

# A radiation of arboreal basal eutherian mammals beginning in the Late Cretaceous of India

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India's Late Cretaceous fossil mammals include the only undisputed pre-Tertiary Gondwanan eutherians, such as *Deccanolestes*. Recent studies have suggested a relationship between *Deccanolestes* and African and European Paleocene adapisoriculids, which have been variably identified as stem euarchontans, stem primates, lipotyphlan insectivores, or afrosoricids. Support for a close relationship between *Deccanolestes* and any of these placental mammal clades would be unique in representing a confirmed Mesozoic record of a placental mammal. However, some paleogeographic reconstructions place India at its peak isolation from all other continents during the latest Cretaceous, complicating reconstructions of the biogeographic history of the placental radiation. Recent fieldwork in India has recovered dozens of better-preserved specimens of Cretaceous eutherians, including several new species. Here, we incorporate these new specimens into an extensive phylogenetic analysis that includes every clade with a previously hypothesized relationship to *Deccanolestes*. Our results support a robust relationship between *Deccanolestes* and Paleocene adapisoriculids, but do not support a close affinity between these taxa and any placental clade, demonstrating that *Deccanolestes* is not a Cretaceous placental mammal and reinforcing the sizeable gap between molecular and fossil divergence time estimates for the placental mammal radiation. Instead, our expanded data push Adapisoriculidae, including *Deccanolestes*, into a much more basal position than in earlier analyses, strengthening hypotheses that scansoriality and arboreality were prevalent early in eutherian evolution. This comprehensive phylogeny indicates that faunal exchange occurred between India, Africa, and Europe in the Late Cretaceous–Early Paleocene, and suggests a previously unrecognized ~30 to 45 Myr “ghost lineage” for these Gondwanan eutherians.

placentals | paleobiogeography | phylogenetics | dispersal

Despite substantial augmentation of the Mesozoic record of mammals and improvements in calibration methods for molecular clock estimators, the age of origin of placental mammals remains hotly debated (1, 2). Molecular clock estimates consistently place the earliest divergences within Placentalia as falling within the Late Cretaceous (99.6–65.5 Mya) (3), or even in the Early Cretaceous (145.5–99.6 Mya) (1), but the existence of placental fossils from pre-Paleocene (older than 65.5 Mya) deposits is highly contentious (2). These ancient molecular divergence age estimates and the absence of Cretaceous placentals can be reconciled by proposing that the first 20 to 40 Myr (or 25–50%) of this group's fossil record is missing entirely. A few recent studies using statistical models that incorporate gaps in the fossil record to estimate divergence times, either from fossil occurrences alone or combined with molecular data, have produced results more similar to molecular clock dates (81–88 Mya) for the origin of Primates (4, 5), but other quantitative analyses based on the fossil record dispute these early divergence estimates (6–8). At least 70 species of eutherians (the clade in-

cluding placentals and their stem relatives) are known from the Late Cretaceous of Laurasia (North America, Europe, and Asia) (9), and although a few have been suggested as possible placentals [e.g., *Protungulatum* (10)], none are unequivocally supported as a Cretaceous placental mammal (2). With over 4,969 small-mammal fossils recovered from Mesozoic deposits worldwide (ref. 9: occurrence matrix downloaded using the parameters taxon = Mammalia, interval = Cretaceous; species data downloaded using the parameters: taxon = Eutheria, interval = Cretaceous), the absence of placentals cannot easily be ascribed to unsuitable preservation conditions across such a broad spectrum of temporal, geographic, and paleoenvironmental settings (11). One possible explanation for the contradiction between the observed record and molecular age estimates is that molecular clocks for placentals may be flawed and inaccurately reconstruct estimated divergence ages. Alternatively, some of the described Cretaceous eutherians may be stem members of particular placental lineages, but had not yet evolved the osteological synapomorphies of their crown clades, the presence of which would be necessary for accurate cladistic placement. Finally, Late Cretaceous placentals may exist, but remain unsampled if placentals originated where the fossil record is poor, specifically in the Late Cretaceous of Gondwana (11) [South America, Africa, Antarctica, Madagascar, India, and Australia: fewer than 5% of Cretaceous fossil mammal localities are Gondwanan (9)].

