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Introduction, Systematic Paleontology, and Geological Context of Vintana Sertichi (Mammalia, Gondwanatheria) from the Late Cretaceous of Madagascar

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INTRODUCTION, SYSTEMATIC PALEONTOLOGY, AND GEOLOGICAL CONTEXT OF *VINTANA SERTICHI* (MAMMALIA, GONDWANATHERIA) FROM THE LATE CRETACEOUS OF MADAGASCAR

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ABSTRACT—*Vintana sertichi* is a sudamericid gondwanatherian mammal known only from the Upper Cretaceous (Maastrichtian) Maevarano Formation in the Mahajanga Basin of northwestern Madagascar. It is based on a single specimen, a well-preserved and virtually complete cranium discovered in 2010 near Lac Kinkony. The cranium is superficially bizarre and constitutes the only cranial remains of the poorly known, phylogenetically enigmatic Gondwanatheria, which are otherwise known only from isolated teeth and fragmentary dentaries. Gondwanatheria are represented by seven other monotypic genera assigned to two families (Ferugliotheriidae and Sudamericidae). Historically, this clade was assigned to Xenarthra, Paratheria (as a sister group to Xenarthra), Multituberculata, Allotheria (as a sister group to Multituberculata), Mammalia incertae sedis, and, most recently, back to Multituberculata or a close relative of Multituberculata. The craniodental evidence provided by *Vintana* supports inclusion in Sudamericidae, the monophyly of Gondwanatheria, and the position of Gondwanatheria as nested within or sister to Multituberculata. In addition to briefly reviewing the taxonomic composition and phylogenetic history of Gondwanatheria, this introductory chapter sets the stage for the other chapters in the volume by (1) briefly summarizing the inferred life habits of gondwanatherians; (2) reviewing the systematic paleontology of *V. sertichi*; and (3) providing overviews of the discovery of the holotypic specimen, its preservation, its preparation, and the imaging and measurement techniques used to study it. The chapter closes with an overview of the geological context of *V. sertichi*, which indicates that the species lived in a coastal floodplain environment and in a highly seasonal, semiarid climate.

INTRODUCTION

Gondwanatherians are a distinctive but enigmatic clade of non-therian mammals currently known only from the Cretaceous and Paleogene of Gondwana. Based to a large extent on a time and place argument, gondwanatherians were originally assigned to Xenarthra (sloths, armadillos, and anteaters), within Paratheria (Scillato-Yané and Pascual, 1984, 1985; Mones, 1987), and were, for a time, considered to be involved in the ancestry of xenarthrans (Bonaparte, 1986a, 1986b, 1986c, 1987, 1988, 1990; Bonaparte and Pascual, 1987). Paratheria, originally regarded as neither marsupials nor placentals (Thomas, 1887), are currently an unrecognized taxon but have in the past also included pangolins, the aardvark, taeniodonts, and enigmatic genera such as *Ernanodon*, *Eurotamandua*, and *Chungchienia* (e.g., Scott, 1904; Gregory, 1910; Minkoff, 1976; Scillato-Yané and Pascual, 1985). Gondwanatherians were subsequently allocated to Multituberculata (Krause and Bonaparte, 1990, 1993; Krause et al., 1992; Bonaparte et al., 1993; Krause, 1993; Kielan-Jaworowska and Bonaparte, 1996) or Allotheria, as a sister group to Multituberculata (Krause et al., 1997; Goin et al., 2012). The discovery of four molariform tooth positions in a dentary of *Sudamerica*, however, led Pascual et al. (1999) to question this assignment; they regarded gondwanatherians as Mammalia incertae sedis, a conclusion supported by Koenigswald et al. (1999) and Kielan-Jaworowska et al. (2004). Nonetheless, multituberculate affinities have been supported by several more recent authors (Gurovich, 2006; Pascual and Ortiz-Jaureguizar, 2007; Rougier et al., 2009, 2010), including Gurovich and Beck (2009), who conducted a phylogenetic analysis that included dental

characters of *Ferugliotherium*, *Gondwanatherium*, and *Sudamerica*. Most recently, a phylogenetic assessment that includes the craniodental anatomy of the taxon described in detail in this volume, *Vintana sertichi*, yielded three broad conclusions: (1) *Vintana* is a sudamericid gondwanatherian; (2) Gondwanatheria are monophyletic; and (3) Gondwanatheria either fit within or are close relatives of Multituberculata (Krause et al., 2014).

The first known species of Gondwanatheria, *Sudamerica ameghinoi*, was described three decades ago on the basis of a single, hypsodont, molariform tooth from the Paleocene of Patagonia. It was considered distinct enough from other species to merit assignment to a new, monospecific family, Sudamericidae (Paratheria, Edentata incertae sedis), by Scillato-Yané and Pascual (1984, 1985). Since then, many more specimens of *S. ameghinoi* have been recovered (Bonaparte et al., 1993; Koenigswald et al., 1999; Pascual et al., 1999; Gurovich, 2006, 2008). Several new gondwanatherian species have been identified from Upper Cretaceous sediments, including three taxa from Patagonia (*Gondwanatherium patagonicum*: Bonaparte, 1986c, 1988, 1990; *Ferugliotherium windhausenii* [= *Vucetichia gracilis*]: Bonaparte, 1986a, 1986b, 1990; Krause et al., 1992; Krause, 1993; *Trapalcotherium matuastensis*: Rougier et al., 2009), one from India (*Bharatherium bonapartei* [= *Dakshina jederi*]: Prasad et al., 2007; Wilson et al., 2007), and two from Madagascar (*Lavanify miolaka*: Krause et al., 1997; *Vintana sertichi*: Krause et al., 2014). Additional sudamericid specimens not assignable to a particular species have been reported from the Late Cretaceous of India (Verma et al., 2012) and Madagascar (Krause, 2013). The earliest known gondwanatherian was discovered in mid-Cretaceous deposits of Tanzania (Krause et al., 2003), and the youngest members of the clade have been recorded from the Eocene of Patagonia (*Greniodon sylvaticus*: Goin et al., 2012), Peru

