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EREMOTHERIUM LAURILLARDI (LUND) (XENARTHRA, MEGATHERIIDAE), THE PANAMERICAN GIANT GROUND SLOTH: TAXONOMIC ASPECTS OF THE ONTOGENY OF SKULL AND DENTITION

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SYNOPSIS For most of the past 150 years the presence of only giant megatheriine ground sloths in the Pleistocene of Brazil has been recognised. However, it has recently been claimed that a dwarf *Eremotherium* species was present sympatrically with the large-sized giant ground sloth in northeastern and southeastern Brazil during the late Pleistocene and that the concept of a single Panamerican species was improbable. Based on analysis of the ontological sequence of skull suture closure and dental development of remains from a single locality, we demonstrate that the 'dwarf' species is based on the remains of immature individuals, at very early ontogenetic stages, of the large-sized species. Further, we reaffirm that the most parsimonious hypothesis is to consider all large-sized *Eremotherium* remains as belonging to a single species of Panamerican distribution.

KEY WORDS Megatheriinae, dwarf megathere, systematics, taxonomy, palaeobiogeography

Contents

INTRODUCTION

The Megatheriinae (giant ground sloths) are known from the middle Miocene (Friasian) to late Pleistocene (Lujanian and possibly Recent) of South America and the late Pliocene (Blancan) to late Pleistocene (Rancholabrean) of North America (De Iuliis & Saint-André 1997; De Iuliis & Cartelle 1999). With few exceptions (notably *Eremotherium eomigrans* De Iuliis & Cartelle, 1999), pre-Pleistocene species are known from sparse remains and knowledge of these species is very incomplete (De Iuliis *et al.* 2004). However, the remains of Pleistocene species are much more abundant, particularly those of *Megatherium americanum* Cuvier, 1796 from the Lujanian of Argentina and, even more so, *Eremotherium laurillardi* (Lund, 1842) from the Lujanian of much of South America north of Argentina and the Rancholabrean of North America. Based on the analysis of numerous remains from various localities spanning from southern Brazil to the northeastern part of the United States, Cartelle & De Iuliis (1995) showed that these represented a single large, intertropical *Eremotherium* species, thus referred to as the Panamerican giant ground sloth, *Eremotherium laurillardi.*

Guérin & Faure (2000), however, claimed that a dwarf *Eremotherium* species was present sympatrically with the Panamerican giant ground sloth in parts of northeastern and southeastern Brazil during the late Pleistocene (and early Holocene?). These authors recognised *E. laurillardi* as the valid name for this dwarf sloth and *E. rusconii* (Schaub, 1935) for the larger Brazilian species and implied that the concept of a Panamerican species was improbable. This report describes aspects of the ontogenetic development of the large Panamerican species, based on remains from a single locality, to demonstrate that the material used by Guérin & Faure (2000) to support the presence of a dwarf species belongs to a very young juvenile of the Panamerican species.

MATERIALS AND METHODS

Our analysis is based on 14 partial or nearly complete skulls in various stages of ontogenetic development from a single locality, Toca das Onças, Jacobina, Bahia, Brazil (Cartelle & Bohórquez 1982; Cartelle, 1992). That the skulls, all from the same level of one locality, may be arranged in an uninterrupted sequence from very young to aged adult individuals conclusively demonstrates that the remains belong to a single species. Also analysed were over 300 isolated molariforms and 200 molariforms implanted in skulls and mandibles from the same level of Toca das Onças. Various of the cranial specimens are noted below and all are discussed at length by Cartelle (1992) and De Iuliis (1996). The molariforms are listed in the Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCL) database.

Terminology and interpretation of the composition of the molariforms follows Ferigolo's (1985) views on *Megatherium americanum*, since the molariforms of *E. laurillardi* are morphologically nearly identical and very probably of similar composition. Nomenclature for the skeletal anatomy follows the *Nomina Anatomica Veterinaria.*

Abbreviations

MCL = Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais, Belo Horizonte, Brazil.
DMAS = Daytona Museum of Arts and Sciences, Daytona Beach, USA.
M = upper molariform.
m = lower molariform.
ROM = Royal Ontario Museum, Toronto, Canada.
UCMP = University of California Museum of Paleontology, Berkeley, USA
USNM = National Museum of Natural History, Smithsonian Institution, Washington, USA.
UFPe = Universidade Federal de Pernambuco, Recife, Brazil.
ZMUC = Zoologisk Museum Universitat Copenhagen, Copenhagen, Denmark.

TAXONOMIC HISTORY OF *E. LAURILLARDI*

A detailed taxonomic history of *E. laurillardi* was given by Cartelle & De Iuliis (1995) so only those aspects relevant to the current paper are given here. Lund (1842) described and figured a molariform (ZMUC 1130) and figured a second molariform (ZMUC 1131) from Lapa Vermelha, a cave in Vale do Rio das Velhas, Lagoa Santa (Minas Gerais, Brazil). These molariforms are approximately one-quarter of the size of those belonging to the larger megatheriine sloths, known then mainly from Argentina as *Megatherium americanum* (or its synonym, *M. cuvieri*). Lund (1842) considered that these smaller teeth represented a megatheriine species about the size of a tapir that he named *Megatherium laurillardi.* Earlier, Lund (1840) had reported a much larger molariform (ZMUC 867) from the caves, which he (Lund 1842) figured and assigned to *Megatherium americanum.* Nearly all subsequent authors (e.g. Winge 1915; Paula Couto 1950) have concluded that the small molariforms assigned to *M. laurillardi* by Lund (1842) represented juveniles of the larger species present in the caves.

The work of various researchers, mainly during the central part of the last century, led to two main developments: (1) recognition that the large megatheriine remains, mainly from intertropical New World countries, did not belong to *Megatherium* but represented a distinct genus, *Eremotherium* (e.g. Spillmann 1948; Hoffstetter 1952; Paula Couto 1954) and (2) a profusion of species were erected for these large *Eremotherium* remains, seemingly one for every country and based usually on small samples of fragmentary material (e.g. Schaub 1935; Spillmann 1948; Osten 1951; Porta 1961). During the latter part of the century, with the gradual acquisition of larger collections, researchers began to doubt the validity of many of these species (e.g. Bocquentin 1979; Cartelle & Bohórquez 1982). Finally, the recovery of the very large collections from Toca das Onças and Daytona Beach Bonebed (Daytona Beach, Florida, USA) allowed Cartelle & De Iuliis (1995) to demonstrate that all large *Eremotherium* remains, ranging from Brazil to the southeastern United States, most probably represented a single species.

