



OVERVIEW OF THE HISTORY OF DISCOVERY, TAXONOMY, PHYLOGENY, AND BIOGEOGRAPHY OF *MAJUNGASAURUS CRENATISSIMUS* (THEROPODA: ABELISAUROIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT—We review the historical sequence of discoveries of *Majungasaurus crenatissimus*, an abelisaurid theropod from the Upper Cretaceous (Maastrichtian) Maevarano Formation, Mahajanga Basin, northwestern Madagascar. For almost a century, beginning in 1895, periodic expeditions conducted by French, Japanese, and Malagasy teams yielded fragmentary and isolated remains of a medium-sized theropod dinosaur from the Maevarano Formation. These materials were first assigned to *Megalosaurus crenatissimus* but later to *Dryptosaurus crenatissimus*, then *Majungasaurus crenatissimus*, and, most recently, *Majungatholus atopus*. The taxon was variously considered to pertain to Tyrannosauridae, “Megalosauridae,” and Abelisauridae. Recent excavations undertaken by the Mahajanga Basin Project (1993 to present) have resulted in abundant and spectacular remains of this theropod. The new material allows us to establish *Majungasaurus crenatissimus* as the valid name for this theropod and to conclusively place it within Abelisauridae. *M. crenatissimus* is currently known from multiple specimens of various size (and presumably age) classes, which cumulatively represent the great majority of the skull and skeleton. Together, these finds establish *Majungasaurus* as among the best known of Gondwanan theropods. *M. crenatissimus* is one of several vertebrate taxa recovered from the Maevarano Formation that indicate close biogeographic ties linking Madagascar with the Indian subcontinent and South America. These data support the hypothesis of a high degree of cosmopolitanism among these landmasses, the result of a persistent subaerial connection between Indo-Madagascar to the east and South America to the west (possibly through Antarctica) until sometime late in the Late Cretaceous.

MALAGASY ABSTRACT (FAMINTINANA)—Nanao jery todika ireo tantara nitranga sy nifanesy tamin'ny fahitana ny *Majungasaurus crenatissimus*, izay abelisaurid theropod hita tao Cretaceous Ambony (Maastrichtian) tao amin'ny Forona (Formation) Maevarano, ao amin'ny Basin an'i Mahajanga, amin'ny faritra avaratr'andrefan'i Madagasikara iny izahay. Efa ho zato taona teo ho eo izao, izay nanomboka ny taona 1895, tamin'ny fidinana an-tsaha isaky ny fotoana voatondro izay notarihin'ny mpikaroka nitambaran'ny Frantsay, sy Japone, ary Malagasy no nahitana silaka sy ampahantolana an'ireo dinozaoro theropod manana vatana salan-tsaly hita tao amin'ny Forona Maevarano. Tamin'ny alalan'ireo taolana ireo no namaritana an'i *Megalosaurus crenatissimus* tamin'ny voalohany ary taorian'izay koa i *Dryptosaurus crenatissimus*, ary nanaraka i *Majungasaurus crenatissimus*, ary vao haingana dia *Majungatholus atopus*. Ny taxon dia nojerena tamin'ny fomba maro samihafa mba hampisehoana ireo izay mitovy sy mifanakaiky amin'ny Tyrannosauridae, “Megalosauridae,” ary Abelisauridae. Tamin'ny alalan'ny fandavahana an-tsaha nataon'ny “Mahajanga Basin Project” nanomboka tamin'ny taona 1993 ka hatramin'izao dia nahita taolana maro sy nahaliana an'io karazana theropod io. Ireo karan-taolana vao hita ireo no nahafahanay nanome ny tena anarana raikitra an'i *Majungasaurus crenatissimus* ho an'io theropod io sy nametrahana azy ho anisan'ny Abelisauridae. Amin'izao fotoana izao *M. crenatissimus* dia fantatatra tamin'ny alalan'ireo fahitana maro karazana izay manana habe samihafa (izay azo heverina mamaritra koa ny taona), ka raha atambatra dia mampiseho ny ankamaroan'ny taolan'ny loha sy ny vatana. Ny fitambaran'ireo taolana ireo dia nahafahana nilaza ihany koa fa *Majungasaurus* dia anisan'ireo theropod-n'i Gondwana tena tsara fantatra indrindra. *Majungasaurus* koa dia iray amin'ireo karazam-biby manana hazon-damosina (vertebrate taxa) hita tao amin'ny Forona Maevarano izay mampiseho ny tsy fahalaviran'i Madagasikara ara-jeografian'ny zava-manana'aina ka nifandraisany subcontinent-n'i Inde sy Amerika Atsimo. Ireo angonam-pikarohana (data) ireo dia manohana ny fiheverana (hypothesis) ny fisiana karazam-pihavian'aina maro dia maro sy samihafa hita tao amin'ireo vongan-tany ireo, izay vokatry ny fitohizana nitohy teo amin'ny Inde sy Madagasikara tany atsinanana ary Amerika Atsimo tany andrefana (izay mety ho tamin'ny alalan'i Antarctica) hatramin'ny faraparan'ny “Late Cretaceous.”

INTRODUCTION

Abelisaurid theropods were, until recently, a poorly known clade of predatory dinosaurs, with most species established on fragmentary remains. The primary exception has been *Carnotaurus sastrei*, from the Late Cretaceous of Argentina

(Bonaparte et al., 1990), based on a nearly complete skeleton. Over the past decade abelisaurid discoveries on several landmasses have greatly increased our understanding of this theropod group (e.g., Sampson et al., 1996, 1998; Coria and Salgado, 2000; Coria, 2001; Coria et al., 2002; Lamanna et al., 2002; Rauhut et al., 2003; Wilson et al., 2003; Sereno et al., 2004). Due in large part to this influx of comparative data, abelisaurids can now be confidently recognized as an assemblage of medium-to-large-sized predators that, together with the smaller-bodied No-

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asauroidea, comprise a monophyletic group, Abelisauroidea. The earliest definitive abelisaurid remains derive from Aptian-Cenomanian deposits in North Africa and South America (Russell, 1996; Calvo et al., 2004; Sereno et al., 2004; Mahler, 2005), and the clade is known to have been widespread by the latest Cretaceous (Campanian-Maastrichtian). The geographic distribution of the clade is heavily biased toward southern hemisphere landmasses, although fragmentary abelisauroid remains are also known from southern Europe (Buffetaut et al., 1988; Le Loeuff and Buffetaut, 1991; Accarie et al., 1995; Carrano and Sampson, 2002). In many respects, abelisaurids appear to have been the Gondwanan equivalents of Laurasian tyrannosaurs, representing the top predators in their respective ecosystems.

Among the most significant of recent abelisaurid finds have been several specimens of *Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955, from the Anembalemba Member, Maevarano Formation, northwestern Madagascar (Sampson et al., 1996, 1998). The Anembalemba Member preserves sediments deposited during flooding events between crystalline highlands to the east and the Mozambique Channel to the west in a lowland floodplain setting reflective of a highly seasonal, semi-arid climate (Rogers et al., 2000, 2005, this volume). This monograph summarizes current knowledge on *M. crenatissimus*, a medium-sized theropod (6–7 m long) that, in addition to being the top predator in its ecosystem, had cannibalistic tendencies (Rogers et al., 2003, this volume).

Majungasaurus crenatissimus is a significant taxon in that it is one of only approximately 25 valid genera of nonavian theropod dinosaurs from the Late Cretaceous of Gondwana (Weishampel et al., 2004). Most importantly, it is represented by abundant materials, including four skulls and three partial but complementary postcranial skeletons, as well as numerous isolated bones and literally thousands of isolated teeth. Virtually all elements of the skeleton of *M. crenatissimus* are now known (Fig. 1), the principal exceptions being parts of the pectoral and pelvic girdles and most of the forelimb distal to the humerus. Given the relatively large number of exceptionally preserved specimens representative of multiple age classes, *M. crenatissimus* is among the best known of Gondwanan theropods. Although the first fossils of this taxon were discovered in 1895 (Depéret, 1896a, b), the vast majority of specimens was discovered as part of the Mahajanga Basin Project, a long-term and ongoing field research project initiated in 1993 and conducted jointly by Stony Brook University and the University of Antananarivo; to date, eight expeditions have been completed (1993, 1995, 1996, 1998, 1999, 2001, 2003, 2005). It should be noted that specimens recovered during the 2003 and 2005 field seasons, which include excellent new skull and skeletal material of *M. crenatissimus*, are not included in this monograph. As of this writing, the specimens have yet to be prepared and studied.

Owing to the relatively complete representation of bony elements, and their exquisite preservation, this monograph is devoted primarily to detailed documentation of the osteology of *Majungasaurus crenatissimus*. The objective of this introductory chapter is to review the checkered taxonomic history and establish the validity of *M. crenatissimus* (including a revised diagnosis), to provide an overview of the history of discovery of the various specimens of this taxon (before and as part of the Mahajanga Basin Project), and to briefly summarize current knowledge of its phylogenetic placement and biogeographic history.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, NY; **FMNH**, Field Museum of Natural History, Chicago, IL; **FSL**, Faculté des Sciences de Lyon, Lyon, France; **MNHN**, Muséum National d'Histoire Naturelle, Paris, France; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1888
THEROPODA Marsh, 1881
CERATOSAURIA Marsh, 1884
ABELISAUROIDEA (Bonaparte and Novas, 1985)
ABELISAURIDAE Bonaparte and Novas, 1985
MAJUNGASAURUS Lavocat, 1955

Majungasaurus Lavocat, 1955:259.

Majungatholus Sues and Taquet, 1979:634.

Type Species—*Majungasaurus crenatissimus* (Depéret, 1896) Lavocat, 1955

Included Species—Type species only.

Etymology—From *Majunga*, in reference to the province of Mahajanga (formerly Majunga), and *saurus*, New Latin, “lizard”, from the Greek *sauros*.

Revised Diagnosis—Abelisaurid theropod with: (1) dorsoventrally deep, fused nasals that are strongly pneumatized via large, bilateral foramina; (2) nasal processes of left and right premaxillae separated by a thin lamina of nasal; (3) maxilla bearing 17 alveoli; (4) frontals rounded rostrally rather than forming a double notch; (5) frontals with a sculptured, median cornual process in adults that is variably pneumatic; (6) pronounced median fossa on sagittal (frontoparietal) crest; (7) dentary bearing 17 alveoli, virtually no extension caudal to last alveolus, and ventral position of lateral sulcus; (8) teeth bearing weakly developed interdental sulci; (9) long, falciform atlantal epiphysis; (10) vertebral centra in cranial dorsal series with dorsoventrally elongate articular surfaces; (11) cranial and caudal borders of mid-cervical transverse processes parallel in lateral view; (12) dorsal and caudal vertebral neural spines dorsally expanded (transversely and craniocaudally); and (13) cervical ribs pneumatized via multiple, enlarged foramina on medial surface of shaft, and accessory foramina on cranial and caudal surfaces of capitulum-tubercular web.

Age and Distribution—Known with certainty only from the Late Cretaceous (Maastrichtian) of Madagascar.

MAJUNGASAURUS CRENATISSIMUS (Depéret, 1896)
Lavocat, 1955

Megalosaurus crenatissimus Depéret, 1896b:188

Dryptosaurus crenatissimus Depéret and Savornin, 1928:263

Majungatholus atopus Sues and Taquet, 1979:634

Type Specimen—MNHN.MAJ 1, fragmentary right dentary of a subadult individual (Lavocat, 1955).

Etymology—From *crenatus*, Latin, “notched or toothed”, and *issimus*, “most or very much”; in reference to “the serrations which are extended along the entire length of the two trenchant ridges of the teeth” (Depéret, 1896b:191).

Type Locality—Listed by Lavocat (1955b) as occurring in a boxed ravine, three meters above the riverbed, two or three km north of the Berivotra hotel. This is almost certainly in error because the Maevarano Formation crops out for only approximately 1.75 km immediately north of the village, whereas the marine Maastrichtian Berivotra Formation and Danian Bet-siboka Limestone lie still further north (see Fig. 2). Yet, despite Lavocat’s apparent slight overestimate of the distance, there is no reason to doubt that the specimen came from this general area and from the same rock unit, the Maevarano Formation, as the other specimens here referred to the species (Rogers et al., 2000).

