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LATE CRETACEOUS GONDWANATHERIAN MAMMALS OF INDIA: DISTRIBUTION, INTERRELATIONSHIPS AND BIOGEOGRAPHIC IMPLICATIONS

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ABSTRACT

Gondwanatheria is a poorly-known extinct order of the class Mammalia. It represents an enigmatic and distinctive non-tribosphenic radiation of mammals in the Southern Hemisphere with fossils documented from the Late Cretaceous and early Middle Eocene of Argentina, Late Cretaceous of Madagascar and India, ?Cretaceous of Tanzania and ?Middle Eocene of Antarctica. The Indian gondwanatherian mammals are known by two taxa (*Bharattherium bonapartei* Prasad *et al.*, 2007a and *Dakshina jederi* Wilson *et al.*, 2007) from the Upper Cretaceous sediments intercalated with the Deccan volcanic flows (= intertrappean beds) of peninsular India. A close examination of the type specimens of both these Indian sudamericids shows that they are morphologically similar, and given that the publication of *Bharattherium* pre-dates *Dakshina*, the latter is regarded here as a junior synonym of the former. In addition, recent fieldwork in central India has resulted in the discovery of a new sudamericid tooth in the Upper Cretaceous (Maastrichtian) intertrappean beds of Kisalpuri, District Dindori (Madhya Pradesh). Though in having two independent transverse lophs, distinct shape of the lophs, and in the absence of infundibulum, perikymata, and enamel islet this tooth differs from *Bharattherium* and other morphological variation of molariforms in different loci on the dentition of sudamericid mammals. Further, the phylogenetic and palaeobiogeographic relationships of gondwanatherian mammals are reviewed in light of recent fossil discoveries from the Late Cretaceous of India.

Keywords: Late Cretaceous, Gondwanatherians, Mammals, Palaeobiogeography, India

INTRODUCTION

Gondwanatheria is an extinct group of highly derived, nontribosphenic mammals restricted to the Gondwanan continents, whose distinctiveness is conspicuous by the earliest development of hypsodont dentition among mammals. These mammals have been documented from all Gondwanan continents except Australia and New Zealand. They first appeared in the fossil record during the Late Cretaceous and survived until the Middle Eocene. Scillato-Yané and Pascual (1984) described the first gondwanatherian mammal, Sudamerica ameghinoi from the Lower Palaeocene sediments of Patagonia. Two years later, Bonaparte (1986a, 1986b, 1990) reported a second gondwanatherian taxon, Gondwanatherium patagonicum from the Upper Cretaceous sediments of Argentina. Originally, these taxa were assigned to the edentate order Xenarthra (Scillato-Yané and Pascual, 1984; Mones, 1987), but latter they were variously referred to paratherians (Scillato-Yané and Pascual, 1985; Bonaparte, 1986a), multituberculates (Bonaparte et al., 1989; Krause et al., 1992; Krause and Bonaparte, 1993), dubious allotherians (Krause et al., 1997), and Mammalia incertae sedis (Pascual et al., 1999). Cladistic analysis of gondwanatherian mammals led Gurovich and Beck (2009) to propose Gondwanatheria as sister group to Multituberculata. Very recently, Goin et al. (2012) assigned gondwantherians to Allotheria. The order Gondwanatheria, Mones (1987) comprises two families, Ferugliotheriidae and Sudamericidae. Ferugliotheriidae, known by two species (Ferugliotherium windhauseni Bonaparte, 1986b and Trapalcotherium matuastensis Rougier et al., 2009), has been reported from the Late Cretaceous deposits of Argentina

(Bonaparte, 1986b; Krause *et al.*, 1992, Rougier *et al.*, 2009). Another doubtful occurrence of indeterminate ferugliotheriid has been reported from the ?Eocene deposits of Perú, in the western South America (Goin *et al.*, 2004). Kielan-Jaworowska *et al.* (2007) reported a doubtful cimolodontan multituberculate taxon, *Argentodites coloniensis* from the Late Cretaceous deposits of Argentina, but it has been argued that the type specimen of *A. colonienis* could be an unworn p4 of *Ferugliotherium* or some related taxon (Gurovich and Beck, 2009; Rougier *et al.*, 2009).

Sudamericidae has a more cosmopolitan distribution with reports coming from South America, Antarctica, ?Africa, Madagascar and India. The sudamericid gondwanatherians are currently represented by G patagonicum Bonaparte, 1986a known from the Campanian-Maastrichtian of Argentina; S. ameghinoi Scillato-Yané and Pascual, (1984) from the Early Palaeocene of Argentina; Lavanify miolaka Krause et al., (1997) from the Maastrichtian of Madagascar and Bharattherium bonapartei (= Dakshina jederi Wilson et al., 2007) Prasad et al. (2007a) from the Maastrichtian of India. In addition, unnamed sudamericid gondwanatherians have also been reported from the ?Cretaceous of Tanzania (Krause et al., 2003), ?Middle Eocene of Antarctica (Goin et al., 2006) and an undescribed possible sudamericid from the Middle Eocene of Perú (Antoine et al., 2012). A new gondwanatherian taxon, Greniodon sylvaticus has very recently been described from the early Middle Eocene sediments of northwestern Patagonia, Argentina (Goin et al., 2012). This taxon extends the age range of gondwantherians up to early Middle Eocene in South America but its specific affinities with ferugliotheriids or sudamericids

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are still not clearly understood.

