the radius is approximately circular in megatheriines, although it may have a greater mediolateral diameter. Its proximal surface is regularly concave and receives the humeral capitulum. The articular circumference, which articulates with the radial notch of the ulna, lies distal to the capitular facet. It is centred on the lateral margin of the radius, and extends onto the posterior and anterior surfaces, following the curve of the
head; it is relatively elongated anteroposteriorly.
The neck is constricted somewhat anteroposteriorly, but is generally mediolaterally subequal to the width of the head in M. americanum (eg., right radius in MLP 44-XII-281). The neck is better defined mediolateraliy in $E$. laurillardi, largely because of a more concave medial margin immediately distal to the head. The radial tuberosity, for the lesser insertion of the biceps, and possibly brachialis, is oval proximodistally, and lies along the posterolateral margin of the radius. The tuberosity lies more proximally in M. americanum than in E. laurillardi.

Distal to the tuberosity the diaphysis deflects medially, more abruptly in $M$. americanum than in $E$. laurillardi. Two features contribute to the abruptness in the former: the degree of deflection is greater, and the length through which the deflection occurs is shorter. The diaphysis resumes a more nearly proximodistal course distally. The confluence of these parts of the diaphysis occurs near the middle of the diaphyseal length in $E$. laurillardi, more proximally in M. americanum. The medial surface is strongly compressed anteroposteriorly into a ridge. The bone surface is rugose, and deflected slightly posteriorly. Probably the pronator teres originated from this region.

The lateral surface of the radius is regularly concave throughout its length in E. laurillardi (Pl. 69A, B). In M.
americanum the surface is "stepped" (Rl. 70A-C). Its proximal part, between the head and radial tuberosity is oriented nearly proximodistally; distally it deflects abruptly medially, and then resumes a nearly proximodistal course. The lateral surface bears, except proximally and distally, a series of variably scarred and rugose patches. These served largely for the attachment of the interosseous ligament between the radius and ulna.

A notable difference between the radii of $M$. americanum and E. laurillardi occurs in the distal half of the diaphysis. A general transverse expansion of the diaphysis occurs distal to the level of the tuberosity for the pronator teres, but a constriction occurs approximately midway between the tuberosity and distal articular surface. The expansion is gradual in E. laurillardi and the diaphysis constricts only slightly. The constriction is considerably and significantly more marked in M. americanum ( $\chi^{2}$ approximation=15.82, $d f=1, \mathrm{p}=0.0001$ ), so the medial and lateral surfaces of the radius appear to be nearly parallel in anterior or posterior views (see Fig. 10).

Distally the diaphysis expands in all directions to support the distal articular surface. Laterally the rough, shallow, and approximately trapezoidal ulnar notch receives the distal end of the ulna. The robust styloid process projects distally from the medial surface.

Three grooves, separated by two well-defined ridges or

FIGURE 10.
Bivariate plot (mm) of Distal width (dswidth) against Length for the radii of Megatherinae.

processes, are usually present on the anterodistal surface of the radius in megatheriines. The medial and central grooves are prominent and easily identified. The lateral groove forms a broad and very shallow depression. Owen (1859) reported that four grooves, separated by three ridges, were present in $M$. americanum. The additional ridge is the weakest and subdivides the lateral depression. This condition does occur in this species, as in BMNH 19953 i and MNHNM 6, but the ridge may apparently be absent, as in MLP 44-XII-28-1.

The medial groove is deep and oriented obliquely. It lies along the anteromedial surface medial to the styloid process for passage of the tendon of the abductor pollicis longus. The latter normally inserts on metacarpal $I$, and acts to abduct and extend digit 1, and to deflect the forepaw medially (see Evans, 1993; McDonald, 1987).

McDonald (1987) suggested that one would expect reduction in the size of the tendon, hence groove, in Scelidotherium, in which the ungual of manual digit 1 atrophies or is absent, as compared to Catonyx or Proscelidodon, which possess a large functional ungual. However, reduction of the groove does not occur in Scelidotherium. McDonald (1987), citing Vassal et al. (1962), noted that digit 1 atrophies in Bradypus tridactylus, but the radius bears a prominent groove for the tendon of the abductor pollicis longus, whose function is
altered to that of an adductor-supinator of the manus. McDonald inferred a similar alteration of function in Scelidotherium.

The radius of Choloepus didactylus bears a prominent groove for the abductor pollicis longus, which inserts on the lateral and volar surfaces of the trapezium. The latter is fused to metacarpal I, which in turn is bound ligamentously to metacarpal II, thus precluding independent movement of metacarpal $I$. The muscle acts as a carpal abductor (radial deviator), and may act as a flexor during extension of the manus (Mendel, 1981).

A prominent groove for the abductor pollicis longus is retained in megatheriines, regardless of the configuration of the medial elements of the manus. In most megatheriines, manual digit $I$ is represented only by a reduced metacarpal I, which is fused to the trapezium. In E. laurillardi digits 1 and 2 are represented by reduced metacarpal $I$ and metacarpal II, respectively, which are fused to the trapezium and trapezoid. Probably the abductor pollicis longus of these megatheriines acted approximately as in tree sloths, and as inferred by McDonald (1987) for Scelidotherium. Eremotherium n. sp. retains a complete pollex, and the abductor pollicis longus probably acted as a normal abductor and extensor of the manus.

The central groove is deep and oriented nearly anteroposteriorly, with the medial margin formed by the
styloid process. The distal margin of the groove forms a notch on the anterodistal margin of the radius. The groove usually serves for passage of the tendons of the extensor digitorum communis in mammals, which often subdivides into a lateral brevis portion to insert on metacarpal III, and a medial longus, to insert on metacarpal II. The subdivisions are present in Choloepus hoffmanni (Mendel, 1981; Windle and Parsons, 1899), and function principally to extend and radially deviate the manus (Mendel, 1981). Jouffroy (1971) indicated that the extensor carpi radialis is undivided in Bradypus, but Windle and Parsons (1899) state that it may be subdivided. Probably the muscle was subdivided in megatheriines.

The lateral, shallow depression usually serves for passage of the tendon of extensor digitorum communis (= extensor digitorum Iongus of Mendel, 1981), which is commonly composed of digital extensors 2-5 in mammals bearing these digits (Evans, 1993). The tendons of other extensor muscles of the manus may cross the lateral depression, but their course cannot be determined confidently. As mentioned above, the radius of some specimens of $M$. americanum bears a ridge weak ridge that separates the shallow lateral depression into medial and lateral portions. The medial depression probably lodged the tendon of the extensor digitorum communis, and the lateral possibly the tendon of the extensor digitorum lateralis.

The distal surface of the radius bears a large, articular surface, transversely and anteroposteriorly concave, and narrower medially (Pl. 69D), which receives the scaphoid medially and the lunar laterally. A weak ridge may partially separate the facets for these carpals. The distal surface is approximately trapezoidal, with its base lateral. In E. Iaurillardi the medial part of the distal surface is comonly, but not always, narrower anteroposteriorly than in M. americanum. The anteromedial margin of the articular surface bears a narrow notch, which is often better defined in E. laurillardi, but is not reliably diagnostic. In some specimens of M. americanum the notch is replaced by an oval, shallow depression in a similar position as the notch, but entirely within the articular surface.

The general morphology of the radius of other megatheriines is usually some combination of the characteristics of $M$. americanum and E. laurillardi. Additionally the radius of other megatherine species possesses individual traits.

The radius of $M$. tarijense (FMNH P14216; Pl. 70D, E), 461 mm long, is considerably shorter than those of $M$. americanum and $E$. laurillardi. It resembles that of $E$. Iaurillardi in that the neck is well-defined, and the distal constriction is slight. It is distinguished from the radius of E. laurillardi and M. americanum by its smaller size, stockier appearance, less deflected diaphysis, relatively
greater distal width of the diaphysis, and the relatively large notch lateral to the styloid process. It resembles the radius of $M$. americanum in that the tuberosity for the pronator teres lies slightly proximal to the middle of the diaphyseal length, although less so than in M. americanum, and the lateral margin is straighter. The lateral margin differs from that of $M$. americanum in that it is not "stepped": the margin extends nearly linearly for nearly all of its length distal to the articular circumference.

The radius of Eremotherium n. sp. is similar to the radius of $E$. laurillardi. It is relatively more slender mediolaterally, thus appearing more elongated and gracile, but shorter. The proximal half of the medial surface deflects less strongly, and the tuberosity for the teres pronator is less prominent.

The radius of FMNH P13665 (Pl. 70F) is similar to that in $M$. americanum, except that the neck is more elongated and slender. Probably this feature is normally variable in $M$. americanum. In other respects FMNH P13665 is indistinguishable from that of $M$. americanum.

FMNE P14511 (Pl. 70G) bears all the features of the radius of $M$. americanum, and is nearly equal in length. However, it is considerably narrower mediolaterally, and is thus more slender and elongated. It is remarkably similar in form and proportions to the radius of Planops martini. However, the radius of the latter is smaller; the radial
tuberosity is more prominent and lies on the medial half of the posterior surface.

MNHNP 1907-15-49 is the right radius of a large megatheriine from Tarija. The radius is larger and more elongated than that of $M$. tarijense, but does not conform to that in M. americanum, and combines features present in the latter and E. laurillardi. The proximal half is slender, and its neck has a distinct, concave lateral surface immediately distal to the articular circumference. The diaphysis is deflected approximately as in E. laurillardi, and the tuberosity for the pronator teres lies approximately at the middle of the diaphyseal length. The distal half of the diaphysis is intermediate in conformation between those of M. americanum and E. Laurillardi. It widens less strongly than in the latter, and the constriction resembles that in $M$. americanum, but the lateral margin is concave, rather than nearly linear as in the latter. The radius is more likely to de confused with one from E. laurillardi. Probably the radius belongs to the same species represented by various skull elements from Tarija in MNHNP, which are clearly more similar to those of M. americanum, and clearly distinct from those of either M. tarijense and $E$. laurillardi.

The right radius EPN V150 is the holotype of $M$. elenense (Hoffstetter, 1952: fig. 9c). It represents an adult individual, as the epiphyses and diaphysis are solidly
fused (Hoffstetter, 1952). The radius, 520 mm long, is considerably smaller than those of $E$. laurillardi and $M$. americanum, and slightly longer than that of M. tarijense. EPN V150 is more slender and gracile than that of the other three species mentioned, particularly in the relationship between its proximal and distal halves, and the neck is thus better-defined. Radius EPN V150 generally resembles the form of the radii of $E$. laurillardi and M. tarijense, rather than of $M$. americanum, but the muscular attachments are less prominent. It widens distally more markedly than in $E$. laurillardi, and thus resembles more that of M. tarijense, but the proximal half is relatively more slender than in the latter. Further, the longitudinal axis of EPN V150 is convex anteriorly.

ULNA
The ulna in Megatheriinae is distinguished from that of other sloths by its transversely expanded proximal end, reduced olecranon process, and elongated diaphysis. The ulna is not known for all megatheriines. It is conservative in morphology with few diagnostic features, and wellrepresented only in Eremotherium laurillardi ( Pl . 71), in which length varies between 828 mm and 639 mm (MCL 8663 and MCL 8675, respectively). In Megatherium americanum (PI. 72) length varies between 693 mm and 574 mm (MACN 10148 and FMNF P13665, respectively); and in Eremotherium n. sp. between 650 mm and 563 mm (UF 121737 and UF 121738, respectively). Single lengths are available only for M. tarijense (FMNH P14216; RI. 73A, B), 483 mm ; FMNH P14511 (P1. 73C, D), 564 mm; M. medinae (SGO PV185), 535 mm .

A notable difference occurs in the prominence of the olecranon process. In M. americanum the olecranon is a relatively well-developed and distinct process, and projects posteroproximally beyond the articular surface (e.g., BMNH 19953i; Pl. 72A, B), whereas in E. laurillardi it ends at approximately the same level as the articular surface (Cartelle, 1992); also, the olecranon extends more medially in M. americanum (cf. Pls. 71A, E and 72A, D, E). These differences may be appreciated by comparing (Tab. 5; App. 4E) the two lengths recorded for ulnae: that measured
between the olecranon and distal ulnar surface (OLENGTH), and that between the proximal margin of the humeral trochlea (vide infra) and the distal ulnar surface (ALENGTH).

The length of the process is variable in $M$. americanum, being relatively short in MACN 10148 and long in MLP 2-79. The orientation of its projection also varies; it is more nearly proximally oriented in MACN 10148 and BMNH 19953i (Pl. 72A), and more posteriorly in MNHNM 6 (PI. 1) and FMNH P13665. The olecranon process in E. laurillardi (Pl. 71C, D) is considerably less distinct, and generally forms a small protuberance posterior to the articular surface. Variation in its length is considerably less noticeable than in M. americanum.

The functional ulnar length (i.e., ALENGTH) is significantly longer $\left(\chi^{2}\right.$ approximation=2.75, $d f=5.3$, $\mathrm{p}=0.038$ ) in E. laurillardi than in M. americanum. However, these species do not vary significantly ( $t=0.14, d f=11$, $\mathrm{p}=0.895$ ) in proximal depth (PDEPTH: Tab. 5; App. 4E; measured between the posterior margin of the olecranon process and the distal margin of the humeral trochlea), so that the ulna of $M$. americanum is relatively robust.

The diaphysis tapers distally and usually curves slightly posteriorly in lateral view. However, it may be nearly rectilinear in M. americanum or E. laurillardi. The diaphysis is generally mediolaterally compressed, but the long axis changes its orientation at the coronoid process.

TABLE 5. Standard Statistics (mm) for the Ulnae of Megatheriinae. Abbreviations: OLENGTH - Olecranon Length, measured between the proximal margin of olecranon process and distal ulnar surface; ALENGTH Articular (or Functional) Length, measured between the proximal margin of the humeral trochlea and distal ulnar surface; PRDEPTH - Proximal Depth, measured between the posterior margin of the olecranon process and the distal margin of the humeral trochlea.

Eremotherium laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :--- | :--- | :--- | :--- | :--- |
| OLENGTH | 6 | 639 | 828 | 726 | 7.38 |
| ALENGTH | 6 | 648 | 835 | 726 | 8.02 |
| PRDEPTH | 6 | 207 | 300 | 245 | 3.95 |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | ---: | ---: | ---: | ---: | ---: |
| - OLENGTH | 11 | 631 | 693 | 664 | 2.15 |
| ALENGTH | 8 | 614 | 660 | 634 | 1.69 |
| PRDEPTE | 7 | 213 | 264 | 247 | 1.70 |

In its proximal third the long axis is oriented obliquely, approximately anteromedially (Pl. 71A). The orientation rotates to a more nearly anteroposterior position in the distal half.

The ulna of Eremotherium n. sp. resembles that of $E$. laurillardi in possessing a reduced olecranon process. It is somewhat more gracile than in E. laurillardi, particularly at its proximal third, because the coronoid process is weak and arises more proximally.

The ulna of $M$. tarijense is relatively short and stout. The olecranon process is elongated compared to that of $E$. laurillardi, and projects posteroproximally, thus resembling that of $M$. americanum, but is more gracile than in the latter (cf. Pls. 71C, D, 72B, C, and 73B).

The ulna of FMNF P14511 is nearly as long as those of M. americanum and E. laurillardi, but its diaphysis, including the coronoid process, is considerably more gracile (cf. Pls. 71C, D, 72B, C, and 73C), as also occurs with its radius. The olecranon process projects only slightly proximal to the articular surface. It is considerably smaller transversely and anteroposteriorly. The weak anconeal process does not overhang the trochlear notch. However, the distal part of the notch, though incomplete, is apparently transversely wider than in M. americanum and E. laurillardi relative to both the olecranon and articular surface for the humeral capitulum (cf. PIs. 71E, 72E, and

73D).
The proximal articular surface is complex, but similar in all megatheriines. It is formed by three articular facets (cf. PI 71A): a large medial trochlear notch for the humeral trochlea; and two smaller lateral facets, one proximal for the humeral capitulum, and one distal for the radius. The coronoid process is large, arises well distal from the articular surface, and forms a buttress for the distal surface of the trochlear facet. This strongly curved facet is concave and oval, with long axis approximately anteroposterior, and circumscribes an arc of approximately $150^{\circ}$, with its distal end projecting anteriorly well beyond the diaphysis. Its proximal and distal parts face approximately anteriorly and proximally, respectively. The ridge of the trochlear notch is wide and low. It extends proximally from the distolateral margin of the coronoid process into the hook-like anconeal process, which overhangs the trochlear notch.

The approximately oval ulnar notch, for insertion of the biceps and possibly brachialis lies on the anterolateral surface of the coronoid process. It is usually smaller and more proximal than the radial tuberosity of the radius.

The transversely elongated to triangular radial notch occupies the distal part of the articular surface lateral to the ridge, and faces anteriorly and slightly distally. A rough, variably shaped depression usually separates the
radial from the trochlear notch. The proximal margin of the radial notch is contiguous with the larger, oval to rectangular facet that articulates with the posterior surface of the humeral capitulum when the antebrachium is extended. The capitular facet is transversely concave, and faces anteriorly and slightly proximally. Its lateral part is apparently narrower proximodistally in E. laurillardi than in other megatheriines. The lateral parts of these facets are supported by a semicircular ridge or flange that flares proximally and laterally from the diaphysis. This flange is usually separated from the ridge supporting the olecranon by a wide, deep, and proximodistally oriented groove, which is continuous proximally with the shallower sulcus on the proximal surface between the articular surface and olecranon process. The flange and groove are very narrow in FMNH P14511. The surface of the ulna between the flange and coronoid process forms a large, deep and nearly triangular depression, which accommodates the proximal third of the radius. A smaller, nearly oval depression lies on the medial surface of the coronoid process. Its distal half and the ulnar surface distal to it is scarred for muscular attachment.

The ulnar surface distal to the ulnar tuberosity is relatively smooth for $10-20 \mathrm{~mm}$. Distal to this the rugose interosseous crest, for the interosseous ligament, extends distally on the anterolateral surface nearly to the ulna's
distal end.
Distally the ulna expands into an anteroposteriorly elongated and rugose knob-like process. Its anterior surface articulates with the radius, but bears no smooth articular surfaces for the carpus, as occurs in other sloths. Rather, its rugose, striated surface suggests a ligamentous connection between carpus and ulna.

Ulnae of M. medinae from Tarapacá, Chile, include SGO PV44, 11, and 185. These are similar to the ulna in M. tarijense, but the olecranon does not project as strongly proximally. However, it apparently is better-developed proximomedially than in E. laurillardi.

The type of Eomegatherium cabrerai, MLP 2-206 (PI. 73E, F), includes the proximal end of a left ulna. The olecranon is distinct, but still projects only slightly beyond the articular surface. It is relatively narrower transversely than in other megatheriines, and so resembles the olecranon process of other ground sloths. However, it is anteroposteriorly deeper than in FMNH P14511. In the latter the olecranon process is relatively distinct, and projects only slightly beyond the articular surface. It is welldeveloped medially, and apparently relatively more prominent than in M. americanum. The medial half of its posterior surface bears a distinct and shallow notch. The anconeal process is prominent, and projects over the articular surface. The distal part of the trochlear notch is rounded
in proximal view and relatively large. It differs from that in other megatheriines in that its diaphysis is very gracile and elongated.

## MANUS

The manus of megatheriines is completely known only in Megatherium americanum, M. tarijense, Eremotherium n. sp. and E. laurillardi. That of E. laurillardi is relatively widest and most robust. Megatheriines follow the general trends, characteristic of most other ground sloths, of phalangeal reduction and co-ossification of the medial metacarpal (MC) and carpal elements. The manus of Eremotherium n. sp. bears five complete digits, each ending in an ungual phalanx (Hulbert et al., 1989). MC II - MC V are completely developed in Megatherium, with unguals borne on MC II - MC IV. Digit 1 is represented by a reduced MC I, fused to the trapezium. Digit five retains only proximal and distal phalanges (De Iuliis and Cartelle, 1993: fig. 1A; P1. 74). MC III - MC V are completely developed in E. laurillardi, with unguals borne on digits 3 and 4 iDe Iuliis and Cartelle, 1993: figs. 1B, 2).

Co-ossification is carried to an extreme in some megatheriines. The trapezium and MC I are fused in most ground sloths, except in the Santacrucian genera for which all the carpal and metacarpal elements are known, such as Hapalops and Schismotherium (Scott, 1904; Schulthess, 1920). The fused trapezium and MC I are referred to here as the 'Metacarpal-Carpal Complex', abbreviated MCC (De Iuliis and Cartelle, 1993). The MCC in Megatherium is thus composed,
but additional elements are involved in Eremotherium (De Iuliis and Cartelle, 1993).

Scaphoid
De Iuliis and Cartelle (1993) described the form and principal variations of the scaphoid in E. laurillardi (Pl. 75) and M. americanum. Further, they demonstrated that a scaphoid, rather than a scaphotrapezium (as supposed by Owen, 1859, Schulthess, 1920, and Scott, 1904), is present in megatheriines. The scaphoid of other megatheriine taxa is known from few specimens, and often only from a single specimen.

The scaphoid of $M$. tarijense is similar to those described by De Iuliis and Cartelle (1993), but requires modification. The principal facet for the lunar is divided by a narrow patch of rugose bone into approximately oval dorsal and smaller palmar articular surfaces. However, this condition is reported in E. laurillardi (Cartelle, 1992). The accessory lunar facets are small. The dorsal is barely perceptible, as its surface is rougher than usual for an articular surface. There is little apparent separation between it and the distodorsal part of the principal lunar facet, as reported by Owen (1859) for M. americanum.

ROM 11668 is similar except that the proximal lunar facet is relatively narrower compared to that on the scaphoids of other species. The MCC and trapezoid facets
are separate. The scaphoid figured by Hoffstetter (1952: fig. 11a) is indistinguishable from that of ROM 11668. In Eremotherium n. sp. the dorsal magnum facet is pedestalled, and thus there is greater separation between it (and the contiguous dorsal accessory lunar facet) and the distodorsal margin of the principal lunar facet. The dorsal magnum facet may be pedestalled in $E$. laurillardi and $M$. americanum (particularly in MNHNP, without catalogue number), but never to the degree as in Eremotherium n. sp. In dorsal view, the dorsal magnum facet and that for the MCC are stepped on two levels, whereas in other species they are nearly in the same plane. Further, these facets are contiguous along a distopalmarly elongate margin in other species, but such a shared margin is restricted in Eremotherium n. sp. and the facets may be separate. The exaggerated pedastalled condition of the dorsal magnum facet occurs in all specimens available, and is presumably the typical, or at least the most common, condition in Eremotheirum n. sp. Laterally the facet for articulation with the MCC is nearly circular, and this condition also occurs in E. laurillardi (e.g.. ROM 4022).

The scaphoid of FMNH P14530 is missing its dorsal surface and dorsal magnum facet, but preserves the following diagnostic features. The apex is prominent relative to that in Megatherium and Eremotherim n. sp. The radial articular surface is smaller, and the non-articular surface is
expanded palmarly, which reflects a more palmar position of the palmar magnum facet. The facet for the MCC is narrow and very elongated.

## Lunar

The lunar is similar in all species. The morphology and principal variations in E. laurillardi are described by Cartelle (1992), but parts of his descriptions are misleading. The lunar of E. laurillardi (PI. 76) differs from that of other megatheriines principally in being relatively wider transversely (Cartelle, 1992). This is reflected in the more medial projection of its proximomedial surface (i.e., that bearing the principal facet for the scaphoid), and less sharply inclined distal articular surfaces. The Iunar of FMNH P14530 is especially compressed transversely.

The proximal surface (PI. 76A) bears a large, proximally convex articular surface for the radius. It is nearly semicircular dorsopalmarly (PI. 76B, C), and less extensive mediolaterally (P1. 76B, C). The principal facet for the scaphoid (PI. 76D) lies on the proximal half of the medial surface of the lunar, is contiguous with the facet for the radius, and reflects the shape of the principal Iunar facet on the scaphoid. The distal surface (Pl. 76B) bears articular facets for the cuneiform, unciform, and magnum, in lateral to medial sequence. The surface has a
complex shape, and is concave dorsopalmarly (Pl. 76C, D). A prominent crest delineates the common margin of the facets for the unciform and magnum. This crest subdivides the articular surface into a lateral portion, which faces laterodistally and includes the facets for the cuneiform and unciform, and a medial portion, which faces distomedially and forms the facet for the magnum (Pl. 76B, E). The facets for the unciform and cuneiform lie in nearly the same plane. The palmar two-thirds of the facets for the magnum and unciform are strongly concave; their dorsal thirds, where the ridge is most prominent, recurve strongly to face dorsodistally (PI. 76C, D).

Cartelle (1992) describes a second common variation, in which two crests are present. The second crest, less prominent than the first, coincides with the common margin between the facets for the cuneiform and unciform. In this variant the facet for the unciform faces nearly distally, that for the cuneiform more nearly (or disto) laterally, and that for the magnum nearly medially. The facet for the unciform is more readily described as sigmoidal, convex dorsally and concave palmarly.

Cartelle (1992) stated that the central part of the distal articular surface articulated with MC III dorsally and the magnum palmarly. This is incorrect. The lunar does not articulate with MC III: the magnum articulates with the distomedially facing surface.

Two small, accessory facets for the scaphoid (Pl. 75D) may be present. They face medially and are contiguous with the medial margin of the facet for the magnum. The palmar accessory facet is crescentic, proximodistally narrow, and lies within the central third of the dorsopalmar length of the lunar. The dorsal accessory facet varies from oval, to triangular and rectangular, lies at the level of the dorsal third of the facet for the magnum, and may be contiguous proximally with the principal facet for the scaphoid. The non-articular surfaces of the lunar are rugose, irregular, and pierced by large foramina, except for the palmar surface, which is rugose, but free of large foramina.

Cuneiform
The cuneiform has been described by Cartelle (1992) and Owen (1859). Its morphology is conservative (PI. 77A-D), and not diagnostic, apart from size. In dorsal view (Pl. 77C) the cuneiform is approximately rectangular, with its long axis oriented mediolaterally. In approximately half of the E. laurillardi specimens a prominent, convex, oval to circular articular surface, variable in size, lies on the medial half of the proximal surface (Pl. 77A, C, D). A similar condition probably occurred in M. americanum, but the sample is too small to permit an estimate of the frequency of its occurrence. The facet is unknown in other species, but few cuneiforms are preserved. Cartelle (1992)
suggested reasonably that the facet articulated with a small sesamoid, as yet unrecovered or unrecognized, located within the ligaments between the ulna and cuneiform. Evidence suggests that the ulna and cuneiform did not articulate in megatheriines for which these elements are known (Hoffstetter, 1958).

The distal surface of the cuneiform is almost entirely covered by the articular facet for the unciform (Pl. 77B). The facet is approximately oval and elongated mediolaterally, with its lateral margin rounded and medial margin angular. Its surface undulates, so that the medial half faces somewhat palmarly, and the lateral half somewhat dorsally (P1. 77D). Distomedially the cuneiform is wedgeshaped and formed from the medial quarter of the unciform facet (Pl. 77C, D). The proximomedially facing part of the wedge is formed by the dorsopalmarly convex facet for the lunar.

The facet for the pisiform (Pl. 77A, D) lies proximodistally on the palmar surface, and is variable in size. Cartelle (1992) suggested that its size was perhaps reduced in M. americanum, relative to that in $E$. laurillardi. However, additional specimens of this species, and of other megatheriines, suggests that the facet for the pisiform reached proportions similar to that in $E$. laurillardi.

## Pisiform

The pisiform (Pl. 77E, F) lies palmarly to the lateral half of the cuneiform. It is compressed mediolaterally (PI.77E), and its long axis lies obliquely from proximolateral to distomedial. Its dorsal surface bears a central, nearly oval, and longitudinally concave facet for the cuneiform.

Metacarpal-Carpal Complex (MCC)
The MCC of E. laurillardi (De Iuiis and Cartelle, 1993:
fig. 6; Pl. 78) is described by Cartelle (1992) and De Iuliis and Cartelle (1993), who also described that for Megatherium, but attempted no diagnosis, because of small sample sizes. Adäitional specimens of M. americanum (P1. 79A, B) suggest that the nodular shape reported by De Iuliis and Cartelle (1993) is largely consistent, although its length varies. A nodular MCC is present in M. tarijense ( $n=1$; De Iuiis and Cartelle, 1993: fig. 5). The MCC in M. elenense $(n=1)$ appears more elongated, with long axis oriented distomedially. That in unidentified megatherine FMNH P14530 is relatively more elongated and expanded medially, suggesting less reduction of MC I than in Megatherium species. The long axis is oriented distomedially, rather than mediolaterally as reported by De Iuliis and Cartelle (1993).

The medial carpal and metacarpal elements in

Eremotherium n. sp. fall into two morphologically distinct categories, which are temporally separate. These are termed the Blancan and Irvingtonian variants. The Blancan variant is known from at least two nearly complete adult individuals; the Irvingtonian from a few remains, largely manual and pedal, of various individuals. The MCC of the Blancan variant includes the trapezoid, trapezium, and MC I. The MCC of the Irvingtonian variant includes the trapezium and MC I. However, in the latter the MCC is distinct from that of Megatherium (De Iuliis and Cartelle, 1993), where the same elements are involved. The Irvingtonian MCC possesses a relatively large and deep facet for the trapezoid, nearly as large as that for MC II, and includes a prominent proximopalmar extension. In other species, but excluding the Blancan variant and E. laurillardi, the facet for the trapezoid contributes a small proximal part to the lateral articular surface of the MCC. Further, the MCC bears distomedially a large, elliptical, and convex articular facet for digit 1.

The MCC of the Blancan variant possesses a facet for digit 1 , but its body is distinct. Its long axis arches gently distomedially, and its body is expanded medially. Three facets lie proximally. The largest, for articulation with the scaphoid, is a complex and irregularly shaped surface that faces largely proximally. The facet for the magnum lies laterally, and is contiguous proximally with
that for the scahoid. Its distal portion is narrowly elongated dorsopalmarly, and about twice the length of its proximal portion. Distally the facet is contiguous with the third facet, for MC II, which is approximately quadrangular and faces distolaterally.

## Trapezoid

The trapezoid is a free element in most megatherines, but fused to the MCC in the Blancan variant of Eremotherium n. sp., and E. laurillardi (De Iuliis and Cartelle, 1993). When free, as in M. americanum (Pls. 74A, 79C) and M. tarijense (Pl. 74B) it is a relatively small, proximodistally compressed element that is wider dorsally than palmarly. Its dorsal and palmar surfaces are nonarticular. The facet for the scaphoid is large, approximately trapezoidal, and occupies nearly all of the proximal surface. Its surface is gently convex transversely, and concave dorsopalmarly.

The facet for MC II, on the distal surface, is nearly as large, and approximately triangular, with apex palmar. Its medial margin is shorter and more strongly curved than the lateral. A broad, approximately dorsopalmarly oriented, keel occupies the medial third of the facet, and fits into the trough-like depression on the proximal surface of MC II (P1. 79E, F). The facet for the magnum is dorsopalmarly elongated, and lies on the medial surface. That for the

MCC, on the medial surface, is shorter.
The trapezoid follows this pattern in all species for which it is known, except for FMNF P14530 and the Irvingtonian variant of Eremotherium n. sp. The trapezoid of the former is relatively deeper, due to a more prominent keel. The facet for the MCC is considerably reduced, and lies more palmarly.

The trapezoid is unknown for the Irvingtonian variant of Eremotherium n. sp. However, the height of the facet for the trapezoid of the MCC is relatively deep, and nearly equal to the width of the facet for the trapezoid of MC II. The facet for the trapezoid of the magnum is relatively deeper, compared to the facet for MC II, than in other species. These features suggest that the trapezoid was uncompressed, at least medially, in the Irvingtonian variant.

## Magnum

The magnum (Pl. 80) has a complex shape. Most surfaces are completely or nearly articular. The magnum is elongated dorsopalmarly. Its palmar half is approximately twice the proximodistal height of the dorsal part (PI. 80C-E). Considerable variation exists in E. laurillardi in the size, shape and arrangements of the articular facets, particularly those for the scaphoid and lunar.

The dorsal surface (PI. 80E) is irregularly hexagonal
and non-articular. It is rugose, and a few relatively large foramina lie distally. The distal surface articulates with MC III (Pl. 80B). The palmar half is gently convex transversely. The dorsal half bears a prominent protuberance for the depression on the dorsoproximal surface of MC III. The protuberance is relatively large in FMNH P14530.

The facet for the unciform (Pl. 80C), semicircular palmarly and narrowly elongated dorsally, lies on the lateral surface. Its distodorsal margin is contiguous with the dorsolateral margin of the facet for MC III. The palmar parts of the facets are separated by rugose, non-articular bone. The surface of the unciform facet is sinuous, convex palmarly and concave dorsally.

In E. laurillardi the facet for the MCC lies distomedially (Pl. 80D), and may be conspicuous or reduced. Its proximal margin is contiguous with the dorsal facet for the scaphoid; its distal margin with that for MC III. The facet may be a single, distopalmarly elongated surface. Often it is subdivided by a ridge into short proximal and elongated distal parts.

The corresponding surface on the magnum of other species, all of which possess a complete MC II, is always subdivided into a proximal facet for the trapezoid, or for the MCC in the Blancan variant of Eremotherium n. sp., and a distal facet for MC II (De Iuliis and Cartelle, 1993: fig.

5B). In Eremotherium n. sp. ( $n=2$ ) the facet for the trapezoid is about half the length of the facet for MC II, and is deeper proximodistally. In M. tarijense ( $\mathrm{n}=1$ ) and $M$. elenese ( $n=1$ ) the facets are approximately equal in length and depth. In M. americanum ( $n=2$ ) the facets may be subequal in depth (BMNH 19953j), or the facet for MC II is longer and considerably deeper than that for the trapezoid (MLP 2-210). Only the dorsal half of the magnum is preserved for FMNH P14530; the facet for MC II is very deep relative to that of the trapezoid. It would be imprudent to suppose that the conditions described are diagnostic, because the samples are few. However, the great depth of the facet for MC II, the more prominent protuberance for articulation with MC III, and the relatively wide facet of MC II for the magnum in FMNF $P 14530$ suggest a combination of features which may be diagnostic.

The facets for the lunar and scaphoid are highly variable in E. laurillardi. All variations present in the magna of other species fall within the range established for E. laurillardi. The facet for the lunar (Pl. 80A, C, E, F) lies proximally, is generally elongated dorsopalmarly, and faces nearly proximally (e.g., ROM 37055) to nearly proximolaterally (eg., ROM 21893). Its surface is generally sinuous, corresponding to the form of the proximal margin of the facet for the unciform, with the dorsal half lying distal relative to the palmax half.

The magnum usually bears two articular surfaces for the scaphoid, of which the dorsal is usually larger (Pl. 80A, D, E, F). It varies in shape and may be deeply concave, nearly flat, or gently convex; and may face medioproximally or nearly medially. It is contiguous distomedially with the facet for the MCC (or trapezoid, in species in which it is a free element), proximally with the facet for the lunar (P1. 80A, D). The smaller, palmar facet (P1. 80A, D, F) for the scaphoid may be nearly flat, or gently concave or convex; nearly triangular, quadrangular, or oval; isolated or contiguous with the facet for the lunar. It may face nearly medially or palmomedially. The dorsal and palmar facets for the scaphoid are usually separated by a narrow patch of rough bone, but may exceptionally be connected by a smooth tract (e.g., ROM 37055). In some specimens the contact between the facets for the lunar and scaphoid forms an approximately median, proximally projecting crest. The crest is particularly prominent palmarly in ROM 21893 (Pl. 80E), in which the facets for the lunar and scaphoid meet in an acute angle.

## Unciform

The unciform (PI. 81) is a complex bone, and has only been inadequately described. It bears smooth articular surfaces on all but the dorsal, palmar, and a small part of the medial, surfaces. The non-articular regions are rugose,
and pitted with large foramina.
In $E$. laurillardi the dorsal surface of the unciform approaches the form of a parallelogram, but with its proximal part projecting laterally (PI. 81E). In other megatheriine species the lateral surface slopes less prominently, and the body is more rectangular.

A prominent, mound-like protuberance projects proximomedially from the proximomedial corner of the body (PI. 81A, E, F). The surface of the protuberance, as viewed dorsally, serves for articulation with the cuneiform laterally and the magnum medially; a dorsal view, however, shows these facets incompletely.

The shape of the facet for the cuneiform is best understood in proximal view (P1. 81A). It is transversely elongated. Its palmomedial part lies on the lateral half of the protuberance and faces proximolaterally; the rest of the facet undulates slightly, but largely faces proximally. There is some variation in shape, but the facet is apparently more elongated in E. laurillardi, and thus appears relatively narrow dorsopalmarly, than in other species.

The facet for the lunar may be observed in medial view (2I. 81D). Its central part is constricted. The smaller dorsal part lies on the medial surface of the body; the rest on the protuberance. The proximal margin of the facet for the magnum is contiguous with that for the lunar (PI. 81D).

It comprises a relatively narrow, elongated dorsal part, and a larger, approximately semicircular, palmar part; these lie dorsally and proximally, respectively, to the non-articular area on the medial surface of the body, and are usually connected by a very narrow articular isthmus.

The distal margin of the dorsal part of the facet for the magnum is contiguous with the facet for MC III (RI. 81B, D), which continues palmarly distal to the non-articular area of the medial surface. It is generally elongated and narrow, expanding dorsally, faces largely mediodistally (Pl. 81F), and occupies the medial part of the distal articular surface (P1. 81B). The facet for MC IV is larger, and lies on the lateral part of the distal articular surface (PI. 81E, F); in distal view, it appears to lie centrally (P1. 81B). Its palmar half is broad transversely, and shallowly concave; its narrower dorsal half is often nearly flat.

The facet for MC V (Rl. 81B, C, F) is approximately triangular, with apex proximolateral, and lies on the lateral surface of the body of the unciform. The facet is relatively larger in E. laurillardi than in other species, and approaches closely, and in some specimens is contiguous palmolaterally with, the facet for the cumeiform. In other species the angle between the facets for $M C$ IV and MC V is apparently more open, approaching $90^{\circ}$, but Cartelle (1992) reports that the facet faces nearly laterally in some specimens of $E$. laurillardi.

The diagnostic features for $E$. laurillardi are that the lateral part of the unciform is relatively compressed proximodistally, the body resembles a parallelogram, and the facet for MC V is relatively large. The unciform of FMNH P14530 differs from that of other megatheriines in several ways. The central part of the distodorsal margin is concave. The mediodistal corner of the body extends further distally relative to the articular surface of the facet for MC III, and overhangs the proximolateral part of MC III. The dorsal half of the facet for MC III is strongly concave dorsopalmarly. These conditions may be approached in other species, but never to the degree observed in FMNH P14530.

Metacarpal II (MC II)
MC II is normally developed in all megatheriines, except for E. laurillardi (De Iuliis and Cartelle, 1993: fig. 1A; Pls. 74; 79C-F). It is conservative in morphology, slightly shorter than MC III, but considerably less slender. Owen (1859) correctly described its general form; the following focuses on the arrangement and shape of the articular facets.

MC II articulates with four elements proximally: the MCC medially and the trapezoid proximally (Pl. 79C, E), the magnum proximolaterally, and MC III distolaterally (P1. 79D). The proximal third of the medial surface bears a depression, which may be approximately triangular or
quadrangular. The dorsal and, particularly, palmar margins are raised and rugose, and probably served for a ligamentous attachment to the MCC. The facet for the MCC occupies the proximal half (rather than lower half, as reported by Owen, 1859), and is distopalmarly elongated and concave. Its proximal margin is strongly concave distally, and contiguous with the facet for the trapezoid. A notch may lie along the distal margin, subdividing the facet into two lobes.

The proximal surface bears a broad facet medially for the trapezoid, and a narrow facet laterally for the magnum (Pl. 79F). The facet for the trapezoid is approximately triangular with a palmar apex. Its medial margin, which lies more distally than the lateral, is strongly concave medially; the lateral less so. A deep, trough-like depression, oriented approximately dorsopalmarly, occupies the medial third of the facet, and receives the keel of MC II. The facet for the magnum faces proximodistally, and is contiguous medially with the facet for the trapezoid, and laterally with that for MC III. Its shape varies, but is usually dorsopalmarly elongated and concave laterally. The facet faces nearly laterally in Eremotherium n. sp., but proximolaterally in other species.

The facet for MC III is generally elongated dorsopalmarly, and deeper dorsally. It faces approximately distolaterally, and is slightly concave laterally. A large, rugose protuberance lies on the middle third of the lateral
surface of MC II, for ligamentous attachment to MC III. Distally MC II expands dorsopalmarly (PI. 79C). Centrally the diaphysis is constricted dorsopalmarly. ic II of Eremotherium n. sp. is relatively robust and less constricted. The distal surface bears an expansive articular surface for the proximal phalanx. The facet is formed principally from a prominent, distopalmarly oriented, median keel. In Eremotherium n. sp. the keel is less regularly curved than in other species, and is formed from a somewhat flattened dorsal and a longer palmar portion. However, manipulation of MC II and the proximal phalanx suggests that free movement occurred at the metacarpalphalangeal joint.

The keel projects distally and somewhat medially, so that the long axis of digit 2 is deviated medially (Pl. 79D). A prominent shelf lies medial to the base of the keel. The plane of the less well-defined lateral shelf lies distal to that of the medial shelf.

The pattern described occurs in all second metacarpals recovered, except for those of FMNH P14530, and the Blancan variant of Eremotherium n. sp. MC II of the former bears the following diagnostic features. The depression of the facet for the trapezoid is considerably deeper. A deep, prominent depression lies proximolaterally, largely occupied by the facet for MC III, which is strongly concave proximodistally. The depression allows a strong
interlocking contact between MC II and MC III. The facet for the magnum extends laterodistally. It hangs over the facet for MC III, and contributes largely to the formation of the depression.

The proximal end of the Blancan variant of Eremotherium n. sp. bears only three articular facets. The facets for MC III and the magnum are similar to those of M. americanum. A single large facet for the MCC lies on its proximal and proximomedial surfaces. The facet is continuous and slopes distomedially. The ridge that separates the facets for the trapezoid and MCC in MC II of other megatheriines is absent in the Blancan variant.

## Metacarpal III (MC III)

Owen (1859) described MC III for M. americanum. That of E. laurillardi is shorter and more robust than that of $M$. americanum (Hoffstetter, 1952; cf. Pls. 74 and 83). MC III articulates proximally with four elements. The facet for MC IV lies laterally and faces distolaterally (P1. 83C). That for MC II, or the MCC in E. laurillardi, is smaller and faces medially (PI. 83D). The lateral and medial surfaces of MC III, distal to the smooth articular facets, are coarsely rugose, and suggest that the metacarpals were tightly bound by strong intercarpal ligaments.

The facet for the unciform (P1. 83A, C, E) lies proximal to the facet for MC IV; it is distopalmarly
elongated and faces lateroproximally. The largest facet is that for the magnum (RI. 83A, D, E), which is oblique, variably concave, and faces largely proximally.

In E. laurillardi a small, usually semicircular facet (21. 83D) is often present and contiguous with part of the distal margin of the facet for MC II. This semicircular facet articulates with a small, nodular element that is wedged between MC III and the MCC (P1. 82D). Cartelle (1992) supposed that the nodular element was possibly a vestigial first digit. However, it lies between MC III and that part of the facet of the MCC representing the articular surface of MC II, and thus more likely may represent a vestigial second digit. The facet for the vestigial digit on the MCC is shown in De Iuliis and Cartelle (1993: figs. $6 \mathrm{~A}, \mathrm{~B})$ and Plates $78 \mathrm{~B}, \mathrm{D}$ and 82 C .

The body of MC III is constricted transversely just distal to the facet for MC IV (PI. 83E). The degree of constriction, though variable, tends to be more pronounced in M. americanum. MC III of the smaller megatheriine species are apparently more elongated and gracile, and the constriction is prominent, particularly in FMNF P14530, whose proximal end is also relatively wider transversely.

The distal surface (PI. 83B) bears a prominent, mediolaterally compressed keel, which is notched centrally (PI. 83C, D). The keel deviates medially approximately $25^{\circ}$ from the long axis of MC III (P1. 83E). Narrow articular
shelves lie to either side (P1. 83B). The medial is wider, smooth, and contiguous with the adjacent margin of the keel; the lateral is somewhat rugose, and is separate from the lateral wall of the keel.

Metacarpai IV (MC IV)
MC IV is the largest bone of the manus. As with MC III, MC IV (Pl. 84) of E. laurillardi is stocky and more robust than that of other species. The distal end (PI. 84C, D) expands dorsopalmarly, more prominently in E.
laurillardi, M. americanum, and Eremotherium n. sp. than in M. tarijense and M. elenense. Owen's (1859) description of the proximal articular surfaces in $M$. americanum serves equally well for those in other megatheriines. Proximally MC IV articulates with three elements. The facet for MC V lies and faces laterally and is nearly flat (Pl. 84B, E). Its proximal margin is contiguous with that of the facet for the cuneiform, which faces proximally and lies on the lateral half of MC IV in proximal view (P1. 84A, E). The facet for MC III, contiguous with that for MC IV, is approximately semicircular and occupies the medial half of MC IV in proximal view (PI. 84A, C). It is concave and faces proximomedially (PI. 84E).

Minor and apparently consistent differences occur in the distal part of MC IV. In E. laurillardi the keel is relatively shorter, and the distal surface of MC IV is
relatively expanded dorsally, palmarly, and laterodorsally to the keel in $M$. americanum, M. tarijense, and M. elenense. The keel, strongly convex and rounded transversely, is gently concave dorsopalmarly (cf. Pl. 84B and C, D).

Two accessory, sesamoidal facets are present ventrally in E. laurillardi (Pl. 84B-E). The medial facet is contiguous with the palmar margin of the medial shelf; this facet is present in all megatheriines. The lateral is contiguous with the palmolateral margin of the keel, and faces largely laterodistally. One or both sesamoid bones may occasionally fuse with MC IV in E. laurillardi. Owen (1859) reported the presence of only the medial facet in $M$. americanum, which is apparently consistent in M. americanum. The palmolateral surface of MC IV suggests that a sesamoid was not fused to MC IV and, thus, that it was absent. A single facet also occurs in M. tarijense. Both facets are present in FMNH P14530.

Metacarpal V (MC V) and Digit 5 (D5) Phalanges MC V of E. laurillardi (PI. 85) was described by Cartelle (1992). It differs from that of other megatheriines in being relatively robust, and bearing a larger articular facet for the unciform. Proximally MC V articulates with the unciform and MC IV. The facet for MC IV occupies the medial half of MC $V$ in proximal view (PI. 85A) and faces nearly laterally (Pl. 85D, E). The facet for

MC V occupies the lateral half in proximal view (Pl. 85A) and faces nearly proximally (Pl. 85E).

The distal surface bears an articular facet, usually partially bilobate, for the proximal phalanx of D5 (Pl. 85B). Small and distopalmarly compressed proximal and distal phalanges usually represent the rudimentary D5. A single fused element only may be present (Cartelle, 1992).

Digit 1 (D1) Phalanges
Phalanges are absent in all megatheriines (save for Cartelle's, 1992, interpretation of a rudimentary phalanx in E. laurillardi), except Eremotherim n. sp. In this species the pollex is formed from proximal and distal, or ungual, phalanges, as is normal in mamals. The phalanges may be separate or fused. The unfused ungual is the smallest of the manus. The phalanges articulate via flattened, irregularly-shaped, palmarly notched facets. Manipulation suggests that little interphalangeal movement was possible.

Digit 2 Phalanx 1 (D2 P1)
Owen's (1859) description for D2 P1 of M. americanum is somewhat imprecise. P1 is approximately quadrangular, and proximodistally compressed, resembling D4 P1 (see below). The proximal surface bears a trough-shaped, dorsopalmarly elongated depression for the keel of MC II. It is shorter dorsopalmarly than the chord of the keel. Contra Owen
(1859), the depression is not subangular, but regularly concave dorsopalmarly to permit free movement between the P1 and MC II. A prominent, smooth, and medial articular shelf is contiguous with the medial margin of the depression; a small, smooth, and lateral articular shelf is present.

Distally a median depression lies between wider, medial and lateral condylar surfaces. These surfaces are angular rather than rounded, and consist of distodorsally and distopalmarly facing surfaces.

Digit 2 Phalanx 2 (D2 P2)
The middle phalanx (Cartelle and De Iuliis, 1995: fig. 1A; Pl. 74) is proximodistally elongated and dorsopalmarly deeper proximally than distally. The proximal surface reflects the angular condition of the condylar surfaces of the proximal phalanx. Lateral and medial articular surfaces bear depressions centrally; that of the lateral surface is deeper. The angular shape of the condylar and trochlear surfaces suggest that only severely restricted movement between P1 and P2 was possible.

The distal surface bears rounded, lateral and medial articular condyles that circumscribe an arc of nearly $180^{\circ}$, and are separated by a relatively shallow, median depression. Free extension and flexion was possible at the distal interphalngeal joint.

The ungual in megatheriines essentially follows that of M. americanum (De Iuliis and Cartelle, 1993: fig. 1A; Pl. 74A), as described by Owen (1859). The sheath is approximately circular in cross section, and the core is relatively wide, but not so much as that in the ungual of D4.

Other Phalanges
The remaining phalanges of the manus are described by Owen (1859) for M. americanum. Cartelle (1992) described and compared those of $E$. laurillardi. The phalanges are illustrated here, however, because they have not been adequately figured. Additional comments are made to expand the descriptions and to clarify the functional morphology of the manus.

Digit 3 (D3)
P1 and P2 of D3 (PI. 86) are fused in all megatheriines. This combined element is considerably more robust than the corresponding P1 and P2 of D2. However, its length is slightly less than that of P 2 of D 2 .

The proximal surface bears a prominent, median, and trough-shaped depression, elongated dorsopalmarly (P1. 86A, E, F). A short and high transverse ridge, articulating with the notch of the keel of MC III, separates the depression
into nearly equal dorsal and palmar halves. A prominent, dorsopalmarly elongated shelf lies medial to the depression. A small, smooth articular surface may lie laterally. In articulation the phalanx lies medially nearly $25^{\circ}$ to the long axis of MC III.

Cartelle (1992) described lateral and medial protuberances projecting palmarly from the proximopalmar surface of MC III, and suggested that they represent fusions of sesamoid bones. His hypothesis is supported by the occurrence of articular facets, in place of the protuberances, in some specimens. A facet also occurs in FMNH P14530. A deep notch lies between the protuberances, probably for the passage of the tendon of the flexor digitorum profundus.

The distal surface of the phalanx bears large, rounded, and nearly semicircular condyles, which circumscribe a chord of approximately $180^{\circ}$. The condyles are larger than those of D2, and are separated by a deep, well-defined, median depression. A shallow, prominent depression lies on the lateral and medial surfaces of the phalanx near the condyles' centre of curvature. The depressions probably served for attachment of the collateral ligaments of the distal interphalangeal joint.

The ungual phalanx (D3 P3; P1. 87A-D) is the largest ungual, and may be nearly as long as MC IV (Cartelle, 1992). The bony sheath is laterally compressed. The core is
elongated, curved, and laterally compressed. The proximal surface bears dorsopalmarly elongated and regularly concave medial and lateral grooves, separated by a prominent median crest, for articulation with the condyles of the proximal phalanx. Considerable extension and flexion of the ungual was possible.

Two large nutrient foramina lie a short distance distal to the proximal articular surface on the palmar surface of the ungual. A large and coarsely rugose region lies distal to the foramina, and probably served for insertion of the flexor tendons.

Digit 4 (D4)
D4 bears three phalanges (Pls. 87E-H, 88). PI (PI. 88A-E), particularly, and P2 (P1. 88F-J) are compressed proximodistally. The proximal surface of P1 (Pl. 88A, E) bears an elongated and broad depression. Its surface is regularly concave transversely, and gently convex dorsopalmarly. An elongated medial shelf is contiguous with the medial margin of the depression (PI. 88A, D, E). A small facet, probably for a sesamoid, is apparently associated with the palmar end of this shelf (PI. 88A, D, E). In articulation P1 deviated strongly medially, from the long axis of MC IV. Distally P1 bears a large and nearly quadrangular articular surface (Pl. 88B, E). It is nearly flat, but slightly convex dorsopalmarly.

The proximal surface of P2 (Pl. 88F, H, J) bears a corresponding, and slightly dorsopalmarly concave facet. Distally it bears broad medial and lateral condylar articular surfaces, separated by a very shallow median depression (Pl. 88G, I, J). The radius of curvature (Pl. 88H) is considerably larger than in D3, such that the condyles of D4 appear less prominent. The condylar surfaces are regularly rounded, and circumscribe arcs of approximately $110^{\circ}$. The distal interphalangeal joint allowed a wide, though less extensive than in D3, range of extension and flexion.

The ungual phalanx ( P 3 ; $\mathrm{Pl} .87 \mathrm{E}-\mathrm{H}$ ) resembles that of D3, but is smaller, and more asymmetrical. The claw core is deflected medially to the long axis of the phalanx, and the tuberosity for insertion of the digital flexors lies on the palmolateral surface of the sheath. The sheath and core of D3 P3 of E. laurillardi are laterally compressed. In M. americanum they tend to be dorsopalmarly compressed (Cartelle, 1992).

FUNCTIONAL MORPHOLOGY OF THE MANUS
A review of the morphology of the manus indicates that movement was largely restricted to the distal interphalangeal joints. Marginal movement was probably possible among the metacarpals, perhaps as a mechanism compensating for changes in stress. Movement between the metacarpal-phalangeal joints varied among digits. Flexion and extension of approximately $30^{\circ}$ probably occurred in D2 of most species; with possibly less in Eremotherium n. sp. Flexion and extension at this joint was not possible in D3 D5. The notched keel and ridge arrangement of MC III and PI precluded dorsopalmar movement as well. Some dorsopalmar motion may have occurred at the semicylindrical joint of D 4 . However, some mediolateral rotation occurred at the metacarpal-phalangeal joints of all digits, and allowed the digits to be neariy aligned with the long axes of the metacarpals. Manipulation suggests that mediolateral rotation at the proximal interphalangeal joints of MC II and MC IV contributed to alignment of the digits.

A considerable, and nearly equal, range of extension and flexion between the distal interphalangeal joints was possible in D2 and D3. Similar movement was possible in D4, although its range is more restricted.

Movement was severely restricted in the proximal interphalngeal joint of D2, and precluded by fusion of P1
and P2 in D3. Some dorsopalmar and mediolateral movement was possible in $D 4$, but the range of movement did not add significantly to the range of dorsopalmar movement of the ungual. Thus, P1 and P2 of D2 and D4 functioned essentially as a unit; in D3, the elements are fused into a unit. The configurations of the metacarpal-phalangeal and interphalangeal joints, with extension and flexion largely allowed only distally in D3 and D4, suggest that one use of the manus would be as a compound 'hook'. This conforms to hypotheses (see Coombs, 1983) that the manus of megatheriines may have functioned in reaching and drawing overhead branches towards the mouth or in digging for roots. The medial deviation of the digits and the mediolateral mobility at the interphalangeal joints may be explained in terms of the weight-bearing functions of the manus and the posture in megatheriines. The structure of the fore- and hindimbs of ground sloths departs radically from the usual graviportal adaptations of mammals such as elephants and rhinoceroses. These adaptations are probably due to a difference in posture and locomotion. Ground sloths were likely capable of assuming a bipedal posture for defense and feeding, and thus were not obligatory quadrupeds (Coombs, 1983; Hirschfeld, 1985; McDonald, 1987). They probably were, however, quadrupedal in locomotion (McDonald, 1987). This topic is discussed further in ICHNOFOSSILS OF MEGATHERIINAE.

As in many ground sloths (e.g.. Thinobadistes; Webb, 1989), the manus was twisted laterally, so that the anatomically dorsal surface faced nearly laterally. Weight was borne largely by the radius through the scaphoid and lunar. In megatheriines the weight-bearing axis then passed obliquely through the carpus, rather than distally as in most quadrupedal mammals, largely to MC V. In some ground sloths, such as Thinobadistes and Glossotherium, weight was probably borne on MC IV and MC V. This is suggested by a relatively more medial position of the facets for the scaphoid and lunar, and the presence of a rudimentary fourth digit. A distinctive feature in megatheriines is the absence of a synovial articular contact between the ulna and cuneiform, which suggests that increased medial deviation was possible. Mendel (1979) suggested that this adaptation was correlated with reach and pull behaviours in Choloepus and some primates.

As a result of the posture of the manus, the digits were thus oriented more nearly medially than distally in megatheriine sloths, a necessary adaptation given the great length of the claws. The mediolateral mobility at the interphalangeal joints is a further modification for medial deviation of the digits.

The shorter first digit of Eremotherium n. sp. apparently did not require medial interphalangeal deviation. When the phalanges are separate little appreciable movement
is possible; when fused, clearly, no movement was possible.

PELVIS
The os coxae (innominate bone, comprised of the ilium, ischium, pubis, and acetabular bones) of megatheriines are poorly known, and few complete specimens are preserved. Incomplete specimens are more readily available for study, but generally insufficient to provide proper understanding of intra- and interspecific variation. Many of the complete, or nearly complete, specimens are mounted on display and thus usually unavailable for detailed study. Further, the mounted pelvis of Eremotherium laurillardi at MNRJ is reconstructed based on that of Megatherium americanum (Cartelle, 1992). An isolated, nearly complete pelvis at MNRJ is from Argentina, but lacks locality information (C. Cartelle, pers. comm., 1991). The pelvis of Pyramiodontherium bergi, MIP 2-66, was unavailable for study, but Roth (1911) considered it as more gracile than that of $M$. americanum.

These general comments are based mainly on two specimens of E. laurillardi from Daytona Beach (Pls. 89, 90, 91A), one each of M. americanum (MACN 1000, a mounted specimen; P1. 90B) and M. cf. tarijense (MNBN BOL V A-585; P1. 918-D), a specimen from Tarija intermediate in some aspects between E. laurillardi and M. americanum, and resembling one or the other species in some features, see below), and descriptions given by Owen (1860) for $M$.
americanum (P1. 91E) and Cartelle (1992) for E. laurillardi. It should be noted that the pelvis described by Owen is improbably from Lujan, Buenos Aires Province, Argentina, as is most of the rest of the remains that be described. Lydekker (1887) indicated that the innominate bones at BMNH are from Uruguay.

The general morphology of the pelvis is similar to those of other large ground sloths, such as Glossotherium (see Stock, 1925: pls. 35-37), with the wing of the ilium flared laterally (Pls. 89-91). Cartelle (1992) stated that the principal differences between the pelves of M . americanum and E. laurillardi occur in the ilium, and described them as follows:

1) The dorsal border of the ilium is further dorsal relative to the sacral vertebrae in M. americanum.
2) The wing is more laterally oriented in $M$. americanum, and projects further laterally and less anteriorly.
3) The sacropelvic surface is more concave in $E$. Iaurillardi.
4) The ventral border is more concave in E. laurillardi, and the lateral thinner. (Cartelle's lateral border probably refers to the ventrolateral part of the iliac crest. Anatomically the iliac crest is the anterior border; a lateral or gluteal surface is usually recognized, but a lateral border is not.)

I agree with Cartelle's general impressions of the
distinctions between the pelves. However, it is unclear whether these are due completely to the modifications he described. For example, features 1 and 2 are perceived in lateral view, and in anterior view for the pelvis described by Owen (1855: pl. 22). M. cf. tarijense is approximately intermediate in these morphological characters. However, in anterior view the ilia are apparently not more dorsal in $M$. americanum, based on MACN 1000, the mounted specimen in Paris, MNHNP 1871-383, and M. cf. tarijense than in E. laurillardi. In dorsal view the projection of the ilia in E. laurillardi and M. cf. tarijense are similar. In fairness to Cartelle, it is difficult to discern what differences actually exist. Apparently, the ilium of $E$. laurillardi is relatively elongated, and the flaring of the wing begins further anteriorly. Possibly contributing to the differences are the greater thickness of the iliac crest and its more posterodorsal orientation in M. americanum. Apparently, the ventral border may be similarly concave based on the mounted specimens at MNHNP 1871-383 and MNHNM 6.

Cartelle (1992) stated that the ischium is laterally expanded in E. laurillardi. This may be observed in dorsal view, when the distal ends of the transverse processes of the posterior sacral vertebrae project to or slightly beyond the lateral margin of the ischium in Megatherium. Possibly this reflects a wider pelvic canal, rather than a thicker
ischium.
Further, Cartelle (1992) stated that the ilio-ischiadic foramen ( $=$ ischio-pubic foramen of Lessertisseur and Saban, 1967; sacro-ischiatic foramen of Stock, 1925) lies further anteriorly in E. laurillardi. However, the relative positions of this foramen are very similar. The plane of the opening is oriented more anteriorly in Megatherium, possibly because of the more prominentiy flared iliac wing. Cartelle (1992) cited differences in shape of the acetabular fossa, round in M. americanum, oval in E. Iaurillardi. It is oval in M. cf. tarijense. It is worth noting that the fossa varies from round to oval in Glossotherium harlani (Stock, 1925). Further, the acetabular notch for the round ligament varies considerably in size. Similar variation occurs in E. laurillardi. Apparently greater separation occurs between the ilio-ischiatic and obturator foramina, which reflects a thicker ischium in this region in E. laurillardi.

Cartelle (1992) considered that intraspecific variation in the angulation and projection of the pubic symphysis and projection of the ischium revealed sexual dimorphism in $E$. laurillardi. Although it is difficult to demonstrate dimorphism on such a small sample, the size of the pelvic canal, may support Cartelle's hypothesis. The DMAS (PI. 89) and ROM (PI. 90) pelves differ considerably in transverse diameter and shape of the canal. In DMAS the canal is
nearly oval. In ROM it comprises a small, nearly semicircular dorsal part, and a large, nearly semioval, ventral part; and the left and right pelvic surfaces of the ischium and pubis are further lateral. This morphology occurs in the pelvis described by Owen (1855: pl. 22). Also, the iliac wing projects more laterally and is relatively larger in DMAS than in ROM. In MNHN BOL V A-585 (P1. 91C) the pelvic canal is smaller relative to the iliac wing, which is also relatively wider transversely than in $E$. laurillardi. In M. americanum the relationship apparently resembles more that in E. laurillardi, based on MNENP 1871383.
E. laurillardi, Megatherium, and Pyramiodontherium bergi are apparently distinguished by the relationship between the width and anterior height of the pelvic canal. The width ranges from $67.2 \%$ to $61.7 \%$ of the height in $E$. laurillardi, $58.3 \%$ to $52.7 \%$ in $M$. americanum, and is $57.5 \%$ in M. cf. tarijense and $36 \%$ in P. bergi (width and height values for M. americanum and $P$. bergi are from Roth, 1911). However, the relationship between width and posterior height in E. laurillardi ( $80.6 \%$ to 71.9\%) and M. cf. tarijense (71.0\%) is less distinct. Posterior heights for $M$. americanum and $P$. bergi are unavailable.

FEMUR
The femora of megatheriines (Pls. 92-104) are large, flattened, and anteroposteriorly compressed, as in mylodonts. They are approximately rectangular in anterior view. The proximal and distal sections are nearly aligned in the parasagittal plane, so that the head is nearly vertically above the medial condyle, and the greater trochanter above the lateral condyle. In most mylodonts the long axis of the diaphysis slopes medially relative to the distal part of the femur (Stock, 1925: pl. 38, fig. 1a, for Glossotherium; McDonald, 1987: fig. 35a, for Scelidotherium; and Hirschfeld, 1985: fig. 16a, for Pseudoprepotherium).

The transverse plane of the femoral diaphysis is twisted; such rotation also occurs in mylodonts. Weob (1989) attributed this feature to the pedolaterally twisted pes of some sloths. However, the direction of rotation is not clearly understood. Webb $(1989: 487)$ stated that the medial condyle lies "posteriorly beyond the major planes of the femur shaft" in Thinobadistes, thus implying a posteromedial rotation of the diaphysis. McDonald (1987:142) stated that "anteriad torsion around the long axis of the femur" occurred in scelidotheres, with the head lying anterior to the plane formed by the shaft, greater trochanter, medial condyle and lateral condyle. This implies an anterior rotation of the proximomedial part of
the femur about the greater trochanter. Hoffstetter (1952:67), in discussing differences between Megatherium and Eremotherium, stated that the greater trochanter in $M$. americanum "est fortement rejeté vers l'arrière", implying a posterior rotation of the greater trochanter about the head. While it is not clear which of the interpretations is correct, the lateral margin of the femur, as Hoffstetter (1952) pointed out for M. americanum, is curvilinear, and suggests that the rotation has been such that the position of either (or possibly both) the lateral proximal or distal extremity of the femur has been adaptively changed.

