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The Late Cretaceous Vertebrate Fauna of Madagascar: Implications for Gondwanan Paleobiogeography

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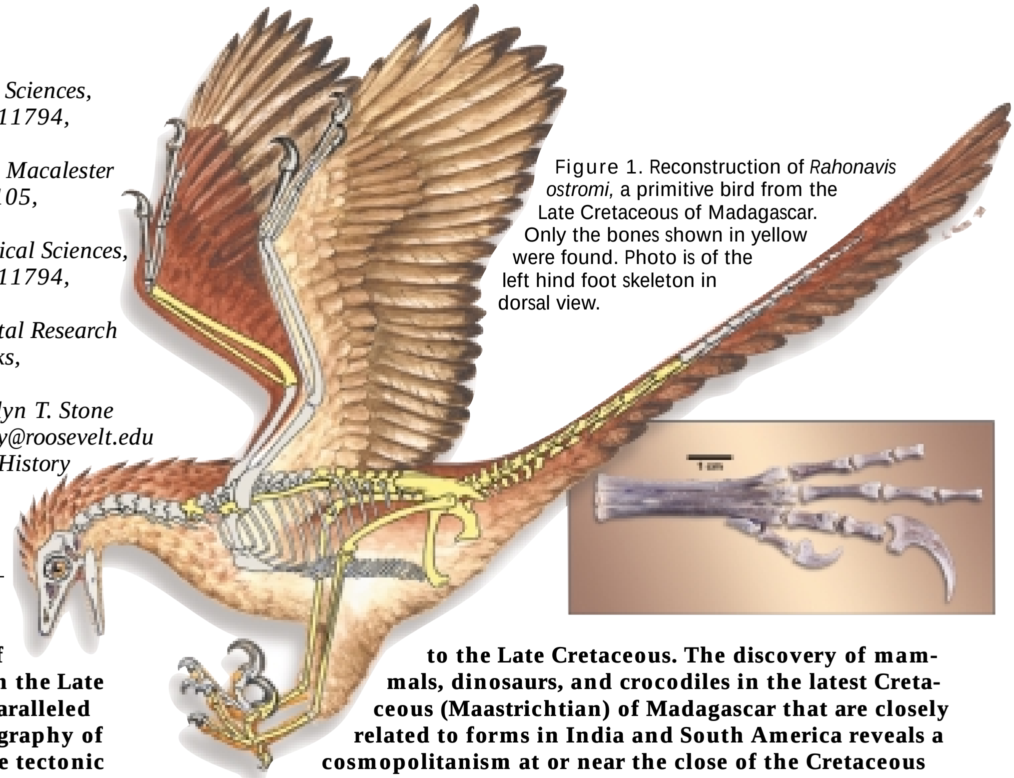

Figure 1. Reconstruction of *Rahonavis ostromi*, a primitive bird from the Late Cretaceous of Madagascar. Only the bones shown in yellow were found. Photo is of the left hind foot skeleton in dorsal view.

ABSTRACT

A rich, newly discovered assemblage of exquisitely preserved vertebrate fossils from the Late Cretaceous of Madagascar provides an unparalleled opportunity to investigate the paleobiogeography of Gondwanan landmasses. Most current plate tectonic models depict widespread fragmentation of Gondwana prior to the Late Cretaceous. The discovery of mammals, dinosaurs, and crocodiles in the latest Cretaceous (Maastrichtian) of Madagascar that are closely related to forms in India and South America reveals a cosmopolitanism at or near the close of the Cretaceous that is paradoxical in the context of these models.

