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## EREMOTHERIUM LAURILLARDI: THE PANAMERICAN LATE PLEISTOCENE MEGATHERIID SLOTH

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**ABSTRACT**—Remains of *Eremotherium*, representing a large-sized megatheriid ground sloth, are known from localities in North, Central, and South America. Usually these remains are currently assigned to the following three species, based largely on geographic provenance: *E. laurillardii* (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 Panamerican species. The range of variation is larger than was suspected and the morphological characteristics used in species distinction are not diagnostically valid.

The valid name for this species is *E. laurillardii* (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. rusconii* (Schaub, 1935) fall as junior synonyms.

### INTRODUCTION

*Eremotherium* comprises a group of small and large, primarily intertropical Pleistocene megatheriid ground sloths that are known from South America, Central America, and North America. Remains of the larger species are assigned currently to *Eremotherium laurillardii* (Lund, 1842), *E. mirabile* (Leidy, 1855), and *E. rusconii* (Schaub, 1935). Those of a possibly smaller species have been described under *E. elenense* (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 *Megatherium* 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 firmly to each other and to the maxillae, and help form a stout and elongated rostrum. The zygomatic arch and orbit lie more ventrally in *Eremotherium*, and the ventral bulge of the mandible is less pronounced in *Eremotherium* than in *Megatherium*. The mandibular symphysis extends posteriorly approximately to m1 in *Eremotherium*, and to m2 in *Megatherium*.

The molariforms of *Eremotherium* and *Megatherium* differ in that the pulp cavity is relatively shorter in the former, comprising approximately half the apicobasal length, whereas in *Megatherium* the cavity occupies approximately the basal three-fourths. However, these differences apparently become manifest during ontogeny, such that molariforms of younger juveniles cannot be consistently distinguished. Fur-

ther, the transverse crests and valleys of the molariforms, particularly 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, well-formed unguals; only metacarpals (MCs) I and II, fused with the trapezium and trapezoid into the Metacarpal-Carpal 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 MC I 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 constitutes 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.N.I. = 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. laurillardii* (Lund, 1842).

### MATERIALS AND METHODS

Specimens and localities used in statistical analyses are listed in Appendix 1. Other material examined is