Manipulation of the hind limb suggests that Hoffstetter's (1952) view of posterior deflection of the greater trochanter is among the more reasonable hypotheses for megatheriines, and possibly for other sloths. If the femur is positioned such that the greater trochanter, head, and medial condyle lie in the same plane, then the axis passing through the distal condyles lies markedly obliquely. This position requires an oblique orientation for the transverse plane through the tibia, which in turn requires that the long axis of the pes be turned markedly medially. If, on the other hand, the head and distal condyles lie in the same transverse plane, the tibia is normally oriented, and imparts a nearly anteroposterior orientation to the pes. The distal end of the femur bears two large articular surfaces. The patellar trochlea is continuous with the
lateral condyle, and separated from the medial condyle by a zone of rugose bone. These distal articular surfaces are nearly separated in the megalonychid Pliomorphus (Kraglievich, 1923; Hoffstetter, 1958), but the trochlea and lateral condyle are linked by a narrow isthmus. In megatheriine taxa for which the femur is known, however, the facets are broadly continuous. In most other ground sloths the patellar trochlear surface is continuous with those of the lateral and medial condyles. In the Plio-Pleistocene nothrotheriines (sensu Hoffstetter, 1958), Megalonyx, and Protomegalonyx (Hoffstetter, 1958; Kraglievich, 1922, 1926) the three facets are separate.

Various authors have commented on the fovea ( $=$ fovea capitis femoris of Evans, 1993) for the round ligament (=1igamentum capitis femoris of Evans, 1993; ligamentum teres of others, e.g., McDonald, 1987; Hirschfeld, 1985; Stock, 1925) in ground sloths. The round ligament extends between the femoral head and acetabulum. In Santacrucian nothrotheres the fovea is connected by a trough to the margin of the articular surface of the head. Two morphologies are considered to have arisen from this condition (Hoffstetter, 1958). In one the fovea is completely enclosed within the articular hemisphere of the head. This condition occurs in the Nothrotheriinae s.s. (Kraglievich, 1923; Hoffstetter, 1958). In the other condition the fovea is reduced to a notch on the posterior
margin of the articular hemisphere, as in mylodontids, megatheriines, planopsines, and some megalonychids (see Hoffstetter, 1958). The form and position of the fovea, if discussed at all, are described as being either contained within the articular surface, or as a notch of variable size on the posterior margin of the head. These features are usually distinct, and there is no reason to believe that previous authors have mistaken the morphological condition in a particular taxon.

However, it is unclear whether proper attention has been given to the interpretation and variation of features associated with the articular hemisphere. This perspective is important for morphological accuracy and phylogenetic usefulness of the fovea.

For example, the form of the fovea is variable. The various morphologies discussed above for sloths may be present in dogs. Evans (1993) observed that in the dog (Canis) the fovea is circular, small, and rather indistinct, and that in some individuals a depressed, moderately rugose, and non-articular strip extends from the fovea to the nearest margin. The condition in Canis is not cited here to imply that similar variation may occur in sloths, but it may be expected. One must remember that the femora of most sloth species is known only from few specimens. Stock (1925) reported considerable variation in the form and size of the foveal notch in Glossotherium; it is absent in one specimen.

With regard to phylogenetic interpretations, the fovea has been cited by some, and ignored by other workers. For example, Hoffstetter (1958) staied that the isolated fovea was characteristic of the Nothrotheriinae s.s. By itself, such a remark suggests that isolated foveae occur only in these nothrotheres and that it is a synapomorphy for the group. However, an isolated fovea also occurs in Acratocnus (e.g., AMNH 17716i; see also Anthony, 1926: fig. 77b; pl. 52: fig. 3c), but its possible significance is not discussed by Hoffstetter (1958) or Matthew and Paula Couto (1959), who were familiar with the works of Kraglievich (1923) and Anthony (1926). Hoffstetter (1961) reported an isolated fovea in Planops, but without discussion of its potential significance. The isolated fovea is likely homoplastic; this may oniy be ascertained through broad cladistic analysis of sloths, which is beyond the scope of this work. The interpretation of the notch as the fovea for the round ligament is more important. Various lines of evidence suggest that in megatheriines, at least, the notch does locate the attachment of the round ligament. A relatively small, nearly circular, slightly depressed, and rugose area lies within the articular surface in the megatheriine femora. It differs from that in Planops, Acratocnus, and nothrotheriines in being relatively shallow. The posterior margins in the latter two taxa lack notches, but one is present in Planops (Hoffistetter, 1961: fig. 10), though it
is broader than is typical in megatheriines. Further, Stock (1925:171) reported that occasionally "a scar extends from the apex of the notch inward toward the centre of the articulating surface". The evidence suggests that the round ligament inserted in this circular region within the articular hemisphere, rather than in the notch, in megatheriines. Perhaps the scars reported by Stock (1925) functioned similarly and indicate a similar position in Glossotherium. Its occasional presence may indicate that the insertion for the round ligament is only sometimes indicated in this genus. The circular region in megatheriines is generally faint, and may have gone unnoticed in the past. Additionally, the surface of the head is often poorly preserved and abraded, which obscures the position of the fovea.

Femora in Eremotherium laurillardi and Megatherium americanum

Differences between the femora of $E$. laurillardi and $M$. americanum have been described by various authors (e.g., Hoffstetter, 1949, 1952; Gazin, 1957; Casamiquela and Sepulveda, 1974; Cartelle, 1992). The femora of these species differ, and typify the two general femoral shapes in megatheriines (Pl. 92), as recognized by Hoffstetter (1949, 1952). However, the specimens on which these descriptions were based represent one extreme of the range of variation
in shape and form of the femora of these species. Since Hoffstetter's work, other specimens have been recovered that provide more complete knowledge of this variation, and is particularly evident from the sample from the Santa Elena Peninsula, Ecuador (Pl. 93). It is worth noting that various authors have used femoral characteristics to help distinguish species of Eremotherium. For example, de Porta (1961) discussed differences between the femora of $E$. "rusconii" and E. "carolinense", but these fall within the observed ranges of variation within samples from single localities. As with other skeletal elements, the recovery of larger samples demonstrate that specific distinctions based on the morphology and size of the femur in Eremotherium (excluding those assigned to M. elenense and Eremotherium n. sp.) are not justified.

The length of the femur, as does that of other elements, varies widely in E. laurillardi. The maximum length (the distance parallel to the long axis of the diaphysis) may be between the transverse planes of the head and lateral condyle, or of the head and medial condyle. Difference between these lengths are minimal, and the distance between the head and medial condyle or medial length is taken as the standard measurement of length. The maximum and minimum lengths in the sample from roca das Onças are 826 (MCL 9524) and 650 mm (MCL 9504), respectively (see also Tab. 6; App. 4F). The latter specimen was not yet
fully adult, as the proximal epiphysis is incompletely fused. Nonetheless, the femur had probably reached its adult length, as its advanced stage of fusion should have precluded further growth. A wider range is represented by the sample from Panama, with maximu and minimum being 867 (USNM V) and 674 mm (USNM 37-57), respectively. The longest femur is 895 mm long (UCMP V420-36884, from El Salvador). The femur in M. americanum is shorter (vide infra), although overlap exists. Its length varies between 780 (MLP 30-VI-81) and 580 mm (BMNH 19953r), or 575 mm if MLP 2-30 (vide infra) is included.

The lateral length of the femur, between the greater trochanter and lateral condyle, is usually less than the medial length. Exceptions are MCL 9523 for E. laurillardi; and ROM 265
and MLP 2-29 for M. americanum.
The femora of $M$. americanum and E. Iaurillardi are clearly distinguished based on the form of the patellar trochlea (vide infra) when all variations are considered, but the differences in femoral shape are less marked than supposed by Hoffstetter (1949, 1952), Casamiquela and Sepulveda (1974), and Cartelle (1992). Further, the variations in form of the femur of $E$. laurillardi suggest that similar variations may be expected in the femora of other megatheriine species.

A narrower, more nearly parallel-sided femur is often

TABLE 6. Standard Statistics (mm) for the Femora of Eremotherium laurillardi and Megatherium americanum. Abbreviations: DSFACETS - Minimum distance between the patellar trochlea and distal medial articular facet; DSWIDTH - Distal width, measured transversely between the epicondyles; LENGTH - Greatest proximodistal length; MSWIDTH - Minimum transverse width at midshaft.

Eremotheruin laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 28 | 605 | 895 | 737 | 63.93 |
| PRWIDTH | 27 | 350 | 451 | 384 | 30.12 |
| DSWIDTH | 29 | 322 | 476 | 392 | 36.82 |
| MSWIDTII | 27 | 236 | 330 | 271 | 23.38 |
| DSFACETS 24 | 9 | 49 | 28 | 11.17 |  |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 27 | 570 | 780 | 684 | 55.31 |
| PRWIDTH | 30 | 297 | 468 | 384 | 39.54 |
| DSWIDTH | 28 | 288 | 473 | 386 | 39.53 |
| MSWIDTH | 28 | 205 | 311 | 262 | 27.44 |
| DSFACETS | 31 | 14 | 71 | 40 | 13.40 |

cited as characteristic of E. laurillardi (e.g., Hoffstetter, 1949, 1952; Casamiquela and Sepulveda, 1974; Cartelle, 1992). This shape (e.g., Cartelle, 1992: figs. 87, 88; Hoffstetter, 1952: fig. 12a; ROM 22057: PI. 93D) is generally viewed as a function of the supposedly greater proximal and distal transverse widths relative to the midshaft width in M. americanum (Pls. 92B, 95-97), which cause the prominently concave diaphyseal margins, so that the femur appears more constricted. It is often true that the femur of $E$. laurillardi appears less constricted, but recently recovered samples of this species indicate that the degree of concavity of the medial and lateral margins vary (P1s. 92A, 93, 94) due to variation in transverse expansion of the greater trochanter and epicondyles, and is perhaps more marked in older individuals. Indeed, the proximal and distal extremities are strongly expanded laterally in some individuals (e.g., ROM 24269: Pl. 94C, D), and the medial and lateral margins resemble those of $M$. americanum (cf. Pls. 93A, C. 92B, and 95B,C).

Despite the variation in shape of the femur of $E$. laurillardi, the femora of this species and M. americanum may usually be distinguished. The distinguishing features include a deeper and more regularly concave lateral margin (vide infra) in $M$. americanum, combined with relatively larger proximal parts, so that its femur appears top-heavy. Thus, the constricted femur of this species is not due
simply to differences in relative widths in proximal, midshaft, and distal widths, or to midshaft width relative to length of the femur.

Additional ideas attempting to explain the differences between the femora of these species have been offered. For example, Gazin (1957) stated that the head tends to project more proximally in E. laurillardi, and Cartelle (1992) that the head is more vertically oriented and projects more proximally. However, the projections of the heads vary, as do the distinctness of the neck, size and projection of the greater trochanter, and depth and shape of the digital fossa, and may resemble those in M. americanum.

Probably the perception shared by various authors that the head projects more medially in $M$. americanum is due largely to the shape of the medial margin of the femur. This surface varies from nearly linear to moderately concave in E. laurillardi; it is always, and usually more markedly, concave in M. americanum. Femora of $E$. laurillardi with moderately concave medial margins may usually be distinguished from those of M. americanum by an apparently more prominent lesser trochanter, which lies and projects more medially and interrupts the smooth curve of the medial margin.

Cartelle (1992) stated that the greater trochanter is larger in M. americanum, citing a larger anteroposterior depth for the trochanter compared to the head, whereas in $E$.
laurillardi the depth of the head exceeds that of the trochanter. Cartelle's observation is confirmed by all other specimens examined. Further, the greater trochanter is apparently wider from its lateral margin to the intertrochanteric crest in M. americanum. In anterior view the larger trochanter is apparently reflected in that the proximal quarter of the lateral margin of the femur projects further laterally and is regularly convex. In $E$.
laurillardi the margin is usually paraxial, or slopes slightly medially, and a small protuberance projects laterally near the distal part of the proximal fourth. The larger size of the greater trochanter contributes to the top-heavy appearance of the femur of $M$. americanum.

Cartelle (1992) stated that the ectepicondyle was larger in $M$. americanum. This is misleading, as the form of the ectepicondyle must be analyzed more carefully for proper assessment. In partial agreement with Cartelle (1992), I concede that the ectepicondyle usually appears as a more prominent structure in M. americanum. However, this probably reflects the fact that it is usually betterdefined. In M. americanum the ectepicondyle is formed from a proximal, distolaterally oriented margin, and a distal, proximolaterally oriented margin. These meet in a prominent and angular protuberance, approximately three-quarters down the length of the femur. In E. laurillardi two extreme forms, with intermediates, occur. In one extreme the
ectepicondyle strongly resembles that in $M$. americanum (e.g., ROM 28911; Pl. 93A). In the other the proximal and distal margins meet at a more obtuse angle, largely because the proximal margin is oriented more vertically (e.g., ROM 22057: Pl. 93D; ROM 24269: Pl. 94C, D). Thus, the ectepicondyle appears reduced in some specimens of $E$. laurillardi, and prominent in others (indeed more so than in M. americanum; cf. Pls. 93A and 95D).

The various explanations and descriptions noted above contribute to our understanding of the nature of the differences between the femora of $E$. laurillardi and $M$. americanum. However, statistical analyses of the following four variables apparently provides a sufficient and rather uncomplex explanation: Length (measured medially between the head and distal condyle), Proximal Width (PRWIDTH, measured between the head and greater trochanter), Midshaft Width (MSWIDTH, measured as the minimum constriction of the diaphysis near its midlength), and Distal Width (DSWIDTH, measured between the epiconyies). PRWIDTH ( $\chi^{2}$ approximation $=0.29, \mathrm{df}=1, \mathrm{p}=0.587$ ), MSWIDTH ( $\chi^{2}$ approximation $=0.84, \mathrm{df}=1, \mathrm{p}=0.358$ ), and $\mathrm{DSWIDTH}(\mathrm{t}=0.57$. $d f=55, p=0.571$ ) do not vary significantly between these species; Length, however, differs significantly (t=3.28, $d f=53, \mathrm{p}=0.0018$ ). Thus, the proximal and distal ends of the femur of M. americanum merely appear to be wider relative to midshaft width. This is due to the shorter femoral length,
or the relatively wider femur compared to that of $E$. Iaurillardi. Further, this also causes the more pronounced curvature of the medial and lateral margins in $M$. americanum.

Rotation of the femur is assessed by the angle formed between the distal articular surfaces and a horizontal plane. The femur is positioned with its posterior surface facing ventrally, such that the head and greater trochanter lie on a horizontal plane (i.e., a table); in this position the medial condyle lies in the same plane and the lateral condyle rises above it (Pl. 98). Torsion is measured as the angle between a line passing through the anteroposterior midpoints of the medial and lateral condyles and the plane. The method of measurement implies torsion of the distal half of the femur relative to the proximal, but this is not certain, as discussed above. The same angle may be obtained by positioning the femur with greater trochanter, and medial and lateral condyles in the same plane, with the head then raised above the plane.

The degree of rotation is highly variable. It tends to be smaller in E. Iaurillardi than in M. americanum, although there is considerable overlap of their ranges. In $E$. laurillardi the maximum, $41^{\circ}$ (USNM $V$; also occurs in three non-Panamanian specimens), and minimum, $10^{\circ}$, occur in the sample from Panama. Rotation in $M$. americanum varies between $57^{\circ}$ (BMNH 19953r) and $31^{\circ}$ (MACN 10683).

Quantification of the angular deviation between the proximal and distal parts of the femur, as measured through the condyles, suggests that the femora of some specimens of E. laurillardi show more torsion than some M. americanum specimens. However, the femur in M. americanum consistently appears to be more twisted, which suggests that angular deviation at the condyles is not the sole determinant of apparent torsion. Two other conditions probably contribute to the appearance of the highly twisted femur of $M$. americanum. One is the greater anteroposterior depth of the greater trochanter. The second is the form of the ectepicondyle. It projects more strongly anteriorly, and a smooth ridge extends proximomedially from it. The greater torsion in M. americanum (P1. 99A) is reflected in the markedly sigmoidal lateral margin of the femur in lateral view, whereas that in E. laurillardi (Pl. 99B-D) is nearly rectilinear.

The shape of the patellar trochlea is consistently different in the femora of E. laurillardi (Pls. 92A, 93, 94A-C, 98A, 100) and M. americanum. It is considerably larger in $E$. laurillardi because it extends further medially on the anterodistal and distal surfaces of the femur than in M. americanum (Hoffstetter, 1949, 1952). Its distolateral part is continuous with the lateral condyle. Its size and shape vary, but it is always clearly distinct from that of M. americanum. The medial margin of the trochlea usually
reaches the plane of the lateral margin of the medial condyle, and often overlaps it. The minimum distance between the facets varies between 9 (MCL 9500) and 4.4 mm (MCL 9524) in E. laurillardi. The trochiea is shallowly concave transversely, or may be nearly flat. The major variations in shape of the trochlear margins are that the central part of the proximal margin may be regularly convex or concave.

The patellar trochlea in M. americanum (Pls. 92B, 9697. 98B, 101), as described by Owen (1860) and Kraglievich (1925a), corresponds approximately to the lateral half of that in E. laurillardi, and thus the minimum separation between the facets is significantly wider ( $t=3.53, \mathrm{df}=53$, $\mathrm{p}=0.0009$ ) than in E. laurillardi. Its morphology may be considered essentially as an anteroproximal extension of the lateral condylar surface. It varies in size and shape, but generally does not reach medially as far as the vertical midplane of the intertrochlear space.

Kraglievich (1925a) noted differences among the trochleae of $M$. americanum and other Megatherium species. These will be assessed later, but it is appropriate here to note the variations in size and shape in $M$. americanum. In anterior view the trochlea in the type, MNHNM 6 (Pl. 95A), is nearly circular and extends somewhat proximally. A measure of possible variation may be appreciated by comparing the trochleae of BMNH 19953r and 19953q (P1. 101B
and C, respectively). These are from Lujan, Buenos Aires Province (Lydekker, 1887), and are from opposite sides, but from different individuals. The proximal and distal margins of BMNH 19953q are arched proximally, the medial and lateral margins are subparallel, and the distal surface of the trochlea is markedly concave transversely. In BMNH $19553 r$ the facet is positioned more medially, is approximately triangular, with a nearly linear distal margin, and its surface is gently concave. The trochlea extends further medially in ZMUC 212 (Pl. 96C), and separation between it and the medial condyle is 280 mm . Greater separations are more common, although variable; for example, the femur of MNHNP 6 and MRB 1 are similar in length, but the minimum separation between the facets is 550 in the former, and 320 mm in the latter. The trochlea in MACN 6410 (P1. 101D) and MUT V413 resembles that of ZMUC 212. In MACN 10683 (RI. 101E) the trochlea is lower proximodistally than is usual, and thus appears transversely elongated and approximately triangular. That of MACN 54 (PI. 101F)-is nearly rectangular, with its long axis proximodistal.

Other megatheriine species of doubtful validity (vide supra) have been described in the past. This section discusses the femur, where known, of these species, and demonstrates that the femur supports no specific distinction from M. americanum.

The type of $M$. gaudryi, MLP 2-60 (P1. 97B), includes
right and left femora. They are largely in pieces, but reasonably well-preserved and properly restored. They generally resemble those of $M$. americanum. They also strongly resemble MACN 54, but with a slightly more concave medial margin, which is entirely normal in this species. The patellar trochlea is reduced essentially as an anteroproximal extension of the lateral condyle, as in $M$. americanum, and is somewhat intermediate between the trochlea of MACN 54 and MNHNM 6. Kraglievich (1925a) stated that the trochlea was somewhat larger and more concave than in M. americanum, and further that the patella was somewhat large, but it is apparently relatively smaller than in MNHNM 6 , and not particularly more concave than in some other specimens. The length of the femur is approximately 610 mm . While relatively small, it is longer than BMNE 19953r, and thus within the range for $M$. americanum.

MLP 2-30 (PI. 97C), the type of M. filholi, includes right and left femora of an individual from the opper Pampean. The femur is 575 mm long, slightly smaller than BMNH 19953r and MLP 2-60. The shape is generally as in M. americanum, but somewhat less prominently transversely expanded proximally and distally. The minimum transverse width occurs approximately at midshaft, as in MACN 54, MNHNM 6, and MUT V413. The projection of the head and form of the ectepicondyle are approximately intermediate between BMNH 19953q and ZMUC 212. The patellar trochlea is gently
concave transversely. It extends medially approximately as in ZMUC 212, but the distomedial part extends further medially, rather than the proximomedial part as in ZMUC 212.

The femur of MACN 5002 (P1. 97D), the type of $M$. gallardoi, is prominently transversely expanded both proximally and distally. It thus appears relatively short and wide, but clearly resembles the femora of individuals of M. americanum. Its length, 725 mm , falls easily within the range for $M$. americanum. The greater trochanter is prominent, and resembles that of MACN 10683 in shape and MUT V413 in proximal extension. The head projects as in ZMUC 212 and MACN 10683. The patellar trochlea of MACN 5002 (Pl. 101G)is approximately as in MNHNM 6, though perhaps not as high proximodistally. Kraglievich (1925a) stated that the trochlea as slightly concave. Kraglievich's (1925a: figs. 5. 6) illustrations compare the trochlea and show that it is nearly flat and slopes strongly medioposteriorly as compared to that of $M$. americanum. However, variation exists in the shape of the facet, and it may be nearly flat in $M$. americanum. The facet does slope posteromedially, but not as prominently as shown by Kraglievich. Further, the relative positions of the trochlea and medial condyle differ from that typical of $M$. americanum, but may be due partially to the prominence of the scar in MACN 5002 between these facets. A scar, variable in size, occurs in this region in other specimens of $M$. americanum, such as MUT V413, ZMUC

212, and MNHMM 6. Further, the relationship between the distal facets varies in $E$. laurillardi, and may be expected in M. americanum.

Femora of Other Megatheriine Species
The femur in Eremotherium n. sp. resembles that of $E$. laurillardi. Its medial margin is nearly rectilinear, with the lesser trochanter projecting beyond this margin. It is shorter than that of $E$. laurillardi and M. americanum. The length of the larger individual is 599 man, which is below the minimum length for E. laurillardi and barely within the low end of the range for $M$. americanum. The femur of the smaller individual is incomplete, but is approximately 100 mm shorter than that of the larger individual.

The head projects proximally and apparently lies more laterally than in E. laurillardi. The notch on the posterior margin of the head's articular surface is relatively elongated and narrow. The greater trochanter is narrower transversely, particularly in its proximal part, so that the femur appears slightly expanded distally. The patellar trochlea extends medially, apparently more so than in E. laurillardi, and is transversely concave. Torsion of the femur is $26^{\circ}$, well within the range for $E$. laurillardi.

The femur of M. tarijense (FMNH P14216: Pl. 102A-C)
resembles that of E. laurillardi and Eremotherium n. sp. in general form, in shape of the patellar trochlea and in
torsion (33 $)$. The trochlea is nearly flat transversely. The notch on the posterior margin of the head is more similar to that of Eremotherium n. sp. The greater trochanter is narrow proximally, as also in Eremotherium n. sp. The medial and lateral margins are nearly linear and parallel, more so than is usual in E. laurillardi. The lesser trochanter is less prominent, and barely projects beyond the medial margin. The epicondyles are less prominent. MUT V411 (Pl. 102D), from the Tarija Fm., differs only in minor ways from FMNH P14216. Both are nearly the same length, but the lesser trochanter and ectepicondyle are slightly larger, and torsion is slightly less in MUT V411. It is clearly referable to $M$. tarijense. The femur of $M$. medinae (SGO PV231, formerly 1 -VII67/64; P1. 103A) is only slightly different from that of $M$. tarijense. Differences include a more prominent lesser trochanter, a smaller notch on the posterior surface of the head, and a greater length. However, the smaller femur (SGO PV185, formerly 9-V-69-1/39), though incomplete, is similar in size to that of $M$. tarijense.

The femur of PIU M4530 (Pl. 103B-D) suggests that the megatheriine from Ulloma may be specifically distinct from those from northern Chile, M. medinae, and Tarija, M. tarijense, supporting the validity of $M$. sundti. The individual is a juvenile, as indicated by non-closure of the skull sutures. In the femur the distal epiphysis is fused
and the proximal is clearly fused, but shows the line of fusion. The length of the femur falls within the range for M. medinae and M. tarijense, but its shape departs radically from that typical for these species. The medial and lateral margins are strongly concave, and the greater trochanter and ectepicondyle are relatively prominent. Its middle portion is markedly constricted transversely (PI. 103B), relatively more so than in the more constricted specimens of $E$. laurillardi, and probably more so than in M. americanum. The patellar trochlea is medially extended and nearly flat transversely, but its medial part is narrower proximodostally than is typical in M. medinae, M. tarijense, and E. laurillardi.
M. istilarti was founded by Kraglievich (1925b: pl. 5) largely on a femur (MACN 9674) of reportedly Chapadmalalan age. The femur is not well-preserved, but various important features can be recognized that support the validity of this species. The proximal and distal extremities of the femur are not as prominently expanded as may occur in $M$. americanum, but it resembles that of $M$. sundti, with moderately concave medial and lateral margins. The entepicondyle is prominent, and resembles that in E. laurillardi ROM 22057. The two features that distinguish this species from others described here are that 1) the patellar trochlea resembles that of $M$. americanum, particularly that of BMNH 19953q, and 2) its very small
size, length $=468 \mathrm{~mm}$, well-below the range for $M$. americanum.

Kraglievich (1925a) based M. nazarrei largely on the form of the patellar trochlea. The type of this genus and species, MACN 7127, includes a few complete skeletal elements, but only the distal portion of the femur (PI. 104A) is preserved. The trochlea is as described by Kraglievich (1925a), and is as in E. laurillardi.

The type of Pyramiodontherium bergi, MLP-66, was discussed by Roth (1911) and includes the femur (P1. 104B), which is reasonably well-preserved but missing most of the central part of its lateral margin. The femur is relatively transversely expanded proximally and distally, and generally resembles that of $M$. americanum. Its length, 511 mm , falls below the lower limit for femora of $M$. americanum, but within the range of most other species (e.g., M. tarijense, M. medinae). The greater trochanter is weaker, particularly proximally, than in $M$. americanum, but may be broken. As preserved, its shape does not strongly resemble that of any other species. The medial margin is relatively concave. Although a considerable part of its lateral margin is missing, the femur was apparently relatively robust. The patellar trochlea resembles that in M. americanum, particularly that in MACN 6410 and ZMUC 212. The morphology of the fovea for the round ligament is notable. It is approximately ovoid and extends by way of a groove, slightly
narrower than the width of the fovea, to the posterior margin of the head. The groove expands near the articular margin to resemble the notch of other megatherines.

Kraglievich (1925a) favourably compared MACN 2817 (PI. 104C-E), a femur from Valle de Santa Maria, Catamarca Province, Argentina, to the femur of Plesiomegatherium. MLP 2-66 was considered to represent this genus at that time, and Kraglievich (1925a) was almost certainly referring to MLP 2-66, because it was the only femur referred to Plesiomegatherium. Kraglievich's (1925a) comparison was reasonable, as both MLP 2-66 and MACN 2817 are from Valle de Santa Maria. MACN 2817 bears a general resemblance to MLP 2-66, particularly in length ( 546 mm ), its proximal and distal expansion, and the shape of the greater trochanter. Despite these resemblances, MACN 2817 bears features that distinguish it from MLP 2-66. The head projects further laterally, with well-defined neck, such that the margin of the digital fossa is wider and considerably less concave. Though the femora are similar in length, MACN 2817 is relatively wider proximally and distally, so that it appears short and very robust. Further, its patellar trochlea is expanded medially and transversely concave, approximately as in E. laurillardi, rather than reduced as in MLP 2-66 and M. americanum. The ectepicondyle is more prominent than in any other megatheriine, particularly on its proximal margin, which is rugose and extends proximally nearly to the level
of the minimal midshaft constriction. This condition may have existed in MLP 2-66, based on the resemblances in its prominent distal width and shape of the ectepicondyle to those of MACN 2817.

The femur of the Toro Negro megatheriine, MLP 68-III-14-1, is relatively narrower, more gracile, and shorter (473 mm ) than the femora of other species. The individual was not quite adult, but not particularly young, because the epiphyseal suture lines, while visible, are nearly obliterated. Probably, the individual was at or near its adult size. The patellar trochlea is medially extended, resembling that in E. laurillardi. While the form of the femur is not particularly striking, the relationship of the length of the femur to that of the tibia distinguishes this individual. The femur is slightiy shorter than the tibia, whereas the femur is generally considerably longer in other species. The status of MLP $68-$ III-14-1 is discussed below in SYSTEMATIC REVIEW OF THE MEGATHERITNAE.

## TIBIA-FIBULA

The tibia of Megatherinae resembles in proportion that of Pseudoprepotherium (Hirschfeld, 1985: fig. 17), and is generally intermediate morphologically between the elongated, gracile tibia of the Santacrucian ground sloths, such as Hapalops (Scott, 1904: pl. 42: fig. 8), most megalonychids (Antiony, 1926: figs. 79, 80), planopsines (Hoffstetter, 1961: fig. 11), and nothrotheres (Stock, 1925: pl. 14: fig. 1), and the relatively short and stocky tibia of mylodonts (Stock, 1925: pl. 40: fig. 1) and scelidotheres (McDonald, 1987: fig. 35b,c). The tibia and fibula are fused proximally in Megatheriinae, a feature perhaps unique among sloths; Stock (1925) reported fusion in a single Glossotherium specimen, which is to my knowledge the only other occurrence of fusion. Only minor morphological differences occur in the Megatheriinae.

## Tibia-Fibula of Eremotherium laurillardi and Megatherium americanum

The tibia of Eremotherium laurillardi (Pl. 105) is relatively well-known, and Hoffstetter (1949, 1952) and Cartelle (1992) provide general descriptions. As in other skeletal elements, considerable morphologic and mensural variation occurs. For example, length varies between 665 mm (UCMP V4201-36885) and 457 mm ( MCL 9570). The tibia of

Megatherium americanum (Pls. 106, 107A-F) is usually shorter, between 594 mm (MACN 54) and 425 mm (BMNH 19953u) long (Tab. 7; App. 4G). However, the tibiae of these species do not vary significantly in length (t=1.79, df=39, $\mathrm{p}=0.081$ ) .

The proximal surface (PI. 105D) arches anteriorly in section, and bears two articular surfaces. The medial articular surface receives the medial femoral condyle and is the main proximal weight-bearing surface of the crus. It is markediy concave transversely and anteroposteriorly, and approximately oval in outline, with its long axis obliquely anteroposterior. The narrower lateral articular surface articulates largely with the lateral femoral condyle. It is usually approximately oval, but may be nearly rectangular, and gently convex anteroposteriorly and transversely. Its surface area is approximately half that of the medial surface. Anteriorly and posteriorly it is contiguous with small, approximately semicircular facets for articulation with sesamoid elements (see Sesamcid Bones, below). The posterior sesamoid facet is occasionally well-demarcated by a low, transverse ridge, but often is barely distinguishable from that for the lateral femoral condyle.

The relatively depressed intercondylar area lacks eminences. The medial margin of the medial articular facet is raised as a narrow crest, and forms the most proximal part of the tibia. The width of the intercondylar area

TABLE 7. Standard Statistics (mm) for the Tibia-Fibula of Eremotherium laurillardi and Megatherium americanum. Abbreviations: LENGTH - Greatest proximodistal length; PWIDTH - Greatest proximal distal width; DWIDTH - Greatest distal transverse width; MSWIDTH - Shaft constriction, minimum transverse width at midshaft; DWWOF - Greatest distal width without fibula, i.e., of tibia only.

Eremotherium laurillardi

| Variable | $\mathbf{N}$ | Minimum | Maximum | Mean | Std Dev |
| :--- | ---: | :---: | :---: | :---: | :---: |
| LENGTH | 23 | 447 | 665 | 555 | 51.8 |
| PWIDTH | 19 | 245 | 405 | 315 | 43.9 |
| DWIDTH | 10 | 227 | 331 | 265 | 30.2 |
| MSWIDTH | 20 | 91 | 144 | 110 | 13.3 |
| DWWOF | 15 | 172 | 271 | 213 | 25.0 |

Megatherium americanum

| Variable | $N$ | Minimum | Maximum | Mean | Std Dev |
| :--- | ---: | :---: | :---: | :---: | :---: |
| LENGTH | 18 | 425 | 623 | 527 | 48.7 |
| PWIDTA | 16 | 246 | 369 | 312 | 38.2 |
| DWIDTH | 11 | 222 | 313 | 284 | 25.8 |
| MSWIDTH | 18 | 810 | 141 | 113 | 14.4 |
| DWWOF | 6 | 182 | 250 | 229 | 26.3 |

varies, but is generally narrower than that of the lateral articular facet. The anterior and posterior intercondylar areas, which serve as attachments for meniscal ligaments, are particularly rugose. The anterior intercondylar area is pierced by large nutrient foramina, particularly lateraily and just posterior to the tibial tuberosity.

The proximal surface in M. americanum (Pl. 106A) is similar morphologically. However, the prominence of the tibial tuberosity and orientation of the medial facet are more variable. In BMNH 19953s (Owen, 1860: pl. 39, fig. 3) the tibial tuberosity is poorly developed, and proximally the tibia is anteroposteriorly constricted in section. However, other specimens (e.g.. ROM 10439) are similar in the arched shape characteristic of E. laurillardi. Cartelle (1992), apparently based on few specimens, stated that the medial facet in tibiae of M. americanum is less obliquely oriented than in E. laurillardi. However, the long axis of this facet may vary between a nearly anteroposterior orientation (e.g., BMNH 19953s), and one nearly $60^{\circ}$ to the transverse plane of the tibia (e.g., MACN 44-XII-28-1). The intercondylar area tends to be wider in M. americanum than in E. laurillardi, but, contra Cartelle (1992), is not always wider than the lateral articular surface.

The tibial tuberosity in E. laurillardi varies in prominence and shape. It ranges from approximately
triangular, with apex distal, to approximately crescentic. The tuberosity is convex in proximal view and bears a weak groove (Pl. 105D). It is centred lateral to the sagittal plane of the tibia and is most prominent laterally, as is common in most ground sloths. In Glossotherium the tuberosity is further lateral (Stock, 1925: pl. 40: figs. 1, 1a). The tibial (cnemial) crest extends distomedially from the tibial tuberosity toward the medial malleolus. The crest forms a narrow, rugose ridge, with height and rugosity diminishing distally. It is not particularly prominent, as is usual in ground sloths. The tibial crest, however, is usually more prominent in M. americanum, as in BMNH 19953 s and, particularly, in ROM 10439 (Pl. 106A and C, respectively).

The tuberosity is morphologically similar in all megatheriines, with variations clearly encompassed by the range in $E$. laurillardi. An exception is that the groove crossing the tibial tuberosity is better-developed in nearly all other megatheriine specimens. The groove is oriented approximately proximodistally and probably served for passage of the patellar ligament. It is most prominent in M. americanum, and best observed in proximal view. Further, the tuberosity lies somewhat more laterally in $M$. americanum, and its apex is more nearly oriented parallel to the long axis of the diaphysis.

The medial and lateral articular facets are supported
largely through the diaphysis, but a buttress supports the posterior part of the lateral facet. The buttress is strongly raised proximally, and diminishes as it extends mediodistally. It is coarsely rugose. A singularly prominent scarline lies along its lateral surface, and probably largely indicates the tibial attachment of the flexor hallucis longus (part of the flexor digitorum profundus). A prominent, nearly pyramidal, tuberosity, with apex distally, projects from the posterior surface between the area of fusion of the tibia and fibula (PI. 105B). Evans (1993) noted that in Canis this region gives rise to the tibialis caudalis; they note, however, that this muscle is completely separated from the heads of the flexor digitorum profundus, in contrast to the condition in hoofed mamals. The arrangement of this musculature in ground sloths is uncertain. However, the tuberosity lies in the region of origin of the flexor hallucis longus, and probably served for part of its insertion. The proximal fifth of the posterior surface, distal to the popliteal notch, is relatively smooth. The surface distal to this region, extending neariy to midshaft and approximately centrally located, is reticulated; possibly it served partly for the origin of the other parts of the flexor digitorum profundus. The proximomedial surface is rugose, and bears a prominent scarline; the popliteus probably attached to this area. The tibial diaphysis is relatively gracile in most
megatheriines. In M. americanum, however, the tibia is robust and its proximal and distal parts are apparently markedly expanded transversely, so that it is relatively short and stocky (Pls. 106B-E, 107A-D). The differences are unambiguous, and it is usually not difficult to recognize the tibiae of $M$. americanum and E. Laurillardi on sight. Despite this ease of distinction, the tibiae of these species do not vary significantly in the following variables assessing width: Proximal Width (PRWIDTH, measured proximally between the medial margin of the tibia and lateral margin of the fibula, which is usually preserved with the tibia; $t=0.23$, $d f=33, p=0.819$ ), Midshaft Width (MSWIDTH, measured as the minimum constriction of the diaphysis, which occurs near its midlength; $\chi^{2}$ approximation=1.55, $d f=1, p=0.214$ ). Distal Width including fibula (DWIDTH, measured distally between the medial margin of the tibia and lateral margin of the fibula; $t=1.53$, $d f=19, p=0.144$ ), and Distal Width excluding fibula (DWWOF; $t=1.29, ~ d f=19, ~ p=0.210$ ).

I agree with Cartelle (1992) that the tibia and fibula do not ankylose distally in E. laurillardi; neither of us has ever observed such fusion. Clearly, the elements were strongly bound together by ligaments, based on the presence of triangular and coarsely rugose apposing areas on the tibia and fibula immediately proximal to the corresponding distal articular facets of these elements. In some
individuals of E. laurillardi the proximal parts of these areas approach each other (ROM 22068; cf. P1 105A and C). probably due to ontogenetic growth, but do not make contact.

In M. americanum ankylosis between these regions usually occurs (in aged individuals according to Hoffstetter, 1952), enclosing a large foramen between tibia and fibula, as in BMNH 19953s (PI. 106B, D), MLP 2-29 (P1. 106E), MPCB 1, and the mounted specimen in MNENP. Fusion is extensive in MACN 2-79, so that the ventral margin of the foramen lies at about the middle of the tibia's length. Examples of largely or completely unfused conditions include MLP 2-31 (PI. 107A), MLP 2-30 (Pl. 107B, C), FMNH P13662 (P1. 107D), and MNHNM 6, the type specimen. The distal apposing surfaces of the tibia and fibula extend further proximally than in E. laurillardi. These regions are generally in contact in the unfused condition in $M$. americanum, and proximally the surfaces of the tibia and fibula curve abruptly toward each other. In E. laurillardi the surfaces of the tibia and fibula approach each other more gradually.

The medial malleolus is prominent in $E$. laurillardi, but barely projects distally beyond the margin of the medial astragalar facet. The posterior surface of the malleolus bears a single, obliquely oriented digital groove (PI. 105B, E), for passage of the digital flexors (Webb, 1989). Its depth varies, and in some specimens is very shallow, largely
due to differential development of the margins of the groove. These may be rugose, raised crests, or low, rounded, and smoother ridges. In some specimens with relatively high crests, the bone surfaces anterior and posterior to the crests resemble grooves; in others, such groove-like structures are obscured because the bone surfaces anterior and posterior to the digital groove had attained a relatively rugose condition.

A single digital groove is also present in $M$. americanum, as is abundantly clear from BMNH 19953s (Pl. 106D) and ROM 10439 (PI. 107E). Its depth varies, but it is wider than in E. laurillardi. However, in some specimens, such as MLP 44-XII-28-1, two grooves appear to be present due to the development of a weaker third crest near the posterodistal margin of the tibia. A similar condition is present in MLP 2-30 (P1. 107C). Based on the morphology of MBNH 19953s, the digital groove in these specimens is that lying more medially.

In unfused tibiae-fibulae the tibia bears two, contiguous articular facets distally for the astragaius and fibula. The small, crescentic facet for the fibula lies laterally and faces laterodistally in E. laurillardi. This facet apparently faces more distally in M. americanum. A prominent, coarsely rugose, and approximately triangular region, with apex proximal, lies proximal to the facet on the tibia's lateral surface. The area served for
ligamentous attachment to the fibula in E. laurillardi, as discussed above. This area is greater in M. americanum, and eventually fused in older individuals with the corresponding surface on the fibula.

The cochlea tibiae in E. laurillardi (PI. 105E), for articulation with the astragalus, is formed from a small, medial part, which received in life the odontoid process of the astragalus, and a larger lateral part, which received the discoid surface of the astragalus. These are contiguous across a concave, obliquely oriented ridge, which is more prominent and sharper anteriorly. The medial margin of the odontoid facet is arched. The facet is concave along its major axes, with its long axis oriented anteromedially. The long axis of the discoid facet lies approximately normal to that of the odontoid facet. The medial part of the discoid facet, adjacent to the ridge, is nearly flat. Its lateral part is strongly concave parallel to the long axis.

The major features of the distal end of the tibia are common to $M$. americanum, and indeed all megatherines. However, some minor diagnostic differences exist. The distal surface of the tibia of $E$. laurillardi is compressed anteroposteriorly relative to that of $M$. americanum (cf. Pls. 105E and 107E). The posterodistal margin is considerably more convex in M. americanum, apparently due to an expanded discoid facet, and the medial malleolus is more prominent. The discoid facet is longer and wider than in E.
laurillardi, as was noted by Cartelle (1992). The odontoid facet, however, is apparently not as long as in E. laurillardi, such that its medial margin is nearly circular. The odontoid facet lies approximately adjacent to the central region of the discoid facet in $M$. americanum, and the posterior part in E. laurillardi. The odontoid process does not appear to lie more anteriorly in $E$. laurillardi, based on the transverse plane. However, Cartelle (1992) stated that the odontoid facet was further anterior with respect to the discoid facet than in M. americanum, and that this resulted in a less oblique position of the pes in $E$. Iaurillardi.

The fibula in E. laurillardi (Pl. 105A-C) is considerably slimmer than the tibia, as in other mamals. Its diaphysis is thinnest centrally, and expands proximally and distally. The fibula may be nearly rectilinear, but in some specimens bows medially. The proximal third of the fibula is anteroposteriorly compressed, but transversely wide, and comprises three surfaces. Its lateral surface is rounded and coarsely rugose. The broad and concave anterior and posterior surfaces converge medially into the narrow, crest-like medial margin. The central third is similar, but transversely narrower. The distal third, formed by three nearly flat surfaces, is triangular in section, with the apical crest lateral; and bears three rugose ridges, one laterally, one anteromedially, and one posteromedially.

In E. laurillardi the fibula bears two contiguous articular facets distally. The proximal, crescentic facet, for the tibia, faces nearly medially. The larger, distal facet, for the astragalus, varies from approximately triangular to nearly oval, and faces mediodistally. The fibula projects distally slightly beyond the tibia.

The fibula of $M$. americanum (Pls. 106B, D, E; 107A, D) is considerably stouter proximally and distally, particularly proximally at its fusion with the tibia. Its surface is generally more irregular due to more prominent ridges.

The crural index (CI, or femorotibial index) = lengths of the tibia/femur $\times 100$ is among the standard limb ratios (Coombs, 1983). The CI is better represented in megatheriines than the brachial index, although there are few individuals known for which both the tibia and femur are preserved. However, CI is apparently useful in taxonomically distinguishing some megatheriines. The CI in M. americanum ranges between 70.5 (MNMN 6) and 82.1 (MLP 229) and is based on seven individuals. Coombs (1983) reported a value of 76.2 from the cast of an individual. CI is known from only two individuals in E. laurillardi, and falls within the range that in M. americanum.

The type of $M$. filholi, MLP 2-30, includes the tibia and proximal part of the fibula. The tibia strongly resembles that of MLP 2-31 in morphology and proportions,
except that it is slightly shorter and the proximal part of the distal articular surface between tibia and fibula is less prominent, as also occurs in FMNH P13662. The proximal fusion is as stout as in other specimens of $M$. americanum. The tuberosity is somewhat less prominent than is usual in M. americanum, but this character is variable; indeed, in proximal view the anteroposterior depth of MLP 2-30 is approximately intermediate between BMNH 19953s (described by Owen, 1860: pl. 39: fig. 3) and the strongly convex anterior surface of most other M. americanum specimens. The morphology, size, and proportions of the tibiae of MLP 2-30 and FMNH P13662 suggest that they represent small individuals of $M$. americanum, and are assigned to this species. The CI values for these individuals fall well within the range for $M$. americanum.

Roselli (1976) assigned a nearly complete right tibia from Uruguay, MPFLR 438, to Perezfontanatherium fiandrai. He distinguished it from that of $M$. americanum based on its shorter length and greater robustness. Although it is relatively robust, MPFLR 438 falls within the ranges of size and morphology for M. americanum.

Tibia-Fibula of Other Megatheriinae
In other megatheriines the proximal surface of the tibia tends to be less strongly arched in section than that of E. laurillardi, but this may be due to individual
variation. The facets and intercondylar width of the proximal tibial surface in Eremotherium n. sp., M. tarijense (Pl. 107F), M. medinae, and M. sundti are approximately as in E. laurillardi.

The tibial diaphysis in M. tarijense (Pl. 107G) is more gracile and elongated than that in M. americanum, resembling that in $E$. laurillardi. In other respects it is closer to that of $M$. americanum. The proximal fusion between tibia and fibula appears stouter. Distally these elements form an extensive contact. They are only partially fused, but the surfaces of the tibia and fibula curve abruptly toward each other. The distal end of the fibula is relatively robust and projects further distally beyond the tibia in M. tarijense. The digital groove is poorly developed, and barely distinguishable (Pl. 107H). The distal tibial surface in $M$. tarijense is somewhat intermediate between those of M. americanum and E. laurillardi (cf. Pls. 105E, 107E, and 107H). Its posterior margin is strongly convex, and the discoid facet is somewhat broader posteriorly than in E. laurillardi, but the odontoid facet and medial malleolus are approximately as large. The CI in $M$. tarijense is 77.3, well within the range for M. americanum.

The tibiae of $M$. medinae (SGO PV231: Pl. 108A) and M. sundti (SGO PV298: Pl. 108B) are known from single specimens. The tibia of M. medinae resembles those of $E$. laurillardi and M. tarijense in its gracile proportions.

The CI of 73.0 is well within the range for that of $M$. americanum. The tibia of M. sundti appears somewhat stockier, transversely expanded proximally and distally, and thus resembles more that of $M$. americanum. The distinction suggested here may be perceived as tenuous because it is based on single specimens. It may, however, be significant that a stockier tibia is associated with a femur that is also transversely expanded proximally and distally in $M$. americanum; and as suggested here for M. sundti. The more gracile tibia of $E$. laurillardi, M. tarijense, and M. medinae is associated with a generally less expanded femur.

The fibulae of $M$. medinae and $M$. sundti are represented only by small, proximal portions fused to the tibia. Distally the tibia and fibula remain unfused, and their morphologies are approximately as in M. tarijense. The tibia, fibula, and their distal relationship in Eremotherium n. sp. closely resemble those in E. laurillardi. The tibia of Pyramiodontherium bergi (PI. 108C) is gracile and generally resembles that of $E$. laurillardi. On the proximal surface the medial articular facet is relatively elongated, with its iong axis considerably more oblique. The intercondylar space is approximately as wide as lateral articular facet. The proximal fusion of the tibia and fibula is less stout than in M. americanum. Distally they are unfused, and their surfaces approach each other gradually. The digital groove is prominent.

Roth (1911) stated that the relative lengths of the femur and tibia clearly distinguish $P$. bergi from $M$. americanum. This is true, although Roth (1911:13)
inaccurately reported the relative lengths of these elements in $P$. bergi in stating that "el fémur es de 3 centimetros más corto que la tibia". MLP 2-66 includes left and right tibiae. The right measures 462 mm in length. The tibia is broken in section near its distal end and the parts are glued together. Apparently, however, some of the diaphysis is missing because the left tibia of this individual, which is better preserved and unbroken, is 499 mun long. The left femur (the right was apparently not recovered) is 511 mm long, and contra Roth (1911) therefore exceeds the tibia in length. The CI is 97.7, whereas the highest value for $M$. americanum is 82.1. While it is unclear that this difference is significant, it is worth noting the CI in $P$. bergi is among the highest recorded not only for megatheriines but all ground sloths. Further, the CI is even higher in another megatheriine (see below). Therefore, I consider the higher CI value in P. bergi as significant and that it may indicate a trend toward a relatively elongated tibia.

The morphology of the tibia of most megatheriine taxa, when known, generally resembles that of E. laurillardi, except as discussed above. The differences are usually minor, and in so much as many of them exist within $E$.
laurillardi, they are perhaps most prudently viewed as individual variations, particularly in light of the small samples.

The tibia of the Toro Negro megatherine (PI. 108D) is similar in to that of Pyramiodontherium bergi also; its fibula, however, is relatively gracile and markedly rectilinear. On the proximal surface the medial facet in the Toro Negro megatheriine resembles that of $P$. bergi, but the intercondylar space is narrower than the width of the lateral facet. The relative lengths of the femur and tibia are significant. The CI value for this individual is 99.6, the highest recorded for any ground sloth, and very similar to that for $P$. bergi (MLP 2-66). While these individuals are also similar in size, and probably geological age, it is unclear whether they are conspecific, as some apparently significant morphological differences exist. It seems reasonable, though, to include the Toro Negro megatheriine in Pyramiodontherium.

Two exceptions must be considered. The proximal and distal ends of the tibia of Plesiomegatherium hansmeyeri (MACN 2895: P1. 109A, B) were found in association with cranial material and form part of the type of this species. The medial facet of the proximal surface is markedly elongated and oriented obliquely ( $35^{\circ}$ ) to the transverse plane. The lateral facet is incomplete. Distally the tibia of $P$. hansmeyeri is distinguished by its nearly triangular
section, which is due to reduction of the anterior part of the odontoid facet of the astragalus. Possibly this morphology results from postmortem compression. Other features tend to be more similar to those of $E$. laurillardi than to $M$. americanum. Its posterior margin is only moderately convex, and the facet for the astragalar odontoid process lies adjacent to the posterior part of the facet for the discoid surface of the astragalus (see PES: Astragalus).

The distal end of the tibia is known in the two species of Megathericulus. That of M. patagonicus (MLP : PI. 109C) is more complete than that of M. primaevus (MLP 39-VI-24-1: Pl. 109D), but both preserve significant information. In M. patagonicus the facet for the astragalar odontoid process is considerably longer transversely than the facet for the astragalar discoid surface, than in other megatheriines, except for $M$. primaevus, and is reflected in the morphology of the astragalus (see PES: Astragalus). Only the posterodistal part of the tibia is known for M. primaevus, but is sufficient, however, to demonstrate that the odontoid process, at least posteriorly, is approximately as wide transversely (and possibly wider than) the discoid facet. Further, the ridge between the facets is low and broad. The digital groove in these species (the posterior margins of the groove are broken in M. patagonicus; Pl. 109C) is very prominent and raised high above the tibia by a buttress arising distally from the posteromedial surface of the
tibia, as occurs also in various other sloths, such as Nothrotheriops (Stock, 1925, pl. 14: fig. 1b), Planops (Hoffstetter, 1961, fig. 11). Prepotherium (Scott, 1904: pl. 61, fig. 2a), and Acratocnus (AMNE 17175a), although the buttress is more prominent in these latter genera. A second, wider digital groove lies posterior to the buttress.

Probably, but not certainly, the tendon of the flexor digitorum longus played over the smaller groove, and that of the flexor hallucis profundus over the wider groove. Possibly, a third groove lay anterior to the buttress. This third groove is approximately as narrow as that for the flexor digitorum longus. However, this structure may be an artifact caused by the shape of the tibial margin.

The buttress is absent in all other megatheriines, although its groove persists. The presence of two digital grooves is considered plesiomorphic for ground sloths (Webb, 1989). It persists as a prominent structure in planopsines, nothrotheres, and megalonychids, and in some mylodontids. Loss of the buttress occurred early in the phylogenetic history of megatheriines. The tendency for reduction is already evident in Megathericulus, where the buttress is smaller than in the contemporaneous sloths that possess it.

Several complete or partial megatherine tibiaefibulae, isolated or associated with other skeletal elements, are known. These are not always clearly assignable to a known taxon, and are discussed below.

The proximal half of a megatheriine tibia, MACN 4956, from Entre Rios was assigned, presumably by MACN staff, to Promegatherium. This is not unreasonable, based on its size, but the megatheriines from Entre Rios are poorly understood (see SYSTEMATIC REVIEW OF THE MEGATHERIINAE). The proximal surface of MACN 4956 generally resembles that described above for Pyramiodontherium bergi. It differs in that the lateral facet appears relatively smaller compared to the medial facet, and the facet for the fabella is relatively large and distinct.

The tibia-fibula of FMNH P14499 (P1. 109E), from Corral Quemado, strongly resembles that of Megatherium tarijense FMNH P14216, from the Tarija Valley. The two are nearly identical in size and morphology. The distal fusion between tibia and fibula is more advanced, and the fibula projects distally further beyond the tibia. However, a CI value of nearly 89 for FMNH P14499 suggests caution in regarding it conspecific with $M$. tarijense.

## Sesamoid Bones

Various sesamoid elements are associated with the knee joint. The largest of these, the patella, is discussed separately later. The smaller and more variable sesamoids are discussed here because the tibia bears evidence for their presence and position. The articular surfaces associated with such sesamoids are variable in
megatheriines, as they are, apparently, in other ground sloths (e.g., Stock, 1925; Hirschfeld, 1985). In E. laurillardi, two small elements are frequently recovered. One is the lunula, a nearly semicircular or crescentic, wedge-shaped bone, with flat, approximately crescentic, articular surfaces separated by a rounded and rugose surface. The other, the cyamella, consists of a flat and approximately oval or irregularly triangular articular surface, topped by an irregular and rugose mound-shaped surface. The positions of these elements have been variably interpreted, because the surfaces with which they articulate are often indistinct.

Among other ground sloths, the position and number of facets vary. McDonald (1987) stated that two facets are generally associated with the lateral facet of the proximal tibial surface in scelidotheres. One lies anterolaterally, for the meniscal sesamoid or lunula; the second posterolaterally, for the cyamella or the sesamoid of the popliteus muscle. Stock (1925) reported a small facet for a fabella on the posterior part of the lateral articular surface, and the occasional presence of a narrow facet contiguous with the medial margin of the medial facet of the proximal surface of the tibia in Glossotherium. Further, a third sesamoid facet lies on the anterolateral surface of the proximal end of the fibula in some specimens. Hirschfeld (1985) noted the presence of a fabellar facet
posteriorly on the lateral articular surface of the tibia in Pseudoprepotherium. The facet on the medial margin of the medial articular surface was absent, except in a single specimen. Webb (1989) reported anterolateral and posterolateral cyamellar facets associated with the lateral margin of the lateral articular facet in Thinobadistes.

The facet located posteriorly on the lateral articular surface in E. laurillardi was mentioned above. Cartelle (1992) stated that it articulated with the fabella or lunula. He believed that the cyamella did not belong to the knee joint in E. laurillardi, but that it articulated with a smooth, articular facet on the dorsal surface of the neural spine of the seventh cervical vertebra, which occurs only in this species, as far as is known. Cartelle's opinion is reasonable for three reasons. First, two sesamoidal facets for the knee joint occur in only a single megatherine specimen (vide infra), which was unknown to Cartelle. Second, a sesamoid very probably did articulate with the neural spine, and likely resembled the cyamella. Third, Cartelle has found that near perfect articulation occurs between the facets on the neural spine and cyamellar-Iike sesamoids (in these cases, the sesamoids may indeed articulate with the spine). However, it is probable that the knee joint contained at least both lunula and cyamella. Nearly complete skeletons of two adults of Eremotherium n. sp. have been recovered from Florida (Hulbert et al., 1989).

Two lunulae and two cyamellae, though disarticulated, are associated with each individual. It is not clear whether the spine of the seventh cervical vertebra bore an articular facet. However, if Cartelle's interpretation were correct, the recovery of a single cyamellar-shaped sesamoid, rather than two, would be expected for each individual. Further, FMNH P14499, the tibia from Corral Quemado assigned above to M. tarijense preserves sesamoidal facets anteriorly and posteriorly on the lateral articular surface (Pl. 109E). The anterior facet is crescentic; it is contiguous with the facet for the lateral femoral condyle, but lies on a distinct plane. Its shape clearly resembles the shape of the articular surfaces of the lunula. The approximately oval posterior facet more nearly resembles the general shape of the articular surfaces of cyamellae. Lunulae and cyamellae are comonly found with other megatheriine remains. Thus, there is no reason to doubt that their positions differed from those of FMNE P14499.

In nearly all megatheriine tibiae a narrow, elongated, and crescentic facet is associated with the anterolateral margin of the proximal medial facet, similar to that reported by Stock (1925) in Glossotherium, and Hirschfeld (1985) in a single specimen of Pseudoprepotherium. This facet occurs in nearly all megatheriine remains, and suggests the presence of a third sesamoid; however, this element has not been recognized or recovered.

The patella is well-known in Eremotherium laurillardi (Pl. 109F-J), and less so in Megatherium americanum. It is subtriangular, with a broad proximal base. The posterior surface is nearly flat and bears a large articular surface for the femur. The tapered apex is non-articular, represents tendinous ossification, and varies in size and orientation (Pl. 109). The patella is convex and coarsely rugose on its free surface, and is mound-shaped in lateral view. Kraglievich (1925b) noted that various authors have incorrectly assigned and figured patellae of other taxa as belonging to Megatherium (e.g., Owen, 1859: pl. 38, fig. 2); see Kraglievich (1925b) for other examples.

There do not appear to be consistent taxonomic differences among known megatheriine patella. Kraglievich (1925b) implied that the patella was reduced in $M$. americanum, reflecting the small decreased size of the patellar trochlea of the femur. However, there is a considerable range in the size of the patella and its femoral facet in E. laurillardi (Pl. 109). Kraglievich's (1925b) hypothesis can be tested only if patella and femur are from a single individual, a condition which is extremely rare for $E$. Laurillardi and M. americanum. A corresponding reduction of the femoral facet of the patella is expected with a decrease of the patellar trochlea of the femur.

However, this apparently does not occur, based on the condition in M. istilarti (Kraglievich, 1925b: pl. 6, fig. 1). Kraglievich (1925b) further stated that the patella of M. gaudryi was distinguished in the greater length of the ventral projection, and in that the height of the articular surface clearly exceeded its width. However, it is not clear that such features are specifically diagnostic.

The pes of megatheriines has undergone complex morphological alteration largely due to the adoption of a partial pedolateral stance. This rotation is present in various ground sloths and is discussed below under Functional Morphology of the Pes.

The surfaces of skeletal elements may be described according to the orientations they assume in life, or the anatomically homologous surfaces in a standard (i.e., primitive) posture. The second is the accepted practice, because anatomically homologous surfaces of most mammals are usually unambiguous. The pes is usually described with reference to a plantigrade stance. Thus, the dorsal surface of the astragalus in canis faces nearly anteriorly, and the distal nearly volarly, due to the animal's digitigrade stance.

Skeletal elements of the pes of megatheriines were described by various authors, e.g., Cabrera (1929), Cartelle (1992), Owen (1860), Paula Couto (1978), and Roth (1911). However, their descriptions may be confusing, due largely to imperfect understanding of the posture of the pes. This creates difficulties in the application of orientational terminology in the descriptions. Cartelle's (1992) description is probably the clearest to date, but contains inconsistencies. For example, the navicular is described in
standard anatomical orientation, but the cuboid apparently is not.

It is sufficient here to note that the pes of large megatheriines has not rotated to the degree suggested by Owen (1860), and that differential rotation has possibly occurred within the pes. Elements are described by standard anatomical orientation, and their position in life is explained briefly.

The pes is almost or completely known in Megatherium americanum, M. tarijense, and Eremotherium laurillardi, although often the astragalus and calcaneum are known for other taxa. Few consistent morphological differences exist among taxa. The tarsus comprises six elements: astragalus, calcaneum, cuboid, navicular, ectocuneiform, and the mesocuneiform-entocuneiform complex; the mesocuneiform and entocuneiform are separate in some individuals of $M$. americanum. Pedal digit 3 is complete and bears an ungual. Metatarsal (Mt) I and Mt II and their digits are apparently absent. Mt IV and Mt V are complete, and bear vestigial đigits.

Astragalus
The astragalus of megatheriines is conservative, and few consistent morphologically diagnostic features at the specific level are recognized in this element in PlioPleistocene megatheriines. Isolated astragali (as for pedal
elements in general) can rarely be confidently identified to species, because of general morphological similarities. Exceptions are those recovered from geographical areas known to yield only remains of $M$. americanum or E. laurillardi, and, clearly, falling within the size ranges of these species (Tab. 8; App. 4H). The description given below is based on the astragalus of $E$. laurillardi; it is followed by discussions of the astragali of other species.

The astragalus has undergone considerable modification. The trochlea tali (PI. 110A, B) is formed from two unequal surfaces. The broad, lateral, approximately semicircular surface, termed the discoid facet, is nearly flat. It is generally convex anteroposteriorly, and more strongly so transversely at its perimeter (Pl. 110B-D). In life the broad, nearly flat part of the discoid facet faced dorsomedially. The medial part of the trochlea, the odontoid facet, occupies the dorsolateral half of the peglike odontoid process of the astragalus (PI. 110A-D), which occurs in various ground sloths, and may correlate with torsion of the pes. The odontoid facet is regularly semicircular; its mediodorsal margin transversely convex. In anterior view it faces dorsolaterally, and meets the discoid surface in a rounded angle between approximately $90^{\circ}$ and $110^{\circ}$ to form a deep and well-defined sulcus (Pl. 110B). The odontoid and discoid facets are subequal in width. The odontoid facet lies centrally relative to the discoid facet,

TABLE 8. Standard Statistics (mm) for the Astragali Eremotherium laurillardi and Megatherium americanum. Abbreviations: LENGTH - Greatest anteroposterior length; HEIGHT - Greatest doroventral height, parallel to the long axis through the astragalar odontoid process.

Eremotherium laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :---: | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 39 | 169 | 259 | 208 | 22.9 |
| HEIGHT | 42 | 175 | 256 | 209 | 19.9 |

Megatherium americanum

| Variable $N$ | Minimum | Maximum | Mean | Std Dev |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 27 | 163 | 238 | 204 | 16.6 |
| HEIGHT | 31 | 169 | 253 | 214 | 19.6 |

so that they appear as balves of concentric semicircles when viewed through the long axis of the odontoid process (Pl. 111A-C; De Iuliis, 1994: fig. 7B). The astragalus lies so that the dorsal margin of the odontoid facet is somewhat dorsal to that of the discoid facet.

The fibular facet is contiguous with the posterior three-fourths of the lateral margin of the discoid facet. Its shape varies considerably (Paula Couto, 1978). It is more prominent anteriorly, and ranges from nearly triangular, with a palmar apex, to variably lobate.

The head of the astragalus is carried by an extremely short and largely indistinct neck (Pl. 110A). The navicular facet lies on its anterior surface. The discoid and navicular facets are separated by a variably narrow tract of rugose bone (Pl. 110B). The navicular facet is approximately oval, with long axis oblique (dorsolateral to ventromedial) and nearly perpendicular to that of the odontoid process. Its dorsolateral half forms a deep circular depression; its ventromedial half is wider and convex. A stout, rugose ridge extends between the dorsomedial margin of the convex part of the facet and the summit of the odontoid process (P1. 110D).

The cuboid facet (PI. 110B, C, E, F) lies ventral to and is continuous with the navicular facet. It varies from nearly oval, trapezoidal, or quadrangular, and is convex along its major axes. In some specimens the cuboid facet is
poorly demarcated from the convex half of the navicular facet and appears continuous with it. In others the facets are contiguous, and separated by a low, blunt ridge, as in Plate 110B.