More recently, a new sudamericid gondwanatherian tooth has been recovered from the Upper Cretaceous Deccan intertrappean beds exposed 1.5 km southwest of Kisalpuri village, Dindori District (Madhya Pradesh), Central India (Fig. 1). The siltstone unit of Kisalpuri site (refer to fig.1 of Prasad et al., 2007a) preserves a relatively diverse microvertebrate fauna represented by fishes, frogs, turtles, lizards, snakes, crocodiles, dinosaurs and mammals (Khosla et al., 2004, 2009; Prasad et al., 2007a, 2007b, 2010; Verma, 2008; Goswami et al., 2011). Based on the similarity of faunas known from other Deccan infra- and intertrappean sites, particularly those of the Naskal, Asifabad, Marepalli and Jabalpur (Khosla and Sahni, 2003; Khosla et al., 2004), a Maastrichtian age and a lacustrine environment of deposition in a coastal-plain milieu have been inferred for this site. The objective of this paper is to describe newly discovered tooth (Sudamericidae indet.), provide upto-date taxonomic and geographical overview of Indian sudamericids, and discuss the phylogenetic relationships and biogeographic implications of sudamericid gondwanatherian mammals in the light of recent fossil finds from India. The specimen is housed in the Palaeontological Laboratory, Indira Gandhi National Open University, New Delhi and has the acronym PL/IGNOU/103.

INSTITUTIONAL ABREVIATIONS

FMNH: Field Museum of Natural History, Chicago, USA; GSI/SR/PAL-G/N: Geological Survey of India, Southern Region, Palaeontological Division, Gokak/Naskal, India; MACN-RN: Museo Argentio de Ciencias Naturales, Rio Negro Collection, Argentina; VPL/JU: Vertebrate Palaeontological Laboratory, University of Jammu, Jammu, India; UA: Universite d' Antananarivo, Antananarivo, Madagascar; and PL/IGNOU: Palaeontological Laboratory, Indira Gandhi National Open University, New Delhi, India.

SYSTEMATIC DESCRIPTION

Class Mammalia Linnaeus, 1758

Order Gondwanatheria Mones, 1987

Family **Sudamericidae** Scillato-Yané and Pascual, 1984 Gen. et sp. indet.

(Pl. I, figs. A-E; Fig. 2 A-C)

Material: PL/IGNOU/103, a well-preserved isolated tooth, tentatively identified as left mf4.

Horizon, locality and age: Siltstone unit of Upper Cretaceous (Maastrichtian) Deccan intertrappean beds exposed near Kisalpuri village in Dindori District, Madhya Pradesh state, Central India.

Description: PL/IGNOU/103 is a well-preserved, hypsodont molariform tentatively identified as a left mf4 on the basis of criteria given in the earlier works (Koenigswald *et al.*, 1999; Pascual *et al.*, 1999; Gurovich, 2006, 2008). We use the term molariform instead of molar or premolar because the existing terminology offers no suggestion as to the position of the teeth on the jaw is concerned owing to poor fossil record. The crown is high and moderately curved along its height, wider at the base and becomes constricted or narrower towards the occlusal surface. The lingual face of the crown is convex while its labial face is concave. The root of the tooth is open and wide. In occlusal view, it has trapezoidal outline with narrow posterior and broad anterior ends (Pl. I, figs. D, E). The flat occlusal surface is divided by a "D-shaped" valley into two asymmetrical independent transverse lophs bounded by

enamel ridges (Pl. I, fig. A, Fig. 2 A). The valley contains cementum and invaginates in the labial and lingual faces of the crown. It has one narrow opening each on the labial and lingual faces. In occlusal view, labial and lingual openings of the valley are in the form of trenchant synclines (e.g., Koenigswald et al., 1999, fig. 1A); the lingual trenchant syncline is more prominent than the labial one. Both anterior and posterior lophs of the crown are labio-lingually elongated. The anterior loph is roughly crescent in shape and about twice as large as the posterior loph and completely filled with dentine. It has a concave posterior face (Pl. I, fig. D) and the enamel border of its lingual face is worn downwards one-third the height of the crown (Pl. I, figs. A, E). The labial face of anterior loph is slightly higher than its lingual face. In occlusal view, a very small, antero-labially to postero-lingually oriented dentine crest occurs on the anterior most margin of the anterior loph (Fig. 2A). The posterior loph is smaller than anterior loph, subcrescent in shape and is situated in a postero-labial position. It is bounded by an enamel band and is filled with dentine. The enamel border of posterior loph is concave anteriorly and rounded posteriorly.