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(Gondwanatheria, gen. et sp. indet.: Campbell et al., 2004; Goin et al., 2004; ‘Sudamericidae’: Antoine et al., 2011), and the Antarctic Peninsula (Sudamericidae, gen. et sp. indet., ‘cf. *Sudamerica ameghinoi*’ or *Sudamerica?* sp.: Reguero et al., 2002, 2013; Goin et al., 2006). The geographic distribution of gondwanatherian occurrences is plotted in Goin et al. (2012:fig. 1), Verma et al. (2012:fig. 3; sudamericids only), and Reguero et al. (2013:fig. 5.19).

All told, there are now eight valid gondwanatherian genera, all of them monotypic, divided into the low-crowned Ferugliotheriidae (*Ferugliotherium*, *Trapalcotherium*) and the high-crowned Sudamericidae (*Bharatherium*, *Gondwanatherium*, *Greniodon*, *Lavanify*, *Sudamerica*, *Vintana*). When originally described by Goin et al. (2012), the familial affinities of *Greniodon* were considered uncertain, but the phylogenetic analysis conducted by Krause et al. (2014) placed it within Sudamericidae. All of the species except *Vintana sertichi* were erected and diagnosed on the basis of isolated teeth; of these, three (*Trapalcotherium matuastensis*, *Lavanify miolaka*, and *Greniodon sylvaticus*) are known from only one or two specimens. Another, currently unnamed gondwanatherian, from the Cretaceous of Tanzania, is known only from a poorly preserved dentary fragment containing teeth and/or alveoli for a single incisor and four cheek teeth (Krause et al., 2003; O’Connor et al., unpubl. data). Four other dentary fragments have been recovered and attributed to various taxa: (1) *Sudamerica ameghinoi*—nearly complete ramus with teeth and/or alveoli for a single incisor and four cheek teeth (Pascual et al., 1999); (2) cf. *S. ameghinoi*—edentulous fragment preserving part of an incisor (Reguero et al., 2002, 2013; Goin et al., 2006; but see Rougier et al., 2009); (3) *Gondwanatherium patagonicum*—edentulous fragment with two complete cheek-tooth alveoli and partial alveoli for an incisor and another cheek tooth (Bonaparte, 1990; Gurovich, 2001, 2006; but see Pascual et al., 1999); and (4) *Ferugliotherium windhausenii*—small fragment with single, laterally compressed, blade-like cheek tooth and partial alveolus for an incisor (Kielan-Jaworowska and Bonaparte, 1996; Kielan-Jaworowska et al., 2004; Gurovich, 2006; Gurovich and Beck, 2009). Of these, only the dentary referred by Pascual et al. (1999) to *S. ameghinoi* is assigned with confidence to the species level.

The lack of specimens other than isolated teeth and a few fragmentary dentaries has also negatively impacted the ability to elucidate the life habits of gondwanatherians. Most attention has been focused on sudamericids, although Gurovich (2008:1084, 1086) speculated that ferugliotheriids, based on their brachydont dentition and small size, “may have had an omnivorous/insectivorous diet” and fed on “insects, large arthropods and/or seeds and nuts.” Based solely on its possession of hypsodont molariform teeth, *Sudamerica* was portrayed as adapted for an abrasive diet by Koenigswald et al. (1999), who also suggested semi-aquatic and fossorial habits (see also Damuth and Janis, 2011). Koenigswald et al. (1999:295) speculated that *Sudamerica*, like the muskrat and beavers, may have fed on “roots, bark and other vegetation” rather than grasses because “increased development of open habitats, and further evolution of grassland environments in Southern South America began in the early Eocene (Pascual & Ortiz Jaureguizar 1990; Pascual et al. 1996) and after gondwanatherians had become extinct.” Koenigswald et al. (1999:294) eliminated arboreality as a possibility because “hypsodonty and arboreal habits do not go together” (but see Pascual and Ortiz-Jaureguizar, 1990). The discovery of phyloliths representing at least five subclades of extant grasses (Poaceae) in the coprolites of large herbivores from the latest Cretaceous of India led to speculation that hypsodonty in sudamericid gondwanatherians evolved as “an adaptation to feeding on abrasive grasses” (Prasad et al., 2005:1180; Strömberg et al., 2012; see also Piperno and Sues, 2005; Prasad et al., 2007; Wilson et al., 2007; Gurovich and Beck, 2009). Conversely, several authors

have pointed out that hypsodonty and grazing are not inextricably linked, because hypsodonty is known in several clades that do not have grazing representatives (e.g., Pascual and Ortiz Jaureguizar, 1990; Williams and Kay, 2001; Damuth and Janis, 2011; Jardine et al., 2012). Hypsodonty is, however, ubiquitously found in mammals that ingest either fibrous or abrasive foods or grit with the foods they eat. Considering body size as well, Gurovich (2008:1086) concluded that sudamericids “were probably browsers with some selective grazing . . . and may have also incorporated fermentation and coprophagy” and that they were probably subterranean, using their incisors for burrowing and their molariform teeth to ingest “plant material as well as abrasive soil particles.”

