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Cosmopolitanism among Gondwanan Late Cretaceous mammals

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Consistent with geophysical evidence for the breaking up of Pangaea, it has been hypothesized that Cretaceous vertebrates on progressively isolated landmasses exhibit generally increasing levels of provincialism^{1–3}, with distinctly heightened endemism occurring at the beginning of the Late Cretaceous⁴. The Cretaceous fossil record from the southern supercontinent of Gondwana has been much too poor to test this hypothesis with regards to mammals (Fig. 1). Early Cretaceous mammals are known only from isolated sites in Argentina⁵, Australia^{6,7}, Cameroon^{8,9} and Morocco¹⁰. Apart from several occurrences in South America¹¹, knowledge of Late Cretaceous Gondwanan mammals is limited to a single site in India that previously yielded a few specimens of placental mammals^{12,13}, and a site in Madagascar that previously yielded only one indeterminate tooth fragment¹⁴. Here we report the occurrence of a highly specialized and distinctive group of extinct mammals, the Sudamericidae (Gondwanatheria), in the Late Cretaceous of Madagascar and India. These new records

comprise the first evidence of gondwanatheres outside South America and the first indication of cosmopolitanism among Late Cretaceous Gondwanan mammals. Antarctica may have served as an important Cretaceous biogeographic link between South America and Indo-Madagascar.

The Gondwanatheria is a group of multituberculate^{15,16} or multituberculate-like¹⁷ mammals previously known only from the Late Cretaceous and Palaeocene of Argentina. Apart from two tentatively referred, fragmentary dentaries (one edentulous and the other bearing a single tooth), Gondwanatheria is based on isolated teeth. The gondwanathere teeth described here are the first identifiable, pre-Late Pleistocene specimens of non-marine mammals known from Madagascar and the first remains of non-placental mammals from the Cretaceous of the Indian subcontinent. The specimens from Madagascar were recovered during joint expeditions by the State University of New York, Stony Brook, and the Université d'Antananarivo in 1995 and 1996 to the continental Upper Cretaceous Maevarano Formation, which, in addition to mammals, has recently yielded a diversity of vertebrate taxa¹⁸. The gondwanathere specimen from India was discovered in 1989 in sediments of the Upper Cretaceous Deccan Intertrappean sequence^{12,13}, but was not identified as that of a gondwanathere until the specimens from Madagascar were examined. None of the lower taxa of mammals from the Late Cretaceous were previously known to be spread across South America, India and Madagascar.

Mammalia Linnaeus 1758

?Allotheria Marsh 1880

Gondwanatheria Mones 1987

Sudamericidae Scillato-Yané and Pascual 1984

Lavanify miolaka gen. et sp. nov.

Etymology. *Lavanify* (la-va-NEE-fee; Malagasy), long tooth; *miolaka* (MYOU-la-ka; Malagasy), curved; in reference to the shape of the cheek-teeth.

Holotype. Université d'Antananarivo (UA) 8653, well-preserved cheek-tooth (Fig. 2a, d).

Referred specimen. Field Museum of Natural History (FMNH) PM 59520, fragmentary cheek-tooth (Fig. 2b).

Localities and horizon. Holotype from locality MAD96-01 and referred specimen from locality MAD93-35, uppermost white sandstone unit of Upper Cretaceous (?Campanian) Maevarano Formation, Mahajanga Basin, near village of Berivotra, northwestern Madagascar.

Diagnosis. The teeth of *Lavanify* differ from those of the only previously known sudamericid genera *Gondwanatherium* and *Sudamerica* in possessing prominent and continuous inter-row sheets of interprismatic matrix in dental enamel and at least one cheek-tooth position that has a single, V-shaped dentine island and lacks enamel on one side of the crown. *Lavanify* further differs from *Gondwanatherium* in having cheek-teeth with vertical furrows that extend to the base of the crown and onto the root.

