
LATE CRETACEOUS TERRESTRIAL VERTEBRATES FROM MADAGASCAR: IMPLICATIONS FOR LATIN AMERICAN BIOGEOGRAPHY¹

David W. Krause,² Patrick M. O'Connor,³
Kristina Curry Rogers,⁴ Scott D. Sampson,⁵
Gregory A. Buckley,⁶ and Raymond R. Rogers⁷

ABSTRACT

The Mahajanga Basin Project, initiated in 1993 and centered in Upper Cretaceous strata of northwestern Madagascar, has resulted in the discovery of some of the most complete, well-preserved, and significant specimens of Late Cretaceous vertebrate animals from the Southern Hemisphere and indeed the world. Among the most important finds are various specimens of crocodyliforms, non-avian dinosaurs, and mammals; these finds have the potential to provide key insights into the biogeographic and paleogeographic history of Gondwana. Madagascar has been physically isolated from Africa for over 160 million years and from all other major landmasses for more than 85 million years. The closest known relatives of many of the Late Cretaceous Malagasy taxa are penecontemporaneous forms from South America (primarily Argentina) and India, thus documenting a previously unrecognized high level of cosmopolitanism among Gondwanan vertebrates near the end of the Cretaceous. The family-level taxa that are shared among Madagascar, South America, and the Indian subcontinent are not known from penecontemporaneous horizons in mainland Africa, but it cannot yet be confidently determined if this is due to differential extinction, poor sampling, true absence (i.e., the taxa were never present on Africa), or some combination thereof. Nonetheless, currently available geologic and paleontologic data are most consistent with the Africa-first model, suggesting that Africa was the first of the major Gondwanan landmasses to be fully isolated prior to the Albian/Cenomanian boundary, and that its terrestrial vertebrate faunas became progressively more provincial during the Cretaceous, while those on other Gondwanan landmasses remained relatively cosmopolitan until the later stages of the Late Cretaceous.

Key words: biogeography, Cretaceous, Madagascar, South America, vertebrates.

RESUMEN

El proyecto de la cuenca de Mahajanga, iniciado en 1993 y centrado en los estratos del Cretácico superior en el noroeste de Madagascar, ha resultado en el descubrimiento de algunos de los especímenes más completos, mejor preservados y más significativos de animales vertebrados del Cretácico tardío del hemisferio sur y de hecho del mundo. Entre los hallazgos más importantes son los varios especímenes de crocodiliformes, dinosaurios no-aviares y mamíferos; estos hallazgos tienen el potencial de adentrarse en puntos claves en la historia biogeográfica y paleogeográfica de Gondwana. Madagascar ha estado físicamente aislada de África por más de 160 millones de años y del resto de masas importantes de tierra por más de 85 millones de años. Los parientes cercanos conocidos de muchos de los taxones malgaches del Cretácico tardío son formas penecontemporáneas de América del Sur (sobre todo de Argentina) y la India, documentando así un alto nivel cosmopolita previamente desconocido entre los vertebrados de Gondwana cerca del final del Cretácico. Los taxones al nivel de familia compartidos entre Madagascar, América del Sur y el subcontinente Indio no se conocen de horizontes penecontemporáneos de África continental, pero todavía no se puede determinar con certeza si esto se debe a extinción diferenciada, escaso muestreo, ausencia verdadera (i.e., los taxones nunca estuvieron presentes en África), o una cierta combinación de esos. No obstante, los datos geológicos y paleontológicos actualmente disponibles son los más consistentes con el modelo de África-primero, que sugiere que África fue la primera de las masas importantes de tierra de Gondwana que estuvo aislada completamente antes del límite del Albiano/Cenomaniano, y que su fauna de vertebrados terrestres se volvió progresivamente más provincial durante el Cretácico mientras que aquellos en las masas terrestres de Gondwana permanecieron relativamente cosmopolitas hasta las fases finales del Cretácico tardío.

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² Department of Anatomical Sciences, Stony Brook University, Stony Brook, New York 11794-8081, U.S.A. dkrause@notes.cc.sunysb.edu

³ Department of Biomedical Sciences, 228 Irvine Hall, Ohio University, Athens, Ohio 45701, U.S.A.

⁴ Paleontology Department, Science Museum of Minnesota, 120 West Kellogg Boulevard, St. Paul, Minnesota 55102, U.S.A.

⁵ Utah Museum of Natural History and Department of Geology and Geophysics, University of Utah, 1390 East Presidents Circle, Salt Lake City, Utah 84112-0050, U.S.A.

⁶ Evelyn T. Stone University College, Roosevelt University, Chicago, Illinois 60605, U.S.A.

⁷ Department of Geology, Macalester College, 1600 Grand Avenue, St. Paul, Minnesota 55105, U.S.A.

The first question that logically might occur to readers of this contribution is “Why is Madagascar relevant to a consideration of Latin American biogeography?” The answer is not intuitively obvious because over 7500 km separate the two landmasses today and Madagascar’s extant biota is highly endemic and imbalanced. However, in the context of a mobilist paradigm of Earth history, the question has different degrees of relevance depending upon the geologic time interval under consideration. We will assert in this paper that near the end of the Late Cretaceous the island-continent of Madagascar hosted a terrestrial vertebrate fauna that was strikingly similar in taxonomic composition to that of South America. This high degree of similarity is unexpected in the context of most recent paleogeographic reconstructions, which depict the southern supercontinent Gondwana as having long been fragmented into its constituent landmasses by this time. Specifically, Madagascar, although still connected to the Indian subcontinent, is usually illustrated as having been physically isolated from all other Gondwanan landmasses since approximately 120 million years ago (Ma). This presents a biogeographic conundrum, as noted by Hay et al. (1999).

The configuration of Gondwana changed dramatically during the Late Jurassic and Cretaceous as it broke apart into isolated landmasses. The dispersion of these landmasses undoubtedly had profound consequences for the geographic distribution and subsequent evolutionary trajectories of the resident terrestrial vertebrate faunas. Reconstructions of the Mesozoic fragmentation of Gondwana, however, are based almost exclusively on geophysical and stratigraphic evidence and remain poorly tested paleontologically. Recent discoveries of fossil vertebrates on southern landmasses, particularly from the Late Cretaceous of Madagascar (cf. Krause et al., 1999; Krause, 2003b), complement those known from South America and elsewhere and have profound implications for testing hypotheses concerning the timing and sequence of Gondwanan breakup. Purportedly isolated in the Indian Ocean for over 85 million years, Madagascar is of unique biogeographic importance; it occupied a central geographic position within Gondwana and was among the first (western margin) and last (eastern margin) major landmasses to be involved in fragmentation of the supercontinent.

The objective here is to provide an overview of the terrestrial vertebrate assemblage recently recovered from the latest Cretaceous stage (Maastrichtian) of Madagascar and to compare it with penecontemporaneous and earlier assemblages from South America and other Gondwanan landmasses in an attempt to elucidate biogeographic patterns. Terrestrial verte-

brates are the focus of this report because they are tied to land (some presumably more than others) and are thus the most appropriate vertebrate animals (i.e., relative to, for example, fishes or birds) for examining biogeographic hypotheses involving subaerial landmasses. We specifically focus on crocodyliforms, non-avian dinosaurs, and mammals for the simple reason that their representation in the Gondwanan terrestrial fossil record is better than for most other terrestrial vertebrate clades and, as a result, their phylogenetic relationships are more highly resolved. This report is not a comprehensive analysis of Gondwanan biogeography. Rather, it is an attempt to compare and evaluate the currently available data provided by terrestrial vertebrate fossils from major southern landmasses, particularly Madagascar and South America, in the context of recent paleogeographic reconstructions of Gondwana. We also strive to identify and draw attention to sampling problems that limit our ability to address particular biogeographic questions.

TERRESTRIAL VERTEBRATES FROM THE LATEST CRETACEOUS OF MADAGASCAR

The sample of latest Cretaceous (Maastrichtian) vertebrates from Madagascar is the most diverse and arguably the most significant in terms of completeness and preservation of specimens among Gondwanan assemblages outside of South America. This is particularly striking considering the small size of Madagascar; indeed, mainland Africa, the largest of the Gondwanan landmasses, is over 50 times larger in area and yet its penecontemporaneous vertebrate fauna is much more poorly known.

The vast majority of specimens known from the Late Cretaceous of Madagascar have been discovered as a result of the Mahajanga Basin Project (MBP), conducted jointly by Stony Brook University and the University of Antananarivo. The MBP was initiated in 1993 and has included eight expeditions, the most recent in 2005. It is focused on the vertebrate paleontology and geology of Upper Cretaceous strata in the Mahajanga Basin of northwestern Madagascar (Fig. 1). Most of the fossil vertebrate specimens have been recovered from a small study area (measuring approximately 20 sq. km) near the village of Berivotra and from one thin stratigraphic interval (measuring some 12 m thick). Existing stratigraphic data indicate that this interval, the Anembalemba Member of the Maevarano Formation, is of Maastrichtian (latest Cretaceous) age; however, we cannot discount the possibility that lower reaches of the member might be Campanian (Rogers et al., 2000). The Anembalemba Member is of fluvial origin and accumulated in a semi-

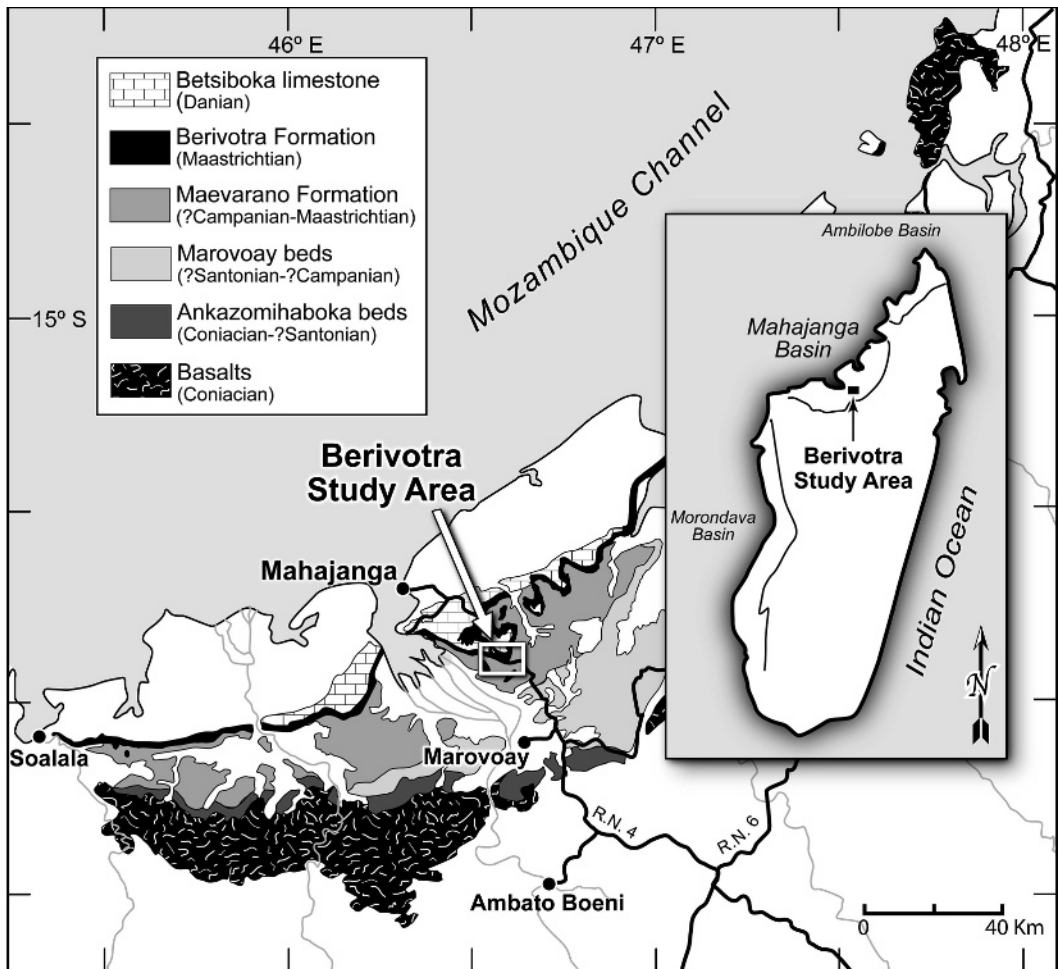


Figure 1. The Berivotra Study Area in the Mahajanga Basin of northwestern Madagascar and the outcrop area of Upper Cretaceous and Paleocene strata in the basin. Question marks indicate uncertainty concerning age estimations.

arid setting characterized by repetitive flood events that triggered fine-grained debris flows. These debris flows in turn served to entomb and preserve massive quantities of vertebrate skeletal material (Rogers et al., 2000; Rogers, 2005).

Our ongoing efforts have dramatically increased the previously known (pre-1993) species diversity of Late Cretaceous vertebrates from the island (cf. Krause et al., 1997a, 1999; Krause, 2003b). The fauna is now known to include fishes, frogs, turtles, lizards, snakes, crocodyliforms, non-avian dinosaurs, birds, and mammals. Many new genera and species have been discovered and many of the higher taxa represented are the first documented occurrences for the pre-Late Pleistocene of Madagascar (e.g., frogs (Asher & Krause, 1998), lizards (Krause et al., 2003a), birds (Forster et al., 1996), mammals (Krause et al., 1994)). Furthermore, some of the higher taxa represent the

only known occurrences from Madagascar, fossil or Recent (e.g., gondwanatheres (Krause et al., 1997b) and marsupials (Krause, 2001) among mammals), and some represent the first Late Cretaceous records from large portions of Gondwana (e.g., lizards, birds, marsupials).

Study of these vertebrate fossils and the sediments that encase them provides important information on the anatomy, paleobiology, ecology, and phylogenetic relationships of several vertebrate higher taxa and has resulted in important insights into, among other topics, the origin and early evolution of birds (Forster et al., 1996, 1998, 2003; Forster & O'Connor, 2000; Chinsamy & Elzanowski, 2001); the Gondwanan diversification and distribution of crocodyliforms (Buckley et al., 1997, 2000; Buckley & Brochu, 1999; Rasmusson, 2002; Rasmusson & Buckley, 2001; Turner, 2004a, b), saurischian dinosaurs

Table 1. Crocodyliform genera from the Anembalemba Member of the Maevarano Formation, Upper Cretaceous (Maastrichtian), Mahajanga Basin, Madagascar.

Mesoeucrocodylia
Metasuchia
Notosuchidae
<i>Simosuchus</i> Buckley, Brochu, Krause & Pol
Peirosauridae
Genus indet.
Trematochampsidae
<i>Trematochampsia</i> Buffetaut & Taquet
Metasuchia <i>incertae sedis</i>
<i>Araripesuchus</i> Price
<i>Mahajangasuchus</i> Buckley & Brochu
Genus indet. A
Genus indet. B

(Sampson et al., 1998, 2001; Curry Rogers & Forster, 2001, 2004; Curry Rogers, 2002, 2005; Carrano et al., 2002, 2004; O'Connor & Claessens, 2005; O'Connor, in press), and mammals (Krause et al., 1997b; Krause, 2001); the biogeographic origins of the highly endemic extant Malagasy vertebrate fauna (Krause et al., 1997a, 1999; Krause, 2003b); and the stratigraphy, sedimentology, and geochronology of Upper Cretaceous rocks in the Mahajanga Basin (Krause & Hartman, 1996; Rogers et al., 2000, 2001; Casey et al., 2003; Rogers, 2005). Perhaps most significantly, these discoveries have profound implications for testing biogeographic hypotheses that, in turn, address broader questions concerning the timing and sequence of Gondwanan fragmentation (Krause et al., 1997a, b, 1999; Sampson et al., 1998; Krause, 2003b).