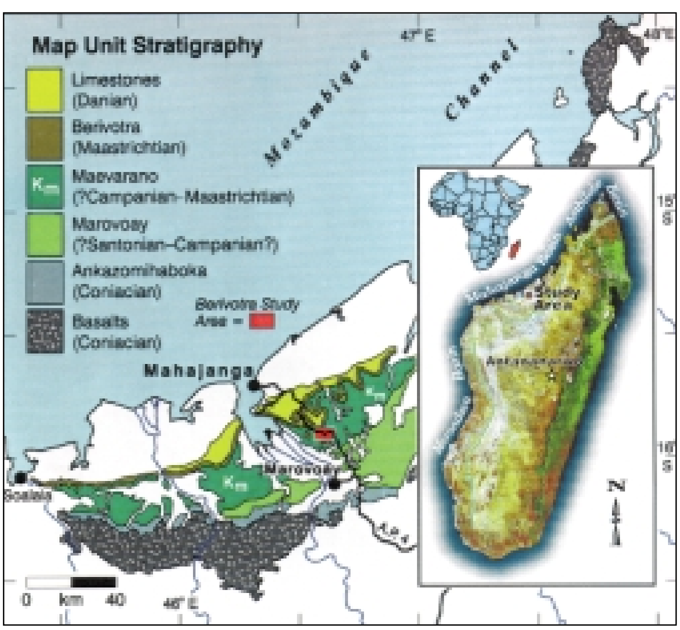

Figure 2. Upper Cretaceous stratigraphy of the Mahajanga Basin. Inset: base map of Madagascar from Satellite Atlas of the World, 1998, National Geographic Society, Washington, D.C., 222 p.

INTRODUCTION

The southern supercontinent of Gondwana fragmented into isolated landmasses during the Late Jurassic and Cretaceous, with dramatic consequences for the associated terrestrial and freshwater vertebrate faunas. Reconstructions of the timing and sequence of this fragmentation are based almost entirely on geophysical evidence and remain poorly tested paleontologically, primarily due to a sparse fossil record. The Mahajanga Basin Project, initiated in 1993 and conducted jointly by the State University of New York at Stony Brook and the University of Antananarivo (Madagascar), has recovered a diverse assemblage of vertebrates, including the primitive bird *Rahonavis ostromi* (Fig. 1), from the Upper Cretaceous Maevarano Formation, Mahajanga Basin, northwestern Madagascar (Fig. 2). This assemblage is one of the richest and best preserved yet known from the Mesozoic of Gondwana. It provides a new opportunity to elucidate distribution patterns among Cretaceous vertebrates from Gondwana and, thereby, to test competing plate tectonic and biogeographic hypotheses.

MALAGASY VERTEBRATE FOSSIL RECORD

The Malagasy record of terrestrial and freshwater vertebrates prior to the Late Cretaceous is sparse but improving, consisting of a diversity of primitive fishes, amphibians (including the frog-like

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IN THIS ISSUE

In Memoriam

Louis C. Conant
Cupertino, California
June 2, 1999

Francis J. Pettijohn
Glen Arm, Maryland
April 23, 1999

Please contact the GSA Foundation for information on contributing to the Memorial Fund.

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Triadobatrachus), and reptiles, as well as spotty occurrences of dinosaurs, therapsids, and crocodiles (Fig. 3; Flynn et al., 1998; Krause, 1999). Depéret (1896) was the first to record Late Cretaceous vertebrates from the island. He described isolated turtle remains and, on the basis of fragmentary bones and teeth, named two dinosaur species from the Maevarano Formation—the meat-eating theropod *Megalosaurus crenatissimus* and the plant-eating sauropod *Titanosaurus madagascariensis.* Intermittent collecting over the course of nearly a century in the same field area by expeditions from France, Madagascar, and Japan yielded additional fragmentary specimens of turtles and dinosaurs, as well as isolated elements of a fish, a snake, two crocodiles, and a purported lizard (see summary in Krause et al., 1997a).

There are no undisputed records of Cenozoic terrestrial and freshwater vertebrates from Madagascar prior to the late Pleistocene, primarily owing to the overwhelming predominance of marine rocks during the era (Krause et al., 1997a). As a result, the biogeographic origins of the highly endemic and imbalanced extant fauna, perhaps best represented by lemurs, remains shrouded in mystery. The late Pleistocene and Holocene record only increases the level of endemism, as it includes several giant lemurs, pygmy hippopotami, the aardvark-like *Plesiorycteropus*, and several other taxa unique to the island.

MAHAJANGA BASIN PROJECT

The Mahajanga Basin Project has focused on the same small set of Maevarano Formation badlands around the village of Berivotra that served as the setting for prior paleontological field efforts. The primary objectives of our four expeditions (1993, 1995, 1996, 1998) have been to discover terrestrial and freshwater vertebrate fossils and to place them in a sound phylogenetic, stratigraphic, paleoenvironmental, taphonomic, and paleobiogeographic context.