With the recognition of *Eremotherium*, Lund's epithet *laurillardi* thus became the oldest available name for the single species. Nearly all authors subsequent to Lund (1842) regarded the molariforms on which the species was based as diagnostically inadequate, mainly because the material belonged to a juvenile. However, Cartelle & De Iuliis (1995) argued that the name was admissable and that one of the molariforms (ZMUC 1130) be considered the holotype by original designation.

Recently, however, Guérin & Faure (2000) claimed that Lund's juvenile molariforms belonged to a young individual of a dwarf *Eremotherium* species, the adult of which is supposedly represented by a left maxilla and molariforms (UFPe 3300 and 3301) from Conceição das Creoulas, Salgueiro, Pernambuco, Brazil. Additional small juvenile molariforms were also reported. Guérin & Faure (2000) considered *E. laurillardi* to be the valid name for this dwarf species and that remains of larger *Eremotherium* individuals from Brazil, at least, belonged to *E. rusconii*.

A LATE PLEISTOCENE PANAMERICAN *EREMOTHERIUM* SPECIES?

The path toward recognising *E. laurillardi* as the only large-sized late Pleistocene *Eremotherium* species with a Panamerican range began definitively with the work of Cartelle & Bohórquez (1982). Their examination of numerous skeletal elements of *E. laurillardi* allowed these authors to determine that: (1) the elements tended to fall into two groups, those of large and small size and (2) each group included both adult and juvenile specimens. These authors interpreted these patterns as indicating size differences due to sexual dimorphism.

Cartelle & De Iuliis (1995: 833) provided quantitative evidence for dimorphism in establishing 'a variation of nearly 35% in linear measurements among both adult and juvenile members of a single population' based on measurements of astragali, among the most frequently recovered skeletal elements, in the sample recovered from Toca das Onças. As there seems to have been some misinterpretation of this evidence (e.g. Guérin & Faure 2000), we offer the following as clarification.

Among adults there is a difference in linear dimensions of nearly 35% between the largest and smallest astragali. There are juvenile astragali (based on unfused or nearly fused epiphyseal articular surfaces) that are nearly the same size as the largest adult astragalus and the smallest adult astragalus. The difference between these juvenile astragali is therefore also nearly 35%. Although Cartelle & De Iuliis (1995) did not state it explicitly, there are, clearly, also many juvenile astragali that are considerably smaller that the smallest adult astragalus. Thus, nearly identical proportions exist among the two groups of larger (presumably mainly male) and smaller (presumably mainly female) adult-sized individuals, but the groups include both adults and juveniles. While the elements tend to fall into these groups, there is no distinct separation between the groups; i.e. a continuous size range exists. The probability of dimorphism in this population is strengthened in that these two parameters are clearly consistent for the long bones and the elements of the manus and pes (Cartelle 1992; De Iuliis 1996); in each case tending to fall into large-sized and small-sized groups, each of which includes adult and juvenile remains. This circumstance is especially notable for the long bones: the juvenile or subadult remains that are nearly as large as the largest adult remains, but considerably larger than many of the adult and subadult remains of the small-size group, are particularly striking examples.

Morphological differences among skeletal elements are relatively minor. More significant, however, is that a nearly identical range of morphological variation exists within the large-sized and small-sized groups, so that there is no morphological justification to support their specific distinction. In other words, the range of morphological variation may clearly be considered intraspecific. This conclusion on intraspecific variation is based on the study of numerous elements, particularly of the manus and pes for which the remains of over 50 individuals have been recovered.

The observations made so far in this section are based on the remains from Toca das Onças and form a body of evidence that strongly suggest that the remains represent a single, probably sexually dimorphic species. Cartelle (1992), Cartelle & De Iuliis (1995) and De Iuliis (1996) provided additional evidence that all the large, late Pleistocene *Eremotherium* remains from North, Central and South America probably represented a single species. This line of reasoning was based mainly on the fact that the two largest collections, from nearly opposite ends of the geographical range of all large, late Pleistocene *Eremotherium* remains, could not be distinguished on either size or morphology. Indeed, as Cartelle & De Iuliis (1995) noted, the Toca das Onças collection alone subsumes nearly all the size variation as well as the morphological variation reported in the literature or observed by these authors. The exceptions are two femora (UCMP V420-36884, from El Salvador, length = 895 mm, and USNM 37-57, from Panama, length = 867 mm) that exceed the longest femur from Toca das Onças (MCL 9524, length = 826 mm) and a centrale (USNM 20872, from Panama) reported by Gazin (1957). The latter is a uniquely anomalous condition representing a medial portion of an unciform that is separate from the main body of this element; other unciform specimens from the same Panama locality are as those from all other localities yielding *E. laurillardi* (Cartelle & De Iuliis 1995).

Two further lines of evidence may be added in support of the idea of a sexually dimorphic Panamerican species. One is based on late Pleistocene pelves from the Daytona Beach Bonebed (DMAS and ROM 4592). De Iuliis (1996) interpreted morphological differences in these pelves, most notably in relative transverse diameter and shape of the pelvic canal, as possible evidence for sexual dimorphism.

The second line of evidence is provided by an earlier large *Eremotherium* species, *E. eomigrans*, from the late Pliocene–early Pleistocene of Florida, described by De Iuliis & Cartelle (1999) as the sister species of *E. laurillardi*. *Eremotherium eomigrans* is best known from the latest Blancan Haile 7C locality, which yielded the remains of large and small adult individuals as well as an immature individual similar in size to the large adult. The size range of the two adults is almost identical to that for the Toca das Onças collection (approximately 35% for linear measurements of the astragalus: see De Iuliis & Cartelle 1999 for further details).