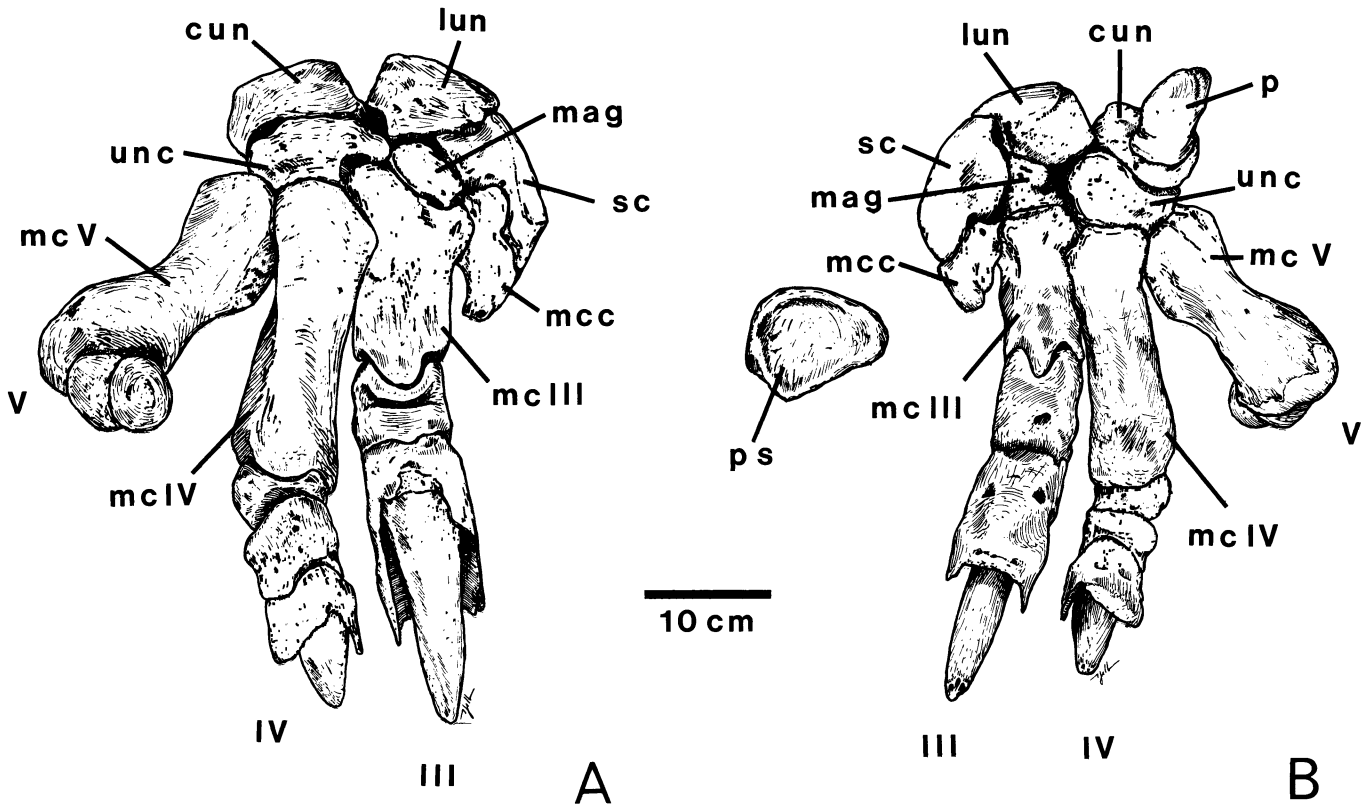


FIGURE 1. Dorsal (A) and palmar (B) views of the right manus of *Eremotherium laurillardi* (MCL 9487). Abbreviations: *cun*, cuneiform; *lun*, lunar; *mag*, magnum; *mc III*, metacarpal III; *mc IV*, metacarpal IV; *mc V*, metacarpal V; *mcc*, metacarpal-carpal complex; *p*, pisiform; *ps*, palmar sesamoid; *unc*, unciform; *sc*, scaphoid. The position of *ps* is uncertain.

too numerous to list, and includes specimens from other localities in Brazil and the United States, and Ecuador, Honduras, Panama, Peru, 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, Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte; MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro; ROM, Royal Ontario Museum, Toronto; UF, Florida Museum of Natural History, Gainesville; UFA, Universidade Federal do Acre, Rio Branco; USNM, National Museum of Natural History, Smithsonian Institution, Washington; ZMUC, Zoologisk Museum Universitat Copenhagen, Copenhagen.

## TAXONOMIC HISTORY

Spillmann (1948) erected *Eremotherium carolinense* for late Pleistocene megatheriine remains from Ecuador. Hoffstetter (1949), without knowledge 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 megatheriine remains from Venezuela. Hoffstetter believed, however, that the material referred to *M. rusconii* was generically distinct from *Megatherium* and erected the genus *Schaubia*. Hoffstetter (1950) discovered that *Schaubia* was occupied and renamed the genus *Schaubitherium*. Hoffstetter (1952) subsequently realized that his Ecuadorian material (*S. rusconii*) was generically identical to Spillmann's *Eremotherium carolinense* and he revised his allocation; however, Hoffstetter maintained the validity of Schaub's *E. rusconii* primarily on the basis of geographic separation.

During the past forty years numerous species have been proposed for *Eremotherium* remains, a circumstance largely due to the sparse and often poorly 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 turtle; 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. rusconii* (Schaub, 1935)  
*E. hudsoni* (White, 1941)  
*E. larensis* (Nectario-Maria, 1941)  
*E. carolinense* Spillmann, 1948  
*E. elenense* (Hoffstetter, 1949)  
*E. venezuelensis* (Osten, 1951)  
*E. lundi* Paula Couto, 1954  
*E. robustum* Porta, 1961  
*E. cucutense* Porta, 1961

Paula Couto (1950) stated that the material mounted at MNRJ 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. lundi*, 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. lundi* 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. lundi* as synonyms of *E. rusconii*. Paula Couto (1979) considered *E. laurillardi* as insufficiently defined and, following Hoffstetter (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. rusconii* 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 Florida; 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 postcranial 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 Brazil; *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-