The remaining two articular facets articulate with the calcaneum. Their surfaces and spatial orientations are not easily described. The smaller, sustentacular facet lies nearly posterior to the cuboid facet, and its anterior margin is contiguous with it (Pl. 110E, F). The remaining margins are free and raised from the surrounding, rugose, non-articular bone, particularly adjacent to the sulcus tali. It is approximately tear-shaped or oval, with its long axis nearly parallel to the sulcus tali, and its tapered end lateral and slightly ventral. The sustentacular facet faces principally posteroventrally and slightly posteromedially (Pl. 110F). Its surface is nearly flat anteroposteriorly, and gently convex transversely.

The ectal facet lies posterodorsal to and is approximately thrice the size of the sustentacular. It varies in shape, but is usually oval, with its long axis oblique. It is oriented nearly anterolaterally to posteromedially, and faces primarily posteroventrally (Pl. $110 \mathrm{C}-\mathrm{E}$ ). The anterolateral half of the facet is nearly flat. The posteromedial half is concave along its major axis and convex along its minor axis. The facet is usually broadest over the convex minor axis.

The rugose sulcus tali is nearly transverse, extending anterolaterally to posteromedially (Pl. 110E). It is usually deep, particularly laterally. The sulcus extends medially into the subodontoid fossa, a shallow, anteroposteriorly broad, and nearly quadrangular, depression at the ventromedial base of the odontoid process (P1. 110F). Its anterolateral and posterolateral margins are formed by the sustentacular and ectal facets, respectively. Its anteromedial margin coincides with the ventromedial margin of the ridge that extends between the navicular facet and sumit of the odontoid process. The posteromedial margin of the fossa is formed by a dorsomedial continuation of the astragalar surface that lies between the discoid and ectal facets posteriorly.

The astragalus of M . americanum (Pls. 111B-F, 112A-D) is similar morphologically to that of E. laurillardi. Gazin's (1957:352; cf. figs. 5,6) claim that the odontoid process was "rather different" is correct, but perhaps not to the degree represented in his diagrams, in which the pes of these species are in somewhat dissimilar orientations. The odontoid process in M. americanum is somewhat rounder and less elongated, and apparently slightly wider, particularly near the discoid facet (cf. Pls. 110D and 111D, E).

The astragali of these species do not vary significantly in height $(t=1.0, d f=71, p=0.32)$ or length ( $\chi^{2}$
approximation $=0.003$, $d f=1, p=0.95$ ), and height and length are highly correlated in E. laurillardi and M. americanum ( $r^{2}=.83, .80$, respectively). However, there is a significant difference ( $F=8.88, \mathrm{p}=0.004$ ) between species in height when covariation in length is considered (see Fig. 11).

Three other characters are apparently diagnostic. Posteriorly the ectal facet and discoid facet approach each other more closely in M. americanum, and may be contiguous. A result of this feature is that the posterior part of the astragalus appears more rounded (cf. Pls. 110D and 111D, E). The anterior margin of the ectal facet lies more anterior relative to the fibular facet in $E$. laurillardi (cf. Pls. 110D and 111D-F; Gazin, 1957). Further, in M. americanum the position of the mediodorsal part of the navicular facet is further ventral compared to the surface or plane of the discoid facet than in E. laurillardi. The difference may be appreciated by comparing the astragali in fibular view, with the long axis of the odontoid process oriented vertically: in $E$. laurillardi the bony ridge between the anterior margin of the odontoid process and the navicular facet is considerably higher relative to the plane of the discoid facet (cf. Pls. 110D and 111B, D, and 112A)

The astragalus of $M$. tarijense (P1. 112E-G) is smaller, and less angular in general appearance. In proportions and morphology it is similar to that of $E$. laurillardi. It
shares with M. americanum a wider and more rounded odontoid process, reduced separation posteriorly between the ectal and discoid facets, and similar positions of the ectal and fibular facets. Also, the dorsomedial part of the navicular facet is further ventral than in E. laurillardi, and approximately intermediate between that of the latter and $M$. americanum. The astragalus of M. medinae (Casamiquela and Sepulveda, 1974: pls. 8, 9) is similar in size and morphology to that of $M$. tarijense.

The astragalus of Pyramiodontherium bergi (MLP 2-66; P1. 113A-C, De Iuliis, 1994: fig 6D) was described by Roth (1911), who noted numerous differences between it and that of M. americanum; some are real, but others are dubious. There are two main sources for the differences described by Roth (1911). First, MLP 2-66 has suffered considerable breakage and, although restored, some distortion remains. Second, Roth (1911) apparently did not consider variation within M. americanum. The differences described by Roth (1911: figs. 3,4) are either due to the use of photographs of the astragali in different perspectives or accentuated by them. Further, P. bergi often differs from M. americanum in the same way as does E. laurillardi, and thus P. bergi does not represent a particularly strange megatheriine.

A few examples of Roth's (1911) supposed differences follow. He described the fibular facet in M. americanum as semilunar, and lacking well-marked margins: that in P. bergi

FIGURE 11.
Bivariate plot (mm) of Height against length for the astragali of Megatheriinae. Equations for regression lines: Eremotherium laurillardi, y =
$0.79 x+4.36 ;$ Megatherium americanum, $Y$ $=1.03 x+0.22$.

as composed of two sections, one approximately circular, the other narrow, with margins raised well above the surrounding bone. However, the shape of the fibular facet can be expected to vary considerably, based on variation in $E$. laurillardi. Indeed, the fibular facet may be bilobate with well-defined margins in some M. americanum (e.g., MNHNP 1871). The fibular facet in $P$. bergi resembles that in $E$. laurillardi in shape, but lies relatively anteriorly. The union between the discoid and fibular facets is more angular in P. bergi than in M. americanum (Roth, 1911) and E. Laurillardi.

Roth (1911) recognized the greater separation posteriorly between the discoid and ectal facets in P. bergi, which resembles that in $E$. laurillardi (in fairness to Roth, this genus was unknown in 1911). However, Roth (1911) stated that the facets are contiguous in $M$. americanum. Contiguity may occur, but the facets are usually separated by a narrow strip of non-articular bone. Similarly, Roth (1911, cf. fig. 3) described the navicular and discoid facets as contiguous anterodorsally in $M$. americanum, but separate in P. bergi. Again, however, contiguity in $M$. americanum is probably exceptional. In other specimens the facets are separated by a patch of nonarticular bone of variable width and depth (e.g., BMNH 19953; MNENP 1871; MLP 44-XII-28-1). Similar variation occurs in E. laurillardi.

The astragalar odontoid process in $P$. bergi is relatively longer and more cylindrical than in M. americanum (Roth, 1911), and resembles that in E. laurillardi. Roth (1911) reported that the odontoid facet was slightly constricted near its union with the discoid facet. However, it is unclear whether this is natural or the result of postmortem damage. Roth (1911) also reported a more angular contact between the odontoid and discoid facets in P. bergi. The angle is approximately $100^{\circ}$, which falls within the range for $E$. laurillardi. Angular variation between these facets is not as well-known in M. americanum, but measurements generally fall between $110^{\circ}$ to $115^{\circ}$.

In $P$. bergi the ridge extending between the navicular facet and summit of the astragalar odontoid process bears a prominent ventromedial expansion, termed the odontoid tuberosity. It is represented by a low nubbin in $M$. americanum (Roth, 1911) and E. laurillardi. The circular depression of the navicular facet is shallower than in Megatherium (Roth, 1911) and Eremotherium.

A difference not noted by Roth (1911) is the position of the navicular facet relative to the discoid facet. In Megatherium and Eremotherium the mediodorsal margin of the navicular facet is nearly (particularly in the former), at the same level as the broad, flat surface of the discoid facet. This feature is best observed in anterior or fibular view, with the long axis of the odontoid process
oriented vertically (vide supra). In these views a small portion of the navicular facet projects above the level of the discoid facet. In P. bergi the facet lies further dorsally, so that a portion of the circular depression of the navicular facet intersects the plane of the discoid surface (cf. Pls. 110D, 111D, and 113A).

The astragali of earlier megatheriines are known from various localities, but the taxonomic identity of some is uncertain. Those that may be assigned confidently to genus and species are MACN (without catalogue number), of Megathericulus patagonicus (Pl. 113C, D; De Iuliis, 1994: fig. 6A), and MLP 39-VI-24-1, of M. primaenus (Pl. 14A-C). A group of astragali are known from Entre Rios Province, Argentina, but precise locality information is unavailable. These include MACN 4941, assigned by museum label to Megatherium antiquum; MACN 13667 (Pl. 114D, E), assigned simply to 'Gravigrada'; and MACN 4992, the type of Eomegatherium nanum (P1. 115A-C). MACN 2904 (PI. 115D-F), apparently from the Hermosense of Monte Hermoso, is assigned by museum label to Megatherium gaudryi. MLP 2-206, from Laguna Blanca, is the type of Eomegatherium cabrerai (P1. 116A, B). The reader is referred to the appropriate sections of SYSTEMATIC REVIEN OF THE MEGATHERIINAE for explanations of the status and taxonomy of these taxa. Although the astragali listed above are generally isolated finds, they are certainly megatheriine and reflect an aspect
of the probable evolutionary history of the megatherine astragalus.

The earliest certain megatheriine is Megathericulus patagonicus. Its type includes the astragalus. Additional remains were reported by Scillato-Yané et al. (1992). The astragalar odontoid process is a tall, peg-like structure. It is better developed than in Eremotherium, Megatherium, and Pyramiodontherium, and strongly resembles that of Glossotherium (Stock, 1917: fig. 1; 1925: fig. 97; and AMNH 16896) and scelidotheriines (Winge, 1915: pls. 32, 33, 41, 42; and AMNH 128738). Further similarities are that the odontoid facet is wider than the discoid facet, and its dorsomedial surface is strongly convex.

An important characteristic shared by various sloths, including the mylodonts mentioned above, Hapalops, planopsines, and Plio-Pleistocene nothrotheres is that the navicular facet projects well dorsal to the discoid facet when the long axis of the astragalar odontoid process is oriented vertically. The fibular facet is relatively large, particularly anteriorly. In Hapalops the facet resembles a coma, rotated $90^{\circ}$ counterclockwise in a right astragalus. Its anteroventral and posteroventral margins are contiguous respectively with the anterolateral and posterolateral margins of the ectal facet. This condition is maintained in M. patagonicus, but the anterior part of the facet is relatively smaller. The facet strongly resembles that of
scelidotheres.
The separation posteriorly between the ectal and discoid facets resembles that in Eremotherium and Pyramiodontherium. The facets are closer together in Hapalops, Megatherium, and scelidotheres. The posterior part of the discoid facet is abbreviated and at an obtuse angle relative to the odontoid surface in Megathericulus, Hapalops, planopsines, and scelidotheriines.

A prominent odontoid tuberosity, similar to that in Pyramiodontherium, is present but somewhat smaller in Megathericulus, possibly due to damage. A smaller tuberosity occurs in Glossotherium and scelidotheriines.

A small, smooth, concave, and approximately oval articular facet lies between the tuberosity and the posteromedial part of the odontoid facet; indeed, the facets are briefly contiguous. The facet probably articulated with a small sesamoid bone. A small facet is present in approximately corresponding position in Hapalops (e.g., AMNH 94743), but an astragalar odontoid process is not developed. The corresponding region in Pyramiodontherium is concave, but the facet apparently absent. A facet may be present in scelidotheriines, based on the available material, and absent in Glossotherium, Eremotherium, and Megatherium.

The sustentacular facet is extended posteriorly into a narrow, tapered, and strongly convex region. A ridge extends between this region and the non-articular surface
posterior to the discoid facet. The ridge and tapered region separate the sulcus tali from the subodontoid fossa. The astragalus of MegathericuIus primaevus, MLP 39-VI-24-1, is smaller than, but morphologically very similar to, that in M. patagonicus (Cabrera, 1939). One difference is that the odontoid tuberosity is less prominent, but remains a distinct structure, approximately as in Glossotherium, rather than the reduced nubbin in Megatherium and Eremotherium. The sesamoidal facet is relatively larger than in Megathericulus patagonicus. The length of the contiguous margins of the ectal facet and the anterior part of the fibular facet is intermediate between that of Prepotherium and M. patagonicus.

The astragali from Entre Ríos Province share various and probably primitive similarities, but apparently represent two forms or types. Among the similarities are: size; a peg-shaped astragalar odontoia process, which leans slightly anteriorly; a navicular facet projecting above the discoid facet; a more nearly triangular sustentacular facet; and separated sulcus tali and subodontoid fossa.

MACN 4992, the type of Eomegatherium nanum, represents a form that more closely resembles the astragalus of $M$. patagonicus. Differences include: reduced dorsal projection of the navicular facet; anterior part of the fibular facet separated from the ectal facet and does not extend so far ventrally; greater separation posteriorly between the ectal
and discoid facets; a less prominent odontoid tuberosity; no or possibly vestigial sesamoid facet; and a more nearly oval sustentacular facet.

MACN 4941 and MACN 13667 represent a second, apparently more derived, form from Entre Ríos Province. The astragalar odontoid process is less peg-shaped. The position of the navicular facet resembles that in Pyramiodontherium, i.e., approximately intermediate between that of Megathericulus and those of Megatherium and Eremotherium. The anterior part of the fibular facet is somewhat rounded ventrally, rather than tapered, and further separated from the ectal facet. The odontoid tuberosity is apparently reduced. The ridge between the sulcus tali and subodontoid fossa is weak.

MACN 2904 is from Monte Hermoso. Its astragalar odontoid process is incomplete, but apparently somewhat more peg-like than in MACN 4941 and MACN 13667. The odontoid tuberosity is apparently more prominent. The navicular facet projects somewhat less beyond the discoid facet. The ridge between the sulcus tali and subodontoid fossa is reduced to a low tuberosity adjacent to the sustentacular facet.

The relationship between the Monte Hermoso astragalus, MACN 2904, and that represented by MACN 4941 and MACN 13667 is unclear. Differences are minor, though possibly diagnostic. The type of Eomegatherium cabrerai is a left astragalus from Laguna Blanca (Chubut Province, Argentina).

MLP 2-206, missing its posterior third. Kraglievich (1930) stated that it was proportionately similar to that of $E$. nanum. The astragali are nearly identical in size, but Kraglievich's statement is somewhat misleading. Indeed, the following features of MLP 2-206 are shared by M. patagonicus and M. primaevus, and not E. nanum. The navicular facet is further dorsal. The anterior margin of the ectal facet is further anterior. The surface of the ectal facet is less inclined the greater inclination in Eomegatherium is shared with the larger megatheriines). The fibular and ectal facets are apparently contiguous anteroventrally. MLP 2-206 is larger than the astragali of M. patagonicus and M. primaevus. Among the astragali discussed in this paragraph, it resembles that of $M$. primaerus most strongly, rather than those of M. patagonicus and $E$. nanum.

The astragalus of the Toro Negro megatheriine (MLP 68-III-14-1; P1. 116C-E) resembles that of the earlier or primitive megatheriines. Thus the odontoid process and position of the navicular facet resemble those in Megathericulus patagonicus. Posteriorly the discoid facet is only slightly larger than in the latter. The oval fibular facet is prominent anteriorly, but small posteriorly.

The morphological changes that occur in the astragali of the following sequence of taxa require comment: Hapalops (AMNH 94743), Prepotherium potens (MACN 4694), Megathericulus primaevus (MLP 39-VI-24-1), M. patagonicus (MACN, without catalogue number), Eomegatherium nanum (MACN 4992), and Eremotherium laurillardi (ROM 22008). This series probably does not represent a phylogenetic progression, but may suggest the probable general trends in the evolution of the megatheriine astragalus. It also serves to sumarize our knowledge of this element in megatheriines. Figure 12 provides calcaneal views of some of these taxa.

In Hapalops the trochlea tali is formed from a wider, longer, and anteroposteriorly convex lateral part, corresponding to the discoid facet, and a smaller medial part, corresponding to the odontoid facet. Its medial surface closely approaches the navicular facet. The sulcus is moderately deep and displaced medially. The trochlea tali appears nearly as in a standard mamalian astragalus in anterior view, but in dorsal view the medial surface is abbreviated anteroposterioriy. In fibular view the medial surface resembles the odontoid surface of later megatheriines, but it is not a separate and distinct structure. The sesamoid facet is oval and concave anteroposteriorly. It lies on the medial surface, opposite
the dorsomedial surface of the medial surface of the trochlea tali (i.e., it is the medial analogue of the fibular facet). The region anterior to it is raised into a small nubbin.

The fibular facet is prominent, and occupies most of the lateral surface. It is crescentic, and considerably more prominent anteriorly. The facet is contiguous laterally with the trochlea tali, and with the ectal facet anteriorly and posteriorly. The ectal facet and lateral part of the trochlea tali approach each other closely posteriorly.

The navicular facet lies dorsal to the lateral surface of the trochlea tali, and its long axis is nearly horizontal. The medial depression of the navicular facet is somewhat oval, rather than nearly circular. The ectal facet is elongate and concave anteroposteriorly. The sustentacular facet is approximately tear-shaped, with tapered end posterior. The anterior two-thirds are flat, the posterior third concave. A ridge continues posteriorly from the tapered end and closes the sulcus tali.

In Prepotherium the medial surface of the trochlea tali is wider than the lateral. It is raised, however, and begins to resemble an odontoid process. Apparently this has occurred through the mediodorsal expansion of the articular surface, medial expansion of the non-articular bone that supports it, and posterodorsal rotation through the long

## FIGURE 12.

Calcaneal view of the right astragalus of Megatheriidae. A. Planopsinae (MACN 4694, diagrammatically reversed from original left); B. Megathericulus primaevus (MLP 39-VI-24-1); C. Megathericulus patagonicus (MACN, without catalogue number): D. Eomegatherium nanum (MACN 4992, diagramatically reversed from original Ieft). Abbreviations: $c$ - cuboidal facet; e - ectal facet for the calcaneum; $n$ navicular facet; ot - odontoid tuberosity; s - sustentacular facet for the calcaneum; so - subodontoid fossa; $x$ - sesamoidal facet. Scale bars represent 50 mm .

axis of the odontoid, so that it assumes a nearly upright position relative to the lateral surface of the trochlea tali, and is displaced from the navicular facet. A small, discrete, subodontoid fossa lies medial to the posterior part of the sustentacular facet. The sesamoid facet is more prominent and concave, and the nubbin increased in size to form a tuberosity. The astragalus is similar to that of Hapalops in other respects.

The astragalus of Megathericulus primaevs is larger, and similar morphologically, except as follows. The odontoid process is more nearly upright and robust. The sesamoid facet, odontoid tuberosity, and subodontoid fossa are relatively larger. The separations between the ectal and discoid facets posteriorly and between the odontoid and navicular facets anteriorly are greater. The astragalus of M. patagonicus is larger. The odontoid process is a large, well-developed, peg-shaped structure, which leans slightly anteriorly. The subodontoid fossa is larger. The sesamoid facet is larger and forms the dorsomedial end of a relatively wide groove adjacent to the posterior margin of the odontoid facet. The navicular and odontoid facets are further separated. The odontoid tuberosity is prominent, resembling that of Pyramiodontherium. The navicular facet does not project as far dorsal to the discoid facet; the plane of the latter intersects the ventral third of the circular depression of the navicular facet.

In MACN 4992, Eomegatherium, the odontoid process is well- formed, nearly upright, with only slight anterior inclination, and separated considerably from the navicular facet. The tuberosity is large, but less distinct than in M. patagonicus, The sesamoid facet is apparently absent, or possibly vestigial, but a well-defined groove remains. The navicular facet is ventral, with the plane of the discoid facet intersecting approximately the centre of the circular depression of the navicular facet. The discoid facet is larger posterior to the odontoid process. The fibular facet is morphologically similar, but separated from the ectal facet. The tapered part of the sustentacular facet is reduced, so that it is more nearly oval, and the ridge extending from it reduced. Thus, there is less complete separation between the large subodontoid fossa and sulcus tali.

In Eremotherium laurillardi the odontoid process is upright. The discoid facet is enlarged posteriorly, so that the odontoid process is nearly central with respect to the discoid facet. The odontoid facet is narrower than the discoid facet. The navicular facet lies further ventrally, with the plane of the discoid facet intersecting the dorsal part of the navicular facet. The subodontoid process is apparently reduced, and does not project as in Megathericulus and Pyramiodontherium. However, it is not a small structure, and its relative smallness may be due to
differential increase of the odontoid process. The sesamoid facet is absent, and the homologous osseous surface is coarse, but a groove remains.

The anterior part of the fibular facet is dorsoventrally abbreviated, and is broadly triangular. The fibular facet is separate from the ectal facet. The sustentacular facet is approximately oval; its posterior end is not tapered and lies well above the non-articular surface. The ridge is extremely reduced, such that the large subodontoid fossa and sulcus tali are continuous.

## Calcaneum

The calcaneum of megatheriines, unlike that of most ground sloths, is elongated and tapers posteriorly. However, it is know in only few genera. Paula Couto (1978) described the calcaneum for Eremotherium laurillardi, Owen (1860) for Megatherium americanum, and Roth (1911) for Pyramiodontherium bergi. Unfortunately, these authors provided little comparative information.

The calcaneum of E. laurillardi (P1. 117) is elongated and relatively narrow, but varies in robustness (cf. PI. 118A and B). The tuber calcanei extends posteriorly as a robust. rugose, and tapered epiphysis. The plane of epiphyseal fusion is raised on the dorsal surface as a posteriorly convex and nodular ridge.

Two prominent sulci constrict the calcaneum between the
articular surfaces and epiphysis. The sulcus for the $m$. flexoris hallucis longus lies anteromedially, posteroventral to the sustentaculum tali; the sulcus for the m. peroneus laterally, posterior to the processus trochlearis.

Three articular facets lie anteriorly. The facets for the cuboid and sustentaculum are contiguous. The latter is approximately teardrop-shaped, with tapered end lateral, gently concave transversely, and faces anterodorsally. The facet for the cuboid lies lateroventral to the sustentacular, and faces nearly anteriorly. It may be similarly shaped, approximately semicircular, or oval, with a narrower medial end. It ranges from approximately onethird to two-thirds the size of the sustentacular facet.

The sulcus calcanei lies dorsal to these facets, oriented nearly transversely, but with its medial end more dorsal. It is usually deeper centrally and shallower medially. Its width varies, depending usually on the width of the ectal facet, which is the third facet of the calcaneum. The latter lies posterodorsal to the facets for the cuboid and sustentaculum, and faces largely anterodorsally. It is approximately oval, with long axis ventrolateral to dorsomedial, but often appears nearly triangular in dorsal and anterior views because the medial part is strongly curved and faces nearly medially. The size of this portion of the facet varies, and may be relatively large. The surface of the facet, particularly
medially, is concave perpendicular to its long axis. The maximum width occurs approximately where the facet curves posteromedially. The ventromedial margin of the facet may be expanded, often coinciding with the maximum width and resulting in a constriction of the sulcus calcanei. The sulcus calcanei may be closed laterally by expansion of the ectal facet, as in ROM 22004. The appearance and orientation of the ectal facet may be considerably altered by relatively minor changes in perspective (vide infra, MLP 68-III-14-1). The stout processus trochlearis projects laterally, and lies between the lateral margin of the ectal facet and sulcus for the $m$. peroneus.

The ventral, or volar, surface of the calcaneum is largely rugose. Various ridges and tuberosities may be recognized, following the terminology of Roth (1911) for Megatherium americanum and Pyramiodontherium bergi; however, their forms vary. A prominent, wide, and rugose ridge lies medially, posterior to the sulcus for the $m$. hallucis longus. It may be separated from or nearly continuous with the rugose region posterior to the facet for the cuboid. A prominent and rugose ridge lies on the lateral margin posterior to the sulcus for the $m$. peroneus. The surface between these ridges is relatively smooth and often depressed.

A stout tuberosity lies ventral to the processus trochlearis and projects posteriorly. It is usually
separated from the medial rugose ridge by the relatively smooth ridge that separates the depression of the ventral surface and the sulcus m. hallucis longus. Occasionally, the tuberosity extends further posteriorly and joins the medial ridge to enclose a nearly circular canal (e.g., ROM 30769) .

A tuberous region extends transversely posterior to the cuboidal facet. An anteroposterior sulcus may divide the region into two tuberosities, but the sulcus may be absent (e.g., ROM 22006) or weakly developed. A wider and approximately transverse sulcus often lies posterior to the tuberous region (or tuberosities), and separates it from the medial ridge. However, it may be missing (e.g., ROM 30770) so that the ridge and tuberosities form a nearly continuous surface.

The calcaneum (Tab. 9) of M. americanum (Pls. 118C, D; 119A) does not vary significantly ( $\chi^{2}$ approximation=0.04, $d f=1, p=0.83$ ) in length from that of $E$. laurillardi, but is significantly wider posteriorly ( $t=4.24, \mathrm{df}=47, \mathrm{p}=0.0001$ ); it is thus less gracile (Fig. 13). A possibly shorter region between the epiphysis and articular surfaces may contribute to this appearance. In fibular view (Pl. 119A) the calcaneum appears less elongated and higher anteriorly than in E. laurillardi.

The sulci for the $m$. hallucis longus and $m$. peroneus generally lie more nearly opposite each other. Variation

TABLE 9. Standard Statistics (mm) for the Calcanea Eremotherium Iaurillardi and Megatherium americanum. Abbreviations: LENGTH - Greatest anteroposterior length; PWIDTH - Greatest posterior transverse

Eremotherium laurillardi

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :---: | :---: | :---: | :---: | :---: |
| LENGTH | 31 | 316 | 508 | 392 | 41.8 |
| PWIDTH | 36 | 119 | 192 | 148 | 18.0 |

Megatherium americanum

| Variable | N | Minimum | Maximum | Mean | Std Dev |
| :--- | :--- | :--- | :--- | :--- | :--- |
| - LENGTH | 15 | 321 | 417 | 387 | 26.0 |
| PWIDTH | 13 | 142 | 190 | 171 | 12.9 |

similar to that of $E$. laurillardi occurs in shape of the ectal facet and, consequently, in the width of the sulcus calcanei. The sustentacular and ectal facets may be fused (Kraglievich, 1926). The processus trochlearis is generally better defined and projects more prominently. A circular canal may be present ventral to the sulcus for the $m$. peroneus (e.g., ROM 10629). Tuberosities, ridges, and sulci on the ventral surface may be arranged as described by Roth (1911), but the sulci may be weak or absent, as in $E$. laurillardi. In ROM 10649 the perimeter of the ventral surface is almost all rugose, because the sulci are very weak, and the tuberosity ventral to processus trochlearis is connected to the lateral ridge.

The type of $M$. tarijense is based on a left calcaneum, MNHNP TAR1269 (P1. 119B, C), from the Tarija Valley, Bolivia, which lacks a small portion anteromedially and has various surfaces eroded. The sustentacular and ectal facets are partially fused across the sulcus calcanei. The calcaneum is relatively short and stocky compared to that of M. americanum, but resembles the latter in fibular view. The processus trochlearis is less prominent, and somewhat rounded and blunt. The relative positions of the sulci for the $m$. hallucis longus and $m$. peroneus are apparently more similar to those in M. americanum than those in $E$. laurillardi. The ventral surface is considerably less rugose than in either. The lateral and medial ridges are

FIGURE 13.
Bivariate plot (mm) of Posterior width (pwidth) and length for the calcanea of Megatheriinae. Equations for regression lines: Eremothgerium Laurillardi, y = $0.35 x+1.09$; Megatherium americanum, $y$ $=0.32 x+4.71$.

absent, and the tuberosity ventral to the processus trochlearis is blunt and poorly developed.

The calcaneum of M. tarijense FMNH P14216 (P1. 119D) is similar in size and morphology to that of MNHNP TAR1269. In FMNH P14216 the sulcus calcanei is uninterrupted, although the margins of the ectal and sustentacular facets approach closely medially. A canal is not present ventral to the sulcus for the $m$. hallucis longus. FMNF P14216 is dorsoventrally higher at the epiphyseal suture. Their minor differences may reasonably be attributed to individual variation. The calcanea of $M$. medinae (Casamiquela and Sepulveda, 1974: pls. 8, 9) are similar in size and shape to those just described for M. tarijense.

The calcaneum of Pyramiodontherium bergi (P1.120A) is more gracile than that of $E$. laurillardi. The relative positions of the sulci for the $m$. hallucis longus and $m$. peroneus are approximately as in E. laurillardi. The description given by Roth (1911) is generally correct, but requires the following qualifications. He stated that the lateral margin of the ectal facet reached the lateral surface of the calcaneum in $P$. bergi, but not in $M$. americanum. However, the margin closely approaches the lateral surface in some individuals of $M$. americanum and $E$. laurillardi. Thus the condition described by Roth (1911) for P. bergi is probably not diagnostic. Similar arguments apply to the arrangements of ridges, sulci, and tuberosities
on the ventral surface of the calcaneum.
The calcaneum of the Toro Negro megatheriine, MLP 68-III-14-1, is relatively short and robust, approximately as in M. tarijense. The relative positions of the sulci appear to resemble those in $M$. americanum, as does the form of the processus trochlearis, except that it is more gracile. Two views of the calcaneum (Pl. 120B, C) demonstrate perceived differences caused by relatively minor shifts in position; note particularly the changes in shape and size of the ectal facet.

Various other, usually isolated, calcanea are known. These cannot be confidently assigned to genus and species, based solely on morphology and size. The calcaneum of $E$. laurillardi varies in length from $500 \mathrm{~mm}(\mathbb{M N R J} 4335)$ to 316 mm (MNRJ 2139). The largest certain M. americanum calcaneum, based on morphology and provenance, is 417 mm (BMNE 19953), the smallest 344 mm (MACN 10147); however the range is probably larger, based on variation in $E$. laurillardi (Tab. 9; App. 4I). Thus, MACN 7063 (Pl. 120D), a left calcaneum from Río Salado, near Esperanza, Santa Fé Province, Argentina, which probably represents $M$. americanum, is only 316 mm long. MACN 11486 (Pl.120E), from the "middle Pampean" of Río Caracarañá, Santa Fé Province, is even smaller at 278 mm long. Morphologically it resembles that of M. americanum, particularly MNHNP 1907-15 from the Tarija Valley, Bolivia. However, it appears
slightly narrower, and intermediate between this species and M. tarijense, and nearly as long as the latter. It is difficult to assign this calcaneum to a species. FMNH P14240, also from the Tarija Valley, strongly resembles $M$. americanum in size and morphology, and is assigned to this species.

Three left calcanea from Entre Ríos Province, Argentina, were studied. These are MACN 4926 (Pl. 120F), MACN 4927 (P1. 120G), and MACN 12303 (P1. 120H), assigned by museum label to Promegatherium smaltatum, Megatherium antiquum?, and Promegatherium, respectively. They are similar in size and share general features of the megatheriine calcaneum. However, they differ markedly in proportions. MACN 12303 and MACN 4927 are similar in width, but the latter differs in a more prominent development of the ventrolateral surface. Such variation may, conceivably, represent intraspecific variation. MACN 4226 is considerably more gracile and elongated, and resembles that of Pyramiodontherium bergi, except that the sulcus $m$. peronaei is wider and posteriorly extended. Probably the calcanea from Entre Ríos Province represent two forms, perhaps Promegatherium and Plesiomegatherium, based on the two types of mandible recovered from Entre Ríos (see MANDIBLE), but precise taxonomic determinations cannot be made.

The navicular (PI. 121A-D) is a broad, elongated, and anteroposteriorly compressed element. It is subrectangular to nearly oval, with long axis oriented dorsolaterally to ventromedially. The posterior surface is almost entirely articular. Its dorsolateral half is formed by a large condylar prominence, which is received by the circular depression of the astragalus. The ventromedial half is concave along both main axes. Anteriorly the navicular is convex along both main axes; and is therefore considerably thicker dorsolaterally than ventromedially. Two articular facets lie on the anterior surface. The larger ectocuneiform facet is nearly triangular to trapezoidal, with narrow end ventromedial. The smaller facet is elongated, with major axis approximately parallel to that of the navicular. It articulates with the mesocuneiformentocuneiform complex, and lies mediodorsally to the facet for the ectocuneiform. The facets are contiguous dorsally, but separated ventrally by an elongated strip of nonarticular bone, which is pierced dorsally by a large nutrient foramen.

The two facets for the cuboid are nearly flat, lie on the ventrolaterally facing surface of the navicular, and are separated by non-articular bone. They are contiguous posteriorly with the astragalar facet. The dorsal facet is nearly semicircular or trapezoidal. Anteriorly it may be
contiguous with or separated from the facet for the ectocuneiform (Cartelle, 1992). The smaller ventral facet may be absent (Cartelle, 1992), but is often crescentic and separate from the facet for the ectocuneiform. The navicular of other megatheriines is morphologically similar. The facets for the cuboid coalesce into a single large articular surface in one navicular of M. americanum (MLP 28-III-16-1) .

Cuboic
The cuboid (Pls. 121E, 122) is irregularly shaped, and articulates with the calcaneum, astragalus, navicular, metatarsal (Mt) IV, and Mt V; and occasionally with the ectocuneiform (Cartelle, 1992). Its non-articular dorsal and ventral surfaces face dorsolaterally and ventromedially, respectively. Its posterior surface bears the calcaneal facet, which is formed from a nearly semicircular, dorsolateral part, and a smaller, tapering, ventromedial part.

The astragalar facet lies on the anatomically medial surface of the cuboid, and is contiguous posteriorly with the facet for the calcaneum. It is approximately oval, with long axis dorsolateral to ventromedial, and concave along both main axes. The facet faces mainly dorsomedially, and slightly posterodorsally. The navicular facets lie along the anteromedial margin of the cuboid. The larger dorsal
facer faces dorsomedially; the smaller nearly laterally. The facet for Mt V lies laterally, and is generally smaller than, but occasionally as large as, the astragalar facet. It varies considerably, but is usually nearly triangular, with its long axis nearly dorsoventral and the apex posterior; its surface is gently convex along both its main axes. The anterior margin, gently convex anteriorly, is contiguous with the lateral margin for the facet for Mt IV. The latter consists mainly of a dorsoventrally elongated lateral portion. Mediodorsally the lateral surface of a median, keel-shaped flange supports an anterodorsal extension of the articular surface. A similar, but less prominent, extension lies ventrally. Cartelle (1992) reported a small, mediodorsal facet for the ectocuneiform in some specimens.

Ectocuneiform
Cartelle (1992) accurately described the morphology and variations of the ectocuneiform and few supplementary comments are required. The ectocuneiform (Pl. 123A-C) is approximately triangular, with base dorsolateral and apex ventromedial, and elongated along this axis. It is strongly compressed anteroposteriorly and curved anteriorly along its main axes. The concave navicular and convex Mt III facets almost comprise its posterior and anterior surfaces, respectively. The facets resemble the ectocuneiform in
shape. The dorsal part of the facet for Mt III is prominently curved across its width.

Mesocuneiform-Entocuneiform Complex
The fused complex (PI. 123D-F) is nearly triangular, with its apex anterior. Its posterior surface bears an elongated facet for the navicular. A small, oval facet lies dorsolaterally for Mt III. In life the long axis of the element was aligned obliquely, as with the ectocuneiform and navicular.

The composite nature of this element was first recognized by Cabrera (1929), who noted that the mesocuneiform and entocuneiform occur separately in some individuals of Megatherium americanum. His observations are confirmed by the presence of unfused elements in other specimens (e.g., MLP 2-79, MLP 44-XII-28-1). Owen (1860) termed the complex the mesocuneiform. Cabrera (1929) noted that it (or another skeletal element) was improperly represented in the left pes by Owen (1860: pl. 25).

Cartelle (1992) generally agreed with and cited Cabrera (1929), but apparently believed that the complex in $E$. laurillardi included the falciform, entocuneiform, and mesocuneiform, essentially following Cabrera (1929), or alternatively the mesocuneiform and Mt II. However, Cabrera (1929) did not include the falciform in the complex, but reported that a falciform articulated with the entocuneiform
in the single specimen MLP 2-30 (unfortunately, this specimen's elements could not be located for reexamination, but there is no reason to doubt Cabrera's observations or figures). He reasoned that it did not represent a vestige of the first or second metatarsal. It appears probable, based on the shape of the complex when compared to the unfused mesocuneiform and entocuneiform, that only these two elements normally fuse. However, there is some evidence that the falciform as identified by Cabrera (1929) may occasionally fuse with the mesocuneiform and entocuneiform into a single element. Normally, the ventromedial surface of the complex, representing the entocuneiform, ends as a blunt, rounded surface. However, in M. tarijense (FMNH P14216) the complex is extended ventromedially by an elongated, tapered process, which may represent the falciform.

It is improbable that the complex is formed from the mesocuneiform and a vestige of Mt II, as Cartelle (1992) alternatively speculated, because it should require articulation between the navicular and Mt II. As far as I am aware, there is only a single sloth specimen (ROM 13077, Nothrotheriops) in which Mt II apparently contacts the navicular. However, comparison with the pes in Stock (1925: pl. 15) suggests that the entocuneiform had fused to Mt II in ROM 13077.

Metatarsal III (Mt III) and Digit 3 (D3)
Mt III was described by Paula Couto (1978) for Eremotherium laurillardi (Pl. 124A-D) and by Owen (1860) for Megatherium americanum. The extreme variation in size and shape of the articular facets was reported by Cartelle (1992). Mt III is relatively short anteroposteriorly and its posterior part is strongly compressed transversely. Its sagittal axis is oblique, following the orientation of the tarsals.

The largest facet, for the ectocuneiform, lies posteromedially, is approximately triangular, with apex medioventral, and prominently concave. The small facet for the mesocuneiform-entocuneiform complex lies dorsomedially and its posterior margin is usually contiguous with the facet for the ectocuneiform (it is separate in MLP 44-XII-28-1, M. americanum).

The facet for Mt IV lies opposite the dorsal part of the facet for the ectocuneiform, and is nearly oval, with its long axis oriented nearly anteroposteriorly or dorsoventrally. Its surface undulates, being concave anteriorly and convex posteriorly. A small accessory facet for Mt IV occurs occasionally on the ventrolateral surface of Mt III. The facet for the proximal phalanx lies on the distal surface. Median, keel-Iike projections lie dorsally and ventrally.

D3 is the only complete pedal digit in megatheriines,
and bears an ungual. Phalanges 1 and 2 are wide, but compressed anteroposteriorly, and usually ankylosed (Cartelle, 1992). The proximal surface bears a broad articular surface; a variable area of the proximal surface is non-articular (cf. Pl. 125A and B). It is notched prominently dorsally and less so ventrally for the keel-like projections of Mt III. The lateral part of the proximal surface extends further volarly than does the medial. A sesamoid may fuse volarly with the phalanx, as in ROM 21953 (P1. 125A). The morphology of the joint allows only very restricted movement. The distal end bears a transversely elongated, and nearly semicylindrical trochlear surface, with a weak median sulcus. The phalanges are oriented obliquely, which deflected the ungual phalanx ventromedially, rather than medially as stated by Cartelle (1992). Paula Couto (1978) reported fusion between the proximal phalanx and Mt III in E. Iaurillardi, which is probably anomalous, because such fusion is otherwise unknown in megatheriines.

The ungual (P1. 126A-D) is the largest pedal phalanx. It is relatively short and stocky, and dorsoventrally higher than wide, particularly distally. The bony core is relatively short and high compared to those of the manus, and projected only slightly beyond the bony sheath. It articulates with the proximal phalanges by a deep, troughlike surface, oriented obliquely to the sagittal plane, and
movement was severely restricted (Owen, 1860; Cartelle, 1992). Cartelle (1992) reported ankylosis of the distal interphalangeal joint in nearly $20 \%$ of adult individuals of E. laurillardi.

Metatarsal IV (Mt IV) and Digit 4 (D4)
Mt IV (Pl. 127), described by Owen (1860) and Paula Couto (1978), is nearly as long as Mt V. Its sagittal axis is gently bowed laterally, and the proximal end is prominently expanded dorsoventrally, its distal less so. The facet for Mt III lies medioposteriorly, and is contiguous posteriorly with the facet for the cuboid, which lies posteriorly and faces posteromedially. The facet for Mt V lies laterally, and is contiguous posteriorly with the facet for the cuboid.

D4 is represented by proximal and distal phalanges. The distal surface of Mt IV bears a small, dorsoventrally elongated facet for the proximal phalanx. A small ventromedial extension of the facet articulated with a sesamoid in M. americanum (Cabrera, 1929). This extension is present in E. laurillardi, but no sesamoid has been recognized or recovered. A distal phalanx articulated with the proximal (Cabrera, 1929; Cartelle, 1992). Occasionally ankylosis occurred between Mt IV and adjacent metatarsals in E. laurillardi (Paula Couto, 1978; Cartelle, 1992).

Metatarsal V (Mt V) and Digit 5 (D5)
Mt V (Pl. 128) is elongated compared to Mt IV, and its proximal end is dorsoventrally expanded. Its sagittal axis is oblique, so that the anatomically lateral surface faces ventrolaterally. The proximal half of the lateral surface is flattened.

The proximal facets are contiguous, and lie on the proximal half of the medial surface, that for the cuboid Iying proximal to that for Mt IV. The plane of the facets is oriented slightly distomedially, making the diaphysis transversely wider centrally than proximally. Proximally Mt $V$ ends as a blunt, rounded surface, nearly coincident with the posterior margin of the facet for the cuboid or extends proximally as a triangular projection. The distal surface of Mt V bears a small, lateroventrally displaced facet for the nodular, anteroposteriorly compressed, and remnant phalanx of D5; occasionally ankylosis occurs between it and Mt V in E. laurillardi (Cartelle, 1992).

## FUNCTIONAL MORPHOLOGY OF THE PES

The Concept of a Pedolateral Posture
The comparative functional morphology of the pes of ground sloths has received little attention. This is surprising, in one sense, because the odd nature of their tarsal elements would seem sufficient to prompt detailed study, building on the initial work of earlier authors such as Owen $(1840,1860)$ and Stock $(1917,1925)$. On the other hand, there are several reasons for the slow progress in the attempt to understand the pes of these animals. Among the more important are that the tarsals, paradoxically, are considerably different from those of most mammals, and that no modern analogue exists. Further, few past studies provide detailed discussion and illustration of the individual elements of the pes (and manus, for that matter), although the seminal efforts of Stock (1925) and Hirschfeld (1985) stand alone in this regard.

The lack of comparative information and the relative paucity in most institutions of comparative collections of ground sloth pedal elements, have probably led most workers to ignore the pes, or to rely on Owen's and Stock's interpretations. Indeed, I have relied on these also during many of my visits to foreign institutions. I noted, for example, that the pes of mounted specimens in MLP was
reassembled with the anatomical sole oriented nearly ventrally, but considered it merely an improper reconstruction, or due to difficulty in reconstructing the pes in a rotated position. Thus, I did not carefully examine the posture of the pes of megatheriines or other large ground sloths. For this reason, a detailed comparison among ground sloths is limited here. However, the pes of megatheriines is herein carefully described and compared with reference to the literature and available specimens at ROM, or those borrowed from other institutions.

The presence in megatheriines and most mylondonts of a well-developed and, in many respects, similar astragalar odontoid process has been interpreted as indicating similarity in structure, posture, and function of the pes. An odontoid process is generally viewed as indicating rotation of the pes so that the anatomical sole faced nearly or entirely medially in life, with the weight borne largely on the lateral surface of Mt V, following Owen (1840, 1860) and Stock (1925). The term pedolateral denotes this position (McDonald, 1977, Webb, 1989). However, the posture in medium- and large-sized megatheriines, at least, apparently does not follow this pattern. I realized this largely during examination of the nearly complete and reasonably well-preserved individual of Megatherium tarijense, FMNH P14216. Two aspects of this specimen facilitated detailed study of the posture of the pes. One,
the elements were bound together by wire (the specimen was once on display); two, the elements are not so massive as to preclude simultaneous manipulation of more than one or two elements, as is the case with those of $M$. americanum and $E$. laurillardi.

The concept of a rotated pes may be traced to Owen (1840: 117) who stated that the pes of Glossotherium, when articulated to the leg, rested "upon the ground by its outer edge, not by its sole, and the peculiarities of the metatarsal structure relate to the inversion of the foot". The plane of the discoid facet (Owen's 'middle division') was described as horizontal; that of the odontoid facet (Owen's 'internal division') as nearly perpendicular to the former.

Owen (1860:815) stated that in M. americanum "the tibia articulates with the side instead of the summit of the tarsus, so that the whole foot is turned inward and rests upon its outer edge instead of its sole", as illustrated in plate 119A. The astragalus is described in similar terms as that of Glossotherium, with the plane of the discoid facet horizontal. The odontoid facet "is wedged into the deeper excavation on the inner part of the tibial articular surface, and forms a kind of pivot on which the foot worked" (Owen, 1860:185). Implicit in his description is that the astragalus, hence pes, rotated about the odontoid process; and the vertical orientation of the latter implied that the
main movement was from side to side in the horizontal plane， rather than the normal flexion and extension in a parasagittal plane．

Owen（1860）apparently deduced a pedolateral posture in M．americanum by noting that the fibular facet of the astragalus faced nearly dorsally when the pes was oriented in a plantigrade stance．Probably he reconstructed the pes in pedolateral position to correct for the position of the fibular facet．This positioned the astragalus so that the long axis of the odontoid process was oriented nearly vertically．Owen＇s interpretation has been followed by subsequent authors，as，for example，the figures given by Gazin（1957），Paula Couto（1978），and Kraglievich（1928）for the astragalus of planopsines and megatheriines．Various authors，following Owen，uncritically linked the presence of an odontoid process with a pedolateral stance in other ground sloths：Stock $(1917,1920,1925)$ and $⿴ 囗 ⿱ 一 一$ irschfeld （1985）for Glossotherium；Stock（1925）for Nothrotheriops； Cartelle and Fonseca（1983）for Nothrotherium；McDonald （1987）for scelidotheriines；and Webb（1989）for Thinobadistes．

The form of the astragalus in mylodontines and lestodontines，particularly in Glossotherium，is considered to represent an advanced pedolateral stance，in which flexion and extension at the tibio－astragalar joint are impossible．The following list of morphological features，
supposedly indicating this condition, is sumarized from Hirschfeld (1985) and McDonald (1987).

1) enlargement or expansion of the medial trochlear surface to form an astragalar odontoid process or tibial knob, which projects proximally into a deep facet in the tibia;
2) an angle of approximately $90^{\circ}$ between the discoid facet and odontoid facet (McDonald, 1987):

3 ) the surface of the discoid facet is flat anteroposteriorly (McDonald, 1987);
4) the discoid surface is posteriorly extended posterior to the odontoid process.

The most important change is the development of the odontoid process, which alters the normal function at the tibioastragalar joint of extension and flexion in the parasagittal plane to one of rotation in a horizontal plane with the odontoid process acting as the pivot (Eirschfeld, 1985; McDonald, 1987).

However, Hirschfeld (1985) and McDonald (1987) were primarily concerned with other ground sloths. McDonald (1987) stated that sceliodotheriines were less specialized. The odontoid process is not as well-developed; the angle between the discoid and odontoid facets is obtuse, ranging between $107^{\circ}$ to $145^{\circ}$; the discoid facet is not expanded posterior to the odontoid process, and is not flat, but retains an anteroposterior convexity. These features
permitted "a restricted degree of anteroposterior movement" (i.e., flexion and extension) at the tibio-astragalar joint in scelidotheriines; similar form and movement probably occurred in Nothrotheriops (McDonald, 1987:166). Hirschfeld (1985:58) stated that the features listed above, and others that she identified with a pedolateral stance (see below), "are just beginning to develop in Pseudoprepotherium."

The Pes in Megatheriines
The astragalus of megatheriines possesses various of the anatomical features listed above. However, manipulation of the pedal elements and the tibia strongly suggests that these ground sloths did not adopt a pedolateral stance. The medial side of the pes is rotated dorsolaterally, but the anatomical sole still faces largely ventrally. A pedolateral stance, as figured by Owen (1860), Gazin (1957), and Paula Couto (1978), requires that the long axis of the odontoid process be oriented nearly vertically. If the tibia is articulated with an astragalus in this orientation, then the tibia deviates approximately $50^{\circ}$ from the vertical. The articular surfaces between tibia and femur indicate that the long axes of these elements were approximately aligned in articulation, and therefore the tibia could not deviate so marikedly. Indeed, given the large bulk of these terrestrial sloths, such a position is clearly impossible. The position of the femur in life cannot be certainly
stated; however, it is reasonable to assume that it was approximately vertical in the transverse plane, as generally occurs in mammals. The tibia thus was also approximately vertically oriented. The distal tibial surface requires that the astragalus lie with the long axis of the odontoid process oriented approximately $15^{\circ}$ from the horizontal. The orientations of the discoid and odontoid facets are discussed above. The most dorsal projection of the odontoid process lies at approximately the same level as, or slightly higher than, that of the discoid facet. The long axis of the navicular facet lies approximately normal to that of the odontoid process, and its surface faces anteriorly and slightly ventrally. In lateral view the odontoid facet is largely or wholly obscured by the fibular facet and lateral part of the discoid facet (Pl. 110C). Contact with the ground is made through the posterior part of the calcaneum, most of the ventrolateral surface of $M t V$, and the proximal and distal parts of the ventrolateral surface of Mt IV. The cuboid is apparently raised off the ground, but may have made a small contact. The third digit, Mt III, ectocuneiform, and the fused mesocuneiform and entocuneiform are raised above the ground (Pl. 129).

The movement at the tibio-astragalar joint is primarily extension and flexion (PI. 129). However, a degree of rotation of the pes occurred during such action, because the sulcus between the discoid and odontoid facets, and the
corresponding ridge on the tibia, are not aligned in the parasagittal plane, but offset between $20^{\circ}-25^{\circ}$ lateral from it. Assuming no (or very restricted) movement between elements of the pes, the obliquity of the sulcus caused the pes to rotate during extension so that the anterior end swung medioventrally, and the posterior end dorsolaterally.

Although some rotation occurred in the pes of megatheriines, the degree of rotation is clearly less than implied by past authors. The orientation of the pes, and its manner of contacting the ground are apparently not radically different from the condition in many plantigrade mammals. However, the distinct morphology of the astragalus and calcaneum and, to a lesser degree, of the remaining tarsals indicates that profound and unique changes had occurred during the evolution of the pes of ground sloths. However, it is unclear how and why these changes occurred, and before proceeding to consideration of these problems, it is worth attempting to analyze, on the available material and iiterature, the possible orientation and movement of the pes in other ground sloths.

The Pes in Other Ground Sloths
Cartelle and Fonseca (1983) stated that the pes of Nothrotherium was turned on its lateral surface during walking so that the sole faced medially; they provide an excellent description of the astragalus. Important
differences are that the odontoid process is less developed and the navicular facet is further medial in Nothrotherium. It is due to this feature that the navicular facet lies dorsal to the plane of the discoid facet when the odontoid process is oriented vertically, as described above for the megatheriine taxa. I add to their observations that the long axis of the navicular facet is apparently oriented more nearly horizontally, and that the navicular facet, as judged by its dorsal margin, is further dorsal with respect to plane of the anterior margin of the discoid facet.

Cartelle and Fonseca (1983:161) stated that in anatomical position "a extremidade medial do processo odontóide sobressai ligeiramente sobre o plano horizontal que passa sobre a crista lateral que marca as facetas articulares para tíbia e fíbula", as occurs in Eremotherium. ROM 13077, a cast of the pes of Nothrotheriops, is similar in all respects to the conclusions of these authors. The position of this pes in natural position differs from the orientation shown in Stock (1925, pl. 15).

The orientation of the long axis of the navicular facet could conceivably explain the pedolateral stance. A more transverse orientation implies a dorsomedial shift with respect to that of Eremotherium. Such modification would tend to rotate the cuboid and metatarsals. However, the difference in orientation does not appear sufficient to cause a significantly greater rotation of the pes than in

Eremotherium. Further, the relative positions of the cuboid facets are similar.

No complete pes of a scelidotheriine is available for study. However, manipulation of the left tibia (ROM 3972) and astragalus (ROM 3953), possibly of Catonyx chiliensis (McDonald, 1987), suggests that the orientation of the scelidotheriine pes is somewhat less pedolateral than that of Catonyx tarijensis as figured by McDonald (1987: fig. 41). The odontoid process in McDonald's illustration is oriented more vertically than in astragalus ROM 3953 when articulated with tibia ROM 3972, in which the odontoid process projects only slightly above the lateral margin of the discoid facet in lateral view. The pes is nonetheless pedolateral, approximately as illustrated by McDonald (1987). However considerable extension and flexion are permitted in the ROM specimens, with some medioventral rotation occurring during extension, as in Eremotherium.

Various elements of the pes, including the astragalus and calcaneum, of Glossotherium are available for study, but no tibia. The margins of the posterior part of the ventral surface of the calcaneum are formed by a thick, raised, rugose ridge. If the pes is pedolateral, then the calcaneum is oriented with the ridge contacting the ground. However, a similar morphology occurs in Eremotherium; that on the medial margin is relatively shorter and is raised above the ground. Stock's (1925: pl. 40, fig. 1) illustration of the
tibia of $G$. harlani suggests that the tibial facet for the odontoid surface lies obliquely to a parasagittal plane through the tibia, which in turn implies a less than vertical orientation for the odontoid process. Thus, the pes was probably less pedolateral than suggested by Stock (1925), but nonetheless more rotated than in Eremotherium.

Interestingly, the tibial odontoid facet is oriented nearly anteriorly in Glossotherium (Stock, 1925: pl. 40. fig. 1b) rather than transversely, as occurs in other ground sloths that I have examined. The result is that the discoid facet lies largely posteriorly, rather than laterally, to the odontoid facet. Hirschfeld (1985: fig. 37a) represents this orientation more accurately and clearly than Stock (1925: pl. 41, fig. 2).

Hirschfeld (1985) stated that the movement of the pes of Glossotherium was rotation in a mediolateral plane. However, a purely rotational movement of the pes is possible only if the odontoid process is oriented vertically. As stated above, the odontoid was probably less vertical than Stock (1925), Hirschfeld (1985), and McDonald (1987) implied, but more so than in megatheriines. This suggests rotation was a larger component of motion. However, some movement occurred in the vertical plane.

Development of a Pedolateral Pes
Hirschfeld (1985:57) stated that the structure of the
pes of Glossotherium represented "an extreme specialization for bipeđalism and weight-bearing, comparable only to the specialization in megatheres among the megalonychoids." However, the pes of the larger megatheriines does not represent the closest comparison among megalonychoids. The pedes of Nothrotherium and Nothrotheriops provide the strongest morphological, structural, and functional resemblances. It is perhaps significant that the largest ground sloths did not have a fully pedolateral pes, but that a considerably smaller sloth did. The locomotory postures among fossil sloths are unclear, although it is nearly certain that several of the smaller taxa were at least partially arboreal (Webb, 1985; White, 1993). Megatheriines have traditionally been regarded as bipedal browsers (and normally bipedal by Casamiquela, 1974; see ICHNOFOSSILS OF MEGATHERIINAE) . MCDonald (1977) suggested that Megalonyx, generally reconstructed with the pes in plantigrade position (Coombs, 1983), Nothrotheriops, and Glossotherium may have been erect or semi-erect, based on the moments of resistance of vertebral centra. Coombs (1983:35) conceded the potential for bipedalism in the former two genera, but that "mylodonts were probably not bipedal browsers".

Possibly the pedolateral position was initially a modification for climbing, based on the ability in Tamandua to turn the pes outward during climbing (Hirschfeld, 1985). Modifications in the pes of sloths "primarily involve loss
of the inner digits; increase in size and massiveness of the outer digits; dorsomedial rotation of the arch of the foot, so that weight is borne on the outer side; caudal extension of the calcaneum; dorsal development of the inner condyle of the astragalus; and a basic reorganization of the structural relationships of various tarsal and metatarsal elements" (Hirschfeld, 1985:58). I agree with most of the components Iisted here, but two seem to require further consideration.

Clearly, the arch of the pes has been turned so that the sole faces medially in pedolateral sloths. However, a satisfactory explanation for the development of this feature has not been proposed. A possible mechanism for such modification may involve the odontoid process. Hirschfeld (1985) and McDonald (1987) noted that the odontoid process. or inner condyle, was expanded in sloths with a pedolateral pes. This seems logical, particularly when compared to the medial trochlear surface of Hapalops, in which an odontoid process is absent. However, if compared to the astragalus of most mamals, the astragalus bearing a well-developed odontoid process is striking in the inequality of the medial and lateral trochlear surfaces, and the depth of the sulcus between them. If the astragaius is oriented so that the odontoid process is directed medially, a number of potentially important relationships are revealed. The facet for the cuboid faces more nearly laterally, and the calcaneal facets are displaced laterally, suggesting the
more normal position in mamals, rather than the ventral position in sloths.

An alternate hypothesis to an increase of the medial trochlear surface is to regard the odontoid process as a product of ventral displacement and anteroposterior reduction of the medial trochlear surface. The rotation of the pes then may be achieved by rotation of the astragalus so that the most dorsal part of the odontoid facet projects somewhat dorsal to that of the discoid facet, which approximates the condition in life. Such movement would rotate the pes approximately $45^{\circ}$, which is nearly the orientation of the pes in larger megatheriines. Further rotation of the pes must be postulated for Glossotherium and Nothrotheriops. It is in this regard that the position of the navicular facet may be important. Compared to megatheriines the facet lies more medially, and thus appears to be dorsal to the discoid facet when the odontoid process is oriented vertically. This relationship may indicate increased rotation of the facet.

As discussed above, the position of the navicular facet in earlier megatheriines (e.g., Megathericulus patagonicus) strongly resembles that of non-megatheriines. This implies that the posture of the pes of these megatheriines was more similar to that in Nothrotheriops and Glossotherium than in Megatherium and Eremotherium; and that the less pedolateral pes of the latter genera is derived.

An impediment to these proposed events for attaining the pedolateral posture is that Hapalops is considered plantigrade (e.g., by McDonald, 1977), and traditionally regarded as morphologically and phylogenetically central among extinct sloths (but see De Iuiis, 1994). The derived astragalar odontoid process is not present, but the position and orientation of the facets for the navicular and cuboid are approximately as in sloths with a pedolateral pes. The navicular is oriented with long axis transverse (Scott, 1903: pl. 33, fig. 4). The resemblance of the medial trochlear surface to an odontoid process is so persuasive that it may be considered either as an incipient or vestigial odontoid process. It is, also, possibile that it is neither. Which of these is the actual case largely depends on the phylogenetic relationships among megatheriines, mylodontids, and megalonychids (s.1.). However, these relationships are not clearly understood (De Iuliis, 1994).

The positions of the cuboid and navicular in Hapalops suggest that the pes, but not the astragalus, were already partly rotated. If the odontoid process was developed by expansion of the medial trochlear surface, and the relationship between astragalus and tibia remained constant, then expansion must have occurred mainly ventrally (i.e., largely forming the non-articular part of the process). Such modification would tend to move the navicular facet,
particularly its medial part, ventrally, thereby rotating the pes in a direction opposite to that required to achieve a pedolateral stance.

The reason for this discussion on Hapalops is to demonstrate that the morphology of its astragalus and position of its pes apparently refute (or is inconsistent with) either hypothesis (i.e., increase or decrease of the medial trochlear surface to form an odontoid process). Possibly this suggests that Hapalops does not represent an ancestral condition of the pedolateral posture.

The pes in Myrmecophagidae, the sister group to the Tardigrada (Engelmann, 1978; 1985), may shed light on the origin and development of the pes of sloths. Hirschfeld (1985) noted various differences in the metatarsals and digits of Tamandua and sloths. Unfortunately, no pes of Tamandua was available for my study; however, that of Myrmecophaga allows various comparisons.

The calcaneum of extinct sloths is notable in the apparent reduction of its anterior end. In Myrmecophaga, and indeed most mammals, the calcaneum extends distally and anteriorly beyond the sustentaculum tali and supports the astragalus from below. The astragalus and cuboid may articulate, but the latter does not support the astragaius. In sloths the sustentaculum tali forms the most distal and anterior part of the calcaneum. The cuboid is relatively posterior, and supports the astragalus ventrolaterally.

This proximal or posterior retraction of the cuboid has apparently also drawn Mt IV and Mt V posteriorly.

The naviculars of Myrmecophaga and sloths are similar in that the astragalar facet is formed from convex and concave parts. The convex part is received by the depression in the navicular facet of the astragalus. Engelmann (1978; 1985) considered this last feature to be a synapomorphy of the Pilosa.

However, a difference exists in the orientation of the navicular. In Myrmecophaga the long axis of the navicular is oriented dorsoventrally with the pes in plantigrade position. In Hapalops it is transversely oriented. In most other extinct sloths it lies somewhere between these positions.

When the pes of Myrmecophaga is in a plantigrade position, the convex surface of the navicular facet of the astragalus lies ventral to the depression of the navicular facet and articulates with the concave part of the astragalar facet of the navicular. However, the convex surface of the navicular facet apparently continues medial to the depression. This implies the potential ability to rotate the navicular mediodorsally around the ball and socket part of the astragalo-navicular joint (Hirschfeld, 1985, hypothesised restricted degree of such movement in Glossotherium). This suggests that Myrmecophaga could turn its pes inward, to present its volar surface nearly
medially.
Hirschfeld (1985) described this ability in Tamandua for tree-climbing, but did not explain the underlying morphological structure that permitted such movement. Unfortunately, I am unable to compare the pes of Tamandua and Myrmecophaga: Further, Myrmecophaga is terrestrial, but Tamandua combines terrestrial and arboreal modes of existence. If rotation of the pes is a modification for tree-climbing in Tamandua, the function of rotation in Myrmecophaga (if indeed it possesses this ability) is unclear. One explanation is that rotation is a primitive feature retained in Myrmecophaga. Further work on the structure and function of the pes of myrmecophagids would probably be useful to understanding the pes of sloths.

## MISCELLANEOUS SKELETAL ELEMENTS

The remaining elements are treated briefly here. They are not described in detail because they are rarely recovered, except for Eremotherium laurillardi or, as with ribs, are fragmented and rarely completely restored. Such elements are either not particularly useful diagnostically, or any possibly diagnostic differences cannot be readily discerned, due to small samples sizes.

Sternebrae
Cartelle (1992) described differences between $E$. Iaurillardi and Megatherium americanum, but noted that marked interspecific variation in size, shape, and arrangement of articular surfaces, particularly in the manubrium, occurs in E. laurillardi. Seven sternebrae are present in E. laurillardi (Cartelle, 1992). Owen (1855: pl. 27) implied that at least eight were present in $M$. americanum; eight are apparently present in MHYNP 1871-383, but only seven in MPCB 1.

Differences in the manubrium of these species include a more concave ventral surface, and a less oblique sternal facet in E. laurillardi. The anterior surface is tapered in the latter, but rounded in M. americanum (Cartelle, 1992) and bears a shallow, median depression. Marked interspecific variation also occurs in the manubrium of $M$.
americanum, particularly in size, robustness, relative proportions of its distal and ventral parts, and shape and orientation of articular facets (cf. MLP 2-132, MLP 44-XII-28-1, and the specimens described by owen, 1855).

## Ribs

The ribs recovered are generally incomplete. Apart from the most anterior few, they can rarely be distinguished, except possibly by size, unless the head is well-preserved. Little can be added to Paula Couto's (1978) description. Vertebrosternal rib 1 is composed of fused vertebral and sternal ribs, the latter representing an ossified costal cartilage (Paula Couto, 1978). Vertebrosternal ribs 2 and 3 may also be thus composed in $M$. americanum (Owen, 1855: pl. 25). However, only the first and second are composed of ankylosed segments in MPCB 1 , and only the first in MNTNP 1871-383.

Vertebrosternal ribs 1-3 in E. laurillardi are formed of fused vertebral and sternal segments. They are similar morphologically to those of $M$. americanum (Owen, 1855: pl. 25), but more gracile and less angular. The medial surface of rib 1 (e.g., ROM 31430, ROM 19704) is less strongly curved, and the sternal segment apparently shorter, particularly ventrally. The articular facets vary considerably. The vertebral facets are separate or contiguous; the sternal are approximately triangular, and do
not bear a distinct ventromedial part as figured by owen (1855: pl. 25, fig. ib) for M. americanum. Vertebrosternal ribs 2 and 3 are also more gracile than in M. americanum, and the sternal part is relatively shorter.

An uncatalogued vertebrosternal rib 1 is known from northern Chile, and probably belongs to $M$. medinae. It resembles more that of M. americanum, but is apparently somewhat stouter, its sternal segment is relatively longer, and the head less oblique in relation to the shaft.