ASPECTS OF ONTOGENETIC DEVELOPMENT

Dentition

Among the abundant material available for study of *E. laurillardi* are developmental stages ranging from neonatal (and possibly fetal) to very aged individuals, a circumstance that also provides considerable data on intraspecific variation. Although little has been published on these themes, Cartelle (1992) described and figured the early stages of dental development and determined the wide range of individual variation that occurs in some of the molariforms, particularly M1 and M5, and Cartelle (1994*a*) noted various modifications that occurred in molariform morphology during the transition

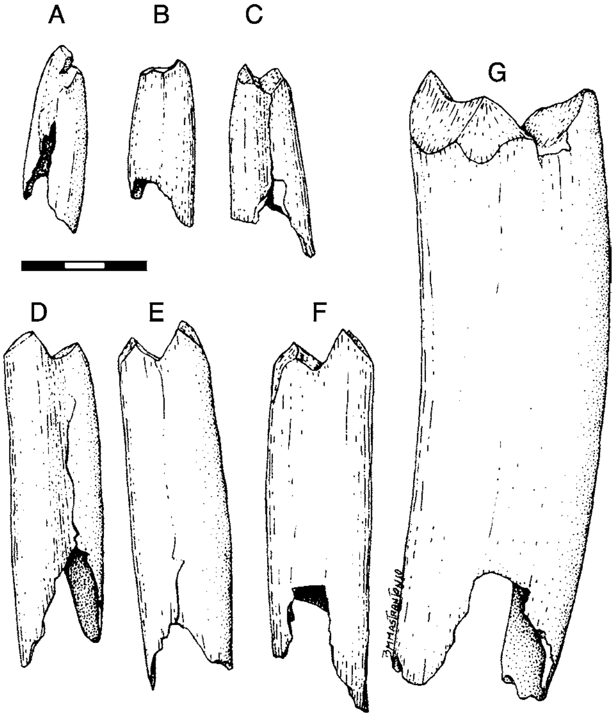

Figure 1 Various stages of growth among molariforms recovered from the same locality (Toca das Onças. Jacobina. Bahia, Brazil). **A**, MCL 3743; **B**, MCL 3902; **C**, MCL 3909: molariforms of very young individuals. The molariforms are pyramidal in form and the occlusal crests are in the process of formation. **D**, MCL 7390; **E**, MCL 7391; **F**, MCL 7374: molariforms of juveniles with prismatic form. These are equivalent in their stage of development to the two molariforms (ZMC 1130 and 1131) assigned by Lund (1842) to *Megatherium laurillardi*. **G**, MCL 7350: molariform of an adult individual. The mesiodistal length is greater at the occlusal surface than at the base of the tooth. This tooth is equivalent in its stage of development to the molariform (ZMC 867) identified by Lund (1842) as *Megatherium cuvieri*. Scale bar = 30 mm.

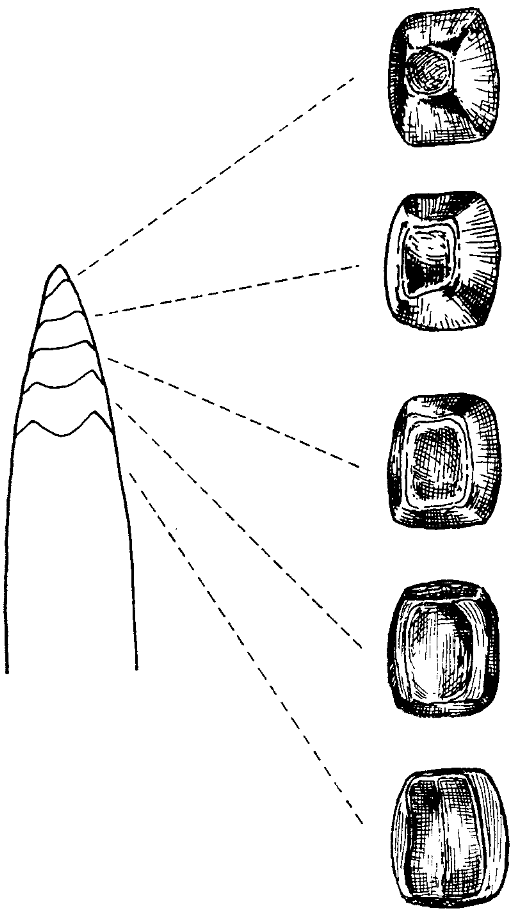

Figure 2 Schematic representation (based on MCL specimens) of wear in the formation of occlusal crests of the molariforms, still pyramidal in form (i.e. of very young individuals). Modified from Cartelle (1992).

from juvenile to adult. The following observations are based, as noted above, on a large sample, including more than 500 molariforms, that has allowed us to formulate various conclusions and outline clearly the ontogenetic development of the dentition so that the stage to which a particular (even isolated) molariform belongs can be determined with a high degree of confidence.

The open-rooted molariforms grew throughout life, as is indicated by teeth belonging to old individuals in which there is no evidence of occlusion of the pulp cavity. The volume of the cavity remained fairly constant throughout life and occupied about two-thirds of the height of the molariform, as determined from specimens that preserve the very thin basal walls of the molariform.

An incomplete dentary (MCL 7235) of a very young, possibly neonatal, individual preserves a nearly unworn m3 and m4 with broken occlusal surface. The mandibular canal, through which passed the ventral alveolar nerve and vascular vessels, was still in the process of formation and thus remains unclosed.

The cranial remains of MCL 7343, another young individual (based on open skull sutures), preserves M1–M4, which display very slight, distal wear on their occlusal apices. The upper and lower molariforms are pyramidal in shape and project to similar degrees beyond the alveolar margins. We may thus conclude that dental eruption occurred simultaneously, as in the scelidotheriine *Catonyx cuvieri* (Lund), the mylodontine *Glossotherium lettsomi* (Owen) (Cartelle 1992) and the nothrotheriine *Nothrotherium maquinense* (MCL 2824). In the latter, dental eruption had occurred in utero, as shown by the fossilised fetus of this species described and figured by Cartelle (1994*b*).

The pyramidal molariforms occurred only in very young juveniles, as described above. In slightly older, but far from nearly mature, individuals the molariforms had already assumed a prismatic form. For example, they are prismatic in individuals in which interdentary symphyseal ossification was in progress, cranial sutures were still open and the occipital condyles still undergoing endochondral ossification. In other words, the molariforms are prismatic even in very young individuals (Figs 1 & 2).

