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SHORT COMMUNICATION

LATE CRETACEOUS SUDAMERICID GONDWANATHERIANS FROM INDIA WITH PALEOBIOGEOGRAPHIC CONSIDERATIONS OF GONDWANAN MAMMALS

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ABSTRACT—Gondwanatherians are a distinctive Cretaceous radiation of Gondwanan mammals. Fieldwork in the intertrappean beds of Karnataka and Andhra Pradesh, India has yielded a substantial collection of Maastrichtian mammals, including nine isolated teeth that represent at least two sudamericid gondwanatherians. We name a new taxon, *Dakshina jederi*, to which we refer six of the specimens and a previously unnamed form (VPL/JU/NKIM/25). The remaining specimens are identified as Gondwanatheria indeterminate. India's Late Cretaceous mammal fauna includes eutherians, a haramiyidan, and sudamericids. Whereas the eutherians likely represent a dispersal event from Laurasia and the haramiyidan represents a relictual distribution on Gondwana, the gondwanatherians are members of an endemic Gondwanan radiation. The sudamericid *Dakshina* possesses several derived features that suggest phylogenetic affinities with *Lavanify* from the Maastrichtian of Madagascar and to a lesser extent with *Sudamerica* from the Paleocene of Argentina. This pattern of phylogenetic relationships agrees with paleogeographic reconstructions for the breakup of Gondwana that hypothesize close biogeographic ties among India, Madagascar, and South America; however, gaps in our temporal and geographic sampling limit our understanding of biogeographic ties that India shares with Africa, Antarctica, and Australia.

INTRODUCTION

Gondwanatherians, more than any other group of Late Cretaceous mammals, have come to underscore the taxonomic similarities among Gondwanan terrestrial biotas and the differences with their Laurasian counterparts (e.g., Van Valen, 1988; Krause et al., 1997; Pascual, 1997). These dentally distinctive taxa were variously assigned to Edentata (e.g., Scillato-Yané and Pascual, 1984; Bonaparte, 1986a, b, 1990), Multituberculata (Bonaparte, 1986a; Krause and Bonaparte, 1990), and tentatively Allotheria (Krause et al., 1997), but have recently been placed *incertae sedis* within Mammalia as an endemic clade with unresolved phylogenetic affinities (Pascual et al., 1999). Whereas Gurovich (2005) maintained that gondwanatherians are multituberculates on the basis of her detailed morphological study and cladistic analysis, most workers have followed the assessment of Pascual and colleagues (1999). Among them, Kielan-Jaworowska and colleagues (2004) modified the contents of Gondwanatheria to exclude several multituberculate-like specimens tentatively assigned to *Ferugliotherium*.

Gondwanatherians have yet to be discovered on the well-sampled Laurasian landmasses, and are known, largely on the basis of isolated teeth, from almost every Gondwanan landmass. The Gondwanatheria consist of the Ferugliotheriidae and Sudamericidae. Ferugliotheriids have brachydont dentition and are represented by the lone species *Ferugliotherium windhauseni*, which occurs in the Campanian-Maastrichtian of Argentina (Bonaparte, 1986a). The more widespread sudamericid gondwanatherians occur in the Campanian-Maastrichtian and Paleocene of Argentina (*Gondwanatherium*, *Sudamerica*, respectively; Scillato-Yané and Pascual, 1984; Bonaparte, 1986b), the Maastrichtian of Madagascar and India (*Lavanify*, unnamed form, respectively; Das Sarma et al., 1995; Anantharaman and Das Sarma, 1997; Krause et al., 1997), the Eocene of Antarctica (unnamed form; Reguero et al., 2002; Goin et al., 2006), and possibly the Cretaceous of Tanzania (unnamed form; Krause et al., 2003). In addition to their pan-Gondwanan distribution, sudamericids have garnered attention as the only Mesozoic mammals to evolve high-crowned cheek teeth (i.e., crown hypsodonty). Initially, their hypsodonty was by default considered an adaptation for the abrasive materials encountered in a semi-aquatic or burrowing lifestyle (e.g., roots, bark, grit; Koenigswald et al., 1999; Patnaik et al., 2001), but with new evidence for Cretaceous grasses in India (Prasad et al., 2005), it is possible that sudamericids were the earliest mammalian grazers. As mammals with definitive "southern" affinities, Indian sudamericids also stand in contrast to Indian eutherian mammals (e.g., *Deccanolestes*) with likely "northern" biogeographic origins (Krause et al., 1997; Rana and Wilson, 2003).

Despite their importance, gondwanatherian taxa from India have not been formally named. Krause and colleagues (1997) published a detailed description of an isolated tooth that was collected in 1989 from Maastrichtian intertrappean beds near Naskal, Andhra Pradesh (Fig. 1). Because the tooth was fragmentary and poorly preserved, the specimen was referred to Sudamericidae but was not named. Subsequent work on the Indian form has largely focused on additional description of its derived enamel microstructure (Koenigswald et al., 1999; Patnaik et al., 2001).

During the 1990's, crews from the Geological Survey of India (GSI) Southern Region undertook paleontological and geological fieldwork in the Maastrichtian infra- and intertrappean beds of Andhra Pradesh and Karnataka (Fig. 1). Underwater screen-washing of nearly 12 tons of matrix from those exposures led to the recovery of a large collection of microvertebrate fossils. The

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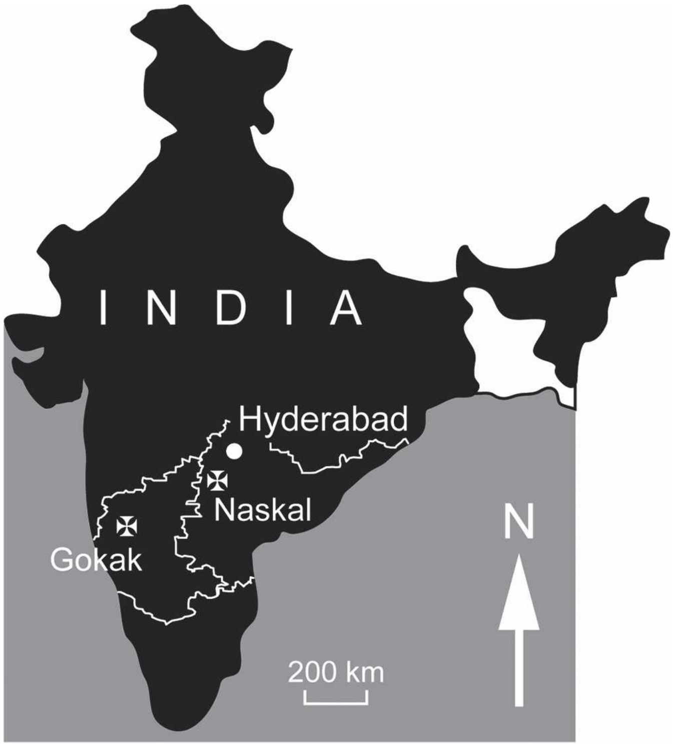

FIGURE 1. Map of India and outline of the states of Karnataka and Andhra Pradesh. Intertrappean mammal fossil localities of Naskal, Andhra Pradesh and Gokak, Karnataka are indicated with crosses. Scale bar equals 200 km. [planned for column width]

mammalian component includes more than 60 isolated teeth, dentulous jaws, and postcranial elements that represent at least two new eutherian taxa, a new "haramiyidan" (Anantharaman et al., 2006), and two sudamericid gondwanatherians. Some of the gondwanatherian specimens from this collection were first mentioned in brief reports (Das Sarma, 1994; Das Sarma et al., 1995; Anantharaman and Das Sarma, 1997), but were never fully described or named. Here we describe the nine isolated gondwanatherian teeth from that collection and refer six of them and the isolated tooth described by Krause and colleagues (1997) to a new genus and species. We also assess the phylogenetic affinities of this new taxon and review the paleobiogeographic significance of India's Late Cretaceous mammal fauna among other Gondwanan mammal faunas.