The record of Late Cretaceous terrestrial vertebrates from Gondwana is spotty at best and therefore difficult to analyze and interpret in a biogeographic context. Among the vertebrate groups represented in the Late Cretaceous of Madagascar, the best known in terms of their completeness and preservation and therefore the most precisely identified, are the crocodyliforms, non-avian dinosaurs, and mammals. These taxa are therefore the most relevant for consideration of biogeographic relationships. The following provides a brief overview of the taxonomic and anatomical diversity of each of these taxa.

CROCODYLIFORMS

At least seven species of crocodyliforms, all metasuchians, are present in the Maevarano Formation (Table 1). This diversity is extraordinary, and it is therefore not surprising that a range of adaptations suggestive of habitat specialization is evident. In addition to extreme differences in body size and form,

ranging from small and gracile to large and ponderous, there is a broad range in skull shape, from robust and broad to long and slender to short and blunt.

Mahajangasuchus insignis (Fig. 2), originally described on the basis of a nearly complete skeleton lacking only the skull, is the first crocodyliform genus and species from the Late Cretaceous of Madagascar to be named on the basis of MBP discoveries (Buckley & Brochu, 1999). Since publication on this specimen, two nearly complete skulls have been discovered (Buckley & Brochu, 2001). *Mahajangasuchus* was a large carnivore, measuring almost 4 m in length, and is distinctive among crocodyliforms in exhibiting an extremely broad and flat, hippopotamus-like snout and deep lower jaw.

Simosuchus clarki (Fig. 3) is a new, bizarre, pug-nosed species represented by a complete skull and articulated anterior half of a postcranial skeleton that were preliminarily described by Buckley et al. (2000). The blunt, shovel-like snout, deep cranium, poster-oventrally positioned occipital condyle, underslung lower jaw, and areas for extensive neck musculature are suggestive of burrowing adaptations, whereas the anteriorly positioned jaw joint and clove-shaped teeth may reflect adaptations for herbivory (Fig. 3).

A new species, *Araripesuchus* sp. indet., is being described by A. Turner (in press). It is known from skulls and skeletons of at least five individuals, all recovered from a single locality, that reveal a small, gracile-limbed form (Fig. 4). *Araripesuchus tsangatsangana* represents the geologically youngest occurrence, yet most primitive known member of the genus (Turner, 2004a, b; in press).

Trematochampsia oblita Buffetaut & Taquet, named on the basis of three fragmentary dentaries, is the only crocodyliform species from the Late Cretaceous of Madagascar that was described prior to inception of the MBP (Buffetaut & Taquet, 1979). A better-preserved dentary, as well as several skull and postcranial elements, were recovered by MBP expeditions (Rasmusson & Buckley, 2001). The new material of *T. oblita* provides the opportunity for a better understanding of phylogenetic relationships of trematochampsids; Rasmusson (2002) determined that trematochampsids are monophyletic, but that the genus *Trematochampsia* is paraphyletic. Although still poorly known, it is clear that *T. oblita*, like *Mahajangasuchus*, was a massive animal and likely one of the top predators of its time.

In addition to these named crocodyliform taxa, there are at least three as yet unnamed species recovered from the Maevarano Formation. One is represented by several skull elements preliminarily identified as peirosaurid. The second is a medium-sized (i.e., smaller than *Mahajangasuchus insignis* and

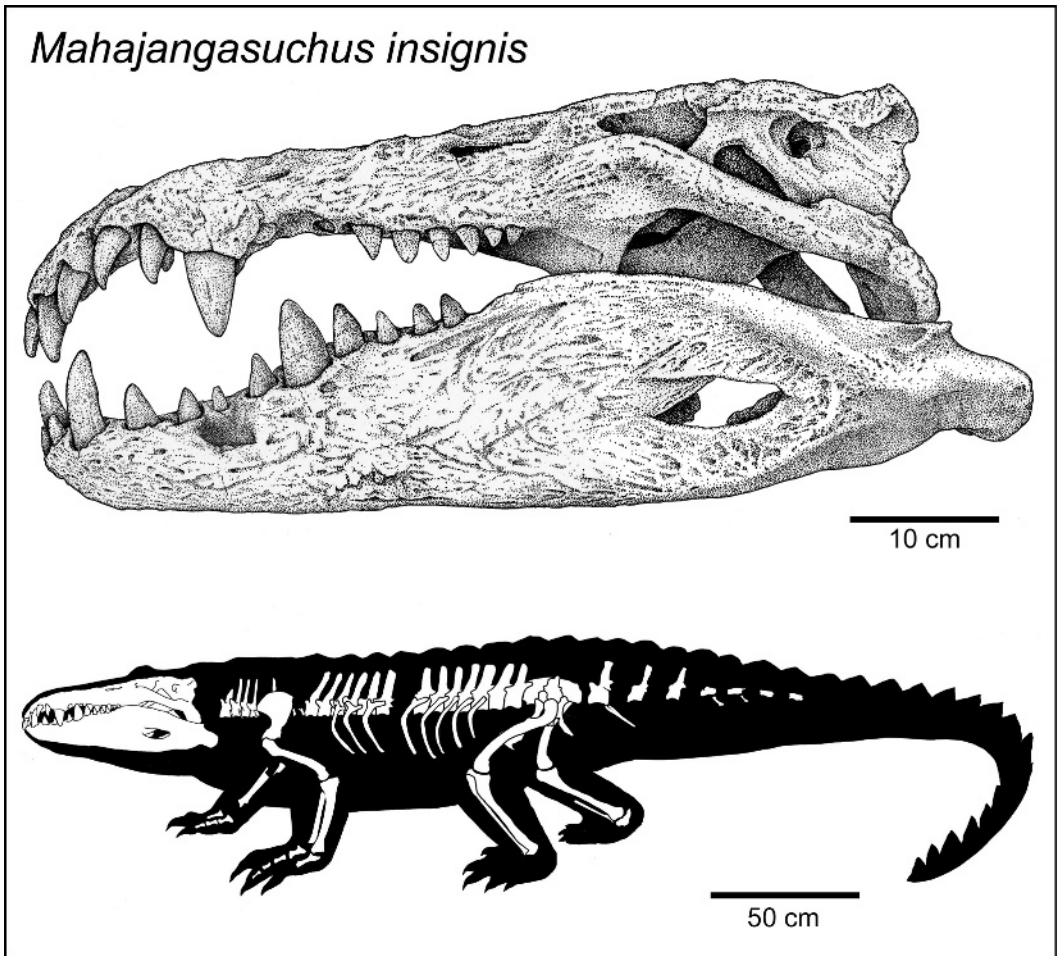


Figure 2. *Mahajangasuchus insignis* Buckley & Brochu, a large, broad-mouthed metasuchian crocodyliform from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

Trematochampsia oblita, but larger than *Araripesuchus* sp. indet.), slender-snouted metasuchian, represented by a partial skull, a complete lower jaw, and considerable postcranial material (Buckley et al., 2003). The third is poorly known, represented only by isolated elements, primarily partial skull and jaw material.

NON-AVIAN DINOSAURS

Dinosaur material is abundant in the Maevarano Formation, but to date is limited to the Saurischia. At least four non-avian species have been discovered: two theropods and two sauropods (Table 2).

The best represented of the two theropods is the mid-sized (approximately 6.2 m in length) abelisaurid *Majungatholus atopus*, previously thought to be a pachycephalosaurid (“dome-headed” ornithischian dinosaur) based on fragmentary skull material (Sues &

Taquet, 1979; Sues, 1980; Fig. 5). One of the most spectacular fossil discoveries of the MBP to date is an exquisitely preserved and virtually complete skull and lower jaws of *M. atopus*, discovered in 1996 (Sampson et al., 1998). The short and deep skull bears fused nasal bones with a large interior pneumatic chamber, and a midline projection or “horn” positioned above the eyes, with a notable parietal eminence capping the skull roof posteriorly. Complementing this specimen are several other, more fragmentary, and less well-preserved skulls discovered recently, in addition to three partial skeletons, one of them representing a juvenile individual; thus, virtually all bones of the skeleton are now represented for this animal (the primary exceptions being parts of the pelvis and the distal portions of the forelimbs). These specimens confirm referral of *Majungatholus* to the Abelisauridae and are described in detail in a monograph-length study (Sampson & Krause, in

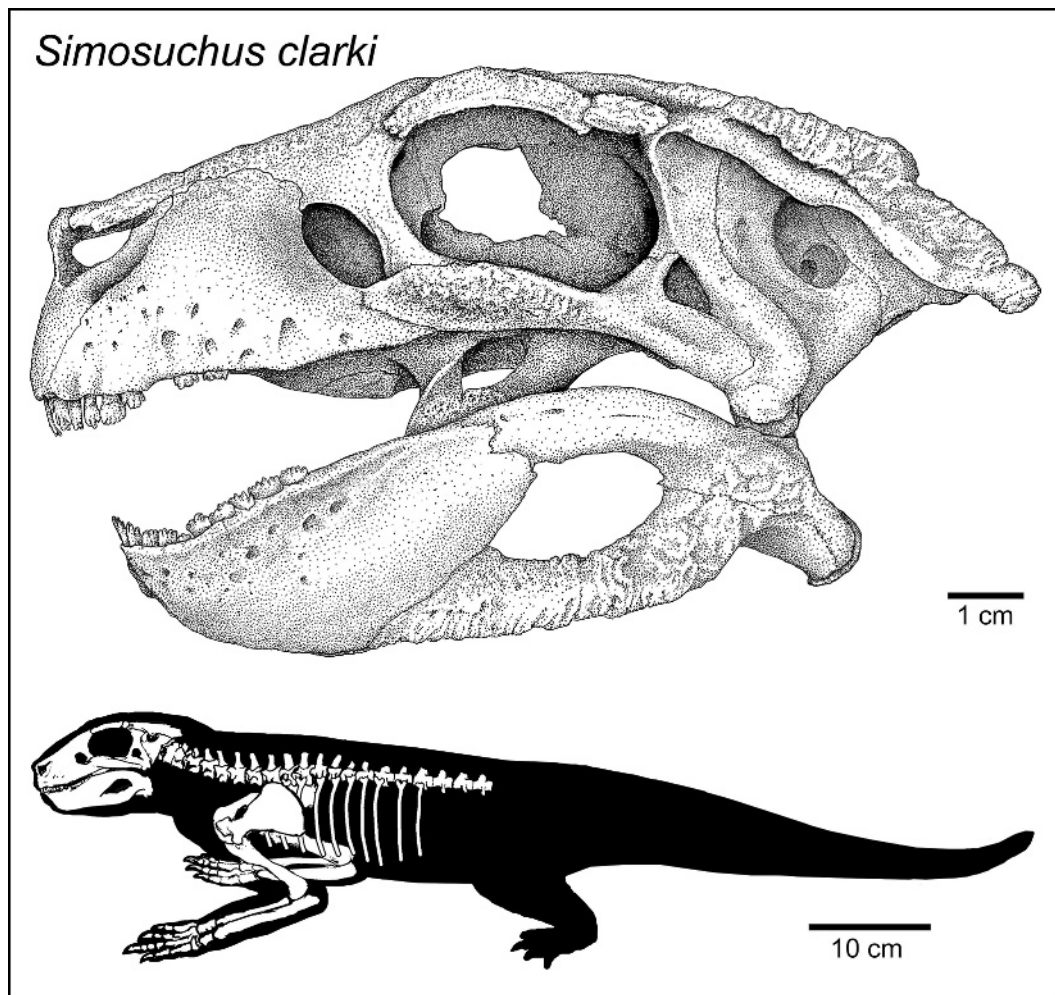


Figure 3. *Simosuchus clarki* Buckley, Brochu, Krause & Pol, a small- to mid-sized metasuchian crocodyliform from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

press). Numerous bones in the Maevarano assemblage exhibit tooth marks (some of which even preserve denticle drag marks) that can be attributed only to *Majungatholus*, thus attesting to its carnivorous habits. Interestingly, many of the bones are those of *Majungatholus* itself, thereby providing the first well-documented evidence for cannibalism among dinosaurs (Rogers et al., 2003).

Masiakasaurus knopfleri, measuring approximately 1.8 m long, was a much smaller and more gracile predator than *Majungatholus atopus* (Fig. 6). It is represented by isolated bones of both the skull and postcranial skeleton and is thus less completely known. *Masiakasaurus* is remarkable, however, in having an anterior dentition that consists of procumbent, spearing teeth, a unique condition among Dinosauria. *Masiakasaurus* was described by Sampson

et al. (2001) and Carrano et al. (2002), who concluded that this Malagasy taxon should be included within the small-bodied abelisauroid clade Noosauridae, previously known only from Argentina. The placement of *Masiakasaurus*—together with the penecontemporaneous Indian form *Laevisuchus*—into Noosauridae (previously known only from Argentina) therefore greatly expanded the geographic range of this clade to encompass much of Gondwana. This finding demonstrates that, at least in a number of ecosystems, noosaurid abelisauroids were small-bodied counterparts to their larger-bodied cousins, the abelisauroids, in a manner parallel to small-bodied maniraptoran coelurosaurs (e.g., troodontids, oviraptorosaurs, dromaeosaurids) and large-bodied tyrannosaurids in many Late Cretaceous Laurasian ecosystems. Recent fieldwork in 2003 and 2005 has produced additional

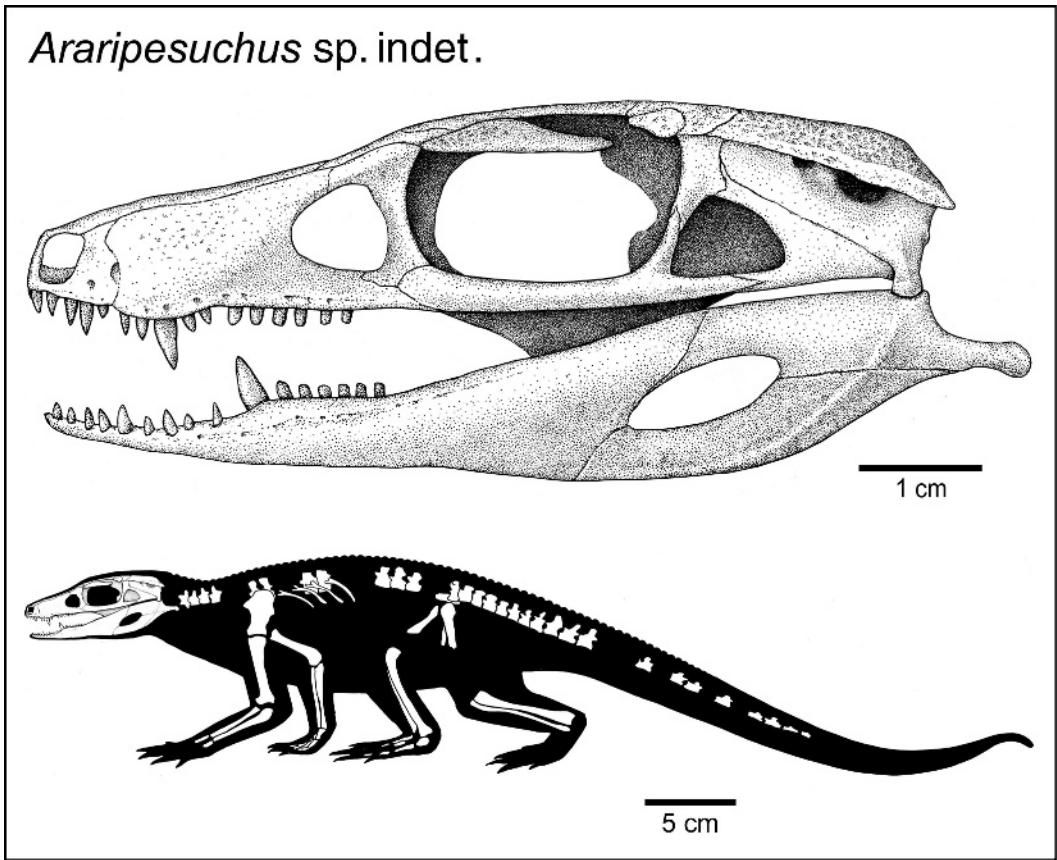


Figure 4. *Araripesuchus* sp. indet., a small, gracile-limbed metasuchian crocodyliform from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

skeletal remains of *Masiakasaurus*, including several key, previously unrepresented cranial and postcranial elements that will significantly increase knowledge of noosaurid anatomy (Carrano et al., 2004, in prep.).