The objective of this volume is to describe in detail and analyze in functional contexts the first cranial material of a gondwanatherian mammal, *Vintana sertichi* (see Krause et al., 2014), from the Upper Cretaceous (Maastrichtian) Maevarano Formation in the Mahajanga Basin of northwestern Madagascar (Figs. 1, 2). The skull is superficially bizarre, exhibiting a highly vaulted nuchal region, large orbits, and huge, scimitar-shaped jugal flanges. It is one of the most complete crania of a Mesozoic mammaliaform yet discovered from Gondwanan landmasses, approximately equivalent in that regard to the best-preserved specimen of *Vincelestes neuquenianus* (see Hopson and Rougier, 1993:fig. 2). It is also the largest known Mesozoic mammaliaform cranium from Gondwana, and second in the world only to *Repenomamus giganticus* (Early Cretaceous, China) in cranial length (Hu et al., 2005), although the cranium of *V. sertichi* is much deeper. The objectives of this introductory chapter are to review the systematic paleontology of *V. sertichi*, the circumstances of discovery and preservation of the holotypic and only known specimen, and the imaging and measurement methods used to study it, and to place this species in geological context, thereby ‘setting the stage’ for the chapters that follow.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

ALLOTHERIA Marsh, 1880

GONDWANATHERIA Mones, 1987

SUDAMERICIDAE Scillato-Yané and Pascual, 1984

VINTANA Krause, Hoffmann, Wible, Kirk, Schultz, Koenigswald, Groenke, Rossie, O’Connor, Seiffert, Dumont, Holloway, Rogers, Rahantarisoa, Kemp, and Andriamialison, 2014

Type Species—*Vintana sertichi* Krause, Hoffmann, Wible, Kirk, Schultz, Koenigswald, Groenke, Rossie, O’Connor, Seiffert, Dumont, Holloway, Rogers, Rahantarisoa, Kemp, and Andriamialison, 2014.

Included Species—Type species only.

Etymology—*Vintana* (Malagasy), *luck*, in reference to the circumstances of discovery of the type and only known specimen (see below).

Diagnosis—As for type and only known species.

VINTANA SERTICHI Krause, Hoffmann, Wible, Kirk, Schultz, Koenigswald, Groenke, Rossie, O’Connor, Seiffert, Dumont, Holloway, Rogers, Rahantarisoa, Kemp, and Andriamialison, 2014 (Fig. 1)

Vintana sertichi Krause, Hoffmann, Wible, Kirk, Schultz, Koenigswald, Groenke, Rossie, O’Connor, Seiffert, Dumont, Holloway, Rogers, Rahantarisoa, Kemp, and Andriamialison, 2014:512, fig. 1.