Maevarano Formation

The Maevarano Formation is well exposed in the Berivotra region, where

J. John Sepkoski 1948–1999

Paleontologist J. John (Jack) Sepkoski Jr., University of Chicago, died May 1, 1999, of heart failure. He was 50.

Sepkoski's research and activity in paleontology played a major role in reshaping the discipline during the past 25 years. His major contributions included documenting and analyzing large-scale patterns of origination and extinction, major changes in the diversity of life over time, and the environmental and ecological context of biotic diversification. He had taught at the University of Chicago since 1978. He was a member of the Geological Society of America.

Sepkoski served as president of the Paleontological Society, co-editor and associate editor of *Paleobiology,* and associate editor of *Acta Palaeontologica Polonica.* He founded the Paleontological Society International Research Program (PalSIRP), to assist paleontologists in Eastern Europe and in the former Soviet Union. Donations in his honor may be made to PalSIRP, c/o Thomas W. Kammer, Treasurer, Paleontological Society, Dept. of Geology and Geography, West Virginia University, P.O. Box 6300, Morgantown, WV 26506-6300.

ENVIRONMENT MATTERS

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At recent workshops, students openly expressed their gratitude to mentors for spending time and energy to share career information. One young woman was so impressed by what she gained that she talked about how she might be a mentor to younger undergraduate women. Please consider this not only an opportunity to discuss your job highlights and challenges, but also an opportunity to truly be a valuable role model and mentor in the budding career of a future geoscientist. For more information, please contact Stacey Ginsburg at 303-447-2020, ext. 194 or sginsburg@geosociety.org. ■

~100 m of the unit is accessible in surface exposures (Fig. 2). The formation is entirely nonmarine and consists of strata that accumulated on a semiarid, low-relief alluvial plain that was bounded to the southeast by crystalline highlands and to the northwest by the Mozambique Channel. The predominant lithology is coarse-grained, poorly sorted sandstone, which ranges from pervasively cross-stratified to massive. Massive beds tend to show conspicuous evidence of pedogenesis, including well-preserved root traces and caliche. A distinctive 15–20-m–thick interval of extremely fossiliferous sandstone facies caps the formation in the vicinity of Berivotra. Virtually all of the vertebrate fossils known from the Maevarano Formation have been recovered from these upper beds, which accumulated in a shallow channel-belt system.

The nonmarine Maevarano Formation and the marine Berivotra Formation were previously considered to be stacked in layer-cake fashion, the Campanian-Maastrichtian boundary being at their contact (e.g., Besairie, 1972). This interpretation, and similar interpretations of lower rock units, oversimplified the geological history of the Mahajanga Basin and hindered accurate comparisons between Madagascar's record of Late Cretaceous vertebrates and those from other Gondwanan localities. Our work reveals instead that the Maastrichtian marine transgression that led to deposition of the Berivotra Formation was demonstrably diachronous, and that the Maevarano Formation accumulated, at least in part, during this same transgressive event (Rogers and Hartman, 1998). Vertebrate-bearing facies of the upper Maevarano Formation are accordingly reinterpreted as Maastrichtian, and perhaps late Maastrichtian.

Vertebrate Assemblage

We have now established the presence of at least 32 species of terrestrial and freshwater vertebrates in the Maevarano Formation, thus quadrupling the previously known species diversity from the Late Cretaceous of Madagascar. These efforts have provided the first pre–late Pleistocene records of Malagasy frogs, birds, and mammals, and the first records of several groups of vertebrates, fossil or extant, from the island (Krause et al., 1994; Forster et al., 1996; Asher and Krause, 1998; Gottfried and Krause, 1998; Gottfried et al., 1998). Despite varied collecting methods and intensive effort, the purported presence of lizards (Russell et al., 1976) has not been confirmed and is suspect.

Fishes, frogs, turtles, and snakes are now represented in some considerable diversity in the Maevarano assemblage, but their diversity pales in comparison to that of crocodiles, which are represented by as many as seven different species. The crocodiles range in size from the small and gracile *Araripesuchus* to the large and ponderous *Mahajangasuchus* (Fig. 4; Buckley and Brochu, 1999). The 1998 field campaign resulted in the discovery of a bizarre new pug-nosed form with mitten-shaped teeth.

