

New Late Cretaceous mammals from the Intertrappean beds of Rangapur, India and paleobiogeographic framework

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A new mammal-bearing locality from the Intertrappean beds (Maastrichtian) of Rangapur, Andhra Pradesh, India provides isolated teeth referable to *Deccanolestes* and a new eutherian, *Sahnitherium rangapurensis*. Dental comparisons with *Cimolestes*, *Procerberus*, and *Aboletylestes* do not support proposed “palaeoryctoid” affinities for *Deccanolestes*. Although similarities exist with *Otlestes* and *Batodon*, *Deccanolestes* is currently considered to be of uncertain familial affinities. *Sahnitherium rangapurensis* exhibits similarities to *Procerberus*, *Paranyctooides*, *Alostera*, *Aboletylestes*, and *Avitotherium*, but it is here placed within *Eutheria incertae sedis*. Despite family level taxonomic uncertainties, the new material confirms the presence of eutherians on the Indian subcontinent during the Late Cretaceous. A Eurasian connection via an early collision or some other dispersal route may explain these paleobiogeographic data, but other hypotheses are considered. In particular, paleogeographic, paleontological, and molecular systematic data hint that boreosphenidan mammals may have had wider distribution on Gondwana during the Cretaceous than previously supported.

Key words: Mammals, Eutheria, biogeography, Late Cretaceous, Gondwana, India.

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Introduction

The Indian subcontinent, Africa, Antarctica, Australia, Madagascar, and South America formed the southern supercontinent Gondwana during the early Mesozoic. As Gondwana broke apart during the Cretaceous, the Indian subcontinent began its northward drift toward Eurasia. Important aspects of this episode remain unclear, including the timing and sequence of breakup (Smith et al. 1994; Scotese 1997; Hay et al. 1999), land connections while en route to Eurasia (Sahni et al. 1987; Briggs 1989; Chatterjee and Scotese 1999), and the timing of collision with Eurasia (Patriat and Achache 1984; Jaeger et al. 1989). Most paleocoastline reconstructions suggest that the Indian subcontinent and Madagascar separated from the other southern continental landmasses ca. 148 million years ago (mya) (Williams 1986), and the Indian subcontinent docked with Eurasia during the Early Eocene (ca. 50 mya) (Besse et al. 1984; Patriat and Achache 1984; Besse and Couillot 1988).

Because lengthy intervals of geographic isolation are known to foster endemism (classic examples include the modern and Cenozoic biotas of Australia, Madagascar, and South America), one may expect Cretaceous and Early Tertiary biotas from the Indian subcontinent to exhibit similar degrees of endemism. However, intense fieldwork in the lat-

est Cretaceous of India (Infra- and Intertrappean beds; see Prasad and Sahni 1999 for a review) over the last two decades and preliminary fieldwork in the latest Cretaceous of Pakistan (Pab Formation; Wilson et al. 2001) has not supported this prediction. Rather, some elements of the biota have been interpreted as “Gondwanan” whereas others have been interpreted as “Laurasian.” The former imply a prolonged connection with other southern landmasses (e.g., via the Kerguelen Plateau, Krause et al. 1997, or Greater Somalia, Chatterjee and Scotese 1999) or the maintenance of a “Gondwanan” biota during the Indian subcontinent’s isolation (Prasad et al. 1995). The latter argue for a connection to Eurasia, either directly via an early collision (Jaeger et al. 1989) or indirectly via Africa (Briggs 1989), an Iran-Afghanistan plate, or a volcanic island arc (Sahni et al. 1987). However, sampling on the Indian subcontinent and neighboring Gondwanan landmasses is sparse, and the specimens from the Indian subcontinent are often too fragmentary to be certain of taxonomic assignments or biogeographic affinities.

Still Cretaceous mammals from the Indian subcontinent have been highlighted throughout these debates (Thewissen 1990; Jaeger and Rage 1990; Buffetaut 1990; Thewissen and McKenna 1992; Rage and Jaeger 1995; McKenna 1995). Although Cretaceous microvertebrate localities have been sampled in southern, central, and western India, mammals have

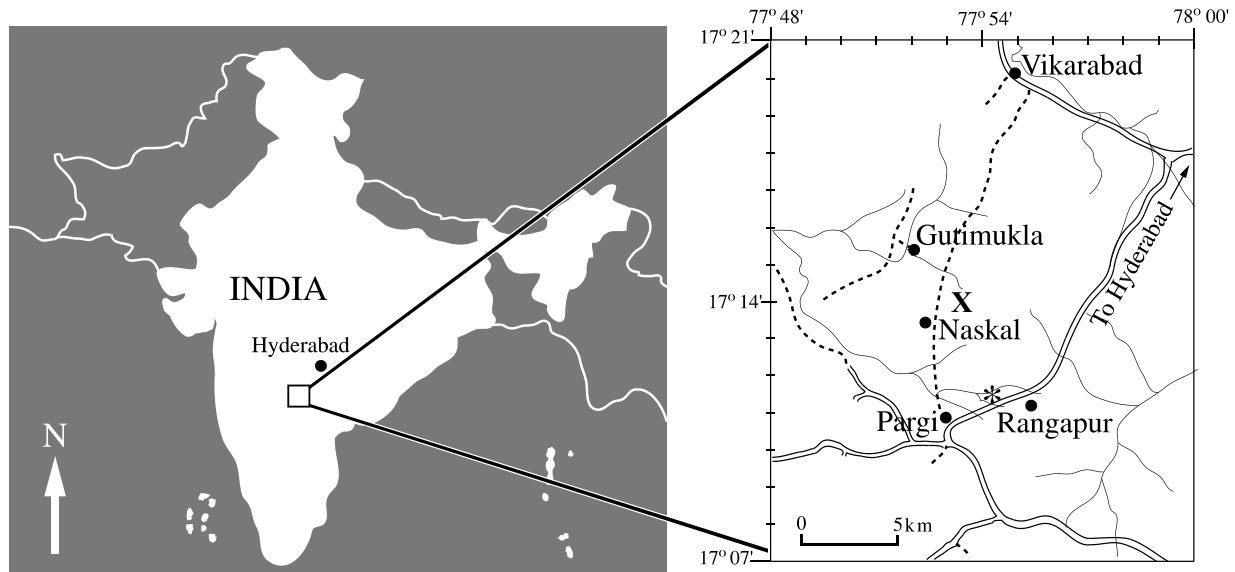


Fig. 1. Map of India and expanded view of Rangapur showing fossil locality (*) and Naskal fossil locality (X). Modified from Rana 1990a.

thus far only been recovered from the Intertrappean beds of Naskal, Andhra Pradesh, Central India (Fig. 1). From this locality, only three taxa are known—two species of *Deccanolestes* and an unnamed gondwanatherid (Prasad and Sahni 1988; Prasad et al. 1994; Krause et al. 1997). *Deccanolestes* is a eutherian mammal—a clade with traditionally accepted Laurasian affinities (Bonaparte and Kielan-Jaworowska 1987; Luo et al. 2001), whereas the distribution of gondwanatherids is restricted to the Late Cretaceous of the Indian subcontinent and Madagascar (Krause et al. 1997), the Late Cretaceous and Early Paleocene of Argentina (Bonaparte 1986a, b; Scillato-Yané and Pascual 1985), and the Eocene of Antarctica (Reguero et al. 2002). These data suggest that the Indian mammal fauna includes both “Gondwanan” and “Laurasian” elements, but more material is needed to better interpret the biogeographic history of the Mesozoic mammals from the Indian subcontinent.

Here we report a new mammal-bearing locality from Rangapur, Andhra Pradesh. Dental remains include fifteen isolated molars and premolars, which are tentatively referred to *Deccanolestes* and a new genus of eutherian mammal—raising the total number of species from the Late Cretaceous of the Indian subcontinent to four. In light of this material, we examine the phylogenetic affinities of these taxa and discuss their paleobiogeographic context.

Geology and age

Upper Cretaceous continental sediments are exposed along the perimeter of the Deccan Traps in peninsular India. The thick sequences stratigraphically below the Deccan basalts and usually deposited on Archaean granite (peninsular gneiss complex) or Gondwana Group are known as Intertrappean (= Lameta Formation) beds. They are generally

considered fluvio-lacustrine coastal plain deposits (Mohabey and Udhoji 1993). The thin (1–5 m) sedimentary beds between basalt flows are known as Intertrappean (= Takli Formation) beds. These sedimentary beds are generally considered to have formed by the sudden blocking of the drainage system immediately after the eruption of Deccan volcanic basalt, resulting in the formation of enclosed basins, separated by interfluvial divides (Rana 1990a). Both the Infra- and Intertrappean beds under study are considered Maastrichtian in age on paleontological, geochronological, and paleomagnetic data (see Khajuria et al. 1994 for a review).

The new mammal-bearing site is located about 7 kilometers southeast of Naskal and 1.5 kilometers northwest of Rangapur village (Fig. 1). The fossiliferous units are situated between basalt flows 4 and 5 (*sensu* Dutt 1975). The basal unit of this local Intertrappean sequence is a white marl bed (10.5 cm), which is overlain by black chert (10.0 cm) followed by black-brown marl (17.5 cm), black chert (10.0 cm), greenish-pink marl (12.5 cm), grey marl with whitish-grey cherty nodules (52.0 cm), and whitish-grey marl beds (42.5 cm), respectively. Fresh water ostracodes, charophytes, and molluscs were recovered from the white marl, black brown marl, and whitish-grey marl beds. Well-silicified leaf impressions, charophytes, ostracodes, and molluscs were recovered from the black chert beds (Rana 1988, 1990a, b; Bhatia et al. 1989). Microvertebrates, including mammals, were recovered from the black-brown marl and whitish-grey marl beds (Rana 1988, 1990a, b).

Materials and methods

The Rangapur locality was investigated by one of us (RSR) during 1986 and then more intensely during a three-year project (1995–1998) sponsored by the Government of India, Department of Science and Technology. In addition to surface

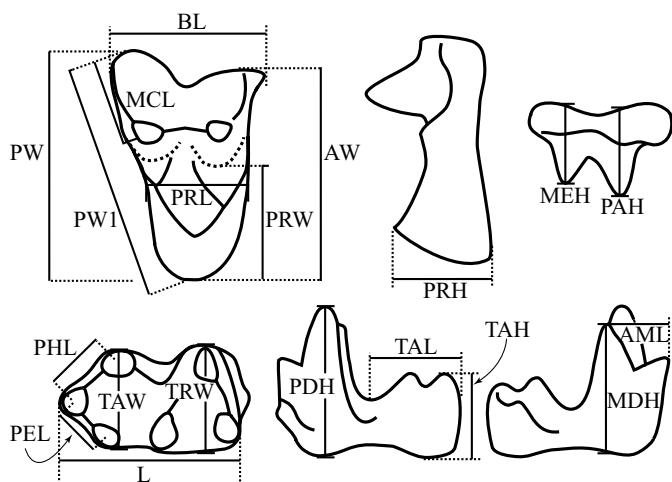


Fig. 2. Diagrammatic sketch of the upper and lower molar measurements. Anteroposterior axes pass through the paracone and metacone for upper molars and through the metaconid and entoconid for lower molars. Abbreviations are as follows: for upper molars, AW, anterior width; PW, posterior width; PW1, posterior width sensu Butler (1990); PRW, protocone shelf width; MCL, postmetacrista length; BL, buccal length; PRL, protocone shelf length; PRH, protocone height; PAH, paracone height; MEH, metacone height; and for lower molars, L, length; TRW, trigonid width; TAW, talonid width; PHL, posthypocristid length; PEL, postentocristid length; PDH, protoconid height; MDH, metaconid height; AML, premetaconid length; TAL, talonid length; TAH, talonid height.

collections, 5000 kilograms of bulk matrix were collected for underwater screenwashing by one of us (RSR). The processed concentrate was sorted in the laboratory under a binocular microscope. Microvertebrate material includes remains from elasmobranchs, bony fish, amphibians, turtles, squamates, crocodiles, and mammals. Only the mammals will be discussed here.