Among Gondwanan landmasses, India has been of particular interest for decades (12), since the discovery of the first undisputed Cretaceous Gondwanan eutherian, *Deccanolestes hislopi* (13). The Indian subcontinent's lengthy northward migration, starting with Gondwanan breakup from the Middle Jurassic (178–161 Mya) to its collision with Asia in the Eocene (14), has fueled discussions about an Indian “Garden of Eden” for placental mammals (12). To date, five species of eutherians have been named from India's Upper Cretaceous (Maastrichtian, 70.6–65.5 Mya) intertrappean beds: *D. hislopi* (13), *Deccanolestes robustus* (15), *Deccanolestes narmadensis* (16), *Sahnitherium rangapurensis* (17), and *Kharmarungulatum vanvaleni* (18). *Sahnitherium* is known from only a single molar and has been qualitatively compared with “zhelestids,” but also shares many morphological similarities with *Deccanolestes* (17) (see *Materials and Methods*). *Kharmarungulatum* is also known from a single, heavily worn

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molar, and was described as a possible placental mammal, specifically a “condylarth” (18).

*D. hislopi* is the only Indian Cretaceous eutherian to have been included in a few previous phylogenetic analyses, which have returned mixed results. Analyses based on the first described, heavily worn dental specimens placed *Deccanolestes* as a stem eutherian, outside of placentals (2), consistent with the “paleoryctid-like” dental morphology noted in its original description (13). In contrast, phylogenetic analyses based on tarsal elements, which show arboreal specializations such as an enlarged peroneal tubercle of the calcaneum and confluence of the navicular and sustentacular facets (19) (Fig. S1), have placed *Deccanolestes* as a stem member of Euarchonta (primates, colugos, and tree shrews), well within Placentalia (20). However, recent qualitative studies have suggested a relationship between *Deccanolestes* and African and European Paleocene adapisoriculids (16, 21, 22)—which have been variably identified as stem euarchontans (21), stem primates (23), lipotyphlan insectivores (24), or afrosoricids (25)—but this relationship has never been tested with a phylogenetic analysis. Support for a close relationship between *Deccanolestes* and any of these placental mammal clades would be unique in representing a confirmed Mesozoic fossil record of a placental mammal. At present then, *Deccanolestes* and *Kharmerungulatum* represent some of the best potential evidence for pre-Tertiary placentals, and thus lie at the heart of resolving the debate over the timing of placental origins.

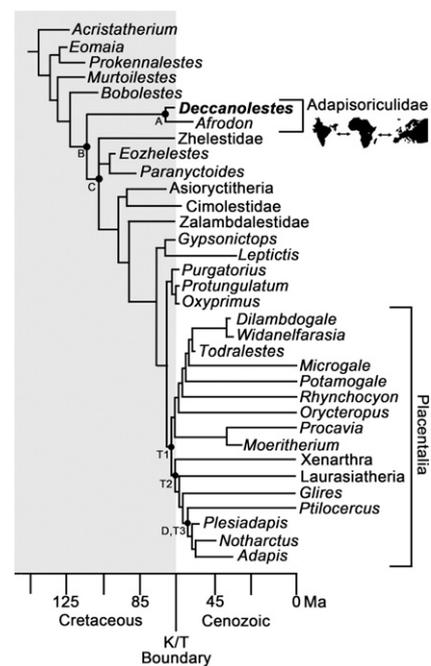
Recent discoveries of many more and better-preserved dental, mandibular (16), and postcranial (22) specimens, the result of years of fieldwork in Central and South India, provide an opportunity to comprehensively assess the affinities of the enigmatic Indian Cretaceous eutherians. We have substantially augmented a previously published data matrix (2, 26) with key taxa, revised character scores from new specimens, and additional postcranial characters derived from new material of *Deccanolestes* (Figs. S1 and S2, and Table S1). This matrix now comprises 415 osteological characters for 80 Jurassic to Recent mammalian taxa, including four Indian Cretaceous eutherians (*Kharmerungulatum* and the three named species of *Deccanolestes*), as well as Paleogene adapisoriculids, euarchontans, and afrosoricids, all groups with previously proposed links to *Deccanolestes* (16, 19–22, 25, 27), and a recently described early eutherian *Acristatherium yanensis* (28). Our recent material results in substantial revisions to the primary data presented in prior phylogenetic studies, including modified interpretations of 67 of the 150 characters previously scored for *Deccanolestes*.