Two species of sauropod dinosaurs have been discovered, both of which belong to the enigmatic Titanosauridae. Each is represented by skeletal material that is among the most complete known

Madagascar *continued on p. 4*

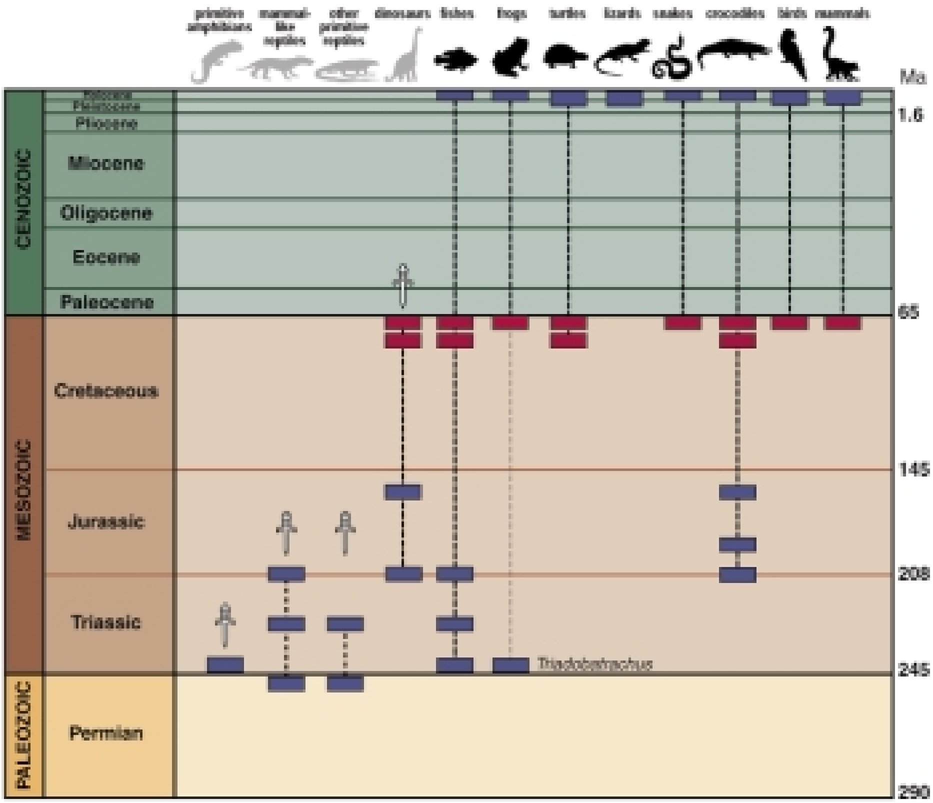

Figure 3. Temporal distribution of the terrestrial and freshwater vertebrates of Madagascar. Late Cretaceous occurrences are from the Maevarano Formation (upper red rectangles) and the Ankazomihaboka beds (lower red rectangles).

Madagascar *continued from p. 3*

for titanosaurids. Perhaps the most spectacular fossil discovery of the Mahajanga Basin Project to date is an exquisitely preserved and virtually complete skull of the mid-sized theropod dinosaur *Majungatholus atopus,* the name now assigned to Depéret's *Megalosaurus crenatissimus* (Fig. 5; Sampson et al., 1998). The skull is complemented by a second specimen consisting of a nearly complete axial skeleton of a juvenile individual. At least one other smaller and as yet unidentified theropod is present in the Maevarano Formation. No ornithischian dinosaurs are represented in the fauna.

Birds are represented by at least five taxa (Forster et al., 1996, 1998). The most significant specimen is a partial skeleton of *Rahonavis ostromi* (Fig. 1), a close relative of the Late Jurassic *Archaeopteryx. Rahonavis* provides strong confirmatory evidence for the dinosaurian origin of birds in that its hind foot bore a robust, hyperextendable killing claw on the second digit, just as in its theropod predecessors. Multiple, independent analyses of fibrous material adhering to the claw of the second digit has revealed that it is keratin from the claw sheath (Schweitzer et al., 1999). This represents by far the oldest documented record of keratin.

Mammals are represented by four species: two possible therians, a multituberculate, and a new species of sudamericid gondwanathere (Krause et al., 1994, 1997b; Krause and Grine, 1996).