Institutional Abbreviations—**GSI/SR/PAL**, Geological Survey of India, Southern Region, Palaeontology Division, Hyderabad, India (repository for specimens described herein); **VPL/JU/NKIM**, Vertebrate Palaeontology Laboratory, Jammu University, Jammu, India, Naskal intertrappean mammals; **FMNH**, Field Museum of Natural History, Chicago, U.S.A.; **MPEFCH**, Museo Paleontológico 'Egidio Feruglio,' Trelew, Argentina; **NMT**, National Museums of Tanzania, Dar Es Salam, Tanzania; **UA**, Université d'Antananarivo, Antananarivo, Madagascar.

Terminology and Assignment of Tooth Positions—We use dental terminology that is standard for gondwanatherians (e.g., Koenigswald et al., 1999; Gurovich, 2005). Cheek teeth are referred to as molariforms, recognizing the uncertainty in distinguishing between premolars and molars. Isolated molariforms are assigned tooth positions on the basis of published criteria (Koenigswald et al., 1999; Pascual et al., 1999; Gurovich, 2005).

MPEFCH 534 is a mandible of *Sudamerica ameghinoi* from the Paleocene of Argentina that preserves two mesial molariforms and alveoli for an incisor and two distal molariforms (Pascual et al., 1999). Relying on MPEFCH 534, Koenigswald and colleagues (1999) classified a sample of 30 isolated molariforms of *S. ameghinoi* into eight morphological categories. The specimens in these categories were then assigned to the four lower molariform positions (mf1, mf2, mf3, mf4) and the presumed four upper molariform positions (MF1, MF2, MF3, MF4). Our working hypothesis is that sudamericids from the Late Cretaceous of India share the same dental formula as the Paleocene *S. ameghinoi*. We also assume that despite differences in morphological details with *S. ameghinoi*, similar criteria may be used to assign tooth row positions to the isolated teeth in our sample. It should be noted that a dentary of a possible gondwanatherian from the Cretaceous of Tanzania (NMT 02067) exhibits a dental formula of five, not four, lower molariforms (Krause et al., 2003). The authors suggested that five lower molariforms may represent the primitive dental formula for gondwanatherians; nevertheless, tooth row positions for the Indian specimens should be considered tentative until dentulous mandibular fragments are known.

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758
GONDWANATHERIA Mones, 1987 (Krause and Bonaparte, 1990)
SUDAMERICIDAE Scillato-Yané and Pascual, 1984
DAKSHINA, gen. nov.

Etymology—*daakshinaatya*, (Sanskrit) means "of the south" referring to the Deccan region of India where the fossils were recovered and the restricted geographic distribution of gondwanatherians on the southern continents.

Type species—*Dakshina jederi* sp. nov.

Diagnosis—As for the type and only species.

DAKSHINA JEDERI, sp. nov.

(Fig. 2-4)

Etymology—*jeder*, nickname of Professor Jeffrey A. Wilson, vertebrate paleontologist from the University of Michigan, honoring the vital role he played in facilitating the current collaboration.

Holotype—GSI/SR/PAL-G074, a well-preserved, right mf4.

Referred Specimens—GSI/SR/PAL-G059, left mf3; GSI/SR/PAL-G070, right mf4, both from the type locality; GSI/SR/PAL-N071, left mf4; GSI/SR/PAL-N210, left i1; GSI/SR/PAL-N212, right mf4; VPL/JU/NKIM/25, left mf4, all from the Naskal locality.

Localities and Horizons—The holotypic locality is from the Maastrichtian intertrappean beds near Gokak, Karnataka, India (Fig. 1; 16° 10′ N, 74° 53′ E). Fossils were found within 1 m thick, red silty-mudstone beds, which lie above 2–3 m thick, gray silty-sandstone beds. The second locality is from Maastrichtian intertrappean beds near Naskal, Andhra Pradesh, India (Fig. 1; 17° 15′ N, 77° 50′ E). Fossils were found within 1–2 m gray sandy-siltstone beds, which lie above a thin (<1m) greenish chert layer. Additional data are available from the GSI.

Diagnosis—Autapomorphies of *Dakshina*: multiple-layered dental enamel (Patnaik et al., 2001), at least one molariform position with a V-shaped enamel islet. Differing from *Gondwanatherium* and *Sudamerica* in: dental enamel with well-developed inter-row sheets of interprismatic matrix (Krause et al., 1997; Koenigswald et al., 1999; Patnaik et al., 2001), molariforms with perikymata, deep infundibula (Koenigswald et al., 1999), and vertical furrows only on lingual side of crowns. Differing from *Gondwanatherium* in: vertical furrows extending to

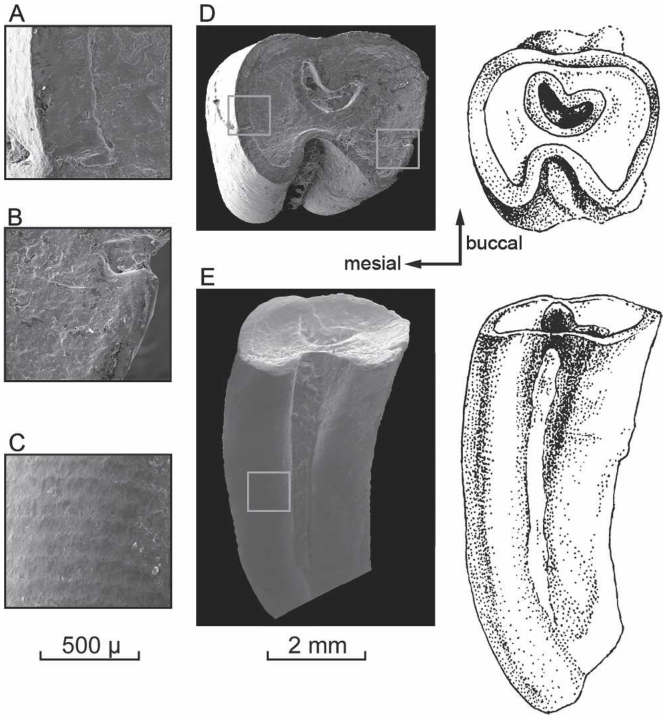

FIGURE 2. Scanning electron micrographs and stipple drawings of the holotype of *Dakshina jederi*, right mf4, GSI/SR/PAL-G074. High-magnification views of **A**, trailing edge of enamel; **B**, leading edge of enamel; **C**, perikymata. Scale bar equals 500 μ. Low-magnification views of **D**, occlusal surface of the crown with gray square outlines indicating position of high-magnification views in **A** (left) and **B** (right); **E**, lingual aspect of the crown with gray square outline indicating position of high magnification view in **C**. Scale bar equals 2 mm. [planned for column width]

