C. R. Palevol 9 (2010) 63–71

Contents lists available at ScienceDirect

Comptes Rendus Palevol

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Systematic palaeontology (Vertebrate palaeontology)

First mammal evidence from the Late Cretaceous of India for biotic dispersal between India and Africa at the KT transition

Premier témoignage par des mammifères du Crétacé supérieur indien, de la dispersion biotique entre Inde et Afrique à la transition KT

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ARTICLE INFO

Article history:
Received 2 September 2009
Accepted after revision 9 November 2009

Presented by Philippe Taquet

Keywords:
Cretaceous
Mammals
Deccanolestes
Afrodon
Adapisoriculids
Dispersal
India
Africa

ABSTRACT

The Late Cretaceous record of mammals from India assumes great significance in view of the fact that it is the only Gondwanan landmass that has yielded definitive eutherian mammals. These mammals have variously been assigned to palaeoryctids, archontans or Eutheria *incertae sedis*. Well preserved lower molars recovered from a new mammal-yielding Deccan intertrappean site near Kisalpuri village, Dindori District, Madhya Pradesh (state), India, are described here under a new species *Deccanolestes narmadensis* sp. nov. The new fossil material indicates close phylogenetic relationship between *Deccanolestes* from India and *Afrodon* (Adapisoriculidae) from the Late Palaeocene of Africa and Europe. In view of older age and more primitive state of *Deccanolestes* teeth, it is inferred that *Deccanolestes* represents an ancestral morphotype from which the African/European adapisoriculid *Afrodon* may have been derived. This is the first compelling terrestrial fossil evidence for an early dispersal between India and Africa. Such a dispersal possibly involved an East African contact with India at the KT transition.

RÉSUMÉ

Mots clés :
Crétacé
Mammifères
Deccanolestes
Afrodon
Adapisoriculidés
Dispersal

Les gisements à mammifères du Crétacé supérieur indien, d'intérêt majeur, ont livré les seuls euthériens connus dans le Gondwana à cette époque. Les espèces indiennes, de parentés longtemps incertaines, ont été identifiées comme des paléoryctidés, des archontes ou des euthériens *incertae sedis*. Un nouveau matériel dentaire bien conservé, découvert dans le nouveau site de Kisalpuri (District de Dindori, Madhya Pradesh), dans les inter-trapp du Deccan, est décrit et rapporté à la nouvelle espèce *Deccanolestes narmadensis* sp. nov. Celle-ci indique des relations phylogénétiques étroites entre le genre indien *Deccanolestes* et

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doi:10.1016/j.crpv.2009.12.003

Inde
Afrique

l'adapisoriculidé *Afrodon* du Paléocène supérieur d'Europe et d'Afrique. En accord avec son âge ancien et sa morphologie primitive, *Deccanolestes* est donc reconnu ici comme représentant le morphotype ancestral dont sont issus les adapisoriculidés cénozoïques tels qu'*Afrodon*. Il s'agit de la première indication fossile précise à l'appui d'une dispersion ancienne entre l'Afrique et l'Inde. Celle-ci a probablement impliqué une connexion Est-Africaine à la transition KT.

1. Introduction

The fossil record of Cretaceous mammals is very scanty from the Gondwanan continents. Although known from the Early Cretaceous of Australia and Africa, until now, no definitive mammals have been recorded from the Turonian–Maastrichtian interval (ca. 94–65 m.y.) of these continents. Late Cretaceous mammals are known only from South America, Madagascar and India. The Late Cretaceous mammal fauna of South America is represented by gondwanatheres (a specialized Gondwanan group), dryolestoids, and triconodontids (Bonaparte, 1990). Likewise, Late Cretaceous Madagascan mammal fauna is known by gondwanatheres (Krause et al., 1997), a possible marsupial (Krause, 2001) or zhelestid eutherian (Averianov et al., 2003) and some unidentified forms (Krause et al., 1994). A probable gondwanathere mammal was also documented from the Cretaceous rocks of Tanzania, the precise age of which is yet to be confirmed (Krause et al., 2003). As compared to this, India is the only Gondwanan continent that yielded undoubted Late Cretaceous eutherian mammals, and thus it is very important for understanding the evolution of eutherian mammals in the Gondwanan continents. These mammals were first reported from the sedimentary beds sandwiched between the Deccan volcanic flows 2 km north-east of Naskal, Rangareddi Distrit, Andhra Pradesh (Fig. 1) and were assigned to *Deccanolestes hislopi* with possible affinities to the Laurasian insectivore family Palaeoryctidae (Prasad and Sahni, 1988) (cimolestids of Kielan-Jaworowska et al., 2004). Following this, additional fossils belonging to *D. hislopi* and a second species *D. robustus* were described from the same site (Prasad et al., 1994). The dental morphology of *Deccanolestes* was regarded closely comparable to that of North American cimolestids (*Cimolestes* and *Procerberus*) and basal eutherians from Asia (*Kennalestes* and *Otlestes*) (Prasad et al., 1994). In addition to the dental remains of *D. hislopi* and *D. robustus*, ankle bones falling within the size range of these two species have also been described (Godinot and Prasad, 1994; Prasad and Godinot, 1994). Based on close similarity of tarsal morphology to that of archontans, it was inferred that *Deccanolestes* adapted for an arboreal way of life and archontans had possibly originated on the Indian subcontinent from *Deccanolestes*-like animal