The quality of preservation of the fifteen isolated molars and premolars from Rangapur is variable. The original enamel surface is worn, and pitting from chemical erosion has roughened the surface of most specimens. A few specimens have suffered damage through postdepositional breakage, but those cases are minor. Specimen images were obtained using a scanning electron microscope. Measurements were taken using an Ehrenreich Photo-Optical Industries (EPOI) "Shopscope" with capability of reading directly to 0.001 millimeters (Lillegraven and Bieber 1986).

Institutional abbreviations.—ITV/R/Mm, Intertrappean vertebrates/Rangapur/Mammal catalogue numbers for the Department of Geology, HNB Garhwal University, Srinagar, Uttaranchal, India. VPL/JU/NKIM, Vertebrate Paleontology Laboratory, Jammu University, Naskal Intertrappean Mammals catalogue numbers. THR, Adrar Mgorn 1, collections of the Université des Sciences et Techniques du Languedoc, Montpellier II catalogue numbers.

Dental morphology and abbreviations.—Dental terminology follows Bown and Kraus (1979) and Nessov et al. (1998). Dental measurements and their abbreviations follow Butler (1990) with four modifications: TAH, talonid height

from labial base to the highest point (Archibald et al. 2001); PEL, postentocristid length between the hypoconulid and entoconid apices; PW, posterior width sensu Archibald (1982); and PW1, posterior width sensu Butler (1990). Fig. 2 provides diagrammatic explanations for all measurements.

Systematic paleontology

Subclass Theria Parker and Haswell, 1897

Infraclass Eutheria Gill, 1872

Order and family *incertae sedis*

Genus *Deccanolestes* Prasad and Sahni, 1988

Type species: Deccanolestes hislopi Prasad and Sahni, 1988. Late Cretaceous (Maastrichtian) of Naskal, Andhra Pradesh, India.

Deccanolestes cf. *hislopi* Prasad and Sahni, 1988

Tables 1, 2; Fig. 3.

Material.—ITV/R/Mm-2, right M2; ITV/R/Mm-7, right m1 or m2; ITV/R/Mm-10, right m1 or m2; ITV/R/Mm-11, left m3; ITV/R/Mm-12, right m3.

Distribution.—Late Cretaceous (Maastrichtian) Intertrappean beds of Naskal and Rangapur, Andhra Pradesh, India.

Description.—**Upper dentition** (Fig. 3C): Specimen ITV/R/Mm-2 is identified as an isolated right upper molar, most likely M2. Labial roots are missing, but a lingual root remains. The crown has no breaks and little natural wear on the cusps, but bears some surface pitting. It is transversely wide (anterior width to buccal length ratio; Table 1). The metacone is nearly equal in height to the paracone, and the protocone is slightly shorter than both. The apices of the two labial cusps are well separated from each other. Compared to the metacone, the base of the paracone has greater girth and is more lingually expanded. Centrocrisae are absent. The labial cusps are fused at their bases, but not extending much above the styler shelf (moderate zalambdodonty; sensu Gheerbrant 1992). Rather, the fused cusps form a wide valley that is visible in labial view (Fig. 3C₃). The labial aspect of these cusps is flat and contacts the styler shelf at a steep slope. This flat to valley-like shelf rises labially to a weak ectocingulum. The ectoflexus is deep. Accessory cusps are not present on the styler shelf, and there is no indication of wear or breakage. There is no parastylar hook. The metastylar region is somewhat larger than the parastylar region, and both regions extend slightly beyond the anterior and posterior limits of the main labial cusps. The preparacrista is more distinct than the postmetacrista. Both follow the steep gradient of the labial cusps and trend labially with very little anterior or posterior components. The postmetacrista blends with the posterolabial margin of the tooth, whereas the preparacrista does not quite form the anterolabial margin of the tooth.

The metaconule is taller than the paraconule and is positioned just lingual to the base of the metacone. It has a weak but distinct premetaconule crista that forms a step above the

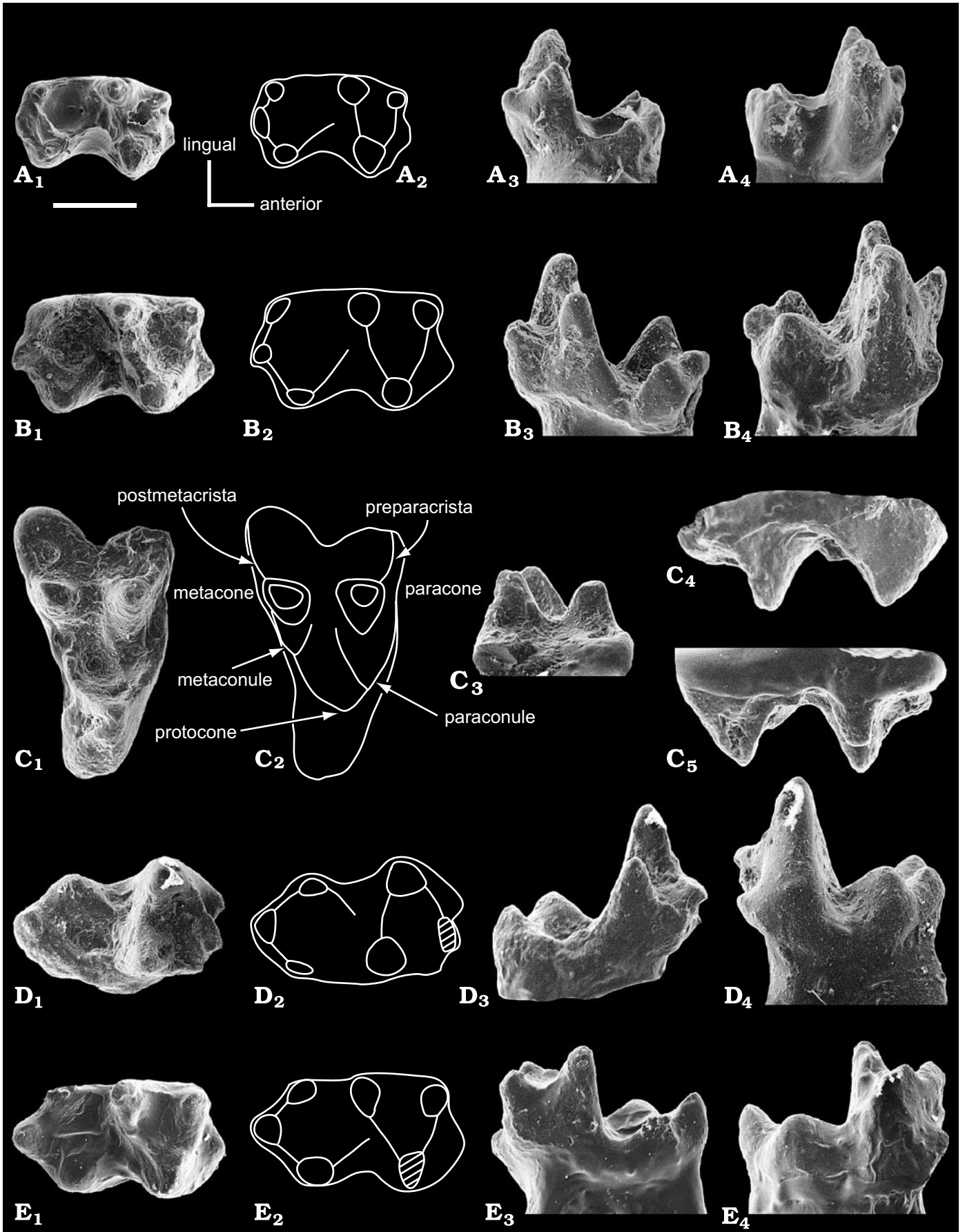


Table 1. Measurements (in mm) and ratios of Rangapur and Naskal upper molars. Abbreviations as follows: AW, anterior width; PW, posterior width; PW1, posterior width *sensu* Butler (1990); PRW, protocone shelf width; MCL, postmetacrista length; BL, buccal length; PRL, protocone shelf length; PRH, protocone height; PAH, paracone height; MEH, metacone height. Naskal data from Prasad et al. (1994).

	Tooth position	AW	PW	PW1	PRW	MCL	BL	PRL	PRH	PAH	MEH	AW/BL	PRW/AW	PRL/BL	MCL/PW	PAH/BL
<i>Deccanolestes hislopi</i>																
VPL/JU/NKIM/10	M1	1.23	–	1.23	0.62	0.40	0.97	0.58	0.36	0.51	0.50	1.27	0.50	0.60	0.33	0.53
VPL/JU/NKIM/11	M3	1.44	–	0.99	0.68	–	0.96	0.47	0.27	0.80	0.60	1.50	0.47	0.49	–	0.83
<i>Deccanolestes cf. hislopi</i>																
ITV/R/Mm-2	M2	1.45	1.45	1.52	0.77	0.46	0.89	0.61	0.60	0.55	0.52	1.63	0.53	0.69	0.30	0.62
VPL/JU/NKIM/15	M2	1.42	–	1.38	0.70	0.38	0.86	0.64	0.56	–	0.46	1.65	0.49	0.74	0.28	–
<i>Deccanolestes robustus</i>																
VPL/JU/NKIM/13	M2	2.21	–	2.10	1.10	0.54	1.65	0.84	0.70	1.20	1.05	1.34	0.50	0.51	0.26	0.73
<i>Sahnitherium</i>																
ITV/R/Mm-1	M1/2	1.20	1.29	1.34	0.64	0.54	1.04	0.59	0.53	0.42	0.61	1.15	0.53	0.57	0.40	0.40

trigon basin. The postmetaconule crista is also distinct but terminates at the posterolingual base of the metacone. The paraconule is closer to the protocone than to the paracone and shifted anteriorly relative to both cusps. The postparaconule crista is weak labially and absent lingually. It forms a short step above the trigon basin. The preparaconule crista flares to produce a wide paracingulum that bows around the anterior aspect of the paracone before blending with the anterior margin of the crown. The trigon basin is deep, with the deepest part closer to the protocone than to the labial cusps. In occlusal outline, there is slight anteroposterior waisting at the posterior margin of the crown in the conular region (Fig. 3C₁, C₂). The apex of the protocone is high and anterolabially deflected, whereas the base is lingually and somewhat anteroposteriorly expanded.