Description. UA 8653, the holotype specimen, is a molariform, hypsodont cheek-tooth (Fig. 2a). Its preserved height is 11.2 mm, and what are interpreted to be its length and width are 3.4 and 3.2 mm, respectively. The crown, as determined from the distribution of enamel, comprises about 85% of the tooth's height. UA 8653 is strongly curved along its height and worn flat on its occlusal surface. In occlusal view, the worn surface consists of a broad, V-shaped dentine island surrounded by enamel (except along one edge, where breakage has occurred). The indentation of the V is formed by a vertical furrow that extends through the entire height of the tooth and is filled with cementum. Enamel is clearly absent from one side of the crown, where two distinct, vertical enamel–dentine edges are evident. UA 8653 possesses small, circular enamel prisms aligned in rows, which are separated by prominent and continuous bands of interprismatic material (Fig. 2d).

FMNH PM 59520 (Fig. 2b) is tentatively referred to *L. miolaka*

because, like UA 8653, it is large (preserved height, 9.8 mm; length and width cannot be determined), molariform, hypsodont, curved along its height (although slightly less so than UA 8653), worn flat on its occlusal surface, and possesses rows of small, circular enamel prisms separated by prominent inter-row sheets. Unlike UA 8653, FMNH PM 59520 possesses an infundibulum that invaginates deeply from the occlusal surface and contains cementum. A cementum-filled furrow or a second, incompletely preserved infundibulum is present as well, but breakage precludes a determination of which of the two possible conditions exist. The presence of an infundibulum and the lesser degree of curvature suggest that FMNH PM 59520 represents a different tooth position from the holotype. In the absence of conclusive evidence to the contrary, and in the light of the considerable range in morphological variation in molariform tooth positions among other gondwanatheres species^{1,15,16}, UA 8653 and FMNH PM 59520 are provisionally considered to represent the same species.

The isolated nature of the two specimens of *Lavanify miolaka*, as well as poor knowledge of all other known gondwanatheres, precludes a confident determination of whether the specimens represent upper or lower teeth, or whether they are molars or molariform premolars.

Sudamericidae incertae sedis
Genus and species indeterminate

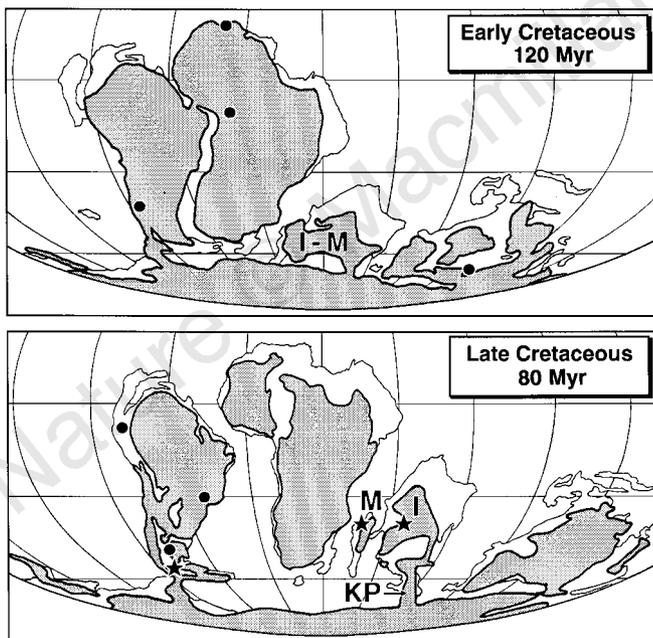


Figure 1 Maps showing distribution of Gondwanan landmasses and known mammal localities in the Early (top) and Late Cretaceous (bottom). Shaded areas indicate the distribution of subaerially exposed land (adapted from ref. 26); dots indicate mammal localities; stars indicate mammal localities that have yielded gondwanatheres. Madagascar (M), with the Indian subcontinent (I) attached to its current eastern margin, separated from Africa ~165 Myr ago and attained its current position relative to the mainland ~124 Myr (refs 23, 25, 29, 30). Strike-slip motion between the Indian subcontinent and Madagascar began ~135 Myr (ref. 25), as India rifted from Antarctica, but they remained in proximity until ~88 Myr (ref. 22), several million years before deposition of the Maevarano Formation¹⁸. Indo-Madagascar (I-M) and eastern Antarctica were connected until at least ~120 Myr (ref. 25), and possibly as late as 80 Myr (ref. 26), across the Kerguelen Plateau (KP). The Antarctic Peninsula remained very close to, or maintained contact with, South America in the Late Cretaceous and into the early Tertiary^{23,24,26}.