## Results

**Phylogenetic Analysis. Unconstrained tree.** The initial search found 67 most parsimonious trees (MPTs) of length 2,521 steps. Further analyses using the traditional search option and these 67 trees as starting topologies found 300 MPTs of the same length as in the initial search. Pruned taxa analysis identified *Kharmerungulatum* (18) and *Montanalestes* (29) as being particularly unstable. A posteriori deletion of these two taxa produced the reduced strict consensus tree shown in Fig. S3.

**Crown Constraint 1: Placental mammals constrained to Exafroplacentalia topology.** The initial search found 220 MPTs of length 2,571 steps. Application of the traditional search increased MPT number to 1,034. *Kharmerungulatum* and *Montanalestes* again were deleted from these MPTs a posteriori to generate the reduced strict consensus tree shown in Fig. 1. Bootstrap and Bremer branch supports are displayed for Crown Constraint 1 in Fig. S4 (see *Materials and Methods*).

**Crown Constraint 2: Placental mammals constrained to Atlantogenata topology.** The initial search produced 227 MPTs of length 2,574 steps. Application of the traditional heuristic search, with the 227 MPTs as starting topologies, yielded a total of 3,102 MPTs of length 2,574 steps. The reduced strict consensus tree (Fig. S5)



**Fig. 1.** Relationships of *Deccanolestes* to other eutherians. Simplified reduced strict consensus tree using the Exafroplacentalia crown group constraint. Shaded area, Cretaceous period (145.5–65.5 Mya). Positions of terminal branches indicate the age of last known occurrence of the respective taxon. *Deccanolestes* and *Afrodon* form a monophyletic clade (node A) that inhabited India, Africa, and Europe in the Late Cretaceous to early Paleogene. Aside from Adapisoriculidae, including *Deccanolestes* and allies, no other undisputed Cretaceous or nonplacental eutherians are known from Gondwanan landmasses. The basal position of this arboreal clade suggests a lengthy ghost lineage for Gondwanan eutherians. Synapomorphies for nodes A, B, C, and the alternative placement of Adapisoriculidae with Euarchonta (node D) are detailed in Table S2. T1, T2, and T3 indicate the alternative positions for *Deccanolestes* and allies tested with Templeton tests.

was recovered after the deletion of *Kharmerungulatum*, *Montanalestes*, and *Lainodon* (30) (see *Materials and Methods*).

The MPTs for all three analyses (unconstrained and constrained) have very similar topologies (2, 26, 28). Although none of the strict consensus trees supported the placement of *Kharmerungulatum* within the placental crown group, the limited dental material for this taxon proved insufficient for resolving its phylogenetic relationships, and so it was removed a posteriori from the MPTs to produce the reduced strict consensus trees. *Deccanolestes* and the African and European Paleocene adapisoriculid *Afrodon* were strongly supported as monophyletic in all analyses (Fig. 1 and Figs. S3–S5). Thus, we assign *D. hislopi*, *D. robustus*, and *D. narmadensis*, as well as the morphologically similar *S. rangapurensis* (17), to the family Adapisoriculidae Van Valen 1967 [sensu Gheerbrant and Russell (31) and Gheerbrant (24)]. Contrary to recent descriptive studies placing the expanded Adapisoriculidae within Placentalia, the improved character data for *Deccanolestes* supports Adapisoriculidae in a much more basal position than previous analyses (Fig. 1), near the base of Eutheria.