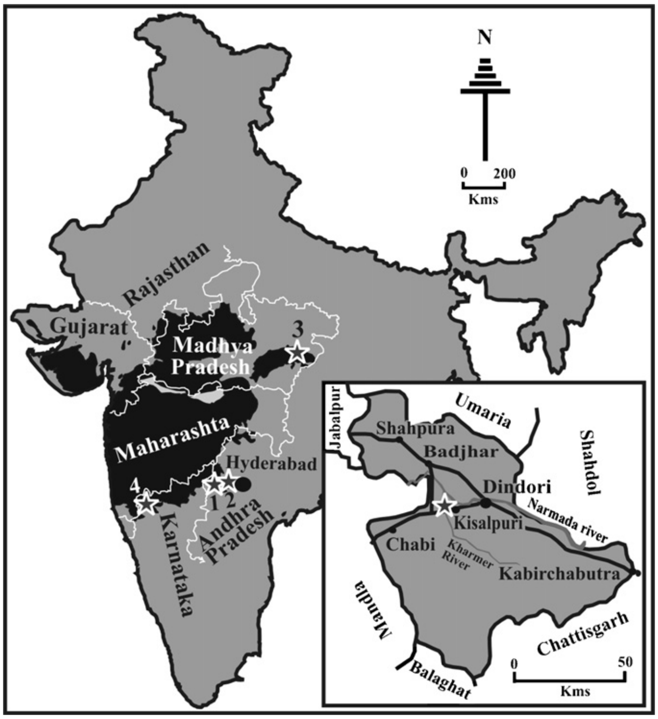

Fig. 1. Map of India showing the location of the Upper Cretaceous mammal-yielding intertrappean sites (denoted by stars). 1. Naskal, 2. Rangapur, 3. Kisalpuri, 4. Gokak.

Fig. 1. Carte de l'Inde montrant la localisation des sites inter-traps pourvoyeurs de mammifères du Crétacé supérieur (indiqués par des étoiles).

(Godinot and Prasad, 1994; Prasad and Godinot, 1994). Rana and Wilson (2003) documented additional fossils represented by *D. hislopi*, *D. robustus* and a new taxon *Sahnitherium rangapurensis* from the intertrappean beds of Rangapur that occur 4 km southeast of Naskal mammal-yielding site along its strike extension (Fig. 1). Rana and Wilson (2003), though accepted the boreoeutherian affinity of these taxa, felt that morphological similarities with *Cimolestes* and *Procerberus* are mostly plesiomorphic and hence placed *Deccanolestes* and *Sahnitherium* in Eutheria *incertae sedis*. In addition to eutherian mammals, gondwanatheres were documented from the intertrappean beds of Naskal and Gokak (Fig. 1) (Das Sarma et al., 1995; Krause et al., 1997; Wilson et al., 2007) and haramiyids from the intertrappean beds in the vicinity of Naskal (*Avashishta bacharamensis*) (Anantharaman et al., 2006). One stumbling block in the interpretation of true phylogenetic relationship of the Cretaceous eutherians from India is the poor preservation of specimens from both Naskal and Rangapur sites. The teeth from these sites, particularly from Naskal, are heavily pitted supposedly due to groundwater action (Khajuria and Prasad, 1998).

More recently, a new Late Cretaceous mammal yielding site was discovered in the eastern Deccan volcanic province about 1.5 km south-west of Kisalpuri village (Fig. 1), Dindori District, Madhya Pradesh situated about 700 km north of Naskal site (Khosla et al., 2004). This site has yielded a new gondwanathere mammal (*Bharattherium bonapartei*) (Prasad et al., 2007a) and an eutherian mammal (*Kharmerungulatum vanvaleni*) (Prasad et al., 2007b) with affinities to archaic ungulates. In addition to these two taxa, several upper and lower teeth that fall within the morphological framework of *Deccanolestes* have also been recovered from the Kisalpuri site. The newly recovered teeth from Kisalpuri are fairly well preserved and provide us with an opportunity to decipher the crown morphology more precisely. In the present article, the new fossil material, especially lower molars, are described and the taxonomic relationship of *Deccanolestes* is reassessed in light of latest comparisons with eutherian mammals of Late Cretaceous age from North America and Asia, Late Palaeocene of Morocco and Germany.

1.1. Institutional abbreviations

VPL/JU/IM: Vertebrate Palaeontology Laboratory, University of Jammu, intertrappean mammal catalogue numbers, **VPL/JU/NKIM**: Vertebrate Palaeontology Laboratory, University of Jammu, Naskal intertrappean mammal catalogue numbers, **ITV/R/Mm**: Intertrappean vertebrates, Rangapur mammal catalogue numbers, Garhwal University, India, **THR**: Adrar Mgorn1, collections of the Université des sciences et techniques du Languedoc, Montpellier II catalogue numbers, CR, CY; Cernay, Bn: Braillon, Ph: Phelzion collections in Muséum national d'histoire naturelle (**MNHN**), Paris, **UCMP**: University of California Museum of Paleontology, Berkeley.

2. Systematic palaeontology

Class	Mammalia Linnaeus, 1758
Infraclass	Eutheria Gill, 1872
Order	? Euarchonta Waddell et al., 1999
Family	Adapisoriculidae Van Valen, 1967
Genus	***Deccanolestes*** Prasad and Sahni, 1988
Species	***Deccanolestes narmadensis*** sp. nov.

2.1. Holotype

VPL/JU/IM/8 (Rm1 or Rm2).

2.2. Referred Material

VPL/JU/IM/7 (Rm1 or Rm2), VPL/JU/IM/6 (Rm3), ITV/R/Mm-8 (Rm1 or Rm2).

2.3. Horizon, type locality and age

Deccan intertrappean beds exposed 1.5 km southwest of Kisalpuri village, Dindori District, Madhya Pradesh, Central India, Upper Cretaceous (Maastrichtian).

2.4. Stratigraphic range

Upper Cretaceous (Maastrichtian) intertrappean beds of Rangapur, Rangareddi District, Andhra Pradesh, South India.