Owen (1855) stated that CV 9, and thus the ninth rib, was the most posterior to retain an osseous connection to the sternum. However, Owen's (1855: pl. 17; 1859: pl. 18) figures indicate that the ninth rib bears no sternal rib. Possibly, Owen (1855) deduced the presence of a sternal rib based on articular facets of the stermal elements but, if so, he did not state it. Vertebrosternal ribs 3-7 bear separate sternal segments in MPCB 1; and 2 to 8 in MNHNP 1871-383. In the latter the eighth sternal rib is fused to the posterior surface of the seventh, and thereby gains attachment to the sternum. This apparently occurs in $E$. laurillardi, based on mounted specimens at USNM. Various of the ribs following the eighth were probably vertebrocostal ribs, linked the sternum or other ribs by costal cartilages.

## Hemal Arches

The hemal arches of the caudal vertebrae are described
by Owen (1855) for M. americanum. The first is composed of separate left and right elements, but those of CD 2 - CD 14 are fused distally to form generally $Y$-shaped arches. The hemal arches of E. laurillardi are not as wide and the distal processes, or apophyses, are shorter (Cartelle, 1992).

Osteoderms
Cartelle (1992) and Cartelle and Bohórquez (1986) reported the recovery of osteoderms associated with various skeletal elements of E. laurillardi from Toca das Onças. Osteoderms have not been recovered, or recognized, from other localities yielding this or other megatherine species, although they are commonly part of the dermal armour of some mylodonts. Nonetheless, the findings of these authors are almost certainly correct. The osteoderms were found in situ on the skull and posterior extremities of the articulated skeletons of two individuals. These remains lay within the highest elevation of the cave from which they were recovered, and apparently were undisturbed by the water that had flowed through the cave. The remains of other taxa, including Glossotherium, were found at lower elevations. Their skeletal elements were generally disarticulated and mixed. The osteoderms of E. laurillardi differ morphologically and histologically from those of Glossotherium, as discussed by Cartelle and Bohórquez

It is perhaps curious that osteoderms have never been reported from other localities yielding remains of $E$. laurillardi, or other megatheriines. However, to my knowledge, no other articulated and apparently undisturbed individual of this species has been recovered, as is probably also true of other megatheriine taxa. Presumably, the osteoderms would be among the first skeletal elements affected by even minimal postmortem disturbance. Further, many excavations, particularly the earlier ones which yielded many of the nearly complete individuals of $M$. americanum, were probably not strictly controlled.

## Hyoid Apparatus

The hyoid apparatus is known completely in $E$. laurillardi (see Cartelle, 1992). Various elements are known for $M$. americanum, and only the stylohyal in $M$. tarijense. The stylohyal is apparently diagnostic, although interspecific variation exists. Generally the proximal part of the stylohyal is more slender in $E$. laurillardi. It is progressively more robust in $M$. medinae (based on a single individual) and M..americanum.

## ICHNOFOSSILS OF MEGATHERIINAE

Casamiquela (1974; in Angulo and Casamiquela, 1982) reported the only probable known ichnofossils of Megatheriinae from which he described two monospecific genera. The ichnofossils consist in both cases of footprints preserved in two or more trackways.

Megatherichnum oportoi is based on footprints contained in two portions, separated by about 300 m , of possibly a single trackway from the type locality of the Rio Negro Formation near Carmen de Patagones, Buenos Aires Province, Argentina, which Casamiquela (1974) considered to be mid to late Pliocene. Marshall et al. (1983) assigned the type Rio Negro Formation to the Montehermosan Land Marmal Age, of early and middle pliocene. The footprints are approximately oval, wider anteriorly, and surrounded by a raised border. An elongate depression is often present posterointernally, and probably represents the calcaneum (Casamiquela, 1974). The form of the prints suggests that the long axis of the pes was oriented slightly obliquely, from posterointernal to anterolateral (Casamiquela, 1974). This position is corroborated by the functional morphology of the pes: slight anterolateral deflection of the astragalus occurs during extension (see FUNCTIONAL MORPHOLOGY OF THE PES). The prints, however, are apparently not regularly elliptical, judging from illustrations in

Casamiquela (1974). The lateral margin is gently and regularly rounded, but the internal is more nearly linear. Further, some prints are slightly, though unevenly, reniform (see Casamiquela, 1974: pl. 2, bottom figure, and pl. 3).

The prints vary in length, with the longest approximately 720 mm , and the shortest 660 mm . Their widths are apparently more variable, with maximum widths between $620-460 \mathrm{~mm}$, and minimum widths between $240-170 \mathrm{~mm}$. Pace or stride length varies between $600-450 \mathrm{~mm}$ (Casamiquela, 1974).

Falsatorichnum calceocannabius is represented by various trackways. The type trackway comprises three footprints from a "Nivel impreciso de la Formación Río Negro (típica)" near Punta Mejillón, Río Negro Province, Argentina, and assigned to the Montehermosan Land Mamal Age (Angulo and Casamiquela, 1982:51). The prints resemble those of M. oportoi, but are smaller. Lengths of the prints of $F$. calceocannabius, including those from a second trackway near Punta Mejillón, vary between 460-310 mm, and maximum width between $260-200 \mathrm{~mm}$. The prints are therefore slightly larger than half the size of those of M. oportoi (Casamiquela, 1974). Stride length is given as approximately 800 mm , which is, curiously, longer than that for M. oportoi. Probably this value is incorrect, judging from illustrations in Angulo and Casamiquela (1982: pl. 1).

Casamiquela (1974) interpreted the prints of M. oportoi as indicating the bipedal gait of a large, plantigrade
mammal, and reasoned that they were very probably megatheriine based on the distributions and sizes of known mammalian taxa. It is indeed probable that M. oportoi belongs to the Megatheriinae, but it is likely that they belong to an already named taxon. Casamiquela (1974) estimated an average length of approximately 650 mm for the footprints (including those from trackways other than the type trackway). The complete pes of Megatherium americanum (BMNH 19953v) is nearly 664 mm long. The correspondence in size seems more than coincidental. However, this species has not been undoubtedly reported from the Pliocene. Although synonymy between Megatherichnum oportoi and Megatherium americanum is possible, it cannot currently be reasonably demonstrated.

Angulo and Casamiquela (1982:52) referred Falsatorichnum calceocannabius provisionally to the Megatheriinae, but that "es imposibile descartar a los megaloniquidos". It is worth noting, with regard to the latter group, that the footprints of Glossotherium are nearly and evenly reniform (Stock, 1917, 1925, 1936). The prints of $F$. calceocannabius, based on shape, may represent a smaller megatherine species, but may also belong to a smaller or juvenile individual of M. oportoi. Angulo and Casamiquela (1982) assigned additional prints to M. oportoi from localities near those yielding F. calceocannabius. Length of one print was given as 540 mm , approximately
intermediate between the types of these two species.
Casamiquela (1974:254) inferred a nearly erect, bipedal stance for megatheriines based on the trackways, stating that the animal which left the prints was "functionalmente bípedo y plantígrado". It is clear from Casamiquela's (1974:282, pl. 14) illustration that he considered it an obligate biped, with "los miembros posteriores extendidos; Ios anteriores se les oponen de manera alternada", so that the tail cleared the ground during locomotion. Apparently, the absence from the trackways of features that might indicate a dragging tail strongly influenced Casamiquela's (1974) reconstruction. Further, the variation among prints of single trackways, particularly in minimum and maximum widths, was apparently considered insignificant.

Casamiquela's (1974) reconstruction essentially follows that of Abel (1911) and contrasts markedly from the traditional view of posture in megatheriines (and Gravigrada in general) as described, for example, by Cabrera (1929) and Hoffstetter (1958), and illustrated by Lankester (1905), Scott (1913), Cartelle (1995), and Plate 2. The traditional reconstruction postulates that megatheriines were capable of sitting or raising themselves on their hindquarters, and using their heavy, robust tail as a prop or balancing organ, or their fore limbs to lean against tree trunks and branches. This view is largely a refinement of Owen's (1842) opinions (Coombs, 1983).

This reconstruction seems intuitively to be a more plausible posture for mamals with the body proportions of megatheriines. The larger megatheriines had considerable body masses, resembling those of elephants (Hoffstetter, 1958). The trunk is relatively elongated, placing the centre of gravity well-forward of the hind limbs. Casamiquela (1974), recognizing the relatively posterior position of the hind limbs and robustness of the tail, postulated that the condition of the tail, with welldeveloped hemal arches, reflected "la segura presencia de múscolos caudo-femorales (-crurales) potentes". The muscles acted against the hind limb, which was braced firmly to the ground, to rotate the vertebral column about the acetabular joint, and thereby raise the trunk anteriorly. The robust and transversely expanded femur of gravigrades, and particularly of megatheriines, is attributed to the presence of this powerful musculature (Casamiquela, 1974).

With regard to the correlation between the morphology of the footprints and locomotion, the footprints of the mylodont sloth Glossotherium from near Carson City: Nevada, USA, described and illustrated by Stock (1917, 1925, 1936), are relevant. The footprints are similar to those of $M$. oportoi in that each is similar in shape and indicate a relatively short gait, are wider anteriorly, and are surrounded by "a raised border where the soft mud bulged upward along the side of the foot as pressure was exerted
downard when the animal walked across the surface of the ground" (Stock, 1925:198). They differ in being smaller and nearly evenly reniform.

The body proportions of Glossotherium generally resemble those of megatheriines, but the trunk is relatively slightly longer, the centre of gravity is well-forward of the hind limbs, as in any normal quadruped, and the front limb is shorter relative to the hind limb. Glossotherium has always, to my knowledge, been reconstructed as a quadruped, as by Stock (1920, 1925). Coombs' (1983) investigation of numerous anatomical and other variables (e.g., coprolites) suggested that Glossotherium was improbably a bipedal browser. Indeed, quadrupedal locomotion is postulated for most large ground sloths; and a robust, transversely expanded femur and powerful tail are characteristic of many of these, particularly scelidotheres and mylodonts. It seems thus improbable that the tail and femur morphologies result simply from muscular adaptations to raise the anterior part of the body about the acetabular joint. It should be noted that McDonald (1977) suggested that Glossotherium, Megalonyx, and Nothrotheriops were possibly capable of erect or semi-erect postures, similar to that of Ursus americanus, based on the moments of resistance of vertebral centra. Coombs (1983:33) suggested that some sloths, including Megatherium, "seem to have been well adapted for bipedal browsing . . . and had long reach
combined with hindlimb adaptations for standing erect". Casamiquela (1974) apparently reconstructed a bipedal gait for megatheriines based on the following features of the footprints: the gait is short, the footprints are similar in shape, and there is no evidence for the tail. To account for these, Casamiquela (1974) reconstructed the animal as plantigrade; its massive weight required that it take short steps made by the hindlimbs only (explaining why the prints are similar); the femur and crus were oriented nearly vertically so that the tail cleared the ground. Stock (1925, 1936:27), however, explained the very similar conditions associated with the footprints of Glossotherium by an altogether different hypothesis: the animal was quadrupedal, and the prints largely represent the hindpaw because "superposition of the print of the hind foot on that of the front has obliterated all signs of the latter". Occasionally, however, some prints do preserve an impression of the claw of the frontpaw (Stock, 1925, 1936).

I see no reason why a similar explanation should not also have been true for the megatheriine ichnofossils. It conveniently explains the similarity of prints and lack of any marking that might have been made by a tail. Further, it is worth noting that not all prints in the trackway of Megatherichnum oportoi are nearly identical in shape. Indeed, some are smaller than others. This would be unexpected if the prints were made only by the hindpaws of a
massive, obligatory biped, because each print would represent the pes that bore the full weight of the animal. Some prints in the trackway illustrated by Casamiquela (1974: pl. 1) are notably different, e.g.. the print above the right half of the ruler; and what appears to be a weak print between the two, central, large prints. I suggest that these impressions may have been left by the manus, which is shorter and less robust than the pes.

## SYSTEMATIC REVIEW OF THE MEGATHERIINAE

A thorough systematic review involves a taxonomic revision and the recovery of phylogenetic relationships of the taxa. Taxonomic revisions include morphologic, biometric, and biostratigraphic analyses of numerous fossil specimens often housed in international museums or other research institutions so that species, the basic biological unit, may be recognized. These exercises also involve diligent searches of the literature, and determinations of priority and synonymy of taxonomic names. Hypotheses of phylogenetic relationship are generated by character analysis and cladistic methodology, as is appropriate for assessing the polarities of characters and analyzing their distribution among the taxa.

This systematic revision is based on the efforts of many earlier authors who proposed their own arrangements and interpretations of relationships among the specimens. In some cases they justified their decisions, but too often, however, diagnoses are incomplete, lack context or detailed comparisons with other material, and original descriptions included minimal explanations for the choice of diagnostic characters. McDonald (1987) noted similar circumstances in his revision of Scelidotheriinae.

Numerous, and often controversial, taxonomic and phylogenetic interpretations have been proposed throughout
the paleontological discovery of the Megatheriinae, and have led to a maze of opinions. However, such confusion is not restricted to paleontology: it is generally acknowledged that scientific knowledge does not advance linearly by an orderly accumulation of facts and observations.

The rate of discovery of megatheriine remains increased markediy during the latter half of the nineteenth century, largely through field work in Argentina, but also in Chile and Bolivia. A few discoveries furnished relatively complete knowledge of most skeletal elements of individuals. However, the majority of the discoveries were of a few associated or isolated, and often incomplete, elements. These specimens were studied and interpreted by a relatively small coterie of scientists, with Florentino Ameghino being the most productive.

Controversy soon arose among these scientists as they argued over the priority of taxa that were based on relatively minor morphological and quantitative differences. The causes of the arguments were largely due to the nature of the specimens, which were generally scarce and incomplete, and thus could be used to support various interpretations. Further disagreement reflected a poor knowledge of biological diversity and evolution, and to the disputatious personalities of some of the scientists!

Discovery of megatheriines continued, almost exclusively in Argentina, through the first forty years of
the twentieth century when Lucas Kraglievich was the leading student of megatheriine systematics. Since about the 1950's megatheriine remains have been recovered in nearly every country of the Western Hemisphere, with many workers contributing to our knowledge of these sloths.

No general synthesis of the scattered and disparate information was ever formalized or attempted. Instead, most workers focused their attentions on the description of newly discovered material as new taxa, rather than considering it within the context of already described remains, despite advances in the theories of evolution and population structure (some of the reasons for this situation are discussed in Cartelle and De Iuliis, 1995).

I consider here only one historical factor - the nature of the material - because the works of earlier authors may be understood better through consideration of the kinds of specimens available to them. There are two aspects of the material that require explanation. One, that specimens recovered from any single locality comprised usually only a few skeletal elements, and often did not correspond to elements recovered from other localities, and which are now understood to be from the same taxon. Two, many of the elements are of similar size, due to representation of the more numerous "normal" individuals: such bias is usual assuming random fossilization of individuals from a population. It is clear that the path toward an accurate
representation of the evolution of and phylogenetic relationships among megatheriines has been influenced strongly by the kind of material available. Such restrictions are not unique to the study of megatheriines, as is clear from McDonald's (1987:180) statement on systematics in general: "Truth in the realm of systematics . . . is only as valid as the quantity and quality of the sample available to the systematist."

This thesis resolves some of the taxonomic and phylogenetic problems of Megatheriinae, particularly of the larger Pleistocene species. These advances have been possible largely through the discovery and excavation of two large collections, each from a single locality, of Eremotherium laurillardi. The collection from Jacobina, Bahia, Brazil, under the supervision of C. Cartelle, is of paramount importance, because it is the largest collection of a single megatheriine species from one locality, and possibly the largest for any extinct sloth. The Jacobina collection, supplemented by that from Daytona Beach, Florida, USA, forms the basis for this thesis. These collections provide considerable knowledge of the qualitative and quantitative knowledge of a megatheriine species, and permit inferences on the recognition of similar variation in other species.

However, my thesis does not resolve the status of all taxa described in the literature. As in the past, the main
reasons are that specimens are scarce and poorly-preserved, and biostratigraphic knowledge is limited. Nonetheless, the results presented here represent a considerable advance over previous work. They are based on detailed reviews of the specimens and their characteristics, and critical analyses of the taxonomic diagnoses of previous workers. These studies were evaluated within the context of the range of variation in E. laurillardi, and in other species also, whose recognition was influenced by that in E. laurillardi.

The following chapters present, in order, a taxonomic revision of and discussion of phylogenetic relationships among Megatheriinae. The characters used to define each taxon are based on careful studies of the specimens within the context of variation observed in E. laurillardi. Each taxon is discussed in terms of taxonomic history and diagnostic features. Lists of synonymies are included and their reasons discussed.

## TAXONOMIC REVIEW OF THE MEGATHERIINAE

Megatherium Cuvier, 1796<br>Bradypus Pander \& d'Alton, 1821, nec Linnaeus, 1758<br>Essonodontherium Ameghino, 1884<br>Orocanthus Ameghino, 1885, nec Agassiz, 1835<br>Neoracanthus Ameghino, 1889<br>Hebetotherium Ameghino, 1898<br>Paramegatherium Kraglievich, 1925a<br>Pseudomegatherium Kraglievich, 1931

Diagnosis:
Medium- and large-sized megatheriines. Hypsodonty increased over that in Eremotherium laurillardi. Condyles, basicranium, and mandibular fossa lie relatively dorsally to the plane through the alveolar margins. Lower orbital margin lies at or dorsal to this plane. Premaxillae, when known, elongated and robust, and with age fused firmiy to each other and the maxillae. Toothrows are subparallel. Pterygoid blades reduced. Ventral bulge of the dentary is prominent and angular process relatively dorsal compared to that in E. laurillardi. The lateral margin of the humerus, proximal to the ectepicondylar notch, reduced, as is deltopectoral crest. Olecranon process widened
transversely. Ectal and discoid facets of the astragalus approach each other closely posteriorly.

Type Species: M. americanum

Discussion:
The early taxonomic history and generic and specific synonymies were discussed by Boyd (1958) and Hoffstetter (1959); (see also Mones, 1986). Lydekker (1889: 1295) suggested, but did not formally propose, that Megatherium "should properly be Megalotherium, but its antiquity renders it somewhat sacred". Mones (1986: 254), considered Megaiotherium as "emendatio illegitimum per Megatherium", but as it was never formally proposed, it actually has no status.

Kragiievich (1931:630) proposed the genus Pseudomegatherium for the remains of Megatherium medinae because he was convinced that" la especie de Philippi no pertenece estrictamente al genero Megatherium y por este motivo propongo fundar con ella el género Pseudomegatherium". No further justification or diagnosis was given. Schneider (1935) implied that Kraglievich would have provided such information had he not died prematurely, but this unfortunate circumstance in no way makes the new genus properly established. The genus has not been accepted by other authors, although Schneider (1935) attempted to
provide a diagnosis based on divergent mandibular tooth rows, which is inaccurate (see MANDIBLE), and an elongated premolariform maxillar region, which is possibly plesiomorphic.

Kraglievich (1925a) based this genus on scant remains. I consider it a synonym of Megatherium, as discussed under M. nazarrei.

## Megatherium americanum Cuvier, 1796

Bradypus giganteus Pander \& d'Alton, 1821
Megatherium australe Oken, 1816, nec Parodi, 1930
Megatherium cuvieri Demarest, 1822, nec Lund, 1842
Megatherium gervaisii (sic) Gervais \& Ameghino, 1880
Essonodontherium gervaisi (Gervais \& Ameghino, 1880)
Megatherium Iundii Gervais \& Ameghino, 1880
Oracanthus burmeisteri Ameghino, 1885
Neoracanthus burmeisteri (Ameghino, 1885) Ameghino, 1889
Megatherium gaudryi Moreno, 1888
Megatherium filholi Moreno, 1888
Neoracanthus brakebuschianus Ameghino, 1889
Hebetotherium silenum Ameghino, 1898
Megatherium silenum (Ameghino, 1898) Rraglievich, 1934
Megatherium gallardoi C. Ameghino \& Kraglievich, 1921
Megatherium australe Parodi, 1930, nec Oken, 1816
Megatherium parodii Hoffstetter, 1949

Diagnosis:
Large megatheriine. Dorsal skull profile variably, but usually prominently, sigmoidal. Highest degree of hypsodonty among megatheriines, and indeed, all sloths. Condyles, basicranium, and mandibular fossae well dorsal to the alveolar plane. Lower orbital margin dorsal to this plane. Width of the palate equal to or
slightly greater than transverse width of widest molariform. Condyloid foramen is divided with age into anterior and posterior foramina by lateral expansion of the basioccipital. Ventral bulge of the dentary very prominent, and greatest among sloths. Angular process lies dorsal to alveolar plane. Lateral margin of humerus reduced, approximately intermediate between those in M. tarijense and E. laurillardi. Deltopectoral crest less prominent than in latter species. Olecranon process markedly wide transversely. Iliac wings of pelvis flare markedly. Femoral shaft very robust. Depth of the greater trochanter greater than depth of the femoral head, but may approach that of the latter. Patellar trochiea markedly reduced medially, and does not extend medially to the parasagittal plane of the femur. Femur is strongly twisted about its axis, with the plane passing through the head and greater trochanter approximately between $35^{\circ}-50^{\circ}$ to that passing between the distal condyles. Lateral femoral margin strongly sigmoidal. Tibia relatively robust, and with age ankyloses distally with the fibula. Navicular facet of the astragalus oriented so that the plane tangential to the flat surface of the discoid facet intersects the dorsal part of the navicular facet.

Type:
MNHNM 6, a nearly complete skeleton of a single individual.

Type Locality:
Approximately 7.3 km ("un lieu 1/2", Hoffstetter, 1959:542) southwest of Luján, Buenos Aires Province; Pleistocene.

Discussion:
The status of Essonodontherium gervaisii was discussed by Edmund and Hoffstetter (1970). Its type, MNHNP PAM 276 (formerly MNHNP R-360), was distinguished by Gervais and Ameghino (1880) in bearing four upper and three lower molariforms. Edmund and Hoffstetter (1970) demonstrated that this was an anomalous condition, thereby confirming Lydekker's (1894) opinion, in which he added that the skull probably belonged to a female individual of M. americanum.

Ameghino (1885) based Oracanthus burmeisteri on a juvenile right dentary, MLP 2-62, which preserves nearly completely the mandibular body and molariforms, but lacks the symphyseal spout and most of the ascending ramus, from the Pleistocene of Buenos Aires Province. It was distinguished morphologically from other meqatheriines by its smaller size and less prominent bulge of the ventral margin of the dentary. Lydekker (1889) noted that

Oracanthus was occupied, and Ameghino (1889: pl. 78, figs.
2, 2a) replaced it with Neoracanthus and described the species N. brakebuschianus, based on a well-preserved and nearly complete right dentary in MLP. Unfortunately, Ameghino gave no catalogue number, and the specimen could not be located in the museum. However, it strongly resembles the right dentary MACN 855 in size, morphology, and preservation. N. brakebuschianus was distinguished from N. burmeisteri on its smaller size and longer symphysis.

Ameghino (1898) created Hebetotherium silenum based on a nearly complete left dentary, MLP 2-61, probably from the Ensenadan, or lower Pampean (Kraglievich, 1934) near Mar del Plata, Buenos Aires. The specimen is figured in Lydekker (1894: pl. 45, figs. 2, 2a).

Lydekker (1894), Cabrera (1928), and Kraglievich (1934) agreed that Neoracanthus burmeisteri and N. brakebuschianus are based on the remains of juvenile individuals. Lydekker (1894) considered them to belong to Megatherium americanum, Cabrera (1928) and Kraglievich (1934) to some species of Megatherium. Although Kraglievich (1934) considered Hebetotherium to be based on juvenile remains, he upheld, without explanation, the validity of the species Megatherium silenum, founded on the same specimen.

The type specimens of these genera and species clearly belong to juvenile individuals. Indeed, they are probably from very young juveniles because the symphysis is unfused,
and the mesial and distal surfaces of all or some of the molariforms are tapered, rather than parallel. The size differences among these specimens are clearly due to age and are not taxonomically useful.

Ameghino (1889) separated N. burmeisteri from N. brackebuschianus because of the shorter symphysis in the type of the former, which is the larger specimen. However, this distinction is doubtful because the symphyseal region in MLP 2-62 is not well-preserved, so that its posterior margin is not clear.

Cabrera (1928:342) stated that N. burmeisteri was not "entreramente igual a otros ejemplos jóvenes de megaterios pampeanos, generalmente considerados como Megatherium americanum". Cabrera (1928:342-343) attributed this to interspecific variation, even though he recognized that considerable intraspecific morphological changes occurred during ontogeny, as it was believed at that time that several Pleistocene Megatherium species existed in Buenos Aires Province: "pero, desde el momento que sabemos que durante el Pleistoceno existieron en lo que hoy es provincia de Buenos Aires varias especies de este género, es perfectamente natural que no sean idénticos todos los restos juveniles que se encuentran, eso sin contar las notables diferencias de forma que en la mandíbula y en los dientes pueden producirse durante el desarrollo". It is probable, however, that only a single Pleistocene species of

Megatherium existed in this geographical area, as discussed below. Further, the degree of morphological variation among the juvenile specimens from the Pleistocene of Buenos Aires Province is no greater than that observed in the Gruta das Onças collection of Eremotherium laurillardi. As there is no evidence on which to maintain N. burmeisteri, N. brackebuschianus and Megatherium (=Hebetotherium) silenum, I regard them as synonyms of $M$. americanum.

The type of Megatherium iundii is an adult right astragalus, MLP 2-131, from the Late Pleistocene of Mercedes, Buenos Aires Province. Gervais and Ameghino (1880:138) described it as belonging "á un individuo adulto $y$ cuya forma es muy diferente de la que presente el astragalo de M. americanum", and which "alcanza apenas un tercio del tamaño del mismo hueso del M. americanum". Lydekker (1894:74) stated that MLP 2-131 "es referibile á una hembra de" M. americanum (Lydekker's accompanying English version lacks this phrase). The astragalus is not well-preserved. Its margins, particularly laterally and anteriorly, are broken and eroded. The absolute anteroposterior length of MLP 2-131 is 156 mm ; the approximate, restored length is 175 mm .

Moreno (1888:17) stated that the type of Megatherium filholi, MLP 2-30, comprising mandible, vertebral column with complete tail, ribs, scapulae, limbs, possibiy metapodials ("huesos sueltos de las extremidades"), and
calcanea and astragali of a single individual from the Late Pleistocene of the northern part of Buenos Aires Province. Unfortunately, the mandible could not be located in MLP. It was distinguished as "adulto, mitad mas pequeño que el Megatherium americanum, pero mucho mas delgado de formas" (Moreno, 1888:17). The remains are smaller and somewhat more gracile than those usually attributed by researchers to M. americanum near the turn of the twentieth century, but they are clearly not half the size of those of $M$. americanum, as Moreno claimed. Unfortunately, no sample such as that for Eremotherium laurillardi from Toca das Oncas exists for M. americanum. However, the collection at BMNH includes various astragali that show important variation in this species, and demonstrate a much wider range of variation in linear dimensions than has hitherto been suspected. Further, it suggests that the range is similar to that in E. laurillardi. It is significant that the astragali are all from near Luján, Buenos Aires Province, because the type of the species and the material described by Owen (1856-1860) are also from Luján. The sample includes an adult left astragalus, BMNH 19953b¹ (undescribed in Owen, 1859), which is smaller than MLP 2-30 and MLP 2-131. Its anteroposterior length is 169 mm ; the length of the largest BMNH astragalus, BMNH 19953x, is 221 mm.

Moreno (1888:17) discussed the remains of M. filholi as
part of the collections recovered from the "Yacimientos de Arrecifes, Carmen y San Antonio de Areco y Mercedes", near Mar del Plata, Buenos Aires Province, all late Pleistocene. It is worth noting that, following the description of $M$. filholi, Moreno (1888) added that remains of M. americanum were also recovered, although it is not clear if these were associated with, or even from the same horizon as, those of M. filholi. While I often disagree with the identifications of many of the earlier authors, I usually trust, as in this case, allocation of remains to M. americanum, given the narrow concept of this species during the latter half of the nineteenth and first half of the twentieth centuries.

The other skeletal elements of MLP 2-30 fall within the size range established for Eremotherium laurillardi, and for M. americanum, as judged by extrapolation of the variation among astragali. Further, the ratio of lengths of the tibia and femur are as in undoubted individuals of $M$. americanum. Morphologically, the elements are indistinguishable from those usually allocated to M. americanum. They are slightly more gracile, but gracility occurs among smaller individuals of E. laurillardi, and is to expected in smaller individuals of M. americanum. The astragalus (MLP 2-131) of M. Iundi also falls within the range of size variation for $M$. americanum. Its morphology, as far as can be determined, is as expected in M. americanum. As there is no evidence to support these species, I synonymize them with M. americanum.

Mones (1986:255) considered the species Megatherium filholi to be a nomen nudum because it corresponds to "uno de los ejemplares designados genéricamente como "megatéridos" por Moreno, 1890: lám. 5". However. I believe that the name was published with a sufficient, though brief, description, and treat it as a potentially available name, and therefore properly a synonym of $M$. americanum.

The type of Megatherium gaudryi, MLP 2-60, includes an incomplete dentary and various limb elements from an individual from Monte Hermoso, Buenos Aires Province. The validity of M. gaudryi has been consistently maintained in the literature, except by Ameghino (1889), who synonymized it with M. antiquum. Roth (1911), for example, stated that the mandible of $M$. gaudryi differed only in size from that of M. americanum. Cabrera (1928) rejected Ameghino's (1889) synonymy. Kraglievich (1934) considered it a certainty that M. gaudryi would be found to be generically distinct from Megatherium, were it more completely known. Kraglievich (1934) also stated that Cabrera (1928) had noted that $M$. gaudryi should probably be separated from Megatherium, although it is unclear that this is actually what Cabrera had intended.

Moreno (1888:12) stated that the size of M. gaudryi was "inferior á la del Meg. Americanum y mayor que la del Meg. Leidyi, aún cuando la cabeza ha sido mas pequeña á juzgar por la mandíbula inferior". "M. Leidyi" does not appear
elsewhere in the literature, except in Ameghino (1889:33), who questioned Moreno's use of the name. Probably, Moreno (1888) was referring to Leidy's (1855) species "Eremotherium mirabile" (=E. laurillardi). If so, his comparisons are inaccurate. Further, Moreno (1888) believed that the bulge of the ventral margin of the dentary was less pronounced than in M. americanum and E. laurillardi, and similar to that in $M$. medinae. The comparisons with the latter two species are clearly incorrect, and indicate that Moreno was insufficiently versed in Megatheriinae. Moreno (1888:12) considered that the forelimb was most similar to that of $M$. americanum, but that the radius was "completamente diferente del de todos los edentatos pampeanos", which is incorrect, although there is some deformation.

MLP 2-60 is nearly as large an individual as are many other specimens of $M$. americanum. The morphology of its dentary is within the range established by other specimens of this species. Thus, there are no significant morphological or size differences between the skeletal elements of MLP 2-60 and those of known $M$. americanum.

I believe that the only basis for the continued support of the taxonomic recognition of this species is, almost certainly, that it has been considered to be of Montehermosan age, and its slightly smaller size has been interpreted in this light. For example, Lydekker (1894:76) stated that "The bones, so far as can be determined,
indicate an adult animal of about two-thirds the dimensions of M. americanum; and since the mamals of the Monte Hermoso beds are generally inferior in size to their relatives of the Pampean epoch, it is probable that the species under consideration was smaller than the latter".

However, the morphological similarities of the preserved skeletal elements of MLP $2-60$ to those of $M$. americanum are such that I seriously doubted its age determination as Montehermosan. On examination, I was unable to discover any character that clearly differentiated MLP 2-60 from this species. Fortunately, I was able to discuss my concerns with Dr. E. P. Tonni of MLP, who has spent considerable time working in the Monte Hermoso region. He is thus well-acquainted with its geology and the preservational characteristics of the fossils recovered from its deposits. His opinion is that MLP 2-60 was without doubt recovered from Pleistocene deposits in the Monte Hermoso region. Dr. Tonni (pers. comm., 12/19/1991) writes:
"F. Ameghino denominó 'Monte Hermoso' a un amplio sector de la costa SW de la provincia de Buenos Aires (alrededor de 17 km de extensión), incluyendo yacimientos de Edad Montehermosense (Plioceno) y de Edad Lujanense (Pleistoceno tardio-Holoceno temprano)."
"En los yacimientos Montehermosenses se encuentra el clásico de los 'acantilados de Monte Hermoso' actualmente citado como 'Farola Monte Hermoso' o
'acantilados de Punta Alta', mientras que los de Edad Lujanense incluyen a los de "Playa del Barco" situados unos 14 km al Este de los anteriores."
"Del yacimiento de Playa del Barco probablemente procede el atlas humano referido por Ameghino como Tetraprothomo y atribuído en consecuencia al Plioceno ('Araucanense'). Recientemente Aramayo y Manera de Bianco . . . (1989) demostraron la indudable Edad Lujanense del yacimiento. Seguramente de aquí procede el fémur de Megatherium [MLP] 2-60 que en las viejas colecciones figura como 'Araucanense de Monte Hermoso'."

There is another possible reason to consider, although it is not clearly established, and may be somewhat apocryphal. It is well-known that $F$. Ameghino was forced from his position at MLP due to irreconcilable differences with F. P. Moreno, then the director of the museum. Dr. Tonni has suggested that Ameghino, possibly to spite and confuse Moreno, changed locality information for various specimens at MLP, among which may have been the type of $M$. gaudryi.

In view of the Pleistocene age of MLP 2-60, and its morphological similarities to M. americanum (see appropriate sections under ANATOMICAL DESCRIPTIONS OF MEGATHERIINAE), I synonymize M. gaudryi with $M$. americanum.

Megatherium gallardoi is based on MACN 5002, which
includes a relatively complete and well-preserved skull and mandible, femur, humerus, and uina of a possibly subadult individual from the Pleistocene (Ensenadan, or lower Pampean) of the city of Buenos Aires. The skull and mandible of the new species were described by Ameghino and Kraglievich (1921). Detailed comparisons and discussion of the remains of M. gallardoi are given within the ANATOMICAL DESCRIPTIONS, where the reasons for synonymy of this species with M. americanum are made clear.

Megatherium australe was erected by Parodi (1930) based on MLP 13021, a reasonably well-preserved skull, and scant postcranial remains from a single individual, from the coastal Pleistocene of the Patagonian Province of Santa Cruz, between Punta Nava and Cabo Tres Puntas. Hoffstetter (1949) stated that the name was unavailable because Oken's (1916) M. australe was a synonym of M. americanum. I accept Hoffstetter's (1949) opinion, based on that of Gervais and Ameghino (1880), of Oken's species, although I was unable to consult Oken's (1816) work. The synonymy appears correct. However, if Oken published the specific name without description, figure, or indication, then $M$. australe could well be a nomen nudum, and "may be made available later for the same or a different concept" (ICZN, 1985). Detailed comparisons and discussions of the remains of M. parodii are given in SKULL: Anatomical Descriptions of the Skull of Eremotherium laurillardi and Megatherium americanum, where
the synonymy of this specific name is manifest.
Three other names, which are not listed as synonyms, must be noted. Megaterium colossale (sic) and Megaterium cataphractum (sic) appear in the second (unnumbered) table in Larrañaga (1923:341). Larrañaga (1923:341) assigned each to different families (although used in a quite different sense from the usual meaning of this rank), M. colossale to the "Edentatos: defecto de incisivos $y$ caninos $y$ a veces molares", and $M$. cataphractum to the "Tardigrados: defecto de solo los incisivos". Apparently, Larrañaga's 'Tardigrados' includes edentates that retain caniniforms, and thus $M$. cataphractum is probably not a megatheriid; Mones (1986) suggested that it may be a glyptodont. Larrañaga (1923) attributed the latter species to Bonpland. However, it is not clear that Bonpland published this name (Mones, pers. comm., 1994). Mones (1986:254) listed the name as "Megatherium cataphractum Bonpland fide Larrañaga, 1923", and considered it a nomen nudum.

Megaterium colossale appears in Larrañaga's (1923:340) first table (also unnumbered) as "Cuvier: colosalis. . . Megaterium". It is not clear how this name is to be interpreted. Mones (pers. comm., 1994) stated that perhaps the species was authored by Cuvier or was intended as a new species name. No reference to colossale is found in the fourth and later editions of Cuvier's (1836:303-370) "Recherches sur les Ossemens Fossiles". Mones (1986)
regarded $M$. colossale as a nomen nudum, with reference Bonpland fide Larrañaga. However, Larrañaga (1923) did not attribute this name to Bonpland.

I agree with Mones (1986) in regarding M. cataphractum and M. colossale as nomina nuda. The names were published without description or illustration, and apparently not based on particular specimens. However, it seems nearly certain that the names refer to the concept of $M$. americanum.

The species Megatherium piratinium is attributed by Mones (1986) to Tupi Caldas (1939, in Paula Couto, 1940:217219); Paula Couto (1940) published, apparently, the quoted opinion that Tupi Caldas had presented to the State Museum. The name is based on three partial elements from Pinheiro Machado, Rio Grande do Sul, Brazil, and housed in the Museu Júlio de Castilhos, of which the tibia, missing its proximal epiphysis, is the most important. It is clear, from Paula Couto's (1940: pl. 11) figures, that Tupi Caldas confused the distal surface for the proximal, and stated that the distal epiphysis was missing; Paula Couto (1940) did not correct or recognize Tupi Caldas' error. The anteroposterior depth of the distal surface of the tibia is apparently more as in M. americanum, rather than in $E$. laurillardi (which may reflect the perspective of the specimen in Paula Couto, 1940: pl. 111, but the shaft constriction appears more as in the latter. Toledo (1989)
recognized Eremotherium as present in the Pleistocene of Rio Grande do Sul. The status of Megatherium piratinium cannot be certainly determined; but the name is almost certainly a synonym of M. americanum or E. laurillarđi.

Megatherium tarijense H. Gervais \& Ameghino, 1880 Megatherium sp. P. Gervais, 1855

Diagnosis:
Medium-sized megatheriine, with ranges of linear dimensions overlapping the lower end of the ranges of M. americanum and E. laurillardi. Skull is elongated and relatively narrow, with prominent postorbital processes and concave lateral walls. Dorsal skull profile is nearly linear, but gently raised centrally as a dome. Premaxillae are robust and quadrangular, but shorter than in M. americanum, and with age fused firmily together and to the maxillae. Hypsodonty approximately intermediate between that of $M$. americanum and E. laurillardi. Lower orbital margin approximately level with the alveolar plane. Condyloid foramen becomes divided with age into anterior and posterior foramina by lateral expansion of the basioccipital. Ventral bulge of dentary approximately intermediate between those of $M$. americanum and $E$. laurillardi, as is position of angular processes. Clavicle is elongated, and bears an abrupt angle at the junction of its sternal and acromial parts. Humeral ectepicondylar notch much reduced, as is the lateral surface of the humerus proximal to the notch.

Deltopectoral crest reduced compared to that of $M$. americanum. Pelvic girale slightly more elongated than in M. americanum, and iliac wings flare laterally less prominently. Femur relatively gracile and patellar trochlea extends medially, resembling those of $E$. laurillardi. Position of navicular facet approximately intermediate between those of $M$. americanum and $E$. laurillardi.

Type specimen:
MNHNP TAR 1269, a nearly complete left calcaneum of an adult individual; missing small portions anteriorly and posteriorly.

Type locality:
Tarija Formation, Tarija, Bolivia.

Referred specimens:
FMNH P14216, a nearly complete adult skeleton of an individual from the Tarija Formation, Tarija Valley, near Pađcaya, Bolivia.

NRM M4890, articulated skull and mandible from the Tarija Formation. The skull has suffered considerable dorsal crushing. The proximal parts of the premaxillae only, fused to maxillae, are preserved.

Discussion:
The species was named by H. Gervais and Ameghino (1880), as noted by Ameghino (1889), and not "(P. Gervais)" as indicated by H. Gervais and Ameghino (1880:138) or as "Gervais in Gervais \& Ameghino, 1880" by Mones (1986:255). The type was figured by P. Gervais (1855: pl. 12, fig. 6).

Ameghino (1889) explained that M. tarijense was named because material discovered since P. Gervais' (1855) report demonstrated the existence of a species smaller than $M$. americanum. Further, Ameghino (1889) synonymized M. filholi with $M$. tarijense, and stated that its remains had been recovered frequently in the province of Buenos Aires, Argentina. On one of these remains Ameghino (1889) reported that the tibia and fibula remain unfused distally; the specimen was housed at MLP and thus unavailable to Ameghino for detailed study. Ameghino (1904) considered M. sundti (from Ulloma, Bolivia; see below) a synonym of M. tarijense. Strangely, but perhaps not surprisingly, Ameghino (1889; 1904) did not consider his and Gervais' M. Iundi as a synonym of $M$. tarijense. The former species was based on an astragalus from the province of Buenos Aires, and distinguished from M. americanum on its smaller size by Gervais and Ameghino (1880) and Ameghino (1889).

Most authors, however, have doubted the validity of $M$. tarijense. Lydekker (1894) regarded $M$. tarijense as probably an immature female of $M$. americanum; however, this
was based on the tibia-fibula from the province of Buenos Aires in MLP, which was mentioned by Ameghino (1889). Boule and Thèvenin ( $1920: 213$ ) rejected the species and considered it "seulement comme une race, une variété géographique", an opinion probably based largely on the evidence of the material remains included in the Créqui-Montfort collection at MNFN (P). Hoffstetter (1952:50) stated that M. tarijense was considered by certain authors "une simple sous-espèce ou même comme un synonyme de l'espèce génotype". Hoffstetter (1963:195) discussed megatherine remains from Tarija as demonstrating "qu'il s'agit bien d'un vrai Megatherium et qu'il atteignait une taille comparable á celle de l'espèce générotype, dont il ne semble pas séparable". Paula Couto (1954) recognized M. tarijense, but later (1979) stated that it might belong to Eremotherium.

The confusion regarding the recognition of this species is understandable because there are at least two Megatherium species present in the Tarija Formation. The possible existence of a third megatheriine species is discussed below and under SKULL. One is that represented most clearly by the nearly complete individual FMNH P14216. This specimen and a femur, MUT V411, provide strong evidence for the unequivocal recognition of a species distinct from $M$. americanum. The reasons for identification of FMNH P14216, and by extension of other specimens from Tarija, to $M$. tarijense are discussed under the PES: Calcaneum.

The second species from Tarija is M. americanum. The identification of this species in Tarija is based on usually isolated specimens in MUT, MNHN BOL, MNHNP, and FMNH, which are discussed under the appropriate chapters for each skeletal element. The opinions of the authors cited above were undoubtedly influenced by the particular sample of remains available to them for study. It should be noted also that the remains were not particularly abundant and that, for the earlier authors at least, FMNF P14216 was not available for study. For example, the calcaneum and tibia illustrated by Boule and Thèvenin (1920: pl. 24, figs. 7, 8) are clearly of $M$. americanum. Additional material that may be cited are the well-preserved premaxillae MNHNP 1907-1538, and the partial dentary and complete femur MUT V1082 and V413, respectively.

There are additional remains in MNENP, MUT, and FMNH that cannot be assigned confidently to M. americanum or M. tarijense, usually because the specimens are poorly or incompletely preserved, or because the elements preserved are not clearly diagnostic. This is particularly true of the remains of juveniles in MNHNP.

Megatherium nazarrei (Kraglievich, 1925a)

Diagnosis:
Large megatheriine, probably resembling in mass $M$. americanum and E. laurillardi. Humeral diaphysis is nearly cylindrical because the lateral margin proximal to the ectepicondylar notch is markedly reduced, so that no remnant of the lateral projection in $E$. laurillardi is present. The notch itself is so reduced as to be nearly absent. Deltopectoral crest very weak. Clavicle bears an abrupt angle at the junction of its sternal and acromial parts, resembling the condition in M. tarijense, and in contrast to the smoothly sigmoidal clavicles of M. americanum and E. laurillardi. Femoral patellar trochlea medially extended approximately as in E. laurillardi. M. tarijense, and M. medinae.

## Type Specimen:

MACN 7127, preserving scant remains of an individual, and including clavicle, the distal part of a femur, a tibia and the proximal part of a fibula, and 6 articulated and 5 isolated caudal vertebrae.

Type locality:
East bank of the río Agrio, near Cerro Campana,

Mahuida, Lonopue, Neuquen Province, Argentina. Pleistocene.

Discussion:
The species is not well known. Kraglievich (1925a) based the species on MACN 7127, from the level of Locality 2 near Cerro Campana. He assigned additional remains as paratype, MACN 7128, which were recovered from Locality i, and include humerus, clavicle, caudal vertebrae, and numerous molariform fragments. It should be noted, then, that the femur and humerus are not certainly from the same species because they were found separately. However, I accept them as conspecific because the localities are in very close proximity and no other megatheriines are known from the region. Kraglievich (1925a) was uncertain of the age of the deposits, and accepted Groeber's (1925) deduction of a Pleistocene age.

Kraglievich (1925a) distinguished "P." nazarrei generally from megatheriines, and from M. americanum specifically, based on the medially extended patellar trochlea, although he recognized the reduced deltopectoral crest and reduced lateral margin of the humerus. However, the morphology of the patellar trochlea is plesiomorphic; the features of the clavicle and humerus, on the other hand, are apparently derived (vide infra: Phylogeny of the Megatheriinae), and provide evidence of a close relationship between M. tarijense and M. nazarrei.

It is unclear, therefore, whether Paramegatherium merits recognition as a separate genus. Certainly, I would argue against generic status based on a medially extended patellar trochlea, which occurs in many megatheriines, and on the probability that "P." nazarrei and M. tarijense are closely related.

A second option would be to include $M$. tarijense within Paramegatherium, thereby recognizing taxonomically that the two species form a clade. This possibility is feasible, given the hypothesis of relationships presented below. However, I await the inclusion of a new species of cf. Megatherim in an analysis of relationships (in collaboration with P. A. Saint André) before proposing this formally.

A third option is to synonymize Paramegatherium with Megatherium, as I do here. Simpson (1945) did this, but without reasons, although I suspect that he was strongly influenced by the large size and Pleistocene age of "P." nazarrei rather than any affinity to M. americanum through M. tarijense. It is worth noting that Simpson (e.g., 1984 and in Simpson and Paula Couto, 1982) steadfastly rejected generic status for Eremotherium, which implies that he considered the presence of its highly derived features, among other characters, as unimportant. Furthermore Paramegatherium was accepted before and after Simpson's (1945) work by such authors as Cabrera (1928), Rusconi
(1945), and Hoffstetter (1958).

Rusconi (1945) based P. incognitum on a nearly complete right femur, MHNJCM 2, from San Rafael, Mendoza Province, Argentina. Rusconi (1945:5) stated the age simply as "Plioceno?", because it was clearly younger than the "horizonte Tunuyanense". The femur is of a relatively large individual with characteristics approximately intermediate between those of $M$. americanum and E. laurillardi, but perhaps more resembling the former.

I was unable to examine MENJCM 2, and my observations are based on Rusconi's (1945: figs. 1-3) diagrams. The femur is relatively short and stocky, with a large greater trochanter. The shaft is relatively constricted centrally and expanded transversely proximally and distally, and the medial margin is markedly concave, more so than usually occurs in E. laurillardi, but very much as is normal in M. americanum. The shaft is strongly twisted about its long axis, so that the angle between the planes passing through the head and greater trochanter and the distal condyles is approximately $55^{\circ}$, which falls within the high end of the range for $M$. americanum. The patellar trochlea in anterior view extends slightly medially, but essentially lies nearly dorsally to the lateral condyle. Its morphology is apparently not beyond the range observed in $M$. americanum. In distal view, however, the trochlea appears to extend further medially than is usual in the latter species, and
thus is approximately intermediate between those of $M$. americanum and E. laurillardi. I suspect that the femur of "P." incognitum probably represents an individual of $M$. americanum with a slightly analomous patellar trochlea, although a considerably better sample is required before definite decisions are made regarding the former species.

Rusconi (1945) considered Schaub's (1935) Megatherium (?Paramegatherium) rusconii from Venezuela to be sufficiently similar to merit inclusion within Paramegatherium. However, Schaub's (1935) species is a synonym of E. laurillardi (App. 1).

Megatherium medinae Philippi, 1893a
Megatherium meginae Philippi, 1893a, Iapsus
Pseudomegatherium medinae (Philippi, 1893a) Kraglievich, 1931.

Diagnosis:
Medium-sized megatheriine, resembling M. tarijense in size and proportions of known elements, except that: skull is less elongated; lateral surface of humerus projects approximately as in M. americanum; deltopectoral approximately as in latter species.

Type specimen:
SGO PV252 (formerly 1-VI-67-8), an incomplete mandible lacking most of the right ascending ramus, and the region distal to left m4. The tooth-bearing portion of the left ramus is deflected laterally, possibly due to a vertical break through the dentary at the level of the $\mathrm{I} m$ alveolus. $R \mathrm{ml}-\mathrm{m} 3$ are preserved completely; Rm mand L m1-m4 are broken at the level of the alveolar margins.

Type locality:
Pampa del Tamarugal, near Pica, Tarapacá Province, Chile (Marshall and Salinas, 1991).

Discussion:
There are problems with this name. Philippi (1893a, 1893b) published German and Spanish, respectively, versions of his description. These are very similar, except that the Spanish version includes a table of measurements for $\mathrm{M} 3 / \mathrm{m} 3$, the diagrams show slightly more detail, and the arrangement and labelling of the figures differ from the German version. Most workers, particularly South Americans, cite the Spanish version for technical nomenclatural purposes. However, the German version apparently has priority, although I was unable to determine precise dates of publication for either article. This opinion is based on the order in which these articles are listed by Romer et al. (1962), Mones (1986), who stated that the Spanish version is an abbreviated translation of the German, and Marshall and Salinas (1991).

There are, further, two technical nomenclatural problems with the name M. medinae that require clarification. One is that the name was first published by Ameghino (1889) under the synonymy list for M. Iundi. Ameghino (1889) cited the name thrice in his text, and gave a cursory description of the species, stating that $M$. medinae was much more gracile and smaller than $M$. americanum, based on casts that he had received from Philippi. Ameghino (1889) attributed the species to Philippi, but noted that it had not been described. Apparently, "El nombre fué referido por el mismo Philippi a
una fecha once años anterior, y a él aludió Ameghino en 1889; pero realmenteno parece haber sido publicado como nombre válido antes de 1893" (Cabrera, 1928:341). A search for a possibly earlier mention of the name by Philippi has been in vain. Frassinetti (1982:21) includes only the Spanish version of the article as "Philippi, R.A. 18921893", but the date of publication of the volume containing the article is clearly 1893. The second problem is that the species first appears in Philippi's (1893a:91) text as "M. Meginae", although the relevant text is preceded by a diagram (Philippi, 1893a: fig. 5) that is labelled as "Megatherium Medinae".

Technically, M. medinae is a nomen nudum, as suggested by Casamiquela (1967). However, Casamiquela and Sepulveda (1974), and probably all other paleontologists concerned with megatheriine ground sloths, most recently Salinas et al. (1991) and Marshall and Salinas (1991), have long considered the name valid and applied it; Ameghino (1889) is apparently the sole exception. Further, and formally more important, a nomen nudum may be made available later for the same or a different concept (ICZN, 1985). Therefore, M. medinae is the valid name for this species. It is discussed further below together with $M$. sundti, because the taxonomic histories of these species are closely linked.

Diagnosis:
Medium-sized megatheriine, resembling M. tarijense and M. medinae in size and proportions. Differs from these in robustness of its femur, which resembles that of $M$. americanum.

Type Specimen:
SGO PV277 (formerly 5-VI-67/2), an incomplete mandible. Left dentary lacks only the anterodorsal portion of the coronoid process, but right dentary is largely incomplete. Right m1-m4, L m4, and the mesial half of left ml are missing. Left $m 2-m 3$ are broken at the level of the alveolar margins.

## Type Locality:

pleistocene deposits near Ulloma, Bolivia, "in den Uferabhāngen des Rio Desaguadero" (Philippi, 1893a:87). The fossils were recovered from the base of the Ulloma Formation (Sundt, 1892) on the south side of the river (Marshall and Salinas, 1991). The fauna is referrable to the early part of the Lujanian Land Mammal Age, approximately 0.5 Mya (Salinas and Marshall, 1991).

Discussion:
Philippi (1893a:91) distinguished M. medinae and M. sundti based on the relative orientations of the toothrows. He noted that in M. medinae "die beiden Zahnreihen stark divergiren, während sie bei dem Megatherium von Ulloma fast ganz parallel laufen". Philippi (1893a,b) also examined skull remains, but made no attempt to distinguish the species based on this material.

Casamiquela and Sepulveda (1974) considered M. sundti as a junior synonym of $M$. medinae. Frassinetti and Azcarate (1974:38) maintained a distinction between the species, and considered M. sundti to be "un megatérido bastante más pequeño y con las líneas de ambos lados de los molares inferiores paralelas", whereas they are divergent in $M$. medinae. This is based on Philippi's (1893a) original description. However, the characteristic of size is doubtful, and that of the divergent tooth rows misleading. I agree with Casamiquela and Sepulveda (1974) that the divergent tooth rows in SGO PV252 are caused by lateral deformation of the tooth bearing portion of the left ramus.

Casamiquela and Sepulveda (1974) argued that the differences between the skeletal remains from Tarapacá and Ulloma were due to interspecific variation, compounded by age and poor preservation. Marshall and Salinas (1991) agreed with these conclusions.

The synonymy of M. sundti with M. medinae seems
reasonable, given the preservation of the material from these localities, and the scarcity of directly comparable elements. Indeed, it is difficult to distinguish between the cranial and postcranial remains from Tarapacá and Ulloma, particularly on the features discussed by Casamiquela and Sepulveda (1974), and, given only the information available to these workers, I would tend to agree with them.

However, there are subtle differences in the skull and mandible that apparently correlate with considerably different femoral morphologies. The differences in the skulls and mandibles from these localities are discussed under SKULL and MANDIBLE, and may prove to be inconsistent, and therefore not diagnostic, but such an hypothesis may be tested only through the discovery of a considerably larger sample and of better-preserved remains.

Casamiquela and Sepulveda (1974) and Marshall and Salinas (1991) did not compare the femora from Tarpacá and Ulloma, either because they were unaware that a femur from Ulloma, PIU M4530, had been recovered or they were unable to study it. PIU M4530 include the well-preserved remains of most of the skeleton of an older juvenile individual from Ulloma, labeiled by "I. Sefve, 1920" as older than the Puna layers, and thus of Pleistocene age L. Werdelin, pers. comm.. 1993). The animal was not a young juvenile because the bulge of the ventral margin of the dentary was already
prominent. The femur is nearly complete. It is relatively constricted centrally, and transversely expanded proximally and distally, and thus robust, approximately as in Megatherium americanum. This condition contrasts markedly with the nearly parallel-sided femora from Tarapaca, which resemble those of Eremotherium laurillardi. The patellar trochlea of M 4530 is extended medially, as in the Tarapacá and $E$. lauriliardi femora, and in contrast to that of $M$. americanum.

The morphological differences between the Tarapaca and Ulloma megatheriines are considered sufficient to allow recognition of $M$. medinae and M. sundti. The skull of M. tarijense is similar to that of $M$. sundti in inflation over the central part of the dorsal profile, although the skull of the former is relatively elongated and narrow. However, the femur of $M$. tarijense is nearly parallel-sided, as in $M$. medinae and E. laurillardi; and the premaxilla is robust, quadrangular, and elongated, similar to but less prominent than that of $M$. americanum.

Diagnosis:
Small megatheriine. Femur somewhat robust. Patellar trochlea reduced, and essentially an anterodorsal extension of the lateral articular condyle, as in $M$. americanum.

Type specimen:
MACN 9674, complete right femur and left patella.

Type Locality: Left margin of the río Quequen Salada, between Oriente and Irene.

Discussion:
This megatheriine is known only from MACN 9674. The patellar trochlea of the femur is reduced to a degree known elsewhere only in the much larger M. americanum.

> Megatherium elenense (Hoffstetter, 1949)

Megatherium sp. A Hoffstetter, 1948
Megatherium aff. rusconii Schaub (partim). Hoffstetter, 1948: pl. 3, fig. 7)

Schaubia elenense Hoffstetter, 1949
Eremotherium elenense Hoffstetter, 1952

Diagnosis: see Discussion.

Type Specimen:
EPN V150, a right adult radius.

Type Locality:
Upper Pleistocene deposits from Santa Elena Peninsula, Ecuador.

Discussion:
This species is not easily diagnosed, but is apparently slightly smaller than $M$. medinae and its dentary is more gracile. The remains of $M$. elenense are found in the same localities as those of E. laurillardi in the Santa Elena Peninsula. Hoffstetter (1952) maintained this species on its smaller size. Additional remains, from the Talara tar seeps, were subsequently recovered during ROM expeditions to Peru and Ecuador during the late 1958 and 1962.

Cartelle (1992) and Cartelle and Bohórquez (1982) considered these remains as representing small individuals of E. laurillardi. Although the remains of $M$. elenense are possibly somewhat smaller than expected for E. laurillardi, I would agree with these authors if synonymy were based only on size. There are, however, severai features that argue against conspecificity of these species. The relatively deep mandibular bulge and high position of the angular process are discussed under MANDIBLE. Further, the manus of M. elenense bears a complete MC II, known from several specimens from the Santa Elena Peninsula and the Talara tar seeps. The morphology of its proximal surface suggests a Eree trapezoid. Thus, the MCC was probably nodular and contained the trapezium and a reduced MC I, as occurs usually in megatheriines and in contrast to the condition in E. laurillardi. A complete MC II and free trapezoid are unknown in this species, despite the abundant manual elements recovered.
M. elenense is possibly conspecific with one of the medium-sized megatheriines, but its remains are too few to confirm or reject such possibilities. I consider it closer to Megatherium than to E. laurillardi, based on features of its dentary, and thus transfer it to the former genus.

Megatherium Lund, 1842, nec Cuvier, 1796
Ocnopus (partim) Reinhardt, 1875
Schaubia Hoffstetter, 1949, nec Camp, Welles, \& Green, 1949
Schaubitherium Hoffstetter, 1949

Diagnosis:
Large megatheriine, similar in mass to $M$. americanum. Dorsal skull profile gently sigmoidal. Hysodonty low compared to that of $M$. americanum and medium-size Megatherium species. Occipital condyles, basicranium, and mandibular fossae relatively little raised above level of alveolar plane. Lower orbital margin ventral to this plane, so that molariforms often visible in lateral view through lower orbit. Premaxillae triangular, short, and loosely articulated to each other and premaxillae. Maxilla relatively elongated anterior to first molariforms compare to $M$. americanum and medium-sized Megatherium species. Ventral bulge of dentary not prominent. Angular process mainiy ventral to alveolar plane. Humerus bears relatively prominent deltopectoral crest. Lateral surface of humerus proximal to ectepicondylar notch prominent, rugose, and projects laterally. Ectepicondylar notch distinct. Femur gracile, approximately as in M. tarijense and M.
medinae. Patellar trochlea medially extended, as in latter two species. Navicular process lies more dorsally than in Megatherium: plane of flat surface of discoid plane intersects approximately the dorsal third of the navicular facet. Ectal and discoid facets of the astragalus are further separated than in Megatherium.

Type Species: Eremotherium Iaurillardi.
Eremotherium Iaurillardi (Lund, 1842)
Megatherium laurillardi Lund, 1842
Megatherium cuvieri Lund, 1842, nec Desmarest, 1822
Chelonia couperi Harlan, 1842
Megatherium mirabile Leidy, 1855
Megatherium guanajuatense Duges, 1882
Megatherium (?Paramegatherium) rusconii Schaub, 1935
Megatheriumm hudsoni White, 1941
Megatherium Iarensis Nectario-Maria, 1941
Eremotherium carolinense Spillmann, 1948
Megatherium venezuelensis Osten, 1951
Eremotherium (Pseuderemotherium) Iundi Paula Couto, 1954
Eremotherium cucutense Porta, 1961
Eremotherium robustum Porta, 1961

Diagnosis: same as for genus.

Type locality:
Lapa Vermelha, Vale do Rias das Velhas, Lagoa Santa, Minas Gerais, Brazil. Upper Pleistocene.

Type specimen:
ZMUC 1130, an isolated molariform from a juvenile individual.

Discussion:
The taxonomic history and a discussion of this species is presented by Cartelle and De Iuliis (1995). Statistical analyses included in the manuscript demonstrate that no significant variation exists among the height and length among astragali recovered from various localities. Analyses in linear dimensions for other skeletal elements, such as for the humerus, femur, and calcaneum, also demonstrate no significant differences among localities.

## Megatheridium Cabrera, 1928

Diagnosis:
A small megatheriine. Anterior margins of the anterior zygomatic roots well-anterior, approximately at the level of the mesial third of M1. Maxillae elongated anterior to first molariforms, with lateral walls slightly diverging laterally to the anterior.

Type species: M. annectens Cabrera, 1928

Diagnosis: same as for genus.

Type Specimen:
MLP 2-69, incomplete and largely disarticulated skull elements of a juvenile individual, including the occiput, squamosals, and maxillae.

Type Locality:
"territorio de Río Negro, departamento de Coronel Pringles, sección VI, fracción C, lote 16 <<al norte seis leguas de la barranca>s, que equivale próximamente a lat. $40^{\circ} 25^{\prime}$ S. y long. $63^{\circ} 20^{\prime} \mathrm{W}$. (formación probablemente Rionegrense)", Pliocene (Cabrera, 1928:348).

Discussion:
Cabrera (1928:348) erected the species on scant juvenile remains, and considered that the individual "ya no podia ser considerado como joven, y que débia haber alcanzado ya, o estar próximo a alcanzar, el tamano de su especie*. Although I was unable to examine MLP 2-69, evidence from Cabrera's (1928: fig. d; pl. 1) illustrations demonstrates that the individual was probably considerably younger than was supposed by Cabrera. For example, nearly
all the remains are separated along sutural boundaries. The sutures between the supraoccipitals and exoccipitals are incompletely closed, and those between the exoccipitals and basioccipitals are completely unfused, so that the basicranium is missing. These sutures close very early during ontogeny in Eremotherium laurillardi. Therefore, it is improbable that MLP 2-69 was near the adult size for its species.

Few diagnostically useful characters are preserved by MLP 2-69. Cabrera (1928) noted several features that he believed indicated the archaic or primitive nature of the species. This idea was partly due to the then general supposition that Megatherium medinae was a Pliocene species (which, by circular argument, was considered Pliocene largely based on its supposediy primitive features). Cabrera (1928) considered Megatheridium annectens smaller than other Pliocene megatheriines, but MLP 2-69 probably gives no accurate idea of the adult size of its species.

Cabrera (1928) further believed that the molariforms were mesiodistally compressed. However, this appears incorrect and an artefact of preservation. The right maxilla, which is better preserved than the left, suggests that the molariforms were approximately as in most other megatheriines. The alveolus of MI is smaller than those of M2 and M3, but this is the normal pattern. M2 does not appear to be mesiodistally compressed. The alveolus of left

M1 is mesiodistally and asymmetrically compressed, but this is clearly due to distortion. The left M2 alveolus is mesiodistally compressed relative to the right M2 alveolus, but not so much as the left M1 alveolus.

Among the certain features of MLP 2-69 are the position of the anterior zygomatic roots and the premolariform lengths of the maxillae. The roots lie relatively anteriorly, with anterior margin approximately lateral to the mesial third of $M 1$; the posterior margin is not preserved. This position is further anterior than in any other megatheriine in which the root is preserved. It is most similar to that of E. laurillardi, in which the root lies between the middle of M1 to the mesial part of M3 , although the anterior margin may lie somewhat more posteriorly. The position of the root is apparently not influenced by age.

The PMMLI cannot be directly compared with those for other megatheriines because the toothrow and the anterior ends of the maxillae are incomplete. However, the maxilla extended well-anterior to M1, at least to the degree observed in E. laurillardi, and perhaps more. The shape of the muzzle cannot be determined. The lateral walls of the maxillae appear to diverge anteriorly, but less so than in Pyramiodontherium bergi or Megathericulus patagonicus, although this may be due to the incomplete rostrum. Further, divergence of the left maxilla is slightly greater
than of the right and probably reflects distortion, but which represents the actual degree of divergence is unknown.