Table 2. Non-avian dinosaur genera from the Anembalemba Member of the Maevarano Formation, Upper Cretaceous (Maastrichtian), Mahajanga Basin, Madagascar.

Theropoda
Ceratosauria
Abelisauroida
Abelisauridae
<i>Majungatholus</i> Sues & Taquet
Noosauridae
<i>Masiakasaurus</i> Sampson, Carrano & Forster
Sauropoda
Titanosauria
Lithostrotia
Saltasauridae
Genus indet. (Malagasy Taxon B of Curry Rogers, 2002)
Lithostrotia <i>incertae sedis</i>
<i>Rapetosaurus</i> Curry Rogers & Forster

Titanosaurian sauropods were among the first fossils described from Madagascar and are abundant components of the Late Cretaceous fauna. At least two species of lithostrotian titanosaurs are present in the fauna, and at least one possessed osteoderms (“skin bones”) that range in size from small ossicles to bony plates greater than 40 cm in diameter (Depéret, 1896; Dodson et al., 1998).

Rapetosaurus krausei is known from approximately 90% of its skeleton, including several well-preserved associated specimens representing a range of ontogenetic stages (Curry Rogers & Forster, 2001, 2004; Curry Rogers, 2005; Fig. 7). *Rapetosaurus* is particularly significant because it preserves cranial and postcranial data key to elucidating phylogenetic relationships among one of the most temporally and geographically widespread of dinosaurian groups. *Rapetosaurus* has already provided the first cranial data in support of Titanosauriformes monophyly and has helped to increase resolution of lower-level titanosaurian relationships (Curry Rogers & Forster, 2001; Curry Rogers, 2005).

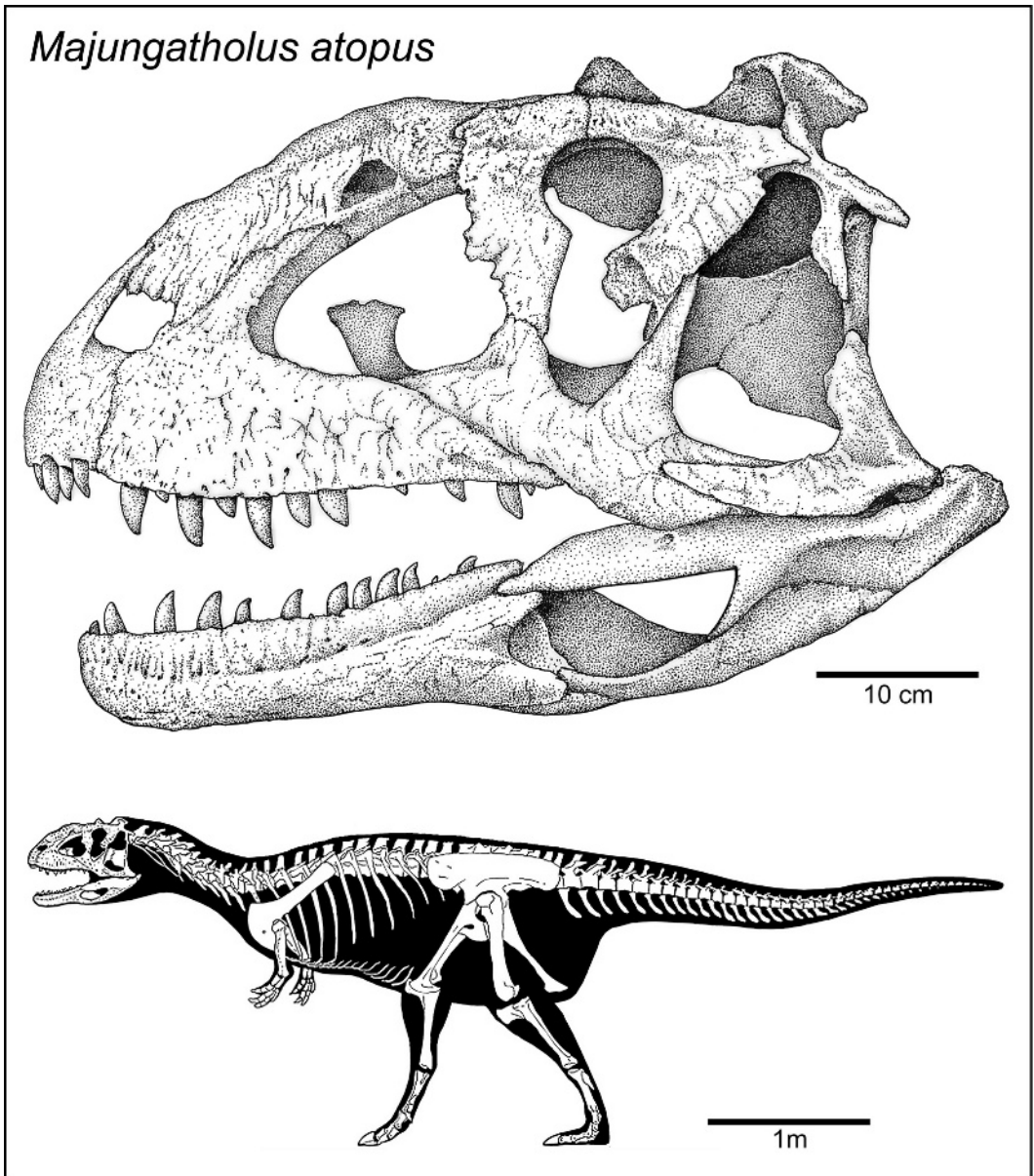


Figure 5. *Majungatholus atopus* Sues & Taquet, a mid-sized theropod dinosaur from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

“Malagasy Taxon B” (Table 2) is the second titanosaur species from Madagascar. Although represented by only several isolated caudal vertebrae, a series of articulated distal caudals, and an isolated coracoid (Curry Rogers, 2002, 2005), Taxon B can be easily distinguished from *Rapetosaurus*. The caudal centra of Malagasy Taxon B are distinctively dorsoventrally compressed and subrectangular in transverse section. In contrast, *Rapetosaurus* caudal centra have subequal height and width dimensions resulting in a round transverse section. Coracoids are also di-

agnostic: Malagasy Taxon B exhibits a square coracoid with broad scapular facet, whereas *Rapetosaurus* has a rounded coracoid with narrow scapular articulation.

Curry Rogers (2005) recently conducted a phylogenetic analysis and concluded that Malagasy Taxon B and *Rapetosaurus* are distant relatives within Titanosauriformes (Curry Rogers, 2005). Even more significantly, the compressed caudal vertebrae and low neural spines of Malagasy Taxon B indicate that it is a member of Saltosaurinae (sensu Wilson & Upchurch, 2003) with close affinities to the South

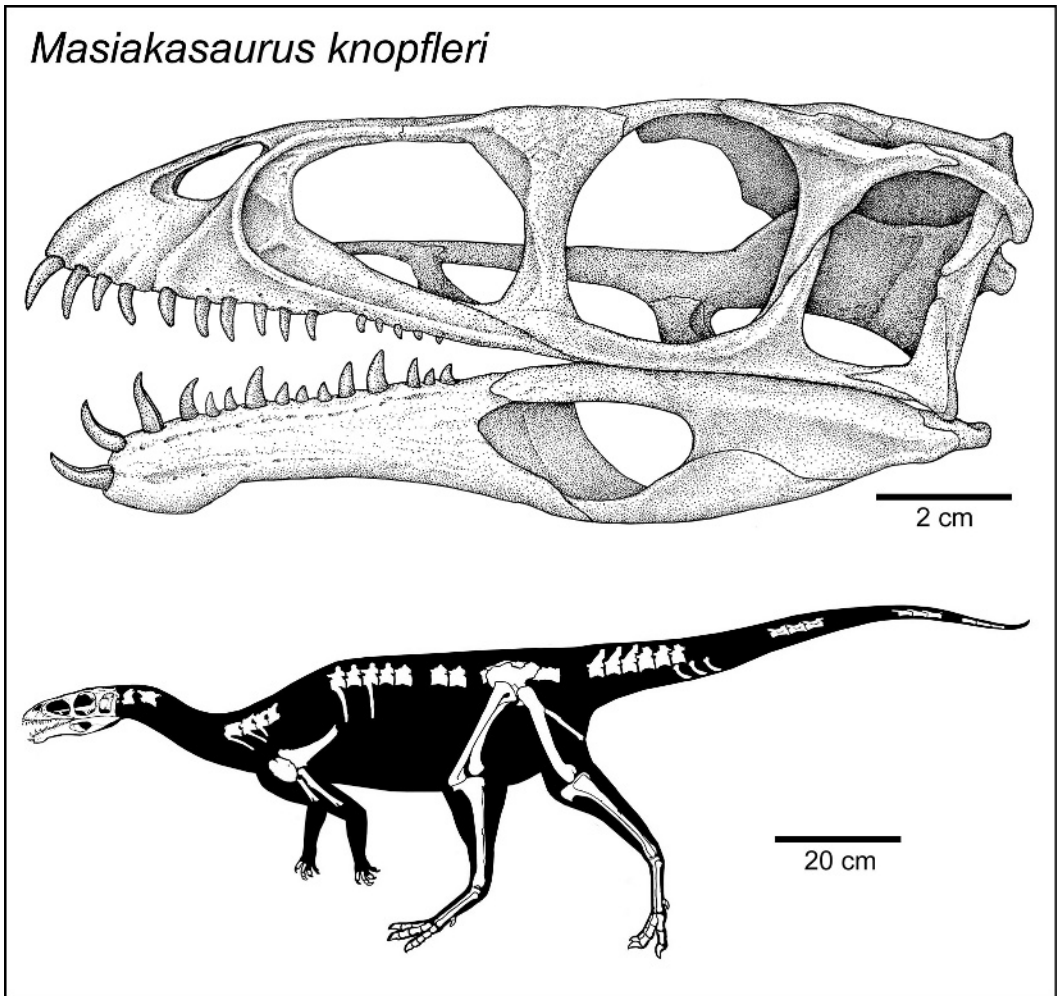


Figure 6. *Masiakasaurus knopfleri* Sampson, Carrano & Forster, a small theropod dinosaur from the Late Cretaceous of Madagascar. Skull in left lateral view and restoration of the skull and skeleton in left lateral view.

American saltasaurine genera *Saltasaurus*, *Neuquensaurus*, and *Rocasaurus*.

MAMMALS

The Late Cretaceous mammalian fauna of Madagascar is still poorly understood. It is represented by five, or perhaps six, taxa, each known from nothing more than a fragmentary tooth or two (Krause et al., 1994, 1997b; Krause & Grine, 1996; Krause, 2001, 2002; Table 3). One still-undescribed taxon, however, is represented by a nearly complete, well-preserved, and articulated skeleton (Krause, 2003a). Interestingly, none of the known taxa can be considered to be potential ancestors of the island's highly endemic extant mammalian fauna, all of which are placentals.

Two fragmentary mammalian teeth were assigned to a new genus and species, *Lavanify miolaka* Krause,

Prasad, von Koenigswald, Sahni & Grine, a sudamericid gondwanatherian (Krause et al., 1997b). Sudamericids are unique among Mesozoic mammals in possessing hypsodont cheek-teeth separated from gliriform incisors by a pronounced diastema. Just as for noasaurid theropods (see above), the discovery of sudamericids in Madagascar and the Indian subcontinent considerably extended the geographic range of the clade (previously known only from Argentina) and provided evidence for a previously unknown high degree of cosmopolitanism that encompassed both western and eastern Gondwana (see below).

At least one other tooth may also be assigned to Gondwanatheria (listed as *Mammalia incertae sedis* Genus indet. A in Table 3), although it is much larger and considerably lower crowned than those assigned to *Lavanify* (Krause, 2000). Still less high-crowned is another isolated tooth that exhibits a complex occlusal

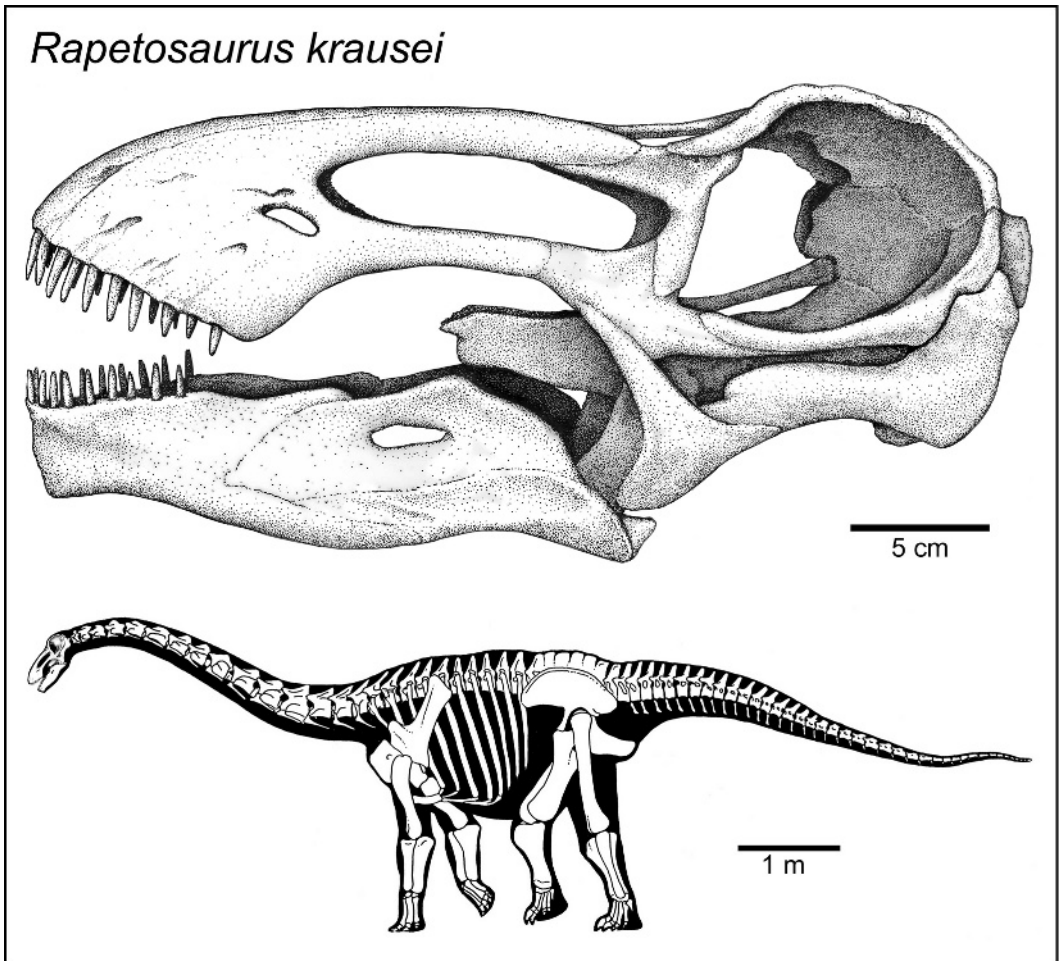


Figure 7. *Rapetosaurus krausei* Curry Rogers & Forster, a titanosaurid sauropod dinosaur from the Late Cretaceous of Madagascar. Subadult skull in left lateral view and restoration of the skull and skeleton in left lateral view.

morphology (W-shaped ridge with two infundibula separating each of the three limbs of the W) on an obliquely-oriented surface. This specimen could conceivably also pertain to Gondwanatheria but,

Table 3. Mammalian genera from the Anembalemba Member of the Maevarano Formation, Upper Cretaceous (Maastrichtian), Mahajanga Basin, Madagascar.