MADAGASCAR PLATE TECTONICS AND BIOGEOGRAPHY

Plate Tectonic Models

There is now general consensus that, prior to rifting, Madagascar lay adjacent to present-day Somalia, Kenya, and Tanzania (see Coffin and Rabinowitz, 1992; Storey, 1995). Sea-floor spreading between the conjugate rifted margins of east Africa and northern Madagascar began in the Late Jurassic. Madagascar moved south-southeastward along the transform fault known as the Davie Fracture Zone until reaching its current position some 400 km off the east coast of Mozambique in the Early Cretaceous (130–125 Ma). Madagascar remained in contact with the Indian subcontinent (through the intervening Seychelles island group) until approximately 88 Ma, at which time the Indian subcontinent and Seychelles block separated from Madagascar and began moving rapidly northeastward toward Eurasia (Storey et al., 1995; Plummer, 1996).

The timing of separation between the Indian subcontinent and Antarctica-Australia, and thus intervening physical connections between Madagascar and South America, is more controversial (Fig. 6). Traditional geophysical interpretations posit a plate reorganization event at about 135–120 Ma that resulted in cessation of movement between Africa and Madagascar-India-Antarctica-Australia and the initiation of separation between India-Madagascar and Antarctica-Australia. Roeser et al. (1996, p. 262), for instance, found evidence for a seaway "along most if not all of the coast of East Antarctica" shortly after chron M0 (124 Ma). Lawver et al. (1992, p. 18) stated that by 110 Ma, "Madagascar, India, and the southern Kerguelen Plateau had cleared Antarctica, and a wide, open seaway existed along that part of the present-day East Antarctic margin." Hay et al. (1999), however, have hypothesized a much longer-lived connection between the Indian subcontinent and Antarctica-Australia across the Kerguelen Plateau, perhaps as late as 80 Ma. The discrepancy in interpretation has crucial implications concerning the biogeographic history of Late Cretaceous terrestrial and freshwater Gondwanan vertebrates (Krause et al., 1997a, 1997b; Sampson et al., 1998).

Biogeographic Scenarios

Madagascar is of unusually high paleobiogeographic interest and intrigue because: (1) it occupies a somewhat central geographic position within Gondwana and was among the first, and last, landmasses to be involved in fragmentation of the supercontinent; (2) it has been isolated from all other Gondwanan landmasses for more than 85 m.y.; (3) it has a highly endemic and imbalanced modern biota;

Figure 4. Postcranial skeleton and lower jaws of the broad-mouthed metasuchian crocodile *Mahajangasuchus insignis* in dorsal view.

and (4) its fossil record of terrestrial and freshwater vertebrates is spotty at best (Fig. 3).

Late Cretaceous vertebrate fossils from Madagascar historically have been most frequently compared to those from the Indian subcontinent, Africa, and South America. The sauropod *Titanosaurus madagascariensis*, for instance, was transferred to the South American genus *Laplatasaurus* and also identified in the Late Cretaceous of India. The theropod *Majungasaurus crenatissimus* (now *Majungatholus atopus*) was identified in the Late Cretaceous of both Egypt and India, and a fragmentary dentary from the Early Cretaceous (Albian?) of Morocco was identified as that of cf. *Majungasaurus* sp. Similar patterns have been noted for non-dinosaurian vertebrates (e.g., crocodiles, snakes) as well.

Many of these identifications, based on fragmentary, isolated specimens, are suspect, and were made before the paradigm of plate tectonics held sway. The reigning stabilist paradigm prompted workers in the late 19th and early 20th centuries to invoke ephemeral land bridges between South America and Africa, Africa and Madagascar, and Madagascar and the Indian subcontinent to explain these distributions (e.g., Blanford, 1890). Alternatively, Huene and Matley (1933), who viewed *Laplatasaurus madagascariensis* as showing affinities between India and South America, speculated upon a polar route including Antarctica.