Lower dentition (Fig. 3A, B, D, E): Two lower molars (ITV/R/Mm-7, ITV/R/Mm-10) are identified as either m1 or m2. ITV/R/Mm-7 (Fig. 3A) is a right lower molar. Roots are not preserved, and there is a small hole that has been eroded at the anterolingual base of the crown. The trigonid is slightly wider and more than one-and-a-half times taller than the talonid (Table 2). In occlusal view, the trigonid appears somewhat anteroposteriorly compressed (Fig. 3A₁, A₂). In lingual view, it is tipped forward relative to the talonid (Fig. 3A₃). The protoconid is slightly taller than the metaconid, which exceeds the very reduced, crest-like paraconid. The paraconid is anteriorly projecting and labially positioned relative to the mesiodistal line formed by the metaconid and entoconid. The metaconid is positioned slightly posterior relative to the protoconid, and its apex is lingually deflected. The protocristid notch rises above the level of the trigonid

basin and is positioned closer to the metaconid than to the protoconid. A paracristid is not evident. A strong anterior buccal cingulid extends from the base of the crown below the protoconid toward the paraconid. An anterior lingual cusplule is not present. The contact between the posterior face of the trigonid and the talonid is slightly oblique.

The cristid obliqua is strong and contacts the trigonid below the protocristid notch. A faint trace of a distal metacristid is present. The hypoconid is the largest of the talonid cusps, followed by the hypoconulid and a slightly smaller entoconid. The talonid cusps are positioned posteriorly on the talonid except a slight anterolabial shift for the hypoconid. The cristid obliqua forms a fairly deep hypoflexid. The hypoconid is connected to the hypoconulid via a high posthypocristid, whereas the entoconid is separated from the hypoconulid by a small notch. The hypoconulid is slightly closer to the entoconid than it is to the hypoconid. The entocristid runs anteroventrally toward the trigonid to form a deep talonid notch that just encloses the talonid basin. The talonid basin is deep and slopes downward in an anterolingual direction. In posterior view, the labial margins of the talonid and protoconid are convex. A postcingulid is absent.

Another right lower molar (ITV/R/Mm-10; Fig. 3B) is also identified as either m1 or m2. Preservation of the crown and both roots is good. The crown length and trigonid width are larger than those of ITV/R/Mm-7. The arrangement of the trigonid is very similar to the latter (ITV/R/Mm-7), except it shows little to no anteroposterior compression. The paraconid is not quite as small nor as crest-like, labially positioned, and anteriorly projecting as in ITV/R/Mm-7. The protocristid is slightly higher and there is a very low paracristid.

← Fig. 3. *Deccanolestes cf. hislopi*. A. Right m1 or m2 (ITV/R/Mm-7) in occlusal (A₁, A₂), lingual (A₃), and labial (A₄) views. B. Right m1 or m2 (ITV/R/Mm-10) in occlusal (B₁, B₂), lingual (B₃), and labial (B₄) views. C. Right M2 (ITV/R/Mm-2) in occlusal (C₁, C₂), labial (C₃), anterior (C₄), and posterior (C₅) views. D. Left m3 (ITV/R/Mm-11) in occlusal (D₁, D₂), lingual (D₃), and labial (D₄) views. E. Right m3 (ITV/R/Mm-12) in occlusal (E₁, E₂), lingual (E₃), and labial (E₄) views. Hatched areas indicate breakage. Scale bar 0.5 mm.

With very few exceptions, the talonid morphology of ITV/R/Mm-10 is as described for ITV/R/Mm-7. Differences relate to an anteroposterior shortening of the talonid, in which the hypoconid is slightly more anterolabially shifted, the hypoflexid is not well excavated, and the talonid basin is deep but not anterolingually sloped.

Two lower molars (ITV/R/Mm-11, ITV/R/Mm-12; Fig. 3D, E) are identified as m3's. Roots are preserved on both specimens, but there is pitting on the crowns. The protoconid on ITV/R/Mm-12 is broken at the base. The paraconid on ITV/R/Mm-11 was chipped after description but prior to imaging. The trigonid morphology for these specimens is very similar to that described for the other lower molars (ITV/R/Mm-7, ITV/R/Mm-10). The paraconids are small and positioned slightly labially. There is very little to no anteroposterior compression of the trigonids. Prominent anterior buccal cingulids are present on both specimens. Furthermore, the posterior faces of the trigonids contact the talonids at a slightly oblique angle.

As expected for m3's, the greatest morphological differences with the other lower molars exist on the talonids. The talonid basins are shallow and encroached by inflated talonid cusps. The cristid obliqua and other talonid cristids are rounded and poorly defined. The hypoflexids and talonid notches are shallow. The talonid lengths are increased by posteriorly expanded hypoconulids, but the talonid widths are somewhat reduced.

Discussion.—Prasad and others (1994) described an upper molar (VPL/JU/NKIM/15) that they referred with uncertainty to *D. hislopi*. They suggested that the differences with the holotypic specimen of *D. hislopi* (VPL/JU/NKIM/10)

may be due to tooth locus but admitted more specimens are needed. We agree that the variation they discussed is commonly found between the M1 and M2 of eutherian mammals (see Lillegraven 1969; Clemens 1973; Archibald 1982; Kielan-Jaworowska and Dashzeveg 1989). Because similar variation exists between ITV/R/Mm-2 and the holotype of *D. hislopi* (VPL/JU/NKIM/10), we suggest that the former may be an M2 of *D. hislopi*. Similarities between ITV/R/Mm-2 and the holotype include a transversely wide crown with a moderately wide styler shelf, moderate zalambodont structure, and a well-developed protocone and metacone. Differences between ITV/R/Mm-2 and the holotype include a greater transverse width, a larger and more lingually placed paraconule, and a bowed paracingulum. ITV/R/Mm-2 further differs from the holotype and a referred specimen (VPL/JU/NKIM/15) in that the parastylar region is less developed than the metastylar region, styler cusps are absent, and the metacrista is not high and blade-like.

Previously, two lower molars of *Deccanolestes* were reported from Naskal (Prasad and Sahni 1988; Prasad et al. 1994). Both were identified as m1's—one referred to *D. hislopi* and the other to *D. robustus*. The four lower molars from Rangapur generally agree with the morphological descriptions of *Deccanolestes* lower molars. Similarities include a trigonid that is more than one-and-a-half times taller than the talonid, a reduced and labial paraconid, a metaconid subequal to protoconid, a tall hypoconid, and a deep talonid notch. Furthermore, ITV/R/Mm-7 is nearly identical in size to the lower molar (m1) from the *D. hislopi* mandibular fragment (VPL/JU/NKIM/16) from Naskal (Table 2). The other lower molars from Rangapur (ITV/R/Mm-10, ITV/R/Mm-11, ITV/R/Mm-12) are larger than ITV/R/Mm-7 and VPL/JU/

Table 2. Measurements (in mm) and ratios of Rangapur and Naskal lower molars. Abbreviations as follows: L, length; TRW, trigonid width; TAW, talonid width; PHL, posthypocristid length; PEL, postentocristid length; PDH, protoconid height; MDH, metaconid height; AML, premetaconid length; TAH, talonid height; TAL, talonid length. Naskal data from Prasad et al. (1994).

	Tooth position	L	TRW	TAW	PHL	PEL	PDH	TAL	MDH	AML	TAH	TRW/L	TAW/TRW	AML/TRW	PDH/L	PEL/PHL	PDH-MDH/L	PHL/L	PDH/TAH
<i>Deccanolestes hislopi</i>																			
VPL/JU/NKIM/16	m1	0.95	0.58	0.56	0.16	–	0.76	0.40	0.36	0.38	–	0.61	0.97	0.66	0.80	–	0.42	0.17	–
<i>Deccanolestes cf. hislopi</i>																			
ITV/R/Mm-7	m1/2	0.91	0.60	0.56	0.22	0.17	0.82	0.41	0.61	0.34	0.49	0.66	0.93	0.57	0.90	0.77	0.23	0.24	1.67
ITV/R/Mm-10	m1/2	1.07	0.72	0.68	0.34	0.28	1.05	0.53	0.76	0.45	0.62	0.67	0.94	0.63	0.98	0.82	0.27	0.32	1.69
ITV/R/Mm-11	m3	1.15	0.70	0.57	0.31	0.24	0.99	0.57	0.67	0.37	0.53	0.61	0.81	0.53	0.86	0.77	0.28	0.27	1.87
ITV/R/Mm-12	m3	1.13	0.68	0.58	0.36	0.29	0.82	0.56	0.67	0.42	0.51	0.60	0.85	0.62	0.73	0.81	0.13	0.32	1.61
<i>Deccanolestes? sp.</i>																			
ITV/R/Mm-9	m1/2	0.97	0.61	0.54	0.21	0.18	0.81	0.45	0.77	0.35	0.49	0.63	0.89	0.57	0.84	0.86	0.04	0.22	1.65
ITV/R/Mm-8	m1/2	1.13	0.67	0.66	0.29	0.29	0.84	0.48	0.74	0.48	0.55	0.59	0.99	0.72	0.74	1.00	0.09	0.26	1.53
<i>Deccanolestes robustus</i>																			
VPL/JU/NKIM/14	m1	1.48	0.94	0.84	0.41	–	1.23	0.67	0.98	0.64	–	0.64	0.89	0.68	0.83	–	0.17	0.28	–
<i>Deccanolestes cf. robustus</i>																			
ITV/R/Mm-6	m2	1.83	1.12	1.05	0.50	0.34	1.42	0.83	1.17	0.68	0.84	0.61	0.94	0.61	0.78	0.68	0.14	0.27	1.69

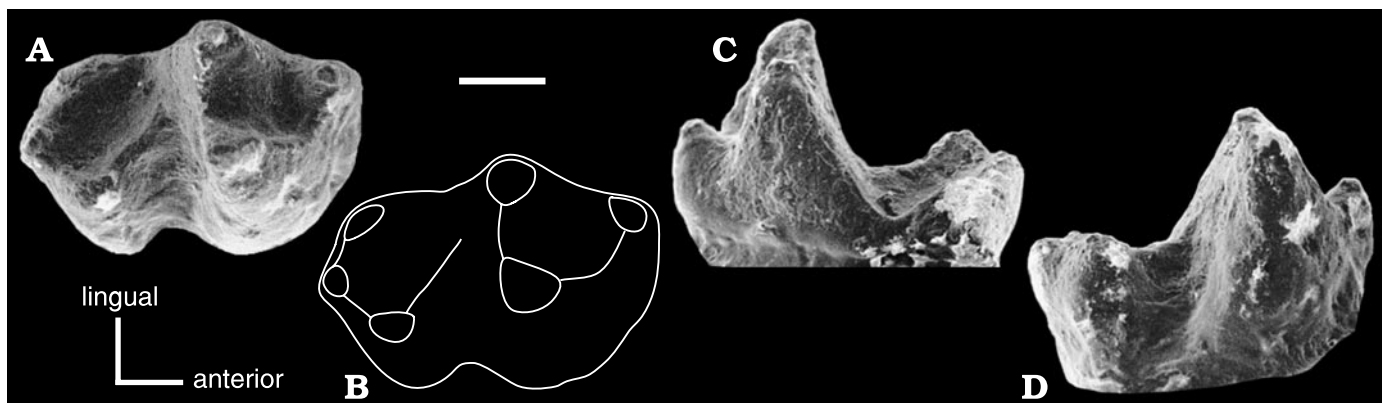


Fig. 4. *Deccanolestes* cf. *robustus*. Right m1 or m2 (ITV/R/Mm-6) in occlusal (A, B), lingual (C), and labial (D) views. Scale bar 0.5 mm.