Referred specimen. Vertebrate Palaeontology Laboratory, Jammu University, Naskal Intertrappean Mammal (VPL/JU/NKIM) 25, fragmentary cheek-tooth (Fig. 2c, e).

Locality and horizon. Naskal Locality, Andhra Pradesh, central India, in Upper Cretaceous (late Maastrichtian) Deccan Intertrappean sequence.

Description. VPL/JU/NKIM/25 is too incomplete to assign to a particular genus and species, but is complete enough to demonstrate clearly that it possesses a range of characteristics unique to the Sudamericidae among Cretaceous mammals. Although smaller (about 6 mm in height), it resembles the cheek-tooth specimens of known sudamericids, including those of *Lavanify miolaka*, in being molariform, hypsodont, and curved along its height, as well as in possessing a flat occlusal surface and an infundibulum that invaginates far into the crown (Fig. 2c). It also exhibits small, circular prisms aligned in rows that are separated by well-developed inter-row sheets of interprismatic matrix (Fig. 2e). Like *Lavanify*

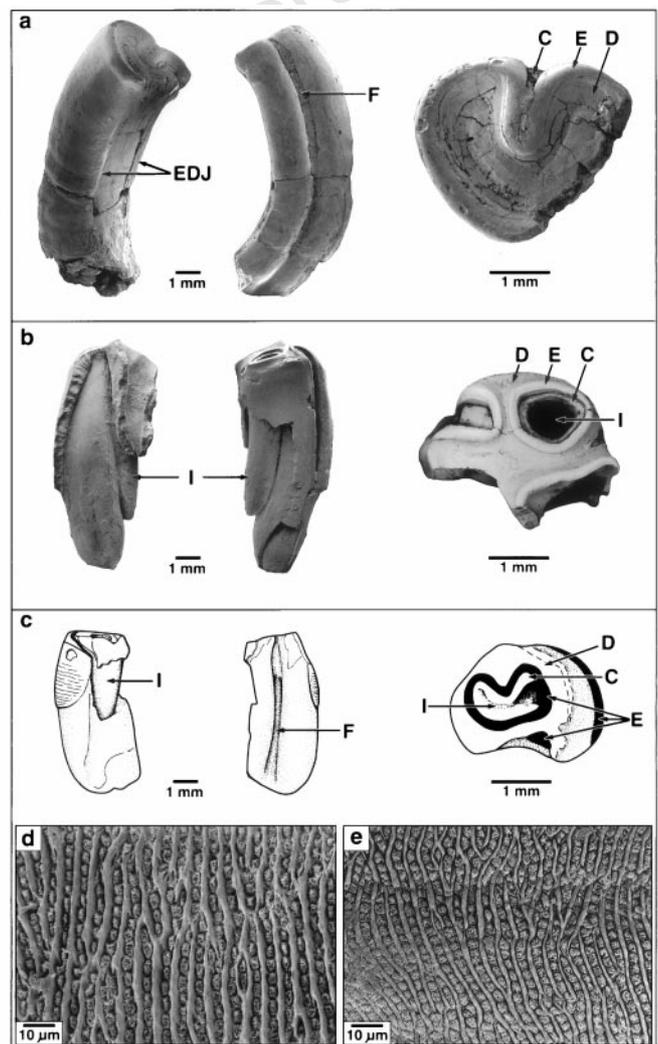


Figure 2 Sudamericids from Madagascar and India. **a, b**, Scanning electron micrographs of cheek-teeth of *Lavanify miolaka* from the Upper Cretaceous Maevarano Formation, Mahajanga Basin, northwestern Madagascar. **a**, UA 8653, holotype, in side (left, middle) and occlusal (right) views. **b**, FMNH PM 59520 in side (left, middle) and occlusal (right) views. **c**, Drawings of cheek-tooth (VPL/JU/NKIM/25) of unnamed Indian sudamericid from the Upper Cretaceous Deccan Intertrappean sequence, India, in side (left, middle) and occlusal (right) views). **d, e**, Scanning electron micrographs of tangential sections of enamel microstructure in *L. miolaka* (UA 8653) and unnamed Indian sudamericid (VPL/JU/NKIM/25), respectively. C, cementum; D, dentine; E, enamel; EDJ, enamel-dentine junction; F, furrow; I, infundibulum.

and *Sudamerica*, the Indian form possesses a prominent, cementum-filled vertical furrow that extends throughout the entire height on the side of the crown. It cannot be demonstrated that enamel is absent on one side of the crown, as in UA 8653, the holotype of *L. miolaka*.

The specimens of *Lavanify* from Madagascar and the unnamed Indian form exhibit several features diagnostic of Gondwanatheria, which were previously known only from Argentina and composed of the ferugliotheriid *Ferugliotherium* (Late Cretaceous, Campanian) and the sudamericids *Gondwanatherium* (Late Cretaceous, Campanian) and *Sudamerica* (early Palaeocene)^{1,15–17}. *Lavanify* and the Indian form are more