The anterior and posterior lophs of the crown are not connected by an enamel bordered ridge or a transverse parasagittal enamel crest (Pl. I, fig. A). In occlusal view, there is no enamel islet. The crown has a thick enamel layer that forms vertical furrows on both labial and lingual faces. The lingual vertical furrow is more prominent, deep, V-shaped and welldeveloped than its labial counterpart, and extends through the entire height of the tooth. It is narrow both at the base and apex of the crown, but wide at its mid-height. The lingual furrow bears only a little cementum near the apex of the crown (Pl. I, fig. C). The labial furrow is restricted to the apical part of the crown (Pl. I, fig. B) and contains no cementum. In occlusal



Fig. 1. Map of India showing outline of states covered by the Deccan basaltic lava flows (black color) and the location of sudamericid gondwanatherian mammal-yielding sites marked by stars. 1. Naskal, 2. Bacharam, 3. Kisalpuri, and 4. Gokak.

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Plate I



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EXPLANATION OF PLATE I

(Scale bar is equal to 1 mm)

view, both lingual and labial vertical furrows join by a "D-shaped" valley.

Measurements in mm: Maximum height of PL/IGNOU/103 (from the occlusal surface to the base of the crown): 5.7 mm; maximum labio-lingual width (measured anteriorly): 1.8 mm; minimum labio-lingual width (measured posteriorly): 1.2 mm; antero-posterior length (in occlusal view): 2.1 mm; and antero-posterior length (at the base of the tooth): 2.7 mm.

Affinities and Comparisons: Any phylogenetic affinities of PL/IGNOU/103 with F. windhauseni Bonaparte. (1986b) and T. matuastensis Rougier et al., 2009 (Family Ferugliotheriidae) are ruled out as the latter has brachydont cheek-teeth (Bonaparte, 1986b; Krause et al., 1992). Several key features, such as hypsodont molariform, flat occlusal surface with two independent asymmetrical lophs separated by a "D-shaped" valley, a lingually well-developed, continuous and deep vertical furrow that extends through the height of the crown, and a small labial vertical furrow, favour the placement of the new tooth in the family Sudamericidae. The molariform shares some fundamental plesiomorphies with G patagonicum: high crown with flat occlusal surface and two asymmetrical transverse lophs with each loph bounded by a thick enamel layer. However, it is distinguished from the holotype (MACN-RN 22) and referred specimens (MACN-RN 23, MACN-RN 25) of G patagonicum in having two isolated or independent asymmetrical enamel lophs rather than three lophs; this difference may be attributed to differing positions on the jaw as it is the case with sudamericid mammals (Koenigswald et al., 1999; Pascual et al., 1999). Furthermore, another referred specimen of G. patagonicum (MACN-RN 24) exhibits close resemblance to PL/IGNOU/103 in having two transverse enamel lophs in occlusal view, but differs from it in having two well developed vertical furrows each on the lingual and labial faces (Bonaparte, 1986a; Gurovich, 2006).

The dental morphology of S. ameghinoi is more derived than that of PL/IGNOU/103 in possessing transverse enamel lophs, formed by lateral and opposed invaginations of the enamel; the deep enamel lophs connected by an anteroposteriorly directed enamel ridge (see Gurovich, 2008, fig. 3A) and by the presence of a central enamel islet (Krause and Bonaparte, 1993; Koenigswald et al., 1999; Pascual et al., 1999; Pascual and Ortiz-Jaureguizar, 2007; Gurovich, 2008). However, S. ameghinoi shares an important apomorphy with the new molariform, i.e. the presence of a deep and well developed "Vshaped" vertical furrow that extends from the base to the crown of the tooth on the lingual side only. Some molariforms of S. ameghinoi (e.g., figs. of MACN Pv-CH 1932 in appendix B-7 and MACN Pv-CH 1484 in appendix B-8 of Gurovich, 2006) have independent transverse lophs bounded by enamel ridges as in the case of new molariform.

The type specimen (UA 8653) of *L. miolaka* is a wellpreserved molariform, hypsodont cheek-tooth (Krause *et al.*, 1997) tentatively identified as a left mf4 (Wilson *et al.*, 2007). It exhibits some similarity with PL/IGNOU/103 in being longitudinally curved with a flat occlusal surface and a vertical furrow that extends through the entire height of the tooth. FMNH PM 59520, a fragmentary cheek-tooth provisionally referred to *L. miolaka* (Krause *et al.*, 1997), has a deep infundibulum filled with cementum and bordered by an enamel layer, and an enamel islet. PL/IGNOU/103 has also a deep valley filled with cementum and bounded by the enamel layers of the anterior and posterior lophs, and is less curved longitudinally



Fig. 2. Schematic drawings of molariforms of suadmericid gondwanatherian mammals. (A-C) Lower molariform of Sudamericidae indet., left mf4 (PL/IGNOU/103), A, occlusal view; B, lingual view; C, labial view. (D-G) Molariforms of *Bharattherium bonapartei* (= *Dakshina jederi* Wilson *et al.*, 2007) Prasad *et al.*, 2007a. (D-E), holotype of *Bharattherium bonapartei* (VPL/JU/IM/33), D, occlusal view; E, lingual view. (F-G), holotype of *Dakshina jederi*, right mf4 (GSI/SR/PAL-G074), F, occlusal view; G, lingual. Figures D – E redrawn after Prasad *et al.* (2007a), and E – G after Wilson *et al.* (2007). d – dentine, dc – dentine crest, edj – enamel dentine junction, e – enamel, f – furrow, i – infundibulum, and v – valley. Scale bars equal to 1 mm.

than in *L. miolaka*. However, *Lavanify* has a single "V-shaped" loph as compared to two distinct lophs on PL/IGNOU/103 in occlusal view.