NKIM/16 but within an acceptable range of variation for species (according to Kielan-Jaworowska and Dashzeveg 1989). Some morphological differences with the Naskal lower molar and among the Rangapur lower molars probably reflect typical variation due to position in the tooth row (see Lillegraven 1969; Clemens 1973; Archibald 1982; Kielan-Jaworowska and Dashzeveg 1989). This variation may include a less labially shifted paraconid, less anteroposterior compression of the trigonid, a deeper hypoflexid, a deeper talonid, or a more posteriorly produced hypoconulid. As discussed in the Appendix, the relative position of the hypoconulid and the contact of the cristid obliqua with the trigonid may represent more significant differences between the samples. Until more material is collected that clarifies variation along the tooth row, we refer the upper and lower molars described above to *Deccanolestes* and tentatively to the species *D. hislopi*.

Deccanolestes cf. *robustus* Prasad, Jaeger, Sahni, Gheerbrant, and Khajuria, 1994

Table 2, Fig. 4.

Material.—ITV/R/Mm-6, right m1 or m2.

Distribution.—Late Cretaceous (Maastrichtian) Intertrappean beds of Naskal and Rangapur, Andhra Pradesh, India.

Description.—ITV/R/Mm-6 is identified as a right lower molar, either m1 or m2. The roots are missing and a small portion of the lingual base of the crown is eroded. The crown is much larger than the other Rangapur specimens (Table 2). The trigonid is just wider than and over one-and-a-half times taller than the talonid. Cusps on the trigonid are well spaced and somewhat inflated. The protoconid is the tallest cusp, but only slightly taller than the metaconid. The paraconid is small, labial, and slightly anteriorly projecting but not crest-like. The metaconid is more distally positioned than the protoconid, and its apex is somewhat lingually deflected. The protoconid is connected to the metaconid by a high protocristid, and to the paraconid by a very low paracristid. A broad notch separates the metaconid and paraconid. The anterolabial face of trigonid is slightly worn but preserves a faint anterior labial cingulid. It runs subvertically from the base of the crown below the protoconid, anterolingually toward the paraconid. It termi-

nates below the notch formed by the paracristid. An anterior lingual cusplule is absent but the inflated base of the paraconid may have served the same function. In labial view, the trigonid appears tipped anteriorly (Fig. 4D).

In occlusal view, the posterior face of the trigonid contacts the talonid at an oblique angle (Fig. 4A, B). The talonid basin is wide but not very deep. It slopes downward in an anterolingual direction and is only weakly closed by a low entocristid on the lingual side. The talonid notch is deep. On the labial side, the cristid obliqua is higher than the entocristid and contacts the base of the trigonid just lingual to the protocristid notch below the base of the metaconid. A faint trace of a distal metaconid is present. The acute angle between the cristid obliqua and the posterior face of the trigonid forms a well-excavated hypoflexid. The hypoconid is more anterior than the entoconid and is labially shifted. The hypoconulid is closer to the entoconid than it is to the hypoconid. The hypoconid is the tallest of the talonid cusps, followed by the hypoconulid, and then the entoconid. In posterior view, the talonid is canted lingually with respect to the trigonid, and the labial margins of the talonid and protoconid are convex. A postcingulid is absent.

Discussion.—In most respects, ITV/R/Mm-6 is very similar to the only known lower molar of *D. robustus* (VPL/JU/NKIM/14, m1). It differs from the latter in both size and in the arrangement of the talonid cusps. ITV/R/Mm-6 is about 24% larger than VPL/JU/NKIM/14 and has a hypoconulid that is closer to the entoconid than it is to the hypoconid (VPL/JU/NKIM/14 has the reverse arrangement). These differences may be due to preservational, intraspecific, or interspecific variation. Because sample sizes are still very small, we tentatively refer this specimen to *D. robustus* rather than to a new taxon.

Deccanolestes? sp.

Table 2, Fig. 5.

Material.—ITV/R/Mm-9, left m1 or m2; ITV/R/Mm-8, right m1 or m2.

Distribution.—Late Cretaceous (Maastrichtian) Intertrappean beds of Rangapur, Andhra Pradesh, India.

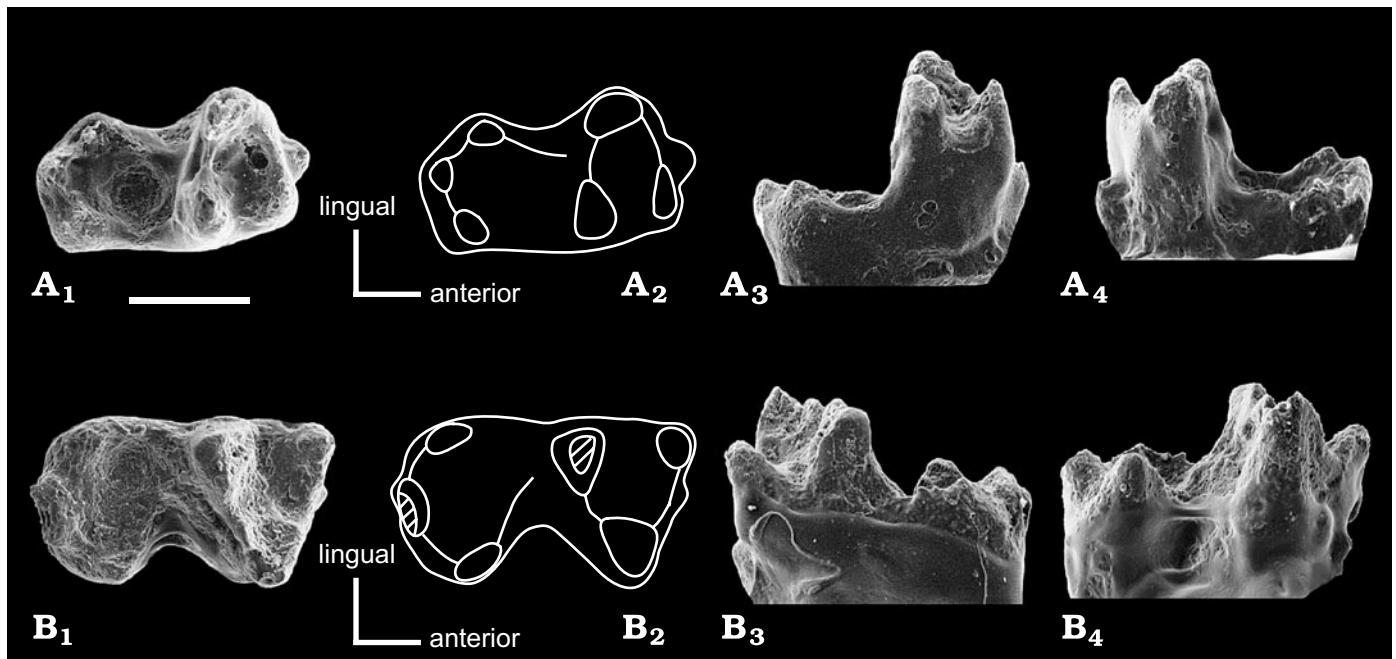


Fig. 5. *Deccanolestes?* sp. **A.** Left m1 or m2 (ITV/R/Mm-9) in occlusal (A₁, A₂), lingual (A₃), and labial (A₄) views. **B.** Right m1 or m2 (ITV/R/Mm-8) in occlusal (B₁, B₂), lingual (B₃), and labial (B₄) views. Hatched areas indicate breakage. Scale bar 0.5 mm.

Description.—ITV/R/Mm-9 is identified as a left lower molar, either m1 or m2 (Fig. 5A). The specimen is well-preserved, except that the anterior root is broken. Paraconid and metaconid are nearly equal in height and slightly shorter than the protoconid. The paraconid is positioned slightly labial relative to the metaconid but does not project anteriorly. The metaconid is robust and positioned slightly posterior relative to the protoconid. The trigonid is anteroposteriorly compressed, but a broad U-shaped notch separates the paraconid and metaconid. A protocristid connects the protoconid and metaconid, and a taller, transverse paracristid connects the protoconid and paraconid. A strong wear facet is visible on the anterior face of the trigonid. In lingual view, the base of the trigonid is level, rather than rising anteriorly (Fig. 5A₃). The trigonid is not tipped forward relative to the talonid. The contact between the posterior face of the trigonid and the talonid is slightly oblique. A distinct cuspule is present low on the anterior face of the trigonid.

The cristid obliqua is strong and contacts the trigonid below the protocristid notch. A distal metacristid is not evident. The entoconid and hypoconulid are nearly equal in height and more developed than the hypoconid. Because the hypoconid is not very anterolabially shifted, the hypoflexid is not deep. In lingual view, the talonid notch is broad and U-shaped, rather than deep and V-shaped (Fig. 5A₃). In occlusal view, the posthypocristid and postentocristid appear sharp (Fig. 5A₁, A₂). The hypoconulid is slightly closer to the entoconid than to the hypoconid. The entocristid and cristid obliqua enclose the deep talonid basin. The basin is a deep circular bowl rather than an anterolingual slope. In posterior view, the labial margin of the protoconid is convex. A postcingulid is absent.

ITV/R/Mm-8 is identified as an isolated right lower molar,

either m1 or m2 (Fig. 5B). The specimen is not as well preserved as the other lower molar (ITV/R/Mm-9). Both roots are missing and the apices of the metaconid and the hypoconulid are chipped. Although the tip of the metaconid is missing, it is clear that the protoconid is the tallest cusp, followed by the metaconid, and a somewhat smaller paraconid. The paraconid is anteriorly projecting and is positioned directly anterior to the metaconid. The metaconid is posterior relative to the protoconid. The trigonid is not anteroposteriorly compressed. The paracristid is a high, sharp, V-shaped crest. A strong wear facet is present on the anterior face of the trigonid. The protocristid is very high and sharp. A deep, broad, V-shaped notch separates the paraconid and metaconid. In labial view, the trigonid is tipped forward relative to the talonid (Fig. 5B₄). In occlusal view, the contact between the posterior face of the trigonid and the talonid is oblique (Fig. 5B₁, B₂). A small cuspule is present on the anterior face of the trigonid.