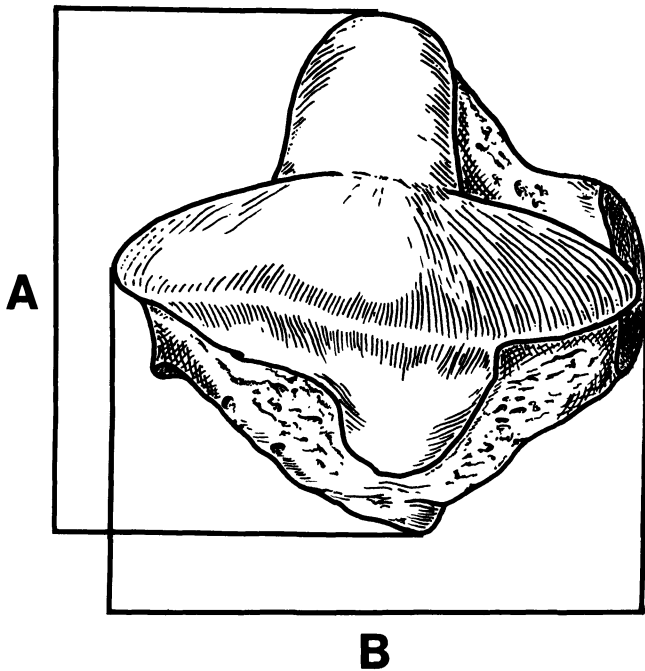


FIGURE 2. Fibular view of the astragalus of *Eremotherium laurillardi* (ROM 22008) demonstrating measurements used in statistical analyses. A = proximodistal height; B = anteroposterior length.

ently on a rather arbitrary geographical basis. Thus, for example, specimens from Brazil have been referred 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 sloth. 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 trapezium with MCs I and II, but figures of the Brazilian manus (Cartelle and Bohórquez, 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 particularly 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 35% 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 1 for samples). Further, the Toca Das Onças 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.

Similarly, the remains from Toca das Onças and Daytona Beach display an extensive variation in shape and form of nearly all skeletal elements and their articular facets, 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 Onças and Daytona Beach collections, except for Gazin's (1957) report of a centrale in one Panamanian specimen, as discussed above. In summary, all supposedly diagnostic and quantitative features of late Pleistocene 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. laurillardii* (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 laurillardii* (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 cuvieri* (= *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 Hoffstetter (1952, 1954), explained that the smaller teeth showed juvenile characteristics and suggested 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