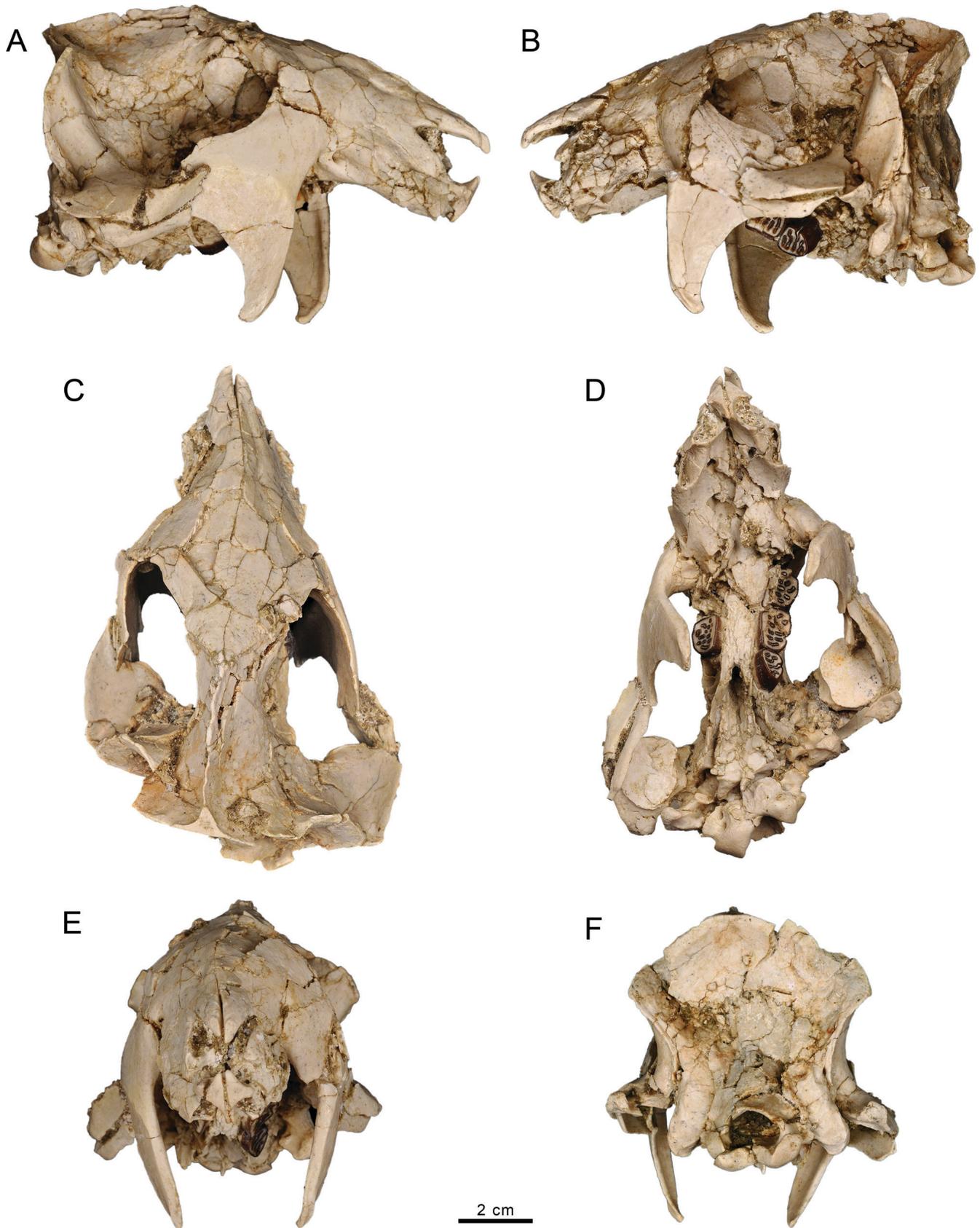


FIGURE 1. The cranium of *Vintana sertichi*, UA 9972, from the Late Cretaceous of Madagascar in **A**, right lateral; **B**, left lateral; **C**, dorsal; **D**, ventral; **E**, anterior; and **F**, posterior views. Enlargements and stereophotographic pairs of these views are presented in the chapters on dental (Krause, this volume) and craniofacial morphology (Krause et al., this volume).

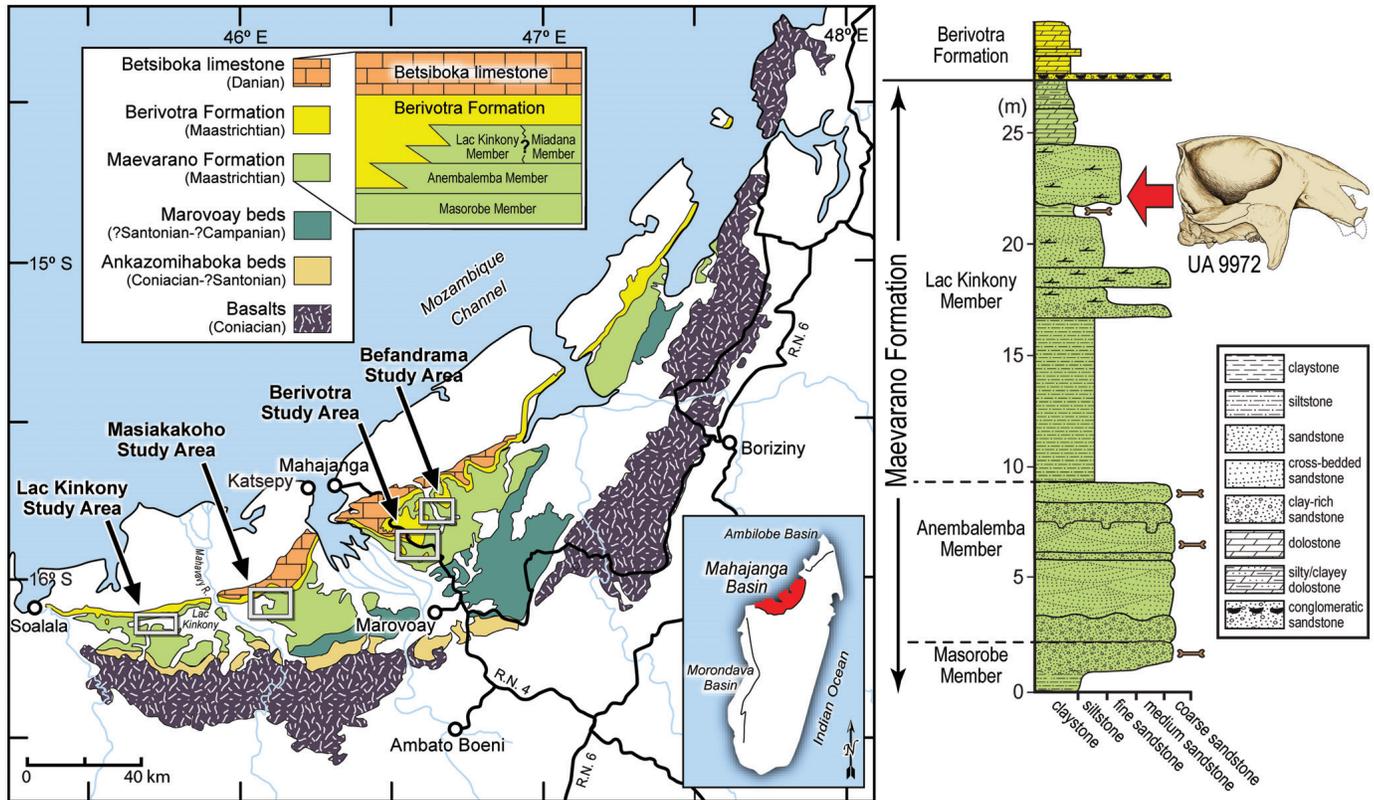


FIGURE 2. Map depicting the outcrop area of Upper Cretaceous (Coniacian through Maastrichtian) and Paleocene (Danian) strata and associated volcanic rocks (Coniacian) in the Mahajanga Basin of northwestern Madagascar (see inset) and the various study areas (Befandrama, Berivotra, Lac Kinkony, and Masiakakoho) of the Mahajanga Basin Project discussed in the text. Composite stratigraphic section at right depicts the Masorobe, Anembalemba, and Lac Kinkony members of the Maevarano Formation, which underlie the Berivotra Formation and crop out in the Lac Kinkony Study Area. The stratigraphic position of locality MAD10-24, which yielded the cranium of *Vintana sertichi* (UA 9972), is indicated by the red arrow.

Holotypic Specimen—UA (Université d’Antananarivo) 9972, virtually complete and well-preserved cranium.

Referred Specimens—None.