Age and Distribution—*Majungasaurus crenatissimus* is known with certainty only from the Upper Cretaceous (Maas-

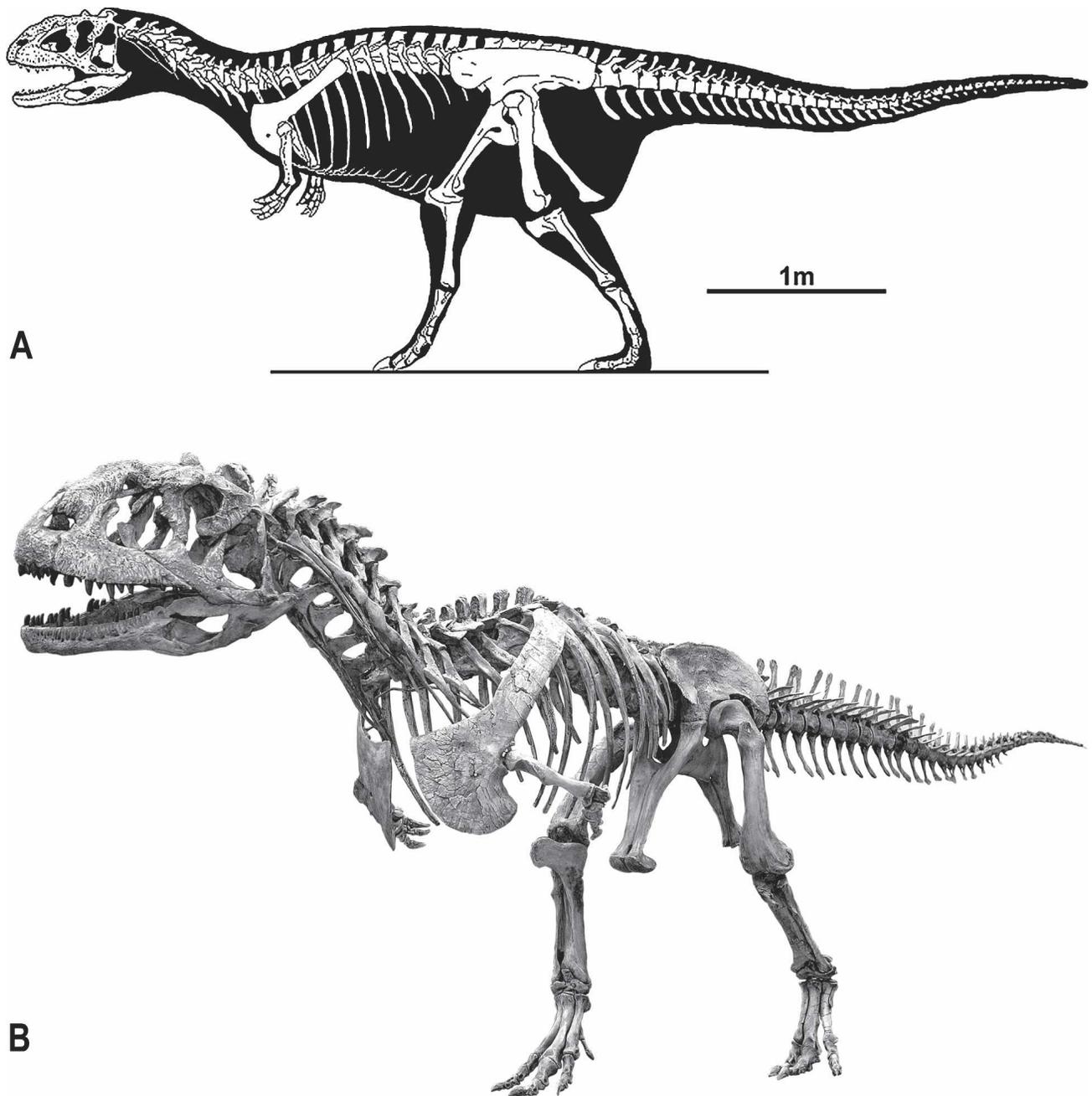


FIGURE 1. Skeletal anatomy of *Majungasaurus crenatissimus* from the Late Cretaceous (Maastrichtian) of Madagascar. **A**, Reconstruction of left lateral view based on a composite of specimens (primarily FMNH PR 2100, UA 8678, and FMNH PR 2278). Scale bar equals 1 m. **B**, Photograph of mounted skeleton (cast) in left anterolateral view on display at Stony Brook University (2006).

trichtian) Maevarano Formation, Mahajanga Basin, northwestern Madagascar, in the small field area surrounding the village of Berivotra, southeast of the port city of Mahajanga. Precise locality data are unknown for the specimens described by Depéret (1896), Lavocat (1955), and Sues and Taquet (1979, 1980), as well as for most of those collected by the Université d'Antananarivo prior to the Mahajanga Basin Project (listed below as UA Bv numbers; except UA 9089, which was catalogued subsequently as part of the Mahajanga Basin Project). However, based on the original descriptions and/or preservational details of the fossil remains, it is logical to assume that these specimens were recovered from the Maevarano Formation in the Berivotra area. The vast majority of specimens collected as part of the

Mahajanga Basin Project were recovered from the 10- to 15-m thick Anembalemba Member, but some specimens (primarily isolated teeth) were also found in the Mesorobe and Miadana members. Though previously regarded as ranging in age from Turonian to Campanian, there is no litho-, bio-, or magnetostratigraphic evidence to suggest anything other than a Maastrichtian age for the Maevarano Formation (Rogers et al., this volume). The localities of the most significant specimens are plotted on Figure 2 and illustrated in Figure 3.

Referred Specimens and Localities—FMNH PR 2008—right premaxilla from locality MAD93-33; FMNH PR 2099—partial skull roof including partially fused frontals with small median cornual process, or 'horncore,' of immature individual from

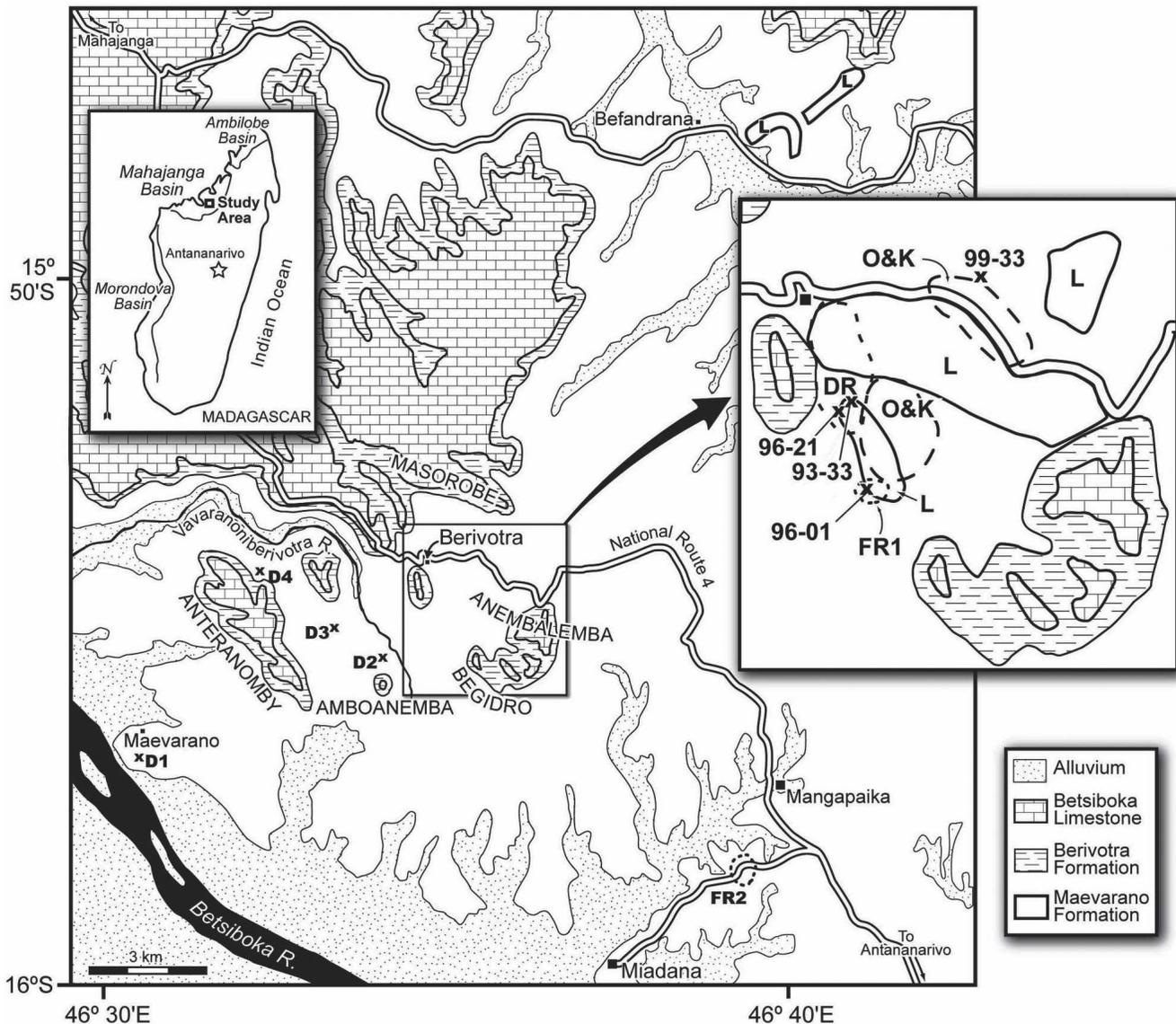


FIGURE 2. Map depicting areas and principal sites from which specimens of *Majungasaurus crenatissimus* have been discovered (see text and Appendix 1 for details). **D1-4**—Deperét's (1896a, b) localities 1-4, Locality D2 being the one from which two teeth were recovered. This vicinity, between the Betsiboka and Vavaranoniberivotra rivers yielded additional material described by Boule (1896) and Thevenin (1907) and was also visited by Lavocat (see map in Lavocat, 1955a:fig.2, reproduced here as Figure 6A); **DR**—area visited by 1974 expedition from the MNHN in Paris (Russell et al., 1976); **FR1** and **FR2**—areas from which Ravoavy (1991) collected dinosaurs in the Berivotra and Miadana regions, respectively; **L**—areas near Maevarano, Berivotra, and Befandrana from which Lavocat (1955a, b, c; 1957) collected in 1954; **O&K**—areas from which the National Science Museum, Tokyo, field crews collected dinosaur material in 1973 and 1975 (Obata and Kanie, 1977; see also Asama, 1977; Asama et al., 1981). Left inset figure: general location map for the Mahajanga Basin. Right inset figure: Berivotra study area in which short dashed lines surround areas collected by Ravoavy (**FR1** and **FR2**), medium dashed lines surround areas collected by Russell et al. (**DR**), long dashed lines surround areas collected by the National Science Museum of Tokyo (**O&K**), and solid lines surround areas collected by Lavocat (**L**). **x**'s on right inset figure indicate Mahajanga Basin Project sites from which significant specimens of *M. crenatissimus* have been recovered.

MAD93-33; FMNH PR 2100—nearly complete, exquisitely preserved, disarticulated skull (missing only left premaxilla, right pterygoid, right ectopterygoid, both epipterygoids, both vomers, and both columellae), with 26 associated caudal vertebrae and 18 haemal arches from MAD96-01 (possibly associated with UA 9089—see O'Connor, this volume); FMNH PR 2278—associated cranial (both premaxillae, both maxillae, left jugal, left quadratojugal, left ectopterygoid, left quadrate, left surangular, left angular, left prearticular, and left articular), and postcranial (two fragmentary cervical neural arches, three fragmentary dorsal vertebrae, one fragmentary caudal vertebra, left scapulocoracoid, partial left ilium, left femur, left and fragmentary right

tibiae, left and partial right fibulae, left astragalocalcaneum, left metatarsals II-IV, right pedal phalanges II-1 and IV-2, and left pedal phalanges IV-2 and IV-3) elements of large near-adult from MAD99-26; FMNH PR 2293—axis (C2) vertebra from MAD95-14; FMNH PR 2294—five articulated caudal vertebrae (the last three fused pathologically) with two haemal arches from MAD93-18; FMNH PR 2295—3rd cervical vertebra (C3) from MAD93-18; FMNH PR 2423—right humerus from MAD93-18; FMNH PR 2424—left tibia from MAD93-18; FMNH PR 2425—left astragalocalcaneum from MAD93-01; FMNH PR 2426—right pedal phalanx II-1 from MAD93-18; FMNH PR 2427—right pedal phalanx II-2 from MAD96-07; FMNH PR 2428—left pedal