derived than other gondwanatheres and are tentatively linked with each other on the basis of the shared possession of prominent and continuous inter-row sheets of interprismatic matrix in the enamel (Fig. 3). Although the interprismatic matrix is thick in *Gondwanatherium* and *Sudamerica*^{15,19}, and is, in places, organized into indistinct inter-row sheets¹⁹, it anastomoses around prisms and the sheets are not nearly as well-organized into continuous separate bands as they are in *Lavanify* and the Indian form. However, because this level of differentiation has been recorded at varying depths (albeit of much thicker enamel) in single molars of extant placental mammal species (caprine bovids)²⁰, we caution that additional samples must be discovered and analysed to assess the range of variation in the development of inter-row sheets within gondwanathere species and, thereby, to validate this synapomorphy. *Lavanify* is considered autapomorphic in possessing at least one cheek-tooth position with a single, V-shaped dentine island and the absence of enamel on one side of the crown.

Within the context of current geophysical models for the sequence of fragmentation of Gondwana (Fig. 1), the discovery of sudamericids in the Late Cretaceous of Madagascar and India, in addition to their occurrence in Argentina, has several profound biogeographic implications. First, the Sudamericidae were distributed much more broadly among Gondwanan landmasses during the Late Cretaceous than previously known. Until now it was not known whether the most well-sampled mammalian fauna from the

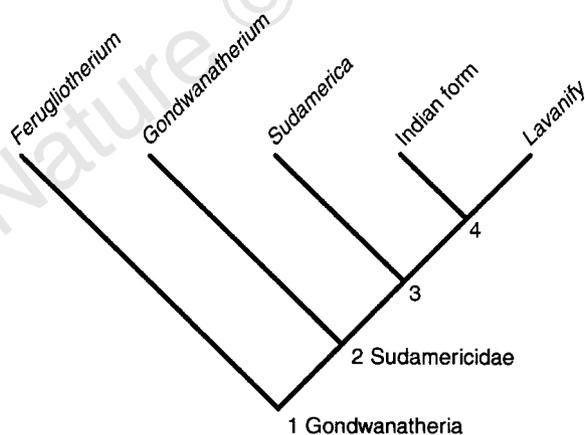


Figure 3 Cladogram showing placement of *Lavanify* and the unnamed Indian sudamericid within Gondwanatheria. The unambiguous synapomorphies diagnosing the nodes are: 1 (Gondwanatheria), prominent transverse ridges and furrows on molariform cheek-tooth crowns, incisors enlarged and procumbent with restricted band of enamel, small and circular enamel prisms; 2 (Sudamericidae), large size, cheek-teeth hypsodont, cheek-teeth curved through height, prominent furrows present on sides of molariform cheek-teeth, infundibula that extend far cervically into molariform cheek-tooth crowns present, cementum present on sides of cheek-tooth crown and inside infundibula, at least one cheek-tooth position with obliquely oriented occlusal plane; 3, presence of furrows on sides of molariform cheek-tooth extending far towards midline of tooth and cervically onto root; and 4, enamel with continuous and prominent inter-row sheets of interprismatic matrix.