Etymology—After Joseph J. W. Sertich, discoverer of the holotypic and only specimen, in recognition of his skill, hard work, prescience, and good fortune in discovering this and numerous other specimens and productive fossil sites in the Late Cretaceous of Madagascar.

Type Locality—Locality MAD10-24 (S16°07’10.3”, E45°44’39.7”) in the Lac Kinkony Study Area of northwestern Madagascar, west-southwest of the port city of Mahajanga, near Lac Kinkony (Fig. 2).

Age and Distribution—Known only from the Upper Cretaceous (Maastrichtian) Lac Kinkony Member, Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Rogers et al., 2013).

Diagnosis—“Differs from all other gondwanatherians in its large size and in exhibiting wear features on molariform tooth crowns indicating a distobuccal (rather than strictly distal) power stroke of the chewing cycle. Differs from ferugliotheriid gondwanatherians in possessing hypsodont and unwaisted molariform cheek teeth with prominent, cementum-filled infundibula. Differs from all other sudamericid gondwanatherians in possessing molariform teeth that are approximately as wide as they are long. Further differs from non-Indo-Malagasy sudamericids in possessing prominent interrow sheets of interprismatic enamel; from *Sudamerica*, *Lavanify*, and perhaps *Bharattherium* in having sidewall furrows that terminate on molariform crowns before reaching roots; from *Bharattherium* and *Lavanify* in having

enamel on all sides of molariform crowns; and from *Sudamerica* in having molariform crowns with furrows on only one side (rather than both buccally and lingually), infundibula that extend far vertically into crowns, and in lacking a parasagittal longitudinal ridge with Type 2 islets (Koenigswald et al., 1999) on the occlusal surface” (Krause et al., 2014:512, S13).

DISCOVERY OF UA 9972

UA 9972, the holotypic and only known specimen of *Vintana sertichi*, was collected in the austral winter of 2010, on July 15, during the 10th joint expedition of the Mahajanga Basin Project, a long-term and still ongoing collaboration between Stony Brook University and the University of Antananarivo. The cranium was fortuitously found in situ and in isolation (i.e., no other parts of the individual [dentaries, isolated teeth, or elements of the postcranial skeleton] were recovered) inside an approximately 70 kg block of sandstone matrix from a microfossil bonebed (sensu Rogers and Kidwell, 2007; Rogers and Brady, 2010) particularly rich in actinopterygian fish fossils at locality MAD10-24 (Fig. 3A, B). This locality occurs on the escarpment approximately 5.1 km northeast of the village of Analalava (‘Antogomena’ on more recent maps) and approximately 1.6 km north of the northern shoreline on the western extension of Lac Kinkony. The bonebed occurs at the base of a 2.6 m thick, cross-bedded sandstone body in the Lac Kinkony Member of the Maevarano Formation (see Rogers et al., 2013, and below).

The fossils collected from the surface of locality MAD10-24 included bones and/or teeth of rays, sharks, anurans, turtles,

