

PALEOENVIRONMENT AND PALEOECOLOGY OF *MAJUNGASAURUS CRENATISSIMUS* (THEROPODA: ABELISAURIDAE) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT —The abelisaurid theropod *Majungasaurus crenatissimus* inhabited the plains of northwestern Madagascar during the Late Cretaceous. It lived alongside other nonavian dinosaurs, including a small-bodied noasaurid theropod (*Masiakasaurus knopfleri*) and a titanosaurian sauropod (*Rapetosaurus krausei*). Although an inhabitant of the expansive floodplains of the Mahajanga Basin, *M. crenatissimus* also frequented the broad and sandy channel belts that drained Madagascar's central highlands. These shallow rivers were populated by a variety of aquatic and semi-aquatic animals, including fish, frogs, turtles, and several species of both large and small crocodyliforms. These animals were likely adapted for seasonal fluctuations in water availability because the sediments that entomb their remains (fine-grained debris flow deposits intercalated with stream flow deposits) indicate a strongly variable discharge regime. Associated oxidized calcareous paleosols with localized accumulations of carbonate nodules suggest that the ambient climate was semiarid. The numerous bonebeds preserved in these same sediments are indicative of localized and recurrent pulses of mortality. *M. crenatissimus* fed on carcasses preserved in these bonebeds, and there is good indication from a wealth of tooth-marked bone derived from two conspecific individuals that it focused on the well-muscled axial skeleton in a fashion similar to that of many modern vertebrate carnivores. This evidence for intraspecific feeding renders *M. crenatissimus* the only theropod dinosaur with demonstrated cannibalistic tendencies.

MALAGASY ABSTRACT (FAMINTINANA) —Ny theropod abelisaurid *Majungasaurus crenatissimus* dia nonina tao amin'ny lemakay ny faritra avaratr'andrefan'i Madagasikara nandrity ny Cretaceous Farany. Tamin 'izany dia niarano-toetra hatrany niaraka tamin'ny dinozaoro tsy avian izy, ka anisan'izany ny theropod noasaurid kely vatana (*Masiakasaurus knopfleri*) sy sauropod titanosaurian (*Rapetosaurus krausei*). Na dia nipetraka maharitra tao amin 'ny lemakay midadasika saforan'ny rano tao amin'ny Basin an'i Mahajanga azo *M. crenatissimus* dia hita matetika koa izy namony ny sisina lehibe sy mamasiky ny lakan-drano, izay manondraka ny anivon-tanin'i Madagasikara (central highlands). Ireo renirano marivo ireo dia nahitana karazam-biby maro izay monina manontolo na am-pahany anaty rano, toy ny trondro, sahona, sokatra, ary karazam-boay maro koa ka hita tamin'izany ireo voay kely sy vaventy vatana. Ireo biby ireo dia toy ny lasa zatra niaina tamin'ny fiovaovan'ny fisian'ny rano satria ireo karazam-batokely madinika notanterin'ny rano izay nandrakotra sy nitahiry ny vatana mbola tavela tamin'izy ireo (tosak'ireo tatitra [sediment] potipotika tena madinika toa miendrika voa izay hifanelanelan'an'y tatitra nentin'ny rano) dia nampiseho mazava ny fisian'ny fiovaovana tamin'ny fametrahana ireo tatitra nentin'ny rano. Ny fisian'ny tany tranainy misy harafesina sy sokay ka niangonan'ny vonganana madinika misy carbonate tamin'ny faritra mazava dia nafahana nilaza fa ny toetr'andro sy toe-tany manodidina teo amin'io toerana io dia maina amin'ny ampahany. Ireo taolana maro hita tany amin'ny faritra ambany tamin'io tatitra io ihany koa dia karazana marika nilaza ny fisian'ny fahafatesana maro niaraka sy tampoka ary niverimberina matetita tamin'ny faritra mazava. *M. crenatissimus* dia nihinana ny vatan'ireo biby voatahiry izay hita tao amin'io toerana niangon'ny taolana io, ary nisy aza filazana mazava tamin'ny taolana nisy dia-nify mazava izay an'ny biby roa avy amin'ny karazana mitovy (conspecific) fa io nify io dia mifandray tamin'ny hozatra matanjaky ny tsangana afovoany ny karana izay miendrika toy ny hita amin'ny hazon-damosin'ireo carnivores mbola amin'izao fotoana izao. Io seho mazava teo fomba fihininana teo amin'ireo biby iray sokajy dia nahatonga ny filazana fa *M. crenatissimus* no hany dinozaoro theropod tokana nampiseho ny mety fisian'ny fifampihinana teo amin'ny biby iray karazana.

INTRODUCTION

Majungasaurus crenatissimus is the largest terrestrial carnivore documented in the Upper Cretaceous Maevarano Formation of northwestern Madagascar. It inhabited an aggrading basin on an island subcontinent that was shifting northward through the southern hemisphere desert belt into tropical latitudes (e.g.,

Royer et al., 1992; Smith et al., 1994; Scoteese, 1998) and roamed a landscape that was characterized by a seasonal and semiarid climate (Rogers et al., 1997, 2000; Miller, 2000; Jerve 2004; Rogers, 2005). *M. crenatissimus* shared its subtropical realm with other nonavian dinosaurs, including the titanosaur *Rapetosaurus krausei* (Curry, 2001; Curry Rogers and Forster, 2001, 2004; Curry Rogers, 2005) and the noasaurid theropod *Masiakasaurus knopfleri* (Sampson et al., 2001; Carrano et al., 2002). Numerous non-dinosaurian animals also lived alongside *M. crenatissimus*, most notably crocodyliforms, which are preserved in consider-

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able abundance and diversity in the Maevarano Formation (Buckley et al., 2000; and see faunal summaries in Krause et al., 1997, 1999, 2006; Rogers et al., 2000; Krause, 2003). The size of *M. crenatissimus* (6–7 m in length), coupled with an apparent lack of other comparably proportioned carnivorous taxa, suggests that it was probably the top predator in the Maevarano ecosystem, at least in fully terrestrial settings (the presumably more aquatic crocodyliforms *Mahajangasuchus insignis* and *Trematochampsia obliqua* were also formidable carnivores).