Late Cretaceous of Gondwana, from the Los Alamos Formation in Patagonia and which consists of non-tribosphenic forms only, was wholly endemic to Patagonia, South America or Gondwana^{1,15–17}. The presence of sudamericids in both Madagascar and India, in addition to their occurrence in South America, demonstrates clearly that at least some Late Cretaceous mammalian taxa were broadly distributed on Gondwana.

Second, the mammalian fauna from the Late Cretaceous of Madagascar was not highly endemic. The modern mammalian fauna of Madagascar is wholly endemic at the species level and includes several suprageneric taxa that are unique to the island (Lemuroidea, Tenrecinae, Nesomyinae, Galidiinae, Euplerinae and Cryptoproctinae)¹⁸. Because *Lavanify* does not bear a close phylogenetic relationship to any of the modern and recently extinct orders of mammals from Madagascar, it contributes no positive evidence to help solve the mystery of their biogeographic origins.

Third, the mammalian fauna from the Late Cretaceous of the Indian subcontinent, like other elements of the biota²¹, has components that are shared with other Gondwanan landmasses. The only other mammalian taxa described from the Indian Late Cretaceous, the palaeoryctid eutherians *Deccanolestes hislopi* and *D. robustus*, have been suggested to have affinities with taxa of Laurasian origin^{12,13}. The tentative phylogenetic placement of the Indian gondwanathere and *Lavanify* as sister taxa is consistent with geophysical evidence indicating that the Indian subcontinent separated from Madagascar approximately 88 million years ago (Myr)²².

Finally, as well as occurring in South America, Madagascar and the Indian subcontinent, sudamericids must have been present on some intervening landmass(es) in the Late Cretaceous or earlier. The three most likely hypotheses to explain the disjunct distribution of sudamericids in Argentina, Madagascar and India are that sudamericids were: found across the whole of Gondwana; also present in Africa alone; or also present in Antarctica alone. Within known geophysical constraints, and acknowledging that Late Cretaceous vertebrate faunas of Gondwana are generally poorly known, the hypothesis that sudamericids were also present in Antarctica seems the most likely. South America was close to or contiguous with the Antarctic Peninsula in the Late Cretaceous and Indo-Madagascar was close to or contiguous with Antarctica until the late Early Cretaceous^{23–25}. A revised palaeogeographic reconstruction of this region²⁶ suggests a connection between Antarctica and Indo-Madagascar across the Kerguelen Plateau that lasted well into the Late Cretaceous (possibly as late as 80 Myr), as shown in Fig. 1. In contrast, a narrow sinuous seaway surrounding southern Africa developed in the late Early Cretaceous and progressively widened in the Late Cretaceous, isolating Africa from South America and Antarctica^{23,26}. Furthermore, the hypotheses that sudamericids were pan-Gondwanan or were also present in Africa alone predict that either they would have evolved by the Late Jurassic, before the breaking-up of Gondwana in general and before Madagascar rifted from Africa in particular, or that they crossed the Mozambique Channel, which is over 400 km wide at its narrowest point, some time later. Basal gondwanatheres may have originated on, and been restricted to, Gondwana by the Late Jurassic. Sudamericids, however, are highly derived, and it therefore seems unlikely that they existed in the Late Jurassic; whether or not they crossed the Mozambique Channel at a later time is currently untestable. Finally, support for Late Cretaceous biotic connections among South America, Antarctica, Madagascar and the Indian subcontinent can also be derived from other terrestrial vertebrate taxa, particularly dinosaurs. For instance, the derived abelisaurid ceratosaurian theropods *Magungasaurus* and *Indosuchus*, from the Late Cretaceous of Madagascar and India, respectively, are sister taxa and are closely related to taxa from the Cretaceous of Argentina²⁷. In contrast, although fragmentary remains of purported abelisaurids have been recently reported from the Early Cretaceous of Africa²⁸ (as well as from the Late Cretaceous of Europe), the Late Cretaceous theropod fauna of

Africa appears to have been dominated by tetanurans, including carcharodontosaurids, spinosaurids and coelurosaur⁴.