The transverse occlusal crests, formed initially from minor wear of the orthodentine layers of the molariforms, developed early (Cartelle 1992, 1994*a*). Indeed, by the time that a molariform had assumed its prismatic form, the wear resulting in the familiar occlusal pattern of megatheriine teeth – two transverse crests separated by a valley – was

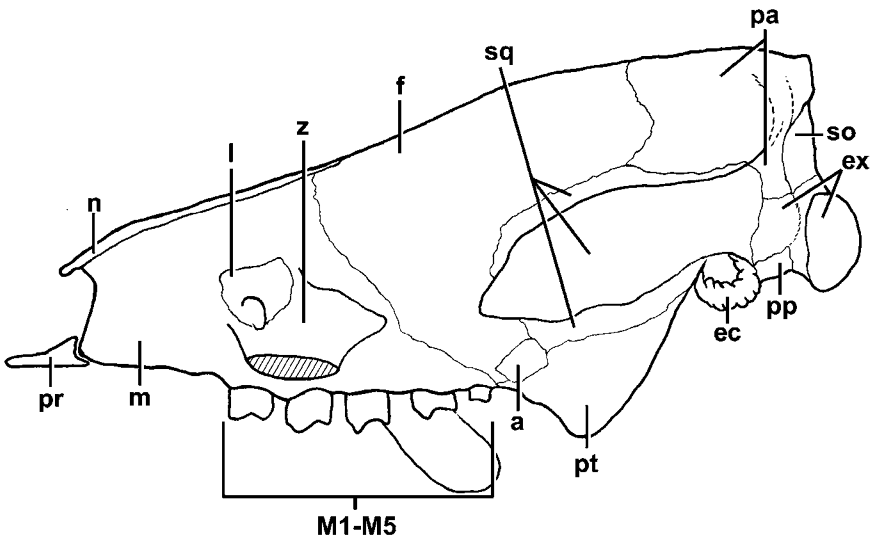

Figure 3 Schematic diagram showing skull sutures of a young individual of *Eremotherium laurillardi* (based on MCL 7230). Abbreviations: a, alisphenoid; ec, ectotympanic; ex, exoccipital; f, frontal; l, lacrimal; M1–M5, upper molariforms; m, maxilla; n, nasal; pa, parietal; pp, paroccipital process; pr, premaxilla; pt, pterygoid; so, suboccipital; sq, squamosal; z, zygomatic.

already in place. Although prismatic, molariforms had to undergo considerable further development before attaining adult form and size: for example, some (M2–M4, m2–m3) could achieve a tenfold increase in volume (Fig. 1).

At the stage in which a prismatic form had just been achieved, most of the cranial sutures were still open. Indeed, the sutures between the basioccipital and exoccipitals, on which the occipital condyles were still forming, had not yet closed. We therefore emphasise that the presumption made by various authors (e.g. Hoffstetter 1952; Guerin & Faure 2000) that a prismatic molariform indicates attainment of adulthood in *Eremotherium* and, in particular, *E. laurillardi*, is incorrect. This had already clearly been stated by Cartelle (1994*a*: 577, translated from the original):

> 'Pyramidal molariforms occur only in very young individuals. In smaller individuals in which the skull sutures were still clearly apparent and the dentaries had just begun to co-ossify the molariforms had already become nearly prismatic. Isolated molariforms of such morpholgy could be considered as having belonged to an adult individual of a small sized species. Indeed, this was Lund's (1842) interpretation in attributing juvenile molariforms, which had already become prismatic, to the species '*Megatherium laurillardi.*' The practice, applied by many authors to extinct sloth species, of equating prismatic teeth with adult individuals is not, in this case, correct.'

As noted, a tooth could experience a tenfold increase in volume once the prismatic stage had been reached. This growth, however, was accompanied by a relative mesiodistal narrowing of the tooth basally. For example, in the large m3 MCL 7360 the extra-alveolar mesiodistal length is 45 mm, whereas basally it is only 33 mm. Thus, contrary to the commonly accepted view (e.g. as by Hoffstetter 1952), the adult molariforms of *Eremotherium* are not prismatic, but are mesiodistally narrower basally than apically. Nearly perfectly preserved specimens are required to appreciate this form (Fig. 1G).

Cranium

The following observations are based on 14 skulls from Toca das Onças (Cartelle & Bohórquez 1982), that represent from probably neonatal to very aged life stages. Most of the specimens are extremely well-preserved. We therefore have a rare situation allowing us to observe and follow numerous aspects of ontogenetic cranial development that occurred in this species and that reflect various ages. For the sutural contacts of the skull bones, see Fig. 3.

In the stage described above in which the molariforms are still pyramidal, none of the maxillar sutures were closed (e.g. MCL 7241). By the time the molariforms had become prismatic (and the individual was still very young), the sutures of the ring-like ectotympanic with the squamosal and entotympanic were nearly closed. All the others remained open. The occipital condyles had not completed their formation and, as noted earlier, the exoccipitals had not fused to the basioccipital (MCL7238 (Fig. 4) and MCL 7237 (Fig. 5)). The specimen described by Guérin & Faure (2000) as a dwarf species of *Eremotherium* apparently belongs to this ontogenetic stage (Fig. 6).

As development progressed, closure of the sutures of the occipital complex occurred (MCL 1702), followed by those of the lacrimomaxillar (MCL 7239) and then by those of the frontoparietal and frontomaxillar sutures (MCL 7240). Co-ossification of the other dorsal bones of the cranium was generally more delayed. For example, the skulls of aged individuals (MCL 7239), based on the fact that the molariforms are in the upper size range and could thus not have increased much more in volume, still have some unfused dorsal cranial sutures (e.g. interparietal suture). In aged individuals with large molariforms (MCL 1700 and 1701: Fig. 7) the median palatal sutures have finally closed, with fusion occurring between the horizontal laminae of the maxillae and palatines. Also, closure of the transverse palatal sutures (between the