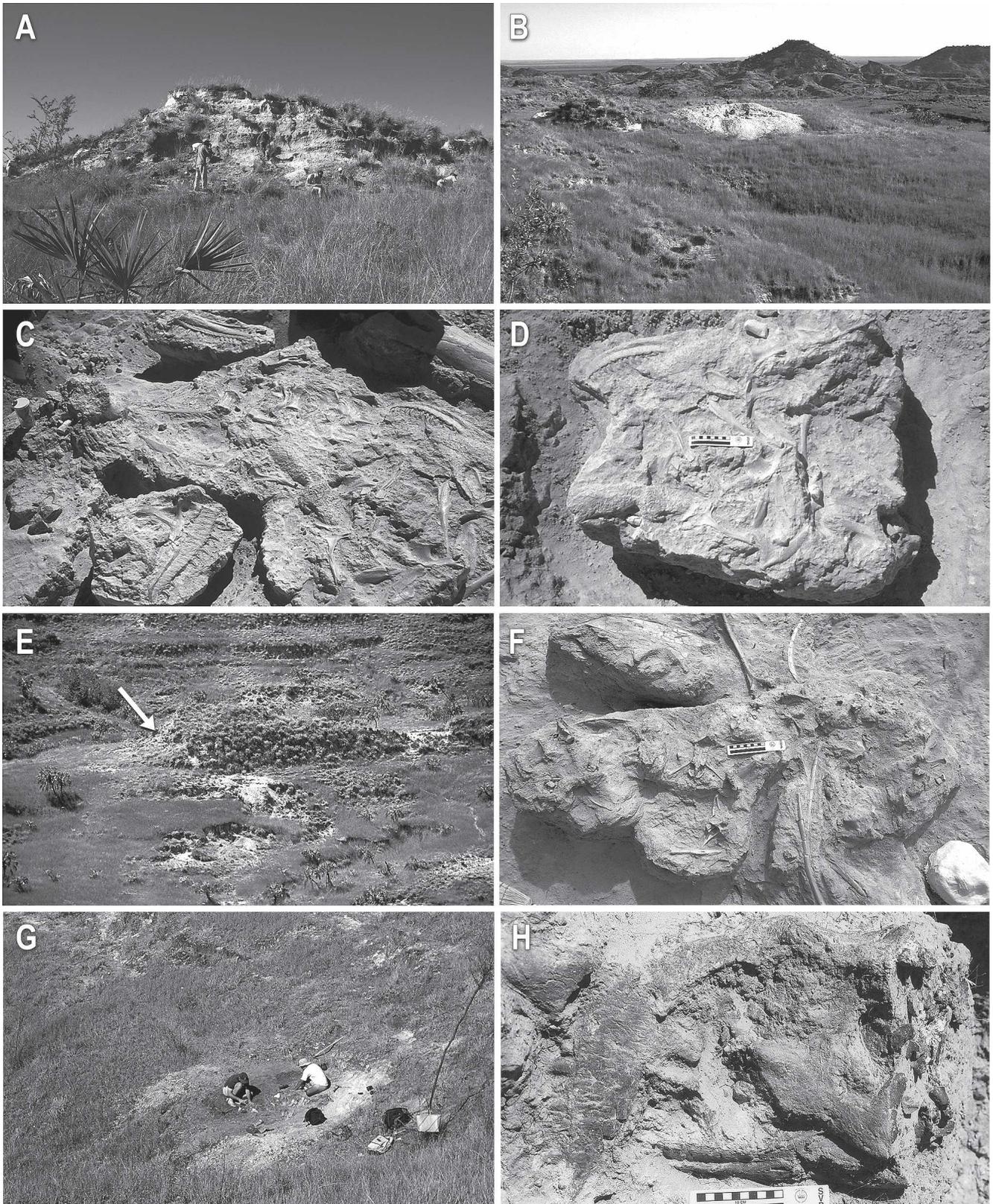


FIGURE 3. Mahajanga Basin Project sites from which significant specimens of *Majungasaurus crenatissimus* were recovered. **A**, MAD93-33, site of recovery of premaxilla (FMNH PR 2008) described by Sampson et al. (1996); **B**, MAD96-01, site of recovery of nearly complete, disarticulated skull (FMNH PR 2100) and associated caudal vertebrae, initially described by Sampson et al. (1998); **C**, and **D**, views of disarticulated skull (FMNH PR 2100) in different stages of excavation at MAD96-01; **E**, MAD96-21, site of recovery of partial skull and postcranial skeleton (UA 8678) of subadult individual, described, in part, by Sampson et al. (1998) (location of MAD93-33 also indicated by arrow); **F**, view of partial skull and postcranial skeleton (UA 8678) at MAD96-21; **G**, MAD99-26, site of recovery of partial skull and postcranial skeleton (FMNH PR 2278); **H**, nearly complete, articulated but poorly preserved skull at MAD99-33 (UA 8709, anterior to left).

phalanges II-3 and III-2 and the distal end of right pedal phalanx II-1 from MAD93-18; FMNH PR 2429—left pedal phalanx III-1 from MAD93-20; FMNH PR 2430—right pedal phalanx IV-1 from MAD99-33; FMNH PR 2431—left pedal phalanx IV-3 from MAD93-19; FMNH PR 2432—left pedal phalanx IV-4 from MAD99-32; FMNH PR 2433—right pedal phalanx IV-4 from MAD93-18; FMNH PR 2434—left pedal phalanx IV-5 from MAD93-18; FSL 92.290—pedal ungual phalanx from unspecified locality in the Berivotra Study Area; MNHN.MAJ 4—partial skull roof with portions of partially fused frontals (with rounded median cornual process), parietals, caudal process of right lacrimal, sphenethmoid, and laterosphenoids from unspecified locality in the ‘Majunga District’; UA 8678—incomplete and disarticulated skull (including left splenial, left prearticular, right surangular, and right squamosal) of subadult individual associated with 23 presacral vertebrae, 13 cervical and 14 dorsal ribs, a partial sacrum, five proximal caudal vertebrae, one middle caudal vertebra, the first haemal arch, and both ilia from MAD96-21; UA 8709—nearly complete, articulated, but poorly preserved skull (including maxillae, nasals, frontals, jugals, lacrimals, right post-orbital and squamosal, pterygoids, ectopterygoids, right palatine, and partial braincase) and both lower jaws from MAD99-33; UA 8716—right premaxilla from MAD99-33; UA 8717—right and left premaxillae from MAD99-33; UA 8718—partial left lacrimal from MAD 93-01; UA 8719—partial skull roof from MAD01-05; UA 8782—distal portion of left quadrate from MAD93-01; UA 9031—left humerus from MAD99-33; UA 9032—left tibia from MAD93-73; UA 9033—right astragalocalcaneum from MAD99-33; UA 9034—left metatarsal II from MAD99-33; UA 9035—left metatarsal IV from MAD99-33; UA 9036—left pedal phalanx II-1 from MAD99-33; UA 9037—right pedal phalanx II-2 from MAD93-33; UA 9038—left pedal phalanx II-3 from MAD95-16; UA 9039—right pedal phalanx III-1 from MAD99-32; UA 9040—right pedal phalanx IV-1 from MAD99-33; UA 9041—right pedal phalanx IV-2 from MAD99-33; UA 9042—left pedal phalanx III-2 from MAD93-32; UA 9043—pedal phalanx IV-5 from MAD96-18; UA 9077—left tibia and fibula from MAD99-33; UA 9078—right fibula from MAD99-33; UA 9079—left metatarsal III from MAD99-33; UA 9081—right pedal phalanx III-1 or III-2 from MAD99-33; UA 9082—astragalus from MAD99-33; UA 9089—four proximal caudal vertebrae from near MAD96-01 (possibly associated with FMNH PR 2100—see O’Connor, this volume); UA Bv 532—left pedal phalanx I-2 from unspecified locality in the Berivotra Study Area; UA Bv 1658—left pedal phalanx I-2 from unspecified locality in the Berivotra Study Area; UA Bv 1260—right pedal phalanx II-1 from unspecified locality in the Berivotra Study Area; UA Bv 1265—left pedal phalanx III-1 from unspecified locality in the Berivotra Study Area; plus literally thousands of isolated teeth (including FMNH PR 2198 and 2228, FSL 92.306a-b, MNHN 1911a-d, MNHN.MAJ 242, MNHN.MAJ 249) from numerous localities in the Berivotra Study Area.

Locality data for specimens collected by joint Stony Brook University/Université d’Antananarivo expeditions are on file at Stony Brook University, the Université d’Antananarivo (where approximately half of the Mahajanga Basin Project specimens are permanently repositied), and the Field Museum of Natural History (where the other half are housed).

Revised Diagnosis—As for the genus (see above).

Discussion—*Majungasaurus crenatissimus* has had a complex taxonomic history. The original sample, collected from several localities near the Betsiboka River, was described by Depéret (1896a, b) and included two teeth, an ungual phalanx, two partial sacral vertebrae, and a partial caudal vertebra. Photographic images of most of these specimens are provided here for the first time (Fig. 4). Depéret named the new species and assigned it to *Megalosaurus*, but he did not designate any of the six specimens comprising the type series as the holotype and, in addition, a type locality was not specified. Nor did Depéret indicate whether the

specimens had been derived from a single individual or, indeed, even the same locality. Depéret and Savornin (1928) later assigned *M. crenatissimus* to *Dryptosaurus*, along with *D. superbus* (= *Erectopus*), *D. aquilunguis*, and *D. saharicus* (= *Carcharodontosaurus*). Depéret (1896b:191) had earlier revealed his inclination for this assignment by stating the following: “The type species *D. aquilunguis* Cope is very large, attaining the size of *M. bucklandi*; the teeth differ entirely from those of *Megalosaurus* in the serrations of the anterior edge, which are extended along the entire length of this edge to near the root, instead of being limited to the upper part of the crown. It is interesting to note that this character is found exactly in the Malagasy and Indian form, therefore the attribution to the genus *Dryptosaurus* is shown as entirely probable.”

Nearly 60 years after publication on the original sample by Depéret (1896a, b), Lavocat (1955a, b) described a dentary from the same general field area (though several km to the north) and convincingly argued that it represented the same species of theropod as the six specimens described by Depéret. This argument was based primarily on dental morphology because several teeth within and associated with the dentary were regarded as identical to the two teeth described by Depéret. This assessment is conclusively confirmed by Smith (this volume). Lavocat, however, recognized that the morphology of the dentary was different from that of other species of *Megalosaurus* and therefore assigned *M. crenatissimus* to a new genus, *Majungasaurus*. Although not explicitly stated, it appears that Lavocat (1955a, b) did not consider any of the specimens in Depéret’s type series to be worthy of designation as the lectotype; instead, he opted to designate the dentary as the neotype of the species.

This same specimen, however, was later considered to be non-diagnostic by Sampson and colleagues (1998), and *Majungasaurus crenatissimus* was thereby regarded as a *nomen dubium*. In its place, Sampson and colleagues (1998) designated *Majungatholus atopus* as the valid name for the Maevarano theropod. This followed the 1996 discovery of a theropod skull with lower jaws, which clearly showed that the skull roof (MNHN.MAJ 4) identified by Sues and Taquet (1979) as representing a new genus and species of pachycephalosaur, *Majungatholus atopus*, instead belonged to a theropod. Sampson and colleagues (1998) argued that, because Depéret did not explicitly designate a holotype for the mid-sized Malagasy theropod, and because Lavocat’s dentary (MNHN.MAJ 1) was non-diagnostic, *Majungatholus atopus* must be the valid name assigned to the mid-sized theropod from the Maevarano Formation.

The recovery and analysis of additional dentary material (Sampson and Witmer, this volume) and especially dental morphology (Smith, this volume), along with detailed comparison to the dentary (MNHN.MAJ 1) and teeth described by Lavocat (1955), compel us to once again reconsider the taxonomic designation of this theropod. The dentary described by Lavocat (1955), MNHN.MAJ 1, is typically abelisaurid in being broad, laterally bowed (in dorsal view), and relatively foreshortened, as well as in possessing a much-enlarged external mandibular fenestra (resulting in a relatively short post-alveolar portion, terminating caudally slightly behind the last alveolus), pronounced longitudinal sulcus on the lateral surface containing neurovascular foramina, and rugose subcutaneous texture on its external surfaces (as on the skull). These same features are found in the dentaries of FMNH PR 2100 and UA 8709 (Sampson and Witmer, this volume). As outlined by Sampson and Witmer (this volume) the adult dentaries of this species can be distinguished from those of other known abelisaurids (e.g., *Carnotaurus* and the Indian taxon represented by AMNH 1960 [referred to *Indosuchus raptorius* by Chatterjee, 1978]) by a suite of features, most notably the presence of 17 alveoli, the virtual lack of an extension of the dentary caudal to the last alveolus, and the ventral position of the lateral sulcus. The subadult dentary,



MNHN.MAJ 1, possesses these same features and is therefore distinctive among theropods. Indeed, Sampson and Witmer (this volume:32) state that “detailed comparisons of MNHN.MAJ 1 with the dentary of FMNH PR 2100 revealed no notable differences other than size (MNHN.MAJ 1 being approximately 25% smaller).”

Furthermore, detailed examination of the teeth preserved in MNHN.MAJ 1 by Smith (this volume) reveals that they fall within the same size and shape parameters as the two isolated teeth (FSL 92.306a-b) described by Depéret (1896a, b), those preserved in the gnathic elements of adult individuals described by Sampson and Witmer (this volume; e.g., FMNH PR 2008, 2100; UA 8709, 8716, and 8717), and the thousands of isolated teeth recovered from the Maevarano Formation by Mahajanga Basin Project personnel and others. The teeth of the Malagasy abelisaurid most closely resemble those of AMNH 1753, 1955, and 1960 from the Late Cretaceous of India (referred to *Indosuchus raptorius* by Chatterjee, 1978) but, importantly, the Malagasy taxon possesses weakly developed interdenticular sulci whereas the Indian specimens lack them (Smith, this volume). These sulci can also be seen on the erupting teeth of MNHN.MAJ 1.