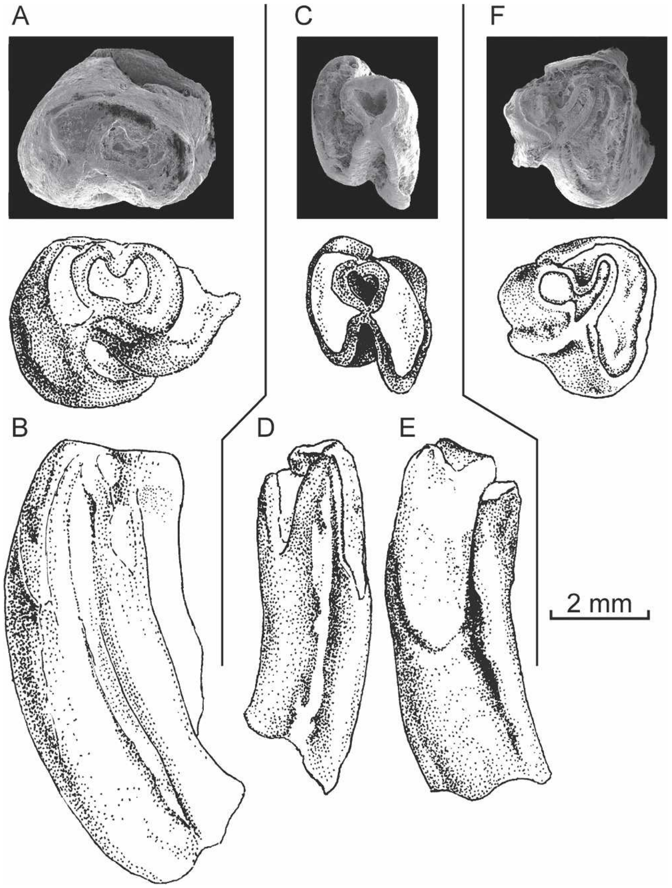

FIGURE 3. Scanning electron micrographs and stipple drawings of specimens of *Dakshina jederi*. **A**, right mf4, GSI/SR/PAL-G070, in occlusal view; **B**, lingual view of same; **C**, left mf4, GSI/SR/PAL-N071, in occlusal view; **D**, lingual view of same; **E**, buccal view of same; **F**, right mf4, GSI/SR/PAL-N212, in occlusal view. Scale bar equals 2 mm. [planned for column width]

base of molariform crowns (Krause et al., 1997). Differing from *Sudamerica* in: molariforms gently tapered towards the occlusal surface. Differing from *Lavanify* in: molariforms without a V-shaped dentine lake, with enamel on all sides of crown (Krause et al., 1997).

Description: Lower Fourth Molariform—The type specimen, GSI/SR/PAL-G074, is a well-preserved, hypsodont molariform tooth that is tentatively identified as a right mf4 (Fig. 2). The crown is oblique to the flat occlusal surface, curved distally and somewhat buccally along its height (Fig. 2E). The enamel is thick and continuous throughout the height of the lingual and mesial aspects of the crown, but it thins ventrally on the buccal and distal aspects of the crown. Transverse wave-like bands and grooves (Fig. 2C) called perikymata are evident on the surface of the enamel along the height of the crown; they relate to striae of Retzius and the pattern of enamel formation (Moss-Salentijn et al., 1997). A vertical furrow, which is partially filled with cementum, extends along the lingual aspect of the crown from near the base to the occlusal surface. The lingual aspect is also convex relative to the flat buccal aspect of the crown. The height measured perpendicularly from the occlusal surface to base of the crown on the lingual and mesial aspects is 7.57 mm. On the buccal and distal aspects, the crown is shorter, in part due to breakage but also possibly due to differential growth and mode of eruption (Pascual et al., 1999). The dimensions of the crown gently taper toward the occlusal surface (L = 3.66 mm; W = 2.99 mm). The root is not preserved on the specimen.

The worn occlusal surface is flat and has a sub-rounded to rectangular outline (Fig. 2D). The vertical furrow that extends along the height of the crown invades the lingual side of the occlusal surface to form a trenchant syncline. Along with the lingual syncline, a shallow indentation on the buccal side separates the occlusal surface into two transverse lophs, each with buccal and lingual lobes. The mesial loph is mesiodistally shorter than the distal loph, and in both lophs, the lingual lobe is wider than the buccal lobe. The enamel band that encircles the occlusal surface is thicker on the mesial and lingual margins than on the distal and buccal margins (Fig. 2A, B, D). It encloses the dentine lakes of the mesial and distal lophs and a broad V-shaped or crescentic enamel islet. The enamel islet is a worn remnant of an infundibulum, an infolding of enamel that also occurs in the teeth of ruminants and horses (Hillson, 1986). The islet, which is partially filled with cementum, is centrally located on the occlusal surface between the mesial and distal lophs. The apex of the V faces the lingual syncline; the mesial arm of the V points toward the shallow, buccal indentation; and the distal arm of the V points towards the distobuccal corner of the occlusal surface. In mesial view, the occlusal surface forms a very shallow, broad, mesiodistally-oriented valley. The buccal rim of the valley is distinctly taller than the lingual rim (Fig. 2E).

Identification of GSI/SR/PAL-G074 as a right lower molariform is based on several morphological features. Gondwanatherians have a palinal chewing motion (Krause et al., 1992), such that the leading and trailing edges on molariform occlusal surfaces can be distinguished based on differentially worn dentine (Costa and Greaves, 1981). On the leading edge, the dentine is protected by enamel and thus, remains flush with the enamel (Fig. 2B); on the trailing edge, the dentine is unprotected and erodes below the level of the enamel (Fig. 2A). The leading edge is thus mesial on upper molariforms and distal on lower molariforms. Determination of buccolingual orientation of GSI/SR/PAL-G074 is based on observations from MPEFCH 534, the dentulous jaw of *Sudamerica ameghinoi*. On lower molariforms, the buccal side of the occlusal surface is taller than the lingual side, and the relative extent of enamel on the lingual face of the crown is greater than it is on the buccal face (Koenigswald et al., 1999; Pascual et al., 1999). Gurovich (2005) argued that in upper molariforms the opposite is the case. Based on these criteria, GSI/SR/PAL-G074 is either a right lower molariform or a left upper molariform. Of the eight morphological categories of *Sudamerica ameghinoi* molariforms (Koenigswald et al., 1999), only mf4 has two-lophs and distobuccal curvature along the height of the crown. Assuming that these features maintain for *Dakshina jederi*, we tentatively identify GSI/SR/PAL-G074 as a right mf4.

Based on the previous features, 4 other specimens are identified as mf4s of *Dakshina jederi*. Morphological and size variation among the mf4s is considered to be primarily due to stage of wear and degree of preservation. Koenigswald and colleagues (1999) showed that in molariforms of *Sudamerica ameghinoi* the shape of the infundibulum varies along its depth, such that the shape of the enamel islet on the occlusal surface varies with stage of wear.