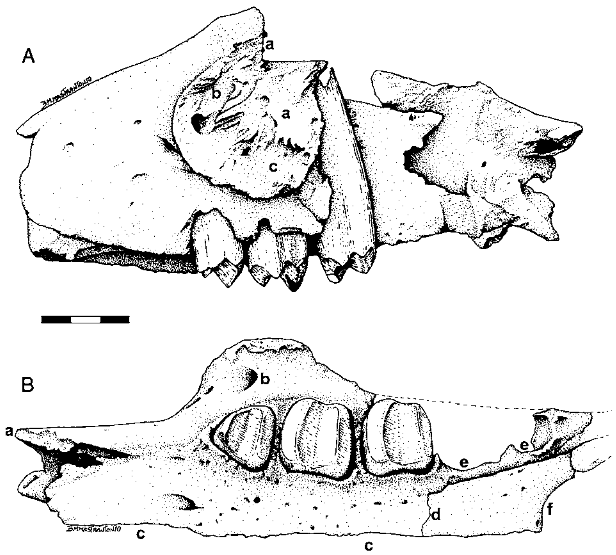

Figure 4 MCL 7238/01. **A.** lateral view of left maxilla, with M1–3, of a juvenile of *Eremotherium laurillardi*. Abbreviations: **a**, rugosities on the sutural surface for the frontal; **b**, rugosities on the sutural surface for the lacrimal; note the opening of the lacrimal canal; **c**, rugosities on the sutural surface for the zygomatic. Despite its very young age, the molariforms of this individual had already become prismatic, as shown in Fig. 1D–F; **B**, ventral view of left maxilla and palatine, with M1–3, of a juvenile of *Eremotherium laurillardi*. Abbreviations: **a**, maximal anterior projection of the lateral part of the maxilla; **b**, infraorbital foramen; **c**, intermaxilar suture in the palatal region; **d**, transverse palatal (maxillopalatine) suture; **e**, lingual alveolar margins of M4–5; the posterior portion of the maxillopalatine suture lies parallel and lingual to the alveolar margin; **f**, posterior margin of palatine, forming choanal border. Scale bar represents 30 mm.

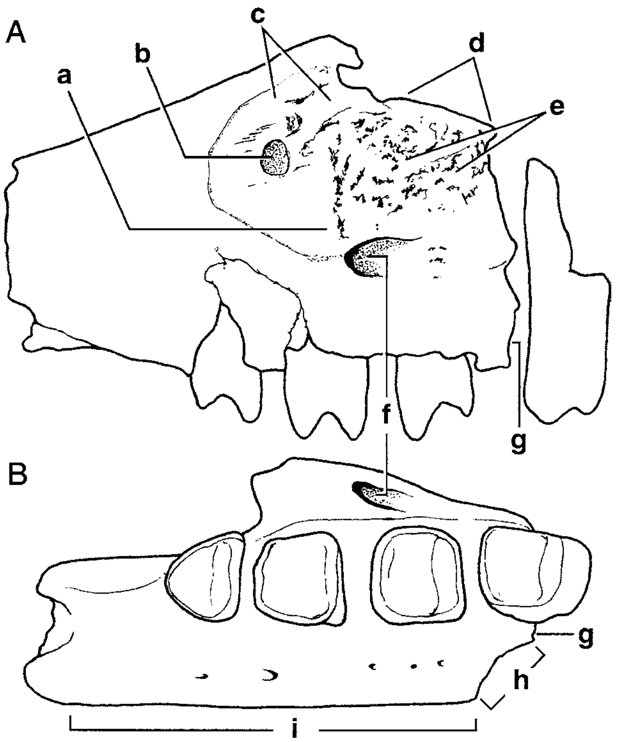

Figure 6 Sketch of UFPe 3300–3301 (modified from Guérin & Faure 2000: fig. 2), indicating the regions discussed in the text. The figure clearly depicts a very young juvenile of *Eremotherium laurillardi* in, **A**, lateral and **B**, ventral views. Abbreviations: **a**, maxillar surface for articulation with the zygomatic; **b**, posterior opening of the lacrimal foramen in the maxilla; **c**, maxillar surface for articulation with the lacrimal; **d**, anterior half of posterodorsal margin of maxilla; **e**, maxillar surface for articulation with the frontal; **f**, posterior opening of infraorbital foramen; **g**, broken edge of maxilla; **h**, anterior portion of palatal maxillopalatine suture; **i**, intermaxillar suture.

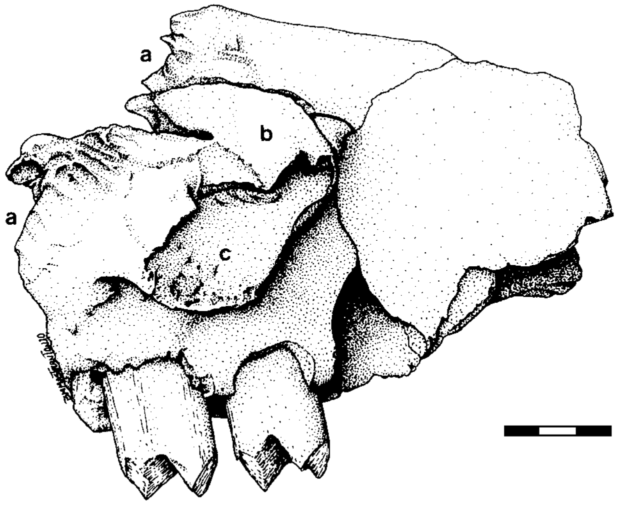

Figure 5 MCL 7237. Lateral view of right partial maxilla, with M2–3 (which had already attained a prismatic form) and partial lacrimal of a juvenile of *Eremotherium laurillardi*. Abbreviations: **a**, articular surface of the maxilla for the frontal; note rugosities typical of a squamous suture; **b**, fragment of lacrimal articulating with, but not yet fused to, the maxilla; **c**, articular surface of maxilla for the zygomatic. Scale bar represents 30 mm.

palatal process of the maxilla and the horizontal lamina of the palatines) occurred.

In even older specimens fusion of the nasofrontal suture had occurred, but the maxillopremaxillar, nasomaxillar, internasal and maxillojugal sutures had not closed (MCL 1700 and 1701). Indeed, not even in the very oldest skulls available is there fusion of the two portions forming the zygomatic arch – the temporal process of the jugal and the zygomatic process of the temporal. To supplement such observations, we are in the process of analysing the progression of sutural closure with respect to relative developmental age in various other skeletal elements, such as those of the hyoid, manus, pes and sacral vertebrae. In addition to considering age, we wish to determine whether the progression of sutural closure was related to gender.

MCL 7237 and MCL 7238/01 are two fairly complete skulls that preserve most of the dentition. The former is at approximately the same developmental stage as the cranial fragment (UFPe 3000) described and figured by Guérin & Faure (2000), whereas MCL 7238/01 is slightly older and can serve as our point of reference. In this specimen the articular facets of the maxilla for the premaxilla bear more strongly developed rugosities than in MCL 7237, indicating a more advanced ontogenetic stage. Certainly, the variations due to age, such as the degree of sutural closure and

Figure 7 MCL 1702/01. Ventral view of anterior part of the skull of a young adult individual, with M5s missing, showing open **a**, intermaxillar, **b**, transverse (maxillopalatine) palatal and **c**, interpalatine sutures. The basal (interalveolar) portions of the molariforms had already become narrower than the exposed portions (crowns). Scale bar represents 30 mm.

development of the molariforms are even clearer in MCL 7237 (Fig. 5), the younger individual, than in MCL 7238 (Fig. 4).