Even later, under a mobilist paradigm, land bridge scenarios were used to explain such distributions, but not without disagreement. While Dietz and Holden (1970) maintained that the Indian subcontinent was an isolated landmass in the Indian Ocean for the entire Jurassic and Cretaceous, Smith and Hallam (1970, p. 960), on the basis of fossil marine invertebrates, envisioned a terrestrial connection between Africa, Madagascar, and the Indian subcontinent until "at least the close of the Cretaceous." Similarly, Colbert (1973, 1984), Sues (1980), Taquet (1982), Briggs (1989), Russell (1993), and others postulated land bridges that allowed dispersal of Cretaceous dinosaurs from Madagascar and/or India to South America through Africa, rather than through Antarctica as proposed by Huene and Matley (1933). In support of this assessment, Le Loeuff (1991) performed a biogeographic analysis of Late Cretaceous Gondwanan vertebrates, which showed closer affinity of the then poorly known Maevarano Formation vertebrate assemblage (Fig. 2) to that of Africa than to that of any other landmass.

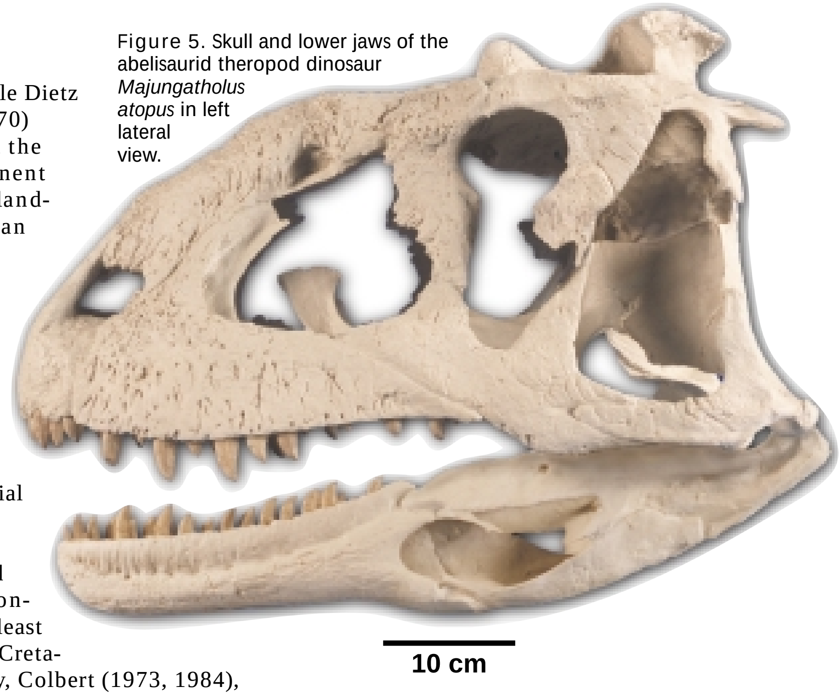

Figure 5. Skull and lower jaws of the abelisaurid theropod dinosaur *Majungatholus atopus* in left lateral view.

With regard to the biogeographic origins of the extant terrestrial and freshwater vertebrate fauna of Madagascar, many workers have speculated that the ancestral stocks were present on the island since the Paleogene, the Late Cretaceous, or even earlier, prior to its rifting from Africa (see review in Krause et al., 1997a). Although it appears that certain taxa (e.g., some birds, bats, and frogs) may be of Indian-Malaysian origin, the consensus is that most taxa arrived by random dispersal (rafting, swimming, and/or island hopping) across the 400 km span of the Mozambique Channel from Africa. McCall (1997, p. 664) recently suggested that "large areas of the Mozambique Channel