GSI/SR/PAL-G070 is a right mf4 (Fig. 3A,B) that suffered breakage on the buccal and distal aspects of the crown and to a slight degree along the lingual vertical furrow. As in all other specimens in the collection, a root is not preserved. The specimen differs from the type specimen in several respects. The crown height (8.40 mm) is greater than that of the type specimen; whereas the length and width at the occlusal surface (2.49 mm, 1.75 mm, respectively) are smaller than those of the type specimen. Although the occlusal surface is relatively flat, the outer enamel covering is not worn through to fully expose the underlying dentine lakes (Fig. 3A). The vertical furrow is tapered abruptly at the occlusal surface, resulting in a less trenchant lingual syncline (Fig. 3A,B). The outline of the occlusal surface is oval rather than sub-rounded to rectangular. The enamel islet is distinct but the V-shaped outline is broader than that in the type specimen. These differences are most likely attributable to stage of wear, which exposes different patterns of the occlusal surface (Koenigswald et al., 1999). Thus, GSI/SR/PAL-G070 is interpreted as a relatively unworn tooth presumably from a younger individual than the type. The curvature along the height of the crown is more pronounced than in the type and may be attributable to the stage of wear and the initial development of a flat occlusal surface (Fig. 3B). At the base of the crown, the length and width measurements of GSI/SR/PAL-G070 and the type are quite similar (L = 3.18 mm, W = 3.18 mm; L = 3.42mm, W = 3.13 mm, respectively).

GSI/SR/PAL-N071 is a fragment of a left mf4 that suffered breakage on all but the distal aspect of the crown (Fig. 3C–E). This damage exposed the internal morphology of the infundibulum in mesial and buccal views (Fig. 3E). The crown height is 7.16 mm, and the infundibulum extends in a ventrodistal direction more than half way down the crown (4.01 mm). The occlusal

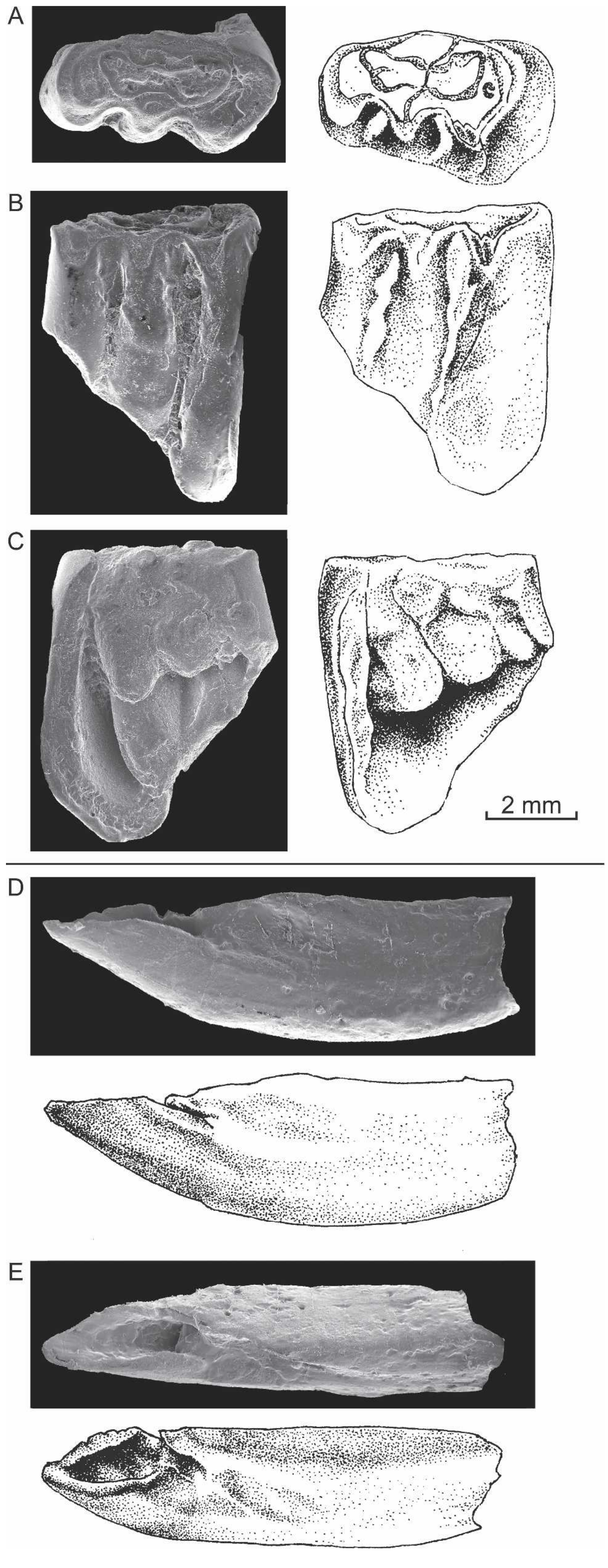

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FIGURE 4. Scanning electron micrographs and stipple drawings of specimens of *Dakshina jederi*. **A**, left mf3, GSI/SR/PAL-G059, in occlusal view; **B**, lingual view of same (SEM shows artificially abrupt mesial aspect of epoxy cast, stipple drawing shows true mesial aspect of actual specimen); **C**, buccal view of same; **D**, left lower incisor, GSI/SR/PAL-N210, in lateral view; **E**, dorsal view of same. Scale bar equals 2 mm. [planned for column width]

morphology is difficult to determine, as the outer enamel border is missing from the mesial, mesiolingual, and buccal margins (Fig. 3C). The dentine on the distal half of the occlusal surface is largely worn down, and is completely missing on the mesial half. The enamel islet is preserved and stands tall above the preserved dentine and outer enamel border on the distal half of the occlusal surface. The enamel islet, which is not filled with cementum, is heart- to V-shaped, and its lingual side (the apex) abuts the lingual syncline. The length measured at the occlusal surface is considerably reduced from breakage but is at least 2.14 mm. The preserved width is 2.42 mm and probably slightly underestimates the actual width.

GSI/SR/PAL-N212 is a right mf4 (Fig. 3F). The enamel on the mesial aspect of the crown is missing and the enamel border on the occlusal surface is broken or missing. The crown curves buccodistally along its height and measures 5.86 mm from the lingual aspect and 1.61 mm from the buccal aspect. The degree of wear indicates that the tooth is from an older individual. The vertical furrow is broad near the base of the crown and narrows dorsally. Although the occlusal morphology is difficult to discern, the enamel border presumably surrounded two dentine lakes and the V-shaped central enamel islet (Fig. 3F). The enamel islet is filled with cementum. The distal, distolingual, and distobuccal aspects of the enamel border have been reduced in height from damage, but the outline is still evident. The distal dentine lake is preserved but also damaged. The mesial dentine lake is missing as is the mesial aspect of the enamel border, exposing the infundibulum ventral to the occlusal surface. It descends buccoventrally to near the base of the crown. At the occlusal surface, the length is at least 2.66 mm and the width is at least 2.04 mm.