Because a recent study questioned the identification of *Montanalestes* as a eutherian mammal (32), we repeated the analysis without *Montanalestes*. Results were entirely congruent with the analysis including *Montanalestes*, suggesting that the position of *Deccanolestes* and other adapisoriculids within the eutherian tree is insensitive to changes in the placement of *Montanalestes*.

**Templeton Tests.** To further test the hypothesis that *Deccanolestes* and allies are closely related or nested within Placentalia, we assessed three alternative positions for the expanded adapisor-

iculid clade using Templeton tests. The first position, labeled T1 in Fig. 1, places *Deccanolestes* and *Afrodon* immediately outside of placental mammals; the second position, labeled T2, places them just inside the basal node of Placentalia; the third tested position, labeled T3, places *Deccanolestes* + *Afrodon* as stem euarchontans, the position suggested by recent descriptive studies. Because the three analyses (unconstrained, Crown Constraint 1, and Crown Constraint 2) all produced remarkably similar results, Templeton tests are here reported for Crown Constraint 1, which was the shorter of the two topologies with placental mammals constrained to relationships supported by molecular data.

When trees produced with Crown Constraint 1 were analyzed for alternative position T1, 104 MPTs were recovered with 2,587 steps (i.e., 16 steps longer than the original MPTs for Crown Constraint 1), with *P* values ranging from 0.0056 to 0.28. The vast majority of these tests have significant *P* values, and most of the small number that “fail” are narrow failures, suggesting that this topology can be rejected. Alternative position T2 produced 8 MPTs of 2,589 steps (18 longer than the original MPTs), with *P* values from 0.0015 to 0.077, with ~90% having significant *P* values. Thus, this topology can also be rejected as significantly longer than the original trees. Alternative position T3 produced 156 MPTs of length 2,580 steps (i.e., 9 steps longer than the original MPTs), with *P* values ranging from 0.081 to 0.628. Although many topologies fail narrowly, none are statistically significant at the *P* < 0.05 level.

As the Templeton tests demonstrate, the minimum number of steps increased with proximity to Placentalia, but they decreased when adapisoriculids were constrained as stem euarchontans, which was the only alternative position that could not be rejected. Because the intermediate positions tested—those between the most parsimonious position near the base of Eutheria and the less parsimonious alternative placement of adapisoriculids as stem euarchontans—create significantly longer trees, and the most parsimonious trees place *Deccanolestes* and other adapisoriculids as basal eutherians, the simplest conclusion is that the postcranial similarities between *Deccanolestes* and euarchontans are convergences related to an arboreal lifestyle rather than synapomorphies.

**Synapomorphies Supporting Key Nodes.** Characters resolved as synapomorphies for *Deccanolestes* and *Afrodon* are detailed in Table S2. Synapomorphies are detailed for the three nodes of particular importance for defining the phylogenetic relationships of *Deccanolestes*: (i) the node that unites *Deccanolestes* and *Afrodon* (node A in Fig. 1); (ii) the node that excludes that clade from a higher position in the tree (i.e., the node immediately above the *Deccanolestes* branch) (node C in Fig. 1); and (iii) the node that unites *Deccanolestes* and *Afrodon* with the clade including placentals (node B in Fig. 1). We note that the listed synapomorphies excluding *Deccanolestes* from a more crownward position pertain only to node C, and thus likely underestimate the total number of synapomorphies, from more crownward nodes, that also bar *Deccanolestes* from a higher position. For brevity, we list the synapomorphies supported in the reduced strict consensus tree using Crown Constraint 1 (Exafroplacentalia), as the basal position and strong support for a *Deccanolestes* + *Afrodon* clade was similar in all three analyses. We also list the characters that supported *Deccanolestes* + *Afrodon* as stem euarchontans (node D in Fig. 1) when constrained for the Templeton test. For all but the last seven characters, character descriptions are as detailed in previous studies (2, 26).