PL/IGNOU/103 shares at least one character with *B. bonapartei*: 1) presence of lingual vertical furrow that extends through the entire height of the crown. However, it differs from *Bharattherium*: 1) in having an occlusal surface divided into

two independent, enamel-bounded, asymmetrical transverse lophs; 2) absence of incremental growth lines (i.e. perikymata); 3) presence of a short labial vertical furrow; 4) absence of an enamel islet; 5) lack of a well-developed infundibulum; and 6) presence of distinct and deep "D-shaped" valley that opens on both labial and lingual ends (Figs. 2 D-G). In the three specimens (GSI/SR/PAL-G070, GSI/SR/PAL-N071, GSI/ SR/PAL-N212) referred to D. jederi, the occlusal surface is not divided into separate lophs as in PL/IGNOU/103. In addition, the new molariform differs from GSI/SR/PAL-G070 and GSI/ SR/PAL-N071 in several other characters: 1) absence of an enamel islet; 2) presence of "D-shaped" valley; and 3) anterior loph higher than the posterior loph resulting in a distinct step between the two lophs. GSI/SR/PAL-G059 is another referred specimen of D. jederi tentatively identified as a left mf3 (Wilson et al., 2007). In occlusal view, it consists of three transverse lophs and preserved lingual aspect of the crown suggests that a single outer enamel band encircled the three transverse lophs, as in the case of the molariform teeth of Sudamerica. In these features, GSI/SR/PAL-G059 is morphologically closer to Sudamerica than to PL/IGNOU/103. Unfortunately, we cannot compare PL/IGNOU/103 with gondwanatherian specimens from Antarctica and Tanzania because of their poor state of preservation. However, it differs from recently described relatively young gondwantherian, G. sylvaticus, known by upper two molariforms that are characterized by having occlusal surfaces which are not flat but labio-lingually concave, strong grooves and deep enamel islets and more transverse lophs (Goin et al., 2012).

From the above comparisons, it is clear that the new molariform from India shares at least one derived feature with S. ameghinoi, L. miolaka and B. bonapartei: a vertical furrow that extends to the base of the teeth on the lingual face (G. patagonicum possesses vertical furrows with varying length as in the case of PL/IGNOU/103, see Krause et al., 1997; Gurovich, 2008). PL/IGNOU/103 and G. patagonicum also share the following features: an occlusal surface consisting of independent transverse lophs bounded by enamel ridges, furrows connecting labial and lingual cusp rows, small occlusal surface in comparison to a wider crown and root, slight curvature throughout the height of the tooth, and a short labial furrow. Even though the overall morphology of new tooth is so unique from that of Sudamerica, Lavanify and Bharattherium and despite the general similarity to that of Gondwanatherium, we do not prefer to place it in a new taxon as there is much uncertainity regarding the variation in dental morphology along the length of the jaw in sudamericid mammals.

TAXONOMIC REVISION OF INDIAN SUDAMERICIDS

Class Mammalia Linnaeus, 1758

- Order Gondwanatheria Mones, 1987
- Family Sudamericidae Scillato-Yané and Pascual, 1984
- *Type Genus* **Bharattherium** Prasad, Verma, Sahni, Krause, Khosla and Parmar, 2007a, p. 19. **Dakshina** Wilson, Sarma and Anantharaman, 2007, p. 522
- Type Species: *Bharattherium bonapartei* Prasad, Verma, Sahni, Krause, Khosla and Parmar, 2007a, p. 19.

Junior Synonym: *Dakshina jederi* Wilson, Sarma and Anantharaman, 2007, p. 522.

Type and only known species

Bharattherium bonapartei Prasad, Verma, Sahni, Krause,

Khosla and Parmar

(Figs. 2. D-G)

Holotype: VPL/JU/IM/33, well-preserved molariform cheek-tooth.

Stratigraphic distribution: Upper Cretaceous (Maastrichtian) Deccan intertrappean sediments of Kisalpuri in Madhya Pradesh, Naskal in Andhra Pradesh and Gokak in Karnataka, India.