2.5. Specific Diagnosis

Differs from *D. hislopi*, *D. robustus* and *Deccanolestes* sp. (ITV/R/Mm-9) in the following traits: anteriorly projecting and lingually placed, large individualized paraconid placed in line with the metaconid rather than crest-like as in *D. hislopi*; trigonid cusps forming an open triangle; paraconid, metaconid and entoconid in line with each other; talonid as wide as and slightly shorter than or as long as the trigonid; and in presence of a postmetacristid.

2.6. Etymology

Species named after Narmada river which flows through the study area.

2.7. Description

The species is known only by lower teeth. VPL/JU/IM/8 has well-preserved cusps except for the abraded metaconid and hypoconid tips. The trigonid cusps are arranged in an open triangle. The protoconid is the highest and largest cusp of the trigonid. The metaconid is slightly smaller than the protoconid and its posterior base is slightly posterior to that of the protoconid which makes the posterior trigonid wall and protocristid slightly obliquely oriented to the transverse axis. The paraconid is the smallest cusp of the trigonid occurring at a lower level than the protoconid and metaconid; it is placed at the lingual margin in line with the metaconid and the entoconid

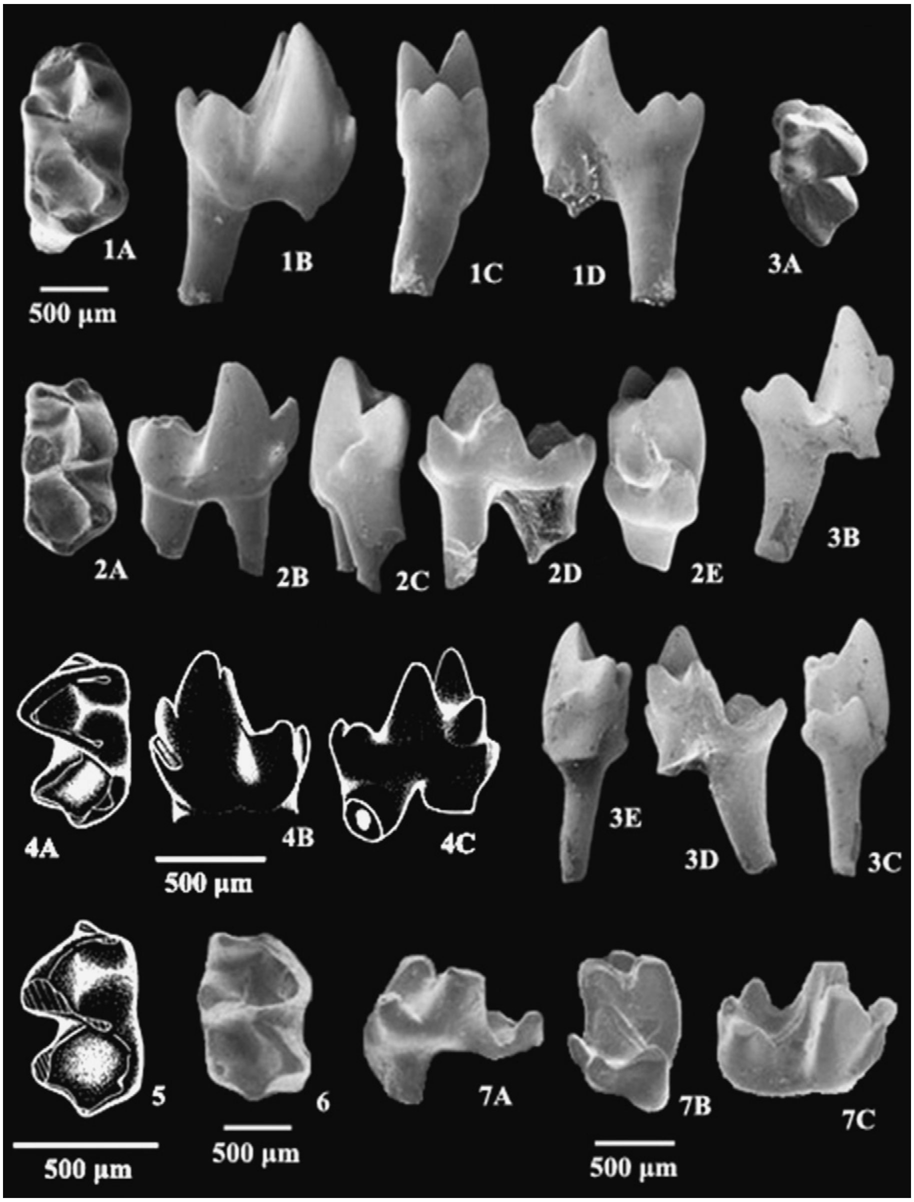

Fig. 2. 1–3. *Deccanolestes narmadensis* sp. nov. from the Upper Cretaceous Kisalpuri intertrappean beds, central India. 1. Right m1 or m2 (VPL/JU/IM/7) in occlusal (1A), labial (1B), posterior (1C) and lingual (1D) views; 2. Right m1 or m2 (VPL/JU/IM/8, holotype) in occlusal (2A), labial (2B), anterior (2C), lingual (2D) and posterior (2E) views; 3. Right m3 (VPL/JU/IM/6) in occlusal (3A), labial (3B), posterior (3C), lingual (3D) and anterior (3E) views. 4. Left m1 of *Afrodon chleuhi* (THR 214) from the Late Palaeocene of Morocco in occlusal (4A), labial (4B) and lingual (4C) views. 5–7. *Afrodon germanicus* from the Late Palaeocene of Germany and France. 5. Left m2 of *A. germanicus* (CY 590) in occlusal view; 6. Right m2 (CR-1-Bn) in occlusal view; 7. Right m1 (Wa/16118B) in lingual (7A), posterior (7B), and labial (7C) views. Figs. 4 and 5 are redrawn from Gheerbrant (1995) and Figs. 6–7 are after Gheerbrant and Russell (1989, fig. 4a–c, 5). Scale bar is same for Figs. 1–3.