The impact of the modified character scores, detailed in *Materials and Methods*, on the phylogenetic reconstruction presented here cannot be overstated when viewed in combination with the list of synapomorphies supporting key nodes. Of the 13

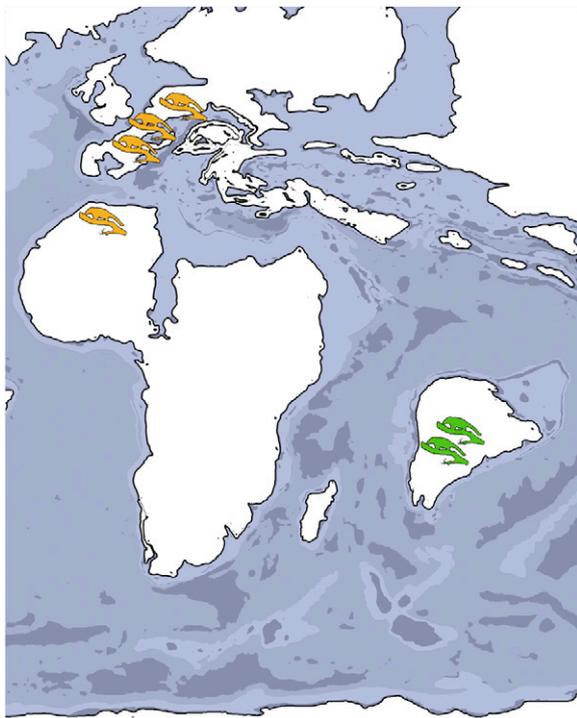
synapomorphies now uniting *Deccanolestes* and *Afrodon*, 11 were identified only in the new specimens of *Deccanolestes* and were either coded differently, coded as missing data, or not included in previous studies (2). Perhaps even more noteworthy is the observation that, of the five characters that now exclude *Deccanolestes* from an more crownward position in the phylogeny (Node C in Fig. 1), only one character (character 65 in ref. 2, upper molar labial styler shelf size) is coded with the same state in previous analyses. Of the new synapomorphies of Node C in this revised analysis, three (characters 41, 70, and 80 in ref. 2, concerning premolar and molar morphology) are coded differently because of the new specimens and another (415, plantar pit on calcaneal cuboid facet) is an entirely new character in this matrix. In contrast, of the six characters that unite the clade of *Deccanolestes* and *Afrodon* with the clade including placentals and most other Late Cretaceous eutherians (to the exclusion of *Eomaia*, *Prokennalestes*, *Murtoilestes*, and *Bobolestes*) (Node B in Fig. 1), only one character (character 79 in ref. 2, metacone and paracone base relationship) is coded differently from previous analyses, and that shift is from a single state to a polymorphic state.

## Discussion

These phylogenetic results have important implications for our understanding of the timing of the origin of placental mammals, the paleoecology of basal eutherians, and mammalian biogeography during the Late Cretaceous. Placement of Adapisoriculidae among the most basal eutherians, and the finding that there is little evidence at present to support recognition of *Kharmerungulatum* as a placental, removes much of the putative fossil evidence for the presence of placentals during the Late Cretaceous. In light of increasing fossil evidence for a diverse Cretaceous eutherian radiation, without compelling evidence that any Cretaceous Indian taxon belongs to a placental clade, it appears unlikely that India was a “Garden of Eden” for placental mammals (11, 12, 33). Recent discoveries of Cretaceous mammals from South America (34), Madagascar (35), Africa (36), and Australia (37), as well as continued Cretaceous mammal discoveries from the Laurasian continents (2), have also failed to recover a definitive placental mammal, although the possibility always remains that future fossil discoveries or molecular analyses will better reconcile the fossil and molecular evidence for the timing of the placental radiation.