Mammalia
Multituberculata
Genus indet.
Marsupialia
Genus indet.
Gondwanatheria
Sudamericidae
<i>Lavanify</i> Krause, Prasad, von Koenigswald, Sahni & Grine
Mammalia <i>incertae sedis</i>
Genus indet. A
Genus indet. B

based on current information, it could equally well belong to a previously unrecognized higher taxon of Mesozoic mammals.

Another isolated tooth, a tribosphenic lower molar, was regarded by Krause (2001) as that of a marsupial and therefore as potentially the earliest evidence of marsupials in the Southern Hemisphere. This identification was confirmed by Case and Krause (2002), but has since been disputed by Averianov et al. (2003); Case (in prep.) is nearing completion of a more detailed analysis that supports the marsupial affinities of the taxon represented by this specimen.

Another isolated specimen is a molar fragment exhibiting cusp-in-line morphology characteristic of multituberculates, a clade that is well represented and extremely diverse in pencontemporaneous, as well as earlier and later, horizons in Laurasia (Krause & Grine, 1996). Multituberculates are poorly known from the Mesozoic of the Southern Hemisphere, previously found

only in the Early Cretaceous of Morocco (Sigogneau-Russell, 1991; Hahn & Hahn, 2003) and possibly the Late Cretaceous (Campanian or early Maastrichtian) of Argentina (Kielan-Jaworowska et al., 2004).

Finally, one recently discovered taxon (listed as *Mammalia incertae sedis* Genus indet. B in Table 3) is represented by a virtually complete, articulated, sub-adult skeleton (Krause, 2003a). This skeleton, still in the process of being prepared and studied, represents the largest and most complete specimen of a mammal yet known from the Mesozoic of Gondwana. It exhibits a striking mosaic of primitive (e.g., septomaxilla with prominent septomaxillary canal, epipubic bone) and derived (e.g., specialized dentition with prominent diastema, well-developed humeral trochlea, reduced fibular-calcaneal contact) features. There is no doubt that this specimen will introduce a substantial amount of character conflict into previous topologies of mammalian phylogeny. It is also safe to conclude, even at this preliminary stage, that this animal cannot be “shoehorned” into any currently recognized higher taxon of mammals; it represents a major new nontherian clade. The relative completeness of this extraordinary specimen promises to elucidate the anatomy, functional morphology, and phylogenetic position of the clade it represents.

TERRESTRIAL VERTEBRATES FROM THE ANKAZOMIHABOKA SANDSTONES

Terrestrial vertebrate fossils have also been recovered from the Ankazomihaboka sandstones, a unit that is purportedly interbedded with, and definitely overlies, basalts of Coniacian age (Besairie, 1972; Storey et al., 1995, 1997). A preliminary report (Curry, 1997) indicates the presence of at least three crocodyliform taxa and two to three taxa of nonavian dinosaurs, including sauropods and theropods; no mammals were found. Subsequent collections have been made and a more extensive analysis of the assemblage from this unit is under way (Curry Rogers et al., in prep.). The taxa derived from the Ankazomihaboka sandstones are not considered here because of the tentative nature of the current identifications and because the age of the rock unit has not been ascertained, although, conservatively, it can be constrained to have been as early as Coniacian and as late as Maastrichtian.

CAMPANIAN/MAASTRICHTIAN CROCODYLIFORMS, NON-AVIAN DINOSAURS, AND MAMMALS FROM OTHER GONDWANAN LANDMASSES

The primary purpose of this section is to compare the latest Cretaceous terrestrial vertebrate assem-

blages of Madagascar and South America. However, the taxonomic similarities between the assemblages from these two landmasses at the end of the Cretaceous make it clear that physical and biotic connections with other landmasses were also involved and must be considered. An overview of penecontemporaneous terrestrial faunas from potentially connected landmasses—namely Antarctica, Africa, and the Indian subcontinent—is therefore warranted. Australia and southern Europe also contained Gondwanan-aspect faunas during the Late Cretaceous, but there is no independent evidence indicating that either was *directly* connected to Madagascar or South America during this interval; as such, and owing to space considerations, their faunas are not considered here.

The faunal lists in Tables 4–6 provide an overview of the generic diversity of crocodyliforms, non-avian dinosaurs, and mammals known from the Campanian and Maastrichtian stages of South America, Africa, Antarctica, and the Indian subcontinent. The Campanian and Maastrichtian, the last two stages of the Late Cretaceous, represent a broader time slice (approximately 18.5 million years) than is likely represented by the Anembalemba Member of the Maevarano Formation in Madagascar. Nonetheless, the uneven comparison is necessitated, at least in part, because of the poor sampling of penecontemporaneous Gondwanan horizons and because of the imprecise dating of productive strata; given these constraints, it is better to be too inclusive rather than too exclusive. The faunal lists have been extracted from numerous sources for crocodyliforms (e.g., Gasparini et al., 1996; Bertini & Carvalho, 1999; Wilson et al., 2001; Prasad & de Lapparent de Broin, 2002), but primarily from Weishampel et al. (2004) for non-avian dinosaurs and Kielan-Jaworowska et al. (2004) for mammals, with other sources noted in table headings.

SOUTH AMERICA

South America has the largest and most diverse samples of Gondwanan Late Cretaceous vertebrates, many from Campanian and Maastrichtian horizons. Indeed, there are over 40 family-level taxa of terrestrial vertebrates known from the Campanian and Maastrichtian of South America, more than double the number from any other Gondwanan landmass. This is in large part the result of intense sampling over the past several decades, much of it owing to the efforts of José Bonaparte of the Museo Argentino de Ciencias Naturales Paleontología (Buenos Aires) and his students.

It is not possible to determine which of the family-level taxa currently unknown from elsewhere were

Table 4. Crocodyliform genera from Campanian and Maastrichtian horizons in South America, Africa, Antarctica, and the Indian subcontinent. List for South America compiled primarily from Gasparini (1996) and Bertini and Carvalho (1999), for Africa from Buffetaut (1982) and Brochu (1997), and for the Indian subcontinent from Wilson et al. (2001) and Prasad and de Lapparent de Broin (2002).

SOUTH AMERICA	
Mesoeucrocodylia	
Metasuchia	
Notosuchidae	
<i>Uruguaysuchus</i>	Rusconi
Baurusuchidae	
<i>Cynodontosuchus</i>	Woodward
<i>Baurusuchus</i>	Price
<i>Stratiotosuchus</i>	Campos, Suarez, Riff & Kellner
Peirosauridae	
<i>Peirosaurus</i>	Price
<i>Lomasuchus</i>	Gasparini, Chiappe & Fernandez
<i>Uberabasuchus</i>	Carvalho, Ribeiro & dos Santos Avilla
Trematochampsidae	
<i>Itasuchus</i>	Price
Metasuchia <i>incertae sedis</i>	
<i>Sphagesaurus</i>	Price
Neosuchia	
Dyrosauridae	
<i>Sulcusuchus</i>	Gasparini & Spalletti
<i>Hyposaurus</i>	Owen (questionably from Maastrichtian)
Eusuchia	
Dolichochoampsidae	
<i>Dolichochoamps</i>	Gasparini & Buffetaut
AFRICA	
Mesoeucrocodylia	
Neosuchia	
Dyrosauridae	
<i>Sokotosuchus</i>	Halstead
ANTARCTICA	
No record	
INDIAN SUBCONTINENT	
Mesoeucrocodylia	
Metasuchia	
Baurusuchidae	
<i>Pabwehshi</i>	Wilson, Malkani & Gingerich
Metasuchia <i>incertae sedis</i>	
Genus indet.	
Neosuchia	
Dyrosauridae	
Genus indet.	

indeed restricted to South America and which were more broadly distributed in the Southern Hemisphere, simply because of the relative paucity of discoveries on other Gondwanan landmasses. However, it is significant to note that of the seven family-level taxa of crocodyliforms (Notosuchidae, Peirosauridae, Trematochampsidae), non-avian dinosaurs (Abelisauridae, Noasauridae, Saltasauridae (including Saltasaur-

inae)), and mammals (Sudamericidae) that have been identified as occurring in the Maastrichtian of Madagascar, *all* are known from the Campanian/Maastrichtian of South America. This is suggestive of close biogeographic ties and, indeed, a degree of cosmopolitanism that was unexpected before the MBP discoveries and that, moreover, is difficult to explain in the context of most recent paleogeographic reconstructions.

Crocodyliforms known from Campanian and Maastrichtian horizons in South America are diverse, comprising at least 12 named genera, most of them metasuchians. In addition to notosuchids, peirosaurids, and trematochampsids, the metasuchian family Baurusuchidae is represented. Neosuchians and eusuchians, for which definitive evidence has yet to be found in the Late Cretaceous of Madagascar, are also present in South America. The non-avian dinosaur fauna from the South American Campanian and Maastrichtian is dominated by saurischians. Among Theropoda, abelisauroid ceratosaurians (including both abelisaurids and noasaurids) are the most diverse and, among the Sauropoda, lithostrotians, including saltasaurines, dominate. Ornithischians are represented by spotty occurrences of ankylosaurs, euornithomorphs, and hadrosaurs. It is intriguing that, in contrast to the dominance of ornithischian herbivores in most Campanian terrestrial ecosystems on Laurasian-derived landmasses, ornithischians appear to be only minor components of Campanian ecosystems on most Gondwanan landmasses, if they are present at all (Currie, 1996). Campanian and Maastrichtian mammals from South America include a diversity of archaic nontribosphenic forms, including Austrotriconodontidae, Bondesiidae, Brandoniidae, Dryolestidae, Ferugliotheriidae, Mesungulidae, Reigitheriidae, and Sudamericidae. Of these, only the Sudamericidae is known to also occur in Madagascar (Krause et al., 1997b). In addition to this diversity of nontribosphenic taxa, there are two species of eutherians and questionable occurrences of "pediomid" and peradectid marsupials.

ANTARCTICA

Not unexpectedly, considering its ice-cover and harsh climate today, Antarctica has grudgingly yielded fossils of Late Cretaceous terrestrial vertebrates. They have been recovered from the Antarctic Peninsula (Vega and James Ross Islands) and include only specimens of dinosaurs (Hooker et al., 1991; Gasparini et al., 1996; Rich et al., 1999; Case et al., 2000, 2003). This appears to be largely the result of "bloat and float" taphonomic scenarios, where carcasses are washed out to sea and skeletal elements are buried in, and recovered from, marine sediments.

Table 5. Non-avian dinosaur genera from Campanian and Maastrichtian horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Weishampel et al. (2004), with additions from Novas and Agnolin (2004), Novas et al. (2004) for South America, Wilson and Upchurch (2003) for India, and Suberbiola et al. (2004) for Africa. Question marks indicate tentative placement.

SOUTH AMERICA

Theropoda

 Ceratosauria

 Abelisauroida

 Abelisauridae

Carnotaurus Bonaparte

 Abelisauridae indet.

 Noasauridae

Noasaurus Bonaparte & Powell

 Tetanurae

 Avetheropoda

Quilmesaurus Coria

 Maniraptora

Unquillosaurus Powell

 ?Oviraptorosauria indet.

 Coelurosauria indet.

 Theropoda indet.

Sauropoda

 Lithostrotia

 Saltisauridae

Saltasaurus Bonaparte & Powell

 Lithostrotia *incertae sedis*

Aeolosaurus Powell

Antarctosaurus Huene

Laplatasaurus Huene

Neuquenosaurus Powell

Pellignisaurus Salgado

Rocasaurus Salgado & Azpilicueta

 Lithostrotia indet.

 Titanosauria indet.

 Sauropoda indet.

Thyreophora

 Ankylosauria

 ?Nodosauridae indet.

 Ankylosauridae indet.

Ornithopoda

 Euornithopoda

 Iguanodontia

Talenkauen Novas, Cambiaso & Ambrosio

 Hadrosauridae

 Hadrosaurinae indet.

 Lambeosaurinae indet.

 Euornithopoda indet.

AFRICA

Theropoda

 Ceratosauria

 Abelisauroida

 ?Abelisauridae

 Genus indet.

 Avetheropoda *incertae sedis*

Bahariasaurus Stromer

Table 5. Continued.

Sauropoda

 Titanosauriformes indet.

ANTARCTICA

Theropoda indet.

Thyreophora

 Ankylosauria

 Nodosauridae indet.

Ornithopoda

 Euornithopoda

 Hadrosauridae indet.

INDIAN SUBCONTINENT

Theropoda

 Ceratosauria

 Abelisauroida

 Abelisauridae

Indosaurus Huene & Matley

Indosuchus Huene & Matley

Rajasaurus Wilson, Sereno, Srivastava, Bhatt,
 Khosla & Sahni

 Genus indet. A

 Genus indet. B

 Noasauridae

Laevisuchus Huene & Matley

 Ceratosauria indet.

 ?Carnosauria indet.

Composuchus Huene & Matley

 Ornithomimidae indet.

 Theropoda indet.

Sauropoda

 Lithostrotia

Isisaurus Wilson & Upchurch

Jainosaurus Hunt, Lockley, Lucas & Meyer

Antarctosaurus

 Titanosauria indet.

 Sauropoda indet.

Thyreophora

 Ankylosauria

 Ankylosauridae indet.

 Stegosauria

 Stegosauridae indet.

This also may account for the lack of discovery of small vertebrate taxa (e.g., lizards, turtles, crocodyli-forms, mammals), although climate may have also played an important role. Interestingly, the dinosaur fossils that have been recovered are of taxa (e.g., Euornithopoda, Hadrosauridae, Nodosauridae) that are not represented in the Campanian/Maastrichtian of Africa, Madagascar, or the Indian subcontinent. Instead they are shared with penecontemporaneous horizons in South America.

AFRICA

Africa is, by far, the largest Gondwanan landmass, roughly 70% larger than the next largest, South

Table 6. Mammalian genera from Campanian and Maastrichtian horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Kielan-Jaworowska et al. (2004), with additions from Rana and Wilson (2003) and Khosla et al. (2004) for the Indian subcontinent. Question marks indicate questionable occurrences and quotation marks indicate paraphyletic taxa.