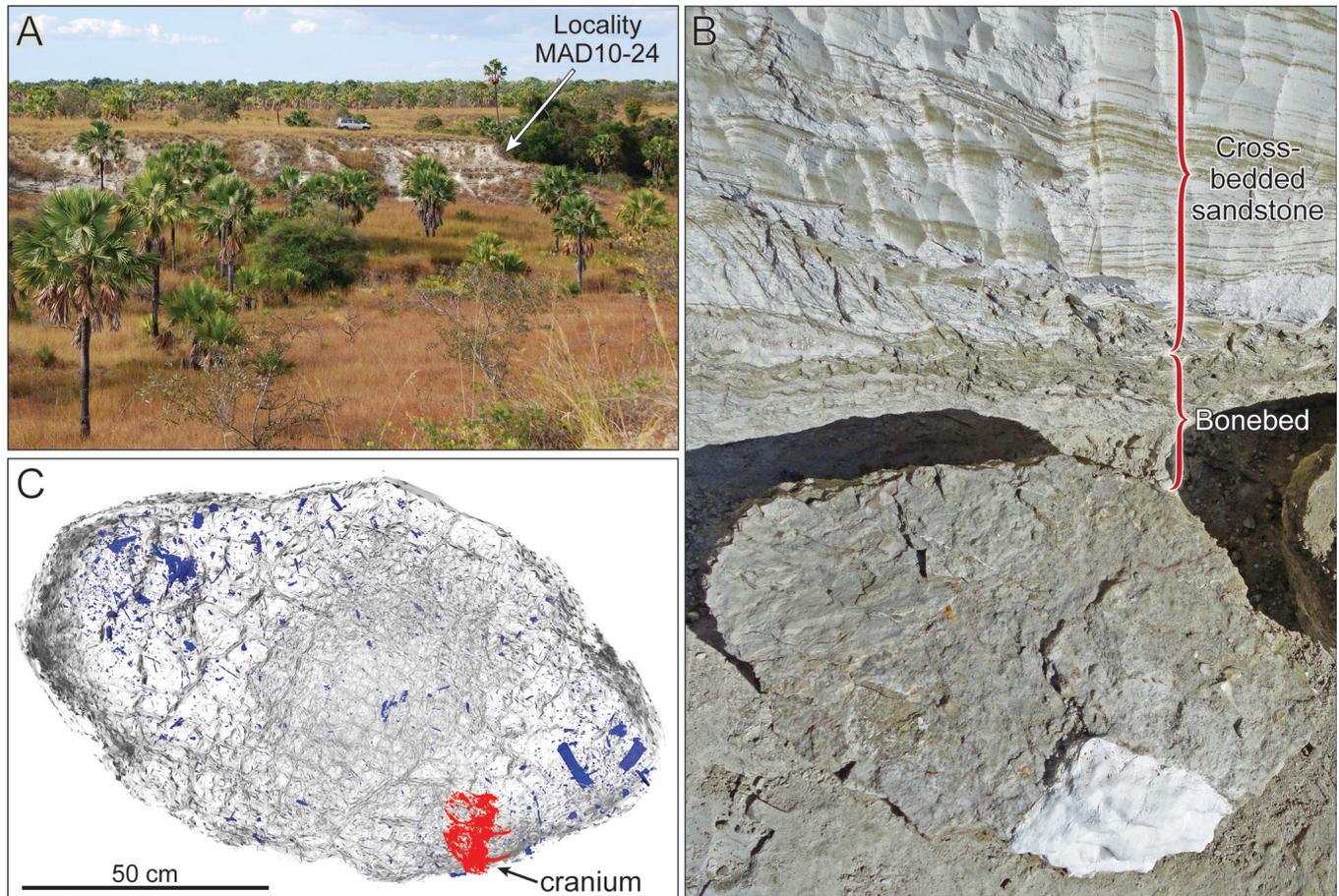


FIGURE 3. Locality MAD10-24, type locality of *Vintana sertichi*, in the Upper Cretaceous (Maastrichtian) Lac Kinkony Member, Maevarano Formation, Mahajanga Basin, northwestern Madagascar. **A**, photograph taken toward the northeast, indicating location of MAD10-24; 4 × 4 vehicle for scale. **B**, close-up view showing bonebed with pre-jacketed block of matrix in situ and overlying cross-bedded sandstone; additional, contiguous blocks were collected in 2010 and 2012. **C**, computed tomography scan of plaster-jacketed block of matrix (the original block shown in **B** was trimmed slightly before final jacketing) showing position of the cranium of *V. sertichi* (UA 9972, in red) and bones (in blue) of other taxa (primarily actinopterygian fishes) embedded in the block.

crocodyliforms, theropod dinosaurs, and especially actinopterygian fishes, as well as coprolites and gastropod steinkerns. At the time the fossiliferous block of matrix was collected, there was no knowledge of the existence of the mammalian cranium inside. The cranium itself was actually discovered via computed tomographic (CT) scanning of the block by one of us (J.R.G.) in June 2011 (Fig. 3C). In addition to UA 9972, the block contained numerous actinopterygian fish bones and teeth, shark teeth, anuran cranial and postcranial elements, crocodyliform teeth and postcranial elements, snake vertebrae (including those belonging to at least one new species; Pritchard et al., 2014), and coprolites.

PRESERVATION OF UA 9972

The cranium of *Vintana sertichi* (UA 9972) was buried resting on its right side (Fig. 3C). Although it is nearly complete and generally well preserved, the cranium suffered some damage, particularly posteriorly on the ventral and ventrolateral surfaces of the left side (the ‘up’ side, as preserved) (Fig. 1B, D). After death and prior to final burial, sediment, fish spines, and other fragmentary elements infilled areas that would have been covered or filled in life with soft tissues (e.g., orbits, temporal fenestrae). Furthermore, all of the teeth of the premaxillae and some

of those of the maxillae had fallen out prior to burial and were not found elsewhere in the block of matrix or in neighboring blocks that were collected and prepared. It is most unlikely that all of them had fallen out during life. These missing teeth include all four incisors (two on the left and two on the right), both pre-molariform teeth (one on the left and one on the right), the first of four molariform teeth on the left side, and all of the molariform teeth except the penultimate one on the right side (Fig. 1D). The four cheek teeth (three on the left, one on the right) that were retained in the cranium are very well to pristinely preserved; description of these teeth, including details of their preservation, is presented in the chapter on the dentition (Krause, this volume).

The cranium exhibits some distortion, particularly on the left side, where the posterior portion was deformed forward and slightly to the right (Fig. 1). As a result, the occipital condyles and other parts of the exoccipitals, as well as the basioccipital, lie oblique, rather than perpendicular, to the median plane (Fig. 1D). This forward displacement also resulted in the left glenoid cavity lying anterior to the level of that on the right side; relative to a plane perpendicular to the longitudinal axis of the skull, the posterior margin of the left glenoid cavity is slightly anterior to the anterior margin of the right glenoid cavity (Fig. 1D). In addition, the anterior margin of the left orbit lies

anterior to that of the right orbit (Fig. 1C). Furthermore, the left zygomatic arch is collapsed forward, resulting in fragmentation and overlap of the constituent elements, the anterior portions of the posterior half lying lateral to the posterior portions of the anterior half (Fig. 1C, D). The forward (and slightly to the right) displacement of the posterior region of the skull also resulted in an oblique angle being formed between the elongate, narrow snout and the rest of the skull (Fig. 1D); the break in angle occurs opposite the anterior margins of the molariform cheek-tooth series.

Additional deformation is evident on the snout, which is deflected slightly to the left such that the left and right nasals are slightly separated anteriorly (Fig. 1C, E). It appears that this deflection to the left is the result of an inward (medial) compression area located just posterior to the level of the external nasal aperture on the left side of the rostrum. As a result of compression that resulted in the posterior portion of the cranium on the left side being pushed forward and the tip of the rostrum being pushed slightly to the left, the anterior midline suture between the nasals is not straight but slightly curved; it is not aligned with the sagittal crest, and the dorsal midline of the skull is therefore an irregular curve that is convex on the right, concave on the left (Fig. 1C).

Even more distortion is evident ventrally (Fig. 1D). Parts of the palate between the level of the distal incisors and the cheek teeth were pushed dorsally into the nasal cavity. The width of the anterior portion of the palate also appears to have been diminished through deformation, perhaps from the event described above that pushed medially from the left side.