Referred specimens: VPL/JU/NKIM/25, fragmentary cheektooth (Krause *et al.*, 1997, fig. 2c; Prasad *et al.*, 2007a, figs. 1km, 4a-f); GSI/SR/PAL-G074, tentatively identified right mf4 (Wilson *et al.*, 2007, figs. 2A-E); GSI/SR/PAL-G070, tentatively identified right mf4; (Wilson *et al.*, 2007, figs. 3A-B); GSI/SR/ PAL-N071, left mf4 (Wilson *et al.*, 2007, figs. 3C-E); GSI/SR/ PAL-N212, right mf4 (Wilson *et al.*, 2007, figs. 3F); GSI/SR/PAL-G059, left mf3 (Wilson *et al.*, 2007, figs. 4A-C) and GSI/SR/ PAL-N210, left lower incisor (Wilson *et al.*, 2007, figs. 4D-E).

Comments on the taxonomic validity of Dakshina jederi: In 2007, two new sudamericid gondwanatherians were described: Bharattherium bonapartei (Prasad et al., 2007a) from the Upper Cretaceous intertrappean beds of Kisalpuri, Madhya Pradesh state and Dakshina jederi Wilson et al. (2007) from the Upper Cretaceous intertrappean beds of Naskal, Andhra Pradesh state and Gokak, Belgaum district, Karnataka state. VPL/JU/IM/33, the holotype of *B. bonapartei*, shares a number of morphological features with GSI/SR/PAL-G074 (fourth lower molariform) designated as the holotype of D. jederi. Both these molariform teeth are characterized by a flat occlusal surface, having subrounded to rectangular outline, curved along their height, prominent vertical furrow on the lingual face, deep infundibulum, and enamel bounded occlusal surface bearing V-shaped or heart-shaped enamel islet. The enamel islet partially filled with cementum lies adjacent to the lingual vertical furrow and extends along the whole height of the crown on the lingual face. Incremental growth lines or transverse wave-like bands known as perikymata are present on the crown of both specimens and occur on the entire height of enamel crown surface of the molariforms. Some minor differences such as shallow indentation on the labial face of GSI/SR/PAL-G074, slightly less developed furrow on the lingual face and absence of enamel on the postero-lingual face of VPL/JU/IM/33, shape of enamel islet (V-shaped on GSI/SR/ PAL-074, heart-shaped on VPL/JU/IM/33) are regarded here as differences due to positional variation on the jaw and/or intraspecific variation. In view of remarkable similarity in the morphology of VPL/JU/IM/33 and GSI/SR/PAL-G074 and as the publication of *B. bonapartei* pre-dates that of *D. jederi*, the former name has priority over the latter. Accordingly D. *jederi* is formally treated here as a junior synonym of B. bonapartei.

Revised diagnosis of B. bonapartei: Differs from *G. patagonicum* and *S. ameghinoi* in that molariforms have well developed, continuous inter-row sheets of interprismatic matrix in the enamel (Krause *et al.*, 1997; Koenigswald *et al.*, 1999; Patnaik *et al.*, 2001), sub-rectangular molariform crowns with a V or U-shaped dentine island enclosing a heart-shaped enamel islet, presence of lingual vertical furrow on the crown, deep

infundibulum, occurrence of perikymata, and in the absence of enamel on the concave labial face of the tooth (Prasad *et al.*, 2007a; Wilson *et al.*, 2007). Differs from PL/IGNOU/103 in that molariforms have a flat occlusal surface not divided into independent transverse enamel lophs, in the presence of enamel islets, and in the absence of a vertical furrow in the labial face. Differs from the holotype of *L. miolaka* by having an enamel islet in 'V' shaped dentine island (Prasad *et al.*, 2007a; Wilson *et al.*, 2007). Further, differs from the referred specimen of *L. miolaka* (FMNH PM 59520) which possesses possibly two deep infundibula (Krause *et al.*, 1997) instead of one in *Bharattherium* (Prasad *et al.*, 2007a).

SPATIAL DISTRIBUTION OF GONDWANATHERIANS IN INDIA

The record of gondwanatherian mammals from India is very poor, represented by isolated and fragmentary cheekteeth and is restricted to the Maastrichtian epoch of the Late Cretaceous. The first specimen of gondwanatherian mammal, a cheek-tooth (VPL/JU/NKIM/25), was discovered in 1989 from the intertrappean beds of Naskal by GVRP. Additional specimens of gondwanatherias were collected by Das Sarma (1994), Das Sarma et al. (1995) and Anantharaman and Das Sarma (1997) from the same site, but none of them were described in detail. While describing the isolated specimens of sudamericid gondwanatherians from Madagascar and India, Krause et al. (1997) provided for the first time a systematic description of the fragmentary gondwanatherian tooth (VPL/ JU/NKIM/25) recovered from the intertrappean beds of Naskal. Krause et al. (1997) considered that VPI/JU/NKIM/25 is too incomplete to name but has preserved morphological details which are adequate enough to demonstrate that it possesses a range of characters unique to the Sudamericidae among Cretaceous mammals. The Indian specimen is smaller (about 6 mm in height) than Lavanify from Malagasy, hypsodont in nature, and curved along its height. It has a flat occlusal surface and an infundibulum that invaginates deep into the crown. Further studies on the enamel microstructure on the Indian sudamericid specimens suggested that VPL/JU/NKIM/25 is quite derived with respect to the South American gondwanatherians and closely related to Lavanify in possessing prominent and continuous inter-row sheets of interprismatic matrix of enamel (Krause et al., 1997; Koenigswald et al., 1999; Patnaik et al., 2001). The current fossil record of sudamericid gondwanatherians from the Indian subcontinent shows that they had a wide geographic distribution during the Late Cretaceous (Maastrichtian) in the subcontinent as their fossil remains are known from four widely separated sites viz., Naskal, located about 70 km west of Hyderabad city, Andhra Pradesh state (Krause et al., 1997); Kisalpuri, located 1.5 km southwest of village Kisalpuri, Dindori District, Madhya Pradesh state (Khosla et al., 2004, 2009; Prasad et al., 2007a; Verma, 2008); Gokak, Belgaum District, Karnataka (Wilson et al., 2007), and Bacharam situated in the proximity of Naskal intertrappean site (Anantharaman et al., 2006) (Fig. 1).