SOUTH AMERICA	
?Docodonta	
Reigitheriidae	
<i>Reigitherium</i> Bonaparte	
Eutricondonta	
Austrotriconodontidae	
<i>Austrotriconodon</i> Bonaparte	
?Multituberculata <i>incertae sedis</i>	
Genus indet.	
Archaic "symmetrodontans"	
Bondesiidae	
<i>Bondesius</i> Bonaparte	
Stem Cladotheria	
Dryolestidae	
<i>Groebertherium</i> Bonaparte	
<i>Leonardus</i> Bonaparte	
Genus indet.	
Mesungulatidae	
<i>Mesungulatum</i> Bonaparte & Soria	
Brandoniidae	
<i>Brandonia</i> Bonaparte	
? <i>Casamiguelia</i> Bonaparte	
Marsupialia	
?Peradectidae	
Genus indet.	
?"Pediomyidae"	
Genus indet.	
Eutheria	
Family <i>incertae sedis</i>	
<i>Perutherium</i> Grambast, Martinez, Mattauer & Thaler	
Genus indet.	
Gondwanatheria	
Sudamericidae	
<i>Gondwanatherium</i> Bonaparte	
Ferugliotheriidae	
<i>Ferugliotherium</i> Bonaparte	
AFRICA*	
No record	
ANTARCTICA	
No record	
INDIAN SUBCONTINENT	
Eutheria	
?Otlestidae	
Genus indet.	
Family <i>incertae sedis</i>	
<i>Deccanolestes</i> Prasad & Sahni	
<i>Sahnitherium</i> Rana & Wilson	
Infraclass <i>incertae sedis</i>	
Gondwanatheria	
Sudamericidae	
Genus indet.	

America. Despite its vast superiority in size among the five Gondwanan landmasses considered here, Africa's diversity of Campanian/Maastrichtian terrestrial vertebrates is the second poorest, little better than that from Antarctica. This is presumably due in large part to the virtual absence of suitable sedimentary depocenters of the right age and environment, but further exacerbated by limited exploration and a lack of definitive age control independent of the vertebrate fossils themselves.

Of the seven identified families of crocodyliforms, non-avian dinosaurs, and mammals represented in Madagascar, only one, Abelisauridae, is represented, albeit questionably, in the Campanian/Maastrichtian of Africa. Among crocodyliforms, Metasuchia, the crocodyliform clade that dominates in penecontemporaneous horizons in South America, Madagascar, and the Indian subcontinent, is absent. Instead, only the neosuchian dyrosaurid *Sokotosuchus* is known. Among non-avian dinosaurs, there is only poorly preserved material, none of which is precisely identified; significantly, however, no ornithischians are currently known. Campanian/Maastrichtian mammals have yet to be discovered from mainland Africa, although the possible gondwanatherian recently described by Krause et al. (2003b) could conceivably be from this horizon.

THE INDIAN SUBCONTINENT

The record of terrestrial vertebrates from the latest Cretaceous of the Indian subcontinent has increased dramatically over the last three decades, largely the result of efforts by Ashok Sahni of Panjab University (Chandigarh) and his students. The assemblage, from below and interbedded within the Deccan Traps (the infra- and intertrapean beds) was recently summarized by Khosla and Sahni (2003). The infra- and intertrapean beds are considered to be of late Maastrichtian age. The diversity of terrestrial vertebrates from the Indian subcontinent is low, and surprisingly low in one clade that is diverse elsewhere, the Crocodyliformes. Two metasuchians (Baurusuchidae and *Metasuchia incertae sedis*) and one neosuchian (Dyrosauridae) are present, but none of the metasuchian families identified in Madagascar (Notosuchidae, Peirosauridae, Trematochampsidae) have been definitively identified on the Indian

←

* A possible gondwanatherian mammal was recently described by Krause et al. (2003b), but the age of the horizon from which it was recovered is of uncertain age within the Cretaceous period.

subcontinent. Non-avian dinosaurs were discovered on the Indian subcontinent over 175 years ago. Many specimens have been discovered since and demonstrate that a diverse fauna existed at this time. Unfortunately, however, few articulated specimens have been recovered and, as a result, the alpha taxonomy remains ambiguous. Nonetheless, it is clear that the most common dinosaurs present at this time in Madagascar (abelisaurid and noasaurid theropods and lithostrotian sauropods) were also present on the Indian subcontinent. The mammalian fauna is represented by fragmentary isolated teeth that have been assigned to at least three eutherian taxa (*Deccanolestes*, *Sahnitherium*, and a possible otlestid) and a sudamericid gondwanathere (Prasad & Sahni, 1988; Godinot & Prasad, 1994; Prasad & Godinot, 1994; Prasad et al., 1994; Krause et al., 1997b; Rana & Wilson, 2003; Khosla et al., 2004).

SUMMARY

It is clear, based on currently available samples, that the greatest similarity in taxonomic composition of known Campanian/Maastrichtian terrestrial vertebrate faunas to that of Madagascar occurs in South America and India.

PRE-CAMPAIAN CRETACEOUS DISTRIBUTION OF
CROCODYLIFORMS, NON-AVIAN DINOSAURS,
AND MAMMALS ON GONDWANAN LANDMASSES

In addition to comparing the taxonomic composition of crocodyliforms, non-avian dinosaurs, and mammals from Campanian/Maastrichtian horizons of Madagascar, South America, Africa, Antarctica, and the Indian subcontinent, it is relevant to record the pre-Campanian Cretaceous distributions of these same clades on these same landmasses in order to potentially reveal deeper histories. As such, Tables 7–9 provide an overview of the generic diversity of crocodyliforms, non-avian dinosaurs, and mammals from the pre-Campanian Late Cretaceous, whereas Tables 10–12 provide the same information for the Early Cretaceous. The pre-Campanian Late Cretaceous and Early Cretaceous distributions are listed individually because there is general agreement among paleogeographers and paleontologists that South America and Africa separated near the Early/Late Cretaceous boundary (see below). Each of the clades will be considered in turn.

CROCODYLIFORMS (TABLES 7, 10)

Notosuchids, but not trematochampsids, are known from the pre-Campanian Late Cretaceous of South

Table 7. Crocodyliform genera from pre-Campanian Late Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. List for South America compiled primarily from Bertini and Carvalho (1999), and for Africa from Buffetaut (1982) and Larsson and Gado (2000).

SOUTH AMERICA	
Mesoeucrocodylia	
Metasuchia	
Notosuchidae	
<i>Notosuchus</i> Woodward	
<i>Mariliasuchus</i> Carvalho & Bertini	
<i>Comahuesuchus</i> Bonaparte	
AFRICA	
Mesoeucrocodylia	
Metasuchia	
Libycosuchidae	
<i>Libycosuchus</i> Stromer	
Trematochampsidae	
<i>Hamadasuchus</i> Buffetaut	
<i>Trematochampsia</i>	
Eusuchia	
Stomatosuchidae	
<i>Stomatosuchus</i> Stromer	
<i>Aegyptosuchus</i> Stromer	
ANTARCTICA	
No record	
INDIAN SUBCONTINENT	
No record	

America, whereas trematochampsids, but not notosuchids, are known from the pre-Campanian Late Cretaceous of Africa. Both notosuchids and trematochampsids, as well as the unplaced metasuchian *Araripesuchus*, are recorded from Early Cretaceous horizons in both South America and Africa. This reveals a deeper history on those landmasses, presumably prior to separation of these landmasses near the Early/Late Cretaceous boundary. Peirosaurids are known from the Early Cretaceous of Africa but not South America and from neither landmass during the pre-Campanian Late Cretaceous. Unfortunately, the record of identifiable pre-Campanian Cretaceous crocodyliforms is nonexistent for Antarctica and the Indian subcontinent.

NON-AVIAN DINOSAURS (TABLES 8, 11)

Pre-Campanian non-avian dinosaur faunas from Gondwana, particularly from Africa and South America, are generally much better characterized than their Campanian/Maastrichtian counterparts, in part owing to the higher incidence of basin formation (with concurrent sedimentation) during these times. Abelisaurids and lithostrotians are known from Africa and South America during both pre-Campanian Late

Table 8. Non-avian dinosaur genera from pre-Campanian Late Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Weishampel et al. (2004), with additions from González Riga (2003) and Apesteguía (2004) for South America and Sereno et al. (2004) for Africa. Question marks indicate tentative placement.

SOUTH AMERICA

Theropoda

 Ceratosauria

Xenotarsosaurus Martinez, Gimenez, Rodriguez & Bochaty

Velocisaurus Bonaparte

 Abelisauroidea

 Abelisauridae

Abelisaurus Bonaparte & Novas

Aucasaurus Coria, Chiappe & Dingus

Ilokelesia Coria & Salgado

 Abelisauridae indet.

 Tetanurae

 ?Coelurosauria

Aniksosaurus Martinez & Novas

 Avetheropoda

 Allosauroidae

Giganotosaurus Coria & Salgado

 Dromaeosauridae

Unenlagia Novas

Megaraptor Novas

 Dromaeosauridae indet.

 Troodontidae indet.

 ?Ornithomimidae indet

 Tetanurae indet

 Theropoda indet.

Sauropoda

 Diplodocoidea

Amazonsaurus Carvalho, Avilla & Salgado

Rayosaurus Bonaparte

 Titanosauria

Andesaurus Calvo & Bonaparte

Argentinosaurus Bonaparte & Coria

Argyrosaurus Lydekker

Bonitasaura Apesteguía

Epachthosaurus Powell

Mendozasaurus González Riga

 Titanosauria indet.

 Lithostrotia

Antarctosaurus

Laplatasaurus

Rinconsaurus Calvo & González Riga

 Lithostrotia indet.

 Saltasauridae

Neuquensaurus Powell

Saltasaurus

 Sauropoda indet.

Ornithopoda

 Euornithopoda

Notohypsilophodon Martinez

 Iguanodontia

Anabisetia Coria & Calvo

Gasparinisaura Coria & Salgado

Table 8. Continued.

 Hadrosauridae

Secernosaurus Brett-Surman

 ?Iguanodontia indet.

 Ornithopoda indet.

AFRICA

Theropoda

 Ceratosauria

 Abelisauroidea

 Abelisauridae

Rugops Sereno, Wilson & Conrad

 Abelisauridae indet.

 Noasauridae

Deltadromeus Sereno, Dutheil, Iarochene, Larsson, Lyon, Magwene, Sidor, Varricchio & Wilson

 Tetanurae

Sigilmassasaurus Russell

 Spinosauroidea

 Spinosauridae

Spinosaurus Stromer

 Avetheropoda

 Carcharodontosauridae

Carcharodontosaurus Stromer

 Avetheropoda *incertae sedis*

Bahariasaurus

 Dromaeosauridae indet.

 Theropoda indet.

Sauropoda

 Diplodocoidea

 Dicraeosauridae

 cf. *Dicraeosaurus* Janensch

 Titanosauria *incertae sedis*

Aegyptosaurus Stromer

 Lithostrotia

Paralititan Smith, Lamanna, Lacovara, Dodson, Smith, Poole, Giegengack, Attia

 Dicraeosauridae indet.

 Lithostrotia indet.

 Sauropoda indet.

Ornithopoda

 Euornithopoda

 Iguanodontia

 Hadrosauridae

 cf. *Ouranosaurus* Taquet*

 Euornithopoda indet.*

 Iguanodontia indet.*

 Ornithopoda indet.

ANTARCTICA

Theropoda indet.

INDIAN SUBCONTINENT

Theropoda

 Theropoda indet.

Sauropoda

 Sauropoda indet. (= *Bruhathkayosaurus* Yadagiri & Ayyasami)

Stegosauria

 Stegosauridae

Dravidosaurus Yadagiri & Ayyasami

* Indicates taxa listed from only Marsa Matruh, Egypt (?Albian–Cenomanian)

Table 9. Mammalian genera from pre-Campanian Late Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Kielan-Jaworowska et al. (2004).

SOUTH AMERICA
Mammalia indet.
AFRICA
Mammalia indet.
ANTARCTICA
No record
INDIAN SUBCONTINENT
No record

Table 10. Crocodyliform genera from Early Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. List for South America compiled primarily from Bertini and Carvalho (1999), and for Africa from Buffetaut (1982) and Larsson and Gado (2000). Question mark indicates tentative placement.

SOUTH AMERICA
Mesoeucrocodylia
Metasuchia
Notosuchidae
<i>Candidodon</i> Carvalho & Campos
Trematochampsidae
<i>Amargasuchus</i> Chiappe
?Trematochampsidae
<i>Caririsuchus</i> Kellner
<i>Metasuchia incertae sedis</i>
<i>Araripesuchus</i>
Neosuchia
Pholidosauridae
<i>Sarcosuchus</i> Marsh
<i>Meridiosaurus</i> Mones
AFRICA
Mesoeucrocodylia
Metasuchia
Notosuchidae
<i>Malawisuchus</i> Jacobs, Winkler, Downs & Gomani
<i>Anatosuchus</i> Sereno, Sidor, Larsson & Gado
Peirosauridae
<i>Stolokrosuchus</i> Larsson & Gado
Trematochampsidae
<i>Hamadasuchus</i>
Libycosuchidae
<i>Libycosuchus</i>
<i>Metasuchia incertae sedis</i>
<i>Araripesuchus</i>
Neosuchia
Pholidosauridae
<i>Sarcosuchus</i>
<i>Neosuchia incertae sedis</i>
<i>Brillanceausuchus</i> Michard, de Broin, Brunet & Hell
ANTARCTICA
No record
INDIAN SUBCONTINENT
No record

Cretaceous and Early Cretaceous intervals, thereby indicating the initial diversification of these clades prior to the breakup of Gondwana. Noosaurids are also known from Africa during these same intervals, but their occurrence in South America is limited to the pre-Campanian Late Cretaceous. The phylogenetic ambiguity resulting from the relatively fragmentary skeletal material of many of these taxa, particularly noosaurids and lithostrotians, however, necessarily limits biogeographic inferences derived from them.

Similar to the situation described above for Campanian/Maastrichtian strata of non-Madagascan Gondwanan landmasses, pre-Campanian Cretaceous deposits, particularly of South America and Africa, also preserve diverse non-avian dinosaur faunas characterized by numerous clades of tetanuran theropods, non-lithostrotian sauropods, ornithopods, ankylosaurians, and stegosaurians. Particularly problematic for Gondwanan-wide biogeographic reconstructions is the virtual absence of Early Cretaceous dinosaur discoveries from Antarctica, India, and Madagascar.

MAMMALS (TABLES 9, 12)

None of the lower-level mammalian taxa recovered from the Maastrichtian of Madagascar are shared with pre-Campanian Cretaceous horizons from other Gondwanan landmasses, but the biogeographic relevance of this information is limited by the extremely poor knowledge of the mammalian fossil record for the entire Cretaceous of Gondwana. With the possible exceptions of a caudal vertebra from Libya (Nessov et al., 1998) and a dentary fragment from Brazil (Bertini et al., 1993), both of which were recovered from poorly age-constrained horizons (Santonian-Campanian), there are no known pre-Campanian Late Cretaceous mammals known from Gondwanan landmasses. In addition to an important assemblage from Australia, Early Cretaceous Gondwanan mammals are known only from Africa and South America. A Barremian site in Cameroon has yielded evidence of at least three nontribosphenic therians, only one of which, the peramurid "eupantotherian" *Abelodon*, has been named (Brunet et al., 1990). By contrast, a diverse mammalian fauna of Berriasian age has been recovered from Morocco and includes eutriconodontans, archaic "symmetrodontans," "eupantotherians," and "tribotherians" (Sigogneau-Russell et al., 1998). A late Hauterivian or early Barremian site in Argentina has yielded numerous skeletal remains of the zatherian *Vincelestes* (e.g., Hopson & Rougier, 1993), but this is the only South American mammal site of definitive Early Cretaceous age.

Table 11. Non-avian dinosaur genera from Early Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. Lists compiled from Weishampel et al. (2004) with additions from Leanza et al. (2004) for South America and Sereno et al. (2004) for Africa.

SOUTH AMERICA

Theropoda

Ceratosauria

Ligabueino Bonaparte

Ceratosauria indet.

Abelisauridae indet.