Ongoing analyses of the stratigraphy, sedimentology, and taphonomy of the Maevarano Formation and associated units (Rogers et al., 1997, 2000, 2003; Rogers, 2005) provide an excellent opportunity to reconstruct the paleoenvironment and paleoecology of *M. crenatissimus*. Data gleaned from the Maevarano Formation and associated rock units that pertain to the age, paleoenvironment, preservation, and paleoecology are presented below.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York, NY; FMNH, Field Museum of Natural History, Chicago, IL; UA, Université d'Antananarivo, Antananarivo, Madagascar.

STRATIGRAPHY AND AGE

Stratigraphic Distribution of *Majungasaurus crenatissimus*

Fossils of *M. crenatissimus* are preserved in strata of the Upper Cretaceous Maevarano Formation, in the central portion of the Mahajanga Basin (Fig. 1). Extensive exposures of the Maevarano Formation crop out in the area surrounding the village of Berivotra, where National Route 4 cuts through spectacularly fossiliferous, highly dissected, and for the most part heavily grassed topography. Localities to the north and south of the Berivotra field area have also yielded bones and teeth of *M. crenatissimus* (see Krause et al., this volume).

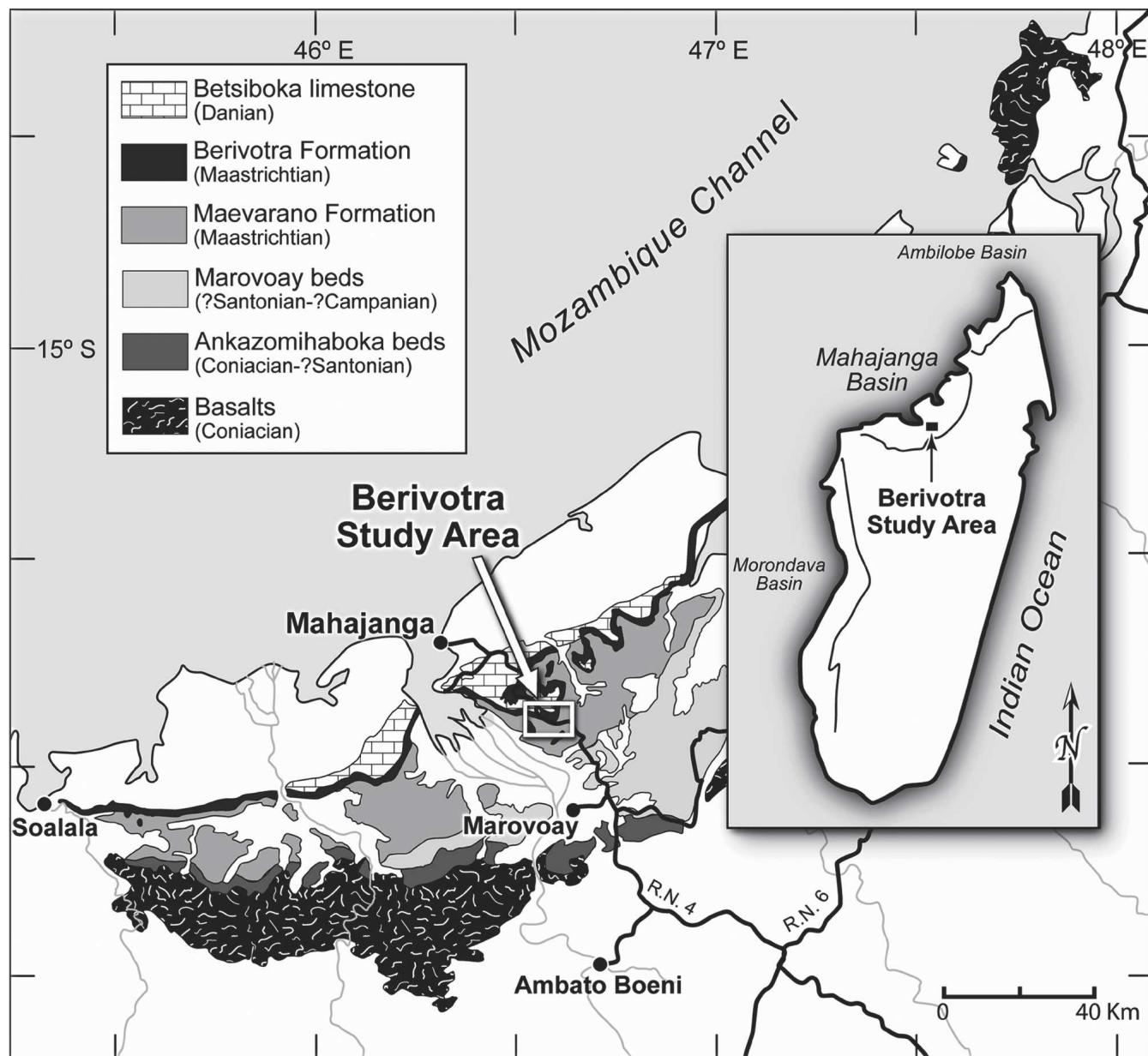


FIGURE 1. Outcrop map of Upper Cretaceous and Tertiary strata in the Mahajanga Basin of northwestern Madagascar. The Maevarano Formation yields abundant fossil remains of the abelisaurid theropod *Majungasaurus crenatissimus*, especially in the Anembalemba Member of the Berivotra study area.

In a recent analysis of the stratigraphy and sedimentology of the Maevarano Formation, Rogers and colleagues (2000) subdivided the formation into the Masorobe, Anembalemba, and Miadana members (Fig. 2). All three members preserve remains of *M. crenatissimus*, though the vast majority and the best-preserved specimens have been recovered from the Anembalemba Member.

The basal Masorobe Member, which is characteristically red and at least 80 m thick (the base of this unit is not exposed in the Berivotra field area), can be traced throughout the Berivotra region (Fig. 3). The unit is composed primarily of coarse-grained, poorly sorted, clay-rich sandstone with intercalations of fine-grained sandstone, siltstone, and claystone. Isolated teeth attributable to *M. crenatissimus* are found in relatively low abundance throughout the Masorobe Member (Rogers et al., 2000).

A disconformity marked by erosional relief and a patchy superjacent lag separates the Masorobe Member from the overlying Anembalemba Member. Locally, the disconformity separates a root-mottled bed of fine- to coarse-grained sandstone with a

red hue from an overlying bed of coarse-grained sandstone with massive structure and an olive green color. The overlying bed marks the base of the Anembalemba Member, which, like the Masorobe Member, crops out throughout the Berivotra region.