VPL/JU/NKIM/25 is the Indian sudamericid specimen that Krause et al. (1997) described, but did not refer to a new taxon. Additional descriptions of the enamel microstructure were also published by Koenigswald and colleagues (1999) and Patnaik and colleagues (2001). On the basis of published morphological descriptions and illustrations (Krause et al., 1997:fig. 2C), we refer this specimen to *Dakshina jederi* and tentatively identify it as a left mf4. The hypsodont crown is curved along its height in what we interpret as the distal direction; however, it is unclear from the illustrations whether the crown also curves in the buccal direction. As in other specimens of *D. jederi*, enamel appears to have been present on all sides of the crown. A cementum-filled vertical furrow travels along the lingual aspect of the crown. Damage to the buccal aspect of the crown reveals a deep infundibulum. The crown height is about 6 mm, which is within the range of crown heights for other mf4s referred to *D. jederi*. The occlusal surface is flat and morphologically very similar to GSI/SR/PAL-G070; the two specimens probably represent similar stages of wear. Some details of the occlusal morphology are difficult to interpret from the published illustrations; the occlusal outline is oval, and the centrally located enamel islet forms a broad V-shape that is almost identical to that of GSI/SR/PAL-G070. The occlusal dimensions of VPL/JU/NKIM/25 ($L \approx 2.5$ mm, $W \approx 1.8$ mm; measured from Krause et al., 1997:fig. 2C) are also almost identical to those of GSI/SR/PAL-G070 ($L = 2.49$ mm, $W = 1.75$ mm).

Description: Lower Third Molariform—GSI/SR/PAL-G059 is a hypsodont molariform with a flat occlusal surface and 3 transverse lophs (Fig. 4A–C). The specimen curves along the height of the crown in the distal direction. The curvature is most noticeable along the height of the mesial loph and progressively less in the shorter distal lophs. Although the buccal aspect of the crown is damaged, it appears that it curves buccally along its height. The height of crown measured from the mesial aspect is 5.97 mm. The height of the crown from the distal aspect is considerably less (2.02 mm). The breakage to the buccal aspect of the crown reveals three distoventrally-oriented infundibula (Fig. 4C). The mesial infundibulum is the deepest, descending more than half the height of the crown; the distal infundibulum is the shallowest. The lingual aspect of the crown is undamaged and preserves two vertical furrows, both of which are broadest dorsally and descend with a slight distal curvature (Fig. 4B). The length of the crown measured near the base is 4.95 mm and the width measured at the mesial base is 2.78 mm. At the occlusal surface, the length is 4.58 mm and the width is at minimum 2.52 mm.

The occlusal surface of GSI/SR/PAL-G059 is moderately preserved (Fig. 4A). Damage to the buccal aspect of the crown has removed most of the enamel band from the buccal margin. Though the occlusal surface is relatively flat, there is a gentle dorsobuccal slope. On the lingual margin, the 2 vertical furrows from the lingual aspect of the crown form synclines that separate the occlusal surface into 3 transverse lophs. The mesial loph appears to be the largest of the lophs, partly due to its rounded mesial cap; the distal loph is the smallest. The lingual lobes of the transverse lophs are wider than the buccal lobes. The outer enamel band surrounds three dentine lakes and three merged enamel islets. In occlusal view, the enamel islets form a single undulating enamel band; however, the buccal view of the crown reveals that the enamel islets are the product of 3 separate infundibula.

Identification of GSI/SR/PAL-G059 as a left mf3 is based on several criteria. Koenigswald et al. (1999) assigned 3-lophed molariforms of *Sudamerica ameghinoi* to mf2, mf3, MF3 or MF4 on the basis of size and curvature along the height of the crown. The current sample of *Dakshina jederi* has only one three-lophed molariform, precluding the use of size. In *S. ameghinoi*, MF3s and MF4s have strong lingual curvature; mf3s have slight distal and buccal curvature; and mf2s do not have curvature along the height of the crown. The distal and possibly buccal curvature along the crown suggests that GSI/SR/PAL-G059 is an mf3. The position of leading and trailing edges on the occlusal surface, the lingual vertical furrows, and the relative heights of the buccal and lingual sides of the occlusal surface suggest that the specimen is from the left side of the jaw. We refer this specimen to *D. jederi* on the basis of size and general morphological similarities with the type, such as the presence of vertical furrows on the lingual but not buccal aspect of the crown. We assume that differences in morphological details reflect differences due to position in the jaw.

Description: Lower Incisor—GSI/SR/PAL-N210 is identified as a left lower incisor (Fig. 4D,E). It is laterally compressed with a flat medial aspect and a more convex lateral aspect. The lateral aspect also has a shallow groove that increases in depth and breadth toward the apical surface (Fig. 4D). At the apical surface, there appears to be some breakage or perhaps some infolding that has left a rim of enamel that follows the margin of the groove on to the dorsal surface (Fig. 4E). The cross-sectional outline at the base of the crown is broad ventrally and tapers dorsally. Although the entire length of the crown is not preserved, the anteroventral margin of the crown follows a gentle arc with a length of 11.76 mm. The depth of the incisor measured along a radius of the arc is 3.39 mm. Poor preservation makes it unclear whether there was a restricted band of enamel along the anteroventral margin of the tooth. The arc length of the dorsal margin excluding the apical surface is 5.39 mm. The apical surface is 5.59 mm in length. The anteroventral margin and the apical surface form an angle of approximately 38 degrees. The acute angle and the gentle curvature of the crown indicate that the tooth is a lower rather than an upper incisor (Krause and Bonaparte, 1993). The size of the tooth suggests that it is referable to *Dakshina jederi*.

Comments—The large proportion of specimens assigned to the lower fourth molariform position raises suspicion that the criteria of Koenigswald et al. (1999) for *Sudamerica* may not directly apply to *Dakshina*. The validity of this assumption awaits further testing with the discovery of additional specimens, particularly dentulous jaw fragments.

Phylogenetic Affinities—*Dakshina jederi* has large, hypsodont molariforms with cementum-filled vertical furrows and a flat occlusal surface that place it within the Sudamericidae. We infer lower-level phylogenetic affinities of *Dakshina* through comparisons with casts of *Sudamerica ameghinoi* (MPEFCH 534), *Lavanify miolaka* (UA 8653, FMNH PM 59520), and the Tanzanian specimen (NMT 02067), and with published descriptions and illustrations of all sudamericid taxa. As fossil material that is more complete becomes available, these hypotheses should be tested in a cladistic framework.

A sudamericid was reported from the middle Eocene La Meseta Formation of Seymour Island, Antarctica and considered to be closely related to *Sudamerica ameghinoi* (Reguero et al., 2002; Goin et al., 2006). The specimens consist of a dentary fragment that preserves the intra-alveolar portion of the lower incisor and a fragmentary upper incisor tentatively referred to the unnamed taxon. In size and preserved gross morphology, the lower incisor from Antarctica is comparable to those of *Dakshina* (GSI/SR/PAL-N210) and other gondwanatherians. The enamel microstructure of the incisors from Antarctica is most similar to and slightly more derived than that of *S. ameghinoi*. Although the enamel microstructure of the lower incisor of *Dakshina* is not known, Goin et al. (2006) suggested that it would be more derived than that of the Antarctic form on the basis of the enamel microstructure of its cheek teeth. We await further fossil discoveries that permit direct comparisons between the Eocene Antarctic form and *Dakshina*.

NMT 02067 is a fragmentary left dentary from the "Red Sandstone Group" of southwestern Tanzania (Krause et al., 2003). It was assigned a Cretaceous age and tentatively referred to the Sudamericidae. The specimen is comprised of dentine stumps of five hypsodont cheek teeth and a large laterally compressed incisor. Indications are that the molariforms of NMT 02067 were smaller than those of *Dakshina jederi*.