Fig. 2. 1–3. *Deccanolestes narmadensis* sp. nov. provenant des lits inter-traps du Crétacé supérieur de Kisalpuri, Inde centrale. 1. m1 ou m2 droite (VPL/JU/IM/7) en vues occlusale (1A), labiale (1B), postérieure (1C) et linguale (1D) ; 2. m1 ou m2 droite (VPL/JU/IM/8, holotype) en vues occlusale (2A), labiale (2B), antérieure (2C), linguale (2D) et postérieure (2E) ; 3. m3 droite (VPL/JU/IM/6) en vues occlusale (3A), labiale (3B), postérieure (3C), linguale (3D) et antérieure (3E). 4. m1 gauche *d'Afrodon chleuhi* (THR 214) du Paléocène tardif du Maroc en vues occlusale (4A), labiale (4B) et linguale (4C). 5–7. *Afrodon germanicus* du Paléocène tardif d'Allemagne et de France. 5. m2 gauche de *A. germanicus* (CY 590) en vue occlusale ; 6. m2 droite (CR-1-Bn) en vue occlusale. 7. m1 droite (Wa/16118B) en vues linguale (7A), postérieure (7B) et labiale (7C). Les Figures 4 et 5 sont redessinées selon Gheerbrant (1995) et les Figures 6–7 selon Gheerbrant et Russel (1989, figs. 4a–c, 5). La barre d'échelle est la même pour les Figures 1 à 3.

(Fig. 2.2A). The paraconid is a relatively large and well individualized cusp slanting anteriorly and separated from the metaconid by a broad 'V' shaped groove (Fig. 2.2D). The paraconid is broken to its base on VPL/JU/IM/7, but in its girth it appears to be substantially large (only slightly smaller than the metaconid) and is placed on the lingual margin (Fig. 2.1A). The paracristid has a 'V' shaped notch. The precingulid is prominent on both the

Table 1
Measurements (millimeters). L: length; TRW: trigonid width; TAW: talonid width; PDH: protoconid height; TAH: talonid height; TAL: talonid length; AML: premetaconid length.
Tableau 1
Mesures en millimètres. L : longueur ; TRW : largeur du trigonide ; TAW : largeur du talonide PDH : hauteur du protoconide ; TAH : hauteur du talonide ; TAL : longueur du talonide ; AML : longueur du prémétaconide.

Specimen number	L	TRW	TAW	PDH	TAH	TAL	AML
VPL/JU/IM/6(m3)	1.23	0.60	0.60	1.33	0.83	0.56	0.56
VPL/JU/IM/7(m1 or m2)	1.32	0.67	0.66	1.34	0.80	0.59	0.56
VPL/JU/IM/8(m1 or m2)	1.25	0.65	0.64	0.97	0.55	0.57	0.58

teeth, stoutly built and subvertical in orientation with a small cuspule at its dorsal end (Fig. 2.1A, 2.2A–C,). The trigonid is nearly as long and as wide as the talonid (Table 1). It is nearly one and half times higher than the talonid (Fig. 2.1B, 2.2B). The hypoconid is the largest and highest cusp of the talonid. The hypoconulid is slightly smaller than the hypoconid. The hypoconulid and entoconid are subequal in size on VPL/JU/IM/8 and the hypoconulid is slightly larger than the entoconid on VPL/JU/IM/7. The hypoconulid is closer to the entoconid than to the hypoconid (Fig. 2.1A, C, 2.2.A, E) The entocristid is short and low. The cristid obliqua joins the trigonid wall below the protocristid notch on VPL/JU/IM/8 and slightly lingual to it on VPL/JU/IM/7. There is a thin distal metacristid at the posterolingual base of the metaconid. It is more prominent on VPL/JU/IM/7 than on VPL/JU/IM/8. Posteriorly, a shallow notch is present between the hypoconid and the hypoconulid. The talonid basin is short, deep, and bowl-like. The hypoflexid is deep.

In m3 (VPL/JU/IM/6), the trigonid is acute-angled (Fig. 2.3A) as compared to that of VPL/JU/IM/7 and 8 and the metaconid is as small as the paraconid. The paraconid is a small, well individualized conical cusp placed lingually in line with the metaconid (Fig. 2.3A). As compared to the metaconid and the paraconid, the protoconid is very high (Fig. 2.3D). The trigonid and talonid junction is lingually twisted. The trigonid basin is open through a wide groove between the paraconid and metaconid. The paraconid tip is broken (Fig. 2.3D–E). Though the paraconid and the metaconid appear subequal in height, in girth the metaconid is slightly smaller than the paraconid (Fig. 2.3D). The distal metacristid descends posterolingually from the protocristid notch in continuation with the lingual crest of protoconid and from the posterior mid-height of metaconid it turns lingually and then descends to the lingual base of metaconid to merge with the entocristid (Fig. 2.3C). The trigonid is shorter and wider than the talonid. The long talonid and posteriorly projecting hypoconulid imply that the tooth represents an ultimate molar (Fig. 2.3A, B, D). Slightly labially shifted hypoconid is the largest cusp of the talonid which is separated from the hypoconulid by a broad notch. The hypoconulid is smaller than the hypoconid, the entoconid and entocristid are completely worn and thus the talonid opens lingually. The cristid obliqua contacts the posterior trigonid wall below the protocristid notch and extends dorsally. The talonid is shallow and slopes anterolingually (Fig. 2.3A).