Tetanurae

Spinosauroida

Spinosauridae

Irritator Martill, Cruickshank, Frey, Small & Clarke

Angaturama Kellner & Campos

Avetheropoda

Allosauroida

Carcharodontosauridae indet.

Tyrannosauroida

Santanaraptor Kellner

Compsognathidae indet.

Oviraptorosauria indet.

Theropoda indet.

Sauropoda

Diplodocoidea

Amargasaurus Salgado & Bonaparte

Rayososaurus

Rebbachisauridae indet.

Titanosauria

Agustinia Bonaparte

Chubutisaurus del Corro

Titanosauria indet.

Thyreophora

Stegosauridae indet.

Ornithopoda

Euornithopoda

Iguanodontia indet.

Ornithischia indet.

AFRICA

Theropoda

Ceratosauria

Spinostropheus Sereno, Wilson & Conrad

Abelisauroidea

Noasauridae indet.

Abelisauridae indet.

Tetanurae

Afavenator Sereno, Wilson, Larsson, Dutheil & Sues

Spinosauroida

Spinosauridae

Spinosaurus

Suchomimus Sereno, Beck, Dutheil, Gado, Larsson, Lyon, Marcot, Rauhut, Sadlier, Sidor, Varricchio, Wilson & Wilson

Spinosauridae indet.

Avetheropoda

Carcharodontosauridae

Table 11. Continued.

Carcharodontosaurus Stromer

Avetheropoda *incertae sedis*

Bahariasaurus Stromer

Coelurosauria *incertae sedis*

Nqwebasaurus de Klerk, Forster, Sampson,

Chinsamy & Ross

Tetanurae indet.

Theropoda indet.

Sauropoda

Diplodocoidea

Rebbachisauridae

Nigersaurus Sereno, Beck, Dutheil, Larsson, Lyon,

Moussa, Sadlier, Sidor, Varricchio, Wilson &

Wilson

Rebbachisaurus Lavocat

Diplodocidae indet.

Macronaria

Jobaria Sereno, Beck, Dutheil, Larsson, Lyon,

Moussa,

Sadlier, Sidor, Varricchio, Wilson & Wilson

Titanosauriformes

Brachiosaurus Riggs

Lithostrotia

Malawisaurus

Lithostrotia indet.

Sauropoda indet.

Thyreophora

Ankylosauria

Nodosauridae indet.

Stegosauria

Paranthodon Nopcsa

Thyreophora indet.

Ornithopoda

Euornithopoda

Iguanodontia

Lurdusaurus Taquet & Russell

Valdosaurus Galton

Hadrosauridae

Ouranosaurus

Iguanodontia indet.

Ornithischia indet.

ANTARCTICA

No record

INDIAN SUBCONTINENT

No record

MADAGASCAR

No record

SUMMARY

Current evidence suggests a number of close biogeographic ties linking pre-Campanian Cretaceous faunas from Africa and South America. However, it must be noted that data to evaluate faunal links with other Gondwanan landmasses, including Madagascar, are minimal. The undescribed faunal assemblage from the Ankazomihaboka sandstones (Curry, 1997; Curry et al., in prep) may have a significant bearing in this regard.

Table 12. Mammalian genera from Early Cretaceous horizons in South America, Africa, Antarctica, and the Indian subcontinent. List compiled from Kielan-Jaworowska et al. (2004), with additions from Hahn and Hahn (2003). Question mark indicates tentative placement and quotation marks indicate paraphyletic taxa.

SOUTH AMERICA	
"Eupantotheria"	
Zatheria	
Vincelestidae	
<i>Vincelestes</i> Bonaparte	
AFRICA	
Mammalia	
Family incertae sedis	
Genus indet. A	
Genus indet. B	
Eutriconodonta	
?"Amphilestidae"	
Genus indet.	
Family indet.	
<i>Dyskritodon</i> Sigogneau-Russell	
<i>Ichthyoconodon</i> Sigogneau-Russell	
Multituberculata	
Hahnodontidae	
<i>Denisodon</i> Hahn & Hahn	
<i>Hahnodon</i> Sigogneau-Russell	
Genus indet.	
Archaic "symmetrodontans"	
Family indet.	
<i>Atlasodon</i> Sigogneau-Russell	
<i>Microderson</i> Sigogneau-Russell	
Thereuodontidae	
<i>Thereuodon</i> Sigogneau-Russell	
Stem Cladotheria ("eupantotherians")	
Family indet.	
Genus indet.	
<i>Afriquamus</i> Sigogneau-Russell	
<i>Minimus</i> Sigogneau-Russell	
Donodontidae	
<i>Donodon</i> Sigogneau-Russell	
Peramuridae	
<i>Abelodon</i> Brunet, Coppens, Dejax, Flynn, Heintz, Hell,	
Jacobs, Jehenne, Mouchelin, Pilbeam & Sudre	
<i>Peramus</i> Owen	
Stem Boreosphenida	
Aegialodontidae	
<i>Hypomylos</i> Sigogneau-Russell	
Family indet.	
<i>Tribotherium</i> Sigogneau-Russell	
ANTARCTICA	
No record	
INDIAN SUBCONTINENT	
No record	

PHYLOGENY AND BIOGEOGRAPHY OF LATE CRETACEOUS
CROCODYLIFORMS, NON-AVIAN DINOSAURS,
AND MAMMALS FROM MADAGASCAR

Of the seven family-level taxa of crocodyliforms, non-avian dinosaurs, and mammals known from the Maastrichtian of Madagascar, all are shared with Campanian/Maastrichtian faunas of South America. This is suggestive of close biogeographic ties and, indeed, a degree of cosmopolitanism that is difficult to explain in the context of most recent paleogeographic reconstructions depicting separation of most Gondwanan landmasses by great distances at this time (e.g., Lawver et al., 1992; Smith et al., 1994; Reeves & de Wit, 2000; Marks & Tikku, 2001; Rotstein et al., 2001; Scotese, 2001; O'Neill et al., 2003; de Wit, 2003; Bernard et al., 2005). According to these reconstructions, Madagascar had long been isolated in the Indian Ocean by the Campanian and, more specifically, any terrestrial continuity with South America, by whatever route, had been severed some 50 million years earlier. However, the record of Late Cretaceous terrestrial vertebrates from Gondwana is spotty at best and therefore difficult to interpret in a biogeographic context. The best possibilities for obtaining a biogeographic signal come from crocodyliforms, non-avian dinosaurs, and mammals, in part because of their relatively good preservation and therefore relatively precise identification, and in part because they are relatively well-studied. Indeed, the recent publication of two monumental works, by Weishampel et al. (2004) on dinosaurs and Kielan-Jaworowska et al. (2004) on mammals, facilitates the compilation of occurrence data that are used herein to reveal distributional patterns for these taxa. Here we document the available taxonomic and phylogenetic information that might have a more immediate bearing on our understanding of Gondwanan biogeography.

CROCODYLIFORMS

Phylogenetic analyses have been presented for only three of the seven species of crocodyliforms known from the Late Cretaceous of Madagascar. The phylogenetic relationship of *Mahajangasuchus insignis* to other metasuchians was examined by Buckley and Brochu (1999) and Buckley et al. (2000). These analyses indicated a clade that consisted of *Trematochampsia* + *Mahajangasuchus* + Peirosauridae, with *Araripesuchus* basal to this clade. This result tends to support the contention of Buffetaut (1988, 1989), who argued that Peirosauridae should be considered a junior synonym of Trematochampsidae. Without more conclusive evidence and a more thorough understanding of trematochampsid taxa, *Mahajangasuchus* was classified as Metasuchia

incertae sedis. Tykoski et al. (2002) and Turner and Calvo (2005) obtained identical results to Buckley and Brochu (1999). Carvalho et al. (2004) did not include any traditional trematochampsids in their analysis, but found *Mahajangasuchus* to be embedded within the Peirosauridae, with *Uberabasuchus* Carvalho, Ribeiro & dos Santos Avilla from the Late Cretaceous of Brazil as its most closely related sister taxon.

Buckley et al. (2000) determined that *Simosuchus* and its closest sister taxon, *Uruguaysuchus*, from the Late Cretaceous of Uruguay, formed a clade with *Malawisuchus*, and that these three taxa were questionable members of the Notosuchidae (which included *Notosuchus* + *Libycosuchus* in their analysis). This relationship was supported by several subsequent analyses. Tykoski et al. (2002) recovered a nearly identical tree, with *Simosuchus* and *Uruguaysuchus* linked as closely related sister taxa within a notosuchian clade. Sereno et al. (2003) placed *Simosuchus* within the Notosuchia (including a *Comahuesuchus* + *Anatosuchus* clade and a *Simosuchus* + *Araripesuchus* + traditional sebecosuchians + *Malawisuchus* + *Notosuchus* clade). Tree topology regarding this clade is nearly identical with the earlier study by Buckley et al. (2000), with the exception of the exclusion of *Araripesuchus* from the Notosuchia. Sereno et al. (2003) additionally recognized an expanded concept of Notosuchia, roughly equivalent to the Ziphosuchia proposed by Ortega et al. (2000), by including *Comahuesuchus*, *Anatosuchus*, and *Baurusuchus* + *Sebecus* Simpson. Pol (2003) recovered a tree similar to those of Buckley et al. (2000) and Sereno et al. (2003), with *Simosuchus* firmly nested within Notosuchia. The constituency of his notosuchian clade strongly reflects that proposed by Ortega et al. (2000) and Sereno et al. (2003), with the only key difference being the exclusion of *Araripesuchus*, as was also proposed by Buckley et al. (2000). It is worth noting that Ortega et al. (2000) and Pol (2003) include several taxa not included in the other two analyses, resulting in a more geographically widespread notosuchian (or ziphosuchian) clade. These taxa include *Chimaerasuchus* Wu, Sues & Sun from the Early Cretaceous of China and *Iberosuchus* Antunes from the Paleogene of Europe. Turner and Calvo (2005) essentially mirrored the earlier results of Buckley et al. (2000) in producing a *Malawisuchus* + *Uruguaysuchus* + *Simosuchus* clade within the Notosuchia.

The most contrary hypothesis regarding the relationship of *Simosuchus* to other mesoeucrocodylians was put forth by Carvalho et al. (2004). They placed the genus, along with *Chimaerasuchus*, within the Chimaerasuchidae, a clade basal to their Notosuchimorpha. Other differences also appear in their results, including the exclusion of *Uruguaysuchus* from the Notosuchia and the placement of *Malawisuchus* within

the Peirosauroidae. It is likely that these discrepancies are due to the authors' reweighting of characters based upon rescaled values, a practice not followed by other studies.

A recent biogeographic study by Turner (2004b) is highly relevant to the question of Cretaceous crocodyliform distribution. Turner (2004b), employing a time-slicing protocol adapted from Upchurch et al. (2002), conducted a cladistic biogeographic analysis of a diverse sample of Cretaceous crocodyliform taxa, mostly from Gondwana. Included in his sample were three taxa known from the Late Cretaceous of Madagascar: *Simosuchus clarki*, *Mahajangasuchus insignis*, and *Araripesuchus* sp. indet. The sister taxon of *Simosuchus* in Turner's analysis is the Late Cretaceous South American form *Uruguaysuchus*, thus supporting an earlier assessment by Buckley et al. (2000). Turner resolved a sister taxon relationship between *Mahajangasuchus* and the South American Peirosauridae, which also supports the earlier analyses of Buckley and Brochu (1999) and Buckley et al. (2000). *Araripesuchus* sp. indet. occurs at the base of a clade of other *Araripesuchus* species from both Africa and South America. In his analysis, Turner also included *Pabwehshi*, a ?Maastrichtian mesoeucrocodylian from the Indian subcontinent recently described by Wilson et al. (2001). Turner (2004b) confirmed inclusion of *Pabwehshi* in the Baurusuchidae, otherwise only known from the Late Cretaceous of Brazil and Argentina. Late Cretaceous crocodyliforms from the Indian subcontinent are poorly known, based almost exclusively on isolated teeth (Prasad & de Lapparent de Broin, 2002). However, based on available information, Malagasy and Indian crocodyliforms share closest affinities with roughly contemporaneous taxa from South America.

Turner (2004b) refined the methods of Upchurch et al. (2002) and revealed two continent-level vicariant events: (1) separation of Africa, South America, and Indo-Madagascar from other non-Gondwanan landmasses earlier in the Cretaceous, and (2) separation of Africa from South America and Indo-Madagascar later in the Cretaceous. Turner (2004b; 2007) states that "this later event depicts a rather non-traditional biogeographic relationship and, in that respect, this study's results are similar to and support the conclusions of Sampson et al. (1998), Buckley and Brochu (1999), Krause et al. (1999), Krause (2001), and the geological data of Hay et al. (1999)."

NON-AVIAN DINOSAURS

It could be argued that non-avian dinosaurs are perhaps better suited than crocodyliforms for revealing biogeographic pattern as it relates to subaerial

landmasses, because they were likely more closely tied to the terrestrial realm. Moreover, most taxa were very large, making it less likely that they would have been able to raft across great distances on floating mats of vegetation, as has been documented for smaller-bodied extant vertebrates (Censky et al., 1998). As for crocodyliforms, the majority of non-avian dinosaur taxa known from the Late Cretaceous of Madagascar share closest affinities with penecontemporaneous taxa from South America and India. Preliminary phylogenetic analyses have been presented for all four of the saurischian taxa known from Madagascar (Sampson et al., 1998, 2001; Curry Rogers & Forster, 2001, 2004; Curry Rogers, 2002, 2005; Carrano et al., 2002).

Majungatholus, an abelisaurid, has been included in several recent phylogenetic analyses. Sampson et al. (1998) placed this Malagasy abelisaurid in a polytomy with *Indosaurus* and *Indosuchus* from the Maastrichtian of India, *Abelisaurus* from the Santonian of Argentina, and *Carnotaurus* from the Campanian-Maastrichtian of Argentina. Relationships within this polytomy were somewhat better resolved by Sampson et al. (2001) and Carrano et al. (2002), who posited that *Majungatholus* and *Carnotaurus* were sister taxa and that they, together, were the sister taxon of *Abelisaurus* (*Indosaurus* and *Indosuchus* were not included in the analyses). These results were in essence supported in a more comprehensive analysis by Tykoski and Rowe (2004). Coria et al. (2002) grouped *Majungatholus* with *Abelisaurus* and *Ilokelesia* in a polytomy that comprised the sister taxon of *Aucasaurus* + *Carnotaurus*. Wilson et al. (2003) described a new abelisaurid, *Rajasaurus*, from the Maastrichtian of India and reported results of another cladistic analysis of abelisaurids (later presented by Sereno et al., 2004), which concluded that *Abelisaurus*, *Rajasaurus*, and *Majungatholus* + *Carnotaurus* occupied successive nodes on a tree. The later study by Sereno et al. (2004) also included a newly named Cenomanian abelisaurid from Africa, *Rugops* (referred to as "Niger taxon 2" in Wilson et al., 2003). Most significantly, despite the shuffling positions among abelisaurid genera, all analyses have concluded that the closest known relatives of *Majungatholus* lie in Campanian-Maastrichtian horizons of Argentina and India.