Cabrera's (1928) reasons for erecting a new genus and species on such scant remains are unclear. The only certain diagnostic feature of $M$. annectens is the very anterior position of its anterior zygomatic root. Cabrera (1928) used the position of the root partly to define his grouping of megatheriines (although he incorrectly believed that the root lay anteriorly in Megatherium americanum; vide infra: Phylogeny of the Megatheriinae). The small size of MLP 2-69 is very probably due to its immaturity. Elongation of the maxillae anteriorly and their divergence are not unique. MLP 2-69 may represent a distinct species, despite its incompleteness. It is more likely, however, that it should be part of a previously described species. At present, it is not possible to invalidate Megatheridium or to synonymize it with another taxon because so little of its morphology is known.

Megatheriops C. Ameghino, 1921
Megatherium Rovereto, 1914, nec Cuvier, 1796

Diagnosis:
Medium-sized megatheriine. Skull relatively short, and cranium dorsoventrally deep. Dorsal profile of cranium bulbous. Rostrum elongated and contact between cranial and rostral profiles abrupt. Toothrows nearly parallel, and palatal intermolariform width approximately equal to that of the largest molariform. Maxillae extend well anterior to M1, with PMML1 approximately 42. Lateral maxillary walls nearly parallel. OCHI and OPTHI are approximately 33. Anterior zygomatic buttress lies between middle of M2 and distal part of M1. Pterygoid blade relatively small. Dentary resembles those of medium-sized Megatherium species. Angular process partly dorsal to the level of the alveolar plane. Symphysis ends near the level of the middle of ml . Humerus bears a rugose lateral projection proximal to the entepicondylar notch. The deltopectoral crest is markedly developed, and its distal end is laterally deflected.

[^0]Discussion: see below

Megatherium rectidens Rovereto, 1914

Diagnosis: same as for genus.

Type specimen:
MACN 2818, includes a nearly complete skull, right dentary, and both humeri of a single individual. The skull is generally well-preserved, except that the left side anterior to the auditory region is crushed medially. In the dentary, the dorsal part of the coronoid process is missing; as are the molariforms, except m 4 .

Type locality:
Huayquerías de San Carlos, Mendoza, Argentina. Pliocene.

Discussion:
Rovereto (1914:210) based this species only on the skull, and considered that its generic characteristics "corresponden suficientement al M. americanum". C. Ameghino (in Ameghino and Kraglievich, 1921) raised the species to generic status as the genus Megatheriops, without explanation. Cabrera (1928) had reservations about its validity, and considered it very similar to

Pyramiodontherium bergi, but maintained its status.
Cabrera (1928:345,347) stated that the difference between the skulls "no tienen mas importancia que las que hay entre dos especies de cualquiera de los generos vivientes de mamiferos, entre Choloepus didactylus y Ch. Hoffmanni, por ejemplo". Further, Cabrera (1928:347) stated that "rectidens ha sido referido por Rovereto al mismo piso en que se encuentra Bergi". The first of these statements may be true, but such arguments are based necessarily and strictly on subjective judgement. I would, for example, consider the differences in general skull form of these species to be of the same nature, and possible to a greater degree, as those between Choloepus and Bradypus.

As for Cabrera's (1928) second statement, Rovereto (1914) assigned both to the "Araucanense". However, this term was then considered to represent a stratigraphic and faunistic unit, but is now understood to span considerably more than a single land mamal age (see GEOLOGY). Further, Megatheriops and Pyramiodontherium are from rather widely separated localities, and precise stratigraphic information is unavailable for Pyramiodontherium. Simpson (1945), followed by Hoffstetter (1958), included Megatheriops within Megatherium, but without explanation.

I consider Megatheriops a valid genus, for it possesses apparently plesiomorphic features, such as an elongated premolariform maxillary region and well-developed humeral
deltopectoral crest, but is derived in its degree of hypsodonty. The skull is dorsoventrally high and relatively short. The dorsal skull profile is distinct from that of other megatheriines. Its cranial portion is curved or bulbous, but unlike the domed profile in M. sundti. The junction between the cranial and rostral profiles is abrupt, and the rostrum is relatively slender. The pterygoid blades are approximately as in Eremotherium laurillardi MCL 1700/01. The right tooth row is apparently linear, and the palatal intermolariform width approximately as wide as the largest molariform. The values for OCHI and OPTHI are both approximately 33. The premolariform portion of the premaxillae is relatively long, with PMMLI value of 42 , as opposed to nearly 47 in Pyramiodontherium. The lateral walls of the maxillae are nearly parallel anteriorly, and in strong contrast to the anteriorly divergent form in Megathericulus and Pyramiodontherium. The anterior zygomatic root lies relatively posteriorly, approximately at the level of the middle part of M2 and the distal part of M3, as in Pyramiodontherium and Megatherium. The ventral margin of the lower orbit in MACN 2818 is reconstructed, but apparently was approximately level with the alveolar margins based on the contours of its preserved parts.

The form of the mandible and the ratio between height of the mandibular body and tooth row length in Megatheriops is intermediate between those of Eremotherium laurillardi
and Megatherium americanum, and therefore similar to those of M. medinae, M. sundti, and M. tarijense. The posterior margin of the symphysis is approximately at the level of the middle of ml , and thus is relatively anterior, as in $E$. laurillardi. The form and height of the angular process is approximately as in M. medinae, M. sundti, and M. tarijense, and therefore somewhat more dorsal than in E. laurillardi. The humerus of Megatheriops is stout and relatively robust. Its lateral surface retains a crest proximal to the ectepicondylar notch, and may be somewhat less rugose than that of $E$. laurillardi, Further, the anterior surface of the humerus of Megatheriops bears a prominent, welldeveloped deltopectoral crest, with distal end deflected. This condition occurs in few megatheriines, such as the Toro Negro sloth, MLP 68-III-14-1, FMNH 14511, from the Corral Quemado Formation, Belen, Catamarca, Argentina, and MACN 4988, the distal end of a probable megatheriine humerus from Entre Rios, Argentina. The lateral deflection, however, occurs in many non-megatheriine sloths (see HUMERUS).

## Plesiomegatherium Roth, 1911

Diagnosis:
Small to medium-sized megatheriine. Ventral bulge of dentary is prominent, and MBI resembles those of $M$. medinae, M. sundti, and M. tarijense. The proximal tibial surface bears an elongated and oval medial articular surface, with its long axis markedly oblique. The distal tibial surface is strongly tapered medially, and bears an elongated discoid facet. The medial or odontoid facet is reduced anteriomedially, and lies relatively posteriorly, suggesting that the astragalar odontoid process was markedly reduced.

Type species: Plesiomegatherium hansmeyeri Roth, 1911

Discussion: see below.

Diagnosis: same as for genus.

Type Locality:
Altiplanicie de Abra Pampa (Cabrera, 1928), near Uschara, Jujuy Province, Argentina.

Type Specimen:
MACN 2895, fragmentary remains of a single individual, including right maxillary and mandibular portions, and the proximal and distal ends of a right tibia. The maxilla preserved M2-M5, the distal part of M1, and the anterior zygomatic root; the dentary $\mathrm{m} 2-\mathrm{m} 4$, and the distal alveolus of ml .

Discussion:
Roth (1911) based this taxon on MACN 2895, and left maxillary and mandibular fragments, the latter preserving mi-m4, which could not be located at MACN; the catalogue number could not be determined. Roth (1911) did not designate a type, and Cabrera (1928) assigned MACN 2895 as lectotype, although Roth (1911: figs. 1, 2) illustrated the left dentary and maxilla. The lectotype is a specimen housed in MACN, and not MLP, as indicated by Mones (1986).

The right and left skull remains are very similar morphologically and in size, and possibly belong to the same individual. However, it is not known whether the specimens were found in association. The remains indicate a small megatheriine, and apparently belonged to an adult, based on the teeth and closure of the tibial epiphyseal sutures.

Roth (1911) based Plesiomegatherium on the oblique orientation of the transverse crests of the first two upper and lower molariforms. The degree of obliquity is particularly pronounced in the left maxillary and mandibular Eragments illustrated by Roth (1911), but is siight in MACN 2895, and is perhaps the reason for Cabrera's (1928) choice of these remains as lectotype. However, this feature is very probably invalid, and the oblique orientations of the crests in the specimens illustrated by Roth (1911) are due to deformation (Cabrera, 1928), and possibly also to individual variation. The crests of the molariforms may be oblique in individuals of Megatherium americanum (Cabrera, 1928) and Eremotherium laurillardi, and often the degree of obliquity varies between opposite-side molariforms in the same individual.

Roth's (1911) description of the cranial and postcranial elements of Plesiomegatherium is based on the nearly complete remains of an individual from Catamarca, which he incorrectly assigned to Plesiomegatherium (Cabrera, 1928; see Pyramiodontherium). Therefore, the genus is based
on a few fragmentary remains, and is poorly understood. The molariforms are essentially squared, approximately as in all other megatheriines so far discussed, and are thus not particularly useful diagnostically. The body of the dentary is relatively deep, with MBI nearly 90 , and the bulge of the ventral margin is prominent. The angular process is missing, but the ventral margin posterior to the bulge suggests that it lay relatively dorsal. In these features, Plesiomegatherium clearly resembles the pattern in the medium-sized Megatherium species (e.g., M. medinae). It differs from the latter, and approaches Eremotherium, in the relatively anterior position of the anterior zygomatic root, which lies approximately between the first alveolar septum and the distal third of M3.

However, Plesiomegatherium is probably not a small Megatherium species, based on the tibial morphology. The proximal surface bears an oval and elongated medial articular surface; its long axis is obliquely oriented. The lateral surface is incomplete. The medial articular surface is consiđerably more elongated and its axis more oblique than in Megatherium. Plesiomegatherium resembles Pyramiodontherium and various other small megatheriines in this feature.

The medial half of the distal tibial surface tapers markedly, in contrast to the condition in other megatheriines, so that the distal surface in nearly
triangular. The articular facet for the discoid surface of the astragalus is relatively narrow and elongated; that for the odontoid process is considerably narrowed medially, particularly anteriorly and lies relatively posteriorly. Furthermore, the ridge between the lateral and medial parts of the distal surface is more prominent than is usual in other megatheriines. This morphology is apparently natural, rather than due to deformation. It suggests a deep astragalar sulcus and reduction of the medial, and presumably odontoidal, form of the medial astragalar facet of the tibia.

Diagnosis:
Medium-sized megatheriine. Skull elongated, with relatively high PMMLI and low hypsodonty. Lower molariforms strongly compressed mesiodistally, uppers less so.

Type specimen:
MLP 26-IV-10-1 (not 24-IV-10-1, as given by Mones, 1986). Nearly complete, but poorly preserved skull, missing premaxillae.

Type locality:
Right bank of the Río Chasicó, near Laguna Chasicó, District of Vilarino, Buenos Aires Province, Argentina.

Discussion:
Cabrera (1928:350) assigned this species to Plesiomegatherium "porque los escasos restos que existen de P. Hans-Meyeri se le parecen bastante en el tamaño $y$ en otros detalles, $Y$, hasta que se disponga de mejor material de uno $y$ otro, me parece innecesario crear un género nuevo, cuyas diferencias son Plesiomegatherium no me sería posible ahora establecer". The general form of the skull is
preserved by MLP 26-IV-10-1, but detailed morphology cannot be determined. The skull has apparently suffered little crushing, but its surface is considerably cracked, and Cabrera's (1928: pl. 2) illustrations make the specimen appear better preserved than it actually is the case.

The skull is possibly, but not certainly, that of an adult individual. There are openings along various of the suture, but these may be cracks, many of which do not coincide with sutural planes. In dorsal view the postorbital constriction is slight, and wider than the rostral width. This condition is more similar to that in adults of Eremotherium laurillardi, and very similar to the juvenile condition of this species, particularly MCL 1702/01, and of Megatherium americanum (MACN 2830). The apparent absence of postorbital processes in MLP 26-VI-10-1, which Cabrera (1928) considered diagnostically important, may be due to imaturity.

MLP 26-IV-10-1 represents a medium-sized megatheriine, approximately as large as M. medinae, although the tooth row is relatively short compared to overall skull length. The anterior margin of the anterior zygomatic root lies approximately at the level of the mesiodistal midpoint of M2. This resembles the condition in many megatheriines, including M. medinae. It is worth noting that Cabrera's (1928:346) diagram indicates that the margin in M. medinae lies nearly at the level of the distal third of M1.

However, the figure is inaccurate, possibly because it is based on a cast, probably of SGO PV273.

Cabrera (1928) noted the elongated premolariform part of the maxilla, and compared it to the similarly elongated maxillae in Pyramiodontherium and Megatheriops. Anteriorly, however, the lateral walls of the maxillae converge slightly in "Plesiomegatherium" halmyronomum, whereas they are nearly parallel in Megatheriops and diverge markedly in Pyramiodontherium. The skull's dorsal profile apparently descends gradually anterioriy, although the cranium is crushed. Cabrera (1928:351) stated that the pterygoid blades "aunque muy deformadas, se conservan casi enteras, y son muy altas $y$ delgadas". However, they do not appear particularly complete, given that their preserved portions lie considerably dorsal to the level of the alveolar plane. Only the left M5 is preserved. All alveoli are present, but generally poorly preserved and distorted; as is shown by those of opposite sides being dissimilar. The relatively short tooth rows suggest that the molariforms were mediodistally compressed, as opposed to generally quadrangular as in megatheriines generally (but see Megathericulus); the left M5 is compressed, but this is normal in megatheriines. Various of the alveoli, particularly the better-preserved left side alveoli, are nearly rounded. However, alveolar form is not necessarily a good indicator of molariform shape, particularly in poorly
preserved specimens.
The shape of the molariforms, even though they are largely missing in MLP 26-IV-10-1, is potentially of great importance for this species. Pascual et al. (1966:pl. 17, figs. a,b) assigned to "P." halmyronomum partial mandibular remains from the Arroyo Chasicó Formation near the Arroyo Chasicó. The preservation of MLP 30-XII-10-21 is approximately as in MLP 26-IV-10-1, with the surfaces considerably cracked. The dentaries are separated. The left is more complete, and preserves all molariforms, most of the body containing the alveoli, and the ventral part of the ascending ramus. The right dentary preserves all molariforms, most of the body containing the alveoli, and the ventral part of the ascending ramus. The right dentary preserves all molariforms, although m3 is broken at the alveolar margin, and most of the symphyseal region.

Significantly, m1-m3 are compressed mesiodistally, in marked contrast to the nearly quadrangular shape in most other megatheriines, and m4 is nearly oval, rather that approximately trapezoidal. Such marked compression of the molariforms is known only in one other genus, Megathericulus, among megatheriines.

The allocation of MLP 30-XII-10-21 to "P." halmyronomum is probably valid. This idea is supported by the form of the alveoli and relatively short toothrow in MLP 26-IV-10-1. Further, the latter and MLP 30-XII-10-21 are the only
megatheriine remains, to my knowledge, reported from the Arroyo Chasicó Formation, and it is probable that they are conspecific.

The ventral bulge of the dentary is not particularly prominent and clearly not as deep as that in Megatherium americanum. The MTRL neariy equals the MBH, a condition which occurs only in M. americanum. However, the relationship between MBH and MTRL in "P." halmyronomum is misleading and not directly comparable to the condition in other megatheriines. This is due largely to the mesiodistal compression of the molariforms, which produces a short toothrow, and consequently overestimates the relative height of the mandibular body.

The ventral margin of the dentary posterior to the bulge is apparently strongly inclined, aithough this may be due to improper reconstruction. The inclination suggests that the position of the angular process in "P." halmyronomum resembled that of species such as $M$. medinae and $M$. tarijense, and therefore more dorsal than in Eremotherium laurillardi.

The relationship between "P." halmyronomum to P. hansmeyeri is unclear. Cabrera (1928) supposedly lacked evidence of the form of the molariforms in noting a sufficient degree of similarity between the remains from Jujuy and Arroyo Chasicó to assign then to the same genus. However, apart from similarity in size, P. halmyronomum
differs, based on molariform morphology, from P. hansmeyeri to the same degree that it differs from all other megatheriines, except Megathericulus; that is, P. bansmeyeri is considerably more similar to M. medinae, M. americanum, and E. laurillardi than to "P." halmyronomum. However, neither species of Plesiomegatherium is sufficiently wellknown to permit unequivocal resolution of their taxonomy. "P." halmyronomum possesses the plesiomorphic feature of mesiodistally compressed molariforms. The presence in $P$. hansmeyeri of nearly quadrangular molariforms (a derived feature present in all other megatheriines except Megathericulus), and the relatively deep dentary and dorsal position of the angular process (derived features characteristic of Megatherium species) could suggest that the $P$. hansmeyeri and "P." halmyronomum are not sister species, and that they should thus be separated generically. It is unclear how this may be done, however. Based on remains currently available, P. hansmeyeri could probably, although not certainly, be accommodated within an existing genus. If future remains demonstrate such inclusion, then plesiomegatherium becomes a junior synonym, and a new name would be required for " $P$." halmyronomum (unless, of course, it too is demonstrated to belong to an already existing genus). If inclusion of $P$. hansmeyeri within another genus is shown to be unlikely, then Plesiomegatherium would be retained for this species, and "P." halmyronomum transferred
to another genus or given a new genus. I consider the species, for the present, as incertae sedis.

Rusconi (1944:2) erected the species P. triangulatum based on a right M1, PVL (ex CR 728; Mones, 1986) from near Villa Ballester, district of San Martin, Buenos Aires Province, Argentina) "de sección casi triangular (triángulo escaleno) con el vértice anterior romo $y$ equivalente a la cara plano-convexa del mismo órgano de Plesiomegatherium Burmeisteri," (=Pyramiodontherium bergi) "P. Hans-Meyeri, etc.". The distinct form attributed by Rusconi (1944) to this molariform is probably unreliable. The mesial margin of MI is unusually bluntly rounded in Eremotherium laurillardi, but occasionally is nearly flat or slightly concave. Similar variation occurs in Megatherium americanum. Further, the left M1 in Pyramiodontherium bergi (MLP 2-66) is bluntly rounded.

The character on which Plesiomegatherium triangulatum is distinguished is therefore invalid. Rusconi (1944) correctly noted that the linear dimensions of the type molariform are smaller than in Pyramiodontherium bergi. However, they are near those of Plesiomegatherium hansmeyeri and "P." halmyronomum, species of which Rusconi (1944) must have been aware.

It is not possible to determine the status of $P$. triangulatum. One is sceptical of the validity of a species based on a single, isolated molariform that does not bear
any diagnostic features. It may be conspecific with a number of approximately contemporaneous megatheriine remains, but probably should be considered as a nomen nudum.

Pyramiodontherium Rovereto, 1914
Megatherium Moreno \& Mercerat, 1891
Plesiomegatherium, partim, Roth, 1911

Diagnosis:
Relatively large megatheriine ground sloth, though smaller than Megatherium americanum and Eremotherium laurillardi. Dorsal skull profile gently convex. OCHI and OPTHI 22 and 31, respectively, resemble those of $M$. tarijense. Skull elongated, narrow, and relatively low. Rostrum tapers markedly anteriorly in lateral view, but not as strongly as in Megatheriops. Maxilla extremely elongated anterior to MI , with PMMLI $=45$. Palate markedly constricted transversely anterior to the molariforms, but further anteriorly, the lateral maxillary walls diverge considerably, resembling the condition in Megathericulus.

Type species: Pyramiodontherium bergi (Moreno \& Mercerat, 1891)

# Pyramiodontherium bergi (Moreno \& Mercerat, 1891) Megatherium burmeisteri Moreno \& Mercerat, 1891 <br> Megatherium bergi Moreno \& Mercerat, 1891 <br> plesiomegatherium burmeisteri (Moreno \& Mercerat, 1891) <br> Pyramiodontherium dubium Rovereto, 1914 

Diagnosis: same as for genus

Type specimen:
MLP 2-66. A reasonably well-preserved and considerable part of the skeleton of a single individual.

Type locality:
Bajo de AndaIhuala, Catamarca Province, Argentina.

Discussion:
Moreno and Mercerat's (1891) cursory description of this species noted that differences existed between it and M. americanum, but made little attempt to describe these differences; although they noted its smaller size and oblique orientation of the transverse crests of the molariforms. "M". bergi (based on MLP 2-78) was distinguished from "M". burmeisteri essentially on its smaller size, and resemblance to M. americanum Cuv. en la đisposición de los dientes" (Moreno and Mercerat, 1891:231).

Lydekker (1894) synonymized "M". burmeisteri and "M". bergi with M. gaudryi, a move generally rejected by earlier paleontologists (e.g., Roth, 1911; Cabrera, 1928). It is argued above that M. gaudryi is a synonym of M. americanum (vide supra). Roth (1911) included "M". burmeisteri in his new genus Plesiomegatherium, which was described largely on MLP 2-66, but based on MACN 2895 from Jujuy Province. Roth (1911) did not discuss "M". bergi. Rovereto (1914) listed "M". burmeisteri and "M". bergi as of uncertain validity. Rovereto (1914) included "M". burmeisteri (but not "M". bergi) in Plesiomegatherium. This genus was tentatively recognized by Rovereto (1914:90), who explained that "En las colecciones que he estudiato, he hallado un solo diente aislado $y$ mal conservado, que no sé si pertenece al Plesiomegatherium o al Megatherium, siéndome por ello imposibile formarme una idea acerca del legitimidad del nuevo genero".

Rovereto (1914) based Pyramiodontherium dubium on MACN 8143, from the Valle de Sante Maria, Catamarca Province, a right maxilla of a very young juvenile, which preserves M2M5 completely and MI broken at the alveolar border. The molariforms are barely worn, and taper markedly apically. They are aligned in a continuous series, and separated by equidistant spaces. Despite this unequivocal megatheriine feature, Rovereto (1914) placed Pyramiodontherium in the Megalonychidae (Cabrera, 1928).

Cabrera (1928:341) recognized that " $M^{*}$. burmeisteri and "M". bergi were conspecific, stating "El trozo de cráneo tipo de $M$. bergi, encontrado en el mismo yacimiento que los restos de M. burmeisteri, teine exactament la misma forma que la parte correspondiente en este último, diferenciándose sólo por su tamaño un poquito más reducido"; further, the details of the morphology of the molariforms, and their measurements given by Moreno and Mercerat (1891) "no tienen el menor valor, pues los pocos dientes que queden están muy rotos $y$ deformados por presión, y otro tanto puede decirse de la forma <<muy particular>> que dichos autores atribuyen al arco cigomático, el qual está representado únicamente por un trozo de su porción malar, completamente desplazado". Further, Cabrera (1928:341) reasoned, correctly in my opinion, that Pyramiodontherium dubium could not be separated from this species: "no hay derecho para considerar como especie distinta un fragmento de cráneo juvenil en el que no hay nada que permita separarlo especificamente de los megaterios adultos hallados en el mismo horizonte $y$ práticamente en la misma localidad".

Cabrera (1928) concluded that this species was generically distinct from Plesiomegatherum. Simpson (1945), Hoffstetter (1958), and Paula Couto (1979) recognized Pyramiodontherium, although the first two considered Megatheriops its junior synonym, with which I disagree. Pyramiodontherium is clearly distinct from the remains of
either species of Plesiomegatherium, but these are so poorly known that the nature of the relationships with Pyramiodontherium is difficult to determine; at least there are no synapomorphies that would clearly unite these two genera. Therefore, it is prudent to retain Pyramiodontherium until additional material is availabie. Cabrera (1928) reasoned that the valid specific name for this species is $P$. bergi, reasoning that burmeisteri was preoccupied as a species of Megatherium. The latter species is considered here to be a synonym of $M$. americanum, as did Lydekker (1894). P. dubium is a junior synonym of P. bergi (Cabrera, 1928).

Diagnosis:
Small megatheriine. Molariforms markedly compressed mesiodistally. M2-M4 are essentially rectangular, but the mesial and distal alveolar margins of M3 and M4 curve mesially. M1 relatively less compressed; its bucal and lingual margins converge slightly mesially. Smallest alveolus is that for M5, which tapers lingually. Premolariform part of maxillae greatly elongated. Lateral maxillary walls diverge anteriorly. A prominent and median $V$-shaped notch, with apex oriented proximally, lies between the premaxillomaxillary articular surfaces, and probably received the medial rami of the premaxillae. Posteroexternal opening of the mandibular canal lies on the anterior margin of the base of coronoid process. Astragalus bears prominent odontoid process. Odontoid tuberosity, sesamoidal facet, and subodontoid fossa are strongly developed. Discoid tibial facet is posteriorly abbreviated. Navicular facet lies dorsally, so that the plane of the discoid intersects it at approximately its middle.

Type species: M. patagonicus Ameghino, 1904.

Discussion:
Megathericulus is the earliest and smallest megatheriine genus. M. patagonicus is certainly a megatheriine, and the diagnosis given above is based on this species. Additional species assigned include $M$. friasensis Kraglievich, 1930a and M. primaevus Cabrera, 1939. The former is based on a partial cranium from río Frias, MLP 2203, which preserves the occipital condyles. This specimen probably represents a scelidothere, as various early authors (see Kraglievich, 1930a) had believed (H.G. McDonald, pers. comm., 1991). M. primaevus is discussed below.

Diagnosis: Same as for genus.

Type specimen:
MACN, without catalogue number, Ameghino Collection. Mones (1986) also lists MLP M-230. The latter, properly MLP M-2-230, is a cast of the type material. The type includes nearly complete maxillae, lacking molariforms but preserving their alveoli, and an associated complete right astragalus.

Type Locality:
Basal layers from near Laguna Blanca, Chubut Province, Argentina.

Discussion:
The form and early stratigraphic age of the type of $M$. patagonicus suggest that this species was a relatively primitive megatheriine in that the molariforms are mesiodistally compressed, the premolariform parts of the maxillae are greatly elongated, the rostrum widens anteriorly, and the navicular facet of the astragalus lies relatively dorsally. Scillato-Yanè et al. (1993) tentatively assigned additional remains, MLP 91-IX-7-18 from Cerro Guenguel (NW Santa Cruz Province, Argentina) and MLP

92-XI-15-2 from Arroyo Pedregoso (SW Chubut) to this species, based on the morphological and size similarities of the astragalus. These remains preserve further evidence of the primitive nature of this species, such as the position of the posteroexternal opening of the mandibular canal, a less prominent bulge of the ventral margin of the dentary, and a prominent and raised tibial process bearing the groove for the digital flexors.

Additional features of the type specimen that were not discussed above are that the intermolariform part of the palate is flat and its width relatively narrow (i.e., less than that of the transverse width of the largest molariform, based on its alveolus), and that the anterior zygomatic root Iies relatively posteriorly, with its anterior margin and posterior margins lying approximately between the levels of the middle part of M2 and M3, respectively. The condition of the palate and position of the root resemble those in Megatherium americanum and allied taxa, rather than of Eremotherium laurillardi. The phylogenetic implications are discussed below.

Megathericulus primaevus Cabrera, 1939
Diagnosis:
Smallest megatheriine known. Astragalus strongly resembles that of $M$. patagonicus, but the odontoid facet is larger and flatter, and the odontoid tuberosity is crest-like. The tibial process bearing the groove for the digital flexors is relatively similar in size to that of M. patagonicus. The patellar trochlea is contiguous with the lateral and medial articular condyles.

Type Specimen:
MLP 39-VI-24-1. Various and mostly fragmentary skeletal remains (of, e.g., rib, radius, femur, tibia, carpal, metacarpal and calcaneum) of a single individual; the right astragalus is complete.

Type Locality:
Cañadon Ftamichi, approximately 5 km from Paso Flores, Neuquen Province, Argentina.

Discussion:
The strong resemblance of the astragalus to that of $M$. patagonicus is discussed above (see PES: Astragalus). Further, the tibial process for bearing the groove for the
digital flexors is prominent and raised, although reduced compared to planopsines and nothrotheriines. Unfortunately, no skull or mandibular remains are known, so that the disposition of the molariforms is unknown.

Probably M. primaerus is a megatheriine, based on astragalar similarities, such as the strong resemblance in general shape, an expanded subodontoid fossa (relative to that of planopsines), and a more nearly circular navicular facet (in contrast to the somewhat reniform facet in planopsines). However, the odontoid tuberosity is not "tuberous", as in M. patagonicus and planopsines. Rather, it is extended as a crest-like structure, and apparently autapomorphic. Further, the distal articular surfaces of the femur are united. The condition is unknown in M. patagonicus, but the patellar trochlea is separate from the medial condyle in all other megatherines. The facets are contiguous in planopsines and Santacrucian nothrotheres. In Plio-Pleistocene nothrotheres the patellar facet is separate from both the lateral and medial condyles.

Diagnosis: see Discussion under Pliomegatherium lelongi.

Type Species: Pliomegatherium lelongi Kraglievich, 1930a

Discussion: see Discussion under Pliomegatherium lelongi.

Pliomegatherium lelongi Kraglievich, 1930a Pliomegatherium paranensis Kraglievich, 1930a

Diagnosis: see Discussion.

Type specimen:
MACN 13213. An incomplete right dentary, preserving the posterior part of the symphysis (including the symphyseal part of the left dentary), and alveoli. The molariforms, ascending ramus, and posterodorsal part of angular process are missing.

Type Locality:
Rio Paraná, Entre Rios Province, Argentina.

Discussion:
Kraglievich (1930a, 1934) recognized Pliomegatherium, Promegatherium, and Eomegatherium as the megatheriines recovered from the "Entrerrianian" banks of the Rio Parana. Kraglievich (1930a) based Pliomegatherium lelongi on MACN 13213 (Mones, 1986, identifies the specimen as Colección Alberto Lelong, Argentina, sin numero). Kraglievich (1930a) distinguished it on the position of the end of the symphysis and moderate bulge of the ventral margin of the dentary. Kraglievich (1930a: figs. 5b, 6b) illustrated MACN 13213
before describing it in his text; further, it is incompletely shown in figure 5b, as the angular process is omitted. Simpson (1945) and Hoffstetter (1958), without justification but probably based on provenance, considered Pliomegatherium a synonym of Promegatherium. This is considered here as improbable, as discussed below.

Kraglievich (1930a) erected a second species, $P$. paranesis, also from the banks of the Río Paraná, on MACN 5269. Mones (1986) listed this species as $P$. paranense. Further, the museum label attached to the surface of MACN 5269 identifies it as P. "caixoi" and the museum catalogue card as "caissoi", but neither name is published. MACN 5269 is also a partial right dentary, not as well-preserved as MACN 13213; it preserves $m 1$ and $m 2$. MACN 5269 is slightly smaller and more gracile than MACN 13213, but clearly within a reasonable range of individual variation. They agree well in morphologic features, and are conspecific.

The molariforms of $P$. Ielongi are approximately quadrangular, as in megatheriines generally. The morphology of the mandible strongly resembles that of Eremotherium laurillardi. The ventral bulge is slight, the angular process relatively low, and the posterior margin of the symphysis falls approximately at the level of the middle of ml , well within the range of variation in E. laurillardi. Kraglievich (1930a) described the posterior margin as lying at the level of or slightly posterior to the mesial margin
of ml , which is misleading. The MTRL of MACN 13213 and 5269 are 144 mm and 142 mm , respectively, similar to, but slightly smaller than in Megatherium medinae and M. sundti. This represents a medium-sized megatheriine. The MBHI is nearly 72 in MACN 13213 (MBH cannot be measured in MACN 5269 because the ventral margin in incomplete), which falls well within the range for $E$. laurillardi. The dentary of Promegatherium is more similar to that of the megatherium species; synonymy of Pliomegatherium with Promegatherium as by Simpson (1945) and Hoffstetter (1958), is therefore improbable.
P. Ielongi thus shares two plesiomorphic features with E. laurillardi. There are no other features which are diagnostically or phylogenetically useful, or any autapomorphies, which suggests that $P$. lelongi should be considered a metataxon. As it cannot be determined whether P. Lelongi and E. laurillardi are sister taxa (there are no derived features to support such an assumption), its proposal would be premature. However, the similarity, while plesiomorphic, occurs rarely among megatheriines, and the possibly exists that the species are congeneric. If this were shown to be true, Pliomegatherium would have priority.

Megatheriines from the Paraná region, Argentina
A proper taxonomy for the megatheres from Paraná cannot be offered, except for the poorly defined Pliomegatherium. This section will review the taxonomic history of the remains from Paraná, identify the taxonomic problems, and suggest possible and informal taxonomic solutions.

The tortuous taxonomic histories of these remains are due to a variety of reasons. The most more important are that the fossils lack stratigraphic and locality data, the stratigraphy and ages of the deposits yielding these remains are only vaguely understood, the identity of which specimens were used or described is unclear, loss of some of these specimens, taxa were created either on wholly inappropriate remains or on skeletal elements different from the types, and apparently arbitrary assignment of newly recovered remains to taxa.

Excluding Pliomegatherium the following three genera and Eive species have been recognized from Paraná:

Megatherium Cuvier, 1796
M. antiquum Ameghino, 1885

Promegatherium Ameghino, 1883
P. smaltatum Ameghino, 1883
P. remulsum Ameghino, 1886
P. parvulum Ameghino, 1891

Eomegatherium Kraglievich, 1926
E. nanum (Burmeister, 1892)

Further, new species, based on material from outside Paraná, were assigned to Promegatherium and Eomegatherium by Frenguelli (1920) and Kraglievich (1930a), respectively.

Ameghino (1883) based $P$. smaltatum on a single molariform, probably MCNA 16 (C.N. Ceruti, pers. comm., 1995), I was unable to examine the specimen, from the Pliocene of Entre Rios, but it is illustrated as actual size by Ameghino (1889: pl. 37, figs. 8, 8a). Ameghino (1883) described its mesiodistal length as 21 mm ; the widest transverse width 25 mm , and the narrowest opposite 21 mm . However, the illustrated molariform is smaller than the one described in the text. Further, the two measurements given for transverse widths imply that the tooth is trapezoidal, but there is considerably less difference between these dimensions in the illustrated tooth, which therefore appears nearly rectangular. Ameghino (1883, 1885) distinguished Promegatherium from Megatherium on the considerably smaller size and the presence (incorrectly) of enamel in the former.

Ameghino (1885) created M. antiquum on various isolated molariforms (MPCNP ?; Mones, 1986) from the river banks in the environs of the city of Parana, which lack enamel and therefore are identical in form and structure to those of $M$. americanum, but one-third the size.

Ameghino (1896) added P. remulsum, based on various fragmented molariforms (MPCNP ?; Mones, 1986) from the

Pliocene of Entre Ríos. Ameghino (1886) believed that these molariforms were of the same internal composition as those of $P$. smaltatum (i.e., enamel was present), but were nearly as large as those of $M$. americanum, and therefore represented a distinct species.

Ameghino (1889: pl. 71, figs. 12, 12a) assigned a molariform (MPCNP ?; Mones 1986) to Ortotherium laticurvatus, but later (1891) referred it to P. parvulum. Kraglievich (1940b) noted some errors in Ameghino's (1891) designation of this specimen. Ameghino (1889: pl. 76, fig. 2) assigned additional remains to $P$. smaltatum, including a left dentary (from the Lelong Collection in MACN: Burmeister, 1892) that was illustrated in lateral view. In this illustration the posterolateral opening of the mandibular canal is shown as lying on the lateral surface of the dentary, a position that does not occur in any known megatheriine dentary.

Burmeister (1892), in blunt and deprecating fashion, responded harshly to Ameghino's opinions. Among other objections, Burmeister (1892) stated that, having examined Ameghino's specimen, the molariforms lacked enamel and the opening of the mandibular canal lay at the base of the anterior edge of the coronoid process. Burmeister rejected Ameghino's species and renamed it Megatherium nanus, which is technically inadmissible.

Ameghino (1892), responding in kind to Burmeister's
criticisms, insisted on the presence of enamel; on the difference in position of the opening, Ameghino suggested that Burmeister must clearly have examined the wrong specimen. Lydekker (1894) maintained Ameghino's species as M. smaltatum, and synonymized M. antiquum and P. remulsum with it.

Kraglievich (1940a, b) devoted two articles in an attempt to reconcile the disagreements between Ameghino and Burmeister. These articles were published posthumously and unedited from Kraglievich's notes, and they contain inconsistencies and errors, but they are useful in explaining some of the events surrounding the controversy. Kraglievich noted that $P$. smaltatum was based on isolated molariforms, and that several others of similar size and morphology had subsequently been recovered. The controversy had arisen essentially over the dentary.

Kraglievich (1940a, b) confirmed Burmeister's opinion that enamel was absent and that the position of the opening was misrepresented in Ameghino's (1889: pl. 76, fig. 2) illustration. In attempting to determine why Ameghino's illustration places the opening on the lateral surface, Kraglievich (1940b) explained that Ameghino had described the dentary based on information sent to him; i.e., he had not examined the specimen directly. Further, the original of the published illustration was drawn by another person. Kraglievich supposed that the original illustration either
represented the opening 1) as in the published illustration (due to inexperience of the artist) or 2) indistinctly (in which case Ameghino must have added the opening as in the published version). Kraglievich (1940b) considered that the latter scenario as the more logical, but still required a reason for Ameghino's decision to place the foramen on the lateral surface of the dentary. At this point in his narrative, Kraglievich (1940b) introduced his "trump card": he had found a cast in Ameghino's personal collection that resembled the illustration and possessed the opening in the same position. In other words, the published illustration was drawn by another person based on dentary MACN 4995 (although this is a right dentary; see MANDIBLE), and the position of the opening was added later by Ameghino based on a cast in his collection. Kraglievich (1940a) presented a nearly identical version of this explanation.

Kraglievich's (1940a, b) attempts to reconcile the controversy between Ameghino and Burmeister may be viewed as bistorically interesting (particularly as neither the dentary nor the cast could be located at MACN), but incidental to the status of P. smaltatum. However, Kraglievich (1940a) used the dentary (i.e., that which Burmeister had examined and on which the original of Ameghino's illustration is based) as the type of Eomegatherium nanum. Thus, he reached a compromise: he maintained Ameghino's genus and species (essentially based
on the cast) and Burmeister's species (based on the actual dentary). Kraglievich (1940a) listed the type as MACN 4993, which is a right dentary; however, the dentary Burmeister examined and on which Ameghino's illustration is based was a left dentary, and referred to as MACN 4995 by Kraglievich (1940b). A search for MACN 4993 proved futile. It is worth noting that the molariforms of MACN 4995 are not mesiodistally compressed.

However, a dentary, either MACN 4993 or 4995, is not the type of Eomegatherium nanum. Kraglievich (1926: fig. 4) illustrated astragalus MACN 4992 as E. nanum; the text explains that the astragalus belongs to a genus, probably Eomegatherium, from Paraná. This suggests 1) that Kraglievich's (1940a, b) posthumously published papers were written before or during 1926, or at least that he had developed the concept of Eomegatherium by this date; and 2) that there is no certain association between MACN 4992 and the dentary used by Kragiievich (1940a) as type of Eomegatherium.

Among the complex and confused published opinions on the megatheriines from Paraná, there are two comments by Burmeister (1892) that are useful. Burmeister (1892) observed that the remains in the Lelong Collection indicate that the lower molariforms are mesiodistally compressed, but that the upper molariforms were less compressed, and more nearly square. This condition resembles that in
"Plesiomegatherium" halmyronomum, and may indicate an affinity between these species. However, the remains of either species are woefully inadequate and insufficient to permit any confident decisions.

There are possibly two other kinds of megatheriines from Paraná. One is Pliomegatherium lelongi, which has mesiodistally uncompressed molariforms and a relatively ventral angular process. The other is represented by MACN 4995, which also possesses mesiodistally uncompressed molariforms, but the bears a more dorsal angular process and more prominent ventral bulge.

I maintain the genera and species PIiomegatherium lelongi (vide supra: MANDIBLE) and Eomegatherium nanum; the latter because it is among the very few specimens from Paraná that is properly established, illustrated, numbered, and available for stucy.

PHYLOGENY OF THE MEGATHERIINAE
The phylogeny of the Megatheriinae has not been seriously considered since the works of Cabrera (1928) and Kraglievich (1930b). Kraglievich (1930b) viewed megatheriine phylogeny as an orthogenetic trend towards increased body size from the late Miocene through the late Pleistocene. He proceeded essentially by arranging taxa in approximate stratigraphic sequence, noted a general increase in size, and interpreted morphological transformations (e.g., increase in depth of the dentary, retrogression of the posterior end of the symphysis) in terms of functional adaptation to size increase. Kraglievich's (1930b) reconstruction of phylogeny included direct ancestordescendant relationships between Promegatherium, Eomegatherium, various Pliocene (as then recognized) species assigned to Megatherium, and culminated in the evolution of the gigantic M. americanum. The few, then recognized, additional Pleistocene species (e.g., M. istilarti) and early, poorly known, species were considered side branches (evolutionary "dead-ends") to the main line. This view of gradual, orthogenetic evolution was generally current in zoological thinking at the time; indeed, Kraglievich (1930b) presented megatheriine phyiogeny as the South American analogue of horse evolution in North America, winich is probably the most "famous" example of the concept of
directed evolution.
Cabrera (1928) viewed megatheriine phylogeny as somewhat more complex or "bushy", and recognized two main lineages. These groups were based largely on the position of the anterior zygomatic root and the length of the maxilla anterior to the molariforms relative to the condylomaxillary length of the skull. Cabrera (1928) recognized that the true length of the rostrum depended mainly on the length of the premaxillae.

At this point, it is worth digressing to discuss the designation of these groups because I have encountered considerable confusion among paleontologists as to Cabrera's (1928) intentions. Cabrera (1928) used the terms longirostral and brevirostral in his discussion of these groups. However, he did not designate the groups as such. Cabrera (1928:345) began his discussion of phylogeny by noting that the relative length of the maxillae anterior to the molariforms varies in megatheriines (at least 20\% of the condylomaxillar length in one group, and less than 17\% in the other); he continued "Podría tal vez decirse que hay megaterios longirrostros y brevirrostros si no fuese porque en estos animales la verdadera longitud del rostro no 10 dan los maxilares, sino los premaxilares, $y$ así vemos que Pyramiodontherium Bergi, teniendo unos maxilares que sobresalen del primer molariforme un 21,3 por ciento de la longitud cóndilomaxilar, debía ser, sin embargo, un
megaterio de rostro bastante corto" (and not brevirostral), based on the length of the symphysis (the premaxillae were known in only the largest Pleistocene species of Megatherium, which probably all belong to M. americanum; vide supra).

Cabrera (1928) correlated a shorter relative length of the maxillae to a more anterior position for the anterior zygomatic roots (between the middle and distal parts of M1); in the group with relatively longer maxillae the root lies between the middle and distal parts of M2. Cabrera (1928:345) stated that these features would contribute "al aspecto respectivamente brevirrostro o longirrostro del craneo", but did not specify the former group as brevirostral and the latter as longirostral, as he had already stated that P. bergi probably had a short rostrum.

Cabrera (1928) included P. bergi and Megatheriops rectidens in the group possessing relatively long maxillae and posterior position of the anterior zygomatic root. The other group contained the Pampean Megatherium species (i.e., M. americanum, M. gallardoi) and M. medinae. One difficulty with Cabrera's (1928) groupings is that the root in Megatherium does not lie in the anterior position. It is demonstrated above (see SKULL) that the root lies anteriorly only in Eremotherium laurillardi, a species unknown to Cabrera.

The efforts of past paleontologists have been hindered
by methodology, inadequate samples, incomplete morphological information, and imprecise biostratigraphical knowledge. Several of these factors continue to impede attempts to generate a defensible hypothesis of relationship. Nearly complete skeletal morphology is available for only three species: Eremotherium laurillardi, Megatherium americanum, and M. tarijense. Less information is available for $M$. medinae and $M$. sundti. However, several presumptive megatheriine taxa may only be recognized as such based on isolated characters in fragmentary (and usually highly incomplete) specimens. Commonly, these latter taxa are represented by remains demonstrating that they are megatheriines; preservation of even one or two informative characters is indeed fortuitous. Such taxa are best excluded from an initial cladistic hypothesis of relationship due to the large proportion of missing data: these taxa would cluster with respect to a few apomorphic characters due to an absence of information.

In any event, phyIogenetic systematic methodology provides a basis or framework to generate falsifiable hypotheses of relationships. Further, recent work (Gaudin, 1994; De Iuliis, 1994) corroborates the traditional grouping of the Megatheriidae as including the Planopsinae and Megatheriinae (contra Engelmann, 1985), and provides an outgroup for resolving relationships within the Megatheriinae. De Iuliis (1994) hypothesized that

Megathericulus patagonicus is the sister-group to all other megatheriines. He also (1994) suggested that the robust, elongated, and approximately quadrangular premaxillae shared by Megatherium americanum and M. tarijense are derived, compared to the premaxillae of Erenotherium laurillardi. Unfortunately the premaxilla is unknown in Planopsinae, but all other ground sloths possess variably short and nearly triangular premaxillae.

A hypothesis of a monophyletic Megatheriinae is corroborated by the possession of $5 / 4$ molariforms or alveoli that have squared corners, are functionally similar, and are spaced equidistantly (Character 1). These are in contrast to the lobate (mylodonts) or nearly oval (megalonychomorphs sensu Gaudin, 1994 and planopsines) molariforms of other sloths. Excluding MegathericuIus patagonicus, for which only the alveoli are known, the molariforms of the remaining megatheriines are unique among sloths in bearing mesial and distal transverse crests separated by a transverse, V-shaped valley (Character 2; De Iuliis and Saint André, in press), in contrast to shearing surfaces located near and usually coinciding in shape with the peripheral margins of the tooth. There are various other characters that are uniquely present in megatheriines; however, they are not known for all megatheriine taxa. They are discussed here, but are unnumbered.

Morphology of the Ectotympanic - The ectotympanic of
megatheriines is relatively large and bears extremely rugose anterior and posterior crura, in contrast to the relatively smooth ectotympanic present in other sloths.

Proximal Fusion of Tibia-Fibula - The tibia and fibula are fused proximally in all megatheriines for which these elements are known.

Length of the Olecranon Process - The olecranon process is relatively elongated and slender in non-megatheriine sloths, as is usual in most mamals. In megatheriines the olecranon process is reduced in length. Among megatheriines the relative length of the process is similar in Megatherium americanum, M. tarijense, and M. medinae, and Eomegatherium cabrerai. It is most reduced in Eremotherium laurillardi.

The following numbered characters are used in the subsequent cladistic analysis:

Character 3. Molariform Length and width.
The mesiodistal length of the molariforms is nearly equal to their transverse width, so that the tooth is almost square. This shape occurs in all megatheriines for which the molariforms or alveoli are known, except for Megathericulus patagonicus and "Plesiomegatherium" halmyronomum . In these latter species the molariforms are mesiodistaily compressed, a state shared with planopsines, as well as megalonychomorphs (sensu Gaudin, 1994). The compressed molariforms are therefore plesiomorphic (0); the
square molariforms derived (1).
Character 4. Position of the Anterior Margin of the Coronoid Process.

The margin lies posteriorly to m 4 . This tooth is thus visible in lateral view in megalonychomorphs, planopsines, and "Plesiomegatherium" halmyronomum. The margin of the coronoid process lies anteriorly in all other megatheriines in which it is known. The posterior position is plesiomorphic (0); the anterior derived (1).

Character 5. Position of the Posterior End of the Symphysis.

The symphysis lies well anterior to the molariforms (or an equivalent position in taxa that possess a diastema between mI and m 2 ) in megalonychomorphs, planopsines, and "Plesiomegatherium" halnyronomum. The symphysis reaches posteriorly at least to the mesial part of ml in all other megatheriines in which the symphysis is known. The anterior position is plesiomorphic (0), the posterior position derived (1).

Character 6. Position of the Posterior Lateral Opening of the Mandibular Canal.

This opening lies dorsally on the surface of the mandibular body (i.e., medial to the lateral margin at the base of the anterior edge of the coronoid process) in all megatheriines. In all other sloths it lies on the lateral surface of the dentary. It may approach the lateral margin
of the coronoid process, but never actually lies dorsally (see App. 2). The lateral position is plesiomorphic (0); the dorsal position derived (1).

Among megatheriines the opening lies either on the anterior edge of the base of the coronoid process, as in Megathericulus patagonicus and "Plesiomegatherium" halmyronomum, or further medially (De Iuliis, 1994: fig. 6B), just lateral to the middle of m 4 , in all other megatheriines in which this character is preserved. This latter state is distinguished as (2).

Character 7. Degree of Hypsodonty.
The molariforms are open-rooted and high-crowned or hypsodont in all megatheriines. The increase causes or is manifested by a suite of morphological changes in the skull and mandible. I consider these part of a functional complex and treat them as a single character. Variable degrees of hypsodonty occurs in megatheriines, and three states may be recognized.

The characters involved are:

1) Position of the lower orbit;
2) $O C H$ (including height of the basicranium and mandibular fossa);
3) MCABH;
4) MBH ;
5) Position of the angular process.

As the height of the upper and lower molariforms
increases, the height of the maxilla and dentary (i.e., MBH) must also increase. In the skull this increase is manifested by: a relatively higher position of the lower orbit, which essentially reflects the position of the zygomatic arch; a higher OCH, i.e., a greater distance between the occipital condyles and alveolar margins of the maxillae (and also of the basicranium, hence mandibular fossa). Changes in the dentary include: increased MCABH, or distance between the mandibular condyle and alveolar margin of the dentary (which compensates for the increase in the position of the mandibular fossa); a more dorsal position of the angular process, possibly as an adaptation to avert dramatic relocation of insertions of various muscle groups (see MANDIBLE).

The condition of these characters in, for instance, "Plesiomegatherium" halmyronomum, and Eremotherium laurillardi, for example, is clearly similar to, although possibly slightly greater than, that of other nonmegatheriine sloths, such as Nothrotherium, Planops, Megalonyx, Hapalops, and scelidotheriines. The condition in several of the derived mylodonts (very shallow dentary, low angular process and basicranium) contrasts with these.

The state observed in E. Iaurillardi is therefore plesiomorphic (0). One derived state (1) occurs in various megatheriines and is approximately intermediate between state 0 and the very high degree of hysodonty observed in

Megatherium americanum (2). Juveniles of this species pass through 0 (see MANDIBLE), which, therefore, supports the ordering of this multistate character as (0) - (1) - (2). Character 8. Presence of the Deltopectoral Crest of the Humerus.

The anterior surface of the humerus of almost all nonmegatheriine ground sloths bears a raised and distinct, though variable, deltopectoral crest, in combination with a smooth and well-defined musculospiral groove. In later, generally Pleistocene megatheriines, a distinct crest is absent. Instead, the humerus bears an elongated, distally tapering ridge that does not rise as a distinct structure from the surface of the humeral diaphysis. However, a raised and distinct deltopectoral crest occurs in some Pliocene megatheriines, such as Megatheriops, the Toro Negro megatheriine, and the humerii from Argentinian Mespotomia, although a comparable groove is apparently absent. The presence of the crest is plesiomorphic (0), its absence derived (I).

Among the later megatheriines, the tapered crest in reduced in Megatherium americanum, M. sundti, and M. medinae compared to that of E. laurillardi. That of M. tarijense and M. nazarrei is further reduced.

Character 9. Form of the Femur.
Non-megatheriine sloths possess elongated and relatively gracile femora. The femur is relatively wider
and therefore robust in megatheriines. Among megatheriines Megatherium americanum possesses the most robust femur. The femur of Pyramiodontherium bergi is also relatively robust, and similar to those of $M$. sundti and M. istilarti. The femur is approximately equally robust in the remaining megatheriines in which it is known. The less robust condition is considered pleisomorphic (0), the more robust condition derived (1); a second derived condition (2) occurs in M. americanum, in which robustness is increased further. Character 10. Shape of the Patellar Trochlea. The patellar trochlea in almost all sloths is transversely broad and variably convex, resembling that of Eremotherium laurillardi, regardless of its relationships to the medial and lateral articular facets. However, the trochlea is reduced in some megatheriines. It is most markedly reduced in Megatherium americanum and M. istilarti, in which the trochlea is essentially an anterodorsal extension of the lateral articular facet (i.e., most of the medial part of the trochlea is absent). The trochlea is somewhat reduced in Pyramiodontherium bergi compared to that of Eremotherium laurillardi. Three unordered states are recognized as no reasonable estimate of the transformation series may be hypothesized: the plesiomorphic state (0), as observed in E. laurillardi; and two derived conditions: that observed in Pyramiodontherium (1), and that in M. americanum and M. istilarti (2).

Character 11. Position of the Navicular Facet of the Astragalus.

The navicular facet lies markedly dorsal to the plane of the discoid facet (or lateral part of the trochlea tali for astragali that do not possess an odontoid process) in all non-megatheriine sloths; this occurs regardless of the shape of the trochlea tali. Slightly more than one-half of the facet lies above the plane.

In megatheriines the position of the navicular facet varies. In the astragalus of the earliest certain megatheriine, Megathericulus patagonicus, it lies approximately at the same level as in other sloths (i.e., one-half lies dorsal to the plane of the discoid facet). In contrast, the dorsal part of the navicular facet lies at nearly the same level as the plane of the discoid facet in Megatherium americanum. Two other positions between these extremes may occur. In one approximately one-third of the navicular facet lies above the discoid facet, as in Eremotherium laurillardi. The other possible position occurs in e.g.. M. tarijense, where the position of the navicular facet is approximately intermediate between those of E. laurillardi and M. americanum.

The position in Megathericulus is clearly plesiomorphic $(0)$ by outgroup comparison. The three other positions are designated (1) - as in E. laurillardi, (2) - as in M. tarijense, and (3) - as in M. americanum.

Character 12. Shape of the Fibular Facet of the Astragalus. The fibular facet extends ventrally nearly to the ectal facet in megalonychymorphs, planopsines, Megathericulus patagonicus, and various other megatheriine astragali that are discussed below, and is plesiomorphic (0). In all other megatheriines the dorsoventral length of the facet is reduced, which is the derived condition (1).

The data were analyzed with PAUP 3.1 , using the exhaustive search option, and Hennig $86,1.5$, using the implicit enumeration option. All multistate characters were run unordered, except Character 7 (vide supra). Phylogenetic analysis of the data matrix (Tab. 10) resulted in 291 most-parsimonious trees of length 19 steps, CI = 0.84, $R I=0.80$, and rescaled $C I=0.67$. Unfortunately, considerable data are missing, and this results in poor resolution. The consensus tree (Fig. 14) indicates that Megatheriinae may be considered to represent a basal group, including Megathericulus patagonicus and "Plesiomegatherium" halmyronomum, and a polytomy of the remaining taxa considered in this analysis. The position of M. patagonicus as a basal megatheriine is strengthened by its early stratigrapinic occurrence. Possibly "P." halmyronomum may be the sister group to the polytomy, based on its nearly square upper and mesiodistally compressed lower molariforms. However, the skull and mandible of this species are not certainly associated.

TABLE 10. Data Matrix Showing the Distribution of 12 Characters among Planopsinae and Nine Megatheriine species.


Further resolution, however, may be hypothesized on the characters and additional taxa, as follows. These groups include a polytomy comprised of Pliomegetherium lelongi, Megatheriops rectidens, Eremotherium laurillardi, and Pyramiodontherium bergi; and a clade including Megatherium.

Pliomegatherium lelongi is known only by its dentary, which indicates that this species is not a basal megatheriine by virtue of its square molariforms. The Megatherium clade is based on 1) a reduction of the deltopectoral crest, and 2) reduction of the lateral surface of the humerus. The deltopectoral crest is relatively large and its lateral surface projects laterally in earlier megatheriines and non-megatheriine sloths. In E. laurillardi the crest is reduced to a large, distally tapered structure on the anterior surface of the humerus. This structure is reduced further in species of Megatherium. The lateral surface of the humerus is rugose and projects laterally in all megatheriines in which it is known, including the earlier taxa, except in the Megatherium clade. Both the deltopectoral crest and lateral surface are strongly reduced in M. tarijense and M. nazarrei (see Taxonomy of the Megatheriinae), and I consider these as sister species based on these character states.

Although only the femur of M. istilarti is known, it preserves a highly significant character. The patellar trochlea is reduced to a degree otherwise known only in $M$.

## FIGURE 14.

Strict consensus tree of 291 most-parsimonius trees based on cladistic analysis of twelve characters (Data Matrix, Tab. 10). Character states: $0=$ plesiomorphic; $1=$ first derived state; $2=$ second derived state.

americanum. I therefore consider these species as sister taxa. M. sundti shares increased robustness of the femur with these species, and is thus included in a clade with them.

The Megatherium clade also possesses a relatively short maxilla anterior to the first molariforms. I suspect that an elongated premaxilla is the plesiomorphic condition among megatheriines, based on its presence in Megathericulus patagonicus and most non-derived megalonychomorphs and mylodontids. In other megatheriines, the premaxilla is shorter than that of $M$. patagonicus, and shortest in the Megatherium clade. While I cannot be certain of the ordering of this transformation series, I hypothesize that the condition in the Megatherium clade is derived.

The Megatherium clade is also recognized by increased hypsodonty. In all but M. americanum hypsodonty is approximately intermediate between the conditions in Eremotherium laurillardi and M. americanum. The condition in the latter is thus probably derived and autapomorphic.

Pyramiodontherium bergi possesses various character states present in some members of the Megatherium clade. Its femur is approximately as robust as that of M. sundti and M. istilarti; the patellar trochlea is reduced compared to that of, e.g., M. tarijense, but not to the degree observed in M. istilarti and M. americanum. Conversely, P. bergi possesses various apparently plesiomorphic features:
the maxillae are extremely elongated anterior to the first molariforms, and the rostrum broadens anteriorly. These states are shared with Megathericulus patagonicus. Also, the OCH and MBI are approximately as in E. laurillardi, suggesting a similar degree of hypsodonty. Thus, the robust femur and somewhat reduced patellar trochlea are regarded as homoplasies.

Megatheriops rectidens shares a degree of hypsodonty present in all members of the Megatherium clade, except $M$. americanum. However, Megatheriops rectidens bears various apparently plesiomorphic features that would seem to exclude it, as with P. bergi, from the Megatherium clade. These include a humerus with a very well-developed deltopectoral crest, with its lateral portion projecting laterally; a rugose and laterally projecting lateral surface of the humerus; and elongated premaxillae anterior to the first molariform. Resemblance in hypsodonty to the Megatherium clade is therefore homoplasic.

Additional taxa that may be discussed include Megathericulus primaevus and Eomegatherium nanum (based on astragalus MACN 4992). The navicular facet in the astragali of these species lies dorsally approximately as in the basal megatheriines. Thus, they may be regarded as members of a basal polytomy.

## SUMMARY AND CONCLUSIONS

TAXONOMY AND PHYLOGENY
Study of the paleontology, biology, and phylogenetic relationships of the Megatheriinae has not kept pace with that of other fossil mamal groups. The main reasons for the neglect of this subfamily over the past fifty years are 1) until quite recently the remains of Megatheriinae were scarce, fragmentary and scattered, excluding a few notable exceptions, and 2) a lack of a proper, appreciation of variation within and among natural populations continued among researchers studying the Megatheriinae well into the 1960's. These factors contributed largely to the proliferation in the literature of taxa named without justification.

The need for a review of the subfamily became evident through numerous inconsistencies in the literature and lack of a general taxonomic consensus of genera and species; many taxa are poorly defined and understood, but consistently appear in recent literature. Such taxonomic instability results in confusion over the paleobiogeography of the group, phylogenetic relationships, and degree of taxonomic diversity.

The present revision undertakes the first comprehensive and extensive morphologic and morphometric study of the remains of Megatheriinae to provide as complete and thorough
an understanding of their history and biology as is permitted by the available data. It includes morphological, biometric, and biostratigraphic analyses of numerous fossil specimens often housed in international museums or other research institutions, extensive literature searches, and determinations of priority and synonymy of taxonomic names. The aims of this thesis are impeded at various levels by the problems that usually hinder paleontological study, such as incomplete stratigraphic and locality information, inadequate samples, and imperfect preservation. However. the result of this broad and comprehensive comparative study (incorporating nearly all known megatheriine remains) has allowed considerable advance in resolving the taxonomy of megatheriines, and better understanding of their phylogenetic relationships. The resulting taxonomic framework permits the recognition of anatomically definable taxa, and identifies which taxa are of ambiguous status and require further study.

The monophyly of the Megatherinae is corroborated by the possession of $5 / 4$ molariforms or alveoli that have squared corners, are functionally similar, and are spaced equidistantly, instead of the lobate or nearly oval molariforms of mylodonts and megalonychomorphs, respectively. Excluding Megathericulus patagonicus, for which only the alveoli are known, the molariforms of the remaining megatheriines are unique among sloths in bearing
mesial and distal transverse crests separated by a transverse, $V$-shaped valley, in contrast to shearing surfaces located near and usually coinciding in shape with the peripheral margins of the tooth. Other characters that are uniquely present in megatheriines, when known, include a relatively large ectotympanic with extremely rugose anterior and posterior crura, proximal fusion of the tibia and fibula, and markedly reduced olecranon process of the ulna.

Fewer genera and species are recognized here than are contained in the older literature. In fact, only a few of the numerous taxa named in the literature are consistently diagnosable. Earlier diagnoses are usually incomplete, lack context or detailed comparisons with other material, and original descriptions included minimal explanations for the choice of diagnostic characters.

Two recent collections of Eremotherium laurillardi (from Jacobina, Bahia, Brazil, and Daytona Beach, Florida, USA) contribute to our understanding of intra-specific variation in megatheriines. These collections preserve nearly all reported morphological and morphometric variations on which species have been erected in the past, and reveal therefore that the diagnoses of many of the aforementioned species are invalid. They demonstrate a degree of variation previously unsuspected. E. laurillardi is the valid name for this Pleistocene species, and $E$. mirabile and E. rusconii, two species currently recognized
as valia in the literature, are synonymized with it. The Panamerican E. laurillardi ranged from northern South America to the southeastern United States.

The degree of morphologic and morphometric variation in E. Laurillardi allows inferences to be made about the possible variation in other megatheriines, particularly those of similar overall mass. Numerous Pleistocene largesized species of Megatherium, nearly all from Argentina, have been erected on similar criteria as were those of Eremotherium, and are improbably valid. This conclusion is based both on the degree of variation in E. laurillardi and the analysis of an undescribed series of astragali at BMNH from near Luján, Buenos Aires Province, the type locality of M. americanum. Many genera and species are synonyms of this species, including Paramegatherium, Pseudomegatherium, M. gallardoi, M. parodii, M. filholi, M. Iundi, and M. gaudryi.

Three medium-sized species of Megatherium are recognized: M. medinae, M. sundti, and M. tarijense. M. sundti has usually been considered as conspecific with $M$. medinae, but there are valid morphological distinctions, particularly in the femur, which suggest that both species should be maintained.
M. tarijense has often been viewed as questionably valid, and commonly a synonym of M. americanum. These hypotheses were reasonable, given the scarce remains of $M$.
tarijense and the probable presence of $M$. americanum in the deposits of the Tarija Valley, Bolivia, from which M. tarijense is known. However, a nearly complete, undescribed skeleton of an individual at FMNH clearly demonstrates that this species is distinct from M. americanum, and probably also from M. medinae and M. sundti.

A fourth, medium-sized species is possibly valid. M. elenense was initially described as Eremotheirum, and was incorrectly synonymized with E. laurillardi. The morphology of its dentary, however, suggests that it belongs to Megatherium. Its remains are poorly known and do not permit unequivocal synonymy with already-named species.

A second large-sized species of Megatherium, M. nazarrei from the early Pleistocene, is recognized. It was described as a distinct genus, Paramegatherium. Although it is poorly known, features of its humerus and clavicle suggest that it is closely related to $M$. tarijense, and therefore transferred to Megatherium.
M. istilarti is a small Megatherium species from the pleistocene. It is known only from its femur, but the shape of its patellar trochlea is otherwise known only in the much larger M. americanum.

Pyramiodontherium bergi is a relatively large Pliocene megatheriine. Its skull is low and elongated. The elongated rostrum diverges anteriorly. The femur is relatively robust and the patellar trochlea somewhat
reduced, but not to the degree observed in M. americanum. Crural index is among the highest known for ground sloths.

The unnamed Toro Negro megatheriine is not well understood, but its remains preserve intriguing features. It is a small to medium-sized megatheriine. Its humerus bears a well-developed and laterally deflected deltopectoral crest. The femur resembles that of $P$. bergi in possessing a somewhat reduced patellar trochlea, and the crural index is nearly 1 , which is the highest known among ground sloths and slightly higher than in P. bergi. These morphological similarities suggest an affinity between the Toro Negro megatheriine and P.bergi. Unfortunately, the skull of the former and the humerus of the latter are not known.