2.8. *Remarks*

D. narmadensis sp. nov. differs from the lower molars of *D. hislopi* and *D. robustus* in having a relatively large paraconid placed at the lingual margin of the trigonid and projecting anteriorly, the talonid nearly subequal in width to the trigonid and slightly shorter or as long as the trigonid, and the hypoconulid slightly closer to the entoconid than to the hypoconid. The paraconid is at a lower level than the protoconid and metaconid and the trigonid lacks the flat triangular area formed by trigonid cusps in *D. hislopi*. In these features and having a paracristid with 'V' shaped notch, a deep and broad 'V' shaped notch separating the paraconid from the metaconid, deep hypoflexid, small precingulid cuspule, and cristid obliqua contacting the trigonid wall slightly lingual to protocristid notch, VPL/JU/IM/7 and VPL/JU/IM/8 compare well with ITV/R/Mm-8 described as *Deccanolestes*? sp. (Rana and Wilson, 2003). Because of this close similarity in crown morphology, ITV/R/Mm-8 is also assigned to the new species. However, in ITV/R/Mm-8, the hypoconulid is equidistant from the hypoconid and entoconid while it is closer to entoconid in the new teeth from Kisalpuri. But this feature is variably present in teeth referred to *D. hislopi*. No comparison is possible with *Sahnitherium*, another eutherian taxon known from the Late Cretaceous of India, as it is based on an upper molar. As the crown morphology of VPL/JU/IM/6-8 and ITV/R/Mm-8 is distinct from that of *D. hislopi* and *D. robustus*, naming of a new species, *D. narmadensis* sp. nov., for these specimens is justified. The mammal collection from the intertrappean beds of Kisalpuri is overwhelmingly represented by lower molars and includes only a few incompletely preserved upper molars. Hopefully, well preserved upper molars referable to *D. narmadensis* sp. nov. may be recovered in future when large scale screen-washing is undertaken at this site.

3. Comparisons

Comparison of *Deccanolestes*, including the new specimens from Kisalpuri, with the casts and original specimens of Late Cretaceous cimolestids (previously described as palaeoryctids) from North America (*Cimolestes, Procerberus Batodon*) and some basal eutherians from Asia (*Kennalestes, Asioryctes*) at UCMP, Berkeley, and Late Palaeocene cimolestids (*Cimolestes, Aboletylestes*) at MNHN, Paris by GVRP and EG indicated that the similarities in the crown morphology between *Deccanolestes* and these taxa are primarily plesiomorphic. *Deccanolestes* is more derived than

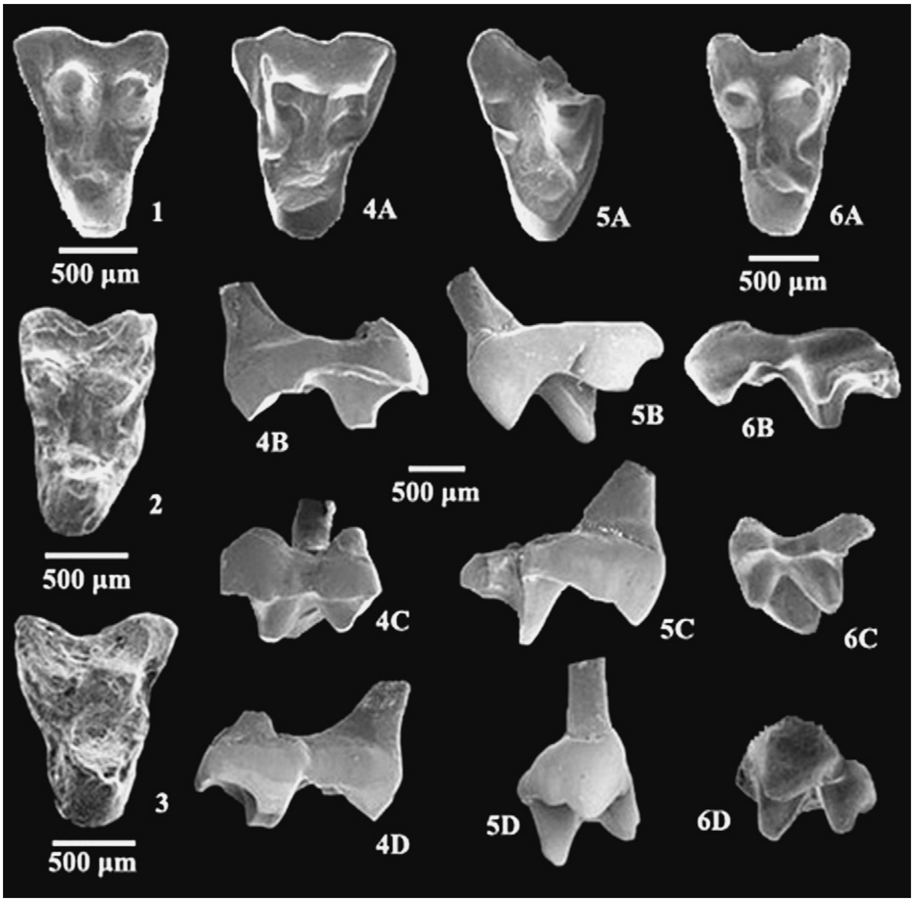

Fig. 3. 1. Left M2 of *Afrodon germanicus* (CR-181-Ph) in occlusal view. 2–3. *Deccanolestes* from the Upper Cretaceous intertrappean beds of Naskal, South India. 2. Right M2 of *Deccanolestes* cf. *D. hislopi* (VPL/JU/NKIM/15) in occlusal view; 3. Right M1 of *D. hislopi* (VPL/JU/NKIM/10, holotype) in occlusal view. 4–5. cf. *Deccanolestes hislopi* from the Upper Cretaceous Kisalpuri intertrappean beds, central India. 4. Left M1 (VPL/JU/IM/17) in occlusal (4A), anterior (4B), labial (4C) and posterior (4D) views; 5. Right M2 (VPL/JU/IM/14) in occlusal (5A), posterior (5B), anterior (5C) and lingual (5D) views. 6. Right M2 of *A. germanicus* (CR-19-Bn) in occlusal (6A), posterior (6B), labial (6C) and lingual (6D) views. Figures 1 and 6 are after Gheerbrant and Russell (1989, figs. 1a–d, 5) and Figures 2 and 3 are after Prasad et al. (1994, figs. 6A, C). Scale bar is same for Figures 4 and 5.