INTERRELATIONSHIPS OF GONDWANATHERIA

The interrelationships of gondwanatherians among the Mesozoic mammals have been much debated due to its poor fossil record and the restricted occurrence of this group in the Gondwanan continents. A few attempts have been made to resolve the phylogeny of these mammals (e.g., Krause *et al.*,

1992; Krause and Bonaparte, 1993; Pascual et al., 1999; Gurovich and Beck, 2009). Initially, they were regarded as early representatives of the Order Xenarthra (Scillato-Yañe and Pascual, 1985). Latter, based on their dental morphology and on the inferred pattern of jaw movement, gondwanatherians were identified as a complex group of Gondwanan multituberculates (Krause and Bonaparte, 1990, 1993; Krause et al., 1992; Kielan-Jaworowaska and Bonaparte, 1996). The phylogenetic relationships of South American gondwanatherians (Ferugliotherium, Gondwanatherium, and Sudamerica) were discussed in detail by Krause and Bonaparte (1993). Based on observed similarities in dental and incisor morphology, enamel ultrastructure and inferred jaw movement, they argued that Ferugliotherium, Gondwanatherium and Sudamerica evolved from a common ancestor, but Gondwanatherium is more derived than Ferugliotherium, and Sudamerica is a sister-taxon of Gondwanatherium. Krause and Bonaparte (1993) also presented a cladogram based on 11 dental characters summarizing the phylogenetic relationships within Gondwanatheria and argued that gondwanatherians appear to represent the plagiaulacid multituberculate grade of evolution.

Pascual et al. (1999), however, raised doubts on the multituberculate affinities of gondwanatherians and placed them in Mammalia incertae sedis based on a newly discovered dentary of Sudamerica bearing two molariform cheek-teeth, the root of an enlarged central incisor and alveoli for two more cheek-teeth distally from the Early Palaeocene of Argentina. Pascual et al. (1999) also inferred that Sudamerica and probably other representatives of Gondwanatheria lacked premolars and apparently had four molariform cheek-teeth, a condition unknown in multituberculates. Kielan-Jaworowska et al. (2004) accepted the argument of Pascual et al. (1999) that gondwanatherians are not related to multituberculates. Latter, Pascual and Ortiz-Jaureguizar (2007) suggested that gondwanatherians form the sister-group to multituberculates, but these authors did not present any phylogenetic analysis in support of this. A very recent phylogenetic analysis of Gondwanatheria based on maximum parsimony and Bayesian analyses by Gurovich and Beck (2009) placed Ferugliotherium and sudamericid gondwanatherians in a clade with cimolodontan and "plagiaulacidan" multituberculates. They also hypothesized that the gondwanatherians are members of Gondwanan multituberculates in which anterior molariforms evolved from blade-like premolars similar to p4 of Ferugliotherium, possibly in response to an adaptation to a hard diet including grasses that appeared in the Gondwanan continents during the Cretaceous.

Based on diagnostic dental characters of *Lavanify* and the Indian sudamericid (VPL/JU/NKIM/25), such as highly specialized hypsodont teeth with flat occlusal surfaces, cementum filled vertical furrows and enamel with continuous and prominent inter-row sheets of interprismatic matrix, Krause *et al.* (1997) suggested that *Lavanify* and the Indian form are more derived than *Gondwanatherium* and *Sudamerica*. The recent reports of *Bharattherium bonapartei* Prasad *et al.*, 2007a (*=Dakshina jederi*) from the Late Cretaceous of India have provided additional data supporting close phylogenetic relationship with *Lavanify* and, to some extent, with *Sudamerica*, as previously suggested (Krause *et al.*, 1997; Koenigswald *et al.*, 1999; Patnaik *et al.*, 2001).