The Pliocene Megatheriops rectidens is known from skull, mandible, and some postcranial remains. The skull is distinguished by its rounded, bulbous cranium. The rostrum is elongated. Increased hypsodonty, approximately to the same degree as in the medium-sized Megatherium species, is indicated by OCHI, MBHI, and the positions of the lower orbit and angular process. The humerus retains a prominent, raised, and laterally deflected deltopectoral crest.

Plesiomegatherium hansmeyeri is the genotype, but is poorly known. It is a small to medium-sized Pliocene megatheriine, known only from partial maxillae, dentaries, and proximal and distal ends of the tibia. The upper and lower molariforms are squared, and the dentary indicates
greater hypsodonty than in E. laurillardi, but the distal end of the tibia suggests a reduced astragalar odontoid process. "P." halmyronomum, a medium-sized Pliocene megatheriine, is also poorly known. Its skull is low and elongated. The lower molariforms are strongly compressed mesiodistally. The upper molariforms are less compressed, so that they are nearly square, rather than rectangular. The MBHI is very high, within the range of $M$. americanum. However, this does not indicate a high degree of hypsodonty, but is an artefact produced by the markedly compressed molariforms. It is improbable that $P$. hansmeyeri and "P." halmyronomum are congeneric, as the compressed molariforms of the latter are plesiomorphic. However, neither species is sufficiently known to permit confident taxonomic decisions. "P." halmyronomum is considered as incertae sedis for the present.

Pliomegatherium lelongi is a medium-sized, poorly known megatheriine from the Argentinian Mesopotamia. Its age is uncertain, but may be late Miocene or early Pliocene. Its molariforms are squared, and its dentary resembles that of E. laurillardi, indicating a relatively low degree of hypsodonty.

Two other megatheriine types, of uncertain age, are known from Mesopotamia. One is apparently Promegatherium smaltatum, a small megatheriine with mesiodistally compressed lower molariforms and relatively low hypsodonty.

The other is represented by MACN 4995, an incomplete dentary with nearly squared molariforms. Features such as a relatively prominent ventral bulge of the dentary and dorsal position of the angular process suggest an increased degree of hypsodonty. Kraglievich (1940b) considered this the type of Eomegatherium nanum. However, the latter is based on an astragalus, MACN 4992, and any association between MACN 4992 and MACN 4995 is uncertain. Probably MACN 4992 belongs to one of the three types from Mesopotamia known from dentaries. Other species of Eomegatherium, such as E. andium and $E$. cabrerai, are based on (and known oniy from) fragmentary and possibly inadequate remains.

Megatheridium annectens is a probably a small to medium-sized Pliocene megatheriine. It is based on the partial skull remains of a very young individual, which are insufficient to allow taxonomic determinations. The combination of an elongated rostrum and very anterior position of the anterior zygomatic roots, however, suggest that the species is distinct.

The late Miocene Megathericulus represents the smallest and earliest known megatheriines. M. patagonicus is the genotype and larger than M. primaevus. The former is known primarily from a partial rostrum and dentary, and complete astragalus. The upper and lower molariforms are markediy compressed mesiodistally, and the rostrum extremely elongated and anteriorly divergent. M. primaevas is smaller
and known from scrappier remains. Its astragalus is approximately intermediate morphologically between those of M. patagonicus and planopsines. Both distal femoral condyles are contiguous with the patellar trochlea, as in planopsines; the femur is not known in M. patagonicus. Unfortunately, no cranial remains of M. primaevus have been recovered.

The phylogenetic relationships among megatheriines are only partially resolvable because most taxa are known from insufficient data. Nearly complete skeletal remains have been recovered only for Eremotherium laurillardi, Megatherium americanum, and M. tarijense, although variation is sufficiently understood only for the former two. The consensus tree of 291 most-parsimonious trees based on the distribution of twelve characters among nine megatheriines (with planopsines as outgroup) suggests that Megathericulus patagonicus and "Plesiomegatherium" halmyronomum fall out as basal megatheriines. The remaining megatheriines (Eremotherium Laurillardi, Megatherium americanum, M. tarijense, M. sundti, M. tarijense, Pyramiodontherium bergi, Megatheriops rectidens), included in this analysis cluster as an unresolved polytomy.

Further resolution may be hypothesized based on additional characters and taxa. Three groups may be recognized: a basal polytomy, including Megathericulus, "Plesiomegatherium" halmyronomum, and Eomegatherium; a
polytomy comprised of Pliomegetherium lelongi, Megatheriops rectidens, Eremotherium laurillardi, and Pyramiodontherium bergi; and the Megatherium clade.

The basal group falls out based on mesiodistally compressed molariforms and a very dorsal position of the navicular facet of the astragalus. The squared molariforms of Pliomegatherium lelongi indicate that this species is not a basal megatheriine; it falls together with Megatheriops rectidens, Eremotherium laurillardi, and Pyramiodontherium bergi as an unresolved polytomy. The Megatherium clade is based on 1) a reduction of the humeral deltopectoral crest, and 2) reduction of the lateral surface of the humerus. The deltopectoral crest is relatively large and its lateral surface projects laterally in earlier megatheriines and nonmegatheriine sloths. In E. laurillardi the crest is reduced to a large, distally-tapered structure on the anterior surface of the humerus. This structure is reduced further in species of Megatherium.

The lateral surface of the humerus is rugose and projects laterally in all megatheriines in which it is known, including the earlier taxa, except in the Megatherium clade. Marked reduction of the deltopectoral crest and lateral surface in M. tarijense and M. nazarrei indicates that they are sister species.

The femoral patellar trochlea of M. istilarti is reduced to a degree otherwise known only in M. americanum,
and suggests that they are sister species. M. sundti shares increased robustness of the femur with these species, and is thus included in a clade with them.

The maxilla is relatively short anterior to the first molariforms in the Megatherium clade. An elongated premaxilla is probably plesiomorphic among megatheriines, based on its presence in Megathericulus patagonicus and most non-derived megalonychomorphs and mylodontids.

The Megatherium clade is also characterized by increased hypsodonty. In all but M. americanum hypsodonty is approximately intermediate between the conditions in Eremotherium laurillardi and M. americanum. The condition in the latter is thus probably derived and autapomorphic.

Pyramiodontherium bergi possesses various character states present in some members of the Megatherium clade. Its femur is approximately as robust as those of $M$. sundti and M. istilarti; the patellar trochlea is reduced compare to that of, e.g., M. tarijense, but not to the degree observed in M. istilarti and $M$. americanum. Conversely, P. bergi possesses various apparently plesiomorphic features: the maxillae are extremely elongated anterior to the first molariforms, and the rostrum diverges anteriorly. These states are shared with Megathericulus patagonicus. Also, the OCH and MBI are approximately as in E. laurillardi, suggesting a similar degree of hypsodonty. Thus, the robust femur and somewhat reduced patellar trochlea are probably
homoplasic.
Megatheriops rectidens possesses relatively high hypsodonty, but bears various apparently plesiomorphic features (e.g.. a very well-developed humeral deltopectoral crest, with its lateral portion projecting laterally; a rugose and laterally projecting lateral surface of the humerus; and elongated premaxillae anterior to the first molariform) that would seem to exclude it, as with $P$. bergi, from the Megatherium clade. Resemblance in hypsodonty to the Megatherium clade is homoplasic.

FUNCTIONAL MORPHOLOGY OF THE MANUS
Movement in the manus was largely restricted to the distal interphalangeal joints. Marginal movement was probably possible among the metacarpals, perhaps as a mechanism compensating for changes in stress. Flexion and extension of approximately $30^{\circ}$ probably occurred between MC II and D2 of most species, but such movement at this joint was not possible in D3 - D5. Some mediolateral rotation occurred at the metacarpal-phalangeal joints of all digits, and allowed the digits to be nearly aligned with the long axes of the metacarpals. Mediolateral rotation at the proximal interphalangeal joints of MC II and MC IV contributed to alignment of the digits.

Considerable extension and flexion occurred in D2 and D3 between the distal interphalangeal joints. Similar movement was possible in D4, although its range was more restricted.

Movement was severely restricted at the proximal interphalngeal joint of D 2 , and precluded by fusion of P 1 and P2 in D3. Some dorsopaimar and mediolateral movement was possible in D4. Thus, P1 and P2 of D2 and D4 functioned essentially as a unit; in D3, the elements are fused into a unit. The configurations of the metacarpal-phalangeal and interphalangeal joints, with extension and flexion largely allowed only distally in D3 and D4, suggest that one use of
the manus would be as a compound hook, possibly used in reaching and drawing overhead branches towards the mouth or in digging for roots.

The medial deviation of the digits and the mediolateral mobility at the interphalangeal joints may be explained in terms of the weight-bearing functions of the manus and the posture in megatheriines. Ground sloths probably assumed a bipedal posture for defense and feeding. They were quadrupedal in normal locomotion, but not obligatory quadrupeds.

As in many ground sloths the manus was twisted laterally, so that the anatomically dorsal surface faced nearly laterally. The weight-bearing axis passed obliquely through the carpus, rather than distally as in most quadrupedal mamals, largely to MC V. In some ground sloths, such as Thinobadistes and Glossotherium, weight was probably borne on MC IV and MC V. This is suggested by a relatively more medial position of the facets for the scaphoid and lunar, and the presence of a rudimentary fourth digit. A distinctive feature in megatheriines is the absence of a synovial articular contact between the ulna and cuneiform, which suggests that increased medial deviation was possible, an adaptation possibly correlated with reaching and pulling.

As a result of the posture of the manus, the digits were thus oriented more nearly medially than distally in
megatheriine sloths, a necessary adaptation given the great length of the claws. The mediolateral mobility at the interphalangeal joints is a further modification for medial deviation of the digits. The laterally twisted manus and medial deviation of the digits allowed the claws to be tucked medially during locomotion.

The astragalar trochlea tali of all megatherinnes bears a well-developed odontoid process medially, as does that of most mylondonts. Its presence has generally been viewed as indicating a rotated or pedolateral pes, so that the anatomical sole faced nearly or entirely medially in life, with the weight borne largely on the lateral surface of Mt V. However, the posture in medium-sized and large megatheriines (the pes is incompletely known in smaller megatheriines) apparently does not follow this pattern.

Past interpretations reconstructed the posture of the megatheriine pes as similar to that of mylodonts, such as Glossotherium: the foot was turned medially and weight borne mainly by its lateral margin. The astragalus was oriented so that the long axis of the odontoid process was nearly vertical. The process thus functioned as a pivot, about which the foot rotated mediolaterally in the horizontal plane, and essentially precluding or severely restricting normal extension and flexion.

However, manipulation of the pedal elements and the tibia strongly suggests that megatheriines did not adopt a pedolateral stance. The medial side of the pes is rotated dorsolaterally, but the anatomical sole still faces largely ventrally. The orientation of the astragalus, hence pes, is constrained by the morphologies and orientations of the
femur and tibia.
The distal tibial surface requires that the astragalus lie with the long axis of the odontoid process oriented approximately $15^{\circ}$ from the horizontal. The most dorsal projection of the odontoid process lies at approximately the same level, or slightly higher, that of the discoid facet. The long axis of the navicular facet lies approximately normal to that of the odontoid process, and its surface faces anteriorly and slightly ventrally. Contact with the ground is made through the posterior part of the calcaneum, most of the ventrolateral surface of Mt $V$, and the proximal and distal parts of the ventrolateral surface of Mt IV. The cuboid is apparently raised off the ground, but may have made a small contact. The third digit, Mt III, ectocuneiform, and the fused mesocuneiform and entocuneiform are raised above the ground.

Movement at the tibio-astragalar joint is mainly extension and flexion. However, a small degree of rotation of the pes occurred during such action, because the sulcus between the discoid and odontoid facets, and the corresponding ridge on the tibia, are not aligned in the parasagittal plane, but offset between $20^{\circ}-25^{\circ}$ lateral from it. Assuming no (or very restricted) movement between elements of the pes, the obliquity of the sulcus caused the pes to rotate during extension so that the anterior end swung medioventrally, and the posterior end dorsolaterally.

Thus, although some rotation occurred in the pes of megatheriines, the degree of rotation is clearly less than implied by past authors. The orientation of the pes, and its manner of contacting the ground are apparently not radically different from the condition in many plantigrade mammals. However, the distinct morphology of the astragalus and calcaneum and, to a lesser degree, of the remaining tarsals indicates that profound and unique changes had occurred during the evolution of the pes of ground sloths. However, it is unclear how and why these changes occurred.

Manipulation of the hind limb elements of some nonmegatheriine sloths, such as scelidotheres, indicates that flexion and extension was also possible at the tibioastragalar joint. The astragalus of scelidotheres also bears a well-developed odontoid process, and its pes has traditionally been viewed as pedolateral. However, its pes functioned similarly to that of megatherines, with considerable extension and flexion possible, although its pes is more pedolateral. The pes of nothrotheriines, Glossotherium, and Pseudomegatherium are apparently markedly pedolateral, but analysis of their functional morphology was not possible because the required elements were unavailable.

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## PLATES CAPTIONS

PLATE 1
Mounted skeleton of the type of Megatherium americanum, MNHNM 6. Scale bar represents 300 mm .

PLATE 2
Mounted composite skeleton of Eremotherium laurillardi at DMAS. Scale bar represents 300 mm .

PLATE 3
Lateral views of skulls of Eremotherium laurillardi. A. Right side, and B. Left side of MCL 1700/01; C. Left side of MCL 1701/01. Scale bars represent 100 mm .

PLATE 4
Lateral views of skulls of Eremotherium laurillardi. A. MCL 1702/01, left side; B. MCL 7240, right side; C. USNM 20872, right side. Scale bars represent 100 mm .

PLATE 5
Lateral views of skulls of Eremotherium laurillardi. A. YPM 14159, right side; B. FMIN P26970, right side; C. ROM 24240, left side. Scale bars represent 100 mm .

PLATE 6
Dorsal views of skulls of Eremotherium laurillardi. A. MCL 1700/01; B. MCL 1701/01. Scale bars represent 100 mm .

PLATE 7
Dorsal views of skulls of Eremotherium laurillardi. A. MCL 1702/01; B. MCL 7240; C. USNM 20872. Scale bars represent 100 mm .

PLATE 8
Dorsal views of skulls of Eremotherium laurillardi. A. YPM 14159; B. FMNH P26970; C. ROM 24240. Scale bars represent 100 mm .

PLATE 9
Ventral views of skulls of Eremotherium laurillardi. A. MCL 1700/01; B. MCL 1701/01. Scale bars represent 100 mm .

PLATE 10
Ventral views of skulls of Eremotherium laurillardi. A. MCL 1702/01; B. MCL 7240; C. USNM 20872. Scale bars represent 100 mm .

PLATE 11
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Skulls of Eremotherium laurillardi. A. and B. Dorsal and ventral views, respectively, of USNM 20867; C. Ventral view of ROM 24239. Scale bars represent 100 mm .
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Skulls of Eremotherium laurillardi. Lateral views of A. and B. Maxilla, MCL 7238, left and right sides, respectively; $C$. and $D$. Skulls, MCL 7230 and MCL 7239, respectively, right sides. Scale bars represent 100 mm .

PLATE 14
Skulls of Eremotherium laurillardi. A. Lateral view of right posterior half of MCL 7230; B. Ventral view of basicranium of MCL 7239; C. Ventral view of posterior half of MCL 7238/01; D. Ventral and slightly posterolateral view of basicranium of MCL 7238/01. Scale bars represent 100 mm .

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Skulls of Eremotherium laurillardi. A. Lateral view of right posterior half, and B. Posterior view of MCL 7230, respectively; C. Lateral view of left posterior half, and D. Posterior view of MCL 7238, respectively. Scale bars represent 100 mm .

PLATE 16
Skulls of Eremotherium laurillardi. A. Dorsal and B. Ventral views, respectively, of MCL 7230; C. Dorsal view of MCL 7238; D. Ventral view of MCL 7239. Scale bars represent 100 mm .

PLATE 17
Lateral views of left sides of skulls of Megatherium americanum. A. MNHNM 6; B. MACN 1000; C. MLP 42-V1-24-2. Scale bars represent 100 mm .

PLATE 18
Lateral views of skulls of Megatherium americanum. A. Left, and B. Right sides, respectively, of BMNH 19953; C. Right side of ZMUC 212. Scale bars represent 100 mm .

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Lateral views of left sides of skulls of Megatherium americanum. A. MLP 2-64; B. MACN, without catalogue number. Scale bars represent 100 mm .

PLATE 20
Dorsal views of skulls of Megatherium americanum. A. BMNH 19953; B. ZMUC 212; C. MACN 42-V1-24-2. Scale bars represent 100 mm.

PLATE 21
Ventral views of skulls of Megatherium americanum. A. BMNH 19953; B. ZMUC 212. Scale bars represent 100 mm .

PLATE 22
Skull of Megatherium americanum, FMNH P14293, in A. Lateral view of right side; B. Dorsal view; C. Ventral view. Scale bar represents 100 mm .

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Skull of Megatherium americanum, MACN 13021, in A. Lateral view of left side; B. Dorsal view; C. Ventral view. Scale bar represents 100 mm .

PLATE 24
Skull of Megatherium americanum, MACN 13021, in A. Lateral view of left side; B. Dorsal view; C. Ventral view. Scale bar represents 100 mm .

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Lateral views of left sides of skulls of Megatherium americanum. A. MACN 2830; B. MACN 2786; C. MMP 430. Scale bars represent 100 mm.

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PLATE 27
Skulls of Megatherium americanum in ventral view. A. MACN 2830; B. MACN 2876; C. MMP 430. Scale bars represent 100 mm .

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Skull and mandibles of Megatherium americanum. A. Lateral view of right side of skull MACN 2831; B. Lateral view of right dentary MACN 10149. Scale bars represent 100 mm.

PLATE 29
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PLATE 30
Skull of Megatherium medinae, SGO PV231, in A. Lateral view of right side; B. Dorsal view; C. Ventral view. Scale bar represents 100 mm.

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Skull of Megatherium medinae, SGO PV275, in A. Lateral view of right side; B. Dorsal view; C. Ventral view. Scale bars represent 100 mm .

PLATE 32
Skulls of Megatherium sundti in Iateral view of right side. A. SGO PV273; B. SGO PV278; C. PIU M4530. Scale bars represent 100 mm .

PLATE 33
Skulls of Megatherium sundti. A. SGO PV273; B. SGO PV278; C. PIU M4530. Scale bars represent 100 mm .

PLATE 34
Skulls of Megatherium sundti in ventral view. A. SGO PV273; B. SGO PV278; C. PIU M4530. Scale bars represent 100 mm .

PLATE 35
Rostrum of MUT V107. A. Lateral view of left side; B. Dorsal view; C. Ventral view. Skull of Megatheriops rectidens, MACN 2818. D. Lateral view of right side; E. Ventral view. Scale bars represent 100 mm .

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Skulls of Megatheriinae. A. Lateral view of right side, B. Dorsal view, and C. Ventral view of skull of Pyramiodontherium bergi, MLP 2-66. D. Ventral view of maxillar fragment of Plesiomegatherium hansmeyeri, MACN 2895. Scale bars represent 100 mm .

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Skulls of Megatheriinae. A. Lateral view of right side, B. Dorsal view, and C. Ventral view of skull of Plesiomegatherium halmyronomum, MLP 26-V1-10-1. D. Ventral view of palate of Megathericulus patagonicus, MACN, without catalogue number. Scale bars represent 100 mm .

PLATE 38
Dentaries of Eremotherium laurillardi. A. MCL 7235, medial view of left dentary; B. MCL 7234, medial view of left dentary; C. MCL 7232, lateral view of right dentary; D. MCL 7221, lateral view of left dentary; E. MCL 7220, lateral view of right dentary. Scale bars represent 100 mm .

PLATE 39
Lateral views of dentaries of Eremotherium laurillardi. A. MCL 7236/02, left dentary; B. MCL 7226, right dentary; C. MCL 7223/01, right dentary; D. MCL 7228, right dentary. Scale bars represent 100 mm .

PLATE 40
Lateral views of dentaries of Eremotherium laurillardi. A. MCL 1702/02, right dentary; B. MCL 7229, left dentary; C. MCL 1701/02, right dentary; D. MCL 7231, left dentary. Scale bars represent 100 mm .

PLATE 41
Lateral views of dentaries of Eremotherium laurillardi. A. MCL 7225, right dentary; B. MCL 1700/02, right dentary; C. MNRJ 3858, left dentary; D. F:AM 95785, right dentary. Scale bars represent 100 mm .

PaATE 42
Occlusal views of mandibles of Eremotherium laurillardi. A. MCL 7234, left dentary; B. MCL 7234, right dentary; C. MCL 7221; D. MCL 7220. Anterior towards top of page. Scale
bars represent 100 mm .
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Occlusal views of dentaries of Eremotherium laurillardi. A. MCL 7236/02, left dentary; B. MCL 7226, right dentary; C. MCL 7223/01, right dentary; D. MCL 7228, right and anterior part of left dentaries. Anterior towards top of page. Scale bars represent 100 mm .

PLATE 44
Occlusal views of mandibles of Eremotherium laurillardi. A. MCL 7222, left dentary; B. MCL 1702/02; C. MCL 7229; D. MCL 1701/02. Anterior towards top of page. Scale bars represent 100 mm .

PLATE 45
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Lateral views of dentaries of Megatherium americanum. A. ZMUC 212, left dentary; B. MLP 28-III-16-2, left dentary ; C. MLP 2-207, left dentary; D. MLP 2-59, right dentary. scale bars represent 100 mm .

PLATE 47
Lateral views of left dentaries of Megatherium americanum. A. MLP 44-12-28-1; B. BMNH 19953f; C. MLP 2-54; D. MLP 2-50. Scale bars represent 100 mm .

PLATE 48
Lateral views of dentaries of Megatherium americanum. A. MEP 2-37, left dentary; B. MLP 2-56, left dentary; C. MACN 5002, left dentary; D. MLP 2-60, right dentary. Scale bars represent 100 mm .

PLATE 49
Occlusal views of mandibles of Megatherium americanum. A. MLP 44-12-28-1; B. BMNH 19953f; C. MLP 2-54, left and anterior part of right dentaries; D. MLP 2-50, left dentary. Scale bars represent 100 mm .

PLATE 50
Lateral views of dentaries of Megatherium americanum. A. MACN 855, right dentary; B. MACN 2830, right dentary; C. MACN 2786, left dentary. Scale bars represent 100 mm .

PLATE 51
Occlusal views of mandibles of Megatherium americanum. A. MACN 855, right dentary; $B$. MACN 2830; C. MACN 2786. Scale bars represent 100 mm .

PLATE 52
Lateral views of dentaries of Megatherium medinae. A. SGO PV252, right dentary; B. SGO pV288, right dentary; C. SGO PV236, left dentary. Scale bars represent 100 mm .

PLATE 53
Occlusal views of mandibles of Megatherium medinae. A. SGO PV252; B. SGO PV288; C. SGO PV236. Scale bars represent 100 mm .

PLATE 54
Lateral views of dentaries of Megatherium sundti. A. SGO PV277, left dentary; B. SGO PV276, right dentary; C. PIU M4530, right dentary. Scale bars represent 100 mm .

PLATE 55
Occlusal views of mandibles of Megatherium sundti. A. SGO PV277; SGO PV276; C. PIU M4530, right dentary. Scale bars represent 100 mm .

PLATE 56
Dentary of A. Megatherium tarijense, FMNH P14216, lateral view of right dentary; B. Lateral, and C. Occlusal views, respectively of dentary of $M$. elenense, EPN V978. Scale bars represent 100 mm .

PLATE 57
Dentary of A. Megatheriops rectidens, MACN 2818, lateral view of right dentary; B. and C. Plesiomegatherium hansmeyeri, right dentary in lateral and occlusal views, respectively. Scale bars represent 100 mm .

PLATE 58
Dentary of A. and B. Pyramiodontherium bergi,

MLP 2-66, left dentary in lateral view and mandible in occlusal view, respectively; $C$. and D. Plesiomegatherium halmyronomum, MLP 30-XII-10-21, left dentary in lateral view and right dentary in medial view, respectively; E. and $F$. Left and right dentaries, respectively, of MLP 30-XII-10-21 in occlusal view. Scale bars represent 100 man.

PLATE 59
Dentaries of A. and B. Pliomegatherium lelongi, MACN 13213, in lateral and occlusal views, respectively; C. and D. cf Promegatherium, MACN 4995, in lateral and međial views, repectively

PLATE 60
Scapulae of Megatheriinae. A. and B. Eremotherium laurillardi, ROM 22117, lateral and medial views, respectively, of left scapula; C. and D. Megatherium americanum, MLP 2-207, lateral and medial views, respectively, of right scapula. Scale bars represent 100 mm .

PLATE 61
Scapulae of Megatheriinae. A. Megatherium americanum, ZMUC 212, lateral view of right scapula; B. Megatherium tarijense, FMNH P142216; C. and D. Toro Negro megatheriine, MLP 68-111-14-1, lateral view of right scapula. Scale bars represent 100 mm .

PLATE 62
Left clavicles of Eremotheirum laurillardi. Top row, dorsal views (sternal towards bottom, posterior towards left); Bottom row, posterior views (sternal towards bottom, dorsal towards right). A. and G. ROM 30799; B. and H. ROM 19762; C. and I. 27328; D. and J. ROM 19763; E. and K. ROM 19764; F. and L. ROM 19761. Scale bar represents 100 mm .

PLATE 63
Clavicles of Megatheriinae. A. Right clavicle of Megatherium americanum, BMNH 19953m, in ventral view; B. Right clavicle of M. americanum, ZMUC 212, in dorsal view; C. Right clavicle of M. americanum, MLP 2-207,in ventral view; D. Left clavicle of $M$. americanum, FMNH P13364, in ventral view. E.

Left clavicle of M. nazarrei, MACN 7127, in ventral view; $F$. and $G$. Left clavicles of $M$. tarijense, FMNH P14216, and FMNE P13365, respectively; H. Left clavicle of Toro Negro megatheriine, MLP 69-III-14-1, in ventral view. Scale bars represent 100 mm .

PLATE 64
Left humerus of Eremotherium laurillardi, ROM 22101. A. Anterior view; B. Posterior view; C. Medial view, anterior towards right; D. lateral view, anterior towards left. Scale bars represent 100 mm .

PLATE 65
Left humeri of Eremotherium laurillardi. A. and B. ROM 19756, anterior and posterior views, respectively; C. and D. ROM 19756, anterior and posterior views, respectively. Scale bar represents 100 mm .

PLATE 66
Humeri of Megatheriinae. A. and B. Eremotherium laurillardi, FMNH P27080, right humerus in anterior and posterior views, respectively; C. and D. Megatherium americanum, BMNH 19953r, Ieft humerus in anterior and posterior views, respectively. Scale bars represent 100 mm .

PLATE 67
Humeri of Megatheriinae. A. and B. Megatherium tarijense, FMNH P14216, anterior view of right and posterior view of left humeri; C. Paramegatherium nazarrei, MACN 7128, right humerus in anterior view (reproduced from Kraglievich, 1925); D. Megatherium sundti, PIU M4530, anterior view of left humerus. Scale bars represent 100 mm.

PLATE 68
Humeri of Megatheriinae. A. and B. Megatheriops rectidens, MACN 2818, anterior and posterior views, respectively, of right humerus; C. FNNH P14511, anterior view of right humerus; D. Toro Negro megatheriine, MLP 68-III-14-1, anterior view of right humerus. Scale bars represent 100 mm.

PLATE 69
Left radius of Eremotherium Iaurillardi, ROM
22107. A. Anterior view; B. Posterior view; C. Ulnar view; D. Distal view, anterior towards top, medial towards left. Scale bars represent 100 mm .

PLATE 70
Radii of Megatheriinae. A. and B. Right radius of Megatherium americanum, BMNH 19953 g , in posterior and anterior views, respectively; C. Left radius of Megatherium americanum, MACN 10148, in posterior view; D. and E. Right radius of Megatherium tarijense, FMNH P14216, in posterior and anterior views, respectively; F. Right radius of Megatherium americanum, FMNH P13365, in posterior view; G. Right radius of FMNH P14511 in posterior view. Scale bars represent 100 mm .

PLATE 71
Left ulna of Eremotherium laurillardi, ROM 28884. A. Anterior view; B. Posterior view; C. Medial view; D. Lateral view; E. Proximal view, anterior towards top, medial towards right. Scale bars represent 100 mm .

PLATE 72
Ulnae of Megatherium americanum. A. and B. Anterior and lateral views, respectively, of left ulna. BMNH 19953i; C. Lateral view of left ulna, MACN 10148; D. and E. Anteromedial and proximal (anterior towards top) views, respectively, of right ulna FMNH P13665. Scale bars represent 100 mm .

PLATE 73
Ulnae of Megatheriinae. A. and B. Anterior and medial views, respectively, of right ulna of Megatherium tarijense, FMNH P14216; C. and D. Lateral and proximal (anterior towards top) views, respectively, of right ulna FMNH 14511; E. and F. Lateral view of proximal part and proximal view (anterior towards top) of left ulna of Eomegatherium cabrerai, MLP 2-206. Scale bars represent 100 mm .

PLATE 74
Manus of Megatherium. Dorsal view of A. Right manus of M. americanum, BMNE 19953j; and B. Left manus of $M$. tarijense, $F M N H$ P14216 (cf. App 3: Fig. 1A). Scale bars represent 100 mm .

PLATE 75
Left scaphoid of Eremotherium laurillardi, ROM 21885. Diagrams indicate articular facets. A. Radial surface, dorsal towards top, medial towards right; B. Distal surface, dorsal towards top, medial towards left; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top; dorsal towards right; E. Palmar view, proximal towards top, medial toward right; F. Dorsal view, proximal towards top, medial towards left. Scale bar represents 100 mm . Abbreviations: 1 - lunar; m magnum; mcc - metacarpal-carpal complex; r radius.

PLATE 76
Left lunar of Eremotherium laurillardi, ROM 22064. Diagrams indicate articular facets. A. Radial surface, dorsal towards top, medial towards right; B. Distal surface, dorsal towards top, medial towards left; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right; E. Dorsal view, proximal towards top, medial towards right. Scale bar represents 100 mm . Abbreviations: c - cuneiform; m - magnum; r - radius, $s^{-}$ scaphoid; u - unciform.

PLATE 77
Cuneiform and pisiform of Eremotherium Iaurillardi. A to D, left cuneiform (ROM 26024) and $E$ to $F$. left pisiform (ROM 28865) of $E$. laurillardi. Diagrams indicate articular facets. A. Proximal surface, dorsal towards top, medial towards right; B. Distal surface, dorsal towards top, medial towards left; C. Dorsal view, proximal towards top, medial towards left; D. Palmar view, proximal towards top, medial towards right; E. Dorsal surface, proximal towards top medial towards left; $F$. Lateral surface, proximal towards top, dorsal towards left. Scale bars represent 100 mm . Abbreviations: c - cuneiform, 1 - Iunar, p -pisiform, u unciform.

PLATE 78
Left metacarpal-carpal complex (MCC) of Eremotherium laurillardi, ROM 35069. Diagrams indicate articular facets. A.

Scaphoidal or proximal surface, dorsal towards top, medial towards right; B. Metacarpal or distal surface, dorsal towards top, medial towards left; C. Dorsal surface, proximal towards top, medial towards left; D. Palmar surface, proximal towards top, medial towards right. Scale bar represents 100 mm . Abbreviations: $m$ - magnum, mc III metacarpal III, s -scaphoid, vp - vestigial phalanx.

PLATE 79
Medial Carpal and Metacarpal Elements of Megatherium americanum. A. and B. Proximal (lateral towards right, dorsal towards top) and lateral (dorsal towards left, proximal towards top) views, respectively, of MCC, BMNH 19953j; C. Medial view of right trapezoid and Mc II, ZMUC 214; D., E., and F. Dorsal (proximal towards top, lateral towards right), medial (proximal towards top, dorsal towards left), and proximal (medial towards right, dorsal towards top) views, respectively, of Mc II, BMNH 19953j. Scale bars represent 100 mm .

PLATE 80
Left magnum of Eremotherium laurillardi, ROM 21893. Diagrams indicate articular facets. A. Proximal view, dorsal towards top, medial towards right; B. Distal view, dorsal towards top, medial towards left; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right; E. Dorsal view, proximal towards top, medial towards left; F. Palmar view, proximal towards top, medial towards right. Scale bar represents 100 mm . Abbreviations: 1 - Iunar; $m$ - magnum, mc III metacarpal III; mcc - metacarpal-carpal complex; s - scaphoid; u - unciform.

PLATE 81
Left unciform of Eremotherium laurillardi, ROM 21900. A. Proximal surface, dorsal towards top, medial towards right; B. Distal surface, dorsal towards top, medial towards left; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right; E. Palmar view, proximal towards top, medial towards right; F. Dorsal view, proximal towards top,
medial towards right. Scale bar represents 100 mm . Abbreviations: c - cuneiform; 1 lunar; $m$ - magnum; mc III - metacarpal III; mc IV - metacarpal IV; mv V - metacarpal V.

PLATE 82
Articulated left proximal carpal row, distal carpal row, and metacarpals, showing corresponding articular surfaces among these units, of Eremotherium laurillardi; cf. diagrams following Plate 82, which indicate articular facets. A. Distal surface of proximal carpal row: scaphoid (ROM 21885), lunar (ROM 22064), cuneiform (ROM 26024), in medial to lateral sequence; medial towards left, dorsal towards top. B. Proximal surface of distal carpal row: metacarpalcarpal complex (ROM 35069), magnum (ROM 21893), unciform (ROM 21900), in medial to lateral sequence; medial towards right, dorsal towards top. C. Distal surface of distal carpal row: elements as in B. medial towards left, dorsal towards top. D. Proximal surface of metacarpals and vestigial phalanx: vestigial phalanx (ROM 35067), metacarpal III (ROM 37958), metacarpal IV (ROM 21907), metacarpal V (ROM 21910), in medial to lateral sequence; medial towards right, dorsal towards top. Scale bar represents 100 mm . Abbreviations: c cuneiform; 1 - Iunar; m - magnum; mc III metacarpal III, mc IV - metacarpal IV; mc V metacarpal V; mcc - metacarpal-carpal complex; s - scaphoid; u - unciform; vp vestigial phalanx.

## PLATE 83

Left metacarpal III of Eremotherium laurillardi, ROM 37058; cf. diagrams following Plate 83 , which indicate articular facets. A. Proximal view, dorsal towards top, medial towards right; B. Distal view, dorsal towards top, medial towards left; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right; E. Dorsal view, proximal towards top, medial towards left. Scale bar represents 100 mm . Abbreviations: m - magnum; mc IV - metacarpal IV: mec - metacarpal-carpal complex; pp proximal phalanx.

PLATE 84
Left metacarpal IV of Eremotherium laurillardi, ROM 21907; cf. diagrams following Plate 84, which indicate articular facets. A. Proximal view, dorsal towards top, medial towards right; B. Distal view, dorsal towards top, medial towards left; $C$. Medial view, proximal towards top, dorsal towards left; D. Lateral view, proximal towards top, dorsal towards right; E. Palmar view, proximal towards top, medial towards right. Scale bar represents 100 mm . Abbreviations: ls - lateral sesamoid; mc III - metacarpal III; mc V - metacarpal V; ms medial sesamoid; ph1 - phalanx 1; u unciform.

PLATE 85
Left metacarpal $V$ of Eremotherium laurillardi, ROM 21910; cf. diagrams following Plate 85, which indicate articular facets. A. Proximal view, dorsal towards top, medial towards right; B. Distal view, dorsal towards top, medial towards left; $C$. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right; E. Dorsal view, proximal towards top, medial towards left. Scale bar represents 100 mm.Abbreviations: mc IV - metacarpal IV; pp proximal phalanx; u - unciform.

PLATE 86
Left proximal phalanx (represents fused phalanges 1 and 2) of digit 3 of Eremotherium laurillardi, ROM 35079. Diagrams indicate articular facets. A. Proximal view, dorsal towards top, medial towards right; B. Distal view, dorsal towards top, medial towards left; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right; E. Dorsal view, proximal towards top, medial towards left; F. Palmar view, proximal towards top, medial towards right. Scale bar represents 100 mm . Abbreviations: mc III - metacarpal III, u - ungual phalanx.

PLATE 87
A. to D. Left ungual phalanx of digit 3 (ROM 35081) and E. to H. Left ungual phalanx of digit 4 (ROM 28867) of Eremotherium
laurillardi. A. and E. Lateral views, proximal towards right, dorsal towards top; B. and F. Palmar views, proximal towards right, lateral towards top; C. and G. Proximal views, dorsal towards top, medial towards right; D. and H. Distal views, dorsal towards top, medial towards left. Scale bars represent $100 \mathrm{~mm} ; A, B$, and $D$ to same scale; E - H to same scale.

PLATE 88
A. to E. Left proximal (ROM 21921) and F. to J. Left middle (ROM 27340) phalanges of digit 4 of Eremotherium laurillardi. A. Proximal view, dorsal towards top, medial towards left; B. Distal view, dorsal towards top, medial towards right; C. Lateral view, proximal towards top, dorsal towards left; D. Medial view, proximal towards top, dorsal towards right: E. Palmar view, proximal towards top, medial towards right; F. Proximal view, dorsal towards top, medial towards right; G. Distal view, dorsal towards top, medial towards left; H. Medial view, proximal towards top, dorsal towards right; I. Dorsal view, proximal towards top, medial towards left; J. Palmar view, dorsal towards top, medial towards right. Scale bar represents 100 mm .

PLATE 89
Pelvis of Eremotherium laurillardi, ROM 4592. A. Anterior view; B. Lateral view of right side. Scale bars represent 100 mm .

PLATE 90
Pelvis of Eremotherium laurillardi, DMAS mount. A. Anterior view; B. Lateral view of right side. Scale bars represent 100 mm .

PLATE 91
Pelves of Megatheriinae. A. Dorsal view of pelvis of Eremotherium laurillardi, ROM 4592; B. Lateral view of left side of pelvis of Megatherium americanum, MACN 1000; C., D., and E. Dorsal, anterior, and lateral (of right side) views, respectively, of $M$. cf. tarijense, MNHN BOL A-585. Scale bars represent 100 mm .

PLATE 92
Femora of Eremotherium laurillardi and Megatherium americanum. Anterior views of A. Left femur of $E$. laurillardi, ROM 22059 (photographically reversed from original right); B. M. americanum, ROM 265. Scale bars represent 100 mm .

PLATE 93
Femora of Eremotherium laurillardi from Coralito, Ecuador. A. Left femur ROM 28911; B. Left femur ROM 19787; C. Right femur ROM 30755; D. Right femur ROM 22057. Scale bar represents 100 mm .

PLATE 94
Femora of Eremotherium laurillardi. A. and B. Right femur FMNH P26970, and FMNH 27080, respectively, from Honduras; C. and D. Left femur ROM 24269 in anterior and posterior views, respectively. Scale bar represents 100 mm .

PLATE 95
Femora of Megatherium americanum in anterior view. A. Left femur in articulation with pelvis, tibia-fibula, and patella MNHNM 6; B. Left femur, MACN 54; C. Right femur MACN 6410; D. Left femur MACN 10683. Scale bar represents 100 mm .

PLATES 96
Femora of Megatherium americanum in anterior view. A. Right femur BMNH 19953r; B. Left femur BMNH 19953q; C. Right femur ZMUC 212; D. Right femur MUT V413. Scale bar represents 100 mm .

PLATE 97
Femora of Megatherium americanum in anterior view. A. Left femur MRN M5626 (the head is reconstructed); B. Left femur MLP 2-60; C. Right femur MLP 2-30; D. Left femur MACN 5002. Scale bars represent 100 mm .

PLATE 98
Distal views of left femora of $A$. Eremotherium laurillardi, ROM 22059 (photographically and diagramatically reversed from the original right); B. Megatherium americanum, ROM 265. Diagrams indicate articular facets. Scale bars
represent 100 mm . Abbreviations: lc lateral condyle; mc - medial condyle; pt patellar trochlea.

PLATE 99
Lateral views of femora of Megatherium americanum and Eremotherium laurillardi. A. Left femur of M. americanum, ROM 265; B. Left femur of E. laurillardi, ROM 22059 (photographically reversed from the original right); C. and D. Right femora of $E$. laurillardi, FMNH P26970 and FMNH P27080, respectively. In A. and B. proximal towards right, anterior towards top; in C. and D. proximal towards left, anterior towards top. Scale bars represent 100 mm .

PLATE 100
Femora of Eremotherium laurillardi. A. Anterior view of distal end of left femur ROM 22059 (photographically reversed from the original right); B. to D. Distal views of right femora DMAS 1L, FMNH P26970, and FMNH P27080, respectively. Scale bars represent 100 mm .

PLATE 101
Femora of Megatherium americanum. A. Distal view of right femur BMNH 19953r; B. Anterior view of distal end of right femur BMNHr; $C$. Anterior view of left femur BMNHq; D. Anterodistal view of right femur MACN 6410; E. Anterior view of distal end of left femur MACN 10683; F. Anterior view of distal end of left femur MACN 54; G. Anterior view of distal end of left femur MACN 5002. Scale bars represent 100 mm .

PLATE 102
Femora of Megatherium tarijense. A. Anterior view of left femur FMNH P14216; B. Distal view of right femur FMNH P14216; C. Anterior view of distal end of right femur FMNH P14216; D. Lateral view of right femur FMNH P14216, proximal towards left, anterior towards top; E. Anterior view of right femur MUT V411. Scale bars represent 100 mm .

PLATE 103
Femora of Megatherium medinae and Megatherium sundti. A. Anterior view of right femur of M. medinae SGO PV231 (from Casamiquela and

Sepulveda, 1974); B. to D. Left femur of $M$. sundti PIU M4530 in B. Anterior view; C. Anterior view of distal end; D. Distal view. Scale bars represent 100 mm .

PLATE 104
Femora of Megatheriinae. A. Anterior view of distolateral part of right femur of Megatherium nazarrei MACN 7127; B. Anterior view of left femur of Pyramiodontherium bergi MLP 2-66; C. to E. Right femur MACN 2817 in C. Anterior view; D. Posterior view; E. Anterior view of distal end. Scale bars represent 100 mm .

PLATE 105
Tibiae-fibulae of Eremotherium laurillardi. A. and B. Anterior and posterior views, respectively, of right tibia-fibula ROM 22068; C. Anterior view of left tibia-fibula MCL 9548; D. and E. Proximal (anterior towards top, medial towards left) and distal (anterior towards top, medial towards right) views, respectively of right tibia-fibula DMAS 4. Scale bars represent 100 mm .

PLATE 106
Tibiae-fibulae of Megatherium americanum. A. Proximal view (anterior towards top, medial towards left) of right tibia-fibula MLP 2-30; B. Anterior view of right tibia-fibula of right tibia-fibula BMNH 19953s; C. Anterior view of right tibia-fibula ROM 10439; D. Posterior view of right tibia-fibula BMNE 19953s: E. Anterior view of right tibiafibula MLP 2-29. Scale bars represent 100 ma.

PLATE 107
Tibiae-fibulae of A. to E. Megatherium americanum, and F. to H. Megatherium tarijense. A. Anterior view of left tibiafibula MLP 2-31; B. and C.Anterior and posterior views, respectively, of right tibia-fibula MLP 2-30; D. Anterior view of right tibia-fibula FMNH P13662; E. Distal view (dorsal towards top, medial towards right) of right tibia-fibula ROM 10439; F. Proximal view (dorsal towards top, medial towards right) of right tibia-fibula FMNH P14216; G. Anterior view of same; H. Distal view (anterior towards top, medial towards
right) of same. Scale bars represent 100 mm .
PLATE 108
Tibiae-fibulae of Megatheriinae. A. Anterior view of left tibia-fibula of Megatherium medinae SGO PV23I; B. Anterior view of left tibia-fibula of Megatherium sundti SGO PV298; C. Anterior view of left tibia-fibula of Pyramiodontherium bergi MLP 2-66. D. Anterior view of left tibia-fibula of the Toro Negro megatheriine MLP 68-III-14-1. Scale bars represent 100 mm .

PLATE 109
Tibiae and Patellae of Megatherinae. A. and B. Proximal (anterior towards top, medial towards left) and Distal (anterior towards top, medial towards right) views, respectively, of right tibia of Plesiomegatherium hansmeyeri MACN 2895; C. Distal view (anterior towards top, medial towards right) of tibia of Megathericulus patagonicus MACN, without catalogue number; D. Distal view (anterior towards top, medial towards right) of posterior part of tibia of tibia of Megathericulus primaevus MLP 39-VI-24-1: E. Proximal view (anterior towards top, medial towards left) of right tibia-fibula of cf. Megatherium tarijense FMNH P14499. F. to H. Femoral views of right patellae of Eremotherium laurillardi ROM 21993, 21994, and 21996, respectively; I. and J. Femoral views of left patellae of $E$. laurillardi ROM 21987 and 21989, respectively. Scale bars represent 100 mm .

PLATE 110
Right astragalus of Eremotherium laurillardi ROM 22008; cf. diagrams following Plate 110 which indicate articular facets. A. Proximal view (anterior towards top), B. Anterior view (proximal towards top). C. Lateral view (proximal towards top), D. Lateroproximal view (anterior towards rigit, with long axis of odontoid process oriented vertically), E. Distal view (anterior towards top), F. Medial view (anterior towards left). Scale bar represents 100 mm . Abbreviations: c cuboid; d - discoid facetof trochlea tali; e ectalfacet for calcaneum; $£$ - fibula; $n$ navicular; s - sustentacular facet for
calcaneum.
PLATE 111
Astragali of Megatheriinae. A. Proximomedial view (anterior towards top) of right astragalus, with long axis of odontoid process oriented vertically, of Eremotherium laurillardi FMNH P26970; B. and C. Proximomedial views (anterior towards top) of right and left astragali of Megatherium americanum MNHNP 1871 and MLP 44-XII-28-1, respectively; D. and E. Lateroproximal views (distal towards bottom) of right and left astragali of $M$. americanum MNHNP 1871 and MLP 44-XII-28-1, respectively; F. Anterior view (proximal towards top) of right astragalus of M. americanum MNHNP 1871. Scale bars represent 100 mm .

PLATE 112
Astragali of Megatheriinae. A., B., and C. Lateroproximal (anterior towards right), anterior (proximal towards top), and proximomedial (anterior towards top) of right astragalus of Megatherium americanum, MLP 230; D. Proximomedial view (anterior towards top) of right astragalus of $M$. americanum, MLP 2-131; E., F., and G. Lateroproximal (anterior towards right), anterior (proximal towards top), and proximomedial (anterior towards top) of right astragalus of $M$. tarijense, FMNH P14216. Scale bars represent 100 mm .

PLATE 113
Astragali of Megatheriinae. A., B., and C. Lateroproximal (anterior towards right), anterior (proximal towards top), and proximomedial (anterior towards top) of right astragalus of Pyramiodontherium bergi, MLP 266; D. and E. Lateroproximal (anterior towards right) and anterior (proximal towards top) views, respectively, of right astragalus of MegathericuIus patagonicus, MACN, without catalogue number. Scale bars represent 100 mm.

PLATE 114.
Astragali of Megatheriinae. A., B., and C. Lateroproximal (anterior towards right), anterior (proximal towards top), and proximomedial (anterior towards top) of right
astragalus of Megathericulus primaevus, MLP 39-VI-24-1; D. Anterior view (Proximal towards top) of right astragalus MACN 13667. Scale bars represent 100 mm .

PLATE 115
Astragali of Megatheriinae. A., B., and C. Lateroproximal (anterior towards left), anterior (proximal towards top), and proximomedial (anterior towards top) views, respectively, of Eomegatherium nanum, MACN 4992; D., E., and F. Lateroproximal (anterior towards right), anterior (proximal towards top), and proximomedial (anterior towards top) views, respectively, of right astragalus MACN 2904. Scale bars represent 100 mm .

PLATE 116
Astragali of Megatheriinae. A. and B. Lateroproximal (anterior towards left) and anterior (proximal towards top), respectively, of left astragalus of Eomegatherium cabrerai, MLP 2-206; C., D., and E. Lateroproximal (anterior towards left), anterior (proximal towards top), and proximomedial (anterior towards top) views, respectively, of Toro Negro megatheriine, MLP 68-III-14-1. Scale bars represent 100 mm .

PLATE 117
Right calcaneum of Eremotherium laurillardi, ROM 23003. A. Dorsal view (anterior towards top), B. Volar view (anterior towards top), C. Lateral view (anterior towards right), D. Anterior view (dorsal towards top). Scale bar represents 100 mm .

PLATE 118
Calcanea of Megatheriinae. A. and B. Dorsal views of right calcanea of Eremotherium laurillardi, ROM 30768 and ROM 23003, respectively; C. Left, and D. Right calcanea of Megatherium americanum in dorsal view, MLP 2-207 and MNHNP 1907-15, respectively. Scale bars represent 100 mm .

PLATE 119
Calcanea of Megatheriinae. A. Dorsal view of right calcaneum of Megatherium americanum, MNHNP 1871; B. Dorsal, and C. Medial views of left calcaneum of M. tarijense, MNENP

TAR1269; D. Dorsal view of right calcaneum of M. tarijense, FMNH P14216. Scale bars represents 100 mm .

PLATE 120
Calcanea of Megatheriinae. A. Dorsal view of left calcaneum of Pyramiodontherium bergi, MLP 2-66; B.and C. Dorsal views of left calcanea of Toro Negro megatheriine, MLP 68-III-14-1, in different perspectives; D. Dorsal view of left calcaneum, MACN 7063; E. Dorsal view of right calcaneum, MACN 11486; F.. G., and H. Dorsal views of left calcanea MACN 4926, MACN 4927, and MACN 12303, respectively. Scale bars represent 100 mm .

PLATE 121
A. - D. Right navicular of Eremotherium laurillardi, ROM 21941, in proximal or astragalar (dorsal towards top, medial towards left), anterior (dorsal towards top, medial towards right), medial (dorsal towards top, posterior towards right), and lateral (dorsal towards top, posterior towards left) views, respectively; E. Dorsal view (anterior or distal towards top, lateral towards right) of articulated right cuboid (ROM 21928) and calcaneum (ROM 22003) of Eremotherium Iaurillardi. Scale bars represent 100 mm .

PLATE 122
Right cuboid of Eremotherium laurillardi, ROM 21932. Anatomical medial surface or astragalar view (anterior towardsleft, dorsal towards top). B. Anatomical lateral surface (anterior towards right, dorsal towards top), C. Anterior view (dorsal towards top, medial towards right), D. Posterior view (dorsal towards top, medial towards left), E. Dorsal view (anterior towards top, medial towards left), F. Ventral view (anterior towards top, medial towards right). Scale bar represents 100 mm .

PLATE 123
A. - C. Right ectocuneiform of Eremotherium laurillardi, ROM 28860, in proximal or posterior (dorsal towards top, lateral towards right), anterior or distal (Corsal towards top, lateral towards left), and medial (dorsal towards top, anterior or distal towards left) views, respectively; D. -
G. Right mesocuneiform-entocuneiform complex of Eremotherium laurillardi, ROM 28861, in medial (dorsal towards top, anterior or distal towards left), lateral (dorsal towards top, anterior towards right), anterior or distal (dorsal towards top, lateral towards left), and posterior or proximal (dorsal towards top, lateral towards right) views, respectively. Scale bar represents 100 mm .

PLATE 124
Right metatarsal III of Eremotherium laurillardi, ROM 21965, in A. Anterior view (dorsal towards top, medial towards right), B. Posterior and slightly medial view (dorsal towards top, medial towards left), C. Posterior and slightly lateral view (dorsal towards top, lateral towards right). D. Lateral view (dorsal towards top, anterior towards right), E. Dorsal view (anterior towards top, medial towards left), F. Ventral view (Anterior towards top, medial towards right). Scale bar represents 100 mm .

PLATE 125
Ankylosed phalanges 1 and 2 of digit 3 of Eremotherium laurillardi. A. Distal (dorsal towards top, lateral towards right) of ROM 21953, left, with both sesamoids fused to ventral or volar surface of ankylosed phalanges: B. - F. ROM 28864, right, with only a medial sesamoid fused to volar surface, in distal (dorsal towards top, lateral towards left), proximal (dorsal towards top, lateral towards right), medial (proximal towards top, dorsal towards right), lateral (proximal towards top, dorsal towards left), and dorsal (proximal towards top, lateral towards left) views, respectively. Scale bar represents 100 mm .

PLATE 126
Right ungual phalanx of digit 3 of Eremotherium laurillardi, ROM 28863, in A. Dorsal (distal towards left, lateral towards top), B. Ventral (distal towards left, medial towards top), C. Medial (distal towards left, dorsal towards top), D. Proximal (dorsal towards top, lateral towards right), and E. Distal (dorsal towards top, lateral towards left) views, respectively. Scale bars represent 100 mm .

PLATE 127
Right metatarsal IV of Eremotherium laurillardi, ROM 28856. A. Dorsal view (proximal towards top, lateral towards left), B. Ventral view (proximal towards top, lateral towards right), C. Lateral view (proximal towards top, dorsal towards right), D. Medial view (proximal towards top, dorsal towards left), Proximal view (dorsal towards top, lateral towards right), F. Distal view (dorsal towards top, lateral towards left). Scale bar represents 100 mm .

PLATE 128
Right metatarsal $V$ of Eremotherium laurillardi, ROM 221973. A. Dorsal view (proximal towards top, lateral towards left), B. Ventral view (proximal towards top, lateral towards right), C. Lateral view (proximal towards top, dorsal towards right), D. Medial view (proximal towards top, dorsal towards left), Proximal view (dorsal towards top, lateral towards right), F. Distal view (dorsal towards top, lateral towards left). Scale bar represents 100 mm .

PLATE 129
Articulated right tibia-fibula (ROM 22068) and astragalus (ROM 22008) of Eremotherium laurillardi in A. and B. Anterior and Lateral views, respectively, with astragalus flexed, and C. and D. Anterior and Lateral views, respectively, with astragalus extended. Scale bar represents 100 mm .

## Plate



## Plate 2



## Plate 3




Plate 5


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## Plate 6



## Plate 7



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## Plate 9



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# Plate 12 



## Plate 13




Plate 15


Plate 16



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## Plate 19




Plate 21


## Plate 22



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Plate 23

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Plate 25


## Plate 26



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## Plate 28




## PLATE 30




# Plate 31 



## Plate 32



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Plate 33


## Plate 34



Plate 35


## Plate 36


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Plate 37


PLATE 38




FLATE 4



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Plate 48


Plate 49




## Plate 52





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## Plate 56



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## Plate 66




PLATE 68



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## Plate 80




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Plate 82


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# Plate 85 




## Plate 86



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## Plate 88




Plate 90



## Plate 92




## Plate 94



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PLATE 9


PLATE 97


## Plate 98



Plate 9!


## Plate 100



Plate 101


## Plate 10



Plate 103




Plate 104



## Plate 106










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## Plate 10\}




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## Plate 11C





# Plate 112 



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## Plate 114



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## Plate 11



## Plate 116



PLate 117


## Plate 118



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Plate 119







## PLATE 122



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## PLATE 123



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## PLATE 127





## PLATE 129



# EREMOTHERIUM LAURILLARDI: THE PANAMERICAN LATE PLEISTOCENE MEGATHERIID SLOTH 

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#### Abstract

ABSIRACT-Remains of Eremotherium, representing a large-sized mepatheriid ground sloth, are lnown from localities in North, Central, and South America. Usually these remains are currently assigned to the following three species, based laryely on geographic provemance: E. laurillardi (Lund), E. mirabile (Leidy), and E. rusconii (Schaub). However, two large, recently recovered collections of Eremotherium remains from Jacobina, Bahia, Brazil, and Daytona Beach, Florida, USA, do not support the separation of these species. Instead, these collections demonstrate the existence of a single Panamericen species. The range of variation is laretr than was suspected and the morphological characteristics used in species distinction are not diagnostically valid.

The valid name for this species is E. laurillandi (Lund, 1842). The type is a juvenile molariform (ZMUC 1130) from the Pleistocene of Lagoa Santa, Minas Gerais, Brazil. E. mirabile (Leidy, 1855) and E. rusconiii (Schanb, 1935) fall as junior synonyms.


## INTRODUCTION

Eremotherium comprises a group of small and large. primarily intertropical Pleistocene megatherïne ground sloths that are known from South America, Central America, and North America. Remains of the larger species are assigned currently to Eremotherium lourillardi (Lumd, 1842), E. mirabile (Leidy, 1855), and E. rusconii (Schaub, 1935). Those of a possibly smaller species have been described under E. elemense (Hoffstetter, 1949), but its diagnosis is not firmly established (De Iuliis and Cartelle, 1994), and this report does not resolve the status of this species.
Eremotherium may be distinguished morphologically from Megotherium primarily through differences in the skull, molariforms, and manus. In Eremotherium the premaxillae are triangular, small, and loosely articulated to each other and to the maxillae, whereas in Megatherium the quadrangular premaxillae are fused firmiy to each other and to the maxilac, and hetp form a stout and elongated rostrum. The zypomatic arch and orbit lie more ventrally in Eremotherizm, and the ventral buige of the mandible is less pronounced in Eremotherium than in Megutherixom. The mandibular symphysis extends posteriorty approximately to ml in Eremotherium, and to $\mathbf{m} 2$ in Megotherium.

The molariforms of Eremotherium and Megatherium differ in that the palp cavity is relatively shorter in the former, comprising approximately half the apicobasal length, whereas in Megatherivm the cavity occupies approximately the basal three-fourths. However, these difierences apparentiy become manifest during ontogeny, such that molariforms of younger juvemiles cannot be consistently distinguished. Fur-
ther, the transverse crests and valleys of the molariforms, particularty of the more mesial ones, tend to be more obliquely oriented in Eremotherium.

The manus of Eremotherium described in the literature (excluding that allocated to E. elenense) retains digits III-V, of which digits III and IV bear large, wellformed unguals; only metacarpals (MCs) $I$ and II, fused with the traperium and trapezoid into the MetacarpalCarpal Complex (MCC), represent the first two digits (Fig 1). The manus of Megatherium possesses digits II-V, of which digits II-IV bear large, well-formed unguals, the trapezium and MCI form the MCC. The relationships among the carpal and metacarpal elements are more fully elaborated elsewhere (De Iuliis and Cartelle, 1994).

Two large collections of Eremotherium remains have recently been made. One constitures remains from Toca das Onças, Jacobina, Bahia, Brazil, and consists of approximately 4,000 skeletal elements (M.N.I. $=36$ ), which are housed at MCL (abbreviations are given below). The second collection, from Daytona Beach Bonebed, Daytona Beach, Florida, USA, consists of approximately 1,300 elements (M.NI. $=11$ ). Most of the latter collection is housed at ROM, but a composite, nearly complete skeleton is mounted at DMAS. These collections demonstrate the existence of a single Panamerican species of Eremotherium during the late Pleistocene. The valid name for this species is $E$. Laurillardi (Lnd, 1842).

## MATERIALS AND METHODS

Specimens and localities used in statistical analyses are listed in Appendix 1. Other material examined is


FIGURE 1. Dorsal (A) and palmar (B) views of the riqht manus of Eremotherium laurillardi (MCI 9487). Abbreviations: cma, cuneiform; lun, lunar; mag, magnum; me III, metracarpal III; meIV, metrcarpal IV; me V, metacarpal V; mec, metacarpalcarpal complex; p, pisiform; ps, palmar sesmoid; une, unciform; se, scaphoid. The position of ps is uncertrain.
too numerous to list, and includes specimens from other localities in Brazil and the United States, and Ecuador, Honduras, Panama, Perr, and Venezuela. The appropriate institution (see text) may be contacted for specimen lists. All measurements are in cm , and were taken with large-size calipers, resembling tree-calipers, constructed by staff of the Department of Zoology, University of Toronto. Statistical analyses were performed using SAS.

Abbreviations: AMNH, American Museum of Natural History, New York, ANSP, Academy of Natural Sciences, Philadelphia; BMNH, British Museum of Natural History, London; DMAS, Daytona Beach Museum of Arts and Sciences, Daytona Beach; FMNH, Field Museum of Natural History, Chicago; MCL, Musen de Ciencias Naturais da Pontificia Universidade Catolica de Minas Gerais, Belo Horizontes, MNRI, Musen Nacional do Rio de Ianeiro, Rio de Janeiro; ROM, Royal Ontario Museum, Toromor UF, Florida Museum of Natural History, Gainesville, UFA, Universidade Federal do Acre, Rio Branco; USNM, National Musem of Natural History, Smithsomian Institution, Washington; ZMUC, Zoologisk Musenm Universitat Copenhagen, Copenhagen.

## TAXONOMIC HISTORY

Spillmam (1948) erected Eremotherium carolinense for late Pleistocene megatheriine remains from Ecuador. Hofitetter (1949), without knowiedge of Spillmann's work, referred material from the same locality as that which had yielded Spillmann's specimens to Megatherium rusconii Schaub, 1935, to which Schaub had allocated megatherine remains from Venezuela. Hoffstetter believed, however, that the material referred to $M$. rusconii was generically distinct from Megatherium and erected the genus Schaubia. Hoffitetter (1950) discovered that Schaubia was occupied and renamed the genus Schoubitherium. Hofistetter (1952) subsequently realized that his Ecuadorian material (S. rusconii) was generically identical to Spillmann's Eremotherium carolinense and he revised his allocation; however, Hoffistetter maintained the validity of Schanb's E. rusconiì primarily on the basis of geographic separation.

During the past forty years numerons species have been proposed for Eremotherium remains, a circumstance laryely due to the sparse and often pooriy preserved nature of the material, but also to the lack of
consideration for either inter- or intraspecific variation of metric or morphological characters. A third reason is that researchers had little opportunity to visit collections in countries in South America. In addition to the species formally proposed for Eremotherium are others originally referred to Megatherium, one (see Mones, 1973) to Scelidotherium, and one (see Ray, 1979) to Chelonia, a marine turtic; these have been reidentified recently as Eremotherium. A list of the names that have appeared in the literature in chronological order follows:
Eremotherium laurillardi (Lund, 1842)
E. couperi (Harlan, 1842)
E. mirabile (Leidy, 1855)
E. quanajuatense (Duges, 1882)
E. rusconií (Schaub, 1935)
E. hudsoni (White, 1941)
E. larensis (Nectario-Maria, 1941)
E. carolinense Spillmann, 1948
E. elenense (Hoffstetter, 1949)
E. venezuelensis (Osten, 1951)
E. Iundi Paula Couto, 1954
E. robustum Porta, 1961
E. cucutense Porta, 1961

Paula Couto (1950) stated that the material mounted at MNRI represented Megatherium laurillardi, which he considered a possibly valid name for Brazilian megatheriine remains. Hoffstetter (1954) decided that the type material of laurillardi and the material discussed by Paula Couto belonged in the genus Eremotherium; he considered E. laurillardi as a possibly valid species, though based on poor material

When Paula Couto (1954) revised the South American Pleistocene megatheriids he recognized five species of Eremotherium: $E$. carolinense, $E$. rusconii, $E$. mirabile, E. elenense, and the new species $E$. lundi. He also proposed the new subgenus Pseudoeremotherium for the material of $E$. hundi, which he considered to be restricted to Brazil. However, the type material of $E$. lundi was largely that which Hoffstetter (1954) had recognized as $E$. laurillardi; if the latter is considered valid, E. fundi would be its junior synonym. Both authors supported the validity of E. rusconii as the Venezuelan species. Later, Paula Couto (1978) considered E. carolinense, E. elenense, and E. hundi as synonyms of E. rusconii. Panla Couto (1979) considered E. Lourillardi as insufficiently defined and, following Hofistetter (1949, 1952), recognized E. elenense as a small eremothere species from South America. Paula Couto (1954) also considered "Megatherium larensis" (sic) Nectario-Maria, 1941 and "M. venezuelensis" (sic) Osten, 1951 to be either synonyms of $E$. rusconii or nomina nuda.