Fig. 3. 1 M2 gauche *d'Afrodon germanicus* (CR-181-Ph) en vue occlusale ; 2–3 *Deccanolestes* des lits inter-traps du Crétacé supérieur de Naskal, Inde méridionale. 2. M2 droite de *Deccanolestes* cf. *D. hislopi* (VPL/JU/NKIM/15) en vue occlusale. 3. M1 droite de *D. hislopi* (VPI/JU/NKIM/10, holotype) en vue occlusale. 4–5. cf. *Deccanolestes hislopi* des lits inter-traps du Crétacé supérieur de Kisalpuri, Inde centrale). 4. M1 gauche (VPL/JU/IM/17) en vues occlusale (4A), antérieure (4B), labiale (4C) et postérieure (4D) ; 5. M2 droite (VPL/JU/IM/14) en vues occlusale (5A), postérieure (5B), antérieure (5C) et linguale (5D). 6. M2 droite de *A. germanicus* (CR-19-Bn) en vues occlusale (6A), postérieure (6B), labiale (6C) et linguale (6D). Les Figures 1 et 6 sont dessinées selon Gheerbrant et Russell (1989, figs. 1a–d, 5) et les Figures 2 et 3 selon Prasad et al. (1994, figs. 6A, C). La barre d'échelle est la même pour les Figures 4 et 5.

Cimolestes, Procerberus, Batodon, Aboletylestes, Kennalestes, Asioryctes, and *Otlestes* in having upper molars with subequal parastylar and metastylar lobes, reduced parastylar hook, labial cusps well separated to their bases (predilambdodonty), reduced transverse width of the crown, and protocone moderately expanded mesiodistally and lingually, and reduced height difference between trigonid and talonid. Therefore, any close relationship with the above mentioned taxa is ruled out for *Deccanolestes*.

Among all known eutherian taxa, the upper and lower tooth morphology of two adapisoriculid species *Afrodon germanicus* known from the Late Palaeocene of Walbeck, Germany and Cernay and Berru localities (France) (Russell, 1964) and *Afrodon chleuhi* documented from the Late Palaeocene (Thanetian) Adrar Mgorn site in Ouarzazate basin, Morocco (Gheerbrant, 1988; Gheerbrant and Russell, 1989) is very similar to that of *Deccanolestes*. The upper molars of *D. hislopi* and *D. robustus* compare well to those of *A. chleuhi* and *A. germanicus* in many derived characters such as the differences listed above from cimolestids (more or less subequal development of parastylar and metastylar lobes, reduced parastylar hook, labial cusps separated as far as their bases (Fig. 3.4C, 3.6C–D) reduced transverse width (Fig. 3.1, 3.2, 3.3, 3.4A, 3.5A, 3.6A), moderate mesiodistal and lingual expansion of the protocone base (Fig. 3.1, 3.2, 3.3, 3.4A, 3.6A), and the paraconule placed between the paracone and the protocone, the metaconule small and closer to the metacone (Fig. 3.1, 3.4A, 3.5A, 3.6A), and moderately labially shifted protocone apex (Fig. 3.4B, D, 3.5B–D, 3.6B). In fact, THR-168, originally described as a didelphodontid (Gheerbrant, 1995), but subsequently identified as a m1 of *A. chleuhi* (Gheerbrant et al.,

1998) is remarkably similar to the holotypes of *D. hislopi* (VPL/JU/NKIM/10) and *D. robustus* (VPL/JU/NKIM/13) in it's crown morphology.

Likewise, the new lower molars assigned to *D. narmadensis* sp. nov. are very similar to those of *A. chleuhi* and *A. germanicus* in having trigonid and talonid subequal in width (Fig. 2.1A, 2.2A, 2.4A, 2.5), reduced height difference between the talonid and trigonid (trigonid nearly one and half times higher than the talonid) (Fig. 2.1B, 2.2B, 2.4B, 2.7C), well individualized and substantially large paraconid slanting anteriorly and placed lingually in line with the metaconid (Fig. 2.2A, D, 2.4A, C, 2.5, 2.7A), the paracristid and protocristid making an angle of more than 50°, metaconid slightly smaller than the protoconid, a large and salient hypoconid, the hypoconulid closer to the entoconid than to the hypoconid (Fig. 2.1A, 2.2A, 2.4A, 2.5, 2.6, 2.7B, C), the distal metacristid along with the cristid obliqua delimiting a deep depression in the linguobasal region of the posterior wall of the trigonid, and a deep bowl-like talonid basin.