Two distinctive sandstone-dominated facies (designated facies 1 and facies 2 by Rogers et al., 2000; see also Rogers, 2005) characterize the Anembalemba Member (Fig. 4). Facies 1 consists of fine- to coarse-grained, poorly sorted sandstone with a considerable silt-clay component. The light greenish gray to white sandstones of facies 1 typically display small- to medium-scale tabular and trough cross-stratification. Facies 2 consists primarily of fine- to coarse-grained clay-rich sandstone characterized by very poor sorting, massive structure, and a light olive gray color. In most exposures of the Anembalemba Member, cross-stratified beds of facies 1 and massive beds of facies 2 are recurrently interbedded, typically with sharp to erosive contacts. Bed thickness and the ability to trace beds laterally vary from outcrop to outcrop.

Vertebrate fossils are strikingly abundant within exposures of the Anembalemba Member, especially within facies 2. It is virtually impossible to traverse outcrops of this unit without encountering vertebrate remains, both as isolated occurrences and as bonebeds. With regard to *M. crenatissimus*, isolated teeth are extraordinarily plentiful. Thousands of *M. crenatissimus* teeth have been collected from the Anembalemba Member over the course of eight field seasons and, to date, seven *M. crenatissimus* individuals represented by associated or articulated cranial and postcranial bones have been identified in the member.

The upper contact of the Anembalemba Member with the marine Berivotra Formation in the vicinity of Berivotra is a laterally continuous and essentially planar disconformity marked by a thin conglomeratic bed that yields teeth of selachians as well as polished bone pebbles (Gottfried and Rabarison, 1997; Rogers et al., 2000; Gottfried et al., 2001). Fine-grained siltstones and claystones of the Berivotra Formation (Rogers et al., 2000) sharply overlie the conglomeratic facies. Several kilometers to the southeast of the Berivotra field area, in the vicinity of the Miadana agricultural station (Krause et al., this volume: fig. 2), exposures of the Anembalemba Member pass up-section into approximately 25 m of intercalated claystone, siltstone, and sandstone beds of the Miadana Member (Rogers et al., 2000). These terrestrial strata, with rare marine intercalations, vary in color from white, to greenish-gray, to deep red, and are characteristically massive, with only rare examples of primary stratification (Fig. 5). Overall, the Miadana Member is finer-grained than either the Masorobe or Anembalemba members. A sharp contact separates the Miadana Member from overlying olive-yellow claystone of the Berivotra Formation. Teeth of *M. crenatissimus* have also been recovered from exposures of the Miadana Member.

Age

The Upper Cretaceous continental sedimentary record in the Mahajanga Basin includes the Maevarano Formation and the underlying Marovoay and Ankazomihaboka beds (Figs. 1, 2). The Ankazomihaboka beds are purportedly intercalated with, and definitely overlie, flood basalts that have been dated to ~88 Ma (Coniacian). These flood basalts are interpreted to reflect the rifting of the Indian subcontinent/Seychelles from Madagascar (Storey et al., 1995, 1997; Torsvik et al., 1998, 2001). Physical stratigraphic correlation of the Miadana and Anembalemba members of the Maevarano Formation with biostratigraphically zoned marine facies of the Berivotra Formation indicates that the formation is, at least in part, Maastrichtian in age (Rogers et al., 2000; Abramovich et al., 2002). The age of the Masorobe Member remains enigmatic, because there is presently no way to ascertain the location of the Campanian–Maastrichtian boundary in the local section. Similarly, there are presently no data that afford reliable age control in the Marovoay and Ankazomihaboka beds (aside from the basalts that purportedly interfinger with the Ankazomihaboka beds). Previous workers in the Mahajanga Basin tended to package Upper Cretaceous strata using stage boundaries (e.g., Besairie, 1972).

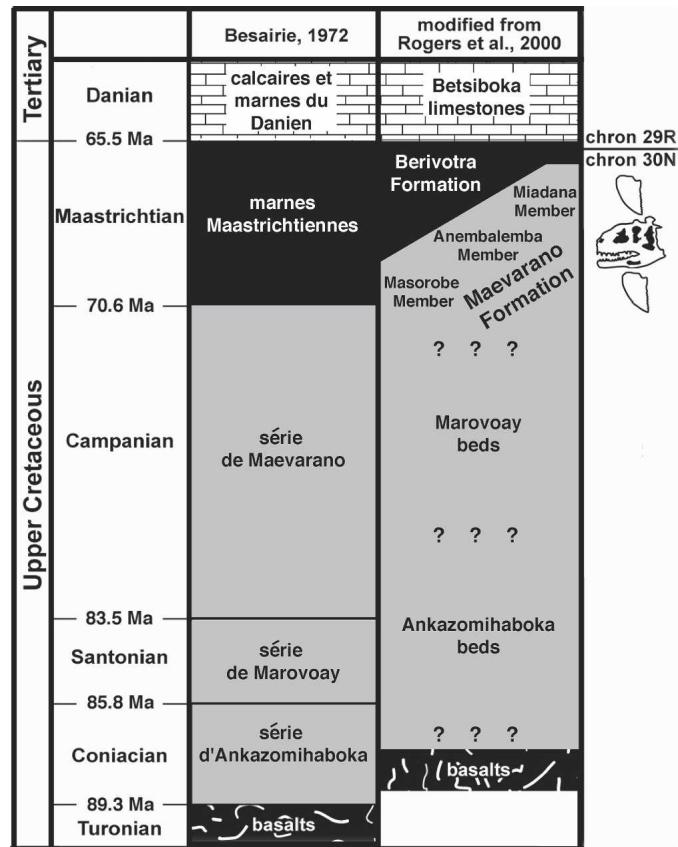


FIGURE 2. Upper Cretaceous stratigraphy of the central Mahajanga Basin in the context of the Cretaceous time scale of Ogg and colleagues (2004). The continental sedimentary record includes the Maevarano Formation and the underlying Marovoay and Ankazomihaboka beds. The Ankazomihaboka beds are underlain by, and ostensibly intercalate with (Besairie, 1972), flood basalts that have been dated to the Coniacian. Physical stratigraphic correlation of the Miadana and Anembalemba members of the Maevarano Formation with biostratigraphically zoned marine facies of the Berivotra Formation indicates that the formation is, at least in part, Maastrichtian in age. The age of the Masorobe Member remains enigmatic, because there is presently no way to ascertain the location of the Campanian–Maastrichtian boundary in the local section. Similarly, there are presently no data that afford reliable age control in the Marovoay and Ankazomihaboka beds (aside from the basalts that purportedly interfinger with the Ankazomihaboka beds). Previous workers in the Mahajanga Basin tended to package Upper Cretaceous strata using stage boundaries (e.g., Besairie, 1972).