The possession of distinctive features in the dentary and teeth described by Lavocat (1955) and their full morphological congruence with other specimens attributed to the mid-sized Malagasy taxon from the Maevarano Formation (not to mention the lack of evidence for any other mid-sized theropod in the Maevarano Formation, despite the recovery of thousands of vertebrate specimens), ineluctably leads to the conclusion that MNHN.MAJ 1 represents a subadult individual of the same taxon represented by other dentaries (FMNH PR 2100, UA 8709) and countless isolated teeth. As such, and according to the Principle of Priority of the International Code of Zoological Nomenclature (1999), MNHN.MAJ 1 must be designated as the valid type specimen and *Majungasaurus crenatissimus* as the valid name of this theropod.

HISTORY OF DISCOVERY AND DESCRIPTION

1895–1993

In 1895, while stationed in Madagascar, French military physician Dr. Félix Salètes led an expedition to a remote region on the northwestern part of the island, approximately 45 km south of the coastal town of Mahajanga (then “Majunga”) and close to the village of Maevarana (then “Mevarana”), on the northeastern (right) bank of the Betsiboka River (Depéret, 1896a, b; Buffetaut, 1987). His mission was to construct a temporary hospital. The French military had been dispatched to Madagascar to occupy the island, which was conquered and formally declared a colony in August of the following year (Brown, 1995). Salètes recognized the paleontological potential of the region but, lacking sufficient leisure time himself, commanded his regimental staff officer, Landillon, to carry out paleontological and geological reconnaissance. Landillon apparently executed his orders with zeal, collecting several vertebrate and invertebrate fossil specimens as well as abundant geological data, all of which were ultimately shipped to the renowned French paleontologist

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FIGURE 4. Photographic images of specimens of *Majungasaurus crenatissimus* originally described by Depéret (1896 a, b) and assigned by him to *Megalosaurus crenatissimus*. Lateral views of **A**, two isolated teeth (Faculté des Sciences de Lyon [FSL] 92.306—see also Depéret, 1896b:pl. 6, figs. 4, 4a, 5, 5a); **B**, pedal ungual phalanx (FSL 92.290—see also Depéret, 1896b:pl. 6, figs. 8, 8a), **C**, caudal vertebra (FSL 92.289—see also Depéret, 1896b:pl. 6, fig. 7); and **D**, fragment of vertebral body (FSL 92.343—see also Depéret, 1896b:pl. 6, fig. 6). Scale bar in A equals 1 cm; scale bar in B–D equals 3 cm.

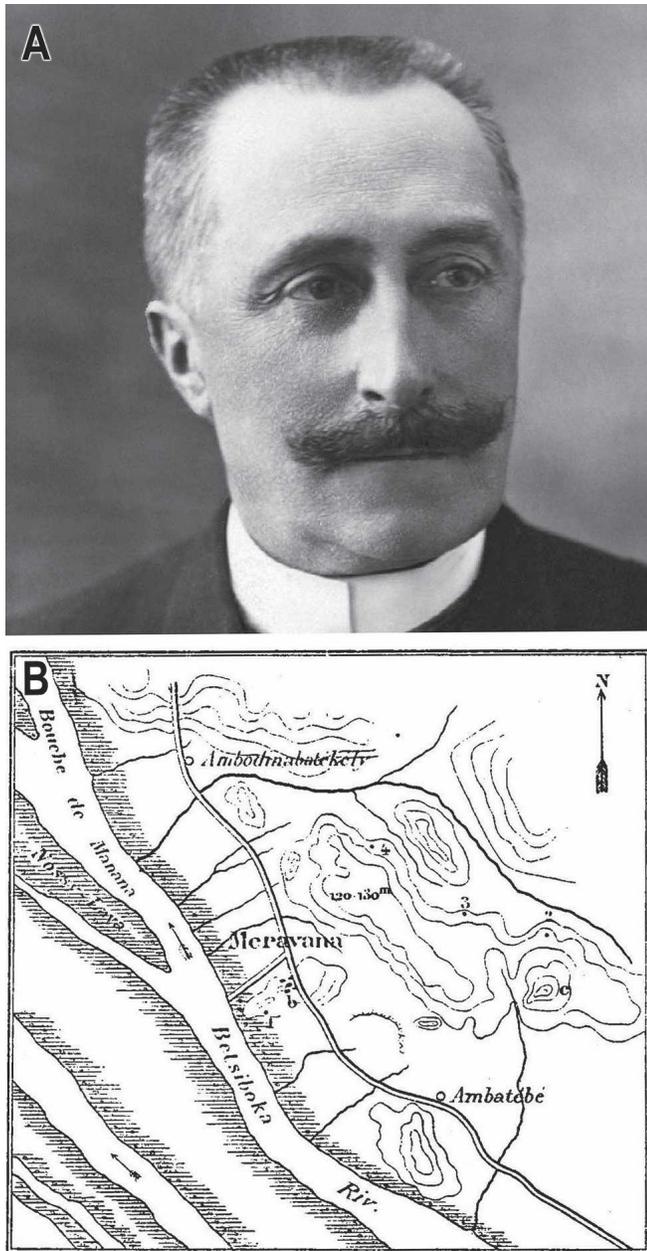


FIGURE 5. **A**, Photograph of Charles Depéret (date unknown but presumed to be just after the turn of the century), who described the first specimens now attributed to *Majungasaurus crenatissimus*. **B**, Topographic map from Depéret (1896b:fig.1) showing original discovery sites of dinosaurs in the Maevarano Formation. Translation of original caption is as follows: "Topographic map of the Mevarana region (after the map of Colonel Beylié, completed by Mr. Landillon, company sergeant major of the marines.-1, 2, 3, 4, localities of dinosaurs." Note that "Mevarana" is misspelled as "Meravana" on map and that current spelling is Maevarana.

Charles Depéret (1854–1929; Roman, 1929; see Fig. 5A) at the Université de Lyon (currently Université Claude Bernard Lyon 1). Depéret (1896a, b), on the basis of the fossils, geological data, and a sketch map provided by Salètes, (1) recognized the presence of two new dinosaur species, the sauropod *Titanosaurus madagascariensis* and the theropod *Megalosaurus crenatissimus*, (2) briefly described the Upper Cretaceous strata from which the fossils had been recovered, and (3) identified and plotted four

localities that had yielded dinosaur fossils (Depéret, 1896b:fig.1). Depéret's map is reproduced here as Figure 5B and his localities are plotted relative to more recently discovered localities in Figure 2.

The original sample assigned to *Megalosaurus crenatissimus* by Depéret (1896a, b) included two teeth, an ungual phalanx, two partial sacral vertebrae, and a partial caudal vertebra (Fig. 4). Depéret (1896b) stated that the two teeth, as well as some turtle bone, came from Locality 2 (Figs. 2, 5B) but the provenance of the other specimens of *M. crenatissimus* was not indicated. Despite inaccuracies in Depéret's (1896b:fig. 1; Fig. 5B) topographic map, it appears that Locality 2 lies just north of the Amboanemba Escarpment (Fig. 2). This area, between the Betsiboka River and one of its tributaries, the Vavananoniberivotra, lies over 2.5 km southwest of the current village of Berivotra. The area was presumably accessed by boat up the broad delta of the Betsiboka River or by a road established by the French military along its northeastern bank (as depicted by Depéret, 1896b:fig. 1; Fig. 5B).

Shortly after Depéret's publications, Marcellin Boule (1896) announced that several shipments of Jurassic and Cretaceous dinosaur bones had been sent from Madagascar to the National Museum of Natural History (MNHN) in Paris by a Mr. Bastard, and that Professor Gaudry (1827–1908) had entrusted Boule (1861–1942) to study them. The Cretaceous samples, however, had been reduced to crumbs during transport. The only theropod materials that survived the shipment were some long bone fragments and a vertebra, none of which were illustrated. Boule implied that these specimens were recovered from the same region, near Maevarana, as those described by Depéret. Boule (1900) later noted that a colonial physician, Dr. Decorse, had sent some theropod teeth, presumably recovered from the same area as the specimens described by Depéret.

Boule, in turn, charged Armand Thevenin (1907) with further study of the dinosaur samples from Madagascar, these being specimens sent by both Mr. Bastard and Dr. Decorse. Thevenin (1870–1918), who died a premature death 11 years later while experimenting with poison gas (Buffetaut et al., 1993), stated that these specimens, which included only an isolated tooth and fragments of hollow bones, also came from the same area as those described by Depéret.

Knowledge of this Malagasy theropod advanced little during the rest of the 20th century prior to the initiation of the Mahajanga Basin Project in 1993. Several expeditions, lead by French, Japanese, and Malagasy paleontologists to the area south of Mahajanga, within what is now known as the central Mahajanga Basin, supplemented the earlier theropod samples and expanded upon the faunal list of vertebrate taxa known from the Late Cretaceous of Madagascar (Priem, 1907, 1924; Piveteau, 1926, 1934; Lavocat, 1955a, b, c, 1957; Hoffstetter, 1961; Russell et al., 1976; Asama, 1977; Obata and Kanie, 1977; Sues and Taquet, 1979; Sues, 1980; Asama et al., 1981; Ravoavy, 1991; B. Rakotosamimanana, pers. comm., 1993; P. Taquet, pers. comm., 1994).

On the advice of the renowned geologist Henri Besairie, René Lavocat (b. 1909; Fig. 6A)—who also surveyed the same area along the Betsiboka River near Maevarana from which the earliest materials of *Majungasaurus crenatissimus* were collected by Landillon, Bastard, Decorse, and others—appears to have been the first to concentrate collecting efforts in the region 2–3 km to the northeast of the original collecting area (but, perhaps importantly in terms of access, on the northeastern side of the Vavananoniberivotra River; see Lavocat, 1955a:fig. 2, reproduced here as Fig. 6B). This new area surrounds (but mainly lies immediately south-southeast of) the village of Berivotra, and is the area that has yielded, and continues to yield, the largest and best-preserved samples of *M. crenatissimus* and other vertebrates. This shift in effort to the Berivotra area is likely owing to the establishment of a road (called the West Road in Lavocat

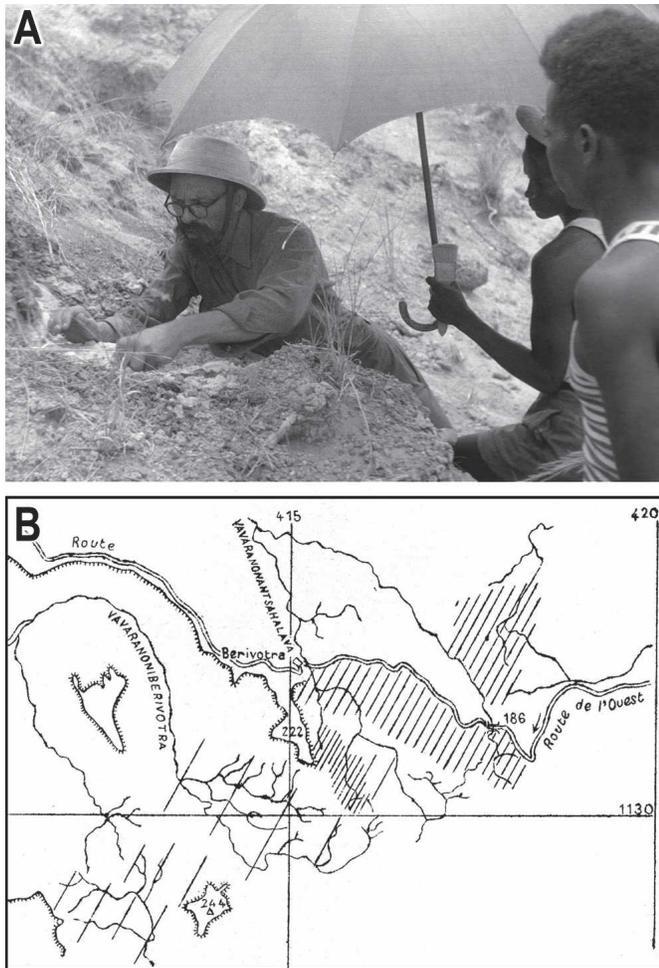


FIGURE 6. **A**, Photograph of René Lavocat (1954, in Madagascar). **B**, Map of Berivotra/Maevarana field area, from Lavocat (1955a:fig. 2). Translation of original caption is as follows: “Map of continental beds with vertebrates in the Berivotra region. In hatching, traversed zones. Fossil richness marked by the density of hatching.”