PALAEOBIOGEOGRAPHIC IMPLICATIONS

The separation of India from Madagascar, a major geotectonic event of the Indian Ocean, took place at about 88 Ma (Storey et al., 1995), following which the Indian subcontinent drifted away from the southern continents across the Tethys Sea to reach its present position. The Late Cretaceous biogeographic history of the Indian mammals has been a subject of debate for long. The reason being, the current state of knowledge of these mammals remains tantalizingly poor and unsatisfactory as a consequence of limited fossil record (Prasad, 2005; Verma, 2008). As a result, Late Cretaceous mammals from India pose more phylogenetic and biogeographic questions than they answer. Among the Late Cretaceous mammals of the Indian subcontinent, gondwanatherians have profound implications for the reconstruction of evolutionary and biogeographic history of Gondwanan mammals (Fig. 3). Prior to 1989, gondwanatherians were known only from Late Cretaceous (Campanian-Maastrichtian) and Middle Eocene of Argentina (Scillato-Yané and Pascual, 1984, 1985; Bonaparte, 1986a) and were considered endemic to South America. However, latter discoveries of sudamericid mammals from Late Cretaceous of India and

Madagascar (Krause *et al.*, 1997), and unnamed taxa from ?Cretaceous of Tanzania (Krause *et al.*, 2003) and ?Middle Eocene of Antarctica (Goin *et al.*, 2006) provided strong evidence for wide geographic distribution of sudamericid gondwanatherians in the Gondwanan continents. The recent discovery of *Bharattherium bonapartei* Prasad *et al.*, 2007a (*=Dakshina jederi* Wilson *et al.*, 2007) from the Late Cretaceous of central India indicated a widespread distribution for this group in India as well.

Although the discovery of an unnamed sudamericid gondwanatherian from the Middle Eocene of Antarctica confirms the cosmopolitan distribution for this group within former Gondwanaland (Reguero *et al.*, 2002; Goin *et al.*, 2006), the discovery of a sudamericid mammal from the Late Cretaceous of Antarctica is crucial for confirming the Late Cretaceous terrestrial connection between South America and Indo-Madagascar via Antarctica and Kerguelen Plateau as suggested by Krause *et al.* (1997). The presence of sudamericid in the Middle Eocene of the Antarctic Peninsula can be explained in three ways: 1) sudamericid mammals may already have been present on Antarctica in the Late Cretaceous and the Middle Eocene record may represent the late survivor of



Fig. 3. Map showing positions and coastlines of Late Cretaceous landmasses (70 Ma) (Smith *et al.*, 1994) and the distribution of sudamericid gondwanatherian sites from Cretaceous-Middle Eocene. Late Cretaceous sites are Campanian-Maastrichtian of Patagonia (A); Maastrichtian of Madagascar (B), Maastrichtian of India (C – Naskal, D – Gokak, E – Kisalpuri, F – Bacharam). Early Palaeocene of Patagonia (G), Middle Eocene of Antarctica (H), and Cretaceous deposits from Tanzania (I). Inset is a life reconstruction of sudamericid mammal drawn by Ezequiel Vera (after Gurovich, 2006).

the pre-existing stock. Absence of these mammals in the Late Cretaceous of Antarctica may be an artifact of unfavourable preservational conditions or limited exploratory work; 2) as the land connection was maintained between South America and Antarctica until the Middle or Late Eocene, it is quite possible that the Middle Eocene record of sudamericid mammals from Antarctica may possibly represent a post-Cretaceous dispersal event; 3) the ancestral stock of gondwanatherian mammals had a pan-Gondwanan distribution prior to the fragmentation of Gondwana landmass. The presence of a tentatively identified gondwanatherian mammal in the Cretaceous of Tanzania (Krause *et al.*, 2003) can be shown in support of a pan-Gondwanan distribution for this group of mammals and Late Cretaceous occurrences can be regarded as relicts of former widely distributed group.

Based on the presence of non-mammalian vertebrates such as abelisaurid dinosaurs, leptodactylid and ranoid frogs, pelomedusoid turtles, and madtosiid and nigerophiid snakes of Gondwanan affinities in the Late Cretaceous of India (see Prasad and Sahni, 1999, 2009), many intra-Gondwanan biogeographic links have been proposed by various workers. These include subaerial connections between South America and Indo-Madagascar via Antarctica and Kerguelen Plateau/ Gunnerus ridge that existed until 88 Ma ago (Krause et al., 1997; Hay et al., 1999; Case, 2002); Late Cretaceous India and South America dispersal route via Ninetyeast Ridge-Kerguelen-Antarctica (Chatterjee and Scotese, 2010); Late Cretaceous land connection between India and Africa through Greater Somalia (Chatterjee and Scotese, 1999; Briggs, 2003); Late Cretaceous dispersal corridor consisting of submerged aseismic tectonic elements of southern Indian Ocean between Indo-Madagascar and Africa (Sahni, 1984), and a terrestrial link between India and Madagascar via the Seychelles plateau at the close of the Late Cretaceous (ca. 65 Ma ago) (Averianov et al., 2003; Rage, 2003). Of all these palaeobiogeographic models, the one proposed by Krause et al. (1997) has been widely debated. According to this model, the Kerguelen plateau was subaerially exposed in the Late Cretaceous (possibly as late as 80 Ma ago) and provided a stable corridor for the dispersal of terrestrial biota between East Antarctica and Indo-Madagascar. However, the recent studies, based on detailed analysis of the current palaeogeographical data on the Kerguelen plateau and Gunnerus ridge, suggested that the Kerguelen plateau - Gunnerus ridge subaerial connections could not have served as a terrestrial link in the Late Cretaceous between Antarctica and India as they were separated from India and Antarctica by extensive stretches of sea-water by late Middle Cretaceous (ca. 80 Ma) (Ali and Aitchison, 2009; Ali and Krause, 2011).