Of the two known species of *Afrodon*, *A. germanicus* appears to be more derived than *A. chleuhi* and *Deccanolestes* in its narrow stylar shelf and in the greater relief and extension of cristid obliqua on to the posterior trigonid wall, sharp cusps on lower molars, proportionately wider talonid with a more labially shifted hypoconid (Fig. 2.6) (linked to a dilambdodont trend) which makes the talonid slightly wider than the trigonid. *A. germanicus* and *A. chleuhi* also differ from *Deccanolestes* in the nature of connection that cristid obliqua makes with the posterior wall of the trigonid. In *Deccanolestes*, the cristid obliqua joins the posterior trigonid wall slightly lingual to the protocristid notch (Fig. 2.1A, 2.2A), while in *A. germanicus* and *A. chleuhi* it meets the posterior trigonid wall in the middle of posterior base of the metaconid (Fig. 2.4A, 2.5, 2.7B). *Deccanolestes* is surprisingly more derived than *Afrodon* in the position of centrocrista on the upper molars. In *Afrodon*, the centrocrista is rectodont (predilambdodonty), whereas in *Deccanolestes* it is labially placed (dilambdodonty). However, in the development of conules and metacingulum *Afrodon* is more derived than *Deccanolestes*. The paraconule and metaconule are well developed in *Afrodon*, while the paraconule is well developed in all upper molars of *Deccanolestes*, the metaconule is either well developed as in VPL/JU/IM/14 (Fig. 3.5A) or weakly developed as in VPL/JU/IM/17 (Fig. 3.4A). Moreover, the metacingulum is absent in *Deccanolestes*, whereas it extends slightly on to the posterior face of the metacone in *Afrodon*. Besides, the postparaconule crest of *Afrodon* continues on to the lingual flank of paracone giving it an angular aspect. On the whole, *Deccanolestes* is more similar to *A. chleuhi* than to *A. germanicus* in the small size of molars, in the presence of robust cusps on lower molars, and in having a talonid nearly subequal in width or slightly narrower than the trigonid and less clearly marked cristid obliqua with a low relief. In these traits, the European species *A. germanicus* is more derived than *Deccanolestes* and *A. chleuhi.*

The m3 VPL/JU/IM/6 referred to *D. narmadensis* sp. nov. is strikingly similar to a left lower third molar (THR-51) assigned to *A. chleuhi* (Gheerbrant, 1995). In both these teeth, the paraconid is a comparatively large, well individualized cusp nearly equal to the metaconid and anterior to it in position; the metaconid is substantially smaller than the protoconid; the trigonid is slightly raised in lingual view as compared to the talonid; the hypoconid is the largest cusp of the talonid; the hypoconulid and entoconid are smaller than the hypoconid and subequal in size; the hypoconulid is median in position; the hypoconid and hypoconulid are separated by a broad notch posteriorly; the talonid basin is shallow and anterolingually sloping and partially open lingually. The trigonid is acute-angled in both THR-51 and VPL/JU/IM/6. The only difference between the two teeth is in the position of cristid obliqua with respect to the posterior trigonid wall. In THR-51, it joins the posterolingual base of the metaconid at its middle and extends up the trigonid wall as compared to its position slightly lingual to the protocristid notch on VPL/JU/IM/6.

4. Discussion

4.1. *Affinities of Deccanolestes*

The marked similarity between the upper and lower teeth of *Deccanolestes* and *Afrodon germanicus* and *A. chleuhi* (Adapisoriculidae) implies close phylogenetic relationship between the two genera. *Decannolestes* is consequently referred here to the Adapisoriculidae family, aside to *Afrodon*. The Indian and African forms appear especially more closely related with respect to the more derived European species *Afrodon germanicus*. Other European adapisoriculids such as *Adapisoriculus* and most remarkably *Remiculus*, are even much more specialized.

A. germanicus and *A. chleuhi* have been assigned to the family Adapisoriculidae (Gheerbrant and Russell, 1989; Gheerbrant, 1995). The phylogenetic relationship of adapisoriculids has remained a vexed problem in palaeontology. Van Valen (1967) created Adapisoriculinae for *Adapisoriculus* (Lemoine, 1883) known from the Late Palaeocene of Cernay, France. *Adapisoriculus*? *germanicus* first described from the Late Palaeocene rocks of Walbeck, Germany (Russell, 1964) was later found in coeval deposits in Cernay and Berru in France. The taxonomic affinity of *Adapisoriculus* has been debated for long and didelphid marsupial (Teilhard de Chardin, 1922), tupaiid (Van Valen, 1965) or mixodectid insectivore (Butler, 1972) relationships have been suggested. Van Valen (1967) placed it in the subfamily Adapisoriculinae (Family Tupaiidae), while Butler (1980) expressed doubts on this familial attribution. Gheerbrant and Russell (1989) placed it in its own family Adapisoriculidae and included predilambdodontids (*Afrodon* and *Bustylus*) and dilambdodontids (*Adapisoriculus, Garatherium,* and *Remiculus*). Gheerbrant (1995) placed adapisoriculids with some reservation in lipotyphlan insectivores. However, in a latest paper (Storch, 2008), small postcranial bones associated with *A. germanicus* (Gheerbrant and Russell, 1989) and *Bustylus* cf. *cernaysi* (Gheerbrant and Russell, 1991) of Late Palaeocene Walbeck fauna of Germany were assigned to Euarchonta and plesiadapiform primates. This hypothesis is interestingly congruent with the tupaiid relationship suggested by Van Valen for *Adapisoriculus* (1967). The close similarity in dental morphology of *Deccanolestes* to *Afrodon* and an arboreal habitat inferred from the postcranial bones morphology of *Deccanolestes* (Godinot and Prasad, 1994; Prasad and Godinot, 1994; Boyer et al., 2009) lends some credence to this interpretation. The currently best available working hypothesis that *Deccanolestes* and the adapisoriculids are euarchontans needs to be further tested in a formal cladistic framework.