As the Cretaceous fossil record of vertebrates on southern landmasses improves, so too will the ability to test the biogeographic conclusions outlined above. Crucial to these tests will be the recovery of mammalian and other vertebrate fossils from the Late Cretaceous of northern South America, mainland Africa, and Australia, to determine whether or not gondwanatheres and other vertebrate taxa were restricted to a high-latitude route involving only Argentina, Antarctica, Madagascar and the Indian subcontinent, or whether they were distributed even more broadly on Gondwana. At the very least, however, our evidence demonstrates that at least some elements of Late Cretaceous vertebrate faunas were broadly shared among Gondwanan landmasses. □

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Biodiversity enhances ecosystem reliability

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Biodiversity may represent a form of biological insurance against the loss or poor performance of selected species¹. If this is the case, then communities with larger numbers of species should be more predictable with respect to properties such as local biomass². That is, larger numbers of species should enhance ecosystem reliability, where reliability refers to the probability that a system will provide a consistent level of performance over a given unit of time³. The validity of this hypothesis has important ecological, management and economic implications given the large-scale substitution of diverse natural ecosystems with less diverse managed systems⁴. No experimental evidence, however, has supported this hypothesis⁵. To test this hypothesis we established replicated microbial microcosms with varying numbers of species per functional group. We found that as the number of species per functional group increased, replicate communities were more consistent in biomass and density measures. These results suggest that redundancy (in the sense of having multiple species per functional group^{6–8}) is a valuable commodity, and that the provision of adequate redundancy may be one reason for preserving biodiversity.

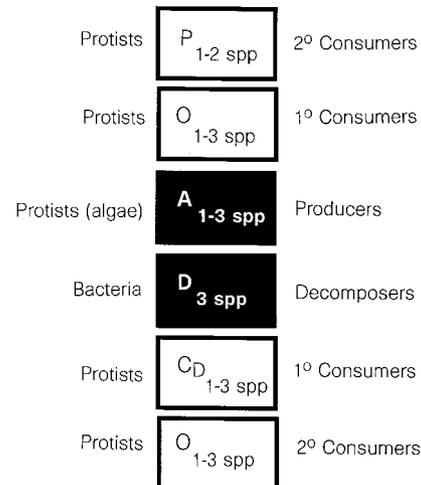


Figure 1 Experimental design. Each microcosm contained two core trophic (functional) groups: autotrophs (A) and decomposers (D). Additional functional groups consisted of species classified as either primary (1°) or secondary (2°) consumers of either A or D. Consumers were all protists species with 1–3 species per functional group, with the exception of top predators (P). Species were chosen at random from the pools of available species (listed below). Because several consumer species were omnivorous (capable of feeding on more than one trophic level) they were classified as omnivores (O). Species in A were *Chlamydomonas reinhardtii*, *Trachelomonas* sp. and *Euglena gracilis*. Species in D were *Serratia marcescens*, *Bacillus subtilis* and *Bacillus cereus*. Consumers of decomposers, C_D, were the ciliate species *Colpidium striatum*, *Spirostomum ambiguum*, *Vorticella* sp., *Stentor* sp. and the flagellate, *Chilomonas paramecium*. Species in O were the ciliates *Euplotes eurystomus*, *Paramecium aurelia*, *Pa. caudatum*, *Pa. multimicronucleatum*, *Blepharisma* sp. and the sarcodinid, *Amoeba proteus*. Species in P consisted of the sarcodinid *Pelomyxa carolinensis* and the ciliate *Didinium nasutum*.