The low cristid obliqua contacts the posterior face of the trigonid below the metaconid. The hypoflexid is very deep. A distal metacristid is present. Although the tip of the hypoconulid is broken, it appears that the hypoconid and hypoconulid were nearly equal in height. The entoconid is slightly shorter. The hypoconid is anterolabially shifted, and the entoconid is anteriorly shifted. The hypoconulid is equidistant from the hypoconid and entoconid. The posthypocristid and postentocristid are low, but the entocristid is rather high. The latter forms the lingual wall for the talonid basin, and consequently, there is no talonid notch. The talonid basin is shallow and slopes lingually and slightly anteriorly. A postcingulid is absent.

Discussion.—Both specimens (ITV/R/Mm-9, ITV/R/Mm-8) are similar in size and somewhat similar in morphology to the

lower molars of *Deccanolestes hislopi*. However, distinct differences prevent us from confidently placing the specimens in that genus. ITV/R/Mm-9 differs from *Deccanolestes* lower molars in that the paraconid is tall, paracristid is high, hypoconid is low and more posteriorly positioned, and the trigonid and its cusps are more erect. ITV/R/Mm-8 differs from *Deccanolestes* lower molars in fewer ways than ITV/R/Mm-9 does. The paracristid and protocristid are both tall and sharp, the height difference between the trigonid and talonid is small, the hypoflexid is very well excavated, and in general, the crown edges and crests are sharp rather than rounded. We feel that these morphological differences may represent species or even generic variation, but we defer any formal taxonomic assignment until more evidence is available.

Genus *Sahnitherium* nov.

Derivation of name: *Sahni*, in honor of Professor Ashok Sahni, a leader in the field of vertebrate paleontology in India and an indispensable advisor on this project. Greek, *therion* (wild beast) common reference to mammals.

Type and only known species: *S. rangapurensis* sp. nov.

Diagnosis.—Same as for the only known species.

Sahnitherium rangapurensis sp. nov.

Table 1, Fig. 6.

Derivation of name: *rangapurensis* from the village of Rangapur near the type locality in the state of Andhra Pradesh, India.

Holotype: ITV/R/Mm-1, isolated right upper molar, M1 or M2.

Type locality: Terminal Cretaceous (Maastrichtian) Intertrappean horizon, Rangapur, Andhra Pradesh, India.

Distribution.—Late Cretaceous (Maastrichtian) Intertrappean beds of Rangapur, Andhra Pradesh, India.

Differential diagnosis.—Similar in size and in some morphological aspects to *Deccanolestes hislopi* but differs in that it is not as transversely wide; the postmetacrista is stronger, longer, and carries the so-called cusp “C”; a stylocone is not present; the metastylar area is more posterolabially expanded and larger than the parastylar region; the ectoflexus is shallower; the labial cusps are labiolingually compressed, convex in labial view, and with steeper lingual slopes; paracone larger and more anterolingually placed; and the protocone height is greater and its labial aspect meets the crown at a steeper angle. The taxon is also diagnosed by a paracone slightly higher and more lingually expanded than the metacone; bases of the labial cusps slightly appressed (moderate zalambdodonty); conular region not anteroposteriorly constricted; conules wing-like with weak internal crests; protocone well-developed and somewhat anteroposteriorly expanded; the apex of the protocone anterolabially recumbent; and no cingula present.

Description.—ITV/R/Mm-1 is identified as a right upper molar, either M1 or M2 (Fig. 6). The posterolabial and lingual roots are preserved. The enamel surface of the crown is pitted in some regions, and a small break can be seen in labial view at the anterolabial end of the crown (Fig. 6C). The break

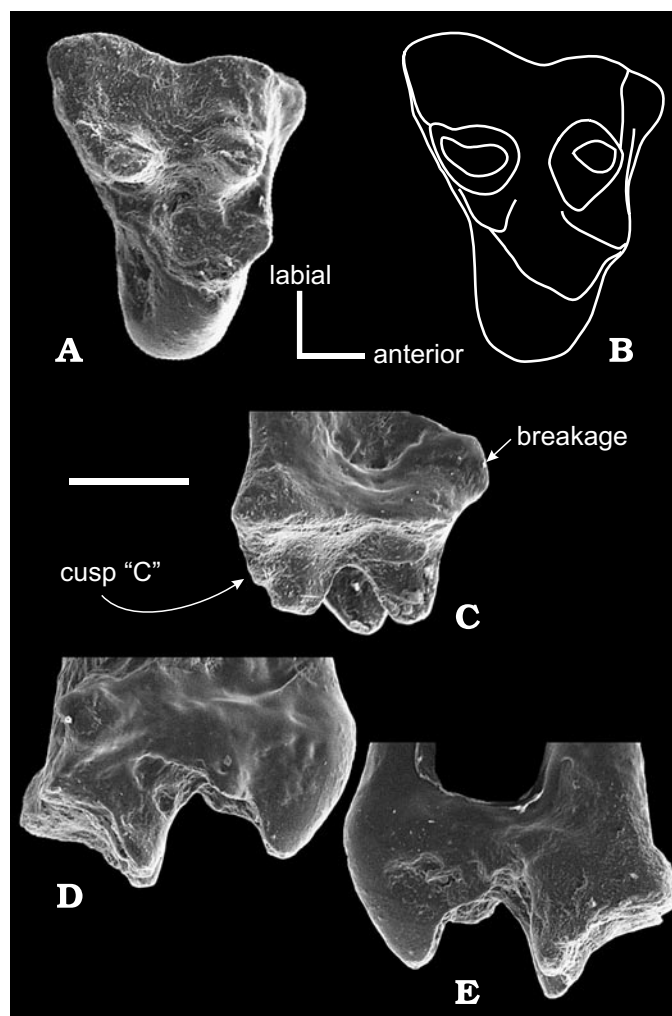


Fig. 6. *Sahnitherium rangapurensis*. Right M1 or M2 (ITV/R/Mm-1), holotype in occlusal (A, B), labial (C), anterior (D), and posterior (E) views. Scale bar 0.5 mm.

removed an anterolabial root and perhaps a parastylar hook and parastyle, if they existed. Otherwise, the labial margin of the crown, including the region where a stylocone would be preserved, is unaffected.

Although the break slightly altered the buccal length and perhaps the anterior width, the crown was clearly not transversely wide (Table 1). The main cusps of the crown are moderately tall and conical. The paracone is the tallest cusp, but it is only slightly taller than the metacone and protocone. The apices of the labial cusps are somewhat labiolingually compressed. The bases of these cusps are fused just above the level of the stylocone (moderate zalambdodonty). Centrocristae are weak. The base of the paracone is somewhat lingually expanded. The labial aspect of the paracone is flat to convex and gently slopes toward the labial margin of the tooth encroaching on the parastylar region. The labial aspect of the metacone is less convex and slopes more steeply toward the labial margin of the crown. The metastylar region slopes and then flattens but is not gutter-like. Also, this region is slightly posterolabially expanded. The postmetacrista is a distinct ridge that

runs along a shallow gradient posterolabially toward the metastylar region. A metacrista cusp (cusp "C") is present. The preparacrista is a less distinct ridge that runs along a steep gradient anterolabially toward the parastylar region. A faint trace of a raised ectocingulum is preserved on the labial margin of the stylar shelf, but a stylocone or accessory cusps are not present. The parastylar region (except a parastylar hook if one existed) is significantly smaller than the metastylar region. The ectoflexus forms a shallow curve.

The paraconule is larger than the metaconule. It is shifted anteriorly and positioned midway between the paracone and protocone. The metaconule is positioned closer to the metacone than to the protocone. The postmetaconule wing terminates at or before the lingual base of the metacone. The preparaconule wing extends labially to the parastylar region. The preparaconule crista runs labially and dorsally along the anterior margin of the crown and becomes a faint trace near the parastylar region. Faint traces of internal wings are present. The trigon basin is deep, especially so toward the labial cusps. The step down to the trigon basin from the metaconule is small and from the paraconule it is negligible. The base of the protocone is somewhat lingually expanded and anteroposteriorly widened. The apex of the protocone is tall and anterolabially deflected. The labial face of the protocone is nearly perpendicular to the rest of the crown, as are the lingual faces of the paracone and metacone (Fig. 6D). In occlusal outline, there is little to no anteroposterior waisting of the crown in the conular region (Fig. 6A). No cingula are present.

Discussion.—The specimen (ITV/R/Mm-1) is similar in size and in some morphological aspects to the M1 of *Deccanolestes hislopi* (VPL/JU/NKIM/10), but it differs in a number of important ways outlined in the diagnosis. Based on evaluation of upper molars from other Cretaceous eutherians, we judge these differences to be greater than preservational, interspecific, or even intrageneric variation. Thus, we erect a new genus and species for the single isolated upper molar because we are unaware of any other Cretaceous or Paleocene boreosphenidan or australosphenidan with this morphology.

Infraclass *incertae sedis*

Table 3, Fig. 7.

Material.—ITV/R/Mm-5, right P3 labial fragment; ITV/R/Mm-19, left p3 or p4; ITV/R/Mm-13, right p3 or p4; ITV/R/Mm-14, left p1 or p2; ITV/R/Mm-15, right p1 or p2; and ITV/R/Mm-17, right p1.

Distribution.—Late Cretaceous (Maastrichtian) Intertrappean beds of Naskal and Rangapur, Andhra Pradesh, India.

Description.—**Lower premolars** (Fig. 7A–C): Specimen ITV/R/Mm-17 is identified as a right p1 (Fig. 7B). The well preserved specimen has a single root and a simple, laterally compressed crown with an incipient talonid heel.

Specimens ITV/R/Mm-14 and ITV/R/Mm-15 are both identified as either p1's or p2's (Fig. 7A). Both specimens have two roots and simple, laterally compressed crowns with

