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ORIGINAL PAPER

New postcrania of *Deccanolestes* from the Late Cretaceous of India and their bearing on the evolutionary and biogeographic history of euarchontan mammals

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Abstract Extant species of the supraordinal mammal clade Euarchonta belong to the orders Primates, Scandentia, or Dermoptera. The fossil record of euarchontans suggests that they underwent their initial radiation during the Paleocene (65–55 million years ago) in North America, Eurasia, and Africa. The time and place of origin is poorly resolved due to lack of definitive fossils of euarchontan stem taxa. We describe a fragmentary humerus and two fragmentary ulnae from the latest Cretaceous of India that bear significantly on this issue. The fossils are tentatively referred to *Deccanolestes* cf. *hislopi* due to their small size and the fact that *Deccanolestes* is the only eutherian dental taxon to have been recovered from the same locality. The new fossils are used to evaluate the existing behavioral hypothesis that *Deccanolestes* was arboreal, and the competing phylogenetic hypotheses that *Deccanolestes* is a stem eutherian versus a stem euarchontan. The humerus resembles those of euarchontans in possessing a laterally keeled ulnar trochlea, a distinct zona conoidea, and a spherical capitulum. These features also suggest an arboreal lifestyle. The ulnar morphology is consistent with that of the humerus in reflecting an arboreal/scansorial animal. Detailed quantitative comparisons indicate that, despite morphological correlates to euarchontan-like arboreality, the humerus of *Deccanolestes* is morphologically intermediate between those of Cretaceous "condylarthran" mammals and definitive Cenozoic euarchontans. Additionally, humeri attributed to adapisoriculids are morphologically intermediate between those of *Deccanolestes* and definitive euarchontans. If adapisoriculids are euarchontans, as recently proposed,

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our results suggest that *Deccanolestes* is more basal. The tentative identification of *Deccanolestes* as a basal stem euarchontan suggests that (1) Placentalia began to diversify and Euarchonta originated before the Cretaceous–Tertiary boundary and (2) the Indian subcontinent, Eurasia, and Africa are more likely places of origin for Euarchonta than is North America.

Keywords Adapisoriculid · *Afrodon* · Paleobiogeography · Palaeoryctoid · Placental · Primate origins · Sweepstakes dispersal

Introduction

Modern primates (= Euprimates, Hoffstetter 1977), the group to which humans belong, are members of a larger group called Euarchonta (e.g., Silcox et al. 2005; Waddell et al. 1999) that also includes flying lemurs (Dermoptera), treeshrews (Scandentia), and plesiadapiforms (probable stem primates) (e.g., Bloch et al. 2007). Euarchonta and two of its orders, Dermoptera and Primates (stem primates + euprimates), are regarded by most paleontologists as having originated in either North America or Asia, while Scandentia is thought to have originated in Asia, and Euprimates in either North America, Africa, or Asia between 65–63 million years ago (Ma=Megannum), at or near the beginning of the Paleocene epoch (e.g., Bloch et al. 2007; Clemens 1974; Silcox et al. 2005; Van Valen and Sloan 1965). Clade divergence estimates based on molecular data suggest a much earlier origin and radiation of Euarchonta and its major component clades early in the Late Cretaceous, at ~97 Ma (e.g., Janečka et al. 2007; Springer et al. 2003).

The discrepancy exists due in part to a lack of Cretaceous (>65 Ma) fossils attributable to euarchontans. However, the fossil mammals *Deccanolestes hislopi* and *Deccanolestes robustus*, from the Cretaceous intertrappean deposits of India (Prasad and Sahni 1988), have been suggested to have euarchontan-like arboreal features of the astragalus and calcaneus (Godinot and Prasad 1994; Prasad and Godinot 1994). Hooker (2001) supported the cladistic inclusion of *D. hislopi* in the Euarchonta based on an analysis of tarsal, dental, and cranial characters. A more recent and more broadly sampled analysis places *Deccanolestes* as a stem eutherian (Wible et al. 2007), based primarily on the plesiomorphic coding of its dental and tarsal morphology (e.g., Hooker 2001; Horovitz 2000; Rana and Wilson 2003). Lastly, Smith et al. (2009) demonstrated that adapisoriculid insectivores from the Paleocene of Belgium have tarsal morphology very similar to that of *Deccanolestes* but with additional resemblances to definitive euarchontans. Storch (2008) had previously suggested that diminutive "plesiadapiform-like" humeri and femora from the Paleocene Walbeck site of Germany belong to adapisoriculids.