Gondwanatherium and *Sudamerica* are sudamericids from Argentina. *Gondwanatherium* is from the Campanian-Maastrichtian Los Alamitos Formation in Río Negro Province (Bonaparte, 1986b); whereas *Sudamerica* is from the lower Paleocene "Banco Negro Inferior" strata in Chubut Province (Scillato-Yané and Pascual, 1984). The dental morphology of these taxa is based on large samples of isolated teeth and a dentulous jaw of *S. ameghinoi* (Krause and Bonaparte, 1993; Koenigswald et al., 1999; Pascual et al., 1999; Gurovich, 2005).

Lavanify is from the Maastrichtian Anembalema Member of the Maeverano Formation in Madagascar (Krause et al., 1997). The holotype of *L. miolaka* (UA 8653) is a well-preserved molariform that may be identified as a left mf4. The crown is missing a small portion of the distobuccal occlusal surface. FMNH PM 59520 is a poorly preserved specimen that was provisionally referred to *L. miolaka*. Morphological differences from the holotype were attributed to tooth position, e.g., FMNH PM 59520 has a deep infundibulum that forms a circular enamel islet on the occlusal surface.

Although the evolutionary polarity of sudamericid dental characters is uncertain, *Dakshina*, *Sudamerica*, and *Lavanify* share a feature that has been interpreted as derived: vertical furrows that extend to the base of the molariform crown. *Gondwanatherium* lacks this feature (Krause et al., 1997). *Dakshina* and *Lavanify* share three additional features that may be derived: (1) molariforms with deep infundibula (except UA 8653) that are not replaced by synclines (Koenigswald et al., 1999); (2) dental enamel with well-developed inter-row sheets of interprismatic matrix (Krause et al., 1997; Koenigswald et al., 1999; Patnaik et al., 2001); and (3) molariforms with transverse wave-like bands and grooves on the enamel surface, i.e., perikymata. *Dakshina* and *Lavanify* share a fourth feature to the exclusion of *Gondwanatherium* and *Sudamerica*, but the polarity of this feature is uncertain. Both have vertical furrows on only the lingual aspect of the molariform crown. *Dakshina* also differs from *Gondwanatherium* and *Sudamerica* in having relatively small molariforms. *Dakshina* and *Gondwanatherium* possess molariforms that gently taper towards the occlusal surface. In contrast, *Sudamerica* possesses what is likely the derived state: molariforms with nearly the same cross-sectional dimensions throughout the height of the crown.

Dakshina has two apparent autapomorphies: (1) mf4s with V-shaped enamel islets; and (2) dental enamel of multiple layers (radial, tangential, and zone of PLEX, Patnaik et al., 2001); whereas autapomorphies of *Lavanify* include possession of at least one molariform position with a V-shaped dentine lake on the occlusal surface and lacking enamel on the distal aspect of the molariform crown (Krause et al., 1997).

On the basis of VPL/JU/NKIM/25, Krause and colleagues (1997) and Koenigswald and colleagues (1999) contended that the sudamericid from India was more closely related to the Malagasy *Lavanify* than either was to the South American sudamericids. Having referred VPL/JU/NKIM/25 to the new taxon *Dakshina jederi*, the larger sample size provides additional morphological data that reinforce previous phylogenetic hypotheses and their biogeographic implications; however, we acknowledge that the Gondwanan fossil record has significant spatial and temporal gaps that must temper our conclusions (Wilson et al., 2003).

The phylogenetic affinities of gondwanatherians to other Mesozoic mammal groups remain unresolved. Central to the debate is whether gondwanatherians are multituberculates, sister group to multituberculates, or an independent clade convergent on multituberculates. Most cladistic analyses of Mesozoic mammals have omitted gondwanatherians because of the limited morphological information available (e.g., Luo et al., 2002; Luo and Wible, 2005). Kielan-Jaworowska and colleagues (2004) placed gondwanatherians *incertae sedis* within Mammalia following Pascual and colleagues (1999), but they removed several specimens from the Ferugliotheriidae and placed them *incertae sedis* within Multituberculata. The specimens include a dentary with a blade-like premolar and isolated, multituberculate-like upper premolars tentatively assigned to *Ferugliotherium* by Kielan-Jaworowska and Bonaparte (1996) and Krause et al. (1992:fig. 2C-F), respectively. Gurovich (2005) retained those specimens in *Ferugliotherium* and on the basis of a cladistic analysis, resurrected the hypothesis that gondwanatherians are multituberculates. Her cladistic analysis incorporated a detailed study of all available gondwanatherian specimens, including some undescribed material from Argentina, and modifications to the matrices of Luo and colleagues (2002) and Kielan-Jaworowska and colleagues (2004). Testing these hypotheses depends upon additional field work to recover specimens with the greater morphological information. For example, a dentulous dentary of *Ferugliotherium* may resolve the debate as to whether gondwanatherians primitively had the multituberculate feature of a blade-like premolar.

GONDWANATHERIA, indet.
(Fig. 5)

Referred Specimens—GSI/SR/PAL-G111, right upper incisor; GSI/SR/PAL-G112, lower incisor; GSI/SR/PAL-G211, tooth of indeterminate position, all from the type locality of *Dakshina jederi*.

Localities and Horizons—Same as the type locality of *Dakshina jederi*.

Description: Upper Incisor—GSI/SR/PAL-G111 is identified as a right upper incisor (Fig. 5A,B). It is a well-preserved, laterally compressed specimen that is broken at its distal end. The apical surface and the anterodorsal margin of the crown form an

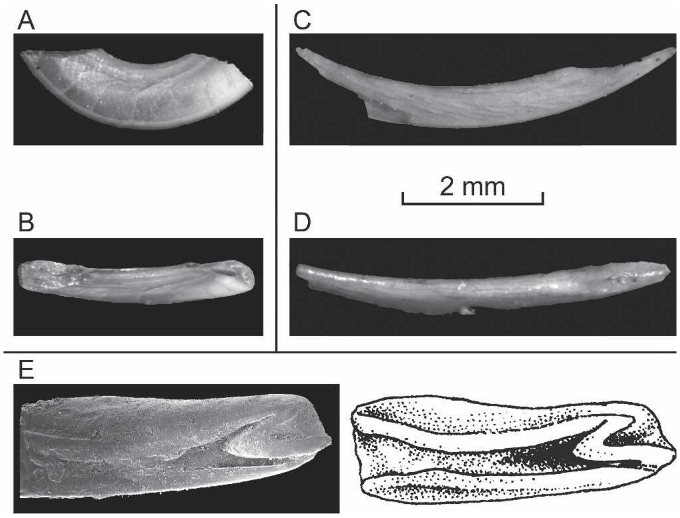

FIGURE 5. Scanning electron micrographs and stipple drawings of specimens of Gondwanatheria indeterminate. **A**, right upper incisor, GSI/SR/PAL-G111, in lateral view; **B**, ventral view of same; **C**, lower incisor, GSI/SR/PAL-G112, in side view; **D**, dorsal view of same; **E**, indeterminate tooth position, GSI/SR/PAL-N211, in side view. Scale bar equals 2 mm. [planned for column width]

angle of approximately 54 degrees. Along with the strong curvature, this relatively less acute angle (see GSI/SR/PAL-G112 below) suggests that the specimen is an upper rather than a lower incisor. In cross-section, we interpret the more convex aspect of the crown as lateral and the less convex to flat aspect as medial, indicating that the specimen is a right upper incisor. As in other gondwanatherians, the specimen has a narrow restricted band of enamel along the anterodorsal margin (Krause and Bonaparte, 1993). The arc length along that anterodorsal margin is 4.07 mm; the arc length of the posteroverntral margin is 1.43 mm; and the length of the apical surface is 1.15 mm. The depth of the crown measured along a radius of the anterodocrsal arc is 1.03 mm. On the basis of morphology, the specimen is referable to Gondwanatheria, but its size is smaller than that predicted for upper incisors referable to *Dakshina jederi*.