[1955a] but now known as National Route 4 [Route Nationale 4 on French maps and Arabem-pirenena 4 on Malagasy maps]) that passes from Mahajanga to the capital city Antananarivo. The road was built during the French invasion of the island in 1895, as troops marched southward to the capital from their staging area in Mahajanga.

The collections of specimens of *Majungasaurus crenatissimus* made prior to initiation of the Mahajanga Basin Project in 1993 are listed in Appendix 1, and the localities from which they were recovered are indicated in Figure 2. These specimens, like those described by Depéret (1896a, b), Boule (1896), and Thevenin (1907), are fragmentary and, with only two notable exceptions, have done little to enhance knowledge of the theropod component of the fauna. The first exception is a dentary (MNHN.MAJ 1; Fig. 7) of a subadult individual described by Lavocat (1955a, b), who designated it as the neotype of *M. crenatissimus*. This specimen is discussed above in the Systematic Paleontology section with regard to the valid name for this species of Malagasy theropod.

The second important specimen—a rugose, partial skull roof with domed frontals (MNHN.MAJ 4; Fig. 8)—was collected at the beginning of the 20th Century from the “Grès de Maevarano” of the “Majunga District,” but exactly when, from where, and by



FIGURE 7. Cast of right dentary, MNHN.MAJ 1 (type specimen), of subadult individual of *Majungasaurus crenatissimus* described by Lavocat (1955b) in **A**, lateral, **B**, superior, and **C**, medial views. Small anterior fragment from the medial side of jaw does not directly attach to posterior fragment but was glued into position for the purposes of this illustration. Scale bar equals 3 cm.

whom is not known (Sues and Taquet, 1979:634; Sues, 1980:957). P. Taquet (b. 1940) rediscovered this specimen in 1976 when a collection of vertebrate fossil specimens from Madagascar with no detailed provenance and collecting information in the “École des Mines de Paris” was transferred to the MNHN (P. Taquet, pers. comm., 2004). Sues and Taquet (1979; see also Sues, 1980) referred this specimen to Pachycephalosauria, erecting a new genus and species, *Majungatholus atopus*. Not only was *M. atopus* the first purported pachycephalosaur described from Madagascar, it was also the only purported pachycephalosaur identified from any Gondwanan landmass. The specific name, *atopus*, refers to the “strangeness” of the specimen, but secondarily means “out of place,” alluding to the biogeographic isolation of this animal. Doubts about the pachycephalosaur affinities of MNHN.MAJ 4 were expressed by a number of authors (Rage, 1988; Giffin, 1989; Sampson et al., 1996, 1998; Krause et al., 1997a) on the basis of several anatomical features not present in any known pachycephalosaur (lack of radiating trabeculae in dome; dome occurring wholly within frontals rather than incorporating parietals; rugose ornamentation) and several derived characteristics (e.g., long, divided olfactory tracts) typical of theropods.

The Mahajanga Basin Project (1993–present)

In addition to a reconnaissance expedition in 1993, seven subsequent field campaigns, conducted jointly by Stony Brook University and the University of Antananarivo, have explored these same Upper Cretaceous deposits in the area surrounding Berivotra village in search of fossil vertebrates. Through a combination of surface collection, dry and wet screen-washing, and large-scale excavations, these expeditions have dramatically increased knowledge about the evolutionary and biogeographic history of terrestrial and freshwater vertebrates of Madagascar, roughly quintupling the known diversity of Late Cretaceous forms (summaries in Krause et al., 1997a, 1999, 2006; Krause, 2003). The

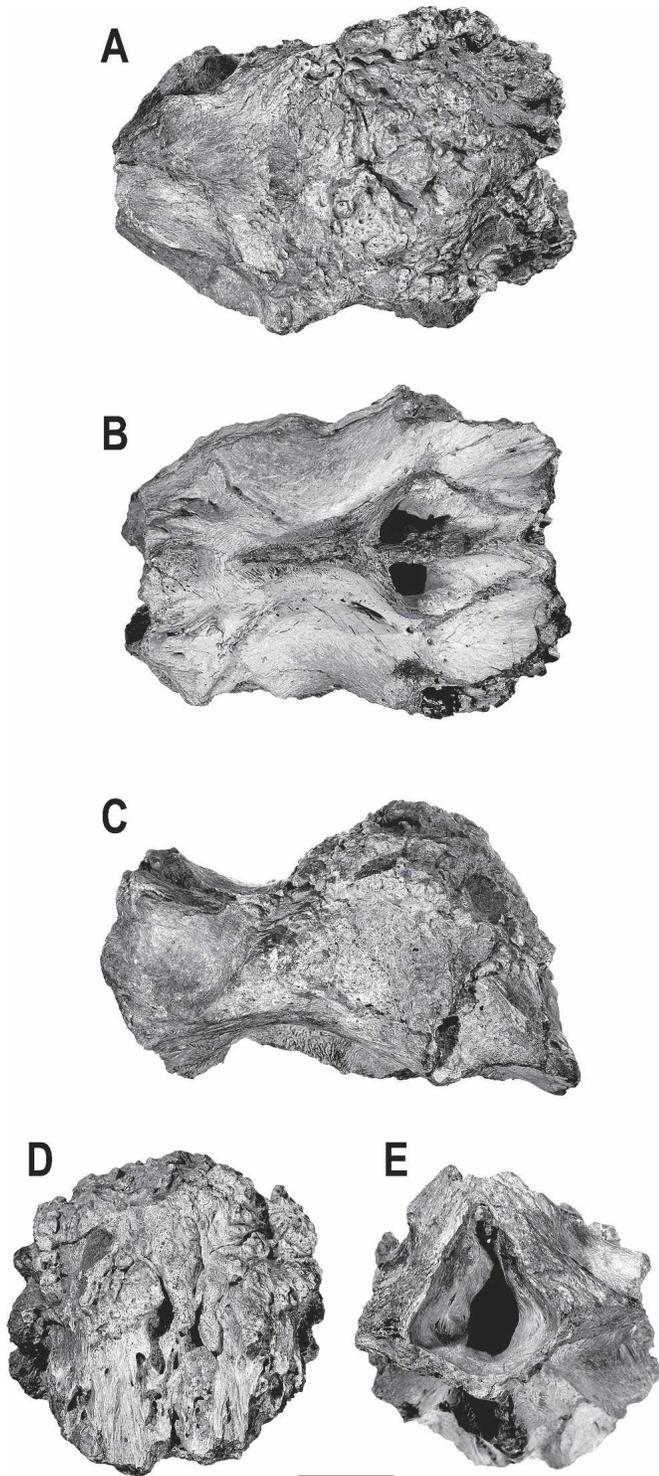


FIGURE 8. Partial skull roof, MNHN.MAJ 4, holotype specimen of *Majungatholus atopus* described by Sues and Taquet (1979) and Sues (1980) in **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; and **E**, posterior views. Scale bar equals 3 cm.

known fauna from the Maevarano Formation now comprises over 40 species of fishes, frogs, turtles, lizards, snakes, crocodyliforms, and mammals, as well as both avian and nonavian dinosaurs.

The initial Mahajanga Basin Project expedition to the Beri-

votra study area in 1993 yielded a plethora, literally hundreds, of isolated theropod teeth from numerous localities (Krause et al., 1997a), as well as an isolated theropod premaxilla (FMNH PR 2008) from locality MAD93-33 (Fig. 3A). The teeth are indistinguishable from those previously assigned to *Majungasaurus crenatissimus* (Sampson et al., 1996:fig. 2). Sampson and colleagues (1996) documented several derived features on the premaxilla shared with that of AMNH 1733 from the Late Cretaceous of India. Although it cannot be identified to the genus level, AMNH 1733 pertains to Abelisauridae, to which Sampson and colleagues (1996) also assigned *Majungasaurus*.

Field efforts in 1996 resulted in the recovery of a nearly complete, exquisitely preserved yet disarticulated skull (FMNH PR 2100; Sampson et al., 1998) of a medium-sized abelisaurid theropod from locality MAD96-01 (Fig. 3B–D). The teeth preserved in the premaxilla, maxilla, and dentary were indistinguishable from the hundreds of isolated teeth recovered previously, and the premaxillary morphology matched that of FMNH PR 2008. More significantly, however, a small, median protuberance projecting dorsally from the fused frontals resembled that of MNHN.MAJ 4, the holotype specimen of *Majungatholus atopus*. This provided conclusive evidence and confirmed suspicions that *M. atopus* is not a pachycephalosaur, as previously postulated by Sues and Taquet (1979) and Sues (1980), but that it is instead a theropod. Sampson and colleagues (1998) considered the type material of *Majungasaurus crenatissimus* to be inadequate, regarding this taxon as a *nomen dubium* and referring other medium-sized theropod specimens from the Berivotra field area to *Majungatholus atopus*, with MNHN.MAJ 4 retained as the holotype.

Continued work in the Berivotra Study Area since 1996 has yielded thousands more isolated teeth of *Majungasaurus crenatissimus*, as well as several partial skulls and skeletons. These specimens form the primary basis for the descriptions in this monograph by Sampson and Witmer (skull and lower jaws), Smith (dentition), O'Connor (postcranial axial skeleton), Carrano (appendicular skeleton), and Farke and O'Connor (paleopathology). As indicated above, the morphology of the dentary and the teeth lead us to conclude that *M. crenatissimus* is the valid name for this Malagasy theropod.

In addition to the specimens of *Majungasaurus crenatissimus* from the Upper Cretaceous (Maastrichtian) Maevarano Formation, several fragmentary Late Cretaceous theropod fossils from landmasses other than Madagascar have been purported to resemble those of *M. crenatissimus* (or its synonyms *Megalosaurus crenatissimus* and *Majungatholus atopus*), or even to be attributable to the same species. These include isolated teeth and two terminal phalanges (*Megalosaurus crenatissimus*) from Egypt (Gemmellaro, 1921; see also Stromer and Weiler, 1930); an isolated tooth (*Megalosaurus crenatissimus*) from India (Gemmellaro, 1921 [figured in Lydekker, 1879]); isolated teeth (Carnosauria, genus and species indet. . . “of the type present in *Genyodectes serus* . . . or in *Majungasaurus crenatissimus*”) from Argentina (Bonaparte and Powell, 1980:25); an incomplete tooth (*Majungasaurus crenatissimus*) from India (Mathur and Srivastava, 1987); and a partial dentary (cf. *Majungasaurus* sp.) from Morocco (Russell, 1996). Furthermore, Curry (1997) identified the presence of *Majungasaurus crenatissimus* in the presumably older (Coniacian?) Ankazomihaboka Sandstones of the Mahajanga Basin, although the fragmentary nature of these specimens renders precise identification problematic. Owing to the difficulty of determining whether or not various fragmentary specimens from these other areas are assignable to *M. crenatissimus*, we conservatively conclude that the species is known with certainty only from the Maevarano Formation in the type area near Berivotra, Mahajanga Basin, northwestern Madagascar. The purported presence of this taxon elsewhere is based on indeterminate abelisaurid materials that were more similar to *Majun-*

gasaurus than to other theropods known at the time of their description.

PHYLOGENY AND BIOGEOGRAPHY

Prior to initiation of the Mahajanga Basin Project in 1993, *Majungasaurus* was poorly known and, as a result, has had a checkered taxonomic history. It had been variously thought to show greatest affinities with ‘megalosaurids’ (Deperét, 1896; Thevenin, 1907), tyrannosaurids (e.g., Charig, 1973; Sues, 1980), and abelisaurids (Bonaparte, 1986; Molnar, 1990, 1991). Sues (1980) ultimately concluded that the remains of *M. crenatissimus* were simply too fragmentary to allow assessment of phylogenetic affinities. Abelisauridae, as a clade, have also been problematic, with the group (or members of it) having been affiliated with allosaurs (Huene and Matley, 1933), tyrannosaurids (Chatterjee, 1978), and ceratosaurs (e.g., Bonaparte et al., 1990).

The relationships of this Malagasy theropod were brought into sharper focus with the discovery in 1993 of FMNH PR 2008, an isolated, well-preserved premaxilla. On the basis of dental morphology, Sampson and colleagues (1996) assigned FMNH PR 2008 to *Majungasaurus crenatissimus*. They also recognized striking similarities between the premaxilla of *Majungasaurus* and AMNH 1753, a pair of premaxillae assigned to *Indosuchus*, a putative abelisaurid from the Maastrichtian of India (Chatterjee and Rudra, 1996). Indeed, the similarities are so striking that Sampson and colleagues (1996:603) remarked: “Based on the available evidence, it would not be unreasonable to assign FMNH PR 2008 to *Indosuchus*.” In this light, Depéret (1896a: 484–485), who originally assigned *M. crenatissimus* to *Megalosaurus*, presciently commented 110 years ago: “It is interesting to note that Mr. Lydekker (*Palaeontologica Indica*, ser. IV, col. I) described from the *Lameta horizon* in India, attributed to the middle Cretaceous, some dinosaur remains from the two genera *Titanosaurus* and *Megalosaurus*, whose presence I have noted in the Upper Cretaceous beds of Madagascar. Moreover, this community of association of the dinosaur genera is an argument to add to those which have already been invoked in favor of a junction between the great island of Madagascar and the Indian continent during the Mesozoic Era.”