A scansorial habitus has been reconstructed for several Cretaceous eutherians, including the oldest known, *Eomaia scansoria* (38). Postcranial remains of *Deccanolestes*, however, suggest that it possessed a greater degree of arboreality than other Cretaceous eutherians (Fig. S1) (19, 22). Its basal placement in the analyses presented here strengthens the hypothesis that eutherian mammals, or even therian mammals, were ancestrally scansorial or arboreal (38–40). Arboreality has recently been linked to lower extrinsic mortality and increased longevity across extant mammals (41), and there may have been strong selective pressure for early eutherians to seek refuge in trees to escape from terrestrial predators, such as dinosaurs, or to explore additional trophic niches. Furthermore, arboreality is correlated with many modifications to the postcranial skeleton to increase flexure, manus and pes rotation, and grasping ability; thus, the prevalence of arboreality and scansoriality in Cretaceous eutherians probably played a key role in shaping the early radiation and later success of the clade.

The phylogenetic relationships of *Deccanolestes* and other adapisoriculids also provide insights into the complex paleobiogeographic history of India during the Cretaceous and Early Tertiary (Fig. 2). As noted above, the timing of the Indian subcontinent’s migration, from the beginning of Gondwanan breakup in the Middle Jurassic to its Eocene collision with Asia (14) has led to the hypothesis that India served as a Garden of



**Fig. 2.** Paleobiogeographic map of the Latest Cretaceous (~65 Mya), with Cretaceous and Paleocene localities of adapisoriculids indicated. Locations of Late Cretaceous occurrences of *Deccanolestes* [Naskal (13)/Rangapur (17) and Kisalपुरi (16), India], indicated with green (to standard color for the Cretaceous) arboreal mammal silhouettes. Early Paleocene (Hainin, Belgium) (21), Middle Paleocene (Walbeck, Germany), and Late Paleocene (Cernay, France; Tremp, Spain; and Ouarzazate basin, Adrar Mgorn, Morocco) localities of *Afrodon* are indicated with orange (standard color for the Paleogene) arboreal mammal silhouettes. White areas indicate subaerial (terrestrial) exposure, and blues represent marine areas, with darker shades of blue reflecting increasing water depth. Paleogeographic reconstruction modified from Ron Blakey, Department of Geology, Northern Arizona University, Flagstaff, AZ (<http://jan.ucc.nau.edu/~rcb7/065Marect.jpg>).

Eden for placental mammals (12), despite ongoing debate about the specific nature and timing of India's connections to other continents. A recent paleogeographic reconstruction suggests that India was connected to East Africa via the Oman-Kohistan-Dras Island Arc in the latest Cretaceous (42), and another suggests that it remained connected to Antarctica into the Late Cretaceous (43). Another recent analysis favored only indirect connection of India with other southern continents, mainly involving overwater dispersal to Africa via Madagascar, from ~83.5 Mya (14). That study placed India at peak isolation from all other continents in the latest Cretaceous (as illustrated in Fig. 2), with an estimated 1,500-km stretch of ocean between India and any northern island arc "stepping stones," although this trans-tethyan route has been proposed for Late Cretaceous lizards and frogs (44). Despite the wide oceanic barriers indicated for this duration, which render it unlikely that large vertebrates were dispersing between Gondwanan landmasses (45), our analyses demonstrate that eutherians dispersed between India, Africa, and Europe, directly or indirectly, during the Late Cretaceous-Early Paleocene.

Among the most intriguing questions regarding the expanded Adapisoriculidae (now including *Deccanolestes*) is that of its geographic origin. Taxa representing the earliest diverging eutherian clades occurred in the Barremian to Cenomanian (130–93.5 Mya) of Asia; the next diverging clades include a series of Aptian to Maastrichtian (125–65.5 Mya) nonplacental eutherians