Masiakasaurus is currently considered to be a noasaurid abelisauroid (Carrano et al., 2004; Sereno et al., 2004; Tykoski & Rowe, 2004). An analysis by Sereno et al. (2004) concluded that *Masiakasaurus* lies in an unresolved polytomy with *Noasaurus* from the ?late Campanian-Maastrichtian of Argentina, an unnamed genus from the Aptian-Albian of Niger, and *Deltadromeus* (originally regarded as a basal coelurosaurian by Sereno et al., 1996) from the Cenomanian

of Morocco. When originally described by Sampson et al. (2001) and Carrano et al. (2002), the relationships of *Masiakasaurus* were also unresolved, although it was recognized that its affinities lay most closely with *Noasaurus*, *Laevisuchus*, *Genusaurus* Accarie, Beaudoin, Dejax, Fries, Michard & Taquet, and *Ilokelesia*, and secondarily with the abelisaurids *Majungatholus*, *Carnotaurus*, *Xenotarsosaurus*, and *Abelisaurus*. Additional remains of *Masiakasaurus* recovered during the 2003 field season are currently under study by M. Carrano, S. Sampson, and M. Loewen. In a preliminary report, Carrano et al. (2004: 44A) regard the Noasauridae to be abelisauroids "from the Cretaceous of Argentina (*Noasaurus*, *Velocisaurus*), India (*Laevisuchus*), Madagascar (*Masiakasaurus*), and possibly Europe and Africa."

Rapetosaurus has been included in several phylogenetic analyses, the most comprehensive by Curry Rogers (2005), but also by Curry Rogers and Forster (2001) and Wilson (2002). All three of these analyses agree in their resolution of a close relationship between *Nemegtosaurus* Nowinski from the Campanian-Maastrichtian of Mongolia and *Rapetosaurus*, but postulate different successive outgroups and close relatives. Curry Rogers and Forster (2001) and Curry Rogers (2005) identify a clade that includes *Malawisaurus* from the Aptian of Malawi and several taxa from India and/or South America (e.g., *Antarctosaurus*, *Agustinia*). Wilson (2002) instead identifies *Malawisaurus* as a more basal lithostrotian, with *Rapetosaurus* as the sister taxon to a clade of more derived titanosaurs including *Isisaurus colberti* Jain & Bandyopadhyay (from the Campanian-Maastrichtian of India) and Saltosauridae (including taxa from North America, Mongolia, and South America).

Malagasy Taxon B has recently been included in a more comprehensive analysis of titanosaur phylogeny (including over 29 purported titanosaurs; Curry Rogers, 2001, 2005); the strict consensus tree clearly resolves it as nested within the Saltosaurinae (sensu Wilson & Upchurch, 2003). Saltosaurines traditionally include only three South American genera (*Saltasaurus*, *Neuquensaurus*, and *Rocasaurus*) and are uniquely characterized by the presence of strongly procoelous, dorsoventrally compressed distal caudal vertebrae.

MAMMALS

Most of the mammalian taxa from the Late Cretaceous of Madagascar provide little biogeographic information, either because the specimens are too fragmentary to permit identification to a lower taxonomic level, or because the taxa represented are unknown from any other landmass. Such is clearly the

case for one isolated tooth of a large taxon and for a nearly complete skeleton (Krause, 2003a); both taxa, if they are different, cannot be identified as yet beyond Mammalia incertae sedis.

The presence of gondwanatheres, however, is important. The two teeth questionably identified as gondwanatherian are relatively uninformative, but the two specimens that have been assigned to *Lavanify miolaka*, a sudamericid, provide important biogeographic data. Sudamericids are elsewhere known from the Late Cretaceous and Paleocene of Argentina, the Late Cretaceous (Maastrichtian) of India, and the Eocene of Antarctica. *Lavanify* appears to be most closely related to the unnamed sudamericid from India (Krause et al., 1997b).

PALEO GEOGRAPHIC RECONSTRUCTIONS: WERE SOUTH AMERICA AND MADAGASCAR CONNECTED IN THE LATE CRETACEOUS?

Despite Madagascar's current position in the Eastern Hemisphere and South America's location in the Western Hemisphere, and despite differing details in depictions of Gondwanan paleogeography, it is clear that the two landmasses were much closer to one another in the Mesozoic than they are today. Prior to the break-up of Pangea, a non-obstructed (by oceanic waters) overland route across Africa spanning some 3000 km separated the two areas of interest; today the straight-line distance between South America and Madagascar is almost 8000 km. With the fragmentation of Gondwana, which is generally agreed to have commenced in earnest in the Late Triassic to Early Jurassic (Lawver et al., 1992; Torsvik et al., 2001; de Wit, 2003; Wells, 2003), Madagascar, as part of "East Gondwana" (also including the Indian subcontinent, Antarctica, and Australia), began to separate from "West Gondwana" (South America and Africa).

Initial rifting between the Indo-Madagascar block and Africa began during the Permo-Triassic, and seafloor spreading between the conjugate-rifted margins of southern Somalia, Kenya, and Tanzania (Western Somali Basin) and northern Madagascar commenced by the late Middle Jurassic (Lawver et al., 1992; Wells, 2003). By the Late Jurassic (approximately 160 Ma), a narrow seaway separated the east coast of Africa from Madagascar and the rest of the East Gondwana block. During the Late Jurassic, Indo-Madagascar shifted southward along the Davie Fracture Zone, ultimately coming to rest some 400 km off the east coast of Mozambique in the Early Cretaceous (130–120 Ma).

At about this same time (mid Early Cretaceous), seafloor spreading commenced between the Indo-Madagascar block and Antarctica-Australia (Lawver

et al., 1992). Most workers (e.g., Lawver et al., 1992; Müller et al., 1993; Roeser et al., 1996; Marks & Tikku, 2001; Coffin et al., 2002; Kent et al., 2002; O'Neill et al., 2003) posit that a through-going seaway intervened between Indo-Madagascar and Antarctica-Australia by the mid to late Early Cretaceous (130–110 Ma) and that subsequent spreading between these landmasses proceeded rapidly. Several recent paleogeographic reconstructions, for instance, illustrate a separation between Antarctica and Indo-Madagascar of approximately 950–1100 km (employing 111 km/degree of latitude conversion) by 96 Ma and 1700–1850 km by 83 Ma (Rotstein et al., 2001: fig. 9; Bernard et al., 2005: figs. 4, 5; Schettino & Scotese, 2005: figs. 4, 33). In part to reconcile the developing record of vertebrate fossils, Hay et al. (1999) boldly proposed an "alternative global Cretaceous paleogeography" in which intermittent land connections persisted between Indo-Madagascar and Antarctica, across the Kerguelen Plateau, well into the Late Cretaceous (perhaps as late as 80 Ma). Case (2002) also proposed a persistent land bridge, although farther west, across the Gunnerus Ridge and Kainan Maru Seamount.

Finally, in the mid Late Cretaceous, another major rifting event linked to the Marion hotspot led to the separation of Madagascar and India. This episode of seafloor spreading was accompanied by an outpouring of flood basalts on both landmasses. Dates from these basalts cluster in age from approximately 91 to 84 Ma (Storey et al., 1995, 1997; Torsvik et al., 1998, 2001). With this final episode of Late Cretaceous rifting, the Indian subcontinent moved rapidly northeastward toward Eurasia (Randrianasolo et al., 1981; Storetvedt et al., 1992; Storey et al., 1995, 1997), and Madagascar, situated several hundred kilometers from mainland Africa across the Mozambique Channel, has remained isolated in the Indian Ocean ever since.

Rifting in "West Gondwana" between South America and Africa commenced in the Early Cretaceous, and by approximately 120 Ma an arm of the South Atlantic extended well northward between the two landmasses (Lawver et al., 1992; Müller et al., 1993; Smith et al., 1994; Scotese, 1998; Hay et al., 1999). Geophysical data indicate that a through-going seaway intervened between South America and Africa by the beginning of the Late Cretaceous (Nürnberg & Müller, 1991; Lawver et al., 1992; Müller et al., 1993; Pletsch et al., 2001), and normal marine communications, as evidenced by the distribution of Cretaceous echinoids and fishes (Maisey, 2000; Néraudeau & Mathey, 2000), were apparently established between the Western Tethys and the Southern Ocean domain by approximately 100 Ma. The Antarctic Peninsula and South Orkney group remained contiguous with the

southern tip of South America throughout the Late Cretaceous and well into the Tertiary (Lawver et al., 1992; Woodburne & Case, 1996; Hay et al., 1999; Reguero et al., 2002; Lawver & Cahagan, 2003).

There remains strong indication that Africa was the first major landmass to become isolated by circumcontinental seaways during the breakup of Gondwana, with both geophysical and biogeographic data suggestive of isolation before the end of the Early Cretaceous (approximately 100 Ma). Whether or not Indo-Madagascar maintained intermittent connections with Antarctica via the Kerguelan Plateau (Hay et al., 1999) and/or the Gunnerus Ridge (Case, 2002) into the later stages of the Late Cretaceous remains debatable. Faunal data described in this report are, however, consistent with a scenario of faunal interchange among "East Gondwana" landmasses (Madagascar-Indian subcontinent-Antarctica) and South America until late in the Late Cretaceous (see below).

GONDWANAN FRAGMENTATION AND LATE CRETACEOUS BIOGEOGRAPHY

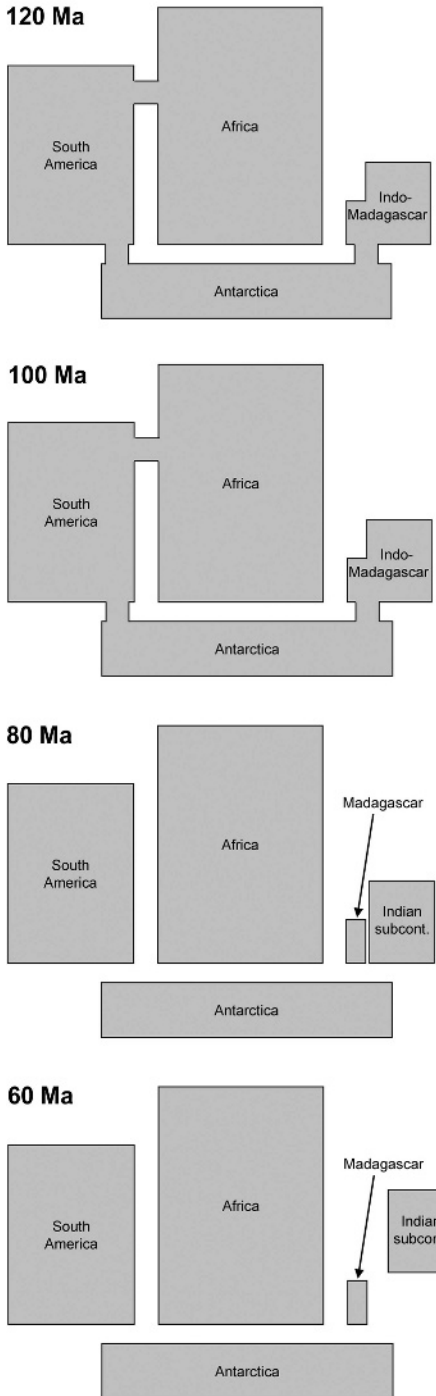
Fragmentation of the Gondwanan supercontinent and dispersion of its constituent landmasses during the latter half of the Mesozoic Era undoubtedly had profound effects on resident faunas of terrestrial vertebrates and their subsequent evolutionary histories. Combining geophysical and stratigraphic data for Gondwanan breakup with observations of faunal distributions provides an unprecedented opportunity to reveal large-scale biogeographic patterns. However, invoking *ceteris paribus*, there is no reason to assume that geologic data, by their very nature, hold priority over paleontologic data or vice versa—yet all things are rarely equal. Unfortunately, for the Cretaceous of Gondwana, seldom are both the geologic and paleontologic data sufficient for specified temporal slices and geographic areas. For some times and places, the geologic data supporting paleogeographic reconstructions are sound, plentiful, and derived from independent sources, and resulting interpretations have been made with confidence. For other times and places, the fossils are numerous, well preserved, and have been incorporated into rigorous phylogenetic frameworks. In this regard, the developing Cretaceous record of terrestrial vertebrates from Gondwanan landmasses is beginning to provide an opportunity to further clarify the timing and sequence of Gondwanan fragmentation.

Tables 4–12 reveal a number of notable patterns in the distribution of Cretaceous Gondwanan terrestrial vertebrates. The same family-level taxa of crocodyli-forms, non-avian dinosaurs, and mammals that were shared among Madagascar, the Indian subcontinent,

and South America during Campanian/Maastrichtian times are not known from pencontemporaneous horizons in mainland Africa or, for that matter, Antarctica. Nonetheless, despite the intensity of recent exploration and collecting, the fossil record is not fully up to the task of testing whether or not this pattern is real, a point made repeatedly by our working group and others (e.g., Krause et al., 1997b, 1999; Forster, 1999; Rogers et al., 2000; Carrano et al., 2002; Lamanna et al., 2002; Krause, 2003b; O'Connor et al., 2006). The geologic stages of the Cretaceous for which the records of terrestrial fossil vertebrates from Madagascar, the Indian subcontinent, and South America are reasonably well sampled are, for the most part, the very stages for which the African record is poor, and vice versa. As emphasized by Krause et al. (1999: 6), "one of the key stumbling blocks ... is the virtual lack of terrestrial and freshwater vertebrates from the post-Cenomanian Late Cretaceous of Africa." The fossil record of terrestrial vertebrates from mainland Africa is much better for the Early Cretaceous and pre-Campanian Late Cretaceous than it is for the later stages of the Late Cretaceous, whereas the reverse is true for the other three landmasses, particularly Madagascar and the Indian subcontinent. To further complicate matters, the record of terrestrial vertebrate fossils from the Cretaceous of Antarctica remains all but nonexistent.

This uneven temporal sampling has inhibited, and still inhibits, definitive testing of two competing biogeographic hypotheses (Fig. 8). The first, recently formulated and labeled the "pan-Gondwana" hypothesis by Sereno et al. (2004), stipulates that various clades of terrestrial vertebrates were broadly distributed throughout Gondwana during the Early Cretaceous and that the much more limited distributions in the post-Cenomanian Late Cretaceous (including in Africa) are the result of poor sampling and/or differential extinction. A corollary of this hypothesis states that land connections between (1) Africa and South America, (2) South America and Antarctica, and (3) Antarctica and Indo-Madagascar were all severed "during a relatively brief interval at the beginning of the Late Cretaceous (ca. 100–90 Myr ago)" (Sereno et al., 2004: 1328). Implicit in this hypothesis, therefore, is the prediction that terrestrial vertebrate faunas on each of these major landmasses would become increasingly endemic during the Late Cretaceous, beginning at approximately 90 Ma. The second hypothesis, formulated by our working group (e.g., Krause et al., 1997b, 1999; Sampson et al., 1998, 2001) and recently dubbed the "Africa-first" hypothesis by Sereno et al. (2004), posits cosmopolitanism of Late Cretaceous terrestrial Gondwanan

PAN-GONDWANA HYPOTHESIS



AFRICA-FIRST HYPOTHESIS

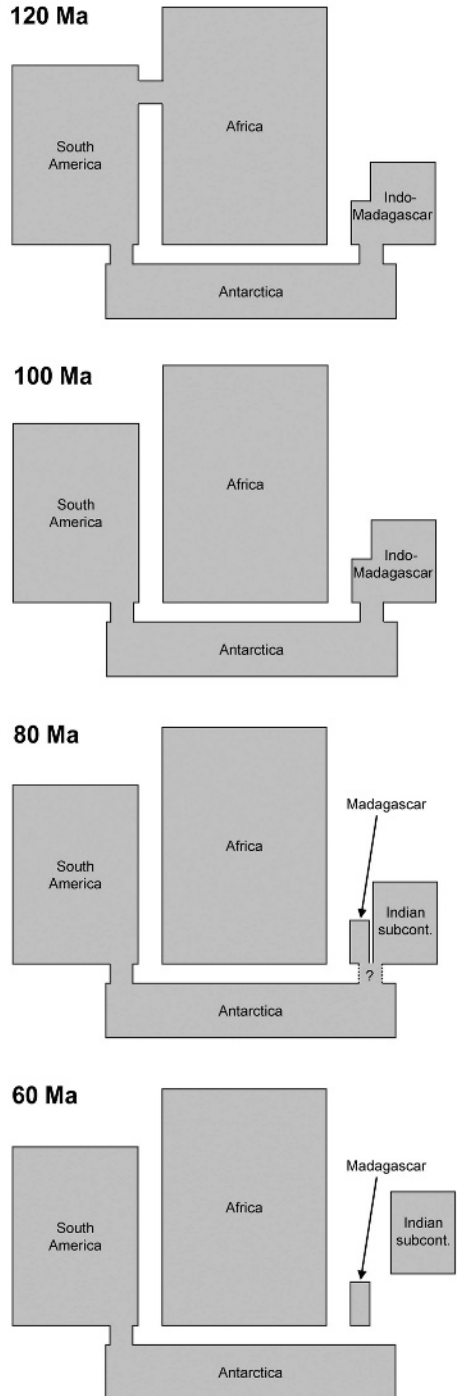


Figure 8. Schematic paleogeographic maps of major Gondwanan landmasses exclusive of Australia and southern Europe at 120, 100, 80, and 60 Ma depicting the major differences in purported land connections between the pan-Gondwana hypothesis (left column) and the Africa-first hypothesis (right column). 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 Ma. The Africa-first hypothesis posits separation of South America from Africa before the beginning of the Late Cretaceous, South America from Antarctica in the Eocene, and Antarctica from Indo-Madagascar late in the Late Cretaceous.

faunas exclusive of Africa. More specifically, the latter model, generally consistent with the paleogeographic reconstruction of Hay et al. (1999), invoked Antarctica (in combination with two key land bridges) as a dispersal route between Indo-Madagascar (the Indian subcontinent plus Madagascar) and South America following isolation of Africa by a circum-African seaway prior to the beginning of the Late Cretaceous. According to this model, terrestrial vertebrate faunas on Africa are predicted to have become progressively more provincial during the Late Cretaceous (after separation between South America and Africa prior to the end of the Early Cretaceous), while those on other Gondwanan landmasses remained relatively cosmopolitan until considerably later in the period.