A phylogenetic tree of Adapisoriculidae showing a proteutherian with zalambdodont structure (otlestid?) as a possible ancestral morphotype for adapisoriculid insectivores was proposed by Gheerbrant (1995, text fig. 2). Gheerbrant (1995) expressed the opinion that *Prokennalestes* is the most directly related form to the hypothetical ancestry of adapisoriculids as far as molar structure is concerned. But at the same time he argued that it is a very old ancestral form going back to more than 45 m.y. before adapisoriculds during which many things could have happened in the early mammalian evolution. *Deccanolestes* with its close resemblance in molar morphology to *A. germanicus* and *A. chleuhi* fills in partially this time gap. In view of the close dental similarity of *Deccanolestes* to *Afrodon germanicus* and *A. chleuhi*, and because of slightly primitive state of *Deccanolestes* molars, we propose here a working hypothesis that the latter represents the ancestral morphotype from which euarchontan adapisoriculids such as *Afrodon* were derived.

4.2. Palaeobiogeographic significance

The Late Cretaceous vertebrate fauna of India exhibits biogeographic affinities with both Gondwanan (Krause et al., 1997; Prasad, 2005; Sahni and Prasad, 2009) and Laurasian fauna (Prasad and Sahni, 1988; Prasad and Rage, 1995; Sahni and Prasad, 2009) during the northward drift phase of India. Based on gondwanathere mammals, abelisaurid dinosaurs and baurusuchid crocodiles, a Late Cretaceous terrestrial connection was envisaged between South America and India–Madagascar via Antarctica and Kerguelen Plateau (Krause et al., 1997; Sahni and Prasad, 2009) (but see Ali and Aitchison (2008) for a contrary view). On the other hand, a northern sweepstakes mode of dispersal between India and Eurasia across Kohistan-Dras island-arc system was suggested for the presence of eutherian mammals, discoglossid frogs and anguimorph lizards of Laurasiatic origin in the Late Cretaceous of India (Prasad and Sahni, 1999; Prasad, 2005; Sahni and Prasad, 2009).

The paleobiogeographic relationships between India and Africa during the Cretaceous and Early Tertiary are enigmatic, especially because of the African fossil gaps (Gheerbrant and Rage, 2006). Some authors suggested that Africa was the main terrestrial link between India and both Laurasian and Gondwanan continents when Greater India was close to the northeastern Africa (Somalia) (Chatterjee and Scotese, 1999; Briggs, 2003). This hypothesis could not be tested rigorously as Late Cretaceous (Turonian–Maastrichtian) fossil yielding sites are not known from Africa and the fossil record from India is mainly from the Upper Cretaceous (Maastrichtian) deposits. The present study espouses a close adapisoriculid taxonomic relationship of *Deccanolestes*, especially with *A. chleuhi* known from the Late Palaeocene rocks of Morocco. Because of the close similarity, but primitive construction and old age with respect to *Afrodon*, we suggest here that *Afrodon* may have evolved from a *Deccanolestes*-like ancestral morphotype. When and how exactly such a morphotype reached Africa/Europe before giving rise to *Afrodon* remains to be understood as there is no documented fossil record of Late Cretaceous mammals from Africa. However, the relationship of *Deccanolestes* and *A. chleuhi* is the most compelling and first direct evidence for an Indo-African dispersal at the beginning of the Tertiary (before the Late Paleocene). The northern dispersal hypothesis that favours sweepstakes mode of dispersal across the Tethys sea via island-arc systems to explain the presence of discoglossid and pelobatid frogs, anguimorph lizards, and eutherian mammals of Laurasiatic origin in the Late Cretaceous of India (Prasad and Sahni, 1999; Sahni and Prasad, 2009) may also hold equally good for the adapisoriculids. The close relationship between *A. chleuhi* and *Deccanolestes* however, weighs in favour of an East-African connection. But this will become clear only when the phylogeny of adapisoriuculids is better understood.

Ali and Aitchison (2008) while refuting the Kerguelen Plateau terrestrial connection between South-America and India–Madagascar suggested that the South American forms may have crossed over the proto-central Atlantic and Mozambique channel to India–Madagascar through West and Central Africa. This is in consonance with the early Late Cretaceous (95 Ma) biotic link suggested by Sereno et al. (2004) between South America and Africa based on abelisaurid dinosaur fossils from the Cenomanian of Niger, Northwest Africa. Another biogeographic link that demands close examination is the Late Cretaceous East African link envisaged for the Indian mobile raft (Chatterjee and Scotese, 1999; Briggs, 2003). Crucial to testing the latter biogeographic model is the Late Cretaceous fossil record of Africa which is poorly documented at present. Further, the East African connection for India needs to be firmly supported by marine geological and geophysical data from the basins west of India and a rigorous phylogenetic analysis of dental and postcranial remains of *Deccanolestes* and *Afrodon* in a cladistic framework (work in progress).

Acknowledgements

GVRP acknowledges Samuel P. & Doris Welles Research Grant, UCMP, Berkeley and the MNHN “Maître de Conférence Invité” grant, which enabled him to undertake comparative study of the Late Cretaceous eutherian mammals of India with those of North America, Asia, Europe and Morocco. Thanks are also due to William A. Clemens and Patricia Holroyd of UCMP and P. Tassy and C. Sagne of MNHN for allowing access to holotypes and casts of Late Cretaceous and Palaeocene eutherian taxa from North America, Europe, Asia, and Africa SEM photomicrography of the mammalian teeth by S. Shome of the Geological Survey of India. Kolkata is duly acknowledged. GVRP acknowledges financial support from the Department of Science & Technology (DST), Govt. of India (Grant No.SR/S4/ES/24/2002) for this work. OV(Grant No.SR/FTP/ES-33/2008) and AK

(SR/S4/Es-382/2008) are also thankful to DST for research grants.

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