Here, we report the discovery of additional postcranial fossils of *Deccanolestes* (Fig. 1) from a Late Cretaceous locality in peninsular India. Analysis of these specimens bears significantly on the hypothesis that *Deccanolestes* and/or Adapisoriculidae are closely related to Euarchonta and, thereby, on hypotheses of the time and place of origin of euarchontan mammals.

Materials and methods

Newly discovered fossils and geologic setting

A humerus (Fig. 1a), two ulnae (Fig. 1b), one calcaneus, and four astragali were recovered by screen-washing ~2 tons of calcareous mudstone from the same locality, Naskal, that originally yielded dentitions and tarsal bones of *D. hislopi* (Prasad and Godinot 1994). The Naskal locality is in southern India, about 70 km west of Hyderabad city and 2 km northeast of Naskal village (Prasad and Sahni 1988; Prasad et al. 1994). The fossiliferous mudstone and marl sequence of the Naskal locality is sandwiched between the fourth and fifth of nine documented Deccan volcanic flows of the area west of Hyderabad (Dutt 1975). In the stratigraphic nomenclature of the Deccan Traps, sedimentary strata occurring interbedded between volcanic flows are generally designated as "intertrappean beds". As for

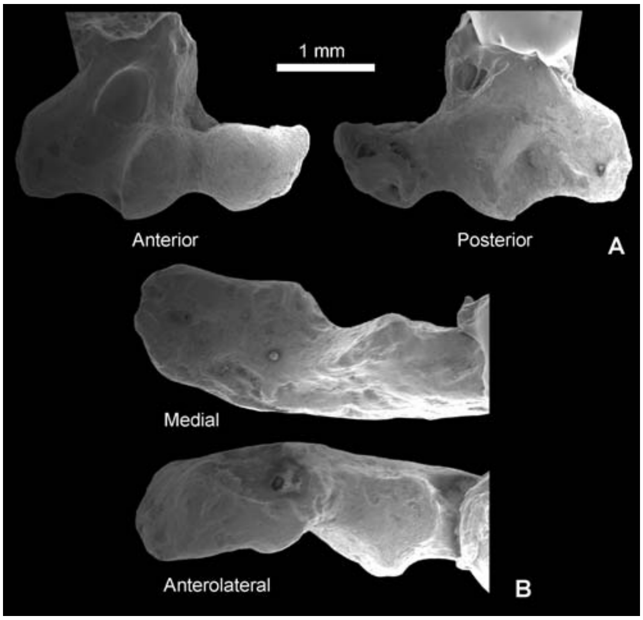

Fig. 1 Scanning electron micrographs of forelimb elements of *D.* cf. *hislopi*. **A** Distal end of left humerus (VPL/JU/NKIM/79). **B** Proximal end of left ulna (VPL/JU/NKIM/81)

most intertrappean beds, the Naskal locality has been confidently dated as Maastrichtian (latest Cretaceous) on the basis of palynofloral and vertebrate fossils (Singh et al. 2006) as well as numerous radioisotopic dates spanning the Deccan Trap basalt sequence (e.g., Allègre et al. 1999; Vandamme et al. 1991).

Taxonomic attribution of new fossils

Three or four mammalian taxa are represented by dentitions at Naskal including *D. hislopi*, *D.* cf. *hislopi*, *D. robustus* (Prasad and Sahni 1988), and *Bharattherium bonapartei* (Prasad et al. 2007a). The new tarsals are identical to those of *Deccanolestes* described by Prasad and Godinot (1994) and Godinot and Prasad (1994) and therefore also are attributable to *Deccanolestes*. They do not preserve any features not also exhibited by the originally referred specimens and therefore are not described here. The humerus and ulnae are of the appropriate size and morphology to articulate with one another (Fig. 2) and are therefore attributed to a single taxon. Specifically, the new humerus (VPL/JU/NKIM/79) and ulnae (VPL/JU/NKIM/81–82) are attributable to either *D. hislopi* or *D.* cf. *hislopi* based on the following evidence: The humerus exhibits features seen only in eutherian mammals (see "Comparisons" section), and it is extremely small. It is unlikely that the humerus and ulnae are referable to *B. bonapartei* because that taxon is a gondwanatherian, not a eutherian, and it is relatively large. Of the two or three species of *Deccanolestes*, *D. robustus* has teeth and tarsals too large for the humerus and ulnae (Prasad and Godinot 1994). We determined this in part by comparison to adapisoriculid material, as adapisoriculids are similar in postcranial morphology: *D. hislopi*, *D.* cf. *hislopi*, and the adapisoriculids *Afrodon chleuhi*, *Afrodon germanicus*, and *Bustylus cernaysi* have similarly sized teeth (Gheerbrant 1988; Gheerbrant and Russell 1989, 1991), which are distinctly smaller than those of *D. robustus* (Fig. 3). Therefore, the observation that the new humerus is close in size to those attributed to adapisoriculids by Storch (2008) supports an attribution to either *D. hislopi* or *D.* cf. *hislopi* (Fig. 3). Because we cannot be sure of the association of postcrania with dentition, we have opted, primarily for ease of