The 1996 discovery of an extremely well-preserved skull (FMNH PR 2100), as well as a partial skull and associated postcranial skeleton (UA 8678), allowed Sampson and colleagues (1998), in a preliminary paper describing these materials, to argue for synonymy of *Majungasaurus* with *Majungatholus*, previously considered a pachycephalosaurid (Sues and Taquet, 1979; Sues, 1980). It also provided an unparalleled opportunity to examine the relationships of the Malagasy taxon to other nonavian theropods. Sampson and colleagues (1998) firmly established *Majungatholus atopus* as a member of the Abelisauridae by documenting 12 abelisaurid synapomorphies and six that are shared between it and *Carnotaurus* (Fig. 9A). As detailed above, however, in light of more recently discovered specimens and further study, we now consider *Majungasaurus crenatissimus* to be the valid name for this taxon.

A number of recent phylogenetic analyses targeting basal theropods support the monophyly of Abelisauridae, Noasauridae, and Abelisauroida within Ceratosauria (e.g., Carrano et al., 2002; Wilson et al., 2003; Rauhut, 2003; Sereno et al., 2004; Carrano and Sampson, in review). However, to date there has been minimal resolution of relationships within Abelisauridae (Fig. 9). Those studies reporting some ingroup resolution have typically regarded *Carnotaurus* and *Majungasaurus* as sister taxa, with *Abelisaurus* as the outgroup to this pair (Sampson et al., 2001; Wilson et al., 2003; Sereno et al., 2004; Tykoski and Rowe, 2004). For example, Carrano et al. (2002) conducted a phylogenetic analysis of basal theropods that included 158 characters distributed across 21 ingroup taxa. A strict consensus cladogram

of these data depicted an unresolved polytomy of abelisaurids (Fig. 9B), consisting of *Abelisaurus*, *Xenotarsosaurus*, *Carnotaurus*, and *Majungatholus*, but a representative most-parsimonious tree indicated a sister-group relationship between *Carnotaurus* and *Majungatholus* (Fig. 9C). The recurrent cladistic linkage of *Carnotaurus* and *Majungasaurus* has led some authors (e.g., Wilson et al., 2003; Sereno et al., 2004) to conclude that the two should be united with other ornate abelisaurids (e.g., *Rajasaurus*) into Carnotaurinae, leaving the relatively unadorned *Abelisaurus* positioned basal to this clade (Fig. 9D).

In the most recent assessment of basal theropod relationships, Carrano and Sampson (in press) conducted a study of 151 characters (including 18 new characters) arrayed across 18 taxa. Figure 10 depicts a portion of the results from the Carrano and Sampson study (cladogram calibrated for time to show stratigraphic occurrences), focusing on abelisaurid relationships. The most striking departure from earlier studies is that *Majungasaurus* and *Carnotaurus* do not share an exclusive sister-taxon relationship. Rather, *Carnotaurus* is allied most closely with another Argentine taxon, *Ilokelesia*, whereas *Majungasaurus* forms a clade with the Indian forms *Rajasaurus* and *Indosuchus*. In addition, *Abelisaurus* no longer occupies a basal position with putatively more ‘derived’ abelisaurids; indeed, this taxon shares several unique character states with *Majungasaurus*. If these conclusions are supported by future analyses, the revised topology would have intriguing biogeographic implications, suggesting the possibility of distinct radiations of abelisaurids in eastern and western Gondwana. The authors of this study note, however, that *Majungasaurus* and *Carnotaurus* also share a number of derived features that could re-unite these two taxa within Abelisauridae; the problem is that these characters are not preserved in other abelisaurids, and thus we currently cannot assess their full distribution.

Nevertheless, based on the above-mentioned studies, it appears that the known closest relatives of *Majungasaurus* lived contemporaneously, or penecontemporaneously, on the Indian subcontinent and in South America. That said, it is important to note that the complete lack of any taxonomically identifiable medium-sized to large theropod remains in the pre-Maastrichtian Cretaceous deposits of Madagascar essentially compels *Majungasaurus* to share a sister-taxon relationship with some non-Malagasy taxon (Carrano and Sampson, 2004). In addition to *M. crenatissimus*, to date the Mahajanga Basin Project has yielded evidence of only one other nonavian theropod from the Maevarano Formation, the much smaller noasaurid *Masiakasaurus knopfleri* (Sampson et al., 2001; Carrano et al., 2002, 2004). Just as *Majungasaurus* (= *Majungatholus*) appears to have had its closest relatives in India and Argentina (Sampson et al., 1996, 1998), so too does *Masiakasaurus* (*Laevisuchus* in India, *Noasaurus* and *Velocisaurus* in Argentina) (Sampson et al., 2001; Carrano et al., 2002, 2004; Agnolín et al., 2003; Sereno et al., 2004; Tykoski and Rowe, 2004).

The pattern of close relationship among latest Cretaceous (i.e., Campanian and Maastrichtian) abelisauroid theropods from Madagascar, India, and Argentina is repeated in certain mammalian (Krause et al., 1997b; Krause, 2001; but see Averianov et al., 2003), crocodyliform (e.g., Buckley and Brochu, 1999; Buckley et al., 2000; Wilson et al., 2001; Prasad and de Broin, 2002; Turner, 2004; Smith and Makovicky, 2006), and sauropod (Curry Rogers, 2002, 2005) taxa. These similarities prompted us (see summaries in Krause et al., 1999, 2006; Krause, 2003) to hypothesize a much higher degree of cosmopolitanism among vertebrate taxa that lived on Gondwanan landmasses during the latest Cretaceous than predicted by most paleogeographic reconstructions based exclusively or primarily on geophysical and geological evidence (e.g., Lawver et al., 1992; Smith et al., 1994; Marks and Tikku, 2001; Reeves and de Wit, 2000; Rotstein et al., 2001; Scotese, 2001; Kent et al., 2002; O’Neill et al., 2003; de Wit, 2003;

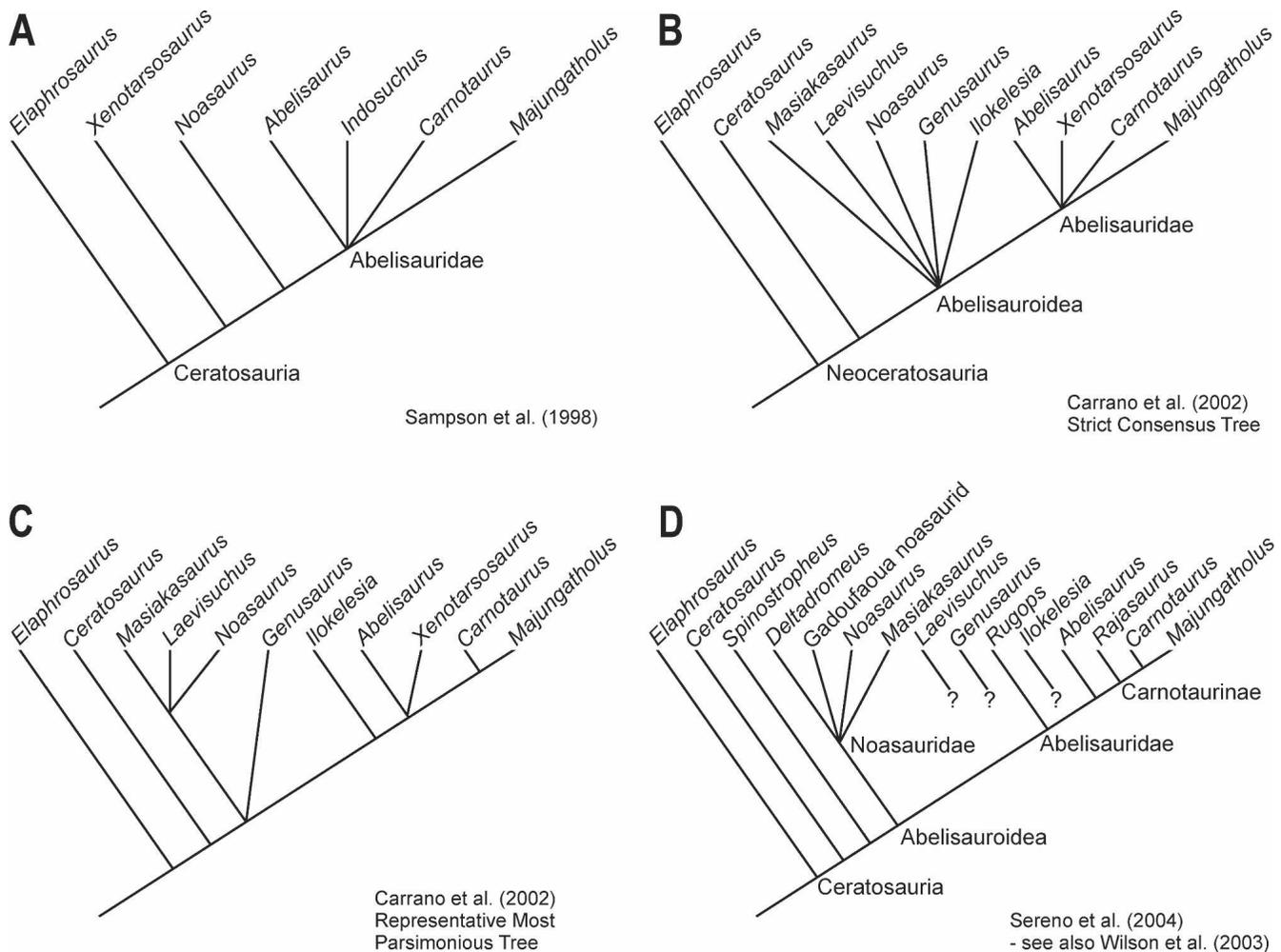


FIGURE 9. Phylogenetic relationships of ceratosaurian theropods as revealed by the analyses of **A**, Sampson et al. (1998); **B**, Carrano et al. (2002)—strict consensus cladogram; **C**, Carrano et al. (2002)—representative most parsimonious cladogram; and **D**, Serenio et al. (2004).

Bernard et al., 2005). These reconstructions (Fig. 11 A, B) posit separation and isolation of Indo-Madagascar (the Indian subcontinent + Madagascar) from all other landmasses by approximately 120 Ma, some 50 Ma before the time that the Maevarano fauna was entombed. The close relationships of terrestrial vertebrates that lived on the Indian subcontinent and Madagascar 70–65 Ma to penecontemporaneous taxa in South America are difficult to explain in light of these paleogeographic reconstructions.

In an attempt to reconcile this conflict, and the apparent absence of derived abelisaurids (carnotaurines of Sereno, 1998) in mainland Africa, Krause and colleagues (1997b, 1999, 2006), Sampson and colleagues (1998, 2001), Carrano and colleagues (2002), Krause (2003), and others in our working group postulated and discussed two alternative paleobiogeographic hypotheses (others have been formulated as well—e.g., Rage, 1988, 2003). The first, referred to as the ‘pan-Gondwana’ model (Serenio et al., 2004), posits that the vertebrate clades in question originated and dispersed throughout Gondwana prior to its fragmentation into isolated landmasses and, thus, that the apparently disjunct biogeographic distributions are simply the result of sampling bias, with representative examples of key taxa yet to be found on Africa, and/or differential regional extinction. The second hypothesis, promoted by our working group, was recently referred to as the ‘Africa-first’ model by Serenio and colleagues

(2004) because it states that mainland Africa was the first of the major Gondwanan landmasses to become physically and biotically isolated (see also Gheerbrant and Rage, 2006). The ‘Africa-first’ hypothesis postulates that the observed cosmopolitanism in vertebrate faunas between Indo-Madagascar and South America is the result of relatively much more recent common ancestry, enabled by persistent subaerial connections among Gondwanan landmasses exclusive of Africa. More specifically, following separation and isolation of the African continent prior to the Early Cretaceous/Late Cretaceous boundary, we postulated that land connections between Indo-Madagascar and South America were maintained via land bridges with Antarctica well into the Late Cretaceous. Plate tectonic reconstructions for the Indian Ocean are subject to many uncertainties, especially prior to 93 Ma (Kent et al., 2002), but this scenario was supported by the paleogeographic model of Hay et al. (1999), who argued for the presence of an early Late Cretaceous large igneous terrain known as the Kerguelen Plateau (e.g., Frey et al., 2000; Rotstein et al., 2001; Wallace et al., 2002) linking Indo-Madagascar with Antarctica (Fig. 11C). Case (2002) has more recently suggested that the connection between Antarctica and Indo-Madagascar was through the Gunnerus Ridge and Kainan Maru Seamount (and thus directly to Madagascar) rather than through the Kerguelen Plateau (and thus to peninsular India) as originally suggested by Hay and colleagues (1999). The large-scale biogeo-