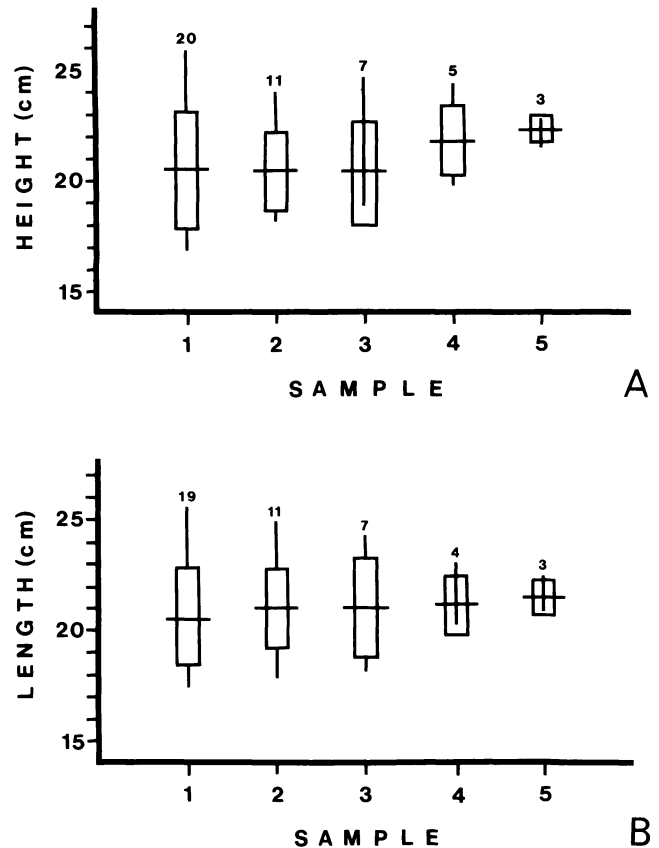


FIGURE 3. Box and Whisker Plot of height (A) and length (B) of astragali of *Eremotherium laurillardii*. Horizontal line indicates mean; vertical line indicates range; box includes one standard deviation above and below the mean; number above vertical line indicates observations (n) for each sample. See Appendix 1 for explanation of samples. Kruskal-Wallis tests indicate that no significant differences exist among samples (for height,  $\chi^2$  approximation = 5.56, DF = 4,  $P$  = 0.2347; for length,  $\chi^2$  approximation = 2.65, DF = 4,  $P$  = 0.6180).

did not permit it to be distinguished from *M. americanum* (Hoffstetter, 1954), because the teeth were fragmentary and morphologically similar to those of *M. americanum*.

The question of the validity of the epithet *laurillardii* 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 Hoffstetter, 1949) considered *E. laurillardii* to be a valid but poorly understood species. In the following paragraph Hoffstetter (1954:746-7) both supported and cast doubt on the validity of *laurillardii*: "Il y a donc une haute probabilité pour que l'espèce de Lagoa Santa soit aussi un *Eremotherium* et doit recevoir le nom de *E. laurillardii* (Lund 1842). Ils s'agit vraisemblablement de la même espèce que