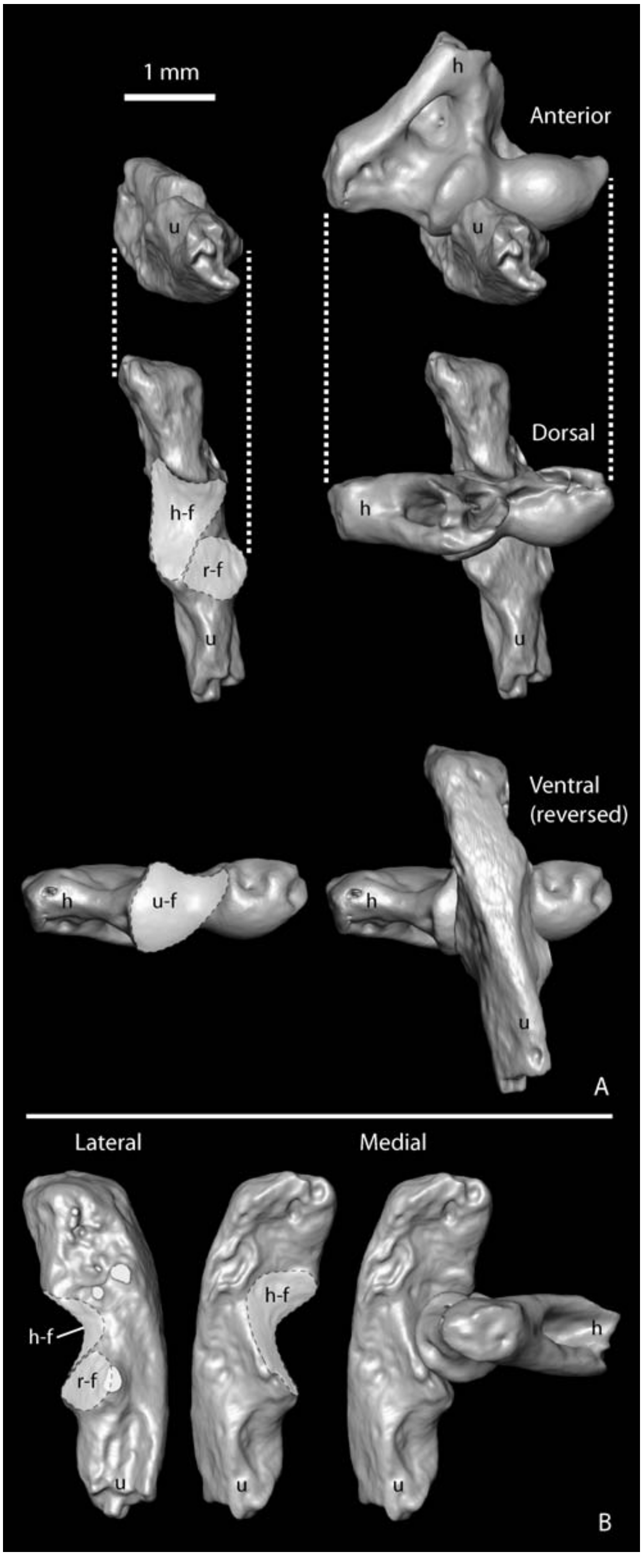

Fig. 2 Micro-CT surface reconstructions of left distal humerus (*h*) and proximal ulna (*u*) of *D.* cf. *hislopi* showing their articular relationships. **A** *Top row* shows ulna in distal view (*left*) and ulna in distal view articulated with humerus in anterior view (i.e., ulna is flexed to 90°, *right*). *Middle row* shows ulna in dorsal view (*left*) and ulna in dorsal view articulated with humerus in proximal view (*right*). *Bottom row* shows humerus in distal view (*left*) and humerus in distal view, articulated ulna in ventral view (*right*). Because the *bottom row* elements have been reversed, the outline of the humerus facet (*h-f*) on the ulna in the *middle row* can be directly compared with the ulna facet (*u-f*) of the humerus in the *bottom row*. The radius facet (*r-f*) faces lateral relative to the humerus facet (*h-f*). **B** The articular surfaces of the ulna shown in lateral (*left*) and medial (*middle*) views and articulation between humerus and ulna shown in medial view (*right*) ▶