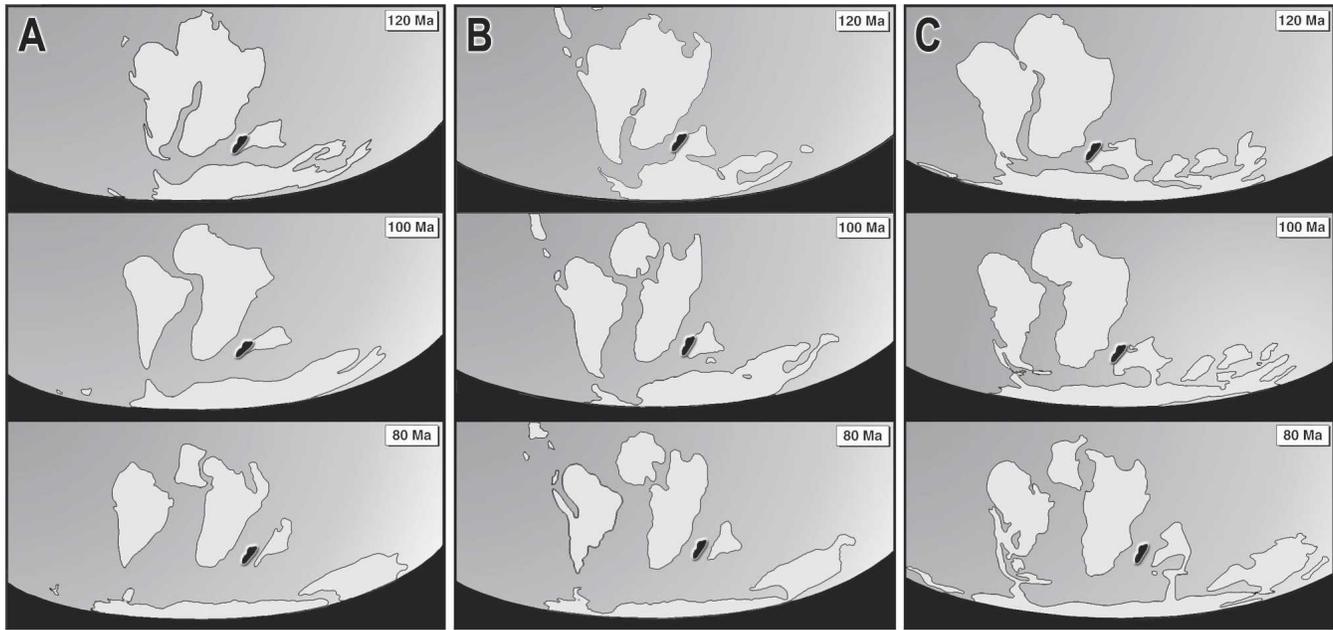


FIGURE 11. Paleogeographic reconstructions of major Gondwanan landmasses during the Late Cretaceous at 120, 100, and 80 Ma, according to **A**, Smith et al. (1994); **B**, Scotese (2001); and **C**, Hay et al. (1999). Madagascar indicated in black. From Krause (2003).

graphic effect, in allowing biotic communication between Antarctica and Indo-Madagascar, however, is the same. Sampson and colleagues (1998:1051) clearly stipulated that both hypotheses (now known as the ‘pan-Gondwana’ and ‘Africa-first’ models) “are equally probable given the data at hand.”

Recent finds of abelisaurid theropods and other Cretaceous vertebrates on Gondwanan landmasses since the description of the skull and partial postcranial skeleton of *Majungatholus* by Sampson and colleagues (1998) are relevant to this discussion. These include several discoveries from Campanian-Maastrichtian horizons of Argentina (*Quilmesaurus* Coria [2001], *Aucasaurus* Coria et al. [2002], and a probable abelisaurid [Kellner and Campos, 2002; Leanza et al., 2004; pers. obs. by MTC]) and India (*Rajasaurus* Wilson et al. [2003]), and one from the Late Cretaceous of Brazil (*Pycnonemosaurus* Kellner and Campos [2002]). The relationships of *Quilmesaurus* and *Pycnonemosaurus*, which are based on fragmentary remains, and *Aucasaurus*, based on a nearly complete but only preliminarily described skeleton, have not been firmly established, although the latter was considered to be the sister taxon of *Carnotaurus* and united with it to form the novel clade Carnotaurini (Coria et al., 2002). Wilson and colleagues (2003), however, conducted a relatively comprehensive phylogenetic analysis of *Rajasaurus* and placed the Indian genus in the Carnotaurinae, as the primitive sister taxon to *Majungatholus* + *Carnotaurus*, on the basis of two synapomorphies: “positioning of the posterior process of the nasal dorsal to the orbit and the presence of a frontal excrescence” (Fig. 9D). *Rajasaurus* was considered by Wilson and colleagues (2003) to be one of three valid abelisaurid genera known from the Late Cretaceous of India (the other two, which were not included in the phylogenetic analysis, being *Indosuchus* and *Indosaurus*). Wilson and colleagues (2003:30) concluded that “carnotaurines are restricted to India, Madagascar, and South America.” Although the above-noted phylogenetic study of Carrano and Sampson (in press) suggests that Carnotaurinae may differ significantly in composition from its ‘traditional’ components (with *Majungasaurus* and *Carnotaurus* residing in separate subclades within Abelisauridae), it supports the conclusion that

derived abelisaurids are currently limited to India, Madagascar, and South America.

Another set of discoveries, from pre-Campanian Cretaceous horizons of South America (Coria and Salgado, 2000; Lamanna et al., 2002; Rauhut et al., 2003; Coria et al., 2004) and Africa (Russell, 1996; Sereno et al., 2004), provide new insights into the early history of Abelisauridae. Importantly, these finds established the pre-Campanian origin of abelisaurids and the wide distribution of the clade across South America and Africa. Of particular note because of the relative completeness of the material (consisting of a partial skull) is the description by Sereno and colleagues (2004) of a basal abelisaurid, *Rugops* (“Niger taxon 2” of Wilson et al., 2003), from the Cenomanian of the Republic of Niger. The discovery of this taxon, if correctly dated (see Jacobs et al. [2006] and O’Connor et al. [2006], who questioned the Cenomanian age and indicated that the generally accepted age, based on Taquet [1976], is Albian), refutes one of the two “equally probable” hypotheses listed by Sampson and colleagues (1998:1050), namely that “abelisaurids originated sometime in the Early Cretaceous after the tectonic isolation of Africa.” Based on the presence of the clade on mainland Africa during the Cenomanian, the authors claimed to have refuted the ‘Africa-first’ model of Gondwanan fragmentation and proposed in its stead a revised ‘pan-Gondwana’ model. The latter model invoked a trans-Atlantic land bridge that, along with those between South America and Antarctica and between Antarctica and Indo-Madagascar, was “severed during a relatively brief interval at the beginning of the Late Cretaceous (ca. 100-90 Myr ago)” (Sereno et al., 2004:1328).

We dispute Sereno and colleagues’ (2004) refutation of the ‘Africa-first’ model. Sereno and colleagues (2004) portrayed the ‘Africa-first’ model as being predicated on separation between Africa and South America as early as 140 Ma, which is not the case. The Gondwanan reconstruction depicted even as late as 120 Ma in Krause and colleagues (1997b, 1999), Sampson and colleagues (1998), and Krause (2003) clearly shows South America and Africa connected at this time (all based on reconstructions generated from the Web site operated by the Hay and

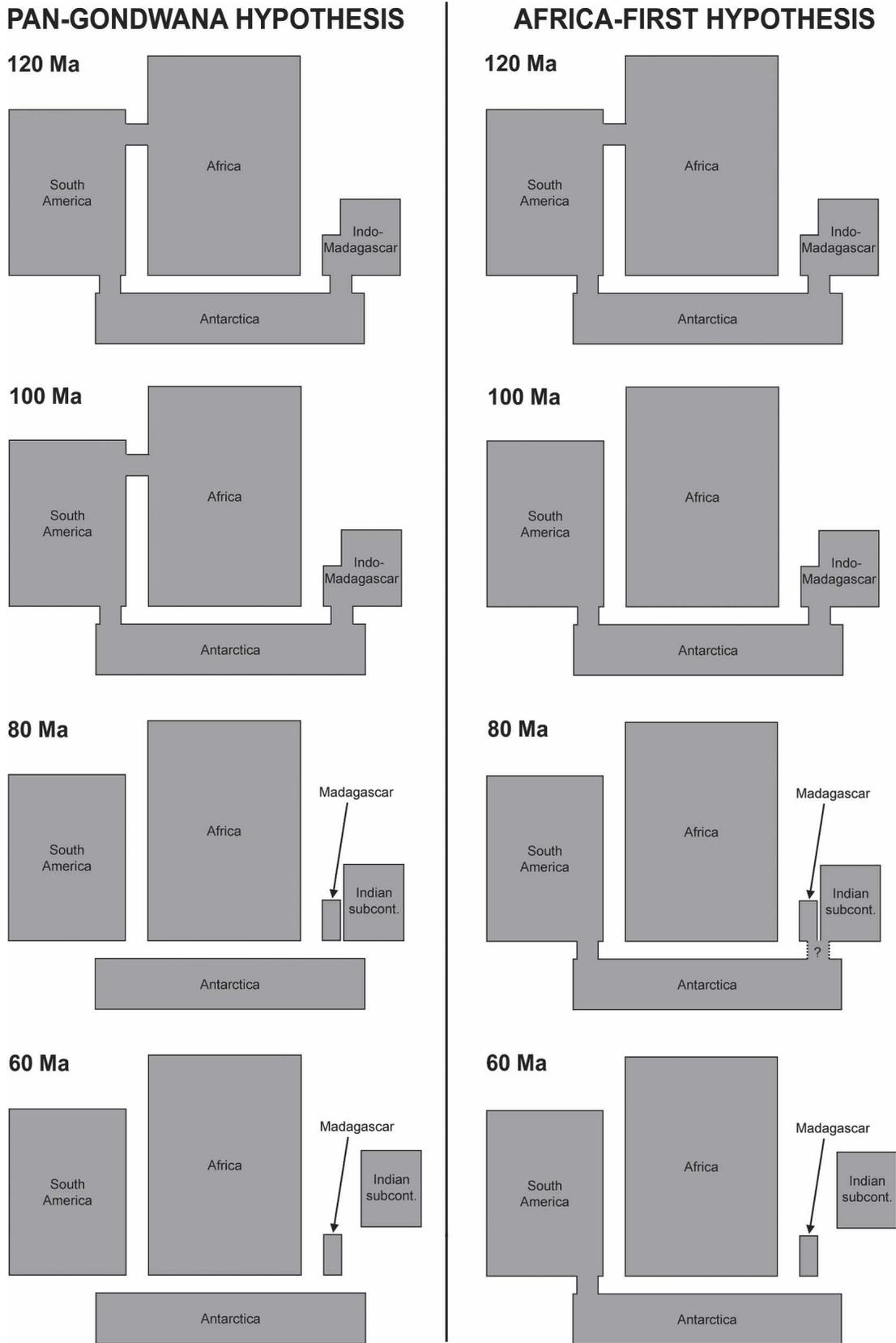


FIGURE 12. Schematic paleogeographic maps of major Gondwanan landmasses exclusive of Australia and southern Europe at 120, 100, 80, and 60 million years ago depicting the major differences in purported land connections between the pan-Gondwana hypothesis (left column) and the Africa-first hypothesis (right column). The pan-Gondwana hypothesis posits separation of South America from Africa, South America from Antarctica, and Antarctica from Indo-Madagascar in a narrow time interval 100-90 million years ago. The Africa-first hypothesis posits separation of South America from Africa before the beginning of the Late Cretaceous, Antarctica from Indo-Madagascar late in the Late Cretaceous, and South America from Antarctica in the Eocene. From Krause et al. (2006).