from Laurasia. Although unstable enough to warrant removal in the reduced strict consensus tree, some trees supported *Montanolestes*, from the Aptian of North America (29), in a more crownward position than Adapisoriculidae, requiring a ghost lineage of at least 45 Myr for Adapisoriculidae. Even excluding consideration of *Montanolestes*, several Cenomanian taxa are present in the sister clade to Adapisoriculidae, requiring a ghost lineage for Adapisoriculidae of ~30 Myr. Whether adapisoriculids had a lengthy Gondwanan history, possibly in Africa or India, and this gap is primarily the result of a poor Gondwanan fossil record, or whether it had an unrecorded earlier Laurasian origin and later dispersed to India (indirectly via Africa or directly across the Tethys Sea) in the Late Cretaceous remains uncertain without further data on Gondwanan Cretaceous mammals. However, vicariance is an unlikely solution, given that the Jurassic breakup of India and Africa likely preceded the divergence of *Afrodon* and *Deccanolestes* by several tens of millions of years. In this regard, resolving the debated affinities of the therian mammal from the Late Cretaceous of Madagascar, which has been described variably as a marsupial (35) or a "zhelestid" eutherian (46), as well as another therian from the earliest Cretaceous of Morocco for which eutherian affinities have been suggested (47), may be relevant to refining the biogeographic relationships of Cretaceous mammals. The results presented here demonstrate the importance of the Cretaceous fossil record from India and other Gondwanan landmasses for revealing previously unappreciated diversity and ecological specialisations during early eutherian evolution, testing hypotheses on the temporal and geographic origin of the placental radiation, and providing direct evidence on continental faunal dispersal abilities and paleogeographic patterns during the latest Cretaceous. Specifically, our recent data, derived from years of fieldwork in Central and South India, definitively demonstrate that eutherian mammals dispersed between India, Africa, and Europe in the Late Cretaceous-Early Paleocene, that arboreality arose early in eutherian evolution, and that *Deccanolestes*, although an adapisoriculid, is not a Cretaceous placental mammal.

## Materials and Methods

**Data Collection.** The bulk of the character matrix used here is derived from recent studies of Cretaceous eutherians (2, 26). We supplemented this dataset with recent data from four eutherian species from the Cretaceous of India (*D. hislopi*, *D. robustus*, *D. narmadensis*, and *K. vanvaleni*), two adapisoriculid species from the Late Paleocene of Morocco (*Afrodon chleuhi*) and France and Germany (*Afrodon germanicus*) (24, 31), three possible afroscricids from the Late Paleocene of Morocco (*Todralestes*) (48, 49) and the Late Eocene of Egypt (*Dilambdogale*, *Widanelifarasia*) (25), an additional extant tenrec (*Microgale*) to represent a generalized member of the Madagascan tenrec radiation, and a recently described early eutherian *A. yanensis* (28). *Sahnitherium* was excluded because of the paucity of information that could be extracted from the single known molar. However, *Sahnitherium* shares many morphological features with *Deccanolestes*, and some of the characters described as diagnostic in *Sahnitherium*, such as a large paraconule overhanging the anterior part of the crown (17), are observed as polymorphic in the new and better preserved specimens of *Deccanolestes*. For this reason, it is likely that *Sahnitherium* and *Deccanolestes* are closely allied. It is hoped that future discoveries of *Sahnitherium* will allow for further testing of the relationship among these taxa.

We also added seven postcranial characters, detailed below, which were coded for all taxa with relevant published material. Finally, following direct study of some taxa, including *Deccanolestes*, *Adapis*, *Cimolestes*, *Notharctus*, *Plesiadapis*, *Zalambdalestes*, and *Zhelestes*, we revised a number of character codings from the original matrix. The complete data matrix, in TNT format, is provided in the *SI Appendix*.

**Specimens.** A total of 30 specimens of eutherian mammals from India's intertrappean beds were examined directly. Of these specimens, 16 are assigned to *D. hislopi*, 7 are assigned to *D. cf. hislopi*, 3 are assigned to *D. robustus*, and 3 are assigned to the recently named *D. narmadensis*. The last specimen is the holotype of the unusual condylarth-like taxon *K. vanvaleni*. Specimen numbers for *Deccanolestes*, *Kharmarungulatum*, and *Afrodon* are



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