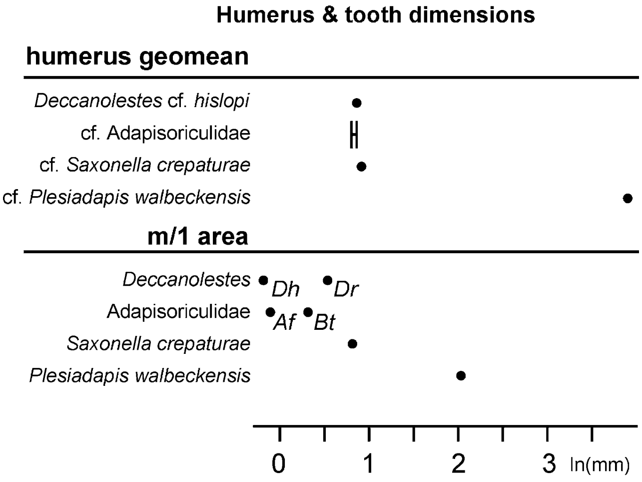

Fig. 3 Comparison of humerus geometric mean values and lower first molar area among *Deccanolestes* species and euarchontans from the Walbeck Fissure fills of Germany. Tooth measurements are averages or single values from Gheerbrant and Russell (1989, 1991), Gingerich (1976), Rana and Wilson (2003), and Russell (1964). Note that teeth of *D. hislopi* (*Dh*) are closest in size to those of *A. germanicus* (*Af*) suggesting that the Naskal humerus and adapisoriculid humeri belong to these taxa, respectively. *D. robustus* (*Dr*) is larger than any Walbeck adapisoriculid, including *Bustylus* (*Bt*). Note that for *D.* cf. *hislopi*, adapisoriculids and cf. *Plesiadapis walbeckensis*, humerus geomean is substantially larger than lower molar area. In contrast, the two values are about equal for cf. *Saxonella crepaturae*, casting some doubt on the correctness of Szalay and Dagosto's (1980) identification of the *Saxonella* humerus

reference, to tentatively and conservatively refer the postcranial elements to *D.* cf. *hislopi* and will use that designation throughout this paper.

Other eutherians known from different intertrappean sites include *Kharmerungulatum* (Prasad et al. 2007b) and an otlestid (Khosla et al. 2004) from Kisalpuri and *Sahnitherium* from Rangapur (Rana and Wilson 2003). The Kisalpuri dental taxa are too large to be attributable to the Naskal taxon represented by the humerus and ulnae (they are even larger than *D. robustus*), while the phylogenetic affinities of *Sahnitherium* are probably so close to *D. hislopi* that the possibility of these bones belonging to *Sahnitherium* is inconsequential relative to the analyses of this paper.

Comparisons, measurements, and analysis

Comparative material includes humeri and ulnae of extant and fossil euarchontan mammals as well as other fossil eutherians (see "Comparisons" section and Table 1). We scanned the new fossils of *Deccanolestes* using a Scanco µCT 40 instrument at Stony Brook University's Center for Biotechnology with a voxel resolution of 10 µm. Comparative material was scanned with the same instrument under resolutions ranging from 10 to 36 µm depending upon the absolute size of the specimen.

Linear measurements (Supplementary Table 1) were taken on scanned bones and/or photographs using Amira 4.1.2 or Sigma Scan Pro 5.0, respectively. Measurements were size-standardized using geometric means, then transformed into natural logarithms, and compared among taxa using principal coordinates analysis (PCOA) of the Euclidean distance matrix relating the specimens. We also compared ratios of (1) trochlea width (TW) to trochlea height (TH) across all specimens−trochlea shape index, (2) entepicondyle width (EEC) to total articular surface width (TW+CW)−entepicondyle size index, and (3) capitulum mediolateral width (CW) to TW−capitulum size index.

Institutional/catalogue

VPL/JU/NKIM—Vertebrate Palaeontology Laboratory University of Jammu, Jammu, India/Naskal Intertrappean Mammal.

Description

VPL/JU/NKIM/79 is a left distal humeral fragment (Figs. 1a, 2, and 4). The bone pristinely preserves the entepicondyle (Fig. 4: *3*) and entepicondylar foramen (Fig. 4: *1*), the distal articular surface including the trochlea (Fig 4: *4*) and capitulum (Fig. 4: *6*), and the ectepicondyle (Fig. 4). The mediolateral width of the complete distal end is 2.83 mm. The mediolateral width of the articular surface (including trochlea, capitulum, and lateral flange) is 1.70 mm.