TABLE 1. Numbers of lower-level taxa of crocodyliforms, non-avian dinosaurs, and mammals reported from Cretaceous horizons in South America, Antarctica, Africa, Madagascar, and the Indian subcontinent.

| | South America | | | Antarctica | | | Africa | | | Madagascar | | | Indian subcontinent | | |
|----------------|---------------|-----|-----|------------|-----|-----|--------|-----|-----|------------|-----|-----|---------------------|-----|-----|
| | EK | ELK | LLK | EK | ELK | LLK | EK | ELK | LLK | EK | ELK | LLK | EK | ELK | LLK |
| Crocodyliforms | 6 | 3 | 12 | 0 | 0 | 0 | 8 | 5 | 1 | 0 | 3 | 7 | 0 | 0 | 3 |
| Dinosaurs | 19 | 37 | 24 | 0 | 1 | 3 | 28 | 19 | 3 | 0 | 2-3 | 4 | 0 | 3 | 17 |
| Mammals | 1 | 1 | 16 | 0 | 0 | 0 | 19 | 1 | 0 | 0 | 0 | 5 | 0 | 0 | 4 |

Note strong disparities in sampling among Gondwanan landmasses from different temporal intervals. Data extracted from Tables 1–12 in Krause et al. (2006). EK = Early Cretaceous, ELK = early Late Cretaceous (pre-Campanian Late Cretaceous), LLK = late Late Cretaceous (Campanian + Maastrichtian).

colleagues working group [<http://www.odsn.de/odsn/services/paleomap/paleomap.html>; see Fig. 11C]; though reconstructions by Smith and colleagues [1994] and Scotese [2001] are consistent in this regard [see Fig. 11A, B]). There is well-constrained geological evidence (e.g., Nürnberg and Müller, 1991; Parrish, 1993; Pletsch et al., 2001) that a permanent marine connection between South America and Africa was initiated in the late Aptian-early Albian (approximately 118–106 Ma; Gradstein et al., 2004). Sereno and colleagues (2004) also incorrectly summarized our previous statements with regard to separations between South America and Antarctica and between Antarctica and Madagascar, claiming that we placed these events 30–50 million years later than the separation between South America and Africa. The most salient distinction between the pan-Gondwana model and the Africa-first model concerning the separation of South America and Africa is that the former posits separation approximately at or soon after the Early/Late Cretaceous boundary whereas the latter posits separation before the boundary. Further, the revised ‘pan-Gondwana’ model posits separation of South America from Antarctica, and Antarctica from Indo-Madagascar, at approximately the same time as the separation between South America and Africa (namely, at or soon after the Early/Late Cretaceous boundary), whereas the Africa-first model suggests markedly different times for these separations: before the Early/Late Cretaceous boundary for the separation of South America and Africa, late in the Late Cretaceous for the separation between Antarctica and Indo-Madagascar, and in the Early Tertiary for the separation between South America and Antarctica. The essential differences between the ‘Africa-first’ and ‘pan-Gondwana’ models, in terms of Gondwanan landmass connections at particular times during the Mesozoic, are depicted in Figure 12 and are discussed in greater detail in Krause and colleagues (2006).

Apart from the inexactitude of the geological/geophysical evidence for landmass fragmentation during the late Mesozoic and the resulting paleogeographic reconstructions, critical to these issues are comparable temporal sampling and documentation of terrestrial faunas from Madagascar, the Indian subcontinent, South America, and mainland Africa (Table 1). Unfortunately, the fossil record of terrestrial vertebrates from mainland Africa is much better for the Early Cretaceous and early Late Cretaceous (pre-Campanian) than it is for the Campanian and Maastrichtian, whereas the reverse is true for Madagascar and the Indian subcontinent (see also, e.g., Lamanna et al., 2002; Wilson et al., 2003). This uneven temporal sampling has precluded definitive testing of the hypotheses articulated above. As we have stressed, “One of the key stumbling blocks for testing the paleobiogeographic hypotheses outlined here is the virtual lack of terrestrial and freshwater vertebrates from the post-Cenomanian Late Cretaceous of Africa” (Krause et al., 1999:6). This statement remains true today. Discovery of the relatively primitive abelisaurid *Rugops* in Niger at ~95 Ma—some 20–30 Ma prior to the occurrences of more derived abelisaurids in South America, India, and Madagascar—while clearly a significant discovery, does not in any way refute an hypothesis that Africa was the first

among Gondwanan landmasses to be fully isolated. What also remains critical is accurate dating of the deposits from which the relevant specimens are recovered; reliable and precise age constraints for much of the African material, for instance, is lacking.

Refutation of the ‘Africa-first’ hypothesis must come in the form of latest Cretaceous nonmarine vertebrate taxa from continental Africa that are more closely related to forms from South America, India, and/or Madagascar than these forms are to each other. With respect to abelisaurids, refutation of this hypothesis does not derive from a Cenomanian(?) taxon (i.e., *Rugops*) from Africa that lies basal to the more derived members of this clade. Even in light of the many significant recent discoveries of abelisaurids from various horizons in Africa, South America, and India, we maintain the same working hypothesis formulated by Sampson and colleagues (1998:1050): “African faunas became increasingly endemic during the Cretaceous after Africa’s isolation from South America, whereas retention of subaerial connections among the remaining Gondwanan landmasses resulted in relatively extensive cosmopolitanism for the associated terrestrial faunas, perhaps until late in the Late Cretaceous.” Recent and ongoing field research in strata of Late Cretaceous age, or potentially Late Cretaceous age, in mainland Africa (e.g., Rauhut and Werner, 1997; Krause et al., 2003; Gottfried et al., 2004; Sertich et al., 2005, 2006; O’Connor et al., 2006; Jacobs et al., 2006), as well as Antarctica (e.g., Hooker et al., 1991; Gasparini et al., 1996; Rich et al., 1999; Case et al., 2000, 2003), provides hope that relevant comparative materials may soon come to light, allowing more rigorous testing of this hypothesis.

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APPENDIX 1. Chronological list of reported discoveries of bones and teeth probably or certainly attributable to *Majungasaurus crenatissimus* found prior to initiation of the Mahajanga Basin Project in 1993.

Author: Depéret (1896a, b).

Collector and Date: Landillon, regimental staff officer of the French Marines, 1895.

Specimens: Two isolated teeth (1896b:pl. 6, figs. 4, 4a, 5, 5a), ungual phalanx (1896b:pl. 6, figs. 8, 8a), two partial sacral vertebrae (one centrum of which is figured in 1896b:pl. 6, fig. 6), partial caudal vertebra (1896b:pl. 6, fig. 7).

Repository: Université Claude Bernard Lyon 1.

Attribution: *Megalosaurus crenatissimus*.

Localities: Near Maevarana, on northeastern bank of Betsiboka River, approximately 46 km south of Mahajanga. The two teeth were recovered from Depéret's (1896b:fig. 1) Locality 2 (Figs. 2, 5B). The localities for the other specimens were not specified.

Author: Boule (1896, 1900).

Collector and Date: Bastard and Decorse, date unknown.

Specimens: Many specimens, but all destroyed in shipment from Mr. Bastard except some hollow limb bone fragments and a vertebra (none illustrated). Some teeth sent by Dr. Decorse.

Repository: National Museum of Natural History, Paris.

Attribution: A theropod of the genus *Megalosaurus*, or close to this genus.

Localities: Near Maevarana, apparently from same area as specimens described by Depéret.

Author: Thevenin (1906, 1907).

Collectors and Date: Bastard and Decorse, late 1890's.

Specimens: Isolated tooth (1907:pl. I, figs. 17, 17a), fragmentary limb bones, vertebrae (caudal vertebra figured in 1907:pl. I, fig. 18).

Repository: National Museum of Natural History, Paris.

Attribution: *Megalosaurus crenatissimus*.

Localities: Near Maevarana, apparently from same area as specimens described by Depéret.

Author: Piveteau (1926).

Collector and Date: Perrier de la Bathie on a trip listed by Piveteau (1926) as recent.

Specimens: Piveteau (1926) lists the presence of teeth and bones of megalosaurids but he does not make it explicit that additional specimens were collected by Perrier de la Bathie.

Localities: Localities in the Marovoay, Miadana, and Mahavavy regions.

Author: Lavocat (1955a, b, c; 1957).

Collectors and Date: Primarily R. Lavocat, from May to October, 1954. The dentary described by Lavocat (1955a, b) was discovered by a Berivotra villager one month prior to Lavocat's arrival. Upon his arrival, and with the assistance of the villager, Lavocat (1955b) collected additional fragments (teeth) of the specimen.

Attribution: *Majungasaurus crenatissimus*.

Specimens: Right dentary of subadult individual (Lavocat, 1955b:fig. 1; Fig. 7), MNHN.MAJ 1, in addition to many isolated teeth and several isolated bones.

Repository: National Museum of Natural History, Paris.

Localities: It appears that the isolated specimens were recovered from a number of localities, some from near Landillon's original discovery sites (in and around butte marked 244 in Lavocat, 1955a:fig. 2; Fig. 6B), some (at least one tooth, noted by Lavocat, 1955a:14, as being larger than those of the 'megalosaurid' in the Berivotra area) from near km 523–524 on what is today National Route 4, and some from in and around the village of Berivotra. The renowned geologist, H. Besairie, had previously collected several bones in the latter area, near km 531 on National Route 4 (it must be noted, however, that recalibrations of distance mean that km 531 in 1955 is not the same as the current km 531), and alerted Lavocat to the fossiliferous potential of the area. The dentary of a subadult individual is listed by Lavocat (1955b) as occurring in a boxed ravine, three meters above the bed of a river, two or three km north of the Berivotra hotel. This is almost certainly in error since the Maevarana Formation does not crop out 2–3 km north of Berivotra, which is indicated in Lavocat's (1955a) figure 2. Another area, east of the village of Befandrana and north of the road between Mahajanga and Ambalabé, that yielded

dinosaur material, as well as specimens of the snake *Madisoia* later described by Hoffstetter (1961:fig. 1), lies approximately 15 km northwest of Berivotra.

Author: Russell et al. (1976).

Collectors and Date: D. and D. Russell, P. Taquet, and H. Thomas; July 1974.

Specimens: Several bones, including elements of the postcranial skeleton. These specimens are also described in the unpublished thesis of Ravoavy (1991, see below).

Repository: University of Antananarivo.

Attribution: *Majungasaurus crenatissimus*.

Localities: Listed as occurring in vicinity of Berivotra, 50 km south of Majunga, along National Route 4.

Authors: Asama (1977), Obata and Kanie (1977), Asama et al. (1981).

Collectors and Date: K. Asama, I. Fujiyama, Y. Hasegawa, Y. Kanie, and H. Ujiié (September, 1973) and K. Asama, Y. Hasegawa, Y. Kanie, S. Matsubara, I. Obata, C. Ramanitrahiraiana, W. Rakotoarivelo, C. Ranaivoson, Y. Ratsimba, and Theodore (September and October, 1975).

Specimens: "A great number of dinosaur bones were collected" (Asama, 1977) but it is unclear how many, if any, of them were of *Majungasaurus crenatissimus*.

Repository: The specimens collected in 1975 were deposited in the Geological Survey of Madagascar whereas those collected in 1973 were initially taken to Japan and then returned to Madagascar (Asama et al., 1981). Our efforts to find these specimens in Madagascar have failed. Photographs (provided by Dr. Makoto Manabe of the National Science Museum, Tokyo) of casts retained at the National Science Museum, Tokyo, do not reveal any material of theropods.

Attribution: *Majungasaurus crenatissimus*.

Localities: From two main areas designated "South of Berivotra" (Obata and Kanie, 1977:figs. 2, 3) and "Berivotra to Amboanemba along Route no. 4" (Obata and Kanie, 1977:fig. 6).

Authors: Sues and Taquet (1979), Sues (1980).

Collector and Date: Collector unknown, specimen rediscovered in MNHN collections by Philippe Taquet in 1976. Thought to have been collected "at the beginning" of the 20th century (Sues, 1980: 954).

Specimens: MNHN.MAJ 4, frontals and incomplete parietals (Sues and Taquet, 1979:fig. 1; Sues, 1980:pl. 1, figs. 1–3, text-fig. 2). See also Fig. 8.

Repository: National Museum of Natural History, Paris.

Attribution: *Majungatholus atopus*.

Locality: Precise locality unknown, listed as Majunga District.

Author: Ravoavy (1991).

Collectors and Date: T. Olivaux and F. Ravoavy, 1987 and 1989 expeditions.

Specimens: Numerous teeth (fig. 21) and three fragmentary long bones (fig. 22), thought to be femora or possibly tibiae. Ravoavy also reported the discovery in 1989 of a series of four anterior caudal vertebrae, but these were not illustrated (they are, however, included in the sample studied by O'Connor, this volume). They were found at Mahajanga Basin Project site MAD96-01 and associated with the skull and additional caudal vertebrae (FMNH PR 2100) discovered seven years later by Mahajanga Basin Project field crews.

Repository: University of Antananarivo.

Attribution: *Majungasaurus crenatissimus*.

Localities: Two sites are mentioned: (1) 30 minute walk SE of Berivotra (indicated in Fig. 2 as Ravoavy Area 1 [FR1]); (2) near Centre Zootechnique de Miadana, Antahialava (indicated in Fig. 2 as Ravoavy Area 2 [FR2]). The location of these areas was confirmed in the field in 1996 by Ravoavy.

Note: Ravoavy also mentions collections made by R. D. E. MacPhee (then of Duke University) and associates in 1984 and by B. Rakotasamimanana (University of Antananarivo) and her students in 1985 in the Berivotra area. It is not stated that theropod material was recovered during these expeditions. MacPhee's collections were deposited in the University of Antananarivo whereas Rakotasamimanana's collections were divided equally and deposited in the University of Antananarivo and the University of Mahajanga.