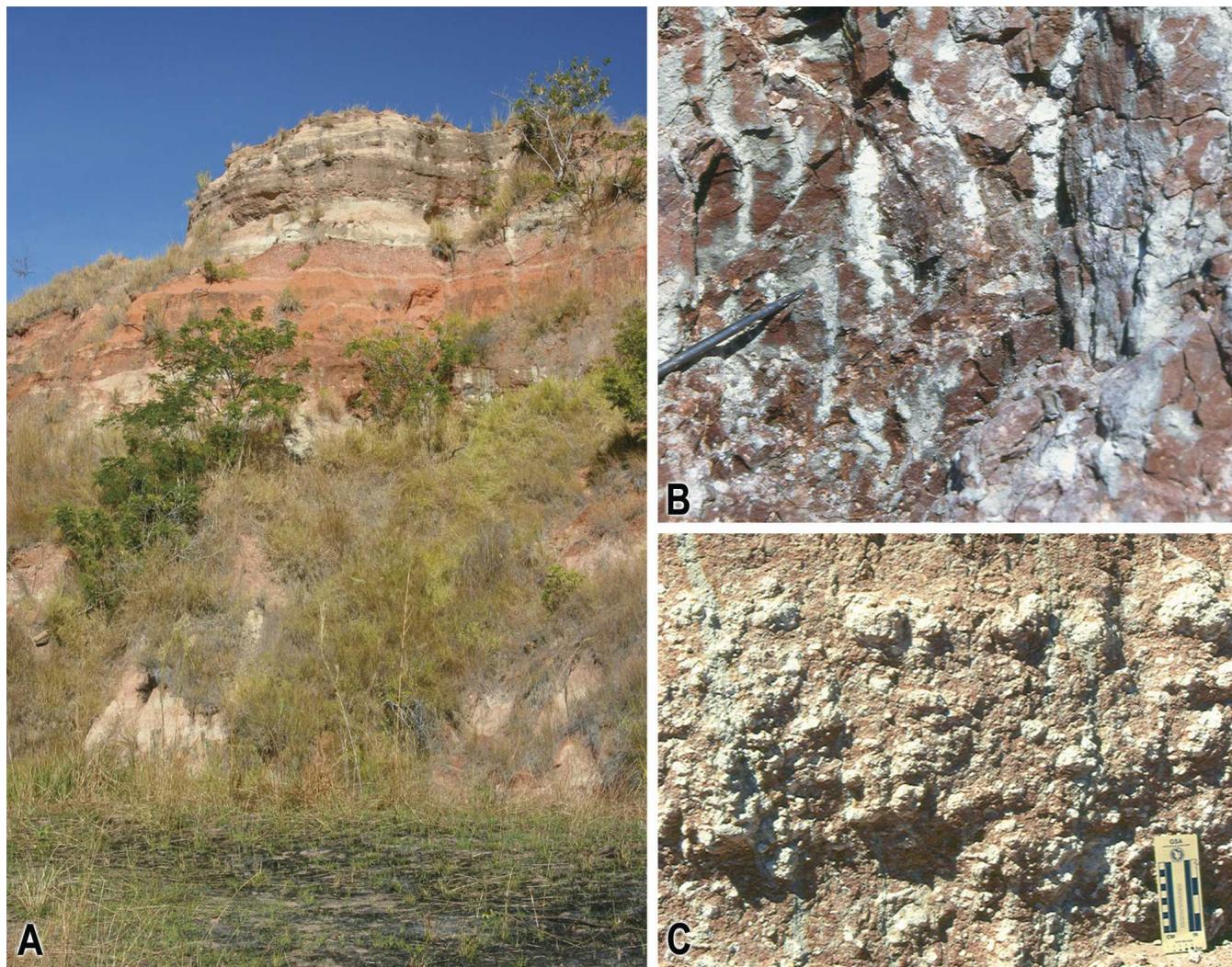


FIGURE 3. **A**, Outcrop view of the ~80 m thick Masorobe Member, exhibiting characteristic red coloration and paleosol-related color banding. **B**, Close-up view of vertical root traces in a clay-rich paleosol horizon within the Masorobe Member. Note drab reduction halos surrounding 2–5 mm diameter root casts and patches of powdery CaCO_3 . **C**, Pedogenic carbonate nodules in Masorobe paleosol. This nodular horizon, which ranges from 30–40 cm thick, is positioned ~1 m below the top of the paleosol.

ary in the local section (Fig. 2). An analysis of the magnetic stratigraphy of the Berivotra and Maevarano Formations is in progress in an effort to better resolve the chronostratigraphy of the Berivotra section (Casey, 2002; Casey et al., 2003; Dennis-Duke, 2005). Preliminary results indicate a reversal near the top of the Berivotra Formation. This reversal is positioned ~2 m beneath the K/T boundary (as defined on the basis of biostratigraphic data), and is interpreted to record the shift, through time, from Chron 30N to Chron 29R, which occurred at approximately 65.8 Ma, only some 300,000 years prior to the end of the Cretaceous Period (Ogg et al., 2004).

Finally, despite many published reports that indicate a Campanian age for the Maevarano Formation (e.g., Hoffstetter, 1961; Karche and Mahe, 1967; Besairie, 1972; Russell et al., 1976; Obata and Kanie, 1977; Buffetaut and Taquet, 1979; Krause and Hartman, 1996; Papini and Benvenuti, 1998), there are currently no data to justify this interpretation. Indeed, it is conceivable that the entire formation was laid down during the Maastrichtian. As such, and until definitive evidence indicates that the lower parts of the formation are older than Maastrichtian the Maevarano Formation, and *Majungasaurus crenatissimus*, are

best considered Maastrichtian in age. Furthermore, given the occurrence of teeth in the Miadana Member, there is strong indication that *M. crenatissimus* survived into the late Maastrichtian (Fig. 2).