Gazin (1957) was the first to recognize the possibility that a single panamerican Eremotherium species existed, based on comparisons of newly discovered Panamanian material. He considered $E$. mirabile to be the valid name for the possible late Pleistocene panamer-
ican species. He allowed, however, for the possibility that distinct South and North American species existed, in which case he considered E. rusconií and E. mirabile, respectively, as valid names. He felt, as had Hoffstetter (1952), that $E$. laurillardi should have been ignored or synonymized with Megatherium americanum. Also, Gazin (1957) agreed with Paula Couto's (1954) reallocation of $M$. mirabile to $E$. mirabile for North American remains. Paula Couto (1954) alluded to M. hudsoni and he (Paulo Couto, 1979) listed E. mirabile and E. hudsoni as North American taxa. E. hudsoni was erected by White (1941) on an incomplete ungual of digit III, possibly of the manus, from Forida; it is thus a poorly established name and is best considered a synonym of $E$. laurillardi. It was mistakenly judged to be a Pliocene species because of its occurrence in the Bone Valley District of Florida; while it is true that in this region Tertiary sediments predominate, Pleistocene sediments are also quite common and have subsequently produced other examples of Eremotherium (S. D. Webb, 1991, pers. comm.), as discussed above.

Bocquentin (1979) synonymized $E$. cucutense, "M. venezuelensis" (sic) and "M. larensis" (sic) with E. rusconii. Cartelle and Bohórquez (1982) synonymized $E$. carolinense with $E$. rusconii, and $E$. quanajuatense and $E$. elenense with $E$. mirabile. The synonymy of $E$. elenense with $E$. mirabile is considered here as incorrect, and will be considered more fully elsewhere. $E$. robustum is based on remains from Fusagasugá, Cundinamarca, Colombia, originally assigned by Bürgl (1957) to Megatherium sp. The material includes a poorly preserved postcranium and a nearly complete dentary. We agree with de Porta's (1961) allocation to Eremotherium, but his description and measurements do not support the erection of a new species, as the attributes ascribed to $E$. robustum fall within the range of variation observed in the new eremothere samples from Daytona Beach and Jacobina. We therefore synonymize E. robustum with E. laurillardi, as explained below.
Cartelle and Bohórquez (1982) considered E. laurillardi to be the valid name for Brazilian eremothere remains, following Paula Couto (1950) and Hoffstetter (1954). Currently, three names are usually recognized in the literature for Eremotherium: E. laurillardi from Brazit; E. mirabile from the United States, and E. rusconii from Colombia (see de Porta, 1961), El Salvador (see Stirton and Gealey, 1949), Ecuador (see Hoffstetter, 1949, 1952; Edmund, 1965), Honduras (specimens in FMNH), Mexico (see Polaco-Ramos, 1981), Panama (see Gazin, 1957), Peru (specimen in ROM), and Venezuela (see Bocquentin, 1979; also specimens in AMNH).

## COMPARISONS

The many specific names erected for eremothere remains during the past forty years were not based on careful comparison with established taxa, but appar-


FIGURE2. Fibular view of the astragalus of Eremotherium lourillardi (ROM 22008) demonstrating measurements used in statistical analyses. $\mathbf{A}=$ proximodistal height; $\mathbf{B}=$ anteroposterior length.
ently on a rather arbitrary geographical basis. Thus, for example, specimens from Brazil have been referted usually to $E$. laurillardi. This practice has resulted, as might be expected, in the unjustifiable use of nearly any quantitative or morphologic character found in exceedingly small samples to justify specific designation. Such diagnoses do not bear close scrutiny in the light of ordinary consideration of variation. For example, Cartelle and Bohórquez (1982) cite a different arrangement of carpals as possibly separating Brazilian eremotheres from Gazin's (1957) Panamanian material, stating that the unciform and centrale are fused in their material, while the centrale is free in Gazin's sioth. However, the occurrence of an unfused centrale in the Panamanian specimen appears to be an anomaly (see below). Cartelle and Bohórquez cited possible fusion of the trapezoid and the magnum, and of the trapexium with MCS I and II, but figures of the Brazilian manus (Cartelle and Bohörquez, 1982.fig. 4b) are nearly identical in this respect to Gazin's (1957: 350-351; fig. 2) description and figure for the Panamanian manus.
Two composite skeletons of E. mirabile from Panama are mounted for exhibition in the USNM, each with reconstruction. The larger of these, mounted bipedally (USNM 20872), is the one for which Gazin (1957) described the manus. Neither manus may be examined in detail because the mount is fragile, the spaces between the skeletal elements are plastered, and
the palmar sesamoid obscures the manus in palmar view. The centrale of the left manus appears to be real. However, it is very similar to the medial portion of a normal unciform, and may represent an anomalous condition in which the medial portion of the unciform is separate from the main body. The right manus could not be examined in detail because it is posed in a raised position, but the centrale appears to be a plaster reconstruction. The smaller mount (USNM 20867) is posed quadrupedally. A centrale is absent, and the unciforms, which probably are not from the same individual, are normal. No other centralia are known to exist. A left unciform in the collection (USNM Field Number 82-51) is normal. It appears, then, that the presence of a centrale is an abnormal variation and is known only from USNM 20872. Unfortunately, Gazin (1957) chose to describe only the anomalous condition.

A second misconception among workers is that eremothere species may be distinguished on the basis of size. Most studies using size to justify specific separation focus on the supposed discrepancy between the size of the South American eremothere remains and that published by Leidy (1855) for the North American E. mirabile. Since the specimen examined by Leidy was not a particularty large one, workers have generally assumed, following Ameghino (1889), that the North American eremotheres were smaller than their South American counterparts. Preliminary statistical analyses of the large collections from Toca das Onças and Daytona Beach do not support these assumptions. Rather, the large Toca das Onças sample demonstrates variation of nearly $\mathbf{3 5 \%}$ in linear measurements among both adult and juvenile members of a single population. Kruskal-Wallis tests for the height and length of the astragalus (Fig. 2) of adults, among the more commonly recovered elements, indicate that no significant differences occur among five samples (Fig 3; see Appendix I for samples). Further, the Toca Das Oncas sample provides evidence, predominantly from long bones, for striking sexual dimorphism, as anticipated by Cartelle and Bohórquez (1982). Dimorphism is suggested in that skeletal elements from near both ends of the size range may belong to adult and juvenile individuals. These new data clearly contravene the previous view that Eremotherium species could be distinguished on the basis of size.
Similarty, the remains from Toca das Oncas and Daytona Beach display an extensive variation in shape and form of nearty all skeletal elements and their articular facers, indicating that the small morphological variations reported in the literature do not constitute valid diagnoses of Eremotherium species. Indeed, all reported differences may be observed in both the Toca das Oncas and Daytona Beach collections, except for Garin's (1957) report of a centrale in one Panamanian specimen, as discussed above. In summary, all supposedly diagnostic and quantitative features of late Pleistocenc eremotheres are subsumed in the new, larger samples from Jacobina and Daytona Beach; thus,

South, Central, and North American Eremotherium remains may be considered conspecific.

## DISCUSSION OF NOMENCLATURE

The oldest specific epithets assignable to Eremotherium are E. laurillardi (Lund, 1842) and E. couperi (Harlan, 1842). The latter was described by Harlan (1842) as the femur of a marine turtle Chelonia couperi, from coastal Georgia, USA (Ray, 1979). Ray (1979: 11) correctly reidentified it as a right clavicle of Eremotherium, and stated that "it seems highly probable that all megatheriid specimens from the late Pleistocene of coastal Georgia, including the holotype of Chelonia couperi, belong to a single species." Ray's hypothesis is justified; the size and morphology of the clavicle fall within the range of variation observed in the Jacobina and Daytona Beach collections. Ray (1979) suggested that couperi be regarded as an unused senior synonym, and that mirabile (Fig. 4), though younger, be used for the North American eremothere, should the two be shown to be conspecific. His reasons were based on maintaining nomenclatural stability, as mirabile was "a name of virtually universal familiarity to vertebrate paleontologists" (Ray, 1979:12), whereas couperi had not "entered into the literature of megatheres at all, and into that of edentates only through the single mention by Hay (1923:370). Other than the few mentions of the taxon cited above, there seems to be no notice of it in the literature of fossil turtles" (Ray, 1979:11). While acknowledging that Ray's (1979) opinion is reasonable, we feel that couperi should be considered as a potentially valid name, because Harlan described and figured the clavicle. The remainder of this discussion continues largely as though couperi did not exist, because the name has not entered into the taxonomic history of eremotheres except for Ray's (1979) work.

Eremotherium laurillardi (Lund, 1842) is based on a molariform (ZMUC 1130) recovered from the caves of Lagoa Santa, Minas Gerais, Brazil. The author reported another molariform (ZMUC 1131), and remarked that the molariforms (Fig. 5) were approximately one-quarter the size of molariforms of Megatherium and indicated the existence of a species the size of a tapir. Only ZMUC 1130 was mentioned, but both were figured by Lund (1842;pl. 35, figs. 6, 7; reproduced in Paula Couto, 1950:pl. 35, figs. 6, 7). Earlier, Lund (1840) had assigned a third tooth (of an adult individual) from the caves to Megatherium cuvieni ( $=$ Megatherium americanum), figured by Lund (1842: pl. 36, figs. 1, 2 ; reproduced in Paula Couto, 1950.pl. 36, figs. 1, 2).

Winge (1915), followed by Hofistetter (1952, 1954), explained that the smaller teeth showed juvenile characteristics and sugested that they probably belonged to the young of the species represented by the larger tooth, which he assigned to M. americanum. Winge's (1915) arrangement was readily supported by subsequent authors, as the material from Lagoa Santa indicated the presence of a megatheriid, but apparently


FIGURE 3. Box and Whisker Plot of height (A) and length (B) of astragali of Eremotherium laurillardi. Horizontal line indicates mean; vertical line indicates range; box includes one standard deviation above and below the mean; number above vertical line indicates observations ( 1 ) for each sample. See Appendix I for explanation of samples. Kruskal-Wallis tests indicate that no significant differences exist among samples (for height, $x^{2}$ approximation $=5.56, \mathrm{DF}=4, P=$ 0.2347 ; for length, $x^{2}$ approximation $=2.65, D F=4, P=$ 0.6180).
did not permit it to be distinguished from M. americamum (Hoffstetter, 1954), because the teeth were fragmentary and morphologically similar to those of $M$. americamum
The question of the validity of the epithet laurillardi resurfaced when continued discovery of new and often more complete material showed that all adequately known megatheres from Brazil belonged to Eremotherium. During the 1940s and 1950s, when the relationships and geographical distribution of Eremotherium were still unclear, Hoffstetter(1949) and Paula Couto (1950, 1954, in Hofftetter, 1949) considered E. laurillardi to be a valid but poorly understood species. In the following paragraph Hoffstetter (1954:7467) both supported and cast doubt on the validity of lourillardi- "Il y a donc une haute probabiité pour que Tespece de Lagoa Santa soit aussi un Eremotherium et doive recevoir le nom de E. lourillardi (Lund 1842). Ils s'agit vraisemblablement de la méme espece que


FIGURE 4. Type specimen of Eremotherium mirabile (USNM 830); A, occlusal; B, hateral views of the mandible.
celle de Bahia, dont létude en cours nous apportera une connaissance détaillée. II est meme possible que se soit la même forme qui a vécu au Venezuela, de sort que $E$. rusconif (Schaub) pourrait tomber en synonymie devant le nom de Lmod, si toutefois ron décide de prendre en consideration le type très insuffisant proposé par le dermier auteur."

Gazin (1957:346) believed that the two teeth comprising the type material of E. laurillardis were "evidently immature and clearly inadequate for diagnostic purposes, hence should probably be ipnored or the name M. lcurillardii be left as a synonym of M. cmericonum as treated by Winge" The latter sugestion is techai-
cally impermissable, but the first has some validity, as even isolated mature teeth of Eremotherium cannot be distinguished consistently from those of Megatherium. Gazin (1957) further proposed that if a single Central and South American species were present, its valid name would be E. rusconiï. Paula Couto (1950) stated that $E$. laurillardi was insufficiently defined, and he (1970) referred to the species from Brazil as $E$. hundi. Later, Paulo Couto (1978) did not refer directily to $E$. laurillarch, but alluded to its invalidity by agrecing with Garin that E. rusconii was valid for the Central and South American species. Paula Conto (1979) stated that $E$. laurillardi was insufficiently defined.

Cartelle and Bohórquez (1982), however, resurrected E. laurillardi for remains from Brazil, based on new material from Toca das Onças (Jacobina), and recognized $E$. mirabile for North American remains and $E$. rusconii for Central and South American remains exclusive of Brazil (see also Cartelle and Bohórquez, 1986). Toledo (1986, 1989) considered E. laurillardi as the valid Brazilian species. Curvello and Guérin (1993) recognized E. lundi as the Brazilian species. They rejected $E$. laurillardi largely because its definition of size did not agree with adult specimens subsequently recovered.

The choice of a valid name for the panamerican eremothere is thus not simply a matter of using the oldest available name. It would seem. based on the work of Hoffstetter (1952, 1954), Gazin (1957). and Paula Couto (1978, 1979) that the epithet laurillardi should be ignored. However, Cartelle and Bohórquez (1982:48) stated that it has priority over other specific names: "Alguns autores . . . inclinam-se para a hipótese de ser o gènero Eremotherium monoespecifico. Caso confirmado tal hipótese, . . . . o nome välido para tal espécie única seria $E$. laurillardi, em cuja sinonimia cairiam todos os demais nomes propostos ..." They (1982:51) justified their assertion by stating that "A diagnose feita por Lund, levando-se em conta a época, parece-nos suficiente para a validade da denominação especifica." A reasonable case may be made in support of this opinion. It is true that Lund's (1842) juvenile molariforms cannot be distinguished from those of Megatherium. but all subsequent diagnostic material from Brazil (see e.g., Cartelle, 1992; Cunha et al.. 1985; Curvello and Guérin, 1993;Guérin, 1991; Oliveira and Damasceno, 1987; Paula Couto, 1975; Rancy. 1981; Rolim. 1974; Simpson and Pauia Couto, 1981: Toledo, 1989) and all intertropical regions of the New World reported up to the present belong to Eremotherium.

The recent discovery by Cartelle of as yet unpublished remains reinforces the probable geographic exclusion of Megatherium from this region. Over the past five vears Cartelle has recovered, from caves in Bahia, remains that offer better understanding of the nature of faunae in intertropical Brazil. The caves contain faunae that preserve synchronous assemblages of typically southern or temperate taxa, such as Morenelaphus sp... Myocastor coypus Molina, Glyptodon clavipes Owen, Toxodon platensis Owen; and those typically intertropical, such as Trigonodops lopesi Roxo, Hoplophorus euphractus Lund, and Xenorhinotherium bahiense Cartelle and Lessa. The discovery of the temperate Lestodon armatus (Paula Couto, 1973) in the State of Sào Paulo is additional support for this possibility, this is the most northern, unambiguous record for this species, as that reported by Simpson and Paula Couto (1981) is uncertain. Further, Cartelle (1992) reported Ocnotherium giganteum (Lund) from Bahia and Minas Gerais, confirming the presence of intertropical Lestodontinae. Such mixed assemblages make it plansible that temperate taxa spread northward during the late Pleistocene, possibly due to changing climatic con-


FIGLRE S. Eremotherium laurillardi. A. type specimen (ZMUC 1130): B, ZMUC 1131 in side view.
ditions. Thus, the migration of Megatherium into what has been considered traditionally intertropical regions might be expected. However, remains of Megatherium have never been found. despite the recovery of various other temperate taxa.

The only possibly valid basis for suppressing the epithet laurillardi would be that its type is not an objective standard of reference by which the application of the name it bears is determined (see ICZN, Art. 61a). As discussed above. various authors have alluded to this apparent deficiency in suggesting that the name be ignored, and replaced by a more suitable type. It is worth considering, then, whether the mandible of $E$. mirabile (USNM 830; Fig. 4), from Skidaway Island, Georgia, USA. figured by Leidy (1855:pl. 15, figs. 1 , 2) adequately represents the panamerican species. Hoffstetter (1952) commented that the jaw possibly represented Plesiomegatherium, but nonetheless designated it as the lectotype for $E$. mirabile. Leidy (1855) figured only the left mandible of this specimen, but the right also exists. Thus, the lectotype is a nearly complete mandible lacking angular and coronoid processes, and rostral portions of the symphyseal spout. The molariforms are incomplete, largely broken at the alveolar border, right ml is absent.

The jaw possesses three characters that identify it as Eremotherium: the presence of a premolariform concavity on the jaw's lateral surface, the shallower ventral projection of the ventral margin of the mandible than in Megatherium: and the more ventral position of the angular process than in Megatherium. However, these features are also present in the recently discovered. large-sized eremothere species from the Blancan of Florida (Hulbert et al. 1989); the formal decription of this species is in progress by De Inlitis and Cartelle. Further, there exists the possibility of confusing the panamerican species with the new species, given the geographical proximity of the localities yielding their remains in Florida. It is clear, on the other hand, that
the numerous remains recovered from the Pleistocene of Brazil represent the same species described by Lund (1842).

Thus. the mandible (USNM 830) is not particularly more adequate as an objective standard of reference than the molariform (ZMUC 1130). Pursuing the search for such standards would. in our opinion, cause considerably more confusion, and the designation of one would be based on somewhat subjective criteria. We agree with Ray (1979:11) that "Absolutely rigorous demands of morphological adequacy for nineteenth century holotypes in vertebrate paleontology are ... contrary to the goal of nomenclatural stability. Old names may often be bolstered by invocation of geographic or stratigraphic propinquity, by the addition of new . . . material." We feel that there is, therefore. no valid reason for suppressing the name Eremotherium laurillardi, and recognize it as a potentially valid name for the panamerican eremothere.

The two oldest available names are thus $E$. laurillardi (Lund, 1842) and E. couperi (Harlan, 1842). The publication date of the latter is July 6, 1842 (C. E. Ray, pers. comm., 1994). We have been unable to determine a more precise date for E. laurillardi; the Royal Danish Academy of Sciences and Letters and the printing house responsible for publication of the journal do not have archives bearing on this matter (T. Hatting, ZMUC, pers. comm.. 1994). Therefore. an objective decision of priority is not possible. We believe that $E$. laurillardi should be given preference because it has entered consistently into the literature of megatheriines, whereas E. couperi is virtually unknown to vertebrate paleontologists. We formally propose, therefore, that $E$. lourillardi be considered the valid name for the Panamerican, large-sized, Pleistocene eremothere. We note that Cartelle (1992) recognized E. mirabile. At that point in our collaboration, we felt that this name would be most appropriate in maintaining nomenclatural stability. We have since realized, clearly, that past objections to $E$. lourillardi could not be justified.

Lund (1842) based $E$. laurillardi on the molariform ZMUC 1130. He did not state this explicitly, but alluded to his figure (1842:pl. 35, fig. 6) of ZMUC 1130 in a footnote, ZMUC 1131 was also figured (1842:pl. 35, fig. 7). Although Lund (1842) did not formally designate ZMUC 1130 as the type, it is clear from his text that he based the species on ZMUC 1130. The ICZN, Art. 73a, i states that a specimen is the holotype by original designation "If an author when establishing a new nominal species-group taxon states in the original publication that one specimen, and only one specimen, is the holotype, or "type", or uses some equivalent expression, ..." However, the specimen is a holotype by monotypy "If the nominal species-group taxon is based on a single specimen, either so stated or inferred in the original publication or demonstrated from evidence derived from outside the work itself ..." (ICZN, Art 73a, ii).
The directions of the Code do not permit an unequivocal designation for ZMUC 1130. Ambiguity
stems from interpretation of the phrase "or some equivalent expression" (Art 73a, i). If the phrase is intended to permit latitude with regard to the use and concept of a type specimen during Lund's time, then we feel that Lund (1842) clearly intended ZMUC 1130 to be regarded as a "type." Therefore, we suggest that ZMUC 1130 be considered the holotype by original designation.

The type locality is Lapa Vermetha, Vale do Rio das Velhas, Lagoa Santa, Minas Gerais, Brazil Lund (1842) stated that ZMUC 1130 and ZMUC 1132 were from Vale do Rio das Velhas, but Lund (1843) listed them as from Lapa Vermelha (see also Paula Couto, 1950: 544). The range of $E$. laurillardi (Fig. 6) extended from South Carolina (Hay, 1923, reported probable remains of this species from New Jersey), USA, to Rio Grande do Sul, Brazil.

The following specimens from Georgia are discussed because of their historical signifance. Leidy (1855) described the posterior part of a cranium (USNM 832), and the left astragalus (part of USNM 837), which were figured by Hodgson (1846:figs. 1, 2, 5, 6). We were unable to locate the ungual phalanx figured in Hodgson (1846:figs. 3, 4). USNM 830, 832, and 837 are catalogued as cotypes (in the sense of syntypes) of $E$. "mirabile." These specimens are from the Pleistocene of Skidaway Island, Georgia, and were collected and donated to the Smithsonian (the National Institute, at the time) by either J. P. Scriven or by Scriven and J. C. Habersham. Still other material described or known to Leidy are USNM 825-829 (isolated molariforms) and USNM 831 (distal end of left humerus). The axis, cervical vertebrae, and head of a femur discussed by Leidy (1855) could not be located.

Additional material from Skidaway Island resides in ANSP, including the molariform (the smaller of two catalogued ANSP 12534) collected by Major Leconte and figured by Leidy (1855:pl. 15, fig. 4). ANSP also houses the $E$. mirabile specimens from Darien and Brunswick Canal, Georgia (collected by J. H. Couper) discussed by Leidy (1855), such as a portion of the left dentary, ANSP 12523. Leidy (1877:pl. 34, figs. 42, 43) also figured a molariform (ANSP 12532) from the Ashley Phosphate Beds, South Carolina, USA.

## CONCLUSIONS

Many species have been proposed for the remains of large-sized Eremotherium remains. Of these species, three are currently recognized in the literature: $E$. lourillardi from Brazil; E. rusconii from Central America and the northern part of South America; and E. mirabile from the United States. The smaller species $E$. elenese is poorly established. Eremotherium is morphologically similar to Megatherium, but may be clearly distinguished on differences in the skull and manus.

The species proposed for Eremotherium over the past half-century were based largely on geographical provenance, without detailed comparison with established taxa. This practice resulted in a series of specific


FIGURE 6. Map showing approximate positions of major localities yielding remains of Enemotherium laurillardi. Brazil: 1 , Rio Grande do Sal; 2, Paraní; 3, Mato Grosso do Sal; 4, Rio de Janciro; 5, Espírito Santo; 6, Minas Gerais; 7, Goiäs 8 , Bahin; 9, Sergipe; 10, Pemambuco; 11, Paraiba; 12. Rio Grande do Norte; 13, Ceara; 14, Piani; 15, Acre. Perry 16, Piura. Ecuador: 17, Guayas. Pemama: 18, Herrera. Colombia: 19, Huila; 20, Cundinamarca; 21, Norte de Santander. Venexuela 22, Lara; 23, Falcom. El Salvador: 24, Sen Migpel Hondurac 25, Copain. Mexico: 26, Tabasco; 27, Jalisco; 28, Guanajuato. USA: 29, Texas, 30, Florida; 31, Georgiar 32, South Carolina.
diagnoses based on relatively minor quantitative and qualitative differences among specimens from inadequate samples. A wide range of variation in size and morphology is observed in large, recently recovered collections of Eremotherium remains from Jacobina and Daytona Beach. These collections demonstrate that the quantitative and qualitative characters cited in the literature in support of specific distinctions are not valid. Instead, the evidence supports the existence of a single. Panamerican, large-sized Eremotherium species.

Eremotherium laurillardi (Lund, 1842) and E. couperi (Harlan, 1842) are the oldest, potentially valid names. An objective decision of priority cannot be made, because a more precise date of publication cannot be determined for $E$. laurillardi. However, it has been used by and is well-known to vertebrate paleontologists, whereas $E$. couperi has largely been ignored. Therefore, E. laurillardi is clearly more appropriate, and recognized as the valid name for the panamerican, large-sized, Pleistocene eremothere. The type is ZMUC 1130 , a juvenile molariform. The range of E. laurillardi extends from South Carolina (and possibly New Jersey), USA, to Rio Grande do Sul, Brazil (Fig. 6). Eremotherium couperi. E. rusconii (Schaub 1935), and E. mirabile (Leidy, 1855) fall as junior synonyms.

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APPENDDX 1. Specimens and localities of astragali used in statistical analyses. Sample 3 comprises specimens from Brazil excluding the single locality samples from Toca das Onças, Jacobina. Bahia (Sample 1) and Permambuco (Sample 2). $L=1=$ left: $\mathbf{R}=$ right.

| Specimen | Side | Locality |
| :---: | :---: | :---: |
| Sample 1 |  |  |
| MCL 9664/02 | R | Toca Das Onças, Jacobina, Bahia, Brazil |
| MCL 9719/02 | R | Toca Das Onças, Jacobina, Bahia, Brazil |
| MCL 9733 | R | Toca Das Orpas, Jacobina, Bahia, Brazil |
| MCL 9736 | R | Toca Das Onças. Jacobina, Bahia, Brazil |
| MCL 9738 | R | Toca Das Onças, Jacobina, Bahia, Brazil |
| MCL 9740 | R | Toca Das Onças, Jacobina, Bahia, Brazil |
| MCL 9744 | R | Toca Das Oncas, Jacobina, Bahia, Brazil |
| MCL 9745 | $R$ | Toca Das Onpas, Jacobina, Bahia, Brazil |
| MCL 9746 | R | Toca Das Ongas, Jacobina, Bahia, Brazil |
| MCL 9749 | R | Toca Das Onças, Jacobima, Bahia, Brazil |
| MCL 9752 | R | Toca Das Ongas, Jacobima, Bahia, Brazil |
| MCL 9754 | R | Toca Das Oncas, Jecohina, Bahia, Brazil |
| MCL 9758 | R | Toca Das Onças, Jacobina, Bahia, Brazil |
| MCL 9759 | R | Toca Das Oncas, Jacobina, Bahia, Brazil |
| MCL 9760 | R | Toca Das Onyas, Jacobina, Balia, Brazil |
| MCL 9761 | R | Toca Das Onpas, Jecobina, Bahia, Brazil |
| MCL 9764 | R | Toca Das Onpas, Jacobina, Bahia, Brazil |
| MCL 9771 | R | Toca Das Oncas, Jacobina, Bahia, Brazil |
| MCL 9772 | R | Toca Das Oncas, Jacobina, Bahia, Brazil |
| MCL 9773 | R | Toca Das Onpas, Jacobina, Bahia, Brazil |
| Sample 2 |  |  |
| MNRJ 99V | R | Pernambuco, Brazil |
| MNRJ 100V | R | Pernambuco, Brazil |
| MNRJ 10IV | R | Pernambuco, Brazil |
| MNRJ 102V | R | Pernambuco, Brazil |
| MNRJ 104V | R | Pernambuco, Branil |
| MNRJ 105V | R | Perpambuco, Brazil |
| MNRJ 106V | R | Permambuco, Brazil |
| MNRJ 107V | R | Pernambuco, Brazil |
| MNRJ 108V | R | Pernambuco, Brazil |
| MNRJ 109V | R | Pernambuco, Brazil |
| MNRJ 110 V | R | Pernambuco. Brazil |
| Sample 3 |  |  |
| MNRJ 417V | L | Conquista, Bahin, Brazil |
| MNRJ 421V | L | Acre, Brazil |
| MNRJ 279V | R | Paraibe, Brazil |
| MNRJ 2130V | R | Boa Nova, Brazil |
| MNRJ 2948V | R | Paraiba, Brazil |
| MNRJ 2972 V | R | Paraiba, Brazil |
| MNRJ 3871V | R | Espirito Santo, Brazil |
| BMNH M5689 | L | Bahia, Brazil |
| Sample 4 |  |  |
| ROM 22013 | L | Daytona Beach Bonebed, Daytona, Florida, USA |
| ROM 22014 | L | Daytona Beach Bonebed, Daytons, Florida, USA |
| ROM 22015 | $L$ | Daytona Beach Boaebed, Deytona, Florida, USA |
| ROM 22016 | L | Daytona Beach Bonebed, Daytom, Fiorida, USA |
| ROM 30773 | $L$ | Daytona Beach Bonebed, Daytoma, Florida, USA |
| Sample 5 |  |  |
| ROM 4036 | L | Coralizo, Santa Elena Penimsula, Ecuador |
| ROM 4037 | L | Coralito, Senta Elem Penizsula, Ecusdor |
| ROM 24257 | L | Coraito, Santa Elema Peninsala, Ecuador |

# REI ATIONSHIPS OF THE MEGATHERIINAE, NOTHROTHERIINAE, AND PLANOPSINAE: SOME SKELETAL CHARACTERISTICS AND THEIR IMPORTANCE FOR PHYLOGENY 

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#### Abstract

The characters used by Engelmann (1985) to mite varioas Nothrotheriinne and Megatheriinae in the Family Metetheriidae are assessed for their suitability as synaponorphies for sach a chade. The elongate, slender premaxillae were cited as a symapomorphy of these subfimilies. $\mathbf{A}$ tendency for the posterior external opening of the mandibular canal to be located medially, topether with the presence of an odontoid tibial articular process of the astragitus, were cited to unite Nothrofherium with megatheres. However, these characters are unsuited to resolving the relationships among Nothrotheriinac, Megatheriinac, and Planopsinace. The Y-shaped premaxillse of some Nothrotheriinae sensu lato may be a synapomorphy of the Plio-Pleistocese and some Santacrucion nothrotheres. These premaxilne are morphologically distinct from the V-shaped, trimgular type seen in Eremotherium, which is probably the plesiomorphic condition in sloths, and the robust, quadrangular, and derived premarillae of Megathariorn. The posterior external opening of the mandibular canal may be located more medially in Nothrotheriops and some species of Brapalops, but not in Nothrocheritut, Nothropiss, and Pronothrotherium. The presence of an odontoid tibial articular process is not rutricted to Nothrotherinae senses stricto and Mepatherïnas. The greater seperation of the astrapilor ectal and tibinl facets (probably a derived condition) occurs only in some mylodonts, and thus is not usefil in distinguishing the significance of the presence of the procest. Other evidence (ains form of the astraplus, anditory repion, and tibial process for the long digital flexors) suapest a closer relationship between Mepatherinae and Planopsinse than some other combination of these subvemition. The astraphar odontoid ribial process is uswally considered to be independently derived in meputheriids and mylodontids, based on the interpretation of other morphological evidence. The alternate hypotheris, that the procers is a synapomorphy of these families, is exploced. Alternate polarities to those usually scoepted for the demtition and dentery are sugaested on the basis of Pserdoghyptodon.


## INTRODUCTION

The phylogeny of the Xenarthra proposed by Engelmann (1985) is a comprehensive attempt to organize a broad ranee of morphologic information as a basis for a classification and phylogeny of tardigrades, vermilingmas, and cingulates. His arrangement is the most useful contribution, to date, for the study of sloth (and other xenarthran) phylogeny, and provides the basis and directions for further research.

Among the Tardigrada sensu Hoffzetter (1958) (=Phyllophaga sensu Engelmann, 1985), Engelmann's (1985) phylogenetic arrangements for the Mylodontidae and Megalonychidae inctude nearly all described taxa, but are controversial. Altemate arrapsements are offired by Hirschfeld (1985), Hofistetuer (1958, 1982), Patherson and Pascual (1972), Patterson et al (1992), Pania Couto (1979), Simpson (1945), Webb and Perripo (1985), and Webb (1989). Relationships among the remaining sloths (Nothrotherimse, Megetherinae, Planopsinac) are even more poorly understood, and Engelimann's analycis includes few described trax.

Engelimann's phylogeny united Hapalops, Nothrotherium, and megetheres, inctuding only Megatherium and Eremotheriven. The Phanopsinge were opmitted from

Engelmann's (1985:59) analysis, as were various megatheriine genera, because "they are based on inadequate material or otherwise unknown to me with regard to useful morphology." It is true that some taxa excluded from his study are not as completely known as other sloths, but their morphology is sufficiently well understood to have some bearing on the characteristics used by Engeimann to unite the nothrotheres and megatheres.
The nodes recognized by Engelmann appear to be weakly supported, as they are supported by only one or two characters, of which some are arguably of dubious systematic value and not corroborated by other evidence. This situation results from Engelmann's (1985) sweeping (and admirable) attempt at inclusion of a wide range of taxa into the phylogeny, but the mossic nature of the distribution of characters among sloths contributes to the presence of weak nodes. This is particulitily applicable to the relationships among nothrotheres, megntheres, and planopsines. A third, and probably most important factor contributing to wealiy stapported phylogenetic statements (inclucting hypotheses of Engetmann and other workers), is a lack of detriled and complatative character descriptions and
illustrations, which might serve as a base for sloth character analyses.

This paper assesses and evaluates the basis for Engelmann's (1985) inclusion of the Nothrotheriinae within the Megatheriidae. The character states he used will be shown to be unsuited to resolving the phyiogenetic relationships among these and other sloth groups.

## ABBREVIATIONS

AMNH-American Museum of Natural History, New York, USA; FMNH-Field Museum of Natural History, Chicago, USA; MACN-Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; MCL-Museu de Ciências Naturais da Pontificia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil; MI.P-Museo de La Plata, La Plata, Argentina; PU-Princeton University, Princeton, U.S.A.: ROM-Department of Paleontology, Royal Ontario Museum, Toronto, Canada. The prefix $\mathbf{R}$ indicates a recent specimen, and the prefix (DM), not formally part of the catalogue number, indicates a specimen from the Department of Mammalogy; UFFlorida Museum of Natural History, Gainerville, USA.

## TAXONOMIC HISTORY

Traditionally the Megatheriidae were considered to include two subfamilies (e.g., Hoffstetter, 1958; Paula Couto, 1954). The Planopsinae (Santacrucian, early Miocene) include only two genera, Planops and Prepotherium. Urumacotherium was assigned to the Planopsinae by Bocquentin-Villanueva (1984), but it is a mylodontid (Santos and De Iuliis, 1993). The Megitherinase (Friasian to Lujamian of South America, middie Miocene to late Pleistocence Irvingtonian to Rancholabrean of Central and North America, middle to late Pleistocene) are generically more diverse and include at least Megathericuius, Pyramiodontherium, Pleviomegatherium, Eremotheriam, and Megatheriunt. The taxonomy of various other megatheriine genera is unsettled and they appear to be questionably valid (eg., Pliomegatherium, Eomegatherium: see Simpson, 1945; Hofistetter, 1958), but are cited in recent literature (eg, Mones, 1988).

The Nothrotherinase (Colhuenspian to Lujanian of South America, late Oligocene to late Pleistocenes Irvingtonian to Rancholabrean of North America; middie to late Pleistocenc) have been grouped with the Megalonychidae (or Megalonychinae) or the Megatheriidae. The Nothrotherimae inctudes various Miocene tava, such as Proschismotherium, Hapaloides, Eut choloeops, Hapalops, Schismotherium, Byperloptus, Pelecyodont and others (see Panla Conto, 1979), and the Pfio-Pleistocene geners Pronothotheritm, Nothropus, Nothrotherium, and Nothrotheriops, termed the Nothrotherinine sensu stricto (Hodistetier, 1958).

The nothrotheres, except Notinotherium, were commonly viewed as mepolonychids or megnlonychines
until some twenty years ago. Near the turn of the century Nothrotherium was grouped with Megatherium in the Megatheriidae or Megatheriinae by most authors (eg., Osbors, 1910; Weber, 1904; Zittel, 1893, 1925), partly, although incorrectly, based on a medial position of the posterior external opening of the mandibular canal (seeZittel, 1925). However, Nothrotherium came to be considered a megalonychid or megalonychine, along with other nothrotheriines, carly in the present century (eg., Scott, 1913; Stock, 1925; Winge, 1915, 1923), probably based largely on Scott's (1903-1904) opinion that Nothrotherium was a direct descendant of Hapalops. Patterson and Pascual (1972:269) suggested that nothrotheres and megatheres "appear to be cioser to each other than either is to the ancestral megalonychids, especially in cranial structure." They offered no further basis for this interpretation, but the apparent concensus among tardigrade specialists is that Patterson and Pascual based their interpretation largely on characteristics of the auditory region, which Patterson had been studying with W. Segall (A. G. Edmund; H. G. McDonald, pers. comm., 1989; Patterson et al., 1992). Patterson and Pascual (1972) make no reference to the planopsines. The inclusion of nothrotheres in the Megatheriidse has been generally followed by later woricers, such as McDonald (1985), Paula Couto (1979), and tentatively by Scillato-Yané et al. (1987) and Scillato-Yané (1979, 1986). Panla Conto (1979) included the Planopsinae, Nothrotheriinae, and Megatheriinae in the Megatheriidae.

Hofistetter (1961), in the most recent review of the Planopsinae, considered the long-held view of ciose affinity between the Planopsinae and Megatheriinae to be overconfidently accepted. He conciuded that planopsines could represent either a lateral branch of the Megalonychidae (sensu lato) with megatheroid tendencies or an carly ofishoot of the Megatherïdae.

Engelmamn (1985:58) stated that the "Megatheriidae includes the megatheres and most, but not necessarily all, of those sloths that have been considered Nothrotheriinae. FIapalops and some other Santa Cruzian sloths belong in this group. All of these sloths are characterized by their narrowiy elongate premaxilla." Engelmann (1985) did not indicate more precisely which Santacrucian genera he considered megatheriids, but the premaxilla is known certainly only in Hapalops, Eucholoeops, and Hyperieptus (see below) among the genera described by Scott (1903-1904).

Engelmann (1985:58) considered Nothrotherium as thesistergenus of megotheres (inciuding only Megatherivm and Eremotherium) and cited as synapomorphies "the common presence of an odontoid tibial articulation of the astraghtus similar to that found in mylodonts, and the tendency of the posterior extemal mandibular foramen to be located medial to the base of the coronoid process."

The character states of the premaxilla, astragalus, and position of the posterior external mandibular foramen used by Engelmant (1985) are amlyzed here for their suitability as symapomorphies for resoking



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FIGURE 2. Ventral view of the palate of $A$, Noohrofherium maquinense, B, Eremotherium mirabite (after Cartele and Bohórques, 1986: figs, 2 and 4, respectively) C, ventril view of premexills of Eremotherivon mirabile (ROM 11461): D, ventral view of palate of Meguherivm americanum (after Owen, 1856.pl. 24). Scale bar equals 2 cm . Abbreviations nan-nasal, and as in Fipure 1.
illae are superficially similar to those of Hapalops and Eucholoeops, but are reduced to "form short, broed, triangular plates with apex directed forwarus the change is due to the relatively great broedening of the posteroexternal branch of each premaxillary" and the palatine fisgures are reduced to very narrow stits (Scott, 19031904:262; pl. 54, fig (A). The premaxilime of Nothrotherium (Fis 2A; Cartelle and Bohórquez, 1980) and Nothrotheriops (Lull, 1929.pl. 3, fies. A, B; Naples, 1987; Wison, 1942:pl. 3, Gig. 1) are similar to those of Hapalops.
In Eremotherium (Fig 2B) the premaxillae are tri-
angular and V-shaped, and lack elongate anterior processes. The lateral ramus is greatly expanded and projects considerably beyond the level of the medial ramus. In some specimens the medial ramus is greatly reduced so that only a nubbin remains, as in MCL 3001/01 (Fir- 2B; Gruta das Oncas, Bahis, Brazil) and ROM 28941 (Daytona Beach Bonebed, Florids, USA). The premaxillae thus open medially as well as posteriorly for the palatine fissure. In other specimens of Eremotherium the medial ramus is well developed (Fig2C), as in ROM 11641 and ROM 35813 (Coralito, Santa Elena Peninsula, Ecuador). In ROM 28944

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FIGURE 4. Fibular view of right astapelins of mylodoatids. A, Glossotherivon harlani (after Stock, 1925ifig, 97B), B, Scelidotherivm sp. (AMME L28738); C, Octodontodherium sp. (after Hofistetter, 1982-fis. 10E); D, Acremylodon campbelfi (Atter Friley, 1986.fig. 9a) Figures 4A, B D ere reversed diagrmatically from original let astrugaii. Scale ber equals 2 cm. Abbreviations ec-ectal articular surfice for celcanewms A-articular surfece for fibulas mo-articular surfice for navicular; al-odontoid tibiat procest th-articular surfice for tibia.

V-shaped and anteroposteriody shortened. In Bradypus the reduction is extreme, particularty that of the lateral ramus. The premaxillae are variously specialired in other sloth genera. In Megalonyx they are considerably reduced, and form two oval plates, sutured to each other at the midline, which lie between and are stightly recessed behind the caminiforms (Leidy, 1855; McDonald, 1987.fig 2). In Mylodon darwini (see Kraglievich, 1934.pls. 3, 5) and Mylodonopsis itseni (see Cartelie, 1991:figs. 1-3) the medial rami fuse and are considerably elongated posteriocty. The hateral mamus is appareatly reduced posterionty (particulariy evident in Kragievich, 1934ppL 3, dorsal view of MACN 5980). A dorsal process is present anteriocty, which contacts the nasals to form an osseous arch. The perimeter of the premarilla is rounded, but cleariy more similar to the $V$-chaped pattern than the $Y$-himped pattern. In Thinobadistes the prempaillse are reduced to rudimentary bets, but lie amterionly beyood the deatition (see Webb, 1989.fic. 4).
Stender, V-shaped patatal processes of the premaxille are abso present in glyptodonts and mymeco-
phagids. In these, however, each premaxilla bears a posterodorsal extension, which lies along the anterior margin of the maxilla and contacts the nasal. The analysis of this character among sloth outgroups by T. J. Gaudin (pers. comm., 1992) demonstrates clearly that the $V$-shaped palatal process of the premaxillae is plesiomorphic for pilosans.
The often cited relationship between the Plio-Pleistocene Nothrotheriinae and Hapalops (and, through it, to the remaining Nothrotheriunae sensulato) was based on a high degree of resemblance in generality of structwre, or more precisely, on characters that have been interpreted consistently as plesiomorphic for sloths. Indeed, it is noteworthy that Frailey (1986:40; 1988) was unable to identify any "derived features that are shared by" Hapalops and the nothrotheres. However, the premaxillae of some of these nothrotheres bear resemblances which may represent synapomorphies of the Plio-Fleistocene nothrotheres and those Sintacrucisp yenera for which the premacillac are known, except Hyperteptus. The premaxilla of thesestre $Y$-shaped rather than $V$-shaped, bear a slender, anterioriy taper-


FIGURE 5. Fibular view of right astraglus of nothrotheres. A, Nothrotherivan maquinense (reversed dingramatically from original left astraglius; after Cartelle and Fonseca, 1983fig, 3); B, Nohiroheriops shasense (after Stock, 1925:fig. 31A). Scale bar equals 2 cm . Abbreviations is in Figure 4.
ing anterior process at the junction of the medial and lateral rami, and have strongly concave lateral margins. The structure of the quadrangular, elongate premaxilla of Megatherium, with robust, prominent anterior processes, is probably autapomorphic.

## Astragalus

Engelmann (1985) cites as a synapomorphy of the Nothrotherium-megathere group the presence of an odontoid tibial articulation of the astragalus. In mylodontids the astragalus, where known, also bears an odontoid process (though it is not equally well developed in all genera), but the mylodontid astragalus is distinguishable from that of megatheriids by the considerable separation posteriorly between the tibial articular surfice and the ectal articular surfice, or that portion corresponding to the ectal surface, for the calcaneum (Engeimamn, 1985). This condition may distinguish between some megatheres and mylodonts. However, it cannot be used consistently to distingnish between other mylodontids, Nothrotherium, Nothrotheriops, and Megatheriunae (including those exchuded from Engelmann's study).

The distance between the ectal and tibial articular surfaces posterioriy is variable in sloths. It is considerable in Glossotherium (Fig 4A), Lestodon, and Thinobadistes, and perhaps Engeimann'sinterpretation was inffuenced by the astragatio of these genera. The distance between these surfaces in the astragali of other mylodontids is considerably smaller than in the mylodontids discussed above, and even less so than that in some megntherines and nothrotheres. Erampies of mylodontids with a smaller separation between ectal and tibial surfices are Scelidotherium and Octodontotherium (Fios 4B, C). In Acremylodon (Fiz. 4D) the distance is similar to that in mequtheciines.

The distance in Nothrotherium and Nothrotheriops
(Figs 5A, B) is similar to that in the megatheriines Megathericulus (Fig. 6A), Promegatherium (? = EOmegatherium) namum (Fig. 6B), P. (cf. E.) cabrerai (MLP 206), Eremotherium (Fis. 6C), and Pyramiodontherium bergi (Fig. 6D). In Megatherium americanum the separation is smaller than in the other megatherïnes, and is approximately as in Octodontotherium (see Owen, $1860:$ pl. 41, fig. 1). This condition is probably derived among megatheriines. The phylogenetic relationships within the Megatheriunae are not well established, but it is probable that Megathericulus is the sister group to other megatheriines, based on its mesiodistally narrow molariforms. The functional ingroup includes the remaining megatheriine genera. The wider separation between facets as occurs in Megathericubus is present in the ingroup geners, except Megatherivm. Therefore, the condition in the latter is probably derived, whereas the wider separation between the ectal and tibial surfaces is probably plesiomorphic.
Within tardigrades the plesiomorphic condition is possibly that exemplified in the megatheriines, exchuding Megatherium, as other non-megatheriine sloths shares similarseparation between ectal and tibial fircets. However, it is doubtfill that this character is of much systematic value above the hierarchical level of subfamily, and its use as a criterion on which to establish frmitial monophyletic groupings is questionable, because this chapreter demonstrates considerable variation across genera within distinct families. Indeed, this character varies considerably within the species Pseudoprepotherivem confiusum (see Birschfeld, 1985:figs. 18B, 19A). However, the character is systematically important within certain ciader, and I recognize that the great separation between the ectal and tibial surfices in Glossotherium and Lestodon is a derived concition and systematically siqnificant.
A more consistent distingrishing criterion for the astragelif of mylodontids and megatheriines is that the


FIGURE 6. Fibular view of astraphas of mepatheriids. A, Megathericubus patagonicus (MACN, catalogne number unaveitable): B, Promegatheriwn nanam (MACN 4992); C, Eremotherivm minabite (ROM 22008; D, Pyamiodontherium bergi (MIP 2-60; E, Ptonops martini (after Hoffitewer, 1961:fit. 12B). Fiqures 6B, E art reversed diequmatically from ociginal left astrualii. Scale ber equals 2 cmi . Abbevintions as in Figure 4.
external, or dorsolateral, trochamter is straight-sided (or nearly so) in mylodontids (although this is not always true it is curved in Glossotherium harlani, AMNH 16896, and semicircular in megatheriines (Fis 7) Some qualifications must, however, benoted. The dorsolnteral trochanter is abso semicircalar in Nohirouneriopss It is similar in Promothrohierium (FMNII P15223) and curved (somewhat intermediate between stright-sided and semicircular, C. Cartelies pers.
comm. 1993) in Nothrotherium. The trochanter is struight-sided in planopsines and in tardigrades lecking an odontoid process, such as megalonychids and other nothrotheriines in which the astraghtus is known. It is tempring to consider the stright-fided dorsolateral trochanter as plesiomophic, especially as it is present in Hapalops, which has long been considered to occupy a central and morpholorically ancestal position among tardigrades. White such a position for Hapalops is not

 after Frailey, 1986:tig, 5B); B, Enemotherium mirabile (ROM 22008). Scale bar equals 4 cm . Abbreviations as in Figure 4.
established, the plesiomorphy of the straight-sided dorsolateral trochanter seems well-established, as it is the condition present in the tardigrade outgroups Myrmecophagidse(Myrmecophaga, ROM(DM)15301, and Tamandua, ROM (DM)95210) and Cingulata (Dasypodidae: Dasypus ROM R2386; Pampatheriinac, sensp Hofstetter, 1958: Chlamytherium, UF 9336, and Holmesina, UF 20947; Glyptodontidae: Selerocalyptus, ROM 408, and Faplophractus, see Cabrera, 1939a: fie 7A). The condition in Bradypus and Choloepus is markedly different from other sloths and xenarthrans, and is almost certhinly derived. The trochanter is concave, more so in Bradypus (see Lessertisseur and Sabem, 1967:fic. 689B) than in Choloepus (ROM R775, ROM R2296), due to the concave fibular fincet of the astragnlus for articulation with the odontoid process of the distal end of the fibula (see Lessertisseur and Saben, 1967:ifig 680). If thesegenera belong to different fimities, as seems probable (see Patterson et al., 1992; Webb, 1985), the condition of the dorsolateral trochanter was derived independently in Bradypus and Choloepus. The semicircular condition was probably derived independentily in megatheriinet, Nothrotheriops, and Pronothrohicrivm, as the monophyiy of nothrotheres appears sufficiently corroborated or other evidence (see following section). It is worth noting here that the occurrence of such homoplasies (ee, the distance between the ectal and tibial surficer; morphology of the donsolateral trochanter) is common among sloths and attests to the mosaicity alloded to in the introduction. Numerous other exomples may be cited, amons which ares the projection and orientation of the odontoid process; the shape of the astragalar cuboid fuces, which is uspally convex in siofiss (a concave ficet is commonly considered a specintized feature of roetidotheres, which poseses an odontoid process, but is present in Acratocmess (AMMNH 17716u), which bects an odontoid process, and in "Ocnopess grocitis" and Chubveheritum ferrollois, the presence of an entepicondylar formmen of the humerus the presence of inflated
pterygoids; position and morphology of the notch for the round ligament on the head of the humerus. These conflicts are not introduced here to dispute any particular classification, but because such examples serve perhaps as a signal that characters traditionally used to differentiate among sloths should be reviewed carefully.

## Postion of Posterior Extermal <br> Openitag of the Mandiliblar Canal

Engelmann (1985) considered a medial position of the posterior external opening of the mandibular canal, or a tendency for it to be located medially, to be a second synapomorphy for the Nothrotherium-megathere group. Before continuing, it is worth clarifying what is the intended meaning of the phrase "a tendency to be located medially." Engeimann is referring to the relatively more medial position of the foramen in Megatheriinae, or pertaps to its uspal position of being somewhat medial to the lateral margin of the coronoid process, but the foramen is never located on the medial surfece of the dentary. Instead, the foramen lies on the dorsal surfice of the mandibular ramus. However, such a position for the opening has not, to my knowledge, been reported for Nothrotherium, in which the foramen clearly lies on the lateral surfice of the dentary (Fig. 8A; Cartelle and Fonsecta, 1983). In Megatherium, Eremotherium (Fig 8B), and Pyramiodomherium the focamen lies between the coronoid process and m4, clearly medial to the lateral edge of the coronoid process. In some specimens the position of the foramen closely appromciess the anterior edge of the bese of the coronoid process. In Promegutherium (MACN 4995) the foramen lies on the medial sarfice of the base of the coronoid process, but it partially visible in lateral view. In Megathericulus patagonicus, certuinly a mesatheriine, the position of the formmen was recently discovered (Scillato-Yané et al, 1993), it lies precisely at the anterior edpe of the bese of the coronoid process.

Srock (1925) and Akersten and McDonald (1991)


FIGURE8. Lateral view of the left dentary (let diagran) and occhasal view of the dentry (rinht dingrum) of A, Nolhrotherium

 mandibular condyles pe-posterior extemal opening of the mandibular camal
reported that the posterior external opening of the mandibular canal is ofter represented by one or two opemings in Nothrotheriops. Varions left or right dentaries demonstrate that the presence of a double foramen is a common occurrence (UF 85984, 84626, 64348, 64352), a single leteral formmen occurs in UF 86121 and 86893. Theright dentary of UF86899 bears a double foramer; itsleft bears a sinjle lateral foramen. The considerably larger and anterior opening Fes on the lateral surface of the dentary, as in Nofisolicrium.

The posterior foramen lies nearily at the amterior edge of the base of the coronoid process, and thus cannot be described properity as lying on the dentary's lateral surfice. The posterior for roment in the mandible figured by Stock (1925:pl. 4, fig. 2) Fies on the lateral surface of the process. A single for amen is present at the base of the coronoid process in the specimen described by Akersten and McDonald (1991:fig- I); its position is simitar to that in Megathericutus, but somewhat more Interal. In Nothrophas (see Burmeister, 1882-pl. 11;

Frailey, 1986:fig 31A) and Pronothrotherium (FMNH P14350, FMNH P14445) the foramen lies on the lateral surface of the dentary, as in Nothrotherium.
The position of the foramen in Megathericulus patagonicus strengthens the argument that a tendency for the foramen to be located medially is a similarity of Nothrotheriops (not Nothrotherium) and the Megatheriinae. However, the following considerations should be noted. Two openings were also reported for the left dentary of the type of Hapalops longiceps by Stock (1925) and Scott (1903-1904), who considered this condition abnormal (one foramen is present in $H$. elongatus, Fig. 8C). The foramen is near the base of the coronoid process in Hapalops grandaevus and $H$. rectangularis, although it faces largely laterally. If the synapomorphic character is a tendency or trend for a medial position of the foramen, then Hapalops (or at least some of its species) should be included within the group, because it demonstrates the potential for the trend. Also, the Plio-Pleistocene nothrotheres very probably form a monophyletic group, atthough the relationships among them are still unsettled (see Frailey, 1986; Paula Couto, 1971, 1979). Thus, a reversal of the trend for medial location of the foramen must be postulated for Nothrotherium, Nothropus, and Pronothrotherium.
Alternatively, it is possible that the position of the foramen in Nothrotheriops and F. longiceps is highly plastic, which would limit its usefulness as a synapomorphy. Although morphoclines and trends within a group have been considered valid for use as synapomorphies (Crisci and Stwessy, 1980), it appears preferable that the monophyly of the group (i.e., the Megatheriinae, Nothrotherium, Nothrotheriops, Nothropus, Pronothrotherium, and H. longiceps) first be established on the basis of synapomorphies discovered through outgroup comparison, as discussed by Maddison et al. (1984).
In Planopainae, Planops (FMNH P13148) and Prepotherium (see Scott, 1903-1904.pl. 59, fig. 2; pl. 60, fig. 1), the formen lies on the lateral surface of the dentary, as in Nothrotherixm. As there is evidence that the Planopsinae are megatheriids, such a position for the foramen in planopsines casts further doubt on the suitability of the position of the formmen as a synapomorphy between megatherines and nothrotherines.

## Relationalitp Between the <br> Planopinac and Mequthertinae

The relationship between the Megatheriinae and Planopsinae should be considered, as it may be relevant to the resolution of this problem. The long held view of the close affinity between these two groups is reflected by the traditional inclusion of the planopsines within the Megatheridae. Hofistetter's (1961) hesithtion in formally recognizing their affinity may have been inffuenced by Cabreva's (19396) assertion that Megathericutus primaevus, recovered from exposures near Paso Flores, Neuquén Province, Argentina, was
a Santacrucian representative of the Megatheriinae, thus excluding the Planopsinae from the ancestry of the Megatheriinae. However, more recent opinion regards the Paso Flores exposures as Colloncurense (Pascual et al., 1978), which is later than the Santacrucian (see Marshall and Salinas, 1990; Marshall and Sempéré, 1991). Further, no skull material of this species is known and its identification as a megatheriine, while probable, is not certain.

The relative reduction of the process of the posteromedial surface of the tibia, which McDonald (1987) and Webb (1989) state is for the long digital fiexors, is a character that possibly may indicate a close association of the planopsines and megatheriines. This process is relatively reduced in Megathericulus patagonicus (Scillato-Yané et al, 1993), as it is in Planops (Hofistetter, 1961:fig. 11) and Prepotherium (Scott, 1903-1904;pl. 51, fig. 2A) as compared to Hapalops (Scott, 1903-1904.pl. 33, fig. 3A), Nothrotheriops (see Stock, 1925:pl. 14, fig. 1B), and Nothrotherium (see Reinhardt, 1878:pL 4, fig. 7). The process in Megathericulus patagonicus and M. primaevus is similar in relative size to that of Planops and, in particular, Prepotherium, and is reduced to a ridge in later Megatheriinae. The process is prominent in all other Santacrucian genera, except Pelecyodon, in which it is absent. It is reduced in Plio-Pleistocene mylodontids, but never to the degree seen in the Plio-Pleistocene Megatheriinae.

The problem with using reduction of the tibial process as a synapomorphy is that, as with the position of the posterior external opening of the mandibular canal discussed above, reliance is placed on a trend. Stronger support for close affinity between planopsines and megatherines may be provided by the astragalus. Descriptions and figures of the astragali of Planops and Prepotherium by Scott (1903-1904) and Hofistetter (1961) indicatecloser morphological similarity of these genera to Megatherium and Eremotherium than to the nothrotheres, especially in the shape of the odontoid process and the region anterior to it, bearing the navicular articular surface. However, the polarity for these characters has not been established.

Frailey (1988:9-10) believed that the planopsines clearly belong within the Megatheriidae, stating that they "foreshadow the features of Megatherium in shape of skull, mandible, and astragalus," but did not document these resemblances. The skull features do not, in my opimion, foreshadow those of Megatherivm any more than do various other Santacrucian sloths, particularly the Friasian mylodontid Pseudoprepotherium (see Firischfeld, 1985:fig. 1A). As for the resemblances in the mandible, I suspect that Frailey based his interpretation on the mandible of Prepotherium moyani, described and figured by Scott (1903-1904:331; pl. 60, fig. 1), who emphesized the "very great vertical depth of the hocizontal ramus in the dentary region, with extremely convex ventral border, which rises steeply behind and becomes concave below the ascending ra-
mus." It is true that the ventral border of the mandible is strongly convex, but the specimen described by Scott is very incomplete, preserving only the middle portion of the ramus, and its appearance may be deceptive. The more complete mandible of Prepotherium filholi (Scott, 1903-1904.pl. 59, fig. 2) is comparable to other Santacrucian sloths in this respect. On the other hand, a nearly complete dentary of Planops (FMNH P13148) has a prominently convex ventral margin. In any event, the significance of depth of the mandible in Santacrucian sloths is not well understood (but see below) and may be exaggerated. The ratio, for example, between the length over $\mathrm{m} 2-\mathrm{m} 4$ and the depth of the mandible is 1.37 in Prepotherium moyani and 1.29 in P. filholi. but 1.6 in Eucholoeops ingens (Scott, 1903-1904.pl. 58, fig. 2).
The greater size of planopsines compared to contemporaneous tardigrades may be a valid synapomorphy of Planopsinae and Megatheriinae, though other Miocene sloths, such as Pseudoprepotherium and the Hu ayquarian Acremylodon, approached the size of the Friasian Megathericulus, the smallest known megatheriine. However, Pseudoprepotherium and Acremylodon clearly share a closer relationship with mylodontids (Hirschfeld, 1985; Frailey, 1986).
Work in progress by T. J. Gaudin (pers. comm., 1992) on the auditory region of pilosans suggests that the inclasion of planopsines in the Megatheriidae is wealdy supported. Gaudin has found no evidence supporting a particularly close association between nothrotheres and megatheriines.

## SUMMMARY AND CONCIUSIONS

Engetmann (1985) considered the Nothrotheriinae and Megatheriinae to be a monophyletic group based on their clongate and slender premaxillae. Within this group, the Megatheriidae, he grouped together Nothrotherium, Eremotherium, and Megatherium, based on the tendency of the posterior external opening of the mandibular canal to be positioned medially, and the common presence of an odontoid tibial articulation of the astragitus. However, there is litule evidence to support a close retationship of Hapalops to nothrotheres, and, through them, the megatheriunes.
The premaxillace of many nothrotheres and Megatherium are similar in being elongate and bearing an anteriorty projecting process, but are structurally distinct. In the former group the premaxilla is $Y$-shaped and bears a slender, tapering anterior process, whereas in Megatherium the premaxilla is quadrangular, robost, and bears a robust process. In Eremotherium, the sister genus to Megatherium, the premaxilla is a triangular, V-shaped structure. These characters are shared among scelidotheres, various other sloths (though in these the premaxille is anteroposterioniy shortened), and sloth outproups. The triangular, V-shaped premaxilla is therefore probably plesiomorphic. The structural similarities of the premacilla of nothrotheres and Megatherium are probably independently derived.
A close relationship between Santacrucion and PlioPleistocenenothrothereshas often been postulited, but
based on plesiomorphic characters (Frailey, 1986, 1988). However, the premaxillae (where known) of Plio-Pleistocene and some Santacrucian nothrotheres provide support for a monophyletic grouping of Hapalops, Eucholoepus, and the Plio-Picistocene nothrotheres. The premaxillae of these taxa share a slender and tapering anterior process at the junction of the medial and lateral rami, and the lateral margins of the premaxilla are strongly concave.
A sister-group relationship for nothrotheres and megatherines, based only on the common presence of an odontoid process of the astragalus, is improbable for two reasons. First, the odontoid is present among mylodonts. Second, the criterion of reduced separation between the ectal and tibial articular surfaces, used by Engelmann (1985) to distinguish between the Noth-rotherium-megathere and mylodontid groups, is not valid. The separation in the astragali of nothrotheres and megatheriines is similar to that in various mylodont genera. The distances between these surfaces is considerably greater in only some mylodonts, such as Glossotherium and Lestodon.
A more consistent distinguishing criterion for the mylodontid and megatherime type astragali is that the dorsolateral trochanter is approximately straight-sided in the former, and semicircular in the latter. The straight condition is present in most other sloths, regardless of the presence of an odontoid process, and probably represents the plesiomorphic condition. The semicircular extemal trochanter of Nothrotheriops and, possibly, Pronothrotherium is probably independently derived from that of megatheriines, as the monophyly of at least the Plio-Pleistocene nothrotheres seems sufficiently established, and other nothrotheres lack a semicircular external trochanter.

A trend toward a medial position for the posterior external opening of the mandibular canal is not a convincing symapomorphy of a Nothrotherium-megathere group. The formmen is medial to the lateral surface of the coronoid process in all megatheres in which it is preserved, except for Megothericulus, the eartiest megatheriine, in which the foramen lies on the anterior edge of the base of the coronoid process and is partially visible in lateral view. The foramen lies on the lateral surface of the dentary, somewhat ventral to the base of the coronoid process, in Nothrotheriam and Nothropus. Two openings may represent the foramen in Nothrotheriops: One lies on the lateral surface of the dentary, as in Nothrohierium, and the other near the base of the coronoid process. A single foramen is present in one specimen, but lies somewhat more laterally than in Megothericutius. Two openings are reported for the left dentary of Hapalops longiceps. The position of the foramen is variable in Hapalops, but usually lies on the lateral surfice of the dentary.
If a trend toward a medial position of the foramen is to beconsidered symapomorphic for the nothrotheremepotheriine group, then Hapalops, or at least some of its species, should be inchuded in that gromp, because they express the potemtial for the trend, and reversils mest be postulated for Notinotherium and Nohiropus.

It is probably best to consider this character as variable or plastic, thus limiting its phylogenetic importance.

An astragalar odontoid process occurs in mylodontids, megatheriines, planopsines, Nothrotherium, Nothrotheriops, and Pronothrotherium. While considerable effort has been devoted in the literature toward demonstrating the differences between mylodontid and megatheriine astragali, it is curious that the great resemblances between them are rarely considered. This is due to the long held view that the odontoid process evolved convergently and independently in thesegroups of sloths, an assumption that may indeed be the best explanation for the distribution of this character in light of the current interpretation of other morphological evidence. However, it may be worthwhile to consider the alternate hypothesis: that the odontoid process is a shared derived character for mylodontids and megatheriines. I do not propose this formally, as the weight of evidence seems to be against it, although this conclusion is partly due to the current and equivocal interpretations of other characters.
One objection, certain to arise, to this hypothesis is the apparent specialization of the dentition of mylodontids and megatheriines, as opposed to the simpler oval or subcircular dentition of Megalonychidae. Because megalonychids are commonly interpreted as a basal group among sloths (Engelmann, 1987), their dentition is assumed to represent the primitive condition; and, in a circular argument, megalonychids are considered a basal group largely because of their early stratigraphic age and simplified dentition, which is superficially similar to the peg-shaped teeth of armadillos. The structure of the dentition in sloths was commonly viewed as a retention of the simplified dentition of the most primitive myrmecophagids, from which sloths were presumed to have descended. The teeth of these eariest (and unknown) myrmecophagids were, in tum, thought to have been inherited from primitive dasypodids (see Winge, 1941:354-55, 359-60).