The entepicondyle is large: The ratio of its mediolateral width to width of the distal articular surface is 0.65 (Fig. 5). Its long axis is aligned with the long axis of the distal articular surface (Fig. 4, distal view). On the anterior aspect of the entepicondyle, a large entepicondylar foramen is oriented at roughly 45° to the axis of the distal articular facet and (likely) to the proximodistal axis of the shaft (not preserved). On its posterior aspect, the entepicondyle sports a large depression, the dorsoepitrochlear pit, for attachment of the ulnar collateral ligament (Fig. 4: *8*). The trochlea for the ulna has a larger maximum radius of curvature than the capitulum (Fig. 4, lateral view); it has a prominent, distally projecting medial keel (Fig. 4: *4*), as well as a subtle, yet distinct lateral keel (Fig. 4: *9*). The trochlea is separated from the capitulum by a distinct zona conoidea, or "gutter" (Fig. 4: *5*). The capitulum itself is notable in being spherical (Fig. 4: *6*), in having a prominent lateral flange (Fig. 4: *7*), and in facing anteroproximally (Fig. 4: *2*). The extensive, proximally facing part of the capitulum suggests a deep supracapitular (humeroradial) fossa (not preserved).

The dimensions of the ulna and its ability to articulate with the humerus suggest attribution to the same species

Table 1 Comparative humeri taxon and specimen list

Taxon	Specimen number and/or measurement reference
Deccanolestes cf. *hislopi*	VPL/JU/NKIM/79
Bug Creek Anthills locality (Eutheria)	
cf. *Procerberus formicarum*	UMVP 1837 (Szalay and Dagosto 1980), AMNH 118456
cf. *Protungulatum donnae*	UMVP 1836 (Szalay and Dagosto 1980), AMNH 119994
Arctocyonidae indet.	USNM 9999 (Szalay and Dagosto 1980)
Walbeck locality (Euarchonta)	
cf. Adapisoriculidae	Storch (2008): Fig. 1a, b
cf. *Saxonellla creparturae*	Szalay and Dagosto (1980)
cf. *Plesiadapis walbeckensis*	Szalay and Dagosto (1980)
Plesiadapidae (Euarchonta)	
cf. *Pronothodectes gaoi*	UALVP 49114
Nannodectes intermedius	USNM 42229
cf. *Plesiadapis rex*	UM 64588
Plesiadapis tricuspidens	MNHN BR 14522, MNHN BR-03-L, MNHN BR 12591, MNHN R 405, Berru (private coll.), MNHN BR-04-L(a), MNHN R 492
Plesiadapis cookei	UM 87990 (L)
cf. *Platychoerops daubrei*	UCMP 102829
Euarchonta (Sundatheria)	
Cynocephalus volans	UF 5969, USNM 144662, USNM 317118, USNM 578084
Ptilocercus lowii	Mean values from Sargis (2002)
Tupaia minor	Mean values from Sargis (2002)
Tupaia glis	Mean values from Sargis (2002)
Euarchonta (Euprimates)	
Adapis parisiensis	Basel QW 1481, Basel QW 1482, AMNH 81001 (Szalay and Dagosto 1980)
Leptadapis magnus	Basel QD 663, Basel QD 664, Basel QD 681 (Szalay and Dagosto 1980)
Smilodectes gracilis	AMNH 11484 (Szalay and Dagosto 1980)
Omomyidae indet.	AMNH 29126, AMNH 113301 (Szalay and Dagosto 1980)
Microchoerine Omomyidae indet.	Basel QD 328, Basel QJ 620, Basel QV 18, Basel QK 989 (Szalay and Dagosto 1980)

This list only includes taxa figured or for which measurements were analyzed in this study

AMNH American Museum of Natural History, New York, *MNHN* Museum National d'Histoire Naturelle, Paris, *UALVP* University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, *UCMP* University of California Museum of Paleontology, Berkley, *UF* University of Florida, Gainesville, *UM* University of Michigan Museum of Paleontology, Ann Arbor, *UMVP* University of Minnesota Vertebrate Paleontology, St. Paul, *USNM* United States National Museum, Washington, D.C., *VPL/JU/NKIM* Vertebrate Palaeontology Laboratory, University of Jammu, Jammu, India