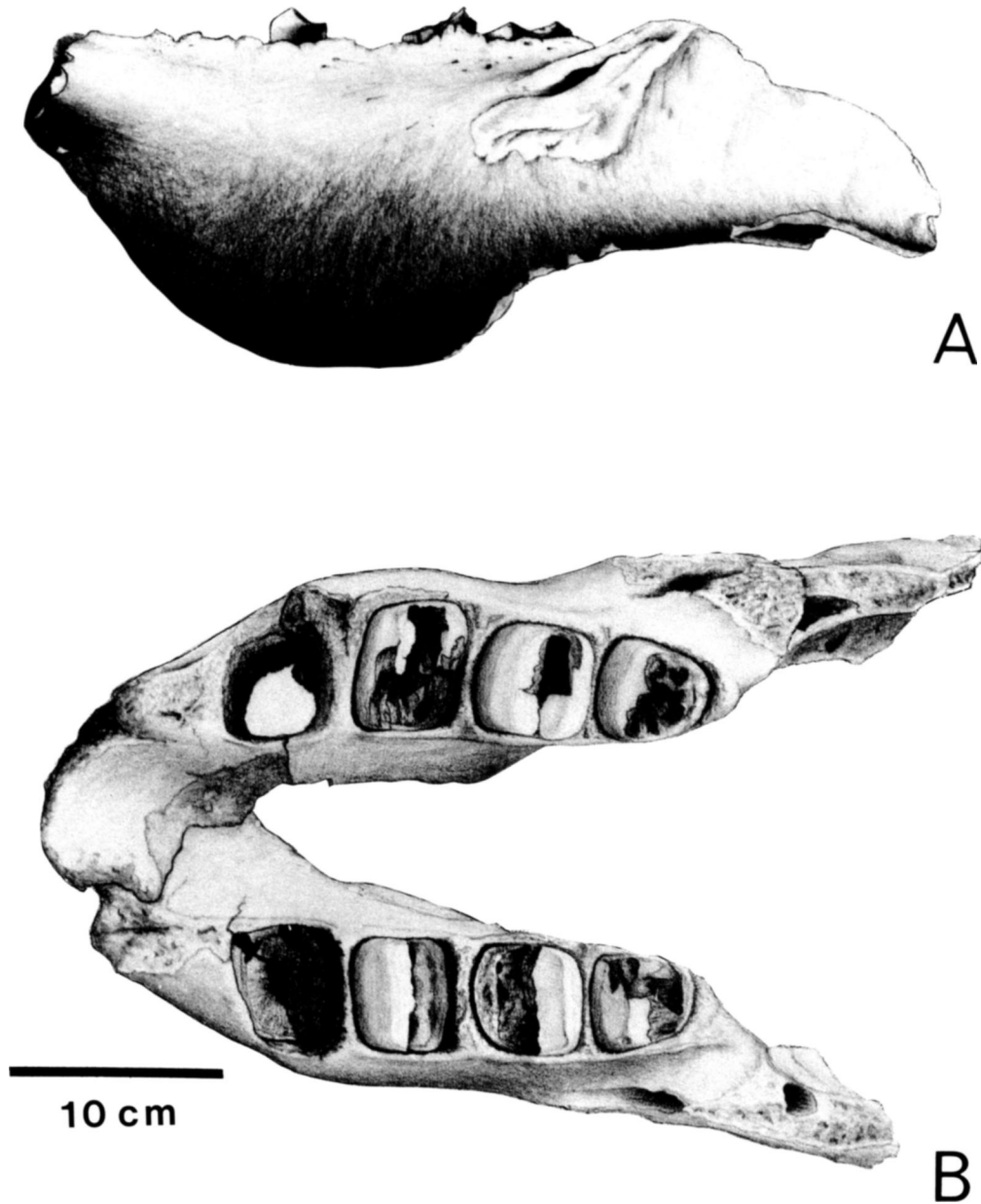


FIGURE 4. Type specimen of *Eremotherium mirabile* (USNM 830); A, occlusal; B, lateral views of the mandible.

celle de Bahia, dont l'étude en cours nous apportera une connaissance détaillée. Il est même possible que se soit la même forme qui a vécu au Venezuela, de sorte que *E. rusconii* (Schaub) pourrait tomber en synonymie devant le nom de Lund, si toutefois l'on décide de prendre en considération le type très insuffisant proposé par le dernier auteur."

Gazin (1957:346) believed that the two teeth comprising the type material of *E. laurillardii* were "evidently immature and clearly inadequate for diagnostic purposes, hence should probably be ignored or the name *M. laurillardii* be left as a synonym of *M. americanum* as treated by Winge." The latter suggestion is techni-

cally impermissible, 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. rusconii*. Paula Couto (1950) stated that *E. laurillardii* was insufficiently defined, and he (1970) referred to the species from Brazil as *E. lundii*. Later, Paulo Couto (1978) did not refer directly to *E. laurillardii*, but alluded to its invalidity by agreeing with Gazin that *E. rusconii* was valid for the Central and South American species. Paula Couto (1979) stated that *E. laurillardii* was insufficiently defined.

Cartelle and Bohórquez (1982), however, resurrected *E. laurillardii* 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. laurillardii* as the valid Brazilian species. Curvello and Guérin (1993) recognized *E. lundii* as the Brazilian species. They rejected *E. laurillardii* 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 *laurillardii* 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 gênero *Eremotherium* monoespecífico. Caso confirmado tal hipótese, . . . , o nome válido para tal espécie única seria *E. laurillardii*, em cuja sinonímia 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 específica." 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 Paula 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 years Cartelle has recovered, from caves in Bahia, remains that offer better understanding of the nature of faunas in intertropical Brazil. The caves contain faunas 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, *Hopliphorus euphractus* Lund, and *Xenorhinotherium bahiense* Cartelle and Lessa. The discovery of the temperate *Lestodon armatus* (Paula Couto, 1973) in the State of São 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 plausible that temperate taxa spread northward during the late Pleistocene, possibly due to changing climatic con-

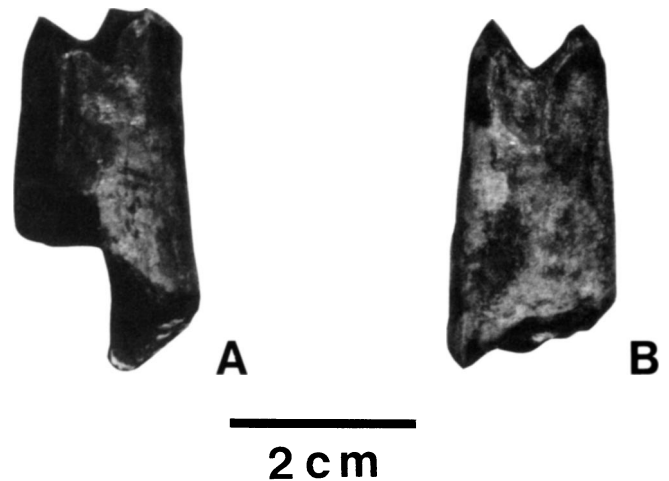


FIGURE 5. *Eremotherium laurillardii*. A, type specimen (ZMUC 1130); B, ZMUC 1131 in side view.