Madagascar *continued on p. 6*

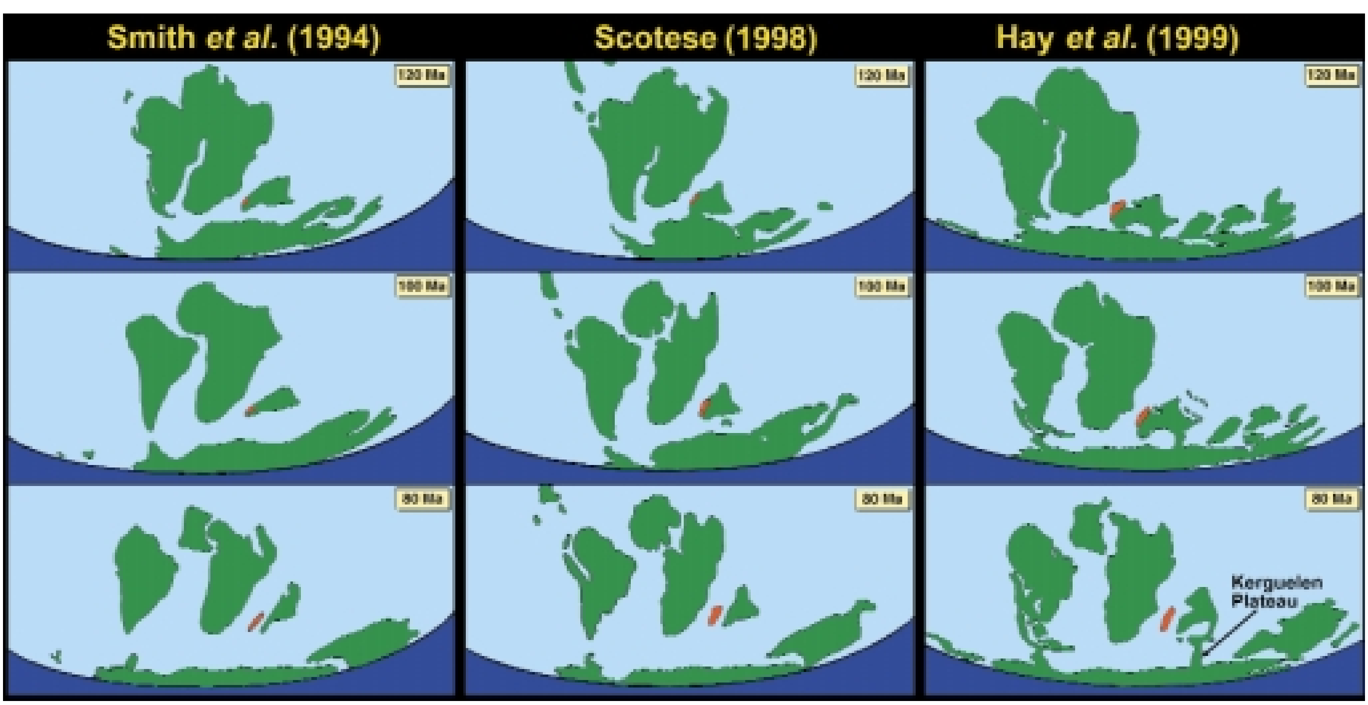

Figure 6. Paleogeographic reconstructions of major Gondwanan landmasses at 120, 100, and 80 Ma modified from authors shown. Land areas in green, except Madagascar, which is indicated in red.

Madagascar *continued from p. 5*

were dry land" during the Paleogene as a result of uplift along the Davie Ridge and that these large areas served as a land bridge for mammalian colonization of Madagascar from Africa. Rage (1996) envisioned a Late Cretaceous land bridge to the east, extending from Madagascar to the Seychelles to the Indian subcontinent to Laurasia, to explain the modern-day presence of iguanid lizards, boine snakes, and perhaps even lemurs on the island.

Biogeographic Significance of the Maevarano Formation Vertebrate Assemblage

The exquisite and relatively complete preservation of skeletal material of Late Cretaceous vertebrates from the Maevarano Formation allows the opportunity to make much better phylogenetic determinations of many taxa that were previously represented only by fragmentary, isolated specimens. This, plus the discovery of several new taxa, has obvious and important consequences for testing paleobiogeographic hypotheses. Two taxa from the Maevarano Formation in particular, gondwanatherian mammals and abelisaurid theropods (and possibly a third, peirosaurid crocodiles), reveal an interesting biogeographic pattern.

Sudamericid gondwanatheres are a highly distinctive but phylogenetically enigmatic group of mammals first known from the Late Cretaceous and Paleocene of Argentina (Krause and Bonaparte, 1993). Their recent discovery in both the Maevarano Formation of Madagascar and the Deccan volcanic-sedimentary sequence of India revealed a previously unknown degree of cosmopolitanism among Gondwanan mammals at the end of the Cretaceous (Krause et al., 1997b). A similar geographic distribution was recently demonstrated among theropod dinosaurs with the discovery of the skull of the abelisaurid *Majungatholus atopus* (Sampson et al., 1998). The skull provides strong evidence that *Majungatholus* is closely related to taxa in both Argentina (*Carnotaurus*) and India (*Indosuchus*). Interestingly, prior to discovery of the skull, *M. atopus* was only known from an isolated skull fragment that had been referred to the Pachycephalosauridae (Sues and Taquet, 1979; Sues, 1980), a group of ornithischian dinosaurs known as "bone-heads" previously reported only from Laurasia. The new, complete skull demonstrates that the fragment of *M. atopus* is that of a theropod and not a pachycephalosaurid. The biogeographic enigma of pachycephalosaurids in the Late Cretaceous of southern Gondwana is thus resolved (Sampson et al., 1998). Finally, peirosaurid crocodiles, whose tentative identification in the Maevarano Formation remains to be confirmed, are otherwise known with certainty only from the Late Cretaceous (Senonian) of South America (Price, 1955; Gasparini et al., 1991).