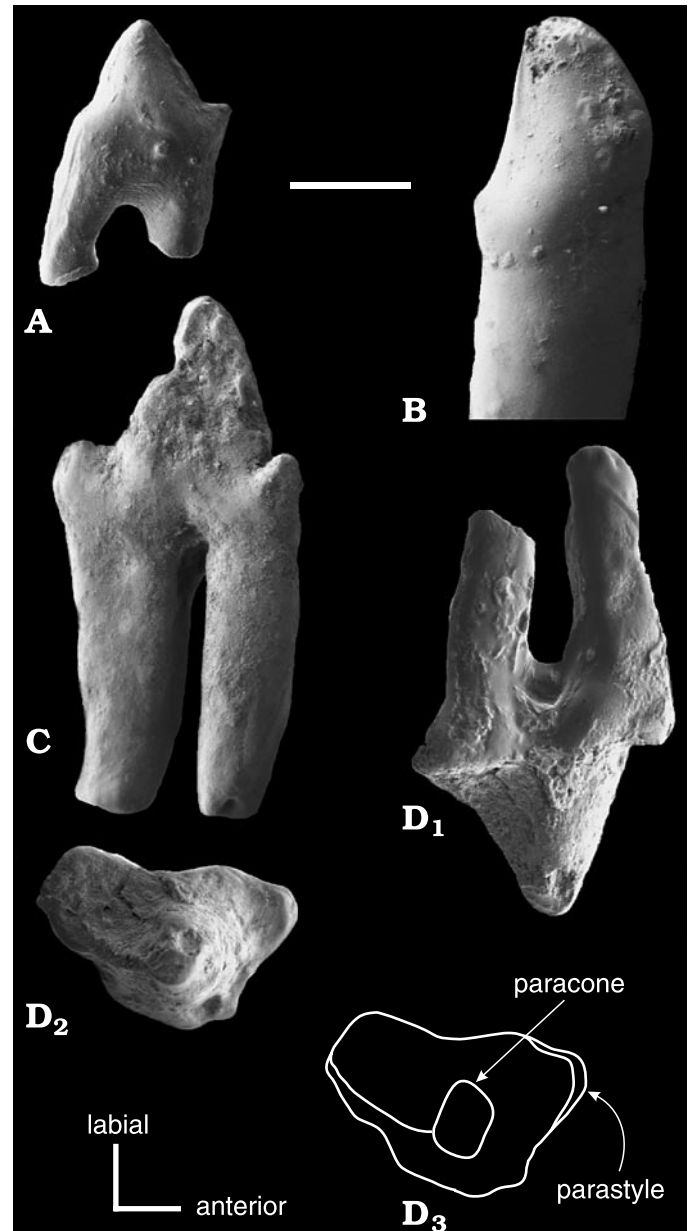


Fig. 7. *Theria incertae sedis*. A. Left p1 or p2 (ITV/R/Mm-14) in labial view. B. Right p1 (ITV/R/Mm-17) in labial view. C. Right p3 or p4 (ITV/R/Mm-13) in lingual view. D. Right P3 (ITV/R/Mm-5) in labial (D₁) and occlusal (D₂, D₃) views. Scale bar 0.5 mm.

a narrow talonid heel. Specimen ITV/R/Mm-14 is significantly smaller than ITV/R/Mm-15.

Specimens ITV/R/Mm-19 and ITV/R/Mm-13 are both identified as either p3's or p4's (Fig. 7C). Both specimens have two roots and somewhat laterally compressed crowns with an anterior cusplule and a two cusped talonid heel.

Upper premolar (Fig. 7D): Specimen ITV/R/Mm-5 is identified as a right P3. The specimen preserves two labial roots, but it probably had a third root in a lingual position. It appears that this third root along with a small lingual portion of the crown was broken off. This lingual portion of the crown likely preserved a small protocone. The remainder of

Table 3. Measurements (in mm) of Rangapur premolars. Abbreviations as follows: L, length and W, width. Asterisk (*) indicates a minimum measurement for a fragmentary specimen.

	Tooth position	L	W
<i>Theria incertae sedis</i>			
ITV/R/Mm-17	p1	0.81	0.55
ITV/R/Mm-14	p1 or p2	0.82	0.46
ITV/R/Mm-15	p1 or p2	1.01	0.56
ITV/R/Mm-13	p3 or p4	1.03	0.56
ITV/R/Mm-19	p3 or p4	1.07	0.56
ITV/R/Mm-5	P3	1.04	*0.67

the crown contains a large, somewhat laterally compressed paracone and a small parastyle. A metacone is not present. A strong crest runs from the apex of the paracone to the posterolabial corner of the crown. A crest from the apex of the paracone to the likely position of the protocone is absent.

Discussion.—Most of the material described above agrees with the descriptions given by Prasad et al. (1994) for the premolars from Naskal. Unfortunately, none of their premolar material was associated with upper or lower molars either. Nevertheless, they tentatively referred this material to *D. hislopi* based on size. Because we recognize a second genus, *Sahnitherium*, that is similar in size to and from the same deposits as *Deccanolestes hislopi*, we cannot confidently refer the isolated premolars in the Rangapur sample to either taxon. One noteworthy difference with the Naskal material is that ITV/R/Mm-17 is a single-rooted p1. Dentary fragments from Naskal do not preserve p1, but alveoli from two specimens (VPL/JU/NKIM/17 and VPL/JU/NKIM/18) indicate p1 was double-rooted. Thus, the combined sample from Naskal and Rangapur probably contains premolars representing at least two taxa.

Phylogenetic affinities

We rely upon previous evolutionary studies of dental characters and cladistic analyses to discuss the phylogenetic position of *Deccanolestes* and *Sahnitherium* with respect to other Cretaceous and Paleocene mammals (Fox 1984; Clemens and Lillegraven 1986; Novacek 1986; Butler 1990; Gheerbrant 1992; Cifelli 1993a, b; Averianov and Skutschas 1999, 2001; Archibald et al. 2001; Luo et al. 2001, 2002). A cladistic analysis that incorporates this dental information and a broad sample of Cretaceous eutherians is needed but is beyond the scope of this paper.

We also note that most paleontologists involved in the initial descriptions and interpretations of the affinities of *Deccanolestes* used “Palaeoryctidae” or “Palaeoryctoidea” in a broadly inclusive sense, similar to that employed by Gheerbrant (1992). In this usage, “Palaeoryctidae” and “Palaeoryctoidea” are most likely paraphyletic (Butler 1972; Novacek 1976, 1986; Wood and Clemens 2001) and, following current convention, the family and superfamily names

are enclosed in quotes. On the other hand, McKenna and Bell (1997) restricted Palaeoryctidae to three genera, which might form a monophyletic clade, and they placed many of the remaining “palaeoryctoids” in the family “Cimolestidae”, which is also most likely paraphyletic. Resolution of these differences is beyond the scope of this paper. Thus, for the purposes of this study, we have chosen to follow the common usage in the literature dealing with *Deccanolestes* and employ “Palaeoryctoidea” as a very inclusive, paraphyletic group. To hopefully mitigate the taxonomic problems caused by the lack of agreement on content of “Palaeoryctoidea”, we focus on individual genera in the following detailed comparisons.

Deccanolestes.—Specimens ITV/R/Mm-9 and ITV/R/Mm-8 will not be addressed in the phylogenetic considerations for *Deccanolestes* because of taxonomic uncertainties explained above. The remaining *Deccanolestes* material from Rangapur (ITV/R/Mm-6, ITV/R/Mm-7, ITV/R/Mm-11, ITV/R/Mm-12, ITV/R/Mm-10, ITV/R/Mm-2) might later be distinguished from *D. hislopi* and *D. robustus* at the species level, but generic-level distinction is not supported. Consequently, the phylogenetic affinities of *Deccanolestes* are based on morphologies found in the specimens from Naskal and Rangapur. The morphological variation in the combined sample is addressed in the Appendix. Based on this treatment, we proceed with a character-based evaluation of the phylogenetic affinities of *Deccanolestes*.

The following is a list of characters for *Deccanolestes* which are derived among Cretaceous eutherians: *Upper molars*—(1) M2 protocone lingually expanded; (2) M1 reduced styler shelf (<29% of AW); (3) parastylar lobe and parastylar hook somewhat reduced; (4) metacone similar to paracone in height and size; (5) labial faces of metacone and paracone flat; (6) protocone height similar to height of labial cusps; (7) protocone somewhat anteroposteriorly expanded; (8) protocone apex with moderate labial position; (9) metacrista cusp “C” absent; (10) lingual slopes of labial cusps long and sloping; (11) parastylar groove reduced or absent; (12) pre-parastyle absent; (13) styler cusp “E” absent. *Lower molars*—(14) metaconid only slightly smaller than protoconid; (15) hypoconulid closer to entoconid; (16) trigonid width similar to talonid width (TRW:TAW < 1.10); (17) trigonid slightly procumbent; (18) trigonid height relative to talonid height reduced (PDH:TAH = 1.5–1.7); (19) trigonid height to total length ratio reduced (< 1.0).

Several of the above characters (9, 12, 13) are widespread among Late Cretaceous eutherians and provide little phylogenetic information. Others have a more restricted distribution among Late Cretaceous eutherians and may better reflect recency of common ancestry. In particular, the initial description of *Deccanolestes* suggested “palaeoryctoid” affinities for the genus (Prasad and Sahni 1988). Subsequent study of additional dental remains referable to *Deccanolestes* confirmed this initial assessment (Prasad et al. 1994) and identified several derived characters shared between *Deccanolestes*, *Cimolestes magnus*, and *Procerberus*. Thus, we

evaluate the phylogenetic affinities of *Deccanolestes* with these taxa and a few other candidates.

Cimolestes magnus and *Deccanolestes* share several derived features (9, 12, 13), but, as mentioned above, all have a broad distribution among Late Cretaceous eutherians (see Archibald et al. 2001). *Cimolestes magnus* is more derived than *Deccanolestes* in a few ways, including a metacingulum that continues labially past the metacone to the metastylar lobe, distinct internal conular cristae, carnassial notches, and incipient protoconular cingula. Yet a larger number of derived features are found in *Deccanolestes* and absent in *C. magnus* (1–8, 10, 11, 14–19). Some overall morphologic similarities exist between these two taxa, but these are likely symplesiomorphic. Thus, phylogenetic affinity between *Cimolestes magnus* and *Deccanolestes* is probably minimal.

Procerberus shares five derived characters (6, 9, 12, 13, 15) with *Deccanolestes*, including those listed for *C. magnus*. The stylar shelves on the upper molars of *Procerberus* are reduced but to a much greater extent than in *Deccanolestes*. *Procerberus* is also more derived than *Deccanolestes* in that the upper molar transverse width is more reduced, the ectoflexus is shallow, the labial cusps are fused above mid-height, and protoconular cingula are incipient. *Deccanolestes*, on the other hand, is more derived than *Procerberus* in that the protoconal apex is more labially positioned, the labial cusps are similar in size and height, the parastylar hook is smaller, and the lower molar trigonids are shorter relative to the talonids. Phylogenetic affinities with *Procerberus* remain possible but are not yet substantiated by the available data.

The Paleocene mammalian fauna from Ouarzazate Basin in Morocco contains a diversity of “palaeoryctoids”—two of which have been compared with *Deccanolestes* (Gheerbrant 1992; Prasad et al. 1994). We agree with Gheerbrant (1992) that the morphological similarities between the Moroccan cf. *Aboylestes hypselus* and *Deccanolestes* are mostly symplesiomorphic. *Cimolestes cusculus* from Morocco also shares morphological similarities with *Deccanolestes* but differs in the presence of accessory cusps along the upper molar pre- and postprotocrista, greater zalambodont structure, a parastylar hook, reduced transverse width, and considerable anteroposterior compression of the m3 trigonid. Few shared derived characters support phylogenetic association with the Moroccan “palaeoryctoids.”

In a cladistic study (Archibald et al. 2001), “zhelestids,” “zalambdalestids,” *Gypsonictops*, *Batodon*, and *Otlestes* were united by three synapomorphies, and the next more exclusive clade (all taxa but *Otlestes*) was united by five synapomorphies. Of these eight synapomorphies, *Deccanolestes* possesses six (2, 4, 6, 16, 18, 19). However, because “zhelestids” and “zalambdalestids” are considerably more derived than *Deccanolestes*, any phylogenetic affinity between *Deccanolestes* and this hypothesized clade is more likely restricted to the basal taxa (*Otlestes* and *Batodon*).