Description: Lower Incisor—GSI/SR/PAL-G112 is tentatively identified as a lower incisor (Fig. 5C,D). The specimen is well preserved, though the distal end is incomplete. The crown is long, laterally compressed, and gently curved along its length. The arc length along the anteroventral margin is 4.84 mm. The depth of the crown measured along a radius of the anteroventral arc is 1.03 mm. The arc length along the dorsal margin is 4.02 mm, and the length of the apical surface is 1.59 mm. The apical surface and the anteroventral margin of the crown form an angle (~22 degrees) that is more acute than that of GSI/SR/PAL-G111. The curvature is also gentler than that in GSI/SR/PAL-G111, indicating that the specimen is a lower incisor. We do not assign GSI/SR/PAL-G112 to either side of the jaw because neither side is more convex than the other in cross-section. It is unclear whether enamel is restricted to the anteroventral margin of the crown.

Description: Indeterminate Tooth—GSI/SR/PAL-G211 is a long, thin tooth that cannot be confidently assigned to a particular tooth position (Fig. 5E). For the convenience of description, we interpret the tooth as an anteriorly projecting lower incisor. The crown gently tapers toward the apical surface, terminating somewhat abruptly in an oblique angled face. The apical surface and the ventral margin of the tooth form an angle of approximately 115 degrees. The apical face is invaginated by a shallow infundibulum that is exposed in what we interpret as the medial view. The shallow infundibulum extends only about one fourth of the depth of the crown. The length of the crown is 4.54 mm and the width is 1.51 mm. The ventral aspect of the tooth is flat in contrast to the more convex dorsal margin. Because of its uncertain position in the jaw and small size relative to teeth of *Dakshina jederi*, we include the specimen as an indeterminate gondwanatherian.

Comments—All 3 specimens are placed within the Gondwanatheria and may ultimately be placed within *Dakshina jederi*; however, their relatively small size suggests that they represent a different species.

DISCUSSION AND CONCLUSIONS

The new gondwanatherian material described previously offers an opportunity to highlight progress in our understanding of Gondwanan Cretaceous mammal biogeography with particular reference to India. Bonaparte and Kielan-Jaworowska (1987) proposed the hypothesis that geographic isolation during much of the Cretaceous led to the evolution of Laurasian and Gondwanan faunas with markedly different taxonomic compositions. Laurasian mammalian faunas were characterized as dominated by multituberculates, with eutherians and metatherians becoming diverse, while triconodontids, dryolestoids, and spalacotheriid “symmetrodontans” went extinct. In contrast, Gondwanan mammalian faunas were characterized, on the basis of the Los Alamitos assemblage of Argentina, as a radiation of dryolestoids with other less diverse forms, such as gondwanatherians, triconodontids, and “symmetrodontans.” Thus, the tectonic separation of Laurasia and Gondwana led to vicariant evolution of multituberculate and tribosphenic mammals on Laurasia and non-tribosphenic endemics and relicts on Gondwana.

“Laurasian” Mammals in Gondwana

Fossil discoveries on the southern continents over the past 30 years have in some ways blurred the biogeographic divide between Laurasia and Gondwana. Prasad and Sahni (1988) reported a eutherian from the Maastrichtian intertrappean beds of India, which at the time was considered evidence of early contact between India and Eurasia. However, a lack of solid geophysical evidence for a pre-Eocene collision (e.g., Clyde et al., 2003) makes such an explanation problematic, unless one invokes an island chain or other dispersal route (see Prasad and Sahni, 1999). Northern tribosphenic mammals (boreosphenidans) are also known from the Early Cretaceous of Morocco (e.g., Sigogneau-Russell, 1991a), but some authors consider northwestern Africa a paleobiogeographic extension of Eurasia (e.g., Luo et al., 2001) despite the lack of evidence for a geographic connection (see Sigogneau-Russell et al., 1998). Nevertheless, additional fossil discoveries have expanded the distribution of supposedly Laurasian mammals during the Cretaceous to other southern landmasses with less controversial geographic histories. Multituberculates have been found in the Campanian-Maastrichtian of Argentina (Kielan-Jaworowska and Bonaparte, 1996), and multituberculates and metatherians have been found in the Maastrichtian of Madagascar (Krause and Grine, 1996; Krause, 2001; but see Averianov et al., 2003). Eutherians and metatherians are known from the Maastrichtian of Peru (Grambast et al., 1967; Sigé, 1972), but the age of these deposits is debated (e.g., Van Valen, 1988). Eutherians have also been found in the middle Maastrichtian of Bolivia (Gayet et al., 2001), and additional eutherian taxa have been found in the Maastrichtian of India (Prasad et al., 1994; Rana and Wilson, 2003; Khosla et al., 2004).

At the very least, these discoveries hint that we still have much left to learn about the geographic distributions of Cretaceous mammals. Even in South America, where we have the best record of Cretaceous mammals of any Gondwanan landmass, sampling is largely restricted to southern Argentina. Importantly, geological and palynofloral data suggest that during the Cretaceous and Paleocene there was a biogeographic barrier between northern and southern South America in the form of an epeiric seaway (Wilson and Arens, 2001). This may possibly explain the absence of eutherians and metatherians in the Cretaceous of Argentina and the absence of gondwanatherians in the Cretaceous and Paleocene of Bolivia and Peru (Van Valen, 1988).

Gondwanan Relicts

Paradoxically, some recent fossil discoveries on the southern continents have bolstered the biogeographic divide between Laurasia and Gondwana. Some non-tribosphenic mammal groups that went extinct on the northern continents by the Cretaceous or earlier persisted as relicts on the southern continents into the Late Cretaceous and Paleocene, in some cases becoming quite successful. For example, dryolestoid taxonomic diversity peaked in Laurasia during the Late Jurassic and dwindled during the Cretaceous (Kielan-Jaworowska et al., 2004). In Gondwana, dryolestoids were present in the Late Jurassic of Tanzania (Dietrich, 1927), the Early Cretaceous of Morocco (Sigogneau-Russell, 1991b) and possibly Australia (Clemens et al., 2003), and underwent an impressive taxonomic radiation in the Late Cretaceous of Argentina (Bonaparte, 1990), surviving into the Paleocene (Gelfo and Pascual, 2001). Haramiyidans are another ancient lineage of Mesozoic mammals that were present on the northern continents during the Late Triassic until at least their last appearance in the Middle Jurassic (Kielan-Jaworowska et al., 2004). On the southern continents, they were present in the Late Jurassic of Tanzania (Heinrich, 1999, 2001) and the Early Cretaceous of Morocco (Sigogneau-Russell, 1991c; Hahn and Hahn, 2003; taxonomic reinterpretation of Butler and Hooker, 2005), and survived well into the Late Cretaceous of India (Anantharaman et al., 2006). *Reigitherium* from the Campanian-Maastrichtian Los Alamitos and La Colonia Formations of Argentina may also represent a Gondwanan relict. Bonaparte (1990) originally described the only known molar as that of a dryolestoid. Then, on the discovery of a lower jaw with three teeth, Pascual et al. (2000) argued that *Reigitherium* is a highly derived docodontan. This taxonomic assignment represents a significant extension to the temporal range of a group that is otherwise only known from the Middle Jurassic and Early Cretaceous of northern continents (Kielan-Jaworowska et al., 2004). Although the interpretation of *Reigitherium* as a relict docodontan has been questioned (Kielan-Jaworowska et al., 2004), the dentition of this mammal remains unquestionably unique and may point to the endemic nature of Gondwanan mammals.