The presence of closely related terrestrial and freshwater animals in Madagascar, the Indian subcontinent, and South America near the end of the Cretaceous is seemingly incompatible with paleogeographic reconstructions (e.g., Smith et al., 1994; Scotese, 1998) in which India-Madagascar is viewed as having been isolated from all other Gondwanan landmasses by 120 Ma (Fig. 6). Rather, this distribution accords with the reconstruction by Hay et al. (1999), which posits a subaerial link between India-Madagascar and Antarctica across the Kerguelen Plateau that persisted well into the Late Cretaceous (Fig. 6).

The Maevarano Formation assemblage also yields substantial, though negative, evidence with regard to the biogeographic origins of the highly endemic and imbalanced modern fauna. We have found no evidence in the Maevarano Formation to support the hypothesis that the basal stocks of extant Malagasy vertebrate taxa were present on the island in the Late Cretaceous (Krause et al., 1997a, 1998). None of the fish, frog, turtle, snake, crocodilian, bird, or mammal taxa now known from the Maevarano Formation appears closely related to the higher taxa of vertebrates on the island today. The basal stocks of the modern taxa must have arrived sometime in the Cenozoic, presumably by crossing a significant marine barrier, a possibility made even more feasible by the recent observation of Caribbean iguanas traversing a distance roughly equivalent to the minimum width of the Mozambique Channel on floating logs (Censky et al., 1998). McCall's (1997) contention that there is geological evidence for a Cenozoic land bridge between Africa and Madagascar along the Davie Ridge is unfounded (see Krause et al., 1997a). Although seamounts that may have been emergent do exist, they would have been but small dots of land in a vast seaway some 400 to 1000 km wide.

PROSPECTUS

A densely sampled fossil record coupled with well-supported phylogenetic hypotheses and sound paleogeographic models are the fundamental building blocks of paleobiogeographic analysis. Although the record of terrestrial and freshwater vertebrates from the Mesozoic of Gondwana has improved dramatically in the last two decades, it is still sparse. One of the key stumbling blocks for testing the paleobiogeographic hypotheses outlined here is the virtual lack of terrestrial and freshwater vertebrates from the post-Cenomanian Late Cretaceous of Africa. Major gaps in the fossil record of other Gondwanan landmasses, including Madagascar (Fig. 3), remain as well.

The Mahajanga Basin Project will continue to exploit the fossil riches of the Maevarano Formation and to test biogeographic hypotheses on the basis of new finds. The number of new taxa discovered in our most recent field season demonstrates that many more await discovery. Our efforts will also extend explorations into other horizons in the basin, most notably the underlying Ankazomihaboka beds (Fig. 2), which have already demonstrated their potential through reconnaissance forays in 1996 (Curry, 1997) and 1998. The Ankazomihaboka beds overlie Coniacian basalts, which have been dated to 87.6 ± 0.6 Ma and purportedly signal the time of separation between Madagascar and the Indian subcontinent (Storey et al., 1995).

Finally, the results of the Mahajanga Basin Project provide focus for future geophysical research. In particular, the paleobiogeographic hypotheses outlined in this report underscore the need for more research in the southern Indian Ocean, with attention being directed toward resolving the time of separation between India-Madagascar and Antarctica and the role that the Kerguelen Plateau may have played in connecting those two landmasses in the Late Cretaceous. Paleontologists and geophysicists have much to gain by working synergistically to provide reciprocal illumination on the sequence and timing of Gondwanan fragmentation.

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Todd Berggren, GSA Information Technology Manager

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