PALEOENVIRONMENT

Majungasaurus crenatissimus inhabited a low-relief alluvial plain that was bounded to the southeast by crystalline highlands and to the northwest by the Mozambique Channel. While *M. crenatissimus* roamed the floodplains and channel belts of the central Mahajanga Basin, the sea transgressed from the northwest and deposited the Berivotra Formation, and, later, the Betsiboka limestone. This marine incursion, which appears to have spanned much of the Maastrichtian and continued into the Tertiary (Lalharisiana and Ferrand, 1994; Rogers et al., 2000; Abramovich et al., 2002), significantly diminished the expanse of the Maevarano alluvial plain, and thus served as a first order control on the nature and availability of habitat. At least some populations of *M. crenatissimus* would have likely encountered a diversity of coastal environments (marshes, beaches, tidal flats), in addition to more inland habitats.

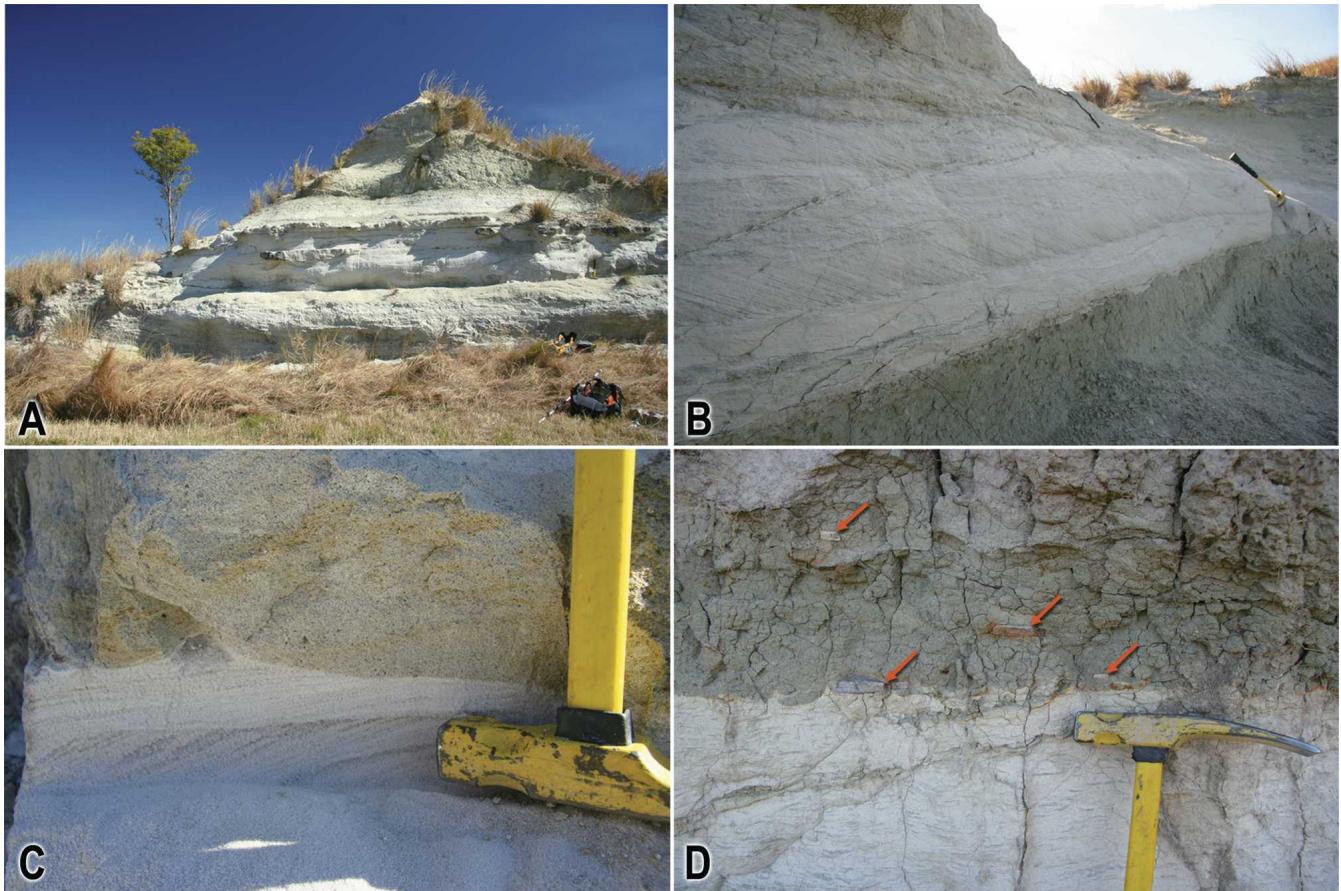


FIGURE 4. **A**, Outcrop view of the Anembalemba Member stratotype (see Rogers et al., 2000). **B**, Stratified light gray to white beds of ‘facies 1’ overlying massive green bed of ‘facies 2.’ Note well-developed planar tabular cross-bedding. **C**, Close-up view of abrupt contact between stratified beds of facies 1 and superjacent massive clay-rich bed of facies 2 in quarry MAD93-18. **D**, Turtle shell fragments and bone fragments (denoted by arrows) at the base of a bed of facies 2.

Paleocurrent data reported in Rogers et al. (2000) from the Anembalemba Member indicate that the rivers that drained the central highlands of Madagascar flowed in a northwesterly direction across the Maevarano alluvial plain to the sea, much as they do today. The sandstone bodies that record the passing of these ancient rivers are interpreted as the deposits of broad and shallow low-sinuosity channel belts, and the bones and teeth of *M. crenatissimus* are found in considerable abundance in their midst. There is good indication from the Anembalemba Member and underlying Masorobe Member that these rivers were characterized by a variable discharge regime. Facies 1 of the Anembalemba Member, which is characteristically cross-bedded and better sorted than facies 2 (Fig. 4), is interpreted to represent ‘normal’ stream flow and the downstream migration of bed-forms. In contrast, facies 2 is interpreted to represent mass flow conditions, specifically the emplacement of fine-grained debris flows (mudflows). Evidence cited by Rogers (2005) consistent with a debris flow origin for the clay-rich beds of facies 2 includes: (1) bimodality in grain size and very poor sorting; (2) matrix support; (3) primary massive bedding; and (4) relatively abundant soft-sediment deformation (Rogers et al., 2000:fig. 8). Sedimentological data presented in Rogers et al. (2000) and Rogers (2005) indicate that sediment-charged slurries rich with sand and clay surged through the Anembalemba fluvial system multiple times, with a minimum of seven distinct debris flow units (‘facies 2’) intercalated in sections that span the member.