Sereno et al. (2004; see also Mahler, 2005) recently reported the important discovery of a number of definitive abelisauroid theropods (abelisaurids and noasaurids) in Aptian-Albian strata of Niger (approximately 110 Ma) and Cenomanian deposits of both Niger and Morocco (approximately 95 Ma), thus providing the first conclusive evidence for the presence of this clade in Africa. These finds support the pre-Late Cretaceous origin of Abelisauroida on Gondwana, as previously indicated by several earlier discoveries in Argentina (Coria & Salgado, 1998; Lamanna et al., 2002; Rauhut et al., 2003). Thus, one alternative hypothesis of Sampson et al. (1998: 1050)—that “abelisaurids originated sometime in the Early Cretaceous after the tectonic isolation of Africa”—is clearly refuted. Based primarily on the new African abelisauroids, Sereno et al. (2004) concluded that the evidence therefore supports the pan-Gondwana hypothesis. We disagree with the latter contention, and regard the Africa-first hypothesis to be more consistent with the available, although admittedly limited, evidence (see below).

Before assessing this issue, it is necessary to address several statements by Sereno et al. (2004). First, these authors claimed that the original formulation of the Africa-first hypothesis by Sampson et al. (1998) included the stipulation that Africa and South America were fully separated by 140–120 Ma. Specifically, Sereno et al. (2004: 1328) stated that the Africa-first model, as portrayed by Sampson et al. (1998), “shows a circum-African seaway in the Early Cretaceous (ca. 140–120 Myr ago) that isolated the continent from other Gondwanan landmasses.” Whereas Sampson et al. (1998: 1050) did state that “South America separated from Africa before 100 Ma” and, in the caption for Figure 4, specified “circa 120 Ma,” claims for separation as early as 140 Ma were not made in that paper, or in any other paper published by our working group. Indeed, all of

the paleogeographic reconstructions presented by us consistently show Africa and South America still joined at 120 Ma (Krause et al., 1997b: fig. 1, 1999: fig. 6; Sampson et al., 1998: fig. 4; Krause, 2003a: fig. 2.17; we specifically did not use the 120 million year reconstruction in Hay et al. (1999: figs. 12, 15), which illustrates full separation between South America and Africa at this time, but instead employed a reconstruction generated from the website operated by the Hay et al. working group (<<http://www.odsn.de/odsn/services/paleomap/paleomap.html>>), which shows these landmasses still connected by a narrow sub-aerial passage at 120 Ma). In any case, the portrayal by Sereno et al. (2004) of our Africa-first hypothesis as requiring isolation of Africa as early as 140 Ma is incorrect.

Second, Sereno et al. (2004: 1328–1329) concluded that “a permanent equatorial seaway of significant depth between South America and Africa was in place no earlier than the end of the Albian,” and that “trans-Atlantic interchange may have been operative as late as 95 Myr ago.” Elsewhere in the same paper, Sereno et al. (2004: 1328) stated that “well-constrained geological evidence (Reyment & Dingle, 1987; Pitman et al., 1993; Maisey, 2000) pinpoints the final separation of South America and Africa in the latest Albian (ca. 100 Myr ago), significantly later than proposed by the “Africa-first” model (ca. 140–120 Myr ago).” To clarify, the three papers cited by Sereno et al. do not make such definitive assessments. Reyment and Dingle (1987: 99) stated that “final continental separation was *probably* completed in Late [not latest] Albian time” (emphasis and bracketed words added), Pitman et al. (1993: 23) stated that “the point in time of final separation must be between 84 Ma . . . and 106 Ma,” and Maisey (2000: 285) concluded that a permanent equatorial seaway joining the South Atlantic and the western Tethys Ocean had developed by the late Aptian (which ends at approximately 112 Ma; Gradstein et al., 2004). That said, it should be pointed out that there is other well-constrained geological evidence (Nürnberg & Müller, 1991; Pletsch et al., 2001) for a permanent marine connection between the central and southern parts of the Atlantic Ocean, separating South America from Africa by the late Aptian-early Albian, approximately 118–106 Ma (Gradstein et al., 2004). Again, we have never argued for separation of Africa and South America as early as 140 Ma, but it must be noted that current geophysical and paleogeographic evidence is suggestive of separation before the end of the Albian. As such, the primary distinction concerning this point is that Sereno’s formulation of the pan-Gondwana hypothesis views separation between South America and Africa as having occurred *after* the end of the

Early Cretaceous, whereas the Africa-first hypothesis supports separation *before* the end of the Early Cretaceous.

Third, Sereno et al. (2004: 1328) made the claim that “other faunal evidence (notosuchian crocodylomorphs (Buckley et al., 2000) and gondwanatherian mammals (Sampson et al., 1998)) no longer supports the “Africa-first” model.” While we agree that this evidence is far from strong or highly resolved, Sereno et al.’s conclusion simply does not follow from their explanatory statement that “African crocodylomorphs of mid-Cretaceous age (Aptian-Albian) are most closely related to taxa of comparable age on South America (Buffetaut & Taquet 1977, 1979; Sereno et al., 2003), and the absence of gondwanatheres reflects only the non-existent record of mammals on Africa during most of the Cretaceous.” Close relationships among African and South American crocodylomorphs of Aptian-Albian age, which we do not dispute, cannot serve as evidence for no longer supporting the hypothesis that Africa was the first major Gondwanan landmass to become isolated. Furthermore, the recent cladistic biogeographic analysis by Turner (2004b), reviewed above, demonstrated that crocodyliform evidence is indeed consistent with the Africa-first hypothesis. Finally, the presence of sudamericid gondwanatheres in the Campanian/Maastrichtian of South America, Madagascar, and India was primarily used to support the hypothesis that this enigmatic clade of mammals was much more cosmopolitan in its distribution in the latest Cretaceous than previously realized (Krause et al., 1997b). The absence of sudamericid gondwanatheres from the Cretaceous of mainland Africa (which, in fact, may not be the case—see Krause et al., 2003b) is no less supportive of an Africa-first hypothesis than it was when the paper by Krause et al. (1997b) was published.

In light of the discussion above, let us reexamine the current evidence and assess the claims and implications of the competing biogeographic hypotheses by focusing on established geologic and biologic constraints. First, the pan-Gondwana hypothesis, as defined by Sereno et al. (2004), posits the existence of three narrow, intermittent land bridges, all severed in the early Late Cretaceous, approximately 100–90 Ma: one between Africa and South America, another between South America and Antarctica, and a third between Antarctica and Indo-Madagascar. Geologic evidence in support of this model was based on the paleocoastline maps of Scotese (2001). In contrast, a revised Africa-first model, incorporating recent data on African abelisauroids from the Albian and Cenomanian, postulates the separation of South America and Africa prior to the Early/Late Cretaceous

boundary, but the persistence of land bridges that permitted faunal exchange through Antarctica between South America to the west and Indo-Madagascar to the east until well into the Late Cretaceous. According to this view, early stocks of abelisaurids (and other vertebrates) were present on at least South America and Africa (and perhaps other Gondwanan landmasses) by the late Early Cretaceous. Rifting of South America and Africa toward the end of the Early Cretaceous isolated at least two stocks of abelisaurids, one on each continent. Currently, there is no reason to assume that they had spread into Gondwanan landmasses outside of Africa and South America at that early stage, although this scenario is not inconsistent with available evidence. Similarly, in the absence of fossil evidence, we cannot yet know what happened to the isolated stock of abelisaurids on Africa during the Late Cretaceous. However, on the rest of Gondwana, a basal stock of Cenomanian abelisaurids (of which there is evidence in Argentina; Lamanna et al., 2002) diversified into closely related forms observed later in the Cretaceous in Argentina, Madagascar, and the Indian subcontinent. Lacking fossil evidence, this hypothesis does not stipulate when during the Late Cretaceous those basal stocks (or their descendants) first arrived on Madagascar and the Indian subcontinent; that is, they may have been present at the time South America and Africa separated or they may have dispersed much later from South America. However, this view is consistent with *all* phylogenetic evidence presented to date (Sampson et al., 1998; Carrano et al., 2002; Coria et al., 2002; Wilson et al., 2003; Sereno et al., 2004) and posits that the derived abelisaurids (including several horned forms) present in the Maastrichtian of India and Madagascar on the one hand, and the Campanian-Maastrichtian of South America on the other, shared a more recent common ancestor than either did with abelisaurids from Africa.

Concerning paleogeographic reconstructions, none, including Scotese (2001), depicted a situation in which all three land bridges were severed at approximately the same time in the early Late Cretaceous, approximately 100–90 Ma. As reviewed above, current evidence suggests that the South America/Africa land bridge ceased to exist prior to the Albian/Cenomanian boundary (i.e., prior to 100 Ma). Indeed, even Scotese (2001) depicted the two continents to be already well separated by 94 Ma (Schettino & Scotese (2000) show separation at 100 Ma). Current geologic evidence is most consistent with the separation of Africa and South America (and thus the isolation of Africa) by 100 Ma (Lawver et al., 1992; Smith et al., 1994; Marks & Tikku, 2001; Scotese, 2001; Kent et al., 2002). By contrast, a land

bridge between South America and Antarctica is thought to have been present throughout the Late Cretaceous and until at least the early Eocene (Lawver et al., 1992; Woodburne & Case, 1996; Hay et al., 1999; Reguero et al., 2002; Lawver & Gahagan, 2003); there is no evidence for a termination of connection 100–90 Ma. Finally, as detailed above, the timing of separation of Antarctica from Indo-Madagascar is controversial. Most reconstructions indicate that Indo-Madagascar became isolated from all other Gondwanan landmasses about 120 Ma, some 50 million years prior to the time that the Maevarano vertebrate assemblage (as well as those from India) was deposited (e.g., Lawver et al., 1992; Smith et al., 1994; Marks & Tikku, 2001; Rotstein et al., 2001; Scotese, 2001; Kent et al., 2002; Bernard et al., 2005). Notably, and in stark contrast, however, the tectonic modeling of Hay et al. (1999) provides support for the scenario posited by the Africa-first hypothesis in that a land bridge between Antarctica and Indo-Madagascar was maintained until approximately 80 Ma (cf. Case, 2002). In neither case is there evidence to indicate synchronicity with the separation of South America from either Africa or Antarctica at 100–90 Ma, as postulated by Sereno et al.'s (2004) pan-Gondwana model.

Concerning faunal evidence, the crocodyliforms, nonavian dinosaurs, and mammals recovered from the Maevarano Formation of northwestern Madagascar are taxonomically most similar to those known from Campanian/Maastrichtian horizons of South America and the Indian subcontinent (Krause et al., 1997b; Buckley & Brochu, 1999; Buckley et al., 2000; Krause, 2001; Wilson et al., 2001; Curry Rogers, 2002; Prasad & de Lapparent de Broin, 2002; Turner, 2004b). Because strength of biogeographic signal is proportional to the number of phylogenetically independent groups possessing the same congruent pattern of area cladograms, it is significant to note that the patterns of similarity are repeated among a growing number of phylogenetically independent groups (e.g., notosuchids, peirosaurids, trematochampsids, and the unclassified metasuchian genus *Araripesuchus* among crocodyliforms; abelisaurids, noasaurids, and saltasaurines among nonavian dinosaurs; and sudamericids among mammals). This provides evidence for a high degree of cosmopolitanism among latest Cretaceous Gondwanan faunas outside of Africa that was not fully appreciated prior to recovery of the Maevarano assemblage and is unpredicted based on most recent paleogeographic reconstructions of the southern supercontinent (e.g., Lawver et al., 1992; Smith et al., 1994; Scotese, 1998, 2001; Marks & Tikku, 2001; Rotstein et al., 2001; Kent et al., 2002; Bernard et al., 2005; Schettino & Scotese, 2005) or

the pan-Gondwanan hypothesis of Sereno et al. (2004).

Finally, the mere presence of abelisaurids and noasaurids on Africa 25 or more million years prior to their occurrence in Madagascar and India does not constitute evidence refuting the Africa-first hypothesis. Although recent discoveries demonstrate the presence of abelisauroids in the Early Cretaceous and earliest Late Cretaceous of mainland Africa, certainly an interesting and significant finding, phylogenetic analysis does not include placement of the recovered forms among the more derived members of this clade (Sereno et al., 2004). Indeed, the abelisaurid *Rugops* is postulated by Sereno et al. (2004) as the basalmost member of the group. Thus, although it appears that Africa did not separate from South America until near the Early/Late Cretaceous boundary, the closest relatives of *Majungatholus* and *Masiakasaurus* from the Maastrichtian of Madagascar are still found in Campanian/Maastrichtian horizons of South America and India. As such, there exists no faunal evidence to refute the hypothesis that Africa was the first among major Gondwanan landmasses to be fully isolated and, perhaps most importantly, that the terrestrial vertebrates of Gondwanan faunas outside of Africa were shared until late in the Late Cretaceous.

In summary, we regard the growing weight of latest Cretaceous biogeographic data as evidence in support of a modified Africa-first hypothesis. The close relationships of terrestrial vertebrates that lived on the Indian subcontinent and Madagascar near the end of the Cretaceous to penecontemporaneous taxa in South America appear incompatible with any proposed lengthy separation of Indo-Madagascar and South America prior to the Maastrichtian, whether that duration was approximately 50 million years, as indicated by most recent paleogeographic reconstructions of Cretaceous Gondwana, or approximately 25 million years, as posited by the pan-Gondwana hypothesis.

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