In addition to the deformation described above, a number of large fractures run through all or part of the skull. The largest crack passes obliquely through the entire skull. In ventral view (Fig. 1D), this crack extends from the anterior margin of the right zygomatic arch, through the alveoli for the right first and second molariform cheek teeth, across the palate, through the mesiobuccal corner of the left penultimate cheek tooth, and finally to just posterior to the left glenoid fossa. In some areas there are relatively few fractures (e.g., both left and right jugal flanges, the right side of the snout, the dorsal aspects of the occipital region), whereas in others there are numerous fractures with considerable displacement that results in broken surfaces wherein relatively little morphology can be discerned (e.g., both left and right sphenoid complexes, the left side of the basicranium). The anterior portion of the palate also exhibits considerable fracturing, particularly medially, beginning opposite the mesial incisors and broadening posteriorly through the region of the diastemata.

Anteriorly, a large, oblique crack, roughly parallel to the more posterior crack described above, passes through the snout from the anterior margin of the right mesial incisor to just anterior to the anterior root of the left zygomatic arch (and the ventral infraorbital foramen; Fig. 1D). The crack results in a portion of the anterior part of the skull, mostly of the left side, that is displaced forward; because the left incisive foramen is on this fragment, it lies slightly anterior to its counterpart on the right side.

PREPARATION, IMAGING, AND MEASUREMENT OF UA 9972

UA 9972 was prepared by J.R.G. in the Vertebrate Fossil Preparation Laboratory at Stony Brook University. After discovery through pre-preparation CT imaging (see below), the focus region of the large plaster-jacketed block of fossiliferous matrix was drilled at several points, and PVA (polyvinyl acetate) B-15 (McGean USA, Midland, Michigan) dissolved in ethyl alcohol was injected to consolidate the loose sandstone matrix and dampen vibration where the jacket was to be opened. A portion of the top of the jacket was then removed, and a pedestal

separating the specimen from the larger block of matrix created. PVA B-15 was used to consolidate the edges of the pedestal, and cyclododecane ($C_{12}H_{24}$; Kremer Pigmente, Aichstetten, Germany) served as a gap filler and penetrant around larger cracks. A Specialist plaster bandage wrapped around the isolated pedestal provided support for complete extraction from the larger block. Mechanical preparation was carried out exclusively with steel insect pins and carbide rods held by pin vices. The specimen was temporarily stabilized and consolidated at various points with cyclododecane and Paraloid B-72 (Dow Chemical Company, Midland, Michigan) dissolved in acetone, respectively. It was transferred twice to new supporting jackets during the process and tacked to those jackets using cyclododecane. Within the extracted jacket, 256 bone fragments were uncovered, photographed in situ, assigned numbers, assessed for their relationship to the cranium, and isolated from the block. Most of these fragments appear to come from fishes, and none was found to fit back onto UA 9972.

Computed tomography occurred throughout the process of preparation, documentation, and description of the specimen. Initial scans used for coarse identification and positioning of specimens within the jacket prior to extraction, and during mechanical preparation, were conducted on a GE Lightspeed VCT 64-source medical scanner in Stony Brook University's Department of Radiology. Subsequent μ CT scanning occurred on several occasions using the GE Phoenix vto me x s240 μ CT scanner (240 kV micro-focus reflection target X-ray tube; DXR250RT detector panel) in the Microscopy and Imaging Facility of the American Museum of Natural History in New York and also on a Nikon Metrology MCT225 industrial μ CT scanner (225 kV micro-focus reflection target X-ray tube; PerkinElmer XRD 1621 AN3 ES detector panel) at Avonix Imaging in Plymouth, Minnesota.

The 16-bit DICOM data from the Lightspeed VCT were reviewed in ImageJ and Avizo 7.1 during preparation; VG Studio Max software created the 16-bit TIFF slices of subsequent μ CT data sets that were utilized during the final stages of preparation. DICOM and TIFF stacks were rendered into surfaces using Avizo 7.1 Isosurface and Volume Rendering options, as well as labeling individual voxels in the Label Field Editor. The particulars of the various μ CT data sets used for morphological descriptions and analyses are presented in the relevant chapters.

Linear measurements of ≤ 10 mm were taken with an ocular micrometer inserted into one of the two eyepieces of a Nikon SMZ1500 stereomicroscope; it was calibrated before each measurement session with a graticule slide; those of > 10 mm were taken using a Mitutoyo CD-8" CSX caliper. Angular measurements were extracted from digital photographs using the Measure Tool in Adobe Photoshop. All measurements are in millimeters.

GEOLOGICAL CONTEXT OF *VINTANA SERTICHI*

The holotypic specimen of *Vintana sertichi*, UA 9972, was recovered from the Lac Kinkony Member of the Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Fig. 2). The Lac Kinkony Member is exposed in the Lac Kinkony Study Area on the shores of Lac Kinkony, west of the Mahavavy River. It was recently recognized as a lithologically distinctive unit by Rogers et al. (2013), thus adding a fourth member to the previously recognized Masorobe, Anembalemba, and Miadana members originally documented in the Berivotra Study Area, approximately 100 km to the east-northeast (Rogers et al., 2000). The Lac Kinkony Member is situated stratigraphically above the fully terrestrial Anembalemba Member, which is particularly rich in exquisitely preserved and frequently articulated vertebrate fossils (see most recent summary in Krause et al., 2006, and revised faunal list in Rogers et al., 2013:table 1),

and below the fully marine Berivotra Formation. The Masorobe and Anembalemba members also crop out in the Lac Kinkony Study Area (as well as in the Masiakakoho Study Area), but the Miadana Member, known from the Berivotra and Befandrama study areas, does not.