(Figs. 1b and 2). This element is represented by two specimens. The following description is based on the better-preserved one (VPL/JU/NKIM/81), which is from the left side. Most of the shaft is missing but the proximal end is relatively well preserved. Enough of the shaft is preserved to observe that there is a lateral sulcus for the extensor *carpi ulnaris* and digital extensors. The dimensions of the shaft where it meets the trochlear notch are 0.90 mm (dorsoventral) by 0.59 mm (mediolateral). On the medial side is a proximally directed fossa, probably for a collateral ligament. The olecranon process is anteriorly canted such that the posterior margin is convex (Fig. 6d: *3*). In anterior view, it flares proximally and appears wedge-shaped (Fig. 6b). Measured from the proximal margin of the trochlear notch, the olecranon process is 1.15 mm long (proximodistal) and 1.04 mm deep (dorsoventral). The maximum mediolateral width of the olecranon process is 0.81 mm. The trochlear notch is shallow (Fig. 6d: *1*) and the coronoid process is small (Fig. 6d: *2*). The dorsoventral distance from the deepest point of the notch to the ventral surface of the shaft is 0.79 mm. The radial facet is flat (Fig. 6g: *4*) and oriented at roughly 39° to the shaft axis (Fig. 6h: *5*) and 130° to the trochlea. The trochlear notch is 1.08 mm long.

Comparisons

Comparisons indicate that the new humerus must pertain to a eutherian mammal. A multituberculate attribution can be ruled out because all described multituberculates have a