Sedimentological data from the underlying and pedogenically overprinted Masorobe Member are also indicative of the recurrent emplacement of debris flow deposits in an overall fluvial setting. Non-uniform flow conditions evidently prevailed in the drainage basin for the duration of Masorobe and Anembalemba deposition, with recurrent episodes of heightened erosion and sediment yield alternating with periods of dilute streamflow. The variable discharge that characterizes the ancient channel belts of the Maevarano Formation presumably reflects seasonality, and perhaps distinct rainy and dry seasons, in the Late Cretaceous ecosystem of *M. crenatissimus* (Rogers et al., 1997, 2000; Rogers, 2005).

The soils upon which *M. crenatissimus* trod are exceptionally well preserved in the Masorobe Member of the Maevarano Formation (Rogers et al., 2000; Miller, 2000; Miller et al., 2000; Jerve, 2004). Masorobe paleosols are predominantly red in color, although drab gray to gray-green root mottling is locally pervasive, with tapering sand-filled casts of roots exhibiting a strong vertical fabric. Some root casts are encrusted with CaCO_3 , and these calcareous rhizoliths are occasionally associated with nodular beds of dispersed to coalesced pedogenic carbonate (Fig. 3). X-ray diffraction analyses confirm that montmorillonite is the dominant clay mineral (Miller, 2000). X-ray fluorescence analyses (Miller, 2000; Jerve, 2004) indicate that soluble elements such as K, Ca, Mg, and Na were mobile within these ancient soils, but were not leached from the relatively unweathered profiles.

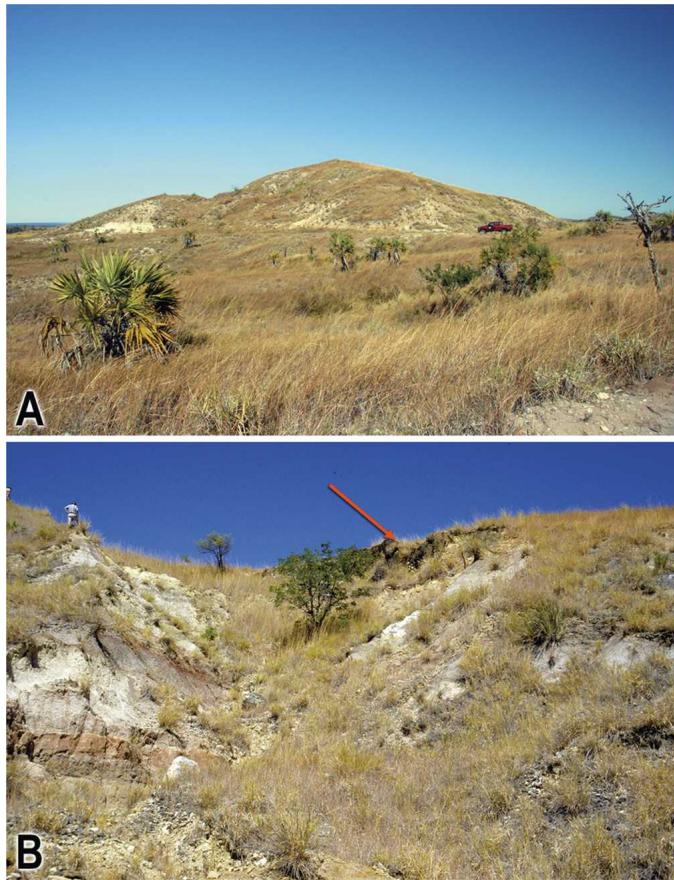


FIGURE 5. **A**, Outcrop view of the type area of the Miadana Member of the Maevarano Formation, in the vicinity of the Miadana Agricultural Station. Truck in right center provides scale. **B**, View of the Miadana Member in the vicinity of kilometer marker 508.4 along National Route 4. Arrow indicates limestone blocks of the marine, Danian-aged Betiboka limestone, which at this locality is separated from the Miadana Member by ~1.5 m of intervening marine Berivotra Formation (Rogers et al., 2000). Individual at top left provides scale.

Essentially all aspects of the Masorobe paleosols suggest that *M. crenatissimus* lived amidst well-drained aggrading floodplains where soils formed under the influence of a semiarid climate. The density of root mottling and vertical fabric of individual root traces indicate that vegetation was relatively abundant (presumably at least on a seasonal basis) and adapted for a relatively dry climate, perhaps not radically unlike that of today. Modern-day Madagascar experiences dry trade-wind conditions in the austral winter (May–September) and tropical storms in the summer (December–March). The western lowlands typically have high mean annual temperatures and abundant annual rainfall but the latter is highly constrained to the summer months (Guilcher and Battistini, 1967; Donque, 1972; Jury, 2003; Wells, 2003). Dongue (1972:130–131), for instance, lists a mean annual temperature of 26.9°C and 1559.1 mm of precipitation for Mahajanga; three of the five dry-season months receive less than 3 mm each, whereas January has 473.8 mm. The high degree of seasonality in Madagascar has a profound effect on the ecology of its vertebrate

inhabitants, resulting in periods of stress in terms of water and food availability in the dry season (e.g., Richard and Dewar, 1991; Wright, 1999; Scholz and Kappeler, 2004; van Schaik and Brockman, 2005).

The interpretation of a highly seasonal, semiarid climate for the Mahajanga Basin in the latest Cretaceous is consistent with paleogeographic reconstructions (e.g., Smith et al., 1994; Scotese, 1998; Torsvik et al., 1998) that position northern Madagascar at approximately 30°S near the end of the Late Cretaceous (but see Royer et al., 1992, who infer its position to have been approximately 25°S at this time), as the island was drifting northward toward the tropics (Berivotra is now at 15°54'S). Such a positioning would have placed the Mahajanga Basin and its inhabitants within the influence of the subtropical desert belt, which Wells (2003) conservatively puts between 24 and 36°S.