Gondwanan Endemics

Fossil evidence of Gondwana's endemism has led paleontologists to overturn long-held notions of early mammalian evolution. Phylogenetic analyses now strongly support an independent southern origin of the tribosphenic molar (Luo et al., 2001; Martin and Rauhut, 2005). Members of the group, Australosphenida, are known from the Early Cretaceous of Australia (e.g., Rich et al., 1997), the Middle Jurassic of Madagascar (Flynn et al., 1999), and the Middle or Late Jurassic of Argentina (Rauhut et al., 2002). Monotremes, which are placed within Australosphenida (Kielan-Jaworowska et al., 2004; but see Rich et al., 2002; Woodburne, 2003), are known by several taxa from the Early Cretaceous of Australia (e.g., Archer et al., 1985; Rich et al., 2001) and a single taxon from the Early Paleocene of Argentina (Pascual et al., 1992; Pascual et al., 2002; Forasiepi and Martinelli, 2003). They provide a second example of this pattern of convergent evolution on Gondwana and Laurasia via their independent acquisition of the tri-ossicular middle ear. The earliest monotreme retained an internal mandibular trough, suggesting that the detachment of certain postdentary bones and their placement in the middle ear occurred independently in monotremes and therians (Rich et al., 2005; but see Rougier et al., 2005; Bever et al., 2005). Further attesting to the endemicity of Gondwanan mammalian faunas, Krause (2003) reported a bizarre new specimen from the Maastrichtian of Madagascar. Although the partially-prepared, incomplete skull and articulated skeleton demonstrate features that suggest it falls among cladotherian mammals and is slightly more derived than *Vincelestes*, the dentition of the Malagasy specimen is so transformed that homologies remain unclear.

Perhaps the most striking example of Gondwanan endemism is the gondwanatherian radiation. These mammals, which are found on all southern continents except Australia, are of uncertain phylogenetic affinities. Although they share derived features with multituberculates, including an inferred palinal jaw motion and laterally compressed lower incisors with a ventrally restricted band of enamel, they are distinct in having at least four molariform teeth and lacking blade-like lower premolars (Pascual et al., 1999). Moreover, the large-bodied sudamericids evolved high-crowned (hypsodont) molariforms with thick enamel—an adaptation that did not become prevalent among Laurasian mammals for at least another 30 million years (Bonaparte, 1988). Whereas most workers agree that the apomorphic features shared by multituberculates and gondwanatherians probably arose convergently (Pascual et al., 1999; Krause et al., 2003; Kielan-Jaworowska et al., 2004), some contend that their apomorphic features derive from a common ancestor (e.g., Gurovich, 2005). Regardless of their phylogenetic relationships with other Mesozoic mammals, gondwanatherians clearly represent a distinct southern radiation of mammals that likely filled ecological roles similar to those of "Laurasian" multituberculates.

This updated view implies that 3 processes shaped Gondwanan Cretaceous mammal faunas. First, as pointed out by Bonaparte and Kielan-Jaworowska (1987), geographic isolation led to vicariant evolution of mammals endemic to Gondwana, such as australosphenidans and gondwanatherians. Second, mammal lineages experienced differential survival, such that some persisted as relicts on Gondwanan landmasses long after their extinction on Laurasian landmasses (e.g., haramiyidans). Third, infrequent dispersal events may explain the rare occurrences of "Laurasian" mammals, such as eutherians and multituberculates, on Gondwanan landmasses.

Summary and Prospectus

In general, australosphenidans and non-tribosphenic endemics and relicts predominated Gondwanan Cretaceous mammal faunas. However, a notable exception to this pattern is the mammalian fauna from the Late Cretaceous of India. Of the 90 mammalian dental specimens from Maastrichtian infra- and intertrappean beds reported in the literature (Prasad and Sahni, 1988; Prasad et al., 1994; Rana and Wilson, 2003; Khosla et al., 2004; Anantharaman et al., 2006; this paper) and accessioned to GSI collections, almost 90% are eutherian mammals, which have phylogenetic affinities to Laurasian taxa. Although other Indian Late Cretaceous vertebrates have been forwarded as "Laurasian" (see Prasad and Sahni, 1999), they are too fragmentary to confidently assess their phylogenetic affinities (e.g., discoglossid and pelobatid frogs, Thewissen and McKenna, 1992; alligatorid crocodiles, Brochu, 1999). The eutherian mammals (*Deccanolestes*, *Sahnitherium*, unnamed forms) thus remain as the only Indian taxa of unchallenged "Laurasian" affinities and as such, pose several unresolved questions (Prasad and Sahni, 1999; Rana and Wilson, 2003). Did eutherians reach the subcontinent via a chain of island arcs or an indirect Gondwanan route? What biogeographic filters allowed their dispersal but prevented the dispersal of other taxa? Was small body size a factor?

Other Indian Late Cretaceous vertebrates (e.g., abelisaurid theropods, baurusuchid crocodyliforms, haramiyidans, sudamericids) share closest ancestry with taxa from southern landmasses, particularly South America and Madagascar (Wilson et al., 2001, 2003; Anantharaman et al., 2006; Krause et al., 1997). The new sample of *Dakshina* provides additional morphological data that strengthen phylogenetic ties to *Lavanify* from Madagascar and to a lesser extent *Sudamerica* from Argentina, as alluded to by other authors (Krause et al., 1997; Koenigswald et al., 1999; Patnaik et al., 2001). All three taxa possess molariforms with vertical furrows that extend the height of the crown; molariforms of *Dakshina* and *Lavanify* also possess deep infundibula, perikymata, and derived enamel microstructure. This nested pattern of sudamericid phylogenetic relationships (*Gondwanatherium* (*Sudamerica* (*Dakshina*, *Lavanify*))) mirrors the sequence of sundered connections among these southern landmasses (South America (India, Madagascar)) proposed by Hay and colleagues (1999). However, any conclusions drawn from this pattern must be balanced by an understanding of the sampling disparity across Gondwanan landmasses. India, Madagascar, and South America are the only southern landmasses with reasonably sampled Late Cretaceous faunas (Wilson et al., 2003), whereas Australia and Africa are only reasonably sampled during the Early and mid-Cretaceous. Thus, a fuller understanding of Gondwanan biogeography will only emerge with even sampling across its constituent landmasses. Among mammalian forms, both eutherians and gondwanatherians will share a central role in elucidating the biogeographic history of India.

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