Otlestes shares at least three derived traits (6, 13, 18) with *Deccanolestes*. However, *Otlestes* differs in that the ratio of trigonid height to talonid height is large (TRH:TAH = 1.8–1.9;

Archibald et al. 2001); the protoconid is considerably bigger than the metaconid; the paracone is higher and larger than the metacone; and the hypoconulid is equidistant between the entoconid and the hypoconid. Prasad et al. (1994) mentioned several derived characters shared between *Deccanolestes* and *Otlestes*, but further comparisons were not made. We find that *Otlestes* is generally more primitive than *Deccanolestes*.

Batodon shares at least seven derived characters (4, 6, 13, 15, 16, 18, 19) with *Deccanolestes*, but the two taxa differ in several ways. *Deccanolestes* is more derived than *Batodon* in that the parastylar groove and hook are reduced, the protocone is more developed and labial, and the metaconid is nearly equal in height to the protoconid. *Batodon*, on the other hand, is more derived than *Deccanolestes* in that the parastyle is larger than the stylocone, the conules are placed midway between the labial cusps and the protocone, cingula are present, the labial cusps are fused at or above mid-height, and the cristid obliqua contacts the trigonid below the protoconid notch (Wood and Clemens 2001).

We must also note that Prasad and Godinot (1994) suggested that the morphology of tarsals attributed to *Deccanolestes* might indicate a close phylogenetic relationship between that taxon and archontans. However, as similar sized eutherians (e.g., *Sahnitherium*) become known from Intertrappean faunas of India the taxonomic attribution of this postcranial material becomes problematic.

In summary, the phylogenetic affinities of *Deccanolestes* remain uncertain. The derived dental characters do not favor a single phylogenetic hypothesis, and they may, in fact, reflect common trends among Late Cretaceous eutherian lineages (homoplasy) rather than shared evolutionary history. Nonetheless, *Deccanolestes* may be derived within a group of one or more “palaeoryctoid” genera, or it may be more closely related to *Otlestes* and *Batodon* (both of which have been considered “palaeoryctoids” by some authors). We conservatively conclude that within Eutheria the phylogenetic affinities of *Deccanolestes* are currently indeterminate but they lie near the base of the clade. This placement is consistent with that presented by McKenna and Bell (1997).

***Sahnitherium*.**—The new Indian genus does not show similarities to Australosphenida, whose representatives are known mostly from lower dentitions. The known australosphenidan upper molars are highly derived and the lower molar morphologies are incompatible (i.e., do not show a predictable occlusal relationship) with the upper molar morphology of *Sahnitherium*. More likely, *Sahnitherium* is a member of Boreosphenida based on the possession of a preprotocrista that extends beyond the paracone into the stylar groove (Luo et al. 2002). Furthermore, the well-developed protocone suggests that *Sahnitherium* falls within crown-group Theria. Beyond this taxonomic level, several possibilities remain open.

Sahnitherium has morphological similarities with Late Cretaceous metatherians. ITV/R/Mm-1 has a broad stylar shelf, a strong metacrista, a paracone and metacone with flat

to convex labial surfaces, a somewhat anteroposteriorly expanded protocone, and a short anterior crown width relative to buccal length (Clemens 1979; Cifelli 1993 a, b). On the other hand, ITV/R/Mm-1 lacks features typical of metatherian upper molars, such as stylar shelf accessory cusps (but some of the parastylar region is broken), well-separated labial cusps, and a lingually extending metacone base (Clemens 1966; Clemens and Lillegraven 1986; Fox 1987; Butler 1990; Cifelli 1993a, b).

We currently favor placement of *Sahnitherium* in Eutheria based on a paracone that is slightly larger and more lingually expanded than the metacone and a paraconule more developed than the metaconule. However, ITV/R/Mm-1 does not possess a postprotocrista that extends beyond the base of the metacone, a trait Rougier et al. (supplementary information 1998) considered synapomorphic for eutherians (also see Cifelli 1993a and Luo et al. 2002). We do note that upper molars of *Procerberus*—an otherwise undisputed eutherian—do not possess this trait either. Thus, based on this working hypothesis, the following characters for *Sahnitherium* are derived among Cretaceous eutherians: (1) M1 or M2 not transverse (AW:BL=1.15); (2) metacone similar to paracone in height and size; (3) protocone height similar to labial cusps; (4) protocone somewhat anteroposteriorly expanded; (5) protocone apex somewhat labially shifted; (6) stylocone absent; (7) paraconule strongly shifted anterolingually; (8) posterior stylar cusps absent; (9) distance between labial cusps and protocone reduced (<45% of crown width).

Evaluation of these traits indicates that *Sahnitherium* shares with *Procerberus* a reduced transverse width, a reduced to absent postprotocrista, and a strong anterolabial paraconule. Yet *Procerberus* differs in that the stylar shelf is reduced, the protocone is not anteroposteriorly expanded or labially shifted, and the paracone is distinctly taller than the metacone and fused to it at or above mid-height.

Several apomorphies of *Sahnitherium* are also reminiscent of *Alostera*, *Avitotherium*, and *Paranyctoides*. All of these taxa have upper molars with reduced transverse width (M1 or M2) (Fox 1984, 1989; Cifelli 1990). *Paranyctoides* has a strong anterolabially placed paraconule, and along with *Avitotherium*, it has a strong postmetacrista. *Avitotherium* has a slightly anteroposteriorly expanded protocone, and this taxon and *Alostera* (as well as several other taxa, see Archibald et al. 2001) also have labial cusps that are similar in height and size and a protocone that is similar in height to the labial cusps. However, these taxa differ from *Sahnitherium* in that they each have a very reduced stylar shelf, a more developed postprotocrista, well-separated labial cusps, a variably present stylar cusp “C” (mesostyle), strong protoconular cingula, and a trapezoidal occlusal outline of their upper molars.

Comparisons were also made with *Aboletylestes robustus*, the Paleocene palaeoryctid from Morocco. Primitively, the M1? of *A. robustus* (THR 184) and ITV/R/Mm-1 share the presence of a wide stylar shelf and a low postprotocrista that doesn't extend labially beyond the metacone. As for derived characters, the two taxa share a paraconule that is

strongly shifted anterolingually, a long, strong postmetacrista, the absence of stylar cusps, an anteroposteriorly wide trigon basin, and a labially shifted protocone apex. Despite the number of shared derived characters, the two specimens differ significantly in the details of those characters and in other characters. THR 184 differs in the presence of a notch on the postmetacrista, a deeper ectoflexus, a stronger, broader ectocingulum, more rounded stylar lobes, a lingually shifted paracone apex (the base is only expanded in ITV/R/Mm-1), greater appression of the labial cusps, a more lingually positioned paraconule, and a more labiolingually transverse occlusal outline. The general similarities, however, certainly warrant additional comparisons when samples of *Sahnitherium* and *A. robustus* are larger. Thus, similarities exist between *Sahnitherium* and a number of taxa, but for the time being we place *Sahnitherium*, along with *Deccanolestes*, in Eutheria *incertae sedis*.

Paleobiogeographic considerations

We agree with Thewissen and McKenna (1992) that the small sample of *Deccanolestes* and now *Sahnitherium* teeth cannot be safely identified at the family level or unambiguously placed within a phylogenetic framework. However, their higher-level affinities indicate that eutherians were present on the Indian subcontinent by the Late Cretaceous. In the traditional context (summarized by Briggs 1989) of a long period of geographic isolation for the Indian subcontinent (~100 my) and an exclusive Laurasian distribution for eutherians, these biogeographic data seem anomalous. Previous hypotheses (see Prasad and Sahni 1999 for a review) have explained this and other seemingly anomalous biogeographic data (e.g., pelobatid and discoglossid frogs, anguid lizards, alligatorids) by way of an early biotic exchange between the Indian subcontinent and Eurasia (via an early collision, island arcs, or an African land bridge). However, as discussed below recent paleogeographic, paleontological, and molecular systematic advances have changed the context of this “biogeographic anomaly” (Patterson and Owen 1991) in three important ways.

First, paleogeographic and paleontological evidence extend the duration of geographic connection between the Indian subcontinent and other southern continents. Geophysical data support a separation between the Indian subcontinent-Madagascar and Africa by approximately 150–160 mya (Rabinowitz et al. 1983; Coffin and Rabinowitz 1987) and between the Indian subcontinent and Madagascar by approximately 88 mya (Storey et al. 1995; Plummer and Belle 1995). However, the Kerguelen Plateau was subaerial and positioned between the Indian subcontinent and Antarctica during much of the Late Cretaceous (Coffin 1992 a, b; Hay et al. 1999). Whether it fully bridged these two landmasses and their biotas is still uncertain. Case (2002) acknowledged the same paleobiogeographic relationships but argued that they arose by dispersal from Antarctica to Madagascar via the Gunnerus Ridge prior

to 82 mya and then to the Indian subcontinent. Regardless of the exact land connections, paleontological evidence and phylogenetic inference from molecular systematic data recognize close affinities between the Late Cretaceous biotas from the Indian subcontinent, Madagascar, and southern South America (see Rogers et al. 2000 and Cracraft 2001). Thus, the geographic isolation of the Indian subcontinent may have been shorter than previously estimated.

Second, a growing amount of fieldwork in Gondwana's Mesozoic deposits has begun to uncover specimens that challenge a strict Laurasian distribution of Cretaceous boreosphenidan mammals. In the past twenty years, boreosphenidans have been reported from Cretaceous sediments on a number of southern continental landmasses (South America, see Mourier et al. 1986; Bertini et al. 1993; Gayet et al. 2001, Africa, see Sigogneau-Russell 1991, 1992, 1994, and Madagascar, see Krause 2001). Admittedly, the condition of many of these specimens makes lower-level identifications difficult. On the other hand, Krause (2001) referred to the Marsupialia a fragmentary tribosphenic lower molar from Late Cretaceous sediments of Madagascar. Furthermore, at least two genera from the earliest Cretaceous (Berriasian) of Morocco clearly document boreosphenidans in Africa prior to its split from South America (Sigogneau-Russell 1991, 1992, 1994). Luo et al (2001) absorbed the latter data into their dual origins hypothesis by arguing that this part of northwestern Africa was contiguous with Eurasia. The phylogenetic affinities of the spinosaurid dinosaur *Baryonyx* from Eurasia with *Suchomimus*, from the Early Cretaceous sediments of Niger, support the northern connection hinted at by the Moroccan specimens (Serenó et al. 1998). Moreover, palynological distributional patterns offer a more detailed paleobiogeographic picture, pointing to strong provinciality within Gondwana during the Cretaceous (Wilson and Arens 2001a, b). Northern South American palynofloras show stronger affinities with other equatorial palynofloras than they do with those from southern South America, suggesting that biogeographic inferences based strictly on the geographically limited vertebrate database may be premature (Wilson and Arens 2001a, b). Thus, growing evidence indicates a wider distribution of boreosphenidan mammals on Gondwana than previously recognized (see Sigogneau-Russell et al. 2001) and a greater biogeographic diversity on Gondwana than currently sampled in the vertebrate record (see Morley 2000).