Vintana sertichi can be confidently established as Maastrichtian in age on the basis of three independent constraints. First, the only relevant radioisotopic date in Mesozoic rocks of the Mahajanga Basin is provided by basalts immediately overlying the Ankazomihaboka sandstones and stratigraphically well below the Maevarano Formation; these rocks have been dated at ca. 88 Ma and have been implicated as directly related to the tectonic event that separated the Indian subcontinent and the Seychelles from Madagascar (Storey et al., 1995, 1997; Melluso et al., 1997, 2003; Torsvik et al., 1998, 2001). Second, Rogers et al. (2000) documented an interfingering relationship of the Anembalemba and Miadana members with lower portions of the Berivotra Formation; the latter is known to be Maastrichtian on the basis of both its invertebrate and vertebrate fossils (Besairie, 1972; Gottfried et al., 2001; Abramovich et al., 2002; Rahantari-soa, 2007; Rogers et al., 2013). Because the Lac Kinkony Member directly overlies the Anembalemba Member and underlies the Berivotra Formation, it is reasonable to also assign it to the Maastrichtian. Third, preliminary magnetostratigraphic data support a Maastrichtian age; a reversal near the top of the Berivotra Formation is interpreted as the shift that occurred at ca. 66.4 Ma, from Chron 30N to Chron 29R (Casey et al., 2003; Dennis-Duke, 2005).

UA 9972 was recovered from a microfossil bonebed at locality MAD10-24, which occurs in a heavily vegetated area, composed primarily of palm savanna, along the escarpment northeast of the village of Analalava (Fig. 3A). The bonebed is intersected by a measured section ("Lac Kinkony 5"; see Rogers et al., 2013: figs. 2, 3) spanning the uppermost ca. 8 m of the Lac Kinkony Member of the Maevarano Formation and almost 4 m of the overlying Berivotra Formation. The bonebed constitutes the basal ca. 30 cm of a 2.6 m cross-bedded sandstone that is in erosional contact with an underlying bed of claystone (Figs. 2, 3B), and it can be traced ca. 600 m to the southwest along the escarpment. In addition to gastropod steinkerns, coprolites, and UA 9972, the bonebed has so far yielded isolated specimens of chondrichthyan and actinopterygian fishes, anurans, turtles, snakes, crocodyliforms, sauropods, and theropods.

Although we have only begun to sample the fossil riches of the Lac Kinkony Member, we have to date discovered over 25 localities yielding vertebrate fossils in the member during brief reconnaissance missions. New turtle (*Kinkonychelys rogersi*) and snake (*Indophis fanambinana*) species have already been described from the Lac Kinkony Member (Gaffney et al., 2009; Pritchard et al., 2014; respectively). The holotypic specimen of *K. rogersi* comes from MAD07-25, and all of the snake material (vertebrae of *I. fanaminana* and two other species) comes from the same bone-bearing facies at locality MAD10-24 as UA 9972.

The Lac Kinkony Member is unique among the members of the Maevarano Formation in exhibiting a strong tidal influence; more specifically, Rogers et al. (2013) interpreted it as representing siliciclastic and carbonate tidal flat facies that were dissected by tidally influenced rivers. The rivers represented in the deposits of the Lac Kinkony Member were of low energy and low sinuosity and flowed northwestward from the central highlands toward the Mozambique Channel, roughly the same direction as today's rivers in the region. A distinctive, laterally traceable ravinement bed separating the Lac Kinkony Member from the superjacent Berivotra Formation and composed of coarse-grained sandstone and cobbles of rounded dolostone marks the full onset of marine transgression.

Previous work on the Maevarano Formation has yielded insight into the paleoecology and paleoclimate of northwestern

Madagascar at the close of the Cretaceous and therefore the paleoenvironmental conditions in which *V. sertichi* lived. Overall, the Maevarano Formation reveals a dryland environment in a terrestrial alluvial floodplain setting with pronounced dry and wet seasons. The Masorobe Member, at the base of the Maevarano Formation, is replete with color banding, abundant calcareous nodules, long, vertical root traces, and other features consistent with an interpretation of parched soils (Rogers et al., 2000). The presence of drought-adapted taxa such as conchostracans in the Anembalemba Member (Stigall and Hartman, 2008) and lungfish in the Masorobe and Anembalemba members (Marshall and Rogers, 2012) confirms an interpretation of a highly seasonal semiarid climate for the Mahajanga Basin in the Maastrichtian, as does the occurrence of abundant feeding traces (e.g., borings, puparial chambers) on vertebrate bone made by necrophagous and osteophagous carrion insects (Roberts et al., 2007; Rogers and Krause, 2007). Also consistent with an interpretation of dry conditions are paleogeographic reconstructions of Gondwana that place the basin in the subtropical desert belt, approximately 15° farther south than it is today (Smith et al., 1994; Scotese, 1998; de Wit, 2003; Wells, 2003; Gaina et al., 2007; Ali and Aitchison, 2008).

The highly variable discharge of the Maevarano Formation river systems is further evidence of distinct dry and rainy seasons. The Anembalemba Member shows abundant evidence of alternating periods of drought and intense rainfall events, as reflected by turbulent downstream-directed deposits of cross-stratified sandstones and massive debris flows relatively rich in claystones. Rogers et al. (2000, 2007, 2013), Rogers (2005), Rogers and Krause (2007), and Krause et al. (2010) have surmised that life during the dry seasons was difficult, as evidenced in part by the repetitive nature and abundance of multitaxic vertebrate fossil bonebeds with articulated and/or associated elements that likely reflect mass mortality in desiccating channel belts. How *V. sertichi* coped with these conditions remains to be determined.

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