PRESERVATION AND PALEOECOLOGY

Taphonomic Overview

Isolated bones and teeth attributable to *Majungasaurus crenatissimus* are found throughout the Maevarano Formation, but are most abundant within the channel-belt deposits of the Anembalemba Member (Rogers et al., 1997, 2000, 2003; Rogers, 2005). These isolated occurrences are fortunately supplemented by several critical localities that have yielded clearly associated partial skeletons. At present, five sites in the Anembalemba Member fit this category (see Krause et al., this volume: fig. 3):

(1) MAD96-01 yielded a nearly complete skull, lower jaws, and associated caudal vertebrae of a single *M. crenatissimus* individual (FMNH PR 2100; Sampson et al., 1998) along with various elements of fish, turtles, crocodyliforms, sauropods, birds, mammals, and the only other known nonavian theropod in the Maevarano Formation assemblage, *Masiakasaurus knopfleri*. Skull elements of *M. crenatissimus* at this site were disarticulated but remained in close association, and they exhibit minimal indication of weathering, breakage, and post-burial distortion.

(2) MAD96-21 yielded several disarticulated skull elements, both ilia, and much of the axial skeleton of a subadult *M. crenatissimus* individual (UA 8678) in association with rare turtle, crocodyliform, and sauropod elements. Bones at this site are again very well preserved, and show only minor indication of degradation prior to final burial.

(3) MAD99-33 yielded a collection of isolated and associated postcranial and cranial elements of *M. crenatissimus* (FMNH PR 2430; UA 8716, 8717, 9031, 9033–9036, 9040, 9041, 9077, 9078), as well as a relatively intact but weathered skull (UA 8709). These specimens were found in association with the bones of *Masiakasaurus knopfleri*, sauropods, and crocodyliforms in an extensive bonebed at the very base of the Anembalemba Member.

(4) MAD99-26 yielded the well-preserved cranial and postcranial elements of a large *M. crenatissimus* individual, including exquisitely-preserved gnathic elements with intact tooth rows (FMNH PR 2278). Unfortunately, several teeth of this specimen were extracted or irreparably damaged by commercial collectors during the excavation phase.

Finally, (5) MAD05-42 yielded at least two well-preserved *M. crenatissimus* individuals, one a nearly complete, partially articulated skeleton (Fig. 6), the other an isolated disarticulated skull of a subadult individual, in association with scattered *Ma-*

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FIGURE 6. Excavation of a mostly articulated *Majungasaurus crenatissimus* specimen from quarry MAD05-42 in July, 2005. This adult individual represents the most complete specimen of the species yet recovered. It rests on its left side, and exhibits marked dorsal flexure of the neck. A second, subadult individual of *M. crenatissimus* is represented in the same bonebed by a disarticulated skull.



siaikasaurus, sauropod, and crocodyliform elements; these have yet to be prepared and studied.

Remains of *M. crenatissimus* are found in association with an array of other animals in several bonebeds within the Anembalemba Member (e.g., localities MAD93-18, MAD96-01, MAD96-21, MAD99-33, MAD05-42). Skeletal remains in these bonebed sites tend to exhibit variable degrees of disarticulation, breakage, and differential weathering, and it is evident that animals perished over a period of time (such as a dry season), as opposed to dying en masse during an instantaneous death event. Several of the bonebeds in the Anembalemba Member also show evidence of carcass utilization in the form of vertebrate feeding traces (Rogers et al., 2003) and invertebrate feeding and reproduction traces (Roberts et al., 2007).

Bone assemblages throughout the Anembalemba Member were typically buried by fine-grained debris flows (Rogers, 2005). The recurrent burial events that served to capture the spectacular bonebeds of the Anembalemba Member were potentially triggered by exceptional rainfalls that signaled the end of prolonged dry spells in the Mahajanga Basin. In turn, these severe dry spells were proposed by Rogers (2005) as the likely agents that led to heightened mortality along the river courses.

Feeding Ecology

Three bonebeds in particular, at localities MAD93-18, MAD96-01, and MAD96-21, provide key insights into the feeding ecology of *M. crenatissimus*. Collections from the quarry at MAD93-18 include an adult *Rapetosaurus* pubis that exhibits conspicuous sub-parallel furrows along the element's distal margin (Rogers et al., 2003:fig. 3). The size, shallow U-shaped morphology, and sub-parallel configuration of the traces are consistent with infliction by the premaxillary teeth of *M. crenatissimus* (Rogers et al., 2003).

Collections from MAD96-01 and MAD96-21 also yield compelling evidence of feeding by *M. crenatissimus*. At least 12 postcranial elements of the *M. crenatissimus* individual preserved in MAD96-01, including five chevrons, three neural arches, two transverse processes, one neural spine, and one rib, exhibit tooth marks, and at least seven ribs and two neural arches derived from the *M. crenatissimus* individual preserved in MAD96-21 also exhibit tooth marks (Fig. 7). Rogers and colleagues (2003) demonstrated that the tooth marks, some containing denticle drag marks, that score *M. crenatissimus* bones from both localities were in fact made by *M. crenatissimus*. Intertooth spacing, eruption patterns, and the morphology and spacing of denticles all serve to link the feeding traces to the jaws of *M. crenatissimus*, and rule out all other potential animals known in the paleofauna. This finding led to the inevitable conclusion that *M. crenatissimus* fed on the remains of conspecifics at both the MAD96-01 and MAD96-21 localities, and was thus a cannibal (Rogers et al., 2003).

Based on the heavily impacted *M. crenatissimus* samples from MAD96-01 and MAD96-21, the feeding focus seems to have been along the axial column, suggestive of late-stage scavenging of degraded carcasses. With regard to the actual ecology behind this feeding strategy, an opportunistic scavenger-based model is certainly consistent with available data. Intraspecific feeding by *M. crenatissimus* may reflect a strategy for dealing with nutritional needs during times of environmental stress (Fox, 1975; Polis, 1981; Polis et al., 1984; Daniels, 1987). In order to survive during stressful periods, *M. crenatissimus* may have thoroughly exploited all available resources, including long dead or dying conspecifics. This scenario is compatible with the high degree of bone modification documented in the Maevarano vertebrate assemblage, and is certainly in line with general taphonomic and paleoenvironmental reconstructions for the Maevarano Forma-