In MCL 7238/01 the molariforms are prismatic and the crests and valleys are formed. Fusion of a few of the cranial sutures had begun, such as between the ectotympanic and squamosal and entotympanic, although the lines of fusion are still clearly discernible. The exoccipitals had also fused with the basioccipital, but all other sutures remain open. In addition, the occipital condyles were still undergoing ossification: they are small in size and entirely rugose.

The relationships of the maxilla with surrounding skeletal elements are clearly discerned in MCL 7238/01 (Fig. 4) and in the younger MCL 7237 (Fig. 5). In discussing these, we will provide observations on later ontogenetic stages as well. The long, oblique nasomaxillar sutures are completely open, but they remain unclosed even in the oldest skulls of *E. laurillardi* (e.g. MCL 1207), as is also true of the premaxillomaxillary suture. The articular surface of the maxilla for the premaxilla is smooth and nearly without rugosities in younger individuals. With increasing age, this surface became more complex and was characterised by irregular rugosites that reinforced the contact between the maxilla and premaxilla.

There are also various other incomplete specimens in addition to the 14 cited and, in all of them, independently of age, the lateral margin of the maxilla extends farther anteriorly than the maxilla's palatal process for articulation with the premaxilla. The anterolateral margin of the maxilla is, particularly in young individuals, delicate and susceptable to wear and fragmentation. As noted above, palatal sutures such as the palatomaxillar remained open for much of the ontogenetic developmental period, as is evident in MCL 7238/01. In the latter, the transverse palatal suture, occuring in the transverse plane between M3 and M4, is also open. A narrow strip of the maxilla forms the lingual borders of the alveoli for M4 and M5 and surrounds the distal surface of the latter tooth. Posteriorly on the palate the palatines form the margin of the internal choanae, but their more posterior portions project distal to M5 (Fig. 4B and see also Fig. 7). In MCL 7238/01 the posterodorsal surface of the maxilla, destined for sutural contact with the frontal, bears rugosities and sulci, indicating a squamous suture that remained open throughout much of ontogenic development (Fig. 4A).

The morphology of the zygomatic process of the maxilla is clear in MCL 7238/01 and 7237 (Figs 4A & 5) and permits unequivocal interpretation of this individual's age. It bears a circular articular surface whose most dorsal portion serves for articulation with the lacrimal. The fusion between the lacrimal and maxilla occurred at the same time as the fusions between the ecto- and entotympanics and between the ectotympanic and the squamosal, as described above, i.e. in very young individuals. In MCL 7237 and 7238/01 fusion between the lacrimal and maxilla had not occurred and, thus, clearly attests to the very young age of these individuals. A small portion of maxilla, ventral to the lacrimal, served for articulation with the jugal, but in none of the specimens, even the oldest, have we observed fusion between the jugal and maxilla.

DISCUSSION AND CONCLUSIONS

The initial observations that eventually led to the recognition of the single Panamerican ground sloth species *E. laurillardi* by Cartelle & De Iullis (1995) was the presence (in all specimens for which it could be studied) of the element that De Iuliis & Cartelle (1994) termed the metacarpal–carpal complex (MCC). The study of different Megatheriidae and of numerous specimens of *E. laurillardi* allowed these authors to identify the elements that had fused to form the MCC and thus to recognise the different skeletal patterns in the manus among Megatheriidae. In concluding that a single Panamerican species had existed during the mid to late Pleistocene over a wide geographical area stretching from southern Brazil to the northeastern USA, these authors (Cartelle 1992; De Iuliis & Cartelle 1994; Cartelle & De Iuliis 1995; De Iuliis 1996) analysed numerous remains of this species from various localities in Brazil, Honduras, El Salvador, Equador, Peru and the USA (see also Toledo 1989 for Brazilian remains). The range of morphological and mensurate variation in the MCC from various Brazilian localities and, in particular, from Toca das Onças (a locality that has yielded the largest sample of remains, including some 3000 pieces), encompasses the variations from other localities. This is also true for nearly all of the other skeletal elements (Cartelle 1992; Cartelle & De Iuliis 1995; De Iuliis 1996), including a unique bony element, termed the cervical sesamoid by Cartelle (1992), that occurs among the Brazilian specimens and was also identified from the Daytona Beach Bonebed.

Following the analysis of numerous remains, Cartelle & De Iuliis (1995) recognised not only the existence of a single Panamerican species, but also confirmed the evidence for the presence of sexual dimporphism within *E. laurillardi*, a hypothesis first proposed by Cartelle & Bohórquez (1982) for the Toca das Onças and other Brazilian remains (and to which, at that time, the name *E. laurillardi* was applied).

Cartelle & De Iuliis (1995) justified the validity of the specific name *E. laurillardi* because the juvenile teeth (which may be referred to stage B in Fig. 1) on which Lund (1842) established the species clearly belong to the same species represented by adult molariforms that the Danish palaeontologist subsequently recovered from Lagoa Santa, Minas Gerais, Brazil. The remains of giant ground sloths from Minas Gerais and neighbouring Brazilian states (Bahia, Espírito Santo, Rio de Janeiro, São Paulo e Goiás), an area covering over 2 million km^2, have been examined by us. Without exception, all may be confidently assigned to the same species, *E. laurillardi*. The only other species to which the molariforms discovered by Lund in Lagoa Santa might be assigned is *Megatherium americanum*, but the latter had an exclusively southern distribution at lower altitudes. Furthermore, the juvenile molariforms are morphologically identical to those found subsequently in the same region and undoubtedly belong to *E. laurillardi*.

In concluding that a single species was present over such a large geographical region (from the northeastern USA to the south of Brazil), Cartelle & De Iuliis (1995) implied that the specimens recovered from the USA were not due to speciation from an earlier Plio–Pleistocene immigrant stock, but that they were conspecific with a form that had originated in the southern hemisphere. It would seem unlikely that separate speciation events, one in the northern and another in the southern hemisphere, would produce such morphologically similar forms, particularly given the near continuous distribution of the populations over the Panamanian isthmus, Central America and Mexico. Hypothetically, the direction of dispersal could have been from north to south as well as from south to north: i.e. a North American origin for *E. laurillardi* of originally South American immigrant ancestral stock, which could have repopulated South America. The biogeographical history of xenarthrans and the near contemporaneous mid to late Pleistocene ages of the remains under consideration suggest that a migration from south to north would be more logical.