Krause *et al.* (2003) also argued that sudamericid gondwanatherians may have had a pan-Gondwana distribution. The pan-Gondwana distribution of sudamericids points to the fact that they may have evolved earlier, may be in Late Jurassic or Early Cretaceous, prior to the fragmentation of the former Gondwanaland. Their absence in Australia and New Zealand may be considered as an artifact of limited field investigations in these areas. Pascual and Ortiz-Jaureguizar (2007) argued that South American gondwanatherians represent a vicariant radiation of well-known Laurasian Mesozoic mammalian lineage Multituberculata, and that this group of mammals lived as Pangaean relicts in Gondwanan landmasses, when the South American continent was still connected to the Antarctic

Peninsula in the south and to North America in the north. On the other hand, based on the Cretaceous tetrapod faunal comparisons of India and South America, Bonaparte (1999) emphasized that the faunal similarities between India and South America do not necessarily imply the existence of direct physical connections, but instead it may point to a broad geographical distribution of faunas prior to the break-up of the Gondwanan landmasses. The pan-Gondwana model, though, seems to be the most likely biogeographical scenario to explain the wide geographic distribution of sudamericid gondwanatherians in the Gondwanan continents, crucial for testing this model are precise dating of gondwanatherian yielding rocks of Tanzania and recovery of sudamericids from rocks older than Late Cretaceous age. Recently, Sereno et al. (2004) based on the presence of abelisaurid dinosaurs from Neocomian of Niger (Africa), proposed that South America and Africa remained connected by a trans-oceanic passage until at least the end of Early Cretaceous (ca. 90 Ma). This may have also facilitated the dispersal of sudamericid mammals into east Africa and from there to Indo-Malagasy across the Mozambique Channel or Arabia. If the east African gondwanatherian specimen shares any derived characters with Lavanify and Bharattherium, it may imply late dispersal between Africa and Indo-Madagascar. A recent study argued that during the Eocene, the ocean currents fueled sweepstakes dispersal of animals from Africa to Madagascar (Ali and Huber, 2010). It may be speculated that similar dispersals of sudamericid gondwanatherians may have occurred between Africa and Indo-Madagascar during Late Cretaceous. However, this needs to be tested with data on Late Cretaceous ocean circulation patterns of the Indian Ocean, particularly from Mozambique Channel and well-preserved and precisely dated sudamericid specimens from Africa.

As far as Cretaceous mammalian fossil record of India is concerned, currently four mammal groups consisting of adapisoriculids, an archaic ungulate, one haramiyidan and probably two sudamericids have been identified from the startigraphically restricted Maastrichtian (latest Cretaceous) strata in India. Among these groups, adapisoriculids (Deccanolestes and Sahnitherium) and archaic ungulate (Kharmerungulatum) represent undisputed eutherians from the Gondwanan continents. Kharmerungulatum has been interpreted as an immigrant from Laurasia or as a product of indigenous evolution (Prasad et al., 2007b). The haramiyid (Avashishta) was considered as a Gondwanan relic (Anantharaman et al., 2006). The Indian adapisoriculids have remarkable similarity with adapisoriculids known from the Early Palaeocene of Belgium and Late Palaeocene of Northwest Africa, Germany and France. As the Indian adapisoriculids (Deccanolestes and Sahnitherium) represent the oldest record of this group, it has been suggested that adapisoriculids had dispersed directly from India to Africa or via Europe close to the Cretaceous-Tertiary boundary (Prasad et al., 2010; Smith et al., 2010; Goswami et al., 2011). Alternatively, the Kohistan, Dras and Oman island-arc systems suggested by Chatterjee and Scotese (2010) may have formed possible terrestrial link between India and Africa in the Late Cretaceous. From the foregoing discussion, it is apparent that dispersals may have played a significant role in the Gondwanan vertebrate biogeography. There are many uncertainties in the current palaeobiogeographic models of the Gondwanan continents as a consequence of limited fossils from the Late Cretaceous rocks.

It is true that lack of vertebrates from the Late Cretaceous of Africa and Antarcto-Australia, and from the Early Cretaceous of South America and Indo-Malagasy has seriously hampered our understanding of Late Cretaceous biogeographic history of the Gondwanan vertebrates. New and additional fossil material from the unsampled Cretaceous outcrops of the Gondwanan continents is required to resolve the issues discussed above.

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