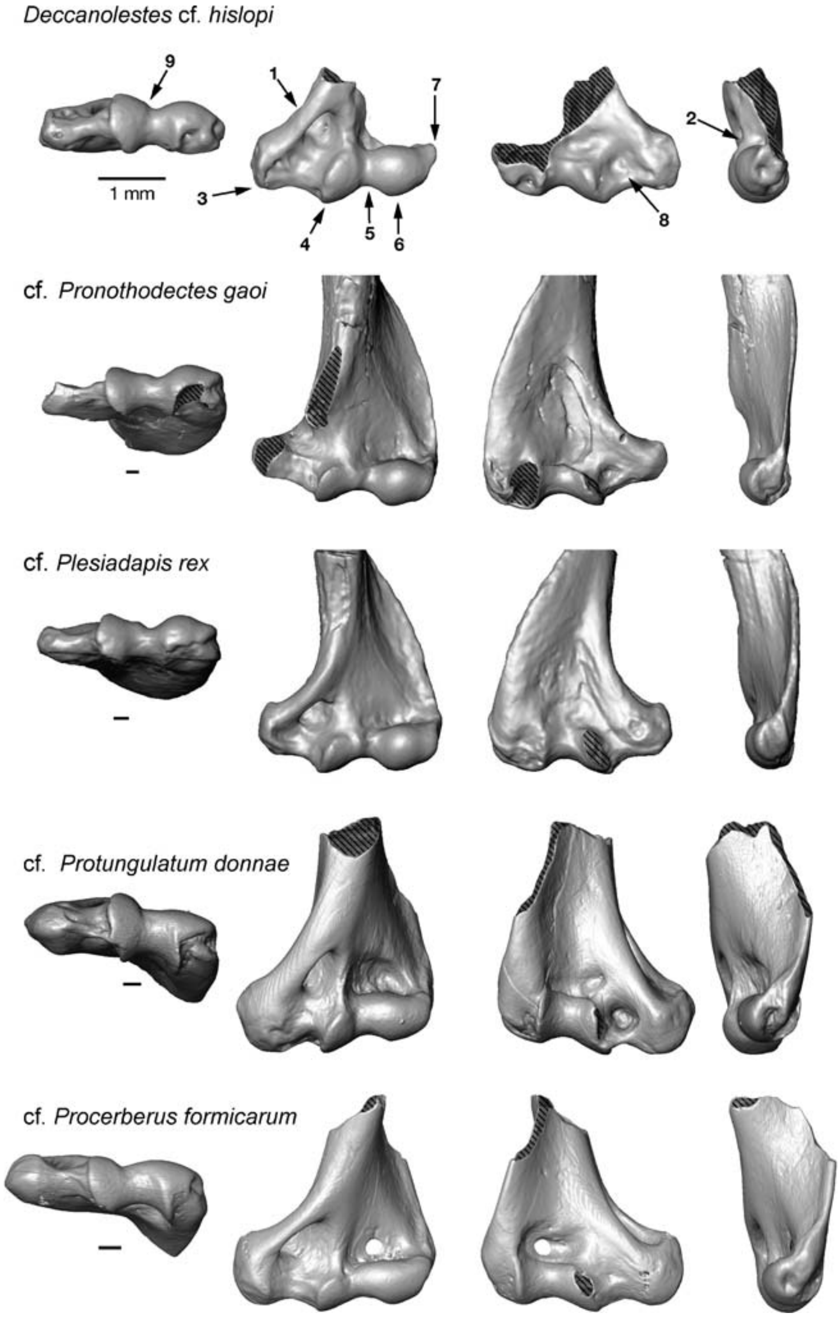

Fig. 4 Humerus of *D.* cf. *hislopi* VPL/JU/NKIM/79 (*Dh*) compared with those of two Paleocene euarchontans (cf. *Pronothodectes gaoi* UALVP 49114 (*Pg*), cf. *P. rex* UM 64588 (*Pr*)), a Late Cretaceous "condylarthran" (cf. *Protungulatum donnae* AMNH 119994 (*Pd*)), and a Late Cretaceous "cimolestan" (cf. *Procerberus formicarum* AMNH 118456 (*Pf*)) in distal, anterior, posterior, and lateral views from *left* to *right*. Note the following features: *1* entepicondylar foramen (present in all), *2* expansive supracapitular fossa and proximally facing radial facet on capitulum (present in all), *3* large entepicondyle (largest in *Dh*, *Pd*, and *Pf*), *4* prominently projecting medial keel on ulnar trochlea (present in all), *5* distinct, deeply invaginated zona conoidea separating trochlea and capitulum (present in *Dh*, *Pg*, and *Pr*), *6* spherical capitulum (present in *Dh*, *Pg*, and *Pr*), *7* lateral flange of capitulum (present in *Dh*, *Pg*, and *Pr*), *8* dorsoepitrochlear fossa (present in *Dh*, *Pg*, and *Pd*), *9* lateral keel of trochlea (present in *Dh*, *Pg*, and *Pr*)

distal articular surface that is much narrower mediolaterally, compared to proximodistally and anteroposteriorly (Krause and Jenkins 1983; Szalay and Dagosto 1980). A metatherian attribution can be ruled out because, according to Szalay and Dagosto (1980), Early Tertiary metatherians have a zona conoidea that tends to be relatively wide and shallow. Furthermore, metatherian humeri that are superficially primate-like lack a dorsoepitrochlear fossa ("medial pit" of Szalay and Dagosto 1980; Szalay and Sargis 2001). Finally, attribution to a multituberculate or metatherian is contraindicated by the lack of dental evidence for these taxa in the intertrappean deposits.

The humerus of *D.* cf. *hislopi* matches that of plesiadapiforms (stem primates) and basal euprimates in several features, while differing in others. To begin with, *Deccanolestes* is similar in having a large entepicondylar foramen (Fig. 4: *1*), a deep supracapitular fossa (inferred), and a proximally facing capitulum (Fig. 4: *2*). However, these features are also shared with early eutherians as basal as *Ukhaatherium* (Horovitz 2003) and therefore can be inferred to be eutherian plesiomorphies. *Deccanolestes*, adapisoriculids, and plesiadapiforms are further similar in at least one feature of the humerus also exhibited by Cretaceous eutherians (such as *Protungulatum* and *Procer-*