The criticism of Guérin & Faure (2000: 477) in this regard is not justified '... il n'y aurait pás eu de spéciation après le passage du genre en Amérique du Nord, ce qui ferait d'*Eremotherium* un cas rare parmi les grands mammifères migrant au Plio-Pléistocène d'un empire biogéographique à un autre.' Migrations of a single species across the Panamanian isthmus, some occurring near the end of the Pleistocene, in either direction were not particularly rare. This suggests that there is no need to consider the migration of *E. laurillardi* necessarily as a rare instance. It is perhaps the only megafaunal-sized mammal that did not speciate, but there are numerous instances where small and large mammals migrated without speciating. Various authors (e.g. Paula Couto 1979; Berta, 1985; Cartelle & Abuhid 1989) have defended the presence of a single *Smilodon* species; Turner & Antón (1997) indicated that there were two species, and that one of them (*S. fatalis*) occurred in both North and South America. *Panthera onca* is widespread from South America to the southern United States (Seymour, 1989, 1993), while the puma (cougar or mountain lion, *Puma concolor*; see Morgan & Seymour, 1997) also occurs in both North and South America (Turner & Antón, 1997). The dire wolf, *Canis dirus*, was present in North and South America and ranged widely from Alberta, Canada, south to Talatra, Peru and Tarija, Bolivia (Berta 1988, Dundas 1999). *Odocoileus virginianus*, of North American origin, occurs in Bahia, Brazil in the late Pleistocene (Cartelle 1999). Furthermore, species of the South American *Tayassu*, *Dasypus*, *Neochoerus* and *Myrmecophaga* have clear representation in the North (Webb 1985; Shaw & McDonald 1987).

Guérin & Faure (2000) defended the existence of a dwarf, intertropical *Eremotherium* species named *E. laurillardi*. However, the descriptions of ontogenetic development provided above, based on a relatively complete series of specimens, invalidates their conclusion. We believe that the only correct conclusion of Guérin & Faure (2000) is that *E. laurillardi* is in fact a valid specific name and, moreover, that it has priority. As was justified in our earlier work (Cartelle & De Iuliis 1995) and reaffirmed here, it is the valid name for the single, giant ground sloth species of *Eremotherium* with a Panamerican distribution.

The supposed dwarf species was founded, without doubt, on a very young juvenile (UFPe 3300) of the giant Panamerican species *E. laurillardi* that Guérin & Faure (2000) mistakenly considered adult for the following reasons:

1. Cartelle & Bohórquez (1986) described the premaxilla of *E. laurillardi*. They noted that the anteroventral surface of the maxilla that articulates with the premaxilla is smooth and lacks the more complex folding or furrowing (i.e. rugosities) that develops with age to reinforce the articulation between the maxilla and premaxilla. The condition of the articular surface in UFPe 3300 simply indicates that it belongs to a very young animal, as in, for example MCL 7238 and 7237.
2. The anterolateral margin of the maxilla is not vertically orientated in any *Eremotherium* adult or juvenile, for which this portion of the element is reasonably complete. Instead it is convex anteriorly. It is clear that the truncated and rectilinear appearance of the anterolateral surface of UFPe 3300 (see Fig. 6) is due to breakage. We have noted above that this portion is very delicate and often broken, particularly in young specimens. The most anterior extension of the maxilla almost certainly occurred laterally in UFPe 3300, as in other *Eremotherium* remains, rather than ventrally as stated by Guérin & Faure (2000). A more anterior ventral extension of the maxilla cannot therefore be demonstrated and its use as a character to diagnose a dwarf species is invalid.
3. Posterodorsally the maxilla has a squamous articulation with the frontal. In all specimens examined by us, the maxilla bears on its posterodorsal surface well-developed striations for this squamous articulation. This suture is open in juvenile specimens, as noted above. In the lateral view of UFPe 3300 (Guérin & Faure 2000: fig. 2) the