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 *laurillardii* 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 description of this species is in progress by De Iuliis 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. laurillardi* 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. laurillardi* 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 Vermelha, 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 significance. 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. laurillardi* 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 *Eremotherium laurillardi*. Brazil: 1, Rio Grande do Sul; 2, Paraná; 3, Mato Grosso do Sul; 4, Rio de Janeiro; 5, Espírito Santo; 6, Minas Gerais; 7, Goiás; 8, Bahia; 9, Sergipe; 10, Pernambuco; 11, Paraíba; 12, Rio Grande do Norte; 13, Ceará; 14, Piauí; 15, Acre. Peru: 16, Piura. Ecuador: 17, Guayas. Panama: 18, Herrera. Colombia: 19, Huila; 20, Cundinamarca; 21, Norte de Santander. Venezuela: 22, Lara; 23, Falcón. El Salvador: 24, San Miguel. Honduras: 25, Copán. Mexico: 26, Tabasco; 27, Jalisco; 28, Guanajuato. USA: 29, Texas; 30, Florida; 31, Georgia; 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 laurillardii* (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. laurillardii*. However, it has been used by and is well-known to vertebrate paleontologists, whereas *E. couperi* has largely been ignored. Therefore, *E. laurillardii* 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. laurillardii* 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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APPENDIX 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 Pernambuco (Sample 2). L = left; R = right.

Specimen	Side	Locality
<b>Sample 1</b>		
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 Onças, 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 Onças, Jacobina, Bahia, Brazil
MCL 9745	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9746	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9749	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9752	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9754	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9758	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9759	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9760	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9761	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9764	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9771	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9772	R	Toca Das Onças, Jacobina, Bahia, Brazil
MCL 9773	R	Toca Das Onças, Jacobina, Bahia, Brazil
<b>Sample 2</b>		
MNRJ 99V	R	Pernambuco, Brazil
MNRJ 100V	R	Pernambuco, Brazil
MNRJ 101V	R	Pernambuco, Brazil
MNRJ 102V	R	Pernambuco, Brazil
MNRJ 104V	R	Pernambuco, Brazil
MNRJ 105V	R	Pernambuco, Brazil
MNRJ 106V	R	Pernambuco, Brazil
MNRJ 107V	R	Pernambuco, Brazil
MNRJ 108V	R	Pernambuco, Brazil
MNRJ 109V	R	Pernambuco, Brazil
MNRJ 110V	R	Pernambuco, Brazil
<b>Sample 3</b>		
MNRJ 417V	L	Conquista, Bahia, Brazil
MNRJ 421V	L	Acre, Brazil
MNRJ 279V	R	Paraíba, Brazil
MNRJ 2130V	R	Boa Nova, Brazil
MNRJ 2948V	R	Paraíba, Brazil
MNRJ 2972V	R	Paraíba, Brazil
MNRJ 3871V	R	Espirito Santo, Brazil
BMNH M5689	L	Bahia, Brazil
<b>Sample 4</b>		
ROM 22013	L	Daytona Beach Bonebed, Daytona, Florida, USA
ROM 22014	L	Daytona Beach Bonebed, Daytona, Florida, USA
ROM 22015	L	Daytona Beach Bonebed, Daytona, Florida, USA
ROM 22016	L	Daytona Beach Bonebed, Daytona, Florida, USA
ROM 30773	L	Daytona Beach Bonebed, Daytona, Florida, USA
<b>Sample 5</b>		
ROM 4036	L	Coralito, Santa Elena Peninsula, Ecuador
ROM 4037	L	Coralito, Santa Elena Peninsula, Ecuador
ROM 24257	L	Coralito, Santa Elena Peninsula, Ecuador