Third, a molecular phylogeny of placentals (crown-group eutherians) by Murphy et al. (2001) suggested a basal split between Afrotheria and Xenarthra + Boreoeutheria. Based on the available fossil evidence for these taxa, they argued that placentals originated on Gondwana rather than Laurasia (but see Hunter and Janis 2002). Furthermore, their molecular divergence estimates for the basal split roughly correspond to estimates for the geographic split between Africa and South America (100–120 mya; Smith et al. 1994), again suggesting that placentals and other crown-group therians (including eutherians) had a deeper history on Gondwana than the fossil record so far indicates.

Thus, better contextual understanding broadens the set of hypotheses that may explain the paleobiogeographic affinities of the Late Cretaceous biota from the Indian subcontinent. Below, we outline phylogenetic predictions for each of these paleobiogeographic hypotheses.

1. Early Asian connection (via an early collision or a series of intermediate island arcs).—This paleobiogeographic hypothesis requires that both the pre-collision Indian subcontinent biota be most closely related to other Gondwanan biotas and that the post-collision Indian subcontinent biota be most closely related to the Asian biota. Workers have predicted that this break in paleobiogeographic affinities may exist between the Infratrappean biota (Gondwanan) and the Intertrappean biota (Asian) (Buffetaut 1990; Prasad et al. 1995). However, the Intertrappean microvertebrate localities still strongly outnumber those from the Infratrappeans. Furthermore, mammals are not yet known from Infratrappean localities.

2. North African connection during the Indian subcontinent's drift.—This hypothesis requires that the pre-connection Indian subcontinent biota be most closely related to other Gondwanan biotas. The post-connection Indian subcontinent biota should be most closely related to the African biota but also closely related to the Eurasian biota. The Synclinal d'Anoual and Ouarzazate Basin mammalian assemblages from the Early Cretaceous and Paleocene, respectively, of Morocco are valuable sources of information, but currently insufficient for testing this hypothesis. Furthermore, faunas from eastern Africa are specifically needed to provide means to test claims of biotic exchange with the east coast of Africa during the Indian subcontinent's northward drift (Morley 2000; Conti et al. 2002).

3. Gondwanan vicariance I.—This hypothesis and the next require a southern distribution of eutherian mammals prior to the breakup of Gondwana. The degree of phylogenetic affinity between the biota from the Late Cretaceous of the Indian subcontinent and those from other Gondwanan landmasses should follow the sequence of sundered connections between them. Paleogeographic reconstructions by Smith et al. (1994) predict that the order from most closely related to the Indian subcontinent biota to the least closely related should be as follows: Madagascar, Antarctica, South America, Africa, and Australia.

4. Gondwanan vicariance II.—Paleogeographic reconstructions by Hay et al. (1999) predict that the order from most closely related to the Indian subcontinent biota to the least closely related should be as follows: Antarctica, South America, Madagascar, Australia, and Africa. Eutherian mammals are not yet represented in the Mesozoic fossil record of Gondwanan landmasses other than the Indian subcontinent, but absences may be due to degree of exploration on these landmasses and the rarity of the taxa. Other vertebrate taxa, like gondwanatherid mammals, baurusuchid notosuchians, and abelisaurid dinosaurs draw a link between the Indian subcontinent, Madagascar, Antarctica, and South America (Krause et al. 1997; Sampson et al. 1998; Bonaparte

1999; Wilson et al. 2001; Reguero et al. 2002), but again most areas, especially Africa, are poorly sampled.

5. North America-South America dispersal route.—A number of workers have recognized biotic exchange between North America and South America during the Late Cretaceous (see Rage 1986 for a review). The paleobiogeographic hypothesis that eutherian mammals arrived on Gondwana via this route requires that the pattern of phylogenetic affinity between eutherians from the Indian subcontinent and eutherians from other continents should follow one of the patterns outlined in hypothesis 3 or 4.

Although further sampling on the southern continents will allow us to further discriminate between the above hypotheses, our data presently provide some insight on the “biogeographic anomaly” of the Indian subcontinent’s Late Cretaceous biota. Without convincing geophysical evidence for an early collision with Asia and without a well-supported biogeographic incongruity between Infra- and Intertrappean biotas, the data do not require an early Asian connection (hypothesis 1). The data also do not provide support for a North African connection during the Indian subcontinent’s drift (hypothesis 2). In our view, the remaining hypotheses (3, 4, 5) garner support from the data and require the fewest *ad hoc* explanations. As argued above, other data suggest the following: the Indian subcontinent’s geographic connections to Gondwana were maintained later than once alleged; biogeographic connections between Gondwana and Laurasia existed during the Cretaceous; boreosphenidans inhabited Africa prior to the final breakup of Gondwana; and therians inhabited South America and Madagascar during the Late Cretaceous. Until the Cretaceous sediments of the southern continents have been more broadly sampled both temporally and geographically, the lack of eutherian fossils outside of the Indian subcontinent is only negative evidence. Within an updated paleobiogeographic and paleogeographic context, occurrences of eutherians (*Deccanolestes* and *Sahnitherium*) on the Indian subcontinent during the Late Cretaceous are not wholly unexpected. The new data are positive evidence that agree with other evidence for a wider distribution of “Laurasian” mammals on Gondwana and a more complex Mesozoic biogeography than previously understood. Currently, we cannot discriminate between hypotheses for Gondwanan vicariance I (according to Smith et al. 1994; hypothesis 3), Gondwanan vicariance II (according to Hay et al. 1999; hypothesis 4), and a North America-South America dispersal route (hypothesis 5). Additional data will help to further evaluate these hypotheses, as well as those not supported here.

Conclusions

The new material from Rangapur adds to our knowledge of the Indian subcontinent’s Late Cretaceous mammalian fauna. The collection of isolated teeth doubles the sample size for *Deccanolestes*, the best-known genus from the Late

Cretaceous of the Indian subcontinent. The larger sample provides a better understanding of the variation in dental morphology for the genus, yet phylogenetic affinities for the genus remain elusive. Synapomorphies previously used to support a close phylogenetic relationship between *Deccanolestes* and “palaeoryctoids” are found to be widespread among Late Cretaceous eutherians. Consequently, we defer familial placement of *Deccanolestes*, but recognize that *Deccanolestes* may share a close phylogenetic relationship with basal members of a proposed clade that includes *Otlestes*, *Batodon*, *Gypsonictops*, “zalambdalestids”, and “zhelestids.”

The Rangapur sample also includes a new taxon, *Sahnitherium rangapurensis*. Although the family-level taxonomy of the new taxon is uncertain, it adds to the diversity of the Indian subcontinent’s Late Cretaceous mammalian fauna. The fauna now consists of four reported mammal species—three of which are eutherians. Along with other purported “Laurasian” taxa from the Late Cretaceous of the Indian subcontinent, the three eutherians contribute to a biota that has been considered biogeographically unexpected for a Gondwanan landmass. Currently, phylogenetic uncertainties, paleogeographic ambiguities, and a sparsely sampled fossil record prevent a resolution for this puzzling biogeographic history. Instead, we outline five hypotheses and their phylogenetic predictions. Previous discussions have concentrated on paleobiogeographic hypotheses 1 and 2 that suggest a localized Laurasian dispersal to the Indian subcontinent, either directly from Eurasia or indirectly through North Africa. Although we do not discount these possibilities, we currently favor a second set of paleobiogeographic hypotheses (3, 4, 5) that suggest a deeper and more extensive history of boreosphenidans on Gondwana. These hypotheses have been largely overlooked in the debate over the Indian subcontinent’s Late Cretaceous biogeographic affinities, but a growing amount of paleontological, paleogeographic, and molecular systematic data provide support for this set of alternatives. Continued geological and paleontological fieldwork, especially underwater screenwashing of microvertebrate localities, on the Indian subcontinent and other southern continents will winnow the possibilities.

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Appendix

The morphological variation in the combined sample of *Deccanolestes* dental specimens from Rangapur and Naskal is discussed below.

Talonid arrangement.—Prasad et al. (1994) suggested that *Deccanolestes* has a talonid arrangement (i.e., hypoconulid closer to hypoconid) distinct from the arrangement we described for the taxon (i.e., hypoconulid closer to entoconid). However, all other Cretaceous eutherians have either the latter arrangement or one in which the hypoconulid is equidistant from the hypoconid and entoconid (Clemens and Lillegraven 1986; Butler 1990). Chemical weathering is evident in the samples from both Rangapur and Naskal (Khajuria and Prasad 1998). Under such conditions, relative observed distances between talonid cusps, especially on small teeth, may not be reliable. Thus, until better-preserved lower molars are available, we contend that *Deccanolestes* possesses the more conservative talonid morphology (i.e., hypoconulid closer to entoconid; Clemens and Lillegraven 1986) or that it is at least the primitive state for the genus.

Cristid obliqua.—In the lower molar specimens from Naskal and ITV/R/Mm-6 (*Deccanolestes* cf. *robustus*) from Rangapur, the cristid obliqua contacts the posterior base of the trigonid lingual to the protocristid notch. In all of the *Deccanolestes* cf. *hislopi* specimens from Rangapur, on the other hand, the cristid obliqua contacts the posterior base of the trigonid directly below the protocristid notch. Because most researchers consider the former condition the primitive state for eutherians (Fox 1984; Butler 1990; Averianov and Skutschas 2001; Archibald et al. 2001), we consider it the

representative morphology in *Deccanolestes*, but acknowledge that molar position may affect this character.

Metastylar area.—The metastylar area is larger than the parastylar area on the undamaged M2 of *Deccanolestes* cf. *hislopi* (ITV/R/Mm-2), almost equal to the parastylar area on the broken M2 of *Deccanolestes* cf. *hislopi* (VPL/JU/NKIM/15), slightly smaller than the parastylar area on M2 of *D. robustus* (VPL/JU/NKIM/13), and smaller than parastylar area on M1 of *D. hislopi* (VPL/JU/NKIM/10). Again, we characterize *Deccanolestes* based on the primitive morphology exhibited by *Deccanolestes* cf. *hislopi*—a metastylar lobe slightly larger than or equal to the parastylar lobe (supplementary information in Archibald et al. 2001).

Stylocone.—Although the lack of a prominent stylocone in the upper molar from Rangapur (ITV/R/Mm-2) may be preservational, other genera and species of Cretaceous eutherians exhibit polymorphism for development of the stylocone (e.g., *Cimolestes*; Novacek 1986). The presence of a prominent stylocone in some *Deccanolestes* specimens is the primitive state (Fox 1984; Averianov and Skutschas 1999), and we consider it the representative morphology for the genus.

Transverse width.—Butler (1990) used M2 as the standard for comparison of transverse widths in upper molars. Following this convention, the anterior width to buccal length ratios for VPL/JU/NKIM/14 and ITV/R/Mm-2 (*Deccanolestes* cf. *hislopi*) are greater than 1.6 (Table 1), whereas the same ratio for VPL/JU/NKIM/13 (*D. robustus*) is 1.34. Until larger samples are reported that clarify the extent of this morphological variation, we conclude that the upper molars of *Deccanolestes* vary in transverse width.