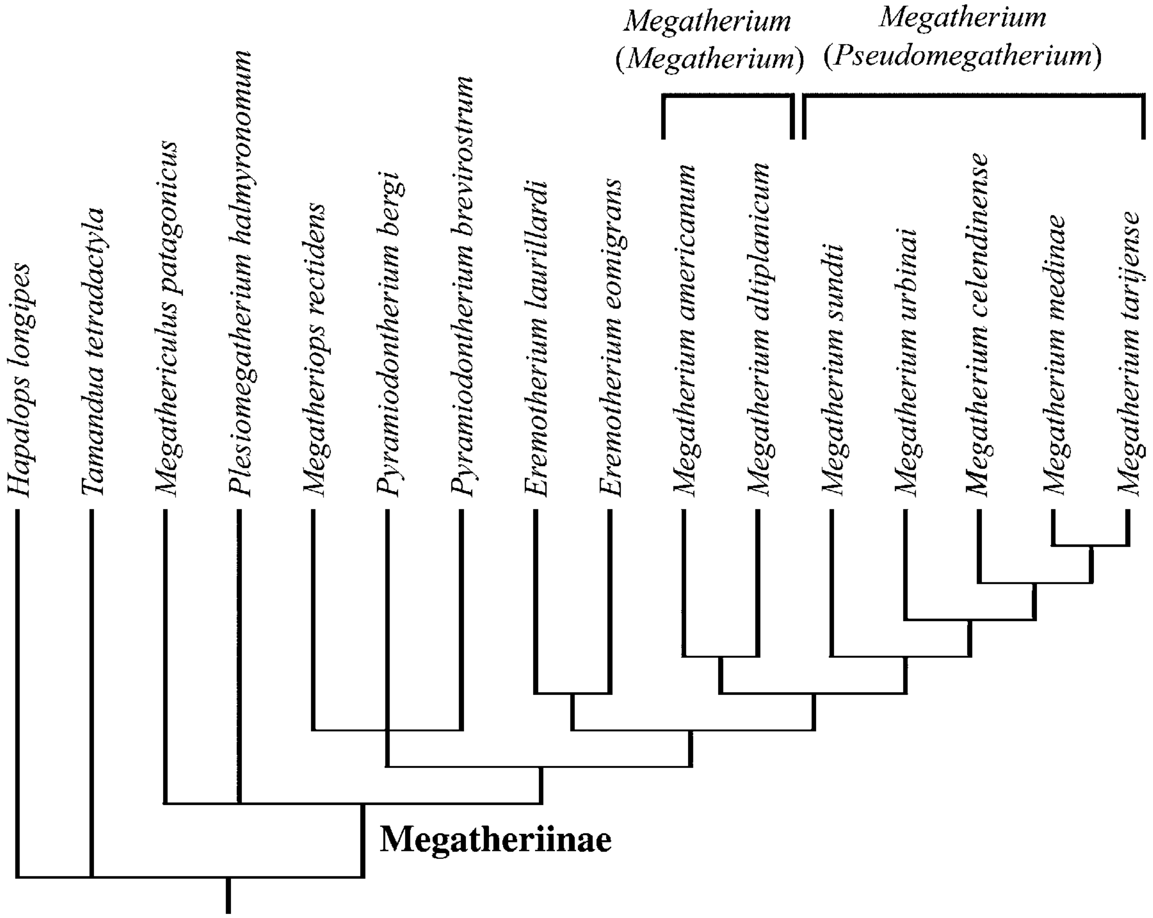

Figure 8 Cladogram showing relationships among Megatheriidae (adapted from Pujos, 2005).

articular striations on the posterodorsal surface of the maxilla for the frontal are clearly visible, indicating, without doubt, that the individual is a juvenile (see Fig. 6). Its small size is thus due to age rather than being a specific character.

4. The same figure of UFPe 3300 clearly shows the large, circular articular surface that surrounds the lacrimal foramen and lies on the zygomatic process of the maxilla. The irregular striations that indicate its articular function are in plain view. The ventral third of this surface served for articulation with the jugal; the portion dorsal to it for the lacrimal. In very young (and perhaps neonate) individuals this bone was not fused to the maxilla. Furthermore, as noted above in the discussion of sequential ontogenetic development of the skull, the lacrimomaxillar contact was ontogenetically among the first sutures to close. Clearly then, as the lacrimal had not yet fused to the maxilla in UFPe 3300 (see Fig. 6), this individual was a very young animal.
5. Guérin & Faure (2000: 478, 480) stated that the palate of UFPe 3300 'est brisé en arrière au niveau de M4/' and 'Il semble en dépit des cassures que le sommet de l'échancrure post-palatine se situe approximativement au niveau de l'avant de M4/, alors qu'il atteint l'arrière de M4/ chez *Eremotherium* et l'arrière de M5/ pour *Megatherium americanum*.' This interpretation for the position of the palatal notch is incorrect. In an adult individual of *Eremotherium* both the median palatal and transverse palatal sutures would be closed. It is clear from the ventral view of UFPe 3300 (Guérin & Faure 2000: fig. 2) that the median suture is open. The form of the medial margin of this specimen cannot correspond to a line of breakage: it is nearly rectilinear and coincides with the median suture of the left and right maxillae. Likewise, the posterior margin of the specimen cannot correspond to the summit of the palatal notch, as asserted by Guérin & Faure (2000); rather it is the transverse palatal suture between the maxilla and the palatine, the latter bone being absent in this specimen. As is shown clearly in Fig. 4 and 7 (MCL 7238/01 and MCL 1702/01), the transverse palatal suture typically begins at the level between M3–M4, curving posterolaterally around and posterior to M5, while the palatal notch lies at the level of M5.
6. The morphological analysis of the molariforms UFPe 3300 and 3301 (Guérin & Faure 2000: fig. 2) and their association with the left maxilla indicate that they do not belong to an adult animal of small size, as Guérin & Faure (2000) assert, but to a very young individual. Guérin & Faure (2000) considered the prismatic form of the molariforms to be strong evidence of adult status of UFPe 3300 and 3301. However, we have demonstrated above that this is incorrect and that the transformation from pyramidal to prismatic form occurred very early in ontogeny. Indeed, given the open sutures described in point 4, above, UFPe 3300 and 3301 themselves become incontrovertible evidence for this early transition.

Phylogenetic aspects

Several recent accounts (De Iuliis 1996; De Iuliis & Cartelle, 1999; Saint-André & De Iuliis, 2001; Pujos, 2005) have considered the phylogenetic relationships among megatheres. All agree on a close relationship between *Eremotherium* and *Megatherium*, with Pujos considering them to be sister taxa (Fig. 8). In describing *Eremotherium eomigrans*, De Iuliis & Cartelle (1999) assigned it to *Eremotherium* on the basis of the rugosity of the ectotympanic and contiguous facets of the atlas and axis. Unfortunately, none of these previous analyses considered juvenile remains, essentially because such remains are insufficiently known. However, none of the features discussed here contradicts the presumed relationships between either *E. laurillardi* and *E. eomigrans* or *Eremotherium* and *Megatherium*. Indeed, De Iuliis & Cartelle (1999) and De Iuliis (1996) found no notable difference in the ontogenetic development of the skull between *E. laurillardi* and *E. eomigrans* and between *E. laurillardi* and *Megatherium americanum*, respectively. These are the only megatheres for which a reasonable amount of ontogenetic information is preserved. The only important skull difference between *Eremotherium* and some species of *Megatherium* (*M. americanum*, *M. tarijense* and *M. altiplanicum*) is that the premaxillae are firmly fused to each other and to the maxillae in the *Megatherium* species, but are isolated in *Eremotherium* (and all other megatheres for which the premaxillae are known). However, De Iuliis (1996) and Saint-André & De Iuliis (2001) were unable to determine the relative timing of fusion of these skeletal elements in *Megatherium*.

In summary, we reject the existence of the supposed intertropical dwarf species of *Eremotherium*. The specimens in Guérin & Faure (2000: fig. 2) clearly belong to a very young individual of the large Panamerican species *E. laurillardi*, as defined by Cartelle & De Iuliis (1995). The age of this individual is attested to both by the form of the molariforms and the unfused sutures of the maxilla. Thus, *E. laurillardi* is the correct specific name for the Panamerican megatheriine giant ground sloth that lived during the latter part of the Pleistocene and (probably) very early Holocene and that ranged from the southeastern part of the United States to the south of Brazil.

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