However, Engelmamn (1987) suggested, primarily on the basis of Pseudoglyptodon sallaense, that some type of lobation is the primitive condition among sloths, and be pointed out that lobation among sloths is not confined to mylodontids. The important character transformation for the dentition of sloths may be a dififerential loss of lobation, with the somewhat lobate teeth of megatherines and the near absence of lobation in megalonychids as extreme examples of its loss.

Other characters used in sloth phylogeny should be reconsidered in light of these possibilities. For example, a deep mandibolar ramus with a convex ventral border appears to be primitive for slotis, again based on the presence of these character states in Pseudoghyptodon. The shallower ramus with approximately linear ventral border, common in myiodontids, may be viewed as derived. Megalonychids and megntheriines retain these primitive states to varying deprees. The shape of the ventral border of Octomylodon robertoscagifiai is more similar to that of the Orophodontidae and Megatheroidea (Scillato-Yane, 1977). The preceding sugestions involving Pseudoglyptodon rest on the
assumption that Pseudoglyptodon is the sister genus (group) to all other sloths. While this assumption is not firmly established, it is based on the carly stratigraphic position of Pseudogtyptodon and the loss of trilobation of the cheek teeth in other sloths.

The phylogenetic relationships among the planopsines, nothrotheriines, and megatheriines are poorly understood. The weight of evidence, though weak, apparently favors a sister-group relationship between planopsines and megatheriines. These subfamilies may be considered for the present as the only taxa within the Megatheriidae. A sister-group relationship is based on similarity of size, aspects of the astragalus, and possibly of the auditory region, and reduction in the tibial process for the long digital flexors. Compelling evidence to support a relationship between nothrotheriines and megatheriines or nothrotheriines and planopsines is lacking. The relationships among nothrotheriines, megatheriines, and other pilosan groups cannot be resolved based on present interpretations of known morphological evidence.

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# THE MEDIAL CARPAL AND METACARPAL ELEMENTS OF EREMOTHERIUM AND MEGATHERIUM (XENARTHRA: MAMMALIA) 

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#### Abstract

Anatomical comparisons suggest that the medial element of the proximal carpal row of Eremotherium and Megatherium is a scaphoid, homologous with that of other Tardigrada, and not a scapho-traperium. The medial process of the scaphoid overhangs the distal carpal row in all sloths. The metacarpal-carpal complex (MCC) is composed of fused elements present medially in the manus of many Tardigrada. In most genera the MCC is a small nodular element incorporating the trapecium and metacarpal I (Mc I). Comparisons of the MCCs of Megatherium and Eremotherium with other sloths suggest that the MCC of Megatherium comprises the trapezium and Me I, and that of Eremotherium the reduced Mc II, Mc I. trapezium, and trapezoid. The morphological similarity of the MCC in the three large size Eremotherium species (E. Laurillardiz, E. mirabile, and E. rusconii) currently recognized in the literature is evidence that species are conspecific.


## INTRODUCTION

The skeletal structures of the manus vary widely among tardigrade species in arrangement, morphology, fusion, and reduction of elements. Generally, the homology of most of these elements is clearly evident. However, the homology of the medial carpal and metacarpal elements in Eremotherium and, to a lesser extent, Megatherium is not as straightforward, and various interpretations have been proposed.

The medial element of the proximal carpal row has been identified alternatively as a scaphoid or scaphotrapezium (reflecting the supposed fusion of the scaphoid and trapezium) in the literature. These designations have determined the identification of the medial element in the distal carpal row as either a co-ossified Mc I and trapezium or a McI, respectively. More extensive fusion of the medial carpal and metacarpal elements in Eremotherium has generated further confusion.

The purpose of this paper is to describe the medial carpal and metacarpal elements in Eremotherium and Megatherium and to establish their homology. A review of the literature and anatomical comparison suggest that the medial element of the proximal carpal row in Megatherium and Eremotherium is homologous with the scaphoid of other Tardigrada. The medial part of the manus of these two genera contains a complex of fused skeletal elements. That of Megatherium is relatively small and incorporates the trapezium and Mc I. The complex in Eremotherium is larger and incorporates a reduced McII, McI, traperium, and trapezoid. We propose that this complex be termed the metacarpal-carpal complex, abbreviated MCC. The more euphonius carpal-metacarpal complex was considered but rejected due to a possibility of a confusion
with the carpometacarpus of Aves. The usefulness of this term may not be readily apparent, given that extensive fusion of the elements is known only in the larger Eremotherium species ( $E$. laurillardi-mirabilerusconii, see below). However, the recently discovered Eremotherium remains from the late Pliccene of Forida (Hulbert et al., 1989) suggests a new species, of which the manus presents two variations of an MCC morphology distinct from each other and from the species discussed here. Furthermore, the term may be applied to the fused Mc I and trapezium of other sloths, and we do so here, though the phrase co-ossified Mc I and traperium is also sufficiently convenient when only these two elements compose the complex.

## ABBREVIATIONS

DMAS-Daytona Beach Museum of Arts and Sciences, Daytona Beach, U.S.A.; EPN-Escuela Politecnica Nacional, Quito, Ecuador; FMNH-Field Museum of Natural Eistory, Chicago, U.S.A.; MCLMuseu de Ciéncias Naturais da Pontificia Universidade Católica de Minas Gerais, Belo Horizonte, Brasil; MLP-Museo de La Plata, La Plata, Argentina; MNHNC-Museo Nacional de Historia Natural de Chile, Santiago, Chile; MNP-Museo Nacional de Panama, Panama City, Panama; ROM-Royal Ontario Museum, Toronto, Canada; UF-Florida Museum of Natural History, University of Florida, Gainesville.

## MANUS OF MEGATHERIUM

A brief review of the structure of the manus of Megatherium americamum ( $\mathrm{Fig}_{\mathrm{g}}$ IA) is given for reference


FIGURE 1. Dorsal view of the right manus of A, Megatherium americanum (redrawn from Owen, 1858.pL. 22), and B, Eremotherium laurillardi (MCL 9487; Toca das Onças, Bahia, Brazil; Pleistocenc-subRecent); cun-cuneiform, Iun-lunar, mag-magnum, mec-metacarpal-carpal complex; meII-metacarpal 2; meIII-metacarpal 3; sc-scaphoid; td-trapezoid; unc-unciform.
and orientation. Owen (1858), Schulthess (1920) and Cabrera (1929) described and discussed the manus of Megatherium, and Hofftetter (1952), Gazin (1957), and Cartelle and Bohórquez (1982) described that of Eremotherium.
The proximal carpal row in the manus of Megatherium consists of cunciform, lunar, and scaphoid, from lateral to medial positions; the pisiform articulates lateroventrally with the cuneiform. The distal row contains in analogous order the unciform, magnum, and trapezoid. Mcs II-V, of which Mcs IH-IV bear unguals, are present; Mc V bears only two reduced phalanges, proximal and distal. The MCC is a relatively small, nodular element formed from the trapezium and Mc L. It articulates laterally with the trapezoid and Mc II, and proximally with the distomedial surface of the scaphoid. A palmar sesamoid is present.
The proximal carpal row, pisiform, palmar sesamoid, Mc V, and the phalanges in the manus of E. tourrillardi-mirabile-rusconiz (Figs 1B, 2) are approximately as in Megutherium. The distal carpal row inclodes the unciform, magnum, and MCC. Mcs III-V are present, of which Mes III-IV bear unguals.

## Scaphoid and Co-ossified Mc I and Trapecium in Mcentierian

Owen (1858) identified the medial element of the proximal carpal row as a scapho-trapezium. He described it as triangular, with its base articulating laterally with the funar and its apex forming a dorsopalmarly twisted process. He considered this process, which extends medially from the articular surface for the trapezoid, as the trapezium. Owen's(1858) opinion was based on the then current assumption (e-g, Cuvier, 1823; Owen, 1866; and Gervais, 1877), that the trapezium and scaphoid were co-ossified in Bradypus and Choloepus. In contrast, Lund (1842), followed by Ameghino (1889) and Winge (1915), suspected that the traperium was fused to Mc I (Cabrera, 1929).

The independent research of Humphry (1870) and Flower (1873; see also 1885), corroborated by Menegaux (1908; 1909a, b) and Poche (1908, 1911), showed that the trapezium was probably fused to Mc I rather than to the scaphoid. This was based on three partly coalesced skeletal elements medial to Mc II and distal to the scaphoid, interpreted by Flower (1873) as the


FIGURE 2. Exploded dorsal view of right manus of Eremotherinat laurillardi (MCL 9464; Toca das Oncas, Bahia, Brazil; Fieistocene-subrecent); cun-cunciform; dp-distal phalanx; lun-lunar; mag-magnum; mec-metacarpal-carpal complex; meIII-metacarpal 3 ; meIV-metacarpal 4; meV-metacarpal $5 ; \mathrm{mp}$-middlephalanx; $\mathrm{p}+$ mp-proximal + middle phalanges; pi-pisiform; pp-proximal phalanx; ps-palmar sesamoid, se-scaphoid; unc-unciform; up-ungual phalanx.
trapecium, proximal epiphysis, and diaphysis of McL, in juvenile specimens of Choloepus. The homology of the scaphoid to that of other sloths was based on morphological similarity and on the lack of evidence for a seperate center of ossification for its medial process. Menegarux (1909b) stated that the process possibly represented a sesamoid, noted by Schiosser (1890) as present between the scaphoid and trapezium in some mammals. Cabrera (1929) admitted this possibility, but concluded correctly that the presence of such an element could not be determined in Megatherium.

In Bradypus the trapezium also fuses with Mc I, but the latter also fuses proximally with Mc II. The trapezoid, however, fuses with the magnum (Anthony, 1909; Schulthess, 1920; Ursing, 1932).

The most reliable method of determining homology is observation of the ontogenetic development of structures. If ontogenetic information is unavailable, inferences on the homology of skeletal structures or parts thereof in one species may be drawn through detailed comparisons of morphology and the association of musculature and skeletal structures in a closely related species for which the ontogeny is known. However, these methods can be applied infrequently with vertebrate fossils and reliance on other methods is required. These include morphotogical similarity, arrangement of articular surfaces, and relationship to other skeletal structures for which the homology is clearly evident.

The morphology of the scaphoid of Megatherium is
similar to that of other sloths. The scaphoid's medial process is a constant character in all sloths, regardless of whether the trapezium is fused to McI (as described above) or is present as a separate element (as in Hapalops). It is highly probable, then, as was realized by Cabrera (1929), followed by Hoffstetter (1952), that the medial process in the scaphoid of Megatherium is not a trapezium, but results from normal development of the scaphoid. Schulthess (1920) was aware that the process is typical for sloths and that the trapezium is co-ossified with Mc I in extant sloths, but followed Owen (1858) in regarding a scapho-trapezium as present in Megatherium.

The trapezium is not present as an independent element in known specimens of Megatherium, and is probably co-ossified with Mc I. The evidence to support this hypothesis is less reliable than that supporting the homology of the scaphoid. It is largely circumstantial and may be used to support fusion of the trapezium and Mc I to form an MCC in Megatherium, but may be insufficient to establish homology with the MCC of non-megatheriid tardigrades. Cabrera (1929), followed by Hoffstetter (1952), reasoned that the trapezium and Mc I, rather than only Mc I, were present in the skeletal element articulating distally with the medial part of the scaphoid, because Cabrera considered articulation between the trapezoid and Mc I improbable, indeed, this does not occur in other xenarthrans and only exceptionally in other mammals. The occasional existence of separated Mc I and trapezium in Nothrotheriops and Glossotherium (Stock, 1925) provides further evidence for the probable fusion of these elements in Megatherium. Co-ossification of the trapezium and Mc I into an MCC is widely recognized as the common or normal condition in post-Santacrucian sloths, eg, as in mylodontids (Stock, 1925; Cartelle, 1980; Webb, 1989), Bradypus tridactylus (Schulthess, 1920), Nothrotheriops (Stock, 1925) and Nothrotherium (Cartelle and Fonseca, 1983). However, a wide range of morphological variation exists among the MCCs of these taxa, and fusion of the traperium and Mc I may not be homologouss i.e, they may represent independently derived fusions.
In summary, it is reasonable to suppose that the Mc I and trapezium are fused into an MOC in tardigrades unless an independent traperium is present, as in Ha palops and Schismotherium; this does not necessarily indicate that the MCC of all tardigrades is homologous. It is probable, however, that the scaphoid is homologous in all Tardigrada.

## THE MEDIAL SKELETAL ELEMENTS OF THE CARPUS AND METACARPUS OF EREMOTHERIUM

Eremotherium and its sister-penus Megatherium (Englemann, 1985) are morphologically similar, but may be distinguished primarily by differences in the skull and, possibly, the manus. As currently understood, Eremotherium comprises large and medium
sized megatherines, but the genus and its species are in need of review.

The manus of the medium sized species E. elenense (Hoffstetuer 1949) is incompletely known. The few remains described by Hoffstetter (1952), among them a complete Mc II, demonstrate that the manus of $E$. elenense is more similar to that of Megatherium than to that of the larger Eremotherium species. The manus of the latter was incompletely known to Hoffstetter and believed by him to be as in Megatherium. He did not state this, but his assumption is revealed by allusion to an absent trapezoid. Hoffstetter (1952) reported only skull fragments of $E$. elenense and he thus referred the smaller megathere remains from Ecuador to Eremotherium primarily on the presence in the same locality of larger and undoubted Eremotherium remains, which he assigned to $E$. carolinense.

Hoffstetter (1952) expressed reservation in erecting the species E. elenense and in allocating it to Eremotherium, but was satisfied that adult remains $70 \%$ the size of those he assigned to $E$. carolinense represented a distinct species, and that the few remains available indicated a closer relationship to Eremotherium than Megatherium. However, more complete material of the larger species subsequently recovered and described by Gazin (1957) and Cartelle and Bohórquez (1982) show that this may be incorrect. At present, the smaller megatheriid remains from Ecuador cannot be assigned with confidence to either genus. It may represent a small species of $M$ egatherium, such as $M$. lundi or M. medinae, or a species of Eremotherium with a primitive hand structure, a supposition rendered piausible by the discovery of an Eremotherium in the Blancan and Irvingtonian of Florida possessing a manus bearing unguals on digits I-IV (Hulbert et al., 1989). The validity of $E$. elenense being uncertain, it is not considered further in this discussion.
The following three species are recognized currently in the literature for the large Eremotherium remains: E. laurillardi, E. mirabile, and E. rusconii. However, there is evidence sussesting that they are conspecific, including the morphology of the MCC (see below); the valid name of this species is E. mirabile (Cartelle and De Iuliis, in progress).
The manus of $E$. laurillardi-mirabile-rusconii was known initially through the discovery of associated skeletons of E. rusconii from El Hatillo, Pamama, described by Gazin (1957). The manus differs from that of Megotherium in that only Mc III-V are completely developed, and the MCC, present medially, articulates with the scaphoid proximally, the magnum lateroproximally, and Mc III laterally (Figs. 1B, 2). Gazin (1957) interpreted the MCC as representing a reduced Mc II fused with the trapezoid and Mc L. Further, he considered that the pollex was represented by a reduced Mc L, as had Owen (1858), and thus implied that the trapezium was fused with the scaphoid to form a sca-pho-traperium. Cartelle and Bohórquez (1982) correctly included the trapezium within the MCC, but improperty considered the trapezoid and magnum to


FIGURE 3. Distolateral view of right scaphoid (reversed diagramatically from original left) of Megatherium americanum (MIP 2-29; near Mar del Plata, Buenos Aires, Argentina; Pleistocene), showing articular surfaces for other manual elements; dorsal surface towards top of page, medial towards right; lun-lunar; mag-magnum; mee-metacar-pal-carpal complex; td-trapezoid.
be co-ossified. The MCCs allocated to E. mirabile (ROM and DMAS specimens) are indistinguishable from those of $E$. rusconii and $E$. laurillardi. The morphological similarity of the MCC provides support (though it is one among various pieces of evidence) for the synonomy of the latter two with $E$. mirabile, and is a diagnostic element of this species.
We show below that the scaphoids of Eremotherium and Megatherium are homologous, based primarily on morphological similarity, and that the MCC includes reduced Mc II, Mc I, trapezium, and trapezoid, based primarily on similarity in morphology and arrangements of articular facets and relationship to adjacent skeletal elements.

## Scaphoid

The scaphoids of Eremotherium and Megatherium are described in detail becanse this has not been done in the fiterature, and will facilitate the detailed comparisons required to establish homology of the scaphoids. Furthermore, the position, arrangement, and shape of the scaphoids' articular surfaces are helpful in the identification of those elements incorporated into the MCC that articulates with the scaphoid.
The scaphoids of Eremotherium and Megatherium are very similar morphologically. Considerable variation exists within either gemus in shape, orientation, and position of articular facets. The scaphoid is roughly triangular in proximal and distal view, with baselateral and with convex dorsal and concave palmar margins. The apex projects medially and is twisted distopalmarly (Fis 4A, C).
The proximal surface bears, except medially, a large, convex facet for the medial half of the distal articular
surface of the radius. The proximal surface of the apex is non-articular and is covered by roughened bone.

The proximal part of the scaphoid's lateral surface articulates laterally with the lunar principally along a smooth, variably sigmoidal and palmarly narrowed facet. The lunar and scaphoid may make further contact by way of two accessory facets further distally, cach of which is contiguous with the lateral margins of the two facets for the magnum. The accessory facets are typically rather small, sometimes inconspicuous or absent, and crescentic, triangular, or trapezoidal (Fig. 4B).

The two facets for the magnum are arranged in dorsopalmar sequence with surfaces proximally convergent on approximately the lateral third of the scaphoid's distal surface (Fig. 4B, C). They are variabie and complex in shape and orientation. Generally the larger the dorsal facet ranges in shape from approximately oval to triangular, and from condylar and pedestalled to nearly flat. The palmar facet is usually oval and may range from flat to slightly convex. The facets may be connected exceptionally by a bony bridge, but they are commonly separated by a deep, narrow groove that expands laterally into a broad, shallow, and perforated surface that separates the principal lumar facet from the accessory lunar facets. Owen (1858) stated that the dorsal part of the principal lunar articular facet is continuous with the dorsal facet for the magnum. There does appear to be a tendency for close approximation of these facets in some specimens, but those that we have examined are consistently separated by at least a narrow tract of roughened bone (e.g., MLP 44-XII-28-1).

The medial margin of the dorsal facet for the magnum is contiguous mediopalmarly with the approximately oval and transversely concave articular surface for the trapezoid in Megatherium, and the proximolateral part of the MCC in Eremotherium (Figs. 3, 4C). The shapes, orientations, and positions of the trapezoid facet are remarkably similar in these genera. In Eremotherium it is commonly contiguous medially with an elongate facet, curved in accordance with the apex of the scaphoid, for the distomedial part of the MCC (Figs. 3, 4C). These facets may be contiguous in Megatherium, as in FMNH P14530 and FMNH P14216, in which case the facet for the MCC (incorporating the traperium and Mc D resembles that for the medial part of the MCC of Eremotherium. However, the facet for the MCC may be isolated in either genus, separated by a variable distance from the facet for the trapezoid (Megatherium) or proximolateral part of the MCC (Eremotherium). The isolated facet may range from elliptical (MNHNC 14) to nearly oval (EPN V. 1001).

## Metacarpal-carpal Complex

The MCC in Megatherium may be nodular, as fisured by Owen (1858.pl 22; see also FMNH P14216, Fig. 5), or mediolaterally expanded, as in FMNH P14530. Its proximal surface conforms to the me-


FIGURE 4. Right scaphoid of Eremotherivan mirabile (ROM 37050: Daytona Beach Bone Bed; Floridas Pleistocene), showing articular surfices for other manual elements. A, proximomedilil view (dorsal towards top; medial towneds left), B, Interal view (proximal towards top; dorsill towards right), C, distolateral view (dorsal towards top; medial towards right), Iun-lunar, mag-magnum; moc-metacarpalcarpal compler, rad-radius.
diodistal orientation of the apex of the scaphoid, for which it bears an articular surface. The facet mirrors the shape of the facet on the scaphoide it may be an isolated oval or ellipse, or an elongate articular surface, contignous (Fig. 5A) with the articular surfice for the trapezoid and Mc II on the lateral surface of the MCC. Some confusion regarding the articular surfice on the MCC is introduced by Owen (1858:270), who described "two sepmate subcircular flat surfices articuFting wint the corresponding facets on the traperial
part of the scapho-trapezium." He (1858:268-269) contradicted this, however, stating that the trapezial part of the scapho-trapezium "articulates with the stunted metacarpal of the pollex .... chiefly by ligament, but also by a small elliptical flat surface."
The articular surface borne on the lateral surface of the MCC is convex. A small proximal part articulates with the trapezoid, the rest with Mc II (Fig. 5B).
The MCC of Eremotherium is larger and more complexly shaped (Fig. 6). It is somewhat wedge-shaped in dorsal view, tapering medially, and in proper position lies with long axis oriented from proximolaterally to distomedially, such that the facet for Mc III faces nearly laterally. The elements that form the MCC cannot be discerned individually because they are greatly reduced, though some specimens do bear scarlines that might be interpreted as planes of fusion.
The facet of the MCC for Mc III (Fig. 6A, B) resembles that on Mc II of Megatherium. It varies in shape, but is longer dorsomedially than proximodistally, and partially divided into large dorsal and smaller ventral parts by a notched distal margin. The palmar part is


FIGURES. Left MCC of Mcgatierium sp. (FMNH 14216; Tarija Formation, Taxij, Bolivia; Pleistocene), showing articular surfices for other manual elements. A, proximomedial view (dorsal towards top; medial towards tight), B, lateral view (dorsal towards left; proximal towards top), meflmetacarper 2 ;sc-scaphoid; $1 d$-traperoid.


FIGURE 6. Left MCC of Eremotherium mirabile (ROM 22135; Daytoma Beach Bone Bed, Florids; Pleistocene), showing articular surfices for other manual elements. A, Lateromedial view (docsil towards left proximal towards top) B, lateral view (docsil towards left proximal towards top); C. proximolateral view (docsal towerds topr medial towards risht); mas-mapuom; mcill-metacarpal 3; ph-phalanx (vestigit): sc-scaphoid.
relatively reduced in Eremotherium. The concave, dorsopalmarly elongate and nearly rectangular facet for the magnum is contiguous distally with the facet for Mc III, and faces approximately proximolaterally (Fis. 6A, B). The morphological similarity and position of the articular facets for Mc III and the magnum in this region of the MCC of Eremotherium suggest that it corresponds to or is homologous with the proximal part of Mc II of Megatherium.
In Megatherium the proximal surface of Mc II, contiguous laterally with the facet for the magnum, is deeply excavated for the trapezoid, which articulates laterally with the magnum by way of a dorsoventrally elongate facet that faces nearly medially. The medial surface of the magnum thus bears distinct, though contiguous, surfaces the proximal articulating with the trapezoid, the distal with Mc II. The magnum in Eremotherium (e.g., ROM 27369) usually possesses a single elongate medial facet, but some specimens bear a facet that resembles the arrangement of the facets for the trapezoid and Mc II in Megatherium. suggesting that the trapezoid contributes to the MCC but that it is usually reduced.

The proximal surface of the MCC in Eremotherium usually bears a single facet for the scaphoid (Fig. 6C). The lateral part is contiguous laterally with the facet for the magnum and resembles the scaphoid facet on the proximal surface of the trapezoid in Megotherium, which suggests that the proximal surface of the trapezoid in Megatherium and the proximal surface of the lateral part of the MCC in Eremotherium are homologous, and thus that the trapezoid participates in the MCC. In most specimens the trapezoid is reduced to such a degree that it appears to be absent entirely from the manus, and that the proximal surface of the Mc II has conformed to the articular facet of the scaphoid. However, this is unlikely in Eremotherium for two reasons. One, there are occasional specimens (ROM 27376, MNP 15) in which the proximolateral part of the MCC is relatively prominent. Comparison of this region in these specimens with that of the articulated trapezoid and McII of Megatherivm reveals close similarity in oustine, offering further evidence that the trapezoid contributes to the MCC in Eremosherium. The second reason involves a new species from the Blancan and Irvingtonian of Florida, which possesses a complete and independent Mc II. Two types of MCC occur, one of which incorporates the trapezoid, traperium, and Mc I (the other lacks the trapezoid, but the MCC is morphologically different from that of Megatherium). The trapezoid in this MCC (e.g., UF 121738) is unreduced and clearly discernable.

The medial part of the facet on the proximal surface of the MCC articulates with the elongate facet on the apical part of the scaphoid. It is dorsopalmariy expandet compared to the homologons and otherwise similar facet on the MCC for the scaphoid in Megatherium (Figs. 5A, 6C). In some specimens of Eremotherium (eg, various MCL specimens; USNM 4571 10) the medial part of this facet is subdivided, producing an
isolated circular or oval facet medially; the scaphoid bears a corresponding facet. The separate factets on the medial surface of the MCC may indicate that the isolated medial facet represents the trapezium and the lateral facet the trapezoid.
Mc I is inferred to contribute to the MCC in Eremotherium on the basis of morphological similarity and because the Mc I contributes to the MCC of Megatherium, the Irvingtonian Eremotherium species from Florida, and other Tardigrada. The medial part of the MCC is nodular, as is the MCC of Megatherium, but is proximodistally compressed in most specimens. However, this medial part may be unreduced, as in MNP 15.

Another facet may be present on the distal surface of the MCC for articulation with a nodular bone, probably representing vestigial phalanges. In some specimens (e.g., ROM 22135) this facet is elongate and contiguous with the distal margin of the facet for Mc III. An analogous facet is present opposite it on Mc III; the vestigial phalanx, probably of digit 2 , is wedged palmarly between these surfaces. In other specimens (e.g., MNP 15) an isolated and approximately oval facet is present on the distomedial part (represeating Mc I) of the MCC, and probably articulated with the vestigial phalanges of digit 1 (Gazin, 1957).

## SUMMARY

Owen (1858) considered the medial element of the proximal carpal row in Megatherium as the scaphotrapezium, refiecting the then current position that the scaphoid and trapecium were fused in Bradypus and Choloepus. Owen was followed by Schulthess (1920) and Cazin (1957), even though Humphry (1870) and Flower (1873) had demonstrated that the trapezium was fused to the Mc I in the extant genera. Cabrera (1929), followed by Hoffstetter (1952), reasoned that an analogous situation was present in Megatherium.

Anatomical comparisons suggest that the medial element of the proximal carpal row of Eremocherium and Megatherium is a scaphoid, homologons with that of other Tardigrada, and not a scapho-trapezium. The medial process of the scaphoid overhangs the distal carpal row in all sioths. As there is no evidence to suggest that it ossifies from a separate center, it should be regarded as a normal ontogenetic feature.

The MCC Complex is a complex of fused elements present medially in the manus of many Tardigrada. In most genera the MCC is a small nodular element incorporating the traperium and Mc I (eg, Thinobadistes, Clossotherium, Nothrotheriops, etc.). Comparisons between the MCCs of Megatherium and other sloths in the position, arrangement of articular facets, and association with adjacent skeletal elements suggest that the MCC of Megatheriam also comprises the trapezium and Mc L. The MCC of Eremotherizm is a langer, more complex element. Analogous comparisons between the MCCs of Eremotherium and Megatherium suggest that the MCC of the former inctudes reduced

Mc II, Mc L, trapezium and trapezoid. This element is present in Eremotherium mirabile, E. laurillardi, and E. rusconii. The morphological similarity of the MCC is strong evidence that the three species are conspecific.

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## APPENDIX 4A. Measurements (mm) for the Skulls of Megatheriinae. Abloreviations as in table 1 ; - juvenile individuals.

## Eremotherium laurillardi

| Specimen | M1OCL | OCH | OPTH | TRL | ANTW | POPW | POCON | POSTW |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| MCL | $1700 / 01$ | 534 | 112 | 170 | 214 | 125 | 191 | 158 | 282 |
| MCL | 170101 | 523 | 110 | 174 | 192 | 133 | 178 | 150 | 245 |
| MCL | 170201 | 464 | 45 | 136 | 185 | 105 | 169 | 151 | 224 |
| USNM | 20872 | 558 | 124 | 167 | 210 | 132 | 202 | 185 | 296 |
| FMNH | 26970 | 497 | 108 | 143 | 197 | 132 | 158 | 142 | 226 |
| ROM, 24240 | 503 | 114 | 154 | 214 | 129 | 194 | 171 | 265 |  |
| MNRJ | 2225 | 504 | 85 | 136 | 207 | 123 | 175 | 126 | 249 |
| MCL | $7240 *$ | 446 | 101 | 152 | 206 | 120 | 185 | 158 | 263 |
| MCL | $7239 *$ | 433 | 106 | 129 | - | 116 | 165 | 140 | 235 |
|  |  |  |  |  |  |  |  |  |  |

Negatherium americanum

| Specim | nen | miocl | OCH | OPTH | TRL | ANTW | POPW | POCON | POSTw |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MUT | 422 V | 465 | 210 | 111 | 207 | 131 | 204 | - | 253 |
| MACN | - | 624 | 204 | 148 | - | - | - | - | - |
| MACN | 5002 | 625 | 230 | 125 | 240 | 177 | 226 | 169 | 310 |
| MACN | 1000 | 466 | 194 | 97 | - | - | - | $\cdots$ | . |
| MLP | 42-VI-24-2 | 601 | 204 | 124 | 220 | 168 | 246 | 173 | 307 |
| MLP | 2-64 | 571 | 211 | 139 | 239 | - | 160 | 172 | 281 |
| BMNH | 19953 | 564 | 221 | 131 | 270 | 167 | 259 | 170 | 290 |
| 2 mNH | P14293 | 553 | 197 | 150 | 223 | 137 | 204 | 130 | 257 |
| zmuc | 212 | 487 | 195 | 92 | 231 | 115 | 217 | 154 | 247 |
| MACN | 13021 | 517 | 144 | 118 | 200 | 129 | 212 | 147 | 259 |
| macn | 2830* | 345 | 120 | 86 | 140 | 97 | 146 | 135 | 178 |
| MACN | 2786* | 342 | 131 | 52 | 158 | 95 | 152 | 129 | 192 |
| MMP | 430* | 383 | 134 | 104 | 166 | 104 | 168 | 131 | 211 |

APPENDIX 4A. Measurements (mm) for the Skulls of Megatheriinae (cont'd).

## Megatherium medinae

| Specimen | M1OCL | OCH | OPTH | TRL | ANTW | POPW | POCON | POSTW |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| SGO | 231 | 423 | 124 | 108 | 168 | 114 | 172 | 125 | 234 |
| SGO | 275 | 385 | 117 | 102 | 162 | 102 | 162 | - | 221 |

जु Megatherium sundti

| Specimen | M1OCL | OCH | OPTH | TRL | ANTW | POPW | POCON | POSTW |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| SGO | 273 | 404 | 131 | 111 | 138 | 105 | 163 | 119 |
| PIU | M4530* | 391 | 155 | 94 | - | 122 | 156 | 123 |

Megatherium tarijense

| Specimen | M1OCL | OCH | OPTH | TRL | ANTW | POPW | POCON | POSTW |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| FMNH P14216 | 432 | 132 | 114 | 170 | 97 | 162 | 108 | 200 |

APPENDIX 4A. Measurements (mm) for the Skulls of Megatheriinae (cont'd).

| Specimen | M20cl | OCH | OPTH | TRL | ANTW | POPW | POCON | POSTW |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MLP 2-66 | 407 | 87 | 114 | 194 | - | - | - |  |

Megatheriops rectidens

| Specimen | M1OCL | OCH | OPTH | TRL ANTW POPW POCON POSTW |  |  |  |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
| MACN 2818 | 365 | 119 | 117 | 173 | - | - | - | - |

Specimen M1OCL OCH OPTH TRL ANTW POPW POCON POSTW

Megatheriinae indet.


APPENDIX 4B. Measurements (mm) for the Dentaries of Megatheriinae. Abbreviations as in Figure 3.

Eremotherium laurillardi

| Specimen |  | MBH | MTRL | MCABH | m1APD |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Adults |  |  |  |  |  |
| MCL | 1700/02 | 152 | 196 | 145 | 461 |
| MCL | 1701/02 | 136 | 186 | 136 | 407 |
| MCL | 1702/02 | 127 | 174 | 138 | 387 |
| MCL | 7225 | 146 | 190 | 146 | 432 |
| MCL | 7229 | 141 | 182 | 156 | 432 |
| MCL | 7231 | 143 | 188 | 127 | - |
| MCL | 7233 | 152 | 194 | - | - |
| MNRJ | 2225 | 153 | 198 | - | - |
| MNRJ | 3858 | 142 | 192 | 135 | - |
| MNP | 44 | 152 | 193 | - | - |
| MNP | 46 | 143 | 186 | - | - |
| USNM | 18498 | 143 | 185 | 149 | 443 |
| USNM | 20867 | 136 | 185 | 138 | 431 |
| ILSB | No \# | 152 | 196 | - | - |
| AMNH | 95742 | 151 | 182 | - | - |
| F:AM | 95785 | 151 | 200 | 114 | 441 |
| ROM | 40324 | 156 | 193 | 123 | - |

Juveniles

| MCL | 7220 | 90 | 124 | - | 278 |
| :--- | :--- | ---: | :---: | :---: | :---: |
| $M C L$ | 7221 | 91 | 116 | 87 | 261 |
| $M C L$ | 7222 | 103 | 144 | - | - |
| $M C L$ | $7223 / 02$ | 107 | 135 | 124 | 330 |
| $M C L$ | 7226 | 95 | 134 | - | - |
| $M C L$ | 7228 | 98 | 144 | 111 | 298 |
| $M C L$ | 7232 | 65 | 085 | - | - |
| $M C L$ | 7234 | 67 | 083 | - | - |
| $M C L$ | $7236 / 01$ | 92 | 127 | 106 | 309 |
| $M C L$ | 7246 | 97 | 130 | - | - |
| F:AM 95790 | 63 | 95 | 69 | 191 |  |

APPENDIX 4B. Measurements (nm) for the Dentaries of Megatherinae (cont'd).

Megatherium americanum

| Specimen | MBH | MTRL | MCABH | m 1 APD |
| :---: | :---: | :---: | :---: | :---: |
| Adults |  |  |  |  |
| MLP 2-37 | 242 | 239 | 222 | 511 |
| MLP 2-50 | 182 | 192 | 170 | 414 |
| $\begin{array}{ll}\text { MLP } & 2-52\end{array}$ | 222 | 220 | - | - |
| MLP 2-54 | 215 | 192 | 136 | - |
| MLP 2-56 | 207 | 200 | 234 | 447 |
| MLP 2-58 | 214 | 201 | 175 | - |
| MLP 2-59 | 191 | 206 | 175 | - |
| MLP 2-60 | 180 | 186 | _ | - |
| MLP 2-207 | 201 | 202 | - | - |
| MLP 28-III-16-2 | 215 | 213 | 180 | - |
| MLP 44-XII-28-1 | 235 | 223 | 210 | - |
| MACN 1000 | 227 | 212 | - | - |
| MACN 2831 | 210 | 237 | - | - |
| MACN 2832 | 216 | 231 | - | - |
| MACN 5002 | 205 | 228 | 217 | 405 |
| MNTENM 6 | 206 | 209 | 192 | - |
| MNEHP R247 | 227 | 211 | - | - |
| MPCB 1 | 235 | 215 | - | - |
| MPLP 559 | 217 | 201 | - | - |
| BMNH 19953 | 254 | 259 | 203 | 488 |
| BMNE 19953f | 227 | 201 | - | - |
| FMNH P14293 | 213 | 216 | - | - |
| ZMUC 212 | 220 | 193 | 176 | - |
| Juveniles |  |  |  |  |
| MACN 855 | 53 | 068 | 57 | - |
| MACN 2786 | 114 | 149 | 122 | 304 |
| MACN 2830 | 110 | 124 | - | 267 |
| MACN 10149 | 134 | 151 | - | - |

APPENDIX 49. Measurements (mm) for the Dentaries of Megatheriinae (cont'd).
M. tarijense

| Specimen | MBH | MTRL | MCABH | m1APD |
| :--- | :---: | :---: | :---: | :---: |
| FMNH P14216 | 140 | 152 | 130 | 330 |
| NRM M4890 | 169 | 204 | 185 | - |

M. medinae

| Specimen | MBH | MTRL | MCABH | m1APD |  |
| :--- | :--- | :--- | :--- | :--- | :---: |
| SGO | PV236 | 161 | 172 | 168 | 413 |
| SGO | PV252 | 142 | 151 | - | - |
| SGO | PV288 | 116 | 142 | - | - |
| SGO PV5000 | 118 | 130 | - | - |  |

M. sundti

| Specimen | MBH | MTRL | MCABH | m1APD |
| :---: | :---: | :---: | :---: | :---: |
| SGO | PV276 | 126 | 149 | 141 |
| SGO | PV277 | 138 | 145 | 122 |
| PIU M4530 | 146 | 154 | - | - |

Megatheriops rectidens

| Specimen | MBH | MTRI | MCABH | mlAPD |
| :--- | :---: | :---: | :---: | ---: |
| $M A C N ~$ | 2818 | 145 | 165 | 117 |

Pyramiodontherium bergi

| Specimen | MBH | MTRL | MCABH |  |
| :--- | :--- | :--- | :--- | :--- |
| MLP | $2-66$ | 154 | 189 | - |

APPENDIX 4B. Measurements (mm) for the Dentaries of Megatheriinae (cont'd).

| Specimen |  | MBH | MTRL | MCABH | m1APD |
| :---: | :---: | :---: | :---: | :---: | :---: |
| EPN | V950 | 51 | 71 | - | - |
| EPN | V948 | 65 | 89 | - | - |
| EPN | V978 | 110 | 144 | - | - |
| ROM | 3756 | 114 | 149 | - | - |


| Specimen | MBE | MTRL | MCABE | m1APD |
| :---: | :---: | :---: | :---: | :---: |
| MNHNU | 194 | 208 | 231 | - |

Perezfontanatherium fiandrai

| Specimen | MBH | MTRL | MCABH | m1APD |
| :--- | :--- | :--- | :--- | :--- |
| $M P F L R ~$ | 396 | 120 | 128 | - |

Pliomegatherium lelongi

| Specimen | MBH | MTRL | MCABH | m1APD |
| :--- | :--- | :--- | :--- | :--- |
| $M A C N ~$ | 13213 | 103 | 144 | - |

Megatherium "rionegrense"

| Specimen | MBH | MTRI | MCABH | m1APD |
| :---: | :---: | :---: | :---: | :---: |
| $M A C N ~ 2833 ~$ | 156 | 149 | - | - |

APPENDIX 4C. Measurements (mm) of Humeri of Megatheriinae. LENGTH measured as the greatest length parallel to the long axis of the diaphysis; Distal Width (DSWIDTH) as the greatest distal transverse width.

Eremotherium laurillardi
$\left.\begin{array}{lcc}\text { Specimen } & \text { LENGTH } & \text { DSWIDTH } \\ \hdashline \text { MCL } & 849 & 782 \\ \text { MCL } & 860 & 739\end{array}\right] 346$

Megatherium americanum

| Specim |  | LENGTH | DSWIDTH |
| :---: | :---: | :---: | :---: |
| MACN | 2321 | 596 | 357 |
| MACN | 5002 | 787 | 368 |
| MACN | 10148 | 738 | 330 |
| MLP | 2-72 | 700 | 350 |
| MLP | 2-79 | 695 | 327 |
| MLP | 2-207 | - | 325 |
| MLP | 28-III-16-2 | 721 | 316 |
| MLP | 41-II-28-1 | 710 | 340 |
| BMNH | 19953d | 664 | 297 |
| BMNH | 19953e | 673 | 305 |
| ZMUC | 3 | 661 | 300 |
| ZMUC | 212 | 626 | 299 |
| MNENM | 6 | 683 | 334 |
| MNENTP | AC7013 | 656 | - |

# APPENDIX 4C. Measurements (mm) of Humeri of Megatheriinae (cont'd). 

Megatherium sundti

| Specimen | LENGTH | DSWIDTH |
| :--- | :---: | :---: |
| PIU M4530 | 531 | 244 |
| Megatherium tarijense |  |  |
| Specimen | LENGTH | DSWIDTH |
| MACN 2818 | 482 | 183 |

Megatheriops rectidens

| Specimen | LENGTH | DSWIDTH |
| :---: | :---: | :---: |
| FMNH P14216 | 527 | 219 |

Toro Negro Megatheriine

| Specimen | LENGTH | DSWIDTH |
| :---: | :---: | :---: |
| MLP $68-$ III-16-2 | 591 | 196 |

APPENDIX 4D. Measurements (mm) for the Radii of Megatheriidae. Abbreviations as in Table 4.

Eremotherium laurillardi

| Specimen | LENGTH | DSWIDTH | MSCONST |
| :--- | :--- | :--- | :--- |
| $M C L$ | 8632 | 802 | 225 |
| MCL | 8635 | 640 | 175 |
| MCL | 8638 | 659 | 171 |
| MCL | 8643 | 690 | 175 |
| MCL | 8645 | 822 | 237 |
| MCL | 8652 | 707 | 210 |
| ROM | 22106 | 730 | 202 |
| ROM | 22107 | 740 | 202 |
| ROM | 10473 | 718 | 204 |
| FMNH | P26970 | 637 | 185 |
| USNM 20867 | 605 | 210 | 116 |
| MNP 41 | 740 | 245 | 125 |

Megatherium americanum

| Specimen | LENGTH | DSWIDTH | MSCONST |
| :--- | :---: | :---: | ---: |
| MNHNM | 6 | 635 | - |
| MPCB | 1 | 675 | 168 |
| MACN | 10148 | 645 | 176 |
| MLP | Sala 9 | 648 | 175 |
| MLP | $28-31-6-2$ | 629 | 162 |
| MLP | $2-34$ | 645 | 169 |
| BMNH | 19953 g | 620 | 163 |
| BMNE | 19953 h | 553 | 136 |
| BMNH | 43232 | 635 | 164 |
| ZMUC | 3 | 603 | 162 |
| ZMUC | 13 | 617 | 161 |
| ZMUC | 121 | 570 | 164 |
| PIMUZ AV0482 | 573 | 150 | 98 |

# APPENDIX 4D. Measurements (mm) for the Radii of Megatheriidae (cont'd). 

Megatherium medinae

| Specimen | LENGTH | DSWIDTH | MSCONST |
| :--- | :---: | :---: | :---: |
| SGO 89 | 578 | 107 | 99 |
| SGO 231 | 528 | 97 | 95 |

Megatherium medinae

| Specimen | LENGTH | DSWIDTH | MSCONST |
| :--- | :---: | :---: | :---: | :---: |
| FMNH P14216 | 461 | 90 | 91 |

Other Radii

| Specimen | LENGTH | DSWIDTH | MSCONST |
| :--- | :---: | :---: | :---: |
| FMNH P13665 | 531 | 140 | 88 |
| FMNH P14511 | 540 | -- | 67 |
| MUT 1530 | 556 | 143 | 99 |
| MUT 2502 | 560 | 143 | 72 |

APPENDIX 4E. Measurements (mm) for the Ulnae of Megatheriidae. Abbreviations: OLENGTH - Olecranon Length, measured between the proximal margin of olecranon process and distal ulnar surface; ALENGTH Articular (or Functional) Length, measured between the proximal margin of the humeral trochlea and distal ulnar surface; PRDEPTH - Proximal Depth, measured between the posterior margin of the olecranon process and the distal margin of the humeral trochlea.

Eremotherium laurillardi

| Spec |  | OLENGTH | ALENGTH | PRDEPTH |
| :---: | :---: | :---: | :---: | :---: |
| MCL | 8663 | 828 | 835 | 300 |
| MCL | 8665 | 805 | 820 | 290 |
| MCL | 8667 | 687 | 673 | 207 |
| MCL | 8669 | 639 | 648 | 216 |
| MCL | 8670 | 699 | 699 | 230 |
| MCL | 8680 | 698 | 683 | 230 |
| MCL | 8675 | 649 | 653 | 222 |

Megatherium americanum

| Specime |  | OLENGTH | ALENGTH | PRDEPTH |
| :---: | :---: | :---: | :---: | :---: |
| MACN | 10148 | 693 | 655 | 248 |
| MLP | 2-34 | 687 | 660 | 262 |
| MLP | 2-72 | 680 | - | - |
| MLP | 2-79 | 690 | - | - |
| MLP | 2-207 | 667 | 638 | 252 |
| MLP | 28-III-16-2 | 667 | 641 | 264 |
| MLP | 44-XII-16-2 | 640 | - | - |
| BMNTE | 199531 | 647 | 618 | 213 |
| zMUC | 212 | 648 | 614 | 243 |
| PIMUZ | - | 631 | 625 | 252 |
| MNHINM | 6 | 655 | 625 | - |

APPENDIX 4E. Measurements (mm) for the Ulnae of Megatheriidae (cont'd).

Megatherium medinae

| Specimen | OLENGTH | ALENGTH | PRDEPTH |
| :--- | :---: | :---: | :---: |
| SGO PV185 | 535 | 510 | 178 |

## Megatherium tarijense

| Specimen | OLENGTH | ALENGTH | PRDEPTH |
| :--- | :---: | :---: | :---: |
| FMNH P14216 | 483 | 462 | 191 |

APPENDIX 4F. Measurements for the femora of Megatheriinae. Abbreviations: DDAF - Distance between the distal articular facets; DWIDTH - Greatest distal transverse width; LENGTH - Greatest proximodistal length; MSCONST Midshaft constriction, i.e., minimum width at midshaft; PWIDTH - Greatest proximal transverse width.

Eremotherium laurillardi

| Specin | nen | LENGTH | PWIDTE | DWIDTH | MSCONST | DDAF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MCL | 9500 | 763 | 351 | 364 | 275 | 9 |
| MCL | 9501 | 724 | 350 | 363 | 281 | 27 |
| MCL | 9524 | 826 | 447 | 432 | 320 | 44 |
| MCL | 9522 | 682 | 352 | 372 | 264 | 39 |
| MNRJ | 3866 | 714 | 365 | 359 | 275 | 14 |
| ROM | 19788 | 723 | 385 | 405 | 280 | 38 |
| ROM | 24268 | 756 | 395 | 426 | 279 | 17 |
| ROM | 27323 | 723 | 385 | 425 | 260 | 10 |
| ROM | 19787 | 700 | 382 | 394 | 275 | 23 |
| ROM | 22059 | 723 | 365 | 379 | 260 | 30 |
| ROM | 30755 | 745 | 394 | 401 | 242 | 43 |
| FMNH | F26970 | 684 | 360 | 356 | 258 | 26 |
| FMNTH | P27080 | 696 | 367 | 364 | 260 | 31 |
| USNM | V | 857 | 451 | 467 | 328 | 49 |
| USNM | 11650 | 816 | 416 | 445 | 300 | 40 |
| USNM | 00 | 758 | 371 | 371 | 255 | 26 |
| MNP | 45 | 828 | 420 | 455 | 255 | 26 |
| MGN | 2000 | 750 | 357 | 388 | 260 | 33 |
| UCMP | V4201 | 895 | 447 | 476 | 330 | 32 |

APPENDIX 4F. Measurements for the femora of Megatherinae ( $\operatorname{con}^{\prime} \mathrm{d}$ ).

Megatherium americanum

| Specimen | LENGTH | PWIDTH | DWIDTH | MSCONST | DDAF |
| :---: | :---: | :---: | :---: | :---: | :---: |
| MACN 54 | 770 | 405 | 415 | 258 | 71 |
| MACN 5002 | 725 | 468 | 455 | 307 | 69 |
| MACN 10683 | 698 | 394 | 385 | 287 | 41 |
| MACN 12826 | 705 | 412 | 395 | 291 | 28 |
| MACN 66 | 679 | 410 | 377 | 274 | 30 |
| MACN 6410 | 650 | 343 | 353 | 236 | 34 |
| MLP SALA9 | 712 | 392 | 409 | 270 | 47 |
| MLP $2-207$ | 735 | 431 | 403 | 260 | 40 |
| MLP 2-29 | 759 | 459 | 473 | 311 | 46 |
| ROM 265 | 673 | 393 | 365 | 267 | 50 |
| BMNH 19953r | 583 | 331 | 326 | 222 | 40 |
| ZMJC 3L (A) | 678 | 374 | 384 | 260 | 42 |
| ZMJC 3L (B) | 665 | 362 | 382 | 246 | 44 |
| ZMUC 121 | 728 | 421 | 398 | 281 | 34 |
| ZMOC 212 | 642 | 376 | 380 | 246 | 28 |
| MHHNM 6 | 735 | 395 | 400 | 257 | 51 |
| $\begin{array}{r} \text { MLP } 28-\text { III- } \\ 16-1 \end{array}$ | 720 | 390 | 390 | 280 | 25 |
| $\text { MLP } \begin{array}{r} \text { 46-III- } \\ \text { 14-1 } \end{array}$ | 690 | 390 | 390 | 280 | 30 |
| MLP 2-60 | 611 | 338 | 326 | 223 | 42 |
| MLP 2-30 | 575 | 299 | 312 | 211 | 26 |
| MUP 2-188 | 570 | 297 | 288 | 205 | 14 |

Megatherium medinae

| Specimen | LENGTH | PWIDTH | DWIDTH | MSCONST | DDAF |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| SGO 17- | 623 | 298 | 313 | 228 | 23 |
| VI-67/64 |  |  |  |  |  |

APPENDIX 4F. Measurements for the femora of Megatheriinae (con'd).

Megatherium sundti

| Specimen | LENGTH | PWIDTH | DWIDTH | MSCONST | DDAF |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| PIU M4530 | 530 | 256 | 266 | 162 | 24 |

Megatherium tarijense

| Specimen | LENGTH | PWIDTH | DWIDTH | MSCONST | DDAF |
| :--- | :---: | :---: | :---: | :---: | :---: |
| FMNH P14216 | 528 | 273 | 266 | 200 | 14 |

Toro Negro Megatheriine

| Specimen | LENGTH | PWIDTH | DWIDTH | MSCONST | DDAF |
| :--- | :---: | :---: | :---: | :---: | :---: |
| MLP $68-$ | 463 | 260 | 253 | 157 | 22 |

Other Femora from the Tarija Valley, Bolivia.

| Specimen | LENGTH | PWIDTH | DWIDTH | MSCONST | DDAF |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| MUT | V2520 | 586 | 295 | 296 | 209 | 36 |
| MUT | V411 | 532 | 284 | 285 | 208 | 49 |
| MUT | V4I3 | 657 | 345 | 341 | 240 | 27 |
| MNINN BOL | 610 | 323 | 330 | 233 | 29 |  |
|  | 1985 |  |  |  |  |  |
|  |  |  |  |  |  |  |

APPENDIX 4G. Measurements for the Tibiae-Fibulae of Megatheriinae. Abbreviations: LENGTK - Greatest proximodistal length; PWIDTH - Greatest proximal distal width; DWIDTH - Greatest distal transverse width; MSWIDTH - Shaft constriction, minimum transverse width at miđshaft; DWWOF - Greatest distal width without fibula, i.e., of tibia only.

Eremotherium laurillardi

| Speci | nen | LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWWOF |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| MCL | 9546 | 545 | 313 | 254 | 100 | - |
| MCL | 9550 | 560 | 285 | - | 113 | 222 |
| MCL | 9551 | 481 | 276 | - | 101 | 191 |
| MCI | 9553 | 589 | 349 | - | 139 | 271 |
| MCL | 9556 | 517 | 261 | - | 91 | 208 |
| MCL | 9558 | 515 | 283 | - | 107 | 189 |
| MCL | 9559 | 531 | 290 | - | 116 | 211 |
| MCL | B | 610 | 369 | 287 | 107 | 257 |
| MCL | 9567 | 447 | 245 | - | 91 | 172 |
| MNRJ | 95 | - | - | - | - | - |
| MNRJ | 96 | 531 | 264 | 227 | 110 | - |
| MNRJ | 404 | 655 | - | 331 | - | - |
| MRRJ | 277 | 550 | - | 234 | 114 | - |
| FMNE | P26970 | 513 | 298 | 248 | 106 | 201 |
| ROM | 22068 | 530 | 306 | 249 | 105 | 199 |
| ROM | 22069 | 557 | 330 | 272 | 114 | 210 |
| ROM | 22070 | 551 | - | - | 113 | 208 |
| ROM | 22139 | 590 | 342 | - | 107 | 220 |
| ROM | 27331 | 588 | 322 | - | 116 | 227 |
| ROM | 30758 | 553 | 316 | - | 95 | 213 |
| TSNM | no\# | 558 | 330 | 266 | 115 | - |
| USNM | 20867 | 512 | - | 281 | - | - |
| USNM | 20872 | 624 | 396 | - | - | - |
| UCMP | V4201 | 665 | 405 | - | 144 | - |

APPENDIX 4F. Measurements for the Tibiae-Fibulae of Megatheriinae (cont'd).

Megatherium americanum

| Specimen | LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWWOF |
| :---: | :---: | :---: | :---: | :---: | :---: |
| MACN 54 | 592 | 325 | 310 | 115 | - |
| MACN 10147 | 475 | 275 | - | 112 | 215 |
| MLP SALA9 | 568 | 330 | 290 | 100 | - |
| MLP 2-79 | 539 | 342 | - | 123 | 246 |
| MLP 2-29 | 623 | 369 | 313 | 141 | , |
| MLP $2-30$ | 446 | 246 | 222 | 81 | 182 |
| MLP $\quad 2-94$ | 553 | 338 | - | 108 | 237 |
| MLP $\quad 2-207$ | 560 | 360 | - | 115 | 245 |
| $\begin{array}{ll} \text { MLP } & 44-X I I- \\ & 28-12 \end{array}$ | 530 | - | - | 114 | - |
| MNEMNM 6 | 532 | 329 | 305 | 117 | - |
| MPCB 1 | 538 | 335 | 302 | 119 | - |
| PIMUZ - | 505 | 332 | 276 | 121 | - |
| BMNH 19953t | 485 | 248 | - | 90 | - |
| BMNH 19953w | 425 | 261 | 279 | 95 | - |
| BMNH 19953s | 525 | 301 | 279 | 121 | - |
| ZMJC 3 | 536 | 301 | 277 | 120 | - |
| ZMUC 212 | 503 | 292 | 266 | 105 | - |
| ROM 10439 | 549 | - | - | 129 | 250 |

Megatherium medinae

| Specimen | LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWWOF |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: |
| - SGO | PV231 | 455 | 236 | - | 92 | - |
| SGO PV298 | 468 | 263 | - | 92 | - |  |

APPENDIX 4F. Measurements for the Tibae-Fibulae of Megatheriinae (cont'd).

Megatherium tarijense

| Specimen LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWWOF |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
| FMNH P14216 | 408 | 214 | 202 | 85 | 156 |

Pyramiodontherium bergi

| Specimen | LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWWOF |
| :--- | :---: | :---: | :---: | :---: | :---: |
| MLP | 266 | 499 | 252 | 228 | 87 |

Toro Negro Megatheriine

| Specimen | LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWOFF |
| :--- | :---: | :---: | :---: | :---: | :---: |
| MLP $68-$ | 472 | 237 | - | 81 | 177 |
| III-14-1 |  |  |  |  |  |

Other Femora from the Tarija Valley, Bolivia.

| Specimen | LENGTH | PWIDTH | DWIDTH | MSWIDTH | DWWOF |
| :--- | :---: | :---: | :---: | :---: | :---: |
| $-M U T$ | V410 | 425 | 249 | 231 | - |
| MMNH P13662 | 447 | 246 | 222 | 96 | 181 |

APPENDIX 4H. Measurements (man) of the Astragali of Megatheriinae.

Eremotherium laurillardi

| Specimen |  | Length | Height |
| :---: | :---: | :---: | :---: |
| MCL | 9664/02 | 191 | 195 |
| MCL | 9719/02 | 259 | 256 |
| MCL | 9733 | 181 | 194 |
| MCL | 9736 | 218 | 214 |
| MCL | 9738 | 205 | 197 |
| MCL | 9740 | 198 | 199 |
| MCL | 9744 | 199 | 190 |
| MCL | 9745 | 212 | 211 |
| MCL | 9746 | 173 | 192 |
| MCL | 9749 | 181 | 175 |
| MCL | 9752 | 196 | 202 |
| MCL | 9754 | 211 | 210 |
| MCL | 9758 | 169 | 179 |
| MCL | 9759 | 204 | 213 |
| MCL | 9760 | 245 | 233 |
| MCL | 9761 | 184 | 191 |
| MCL | 9764 | 188 | 1 |
| MCL | 9771 | 258 | 251 |
| MCL | 9772 | 235 | 232 |
| MCL | 9773 | 187 | 185 |
| MNRJ | 99V | 188 | 179 |
| MNRJ | 100V | 202 | 210 |
| MNRJ | 101V | 208 | 213 |
| MNRJ | 102V | 212 | 229 |
| MNRJ | 104V | - | 193 |
| MNRJ | 105V | - | 208 |
| MNRJ | 106V | - | 225 |
| MNRJ | 107V | 203 | 199 |
| MNRJ | 108V | 195 | 202 |
| MNRT | 109V | 240 | 249 |
| MNRJ | 110 V | 182 | 206 |
| MNRJ | 279V | - | 202 |
| MNRJ | 2130 V | 198 | 205 |
| MNRJ | 2948V | 247 | 243 |
| MNRJ | 2972V | - | 240 |
| MNRJ | 3871V | 192 | 188 |
| ROM | 22013 | 199 | 206 |
| ROM | 22014 | 211 | 206 |
| ROM | 22015 | 212 | - |
| ROM | 22016 | 244 | 230 |
| ROM | 30773 | 220 | 202 |
| ROM | 4036 | 215 | 212 |
| ROM | 4037 | 224 | 209 |
| ROM | 24257 | 228 | 223 |

APPENDIX 4H. Measurements (m) of the Astragali of Megatheriinae (cont'd).

Megatherium americanum


APPENDIX 4H. Measurements (mm) of the Astragali of Megatheriinae (cont'd).

Megatherium medinae

| Specimen | Length | Height |
| :--- | :---: | :---: |
| SGO PV9-V-69/27 | 150 | 134 |
| SGO PVI-VII-67/62 | 148 | 151 |

Megatherium tarijense

| Specimen | Length | Height |
| :---: | :---: | :---: |
| FMNH P14216 | 154 | 144 |

Pyramiodontherium bergi

| Specimen | Length | Height |
| :--- | :---: | ---: |
| MLP 266 | 162 | 165 |

Megathericulus patagonicus

| Specimen | Length | Height |
| :--- | :---: | :---: |
| $M A C N$ | 89 | 96 |

Megathericulus primaevus

| Specimen | Length | Height |
| :---: | :---: | :---: |
| MLP 39-VI-24-1 | 88 | 92 |

APPENDIX 4H. Measurements (mm) of the Astragali of Megatheriinae (cont'd).

## Eomegatherium nanum

| Specimen | Length | Height |
| :---: | :---: | :---: |
| MACN 4992 | 134 | 131 |

Other Astragali from Entre Ríos Province, Argentina

| Specimen | Length | Height |
| :---: | :---: | :---: |
| MACN | 7048 | -- |
| MACN 13667 | 155 | 192 |
| MACN | 4941 | 158 |

Toro Negro Megatheriine
Specimen Length Height

| MLP | $68-I I I-1411$ | 147 |
| :--- | :--- | :--- | :--- |

Other Astragali from the Tarija Valley, Bolivia

| Specimen | Length | Height |
| :--- | :--- | :--- |
| MUT | V407 | 185 |
| MUT | V430 | 180 |
| MUT | V1584 | 196 |
| MUT | V406 | 175 |
| MUT V1585 | 162 | 182 |
| MNEN BOL 3204 | 192 | 189 |
| MNHN BOL 3205 | 197 | 161 |
| MNEN BOL 3206 | 173 | 199 |
| MNHN BOL 3207 | 172 | 185 |

# Appendix 4I. Measurements (min) for Calcanea of Megatheriinae. Abbreviations: PWIDTH - Posterior Width, greatest transverse width across the tuber. 

Eremotherium laurillardi

| Specimen |  | LENGTH | PWIDTH |
| :---: | :---: | :---: | :---: |
| MCL | 2742 | 346 | 136 |
| MCL | 9613 | - | 123 |
| MCL | 9685 | 397 | 155 |
| MCL | 9686 | - | - |
| MCL | 9697 | 366 | 119 |
| MCL | 9700 | 334 | - |
| MCL | 9702 | 357 | 140 |
| MCL | 9704 | 377 | 156 |
| MCL | 9705 | 425 | 162 |
| MCL | 9708 | 440 | 150 |
| MCL | 9711 | - | 126 |
| MCL | 9712 | 382 | 157 |
| MCL | 9720 | 378 | 148 |
| MCL | 9727 | 342 | 123 |
| MCL | 9728 | 362 | 129 |
| MCL | 9730 | - | - |
| MNRJ | 2139 | 316 | - |
| MNRJ | 2949 | 375 | 147 |
| MNRJ | 120 | 381 | 146 |
| MNRJ | 121 | - | - |
| MNRJ | 123 | - | 153 |
| MNRJ | 124 | 376 | 142 |
| MNRJ | 125 | 381 | 151 |
| MNRJ | 277 | 374 | 148 |
| MNRJ | 2781 | - | - |
| MNRJ | 2783 | - | 146 |
| MNRJ | 4335 | 500 | 192 |
| MRRJ | 573 | - | 141 |
| MNRJ | 589 | - | 149 |
| MNRJ | 3878 | 360 | 125 |
| ROM | 22003 | 406 | 154 |
| ROM | 30768 | 415 | 171 |
| ROM | 30769 | - | 183 |
| ROM | 4128 | 418 | 162 |
| ROM | 24260 | 430 | 140 |
| ROM | 24262 | 418 | 136 |
| EPN | 1020 | 409 | 174 |
| EPN | 1021 | 395 | 152 |
| MNP | 33 | 387 | 120 |
| MNP | 34 | 385 | 151 |
| MGN | 2000 | 420 | 149 |
| USNM | 4251 | 508 | 188 |

Appendix 4I. Measurements (ma) for Calcanea of Megatheriinae (cont'd).

Megatherium americanum

| Specimen | LENGTH | PWIDTH |
| :--- | :---: | ---: |
| MACN 5055 | 390 | 170 |
| MACN 6410 | 380 | 182 |
| MACN 10147 | 344 | 155 |
| MIP SALAA | 406 | 166 |
| MLP | $2-79$ | 407 |
| MLP | $2-30$ | 321 |
| MLP $2-207$ | 410 | 142 |
| MIP $44-X I I-28-1$ | 415 | 179 |
| BMNH 19953w | 417 | - |
| BMNH 19953v | 385 | - |
| BMNH 19953y | 388 | 167 |
| BMNH Milan | 385 | 177 |
| ZMUC | 3 | 398 |
| ZMUC 212 | 383 | 190 |
| PIMUZ | - | 376 |

Megatherium medinae

| Specimen | LENGTH | PWIDTH |
| :--- | :---: | :---: |
| SGO PV1-VII-6/76 | 275 | 121 |
| SGO PV9-V-69-2/81 | 252 | 107 |

Megatherium tarijense

| Specimen | LENGTH | PWIDTH |
| :--- | :---: | :---: |
| MNHNP TAR1269 | - | 104 |
| FMNI P14216 | 233 | 105 |

Appendix 4I. Measurements (mm) for Calcanea of Megatheriinae (cont'd).

| Specimen |  |  | LENGTH | PWIDTH |
| :---: | :---: | :---: | :---: | :---: |
|  | MLP | 2-66 | 329 | 116 |
| Toro Negro Megatheriine |  |  |  |  |
|  | Speci | men | LENGTLH | PWIDTH |
|  | MLP | 68-III-1411 | 264 | 110 |
| Other Calcanei from Tarija Valley, Bolivia |  |  |  |  |
| Specimen |  |  | LENGTM | PWIDTH |
| MUT 414 |  |  | 302 | 123 |
| MUT |  | 415 | 352 | 155 |
| MUT |  | 429 | 299 | 115 |
| MUT |  | 2503 | 292 | 112 |
| MUT |  | 2522 | - | 133 |
| MBOL |  | 1487 | 390 | 155 |
|  |  | 3170 | 277 | 124 |

Calcanei from Entre Ríos Province, Argentina

| Specimen | LENGTH | PWIDTH |
| :--- | :--- | ---: |
| MACN | 4926 | 268 |
| MACN | 4927 | 297 |
| MACN 12303 | 266 | 134 |


[^0]:    Type Species: Megatheriops rectidens (Rovereto, 1914)