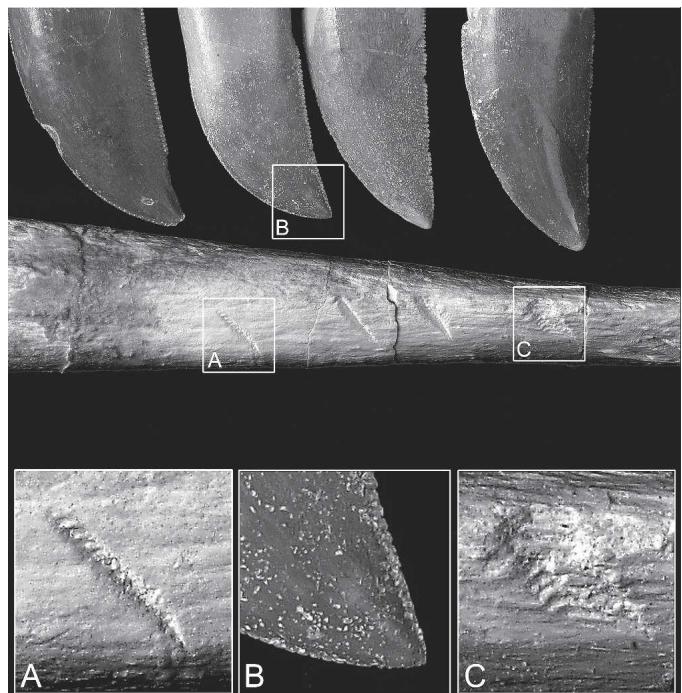


FIGURE 7. Teeth and chevron of *Majungasaurus crenatissimus* from site MAD96-01. Chevron exhibits parallel tooth marks with denticle drag marks (insets A, C). The overall spacing and configuration of tooth marks are consistent with intertooth spacing and eruption patterns in the known jaws of *M. crenatissimus*. Denticle drag marks (insets A, C) match the morphology and spacing of denticles on the teeth of *M. crenatissimus* (inset B).

tion (Rogers et al., 1997, 2000; Rogers, 2005). Alternatively, data could be interpreted to reflect a predatory scenario in which the remains of *M. crenatissimus* in MAD96-01 and MAD96-21 were heavily utilized by persistent individuals. Given present evidence, differentiating between the scavenger- and predator-based scenarios is impossible.

Aside from *M. crenatissimus*, the most often cited example of a dinosaur cannibal is the Triassic theropod *Coelophysis bauri* (Colbert, 1989, 1995), although recent critical reviews of the evidence indicate that claims of cannibalistic feeding by *Coelophysis* are erroneous (Gay, 2002; Nesbitt et al., 2006). Juvenile *Coelophysis* bones traditionally interpreted to represent an ingested meal in one specimen (AMNH FR 7223) in fact probably lie stratigraphically below the rib cage of the proposed cannibal (as opposed to within), and the volume of the purportedly ingested material arguably exceeds reasonable estimates of stomach capacity (e.g., Colbert, 1995:fig. 18). In the other purported *Coelophysis* cannibal (AMNH FR 7224), osseous gut contents do apparently exist, but they derive from a small crocodyliform (Nesbitt et al., 2006). Cannibalism has also been tentatively proposed for Late Cretaceous tyrannosaurids based on the occurrence of tooth marks on tyrannosaurid bone (Jacobsen, 1998). However, several tyrannosaurid species with morphologically indistinguishable teeth occur in the unit that yields the tooth-marked bones, so the evidence remains equivocal. Thus, based on present evidence, *M. crenatissimus* is the only theropod dinosaur with demonstrated cannibalistic tendencies.

Finally, cannibalism as an ecologic strategy is not uncommon among extant animals (Ingram, 1959; Parsons, 1971; Bertram, 1975; Fox, 1975; Auffenberg, 1981; Polis, 1981; Polis et al., 1984), and it should not be considered unexpected or uncommon

among theropod dinosaurs (contra Nesbitt et al., 2006). In fact, if the extant phylogenetic bracket is applied, birds that regularly consume vertebrate tissue (e.g., birds of prey and colonial sea birds) and crocodiles both practice cannibalism (Ingram, 1959; Parsons, 1971; Hutton, 1989). Eliminating *Coelophysis* as a documented dinosaur cannibal does not speak to the prevalence or rarity of cannibalism among non-avian dinosaurs, but rather highlights the dearth of data that relate to dinosaur feeding ecology in general.

CONCLUSIONS

The abelisaurid theropod *Majungasaurus crenatissimus* inhabited the Mahajanga Basin of northwestern Madagascar during the latest Cretaceous, and its remains are recovered within a few meters of the K/T boundary. Shallow sandy rivers flowing from the central highlands northwestward to the Mozambique Channel dissected the landscape of *M. crenatissimus*. Sedimentological data indicate that these rivers were recurrently inundated by fine-grained debris flows, which served as the predominant burial agents in this ancient ecosystem. Red calcareous paleosols associated with the deposits of these ancient rivers are indicative of a seasonal, semiarid paleoclimate. These findings, in turn, are consistent with paleogeographic reconstructions that place the Mahajanga Basin and its inhabitants within the influence of the subtropical desert belt during the Late Cretaceous.

M. crenatissimus shared its habitat with relatively few non-avian dinosaurs, including a small-bodied theropod (*Masiakasaurus knopfli*) and a large titanosaur (*Rapetosaurus krausei*). At least five different species of birds flew overhead, including sickle-clawed *Rahonavis ostromi*, a close relative of *Archaeopteryx* (Forster et al., 1996, 1998; Forster and O'Connor, 2000). Other animals that may have crossed the path of *M. crenatissimus* include at least seven species of crocodyliforms, as well as frogs, turtles, snakes, lizards, and mammals.

Although an inhabitant of the expansive semiarid floodplains of the Mahajanga Basin, *M. crenatissimus* apparently also frequented the broad and sandy rivers. In fact, although bones and teeth of *M. crenatissimus* are preserved throughout the Maevarano Formation, they are most abundant within the channel-belt deposits of the Anembalemba Member. It is thus reasonable to speculate that *M. crenatissimus* hunted and/or scavenged with considerable regularity in this fluvial setting, which was evidently populated by a variety of potential aquatic and semi-aquatic prey, including turtles, crocodyliforms, and frogs. Moreover, given the likelihood of seasonal fluctuations in water availability (and thus perhaps resources in general), it is possible that animals with more terrestrial affinities, such as titanosaurs and abelisauroid theropods, sought refuge in the channel belts during stressful periods. Interestingly, multi-taxon bonebeds with taphonomic attributes consistent with localized and perhaps seasonal pulses of mortality are strikingly common in channel belt facies of the Anembalemba Member. *M. crenatissimus* likely capitalized on the hardship of other animals, including members of its own species, during environmentally stressful periods. There is certainly good indication that it fed upon their remains.

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