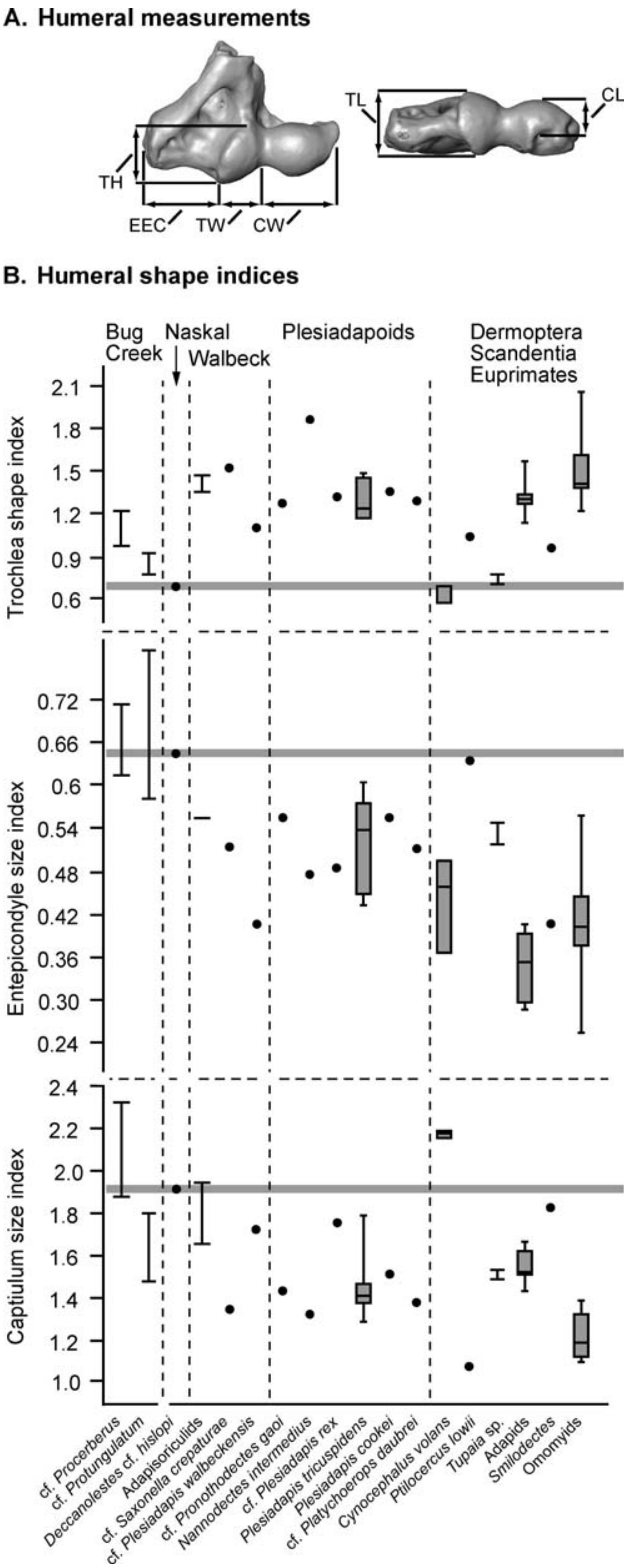

Fig. 5 Metrical comparisons among humeri. **A** Measurements taken on humerus - adapted from Szalay and Dagosto (1980). Measurement abbreviations: *CL* capitulum length, *CW* capitulum width, *EEC* entepicondylar width, *TH* trochlea height, *TL* trochlea length, *TW* trochlea width. See Supplementary Table 1 for specimen measurements. **B** Box plots of humeral shape indices. *Dots* represent *n*=1. *Bars with no box* represent *n*=2. See Table 1 for *n* of other taxa. *Gray horizontal lines* correspond to values for *D.* cf. *hislopi*. *D.* cf. *hislopi* and Walbeck adapisoriculids have a similar capitulum width relative to the trochlea width (CW/TW−capitulum size index), but adapisoriculids have a more plesiadapiform-like entepicondyle size [EEC/(CW+TW)−entepicondyle size index] and trochlea shape (TW/TH−trochlea shape index); see Table 1 for specimen list, see "Comparisons, measurements, and analysis" section of text for description of index calculation and discussion

berus; Sloan and Van Valen 1965) that are later diverging than *Ukhaatherium*; the presence of a distally extended medial trochlear lip (Fig. 4: *4*).

Deccanolestes differs from sampled plesiadapiforms and basal euprimates in having a capitulum that is distally restricted instead of extended (Fig. 4: *6*), an ulnar trochlea that is mediolaterally narrow or small relative to the capitulum and narrow relative to its proximodistal length (Fig. 5), and an entepicondyle that is larger relative to the mediolateral width of its distal end (Fig. 5). In these ways, *Deccanolestes* is more similar to the Cretaceous "condylarth" *Protungulatum* and "cimolestan" *Procerberus*. However, the adapisoriculids from the late Paleocene Walbeck locality in Germany also share with *Deccanolestes* a capitulum that is wide relative to the ulnar trochlea. The dermopteran *Cynocephalus* is similar to *Deccanolestes* in both features of its trochlea (Fig. 5).

Finally and most importantly, *Deccanolestes* is similar to plesiadapiforms, the arboreal treeshrew *Ptilocercus lowii*, and basal euprimates in several humerus features much more rarely exhibited among eutherian mammals. These include a deep zona conoidea (Fig. 4: *5*), a raised lateral trochlear ridge (Fig. 4: *9*), and a spherical capitulum (Fig. 4: *6*).

The ulna provides less insight into the potential phylogenetic affinities of *Deccanolestes* because of its more generalized form. It does not help that the ulnae also are less well preserved than the humerus. All that can really be said is that the radial facet of the ulna of *Deccanolestes* is similar in shape and orientation to those of plesiadapiforms and other arboreal mammals with an axially mobile forearm. For instance, the ulna of cf. *Plesiadapis rex* has its radial facet oriented at 39° to the plane of the shaft and 140° to the trochlear facet (Fig. 6h: *5*). This humeroradial articular surface is thus slightly more open than in *Deccanolestes*, which is consistent with the less sloping, more mediolaterally expanded ulnar trochlea on the humerus of cf. *P. rex* (Figs. 4, 6g: *4*). On the other hand, the ulna of *Deccanolestes* notably lacks the proximal "narrowing" of the olecranon fossa that has been described

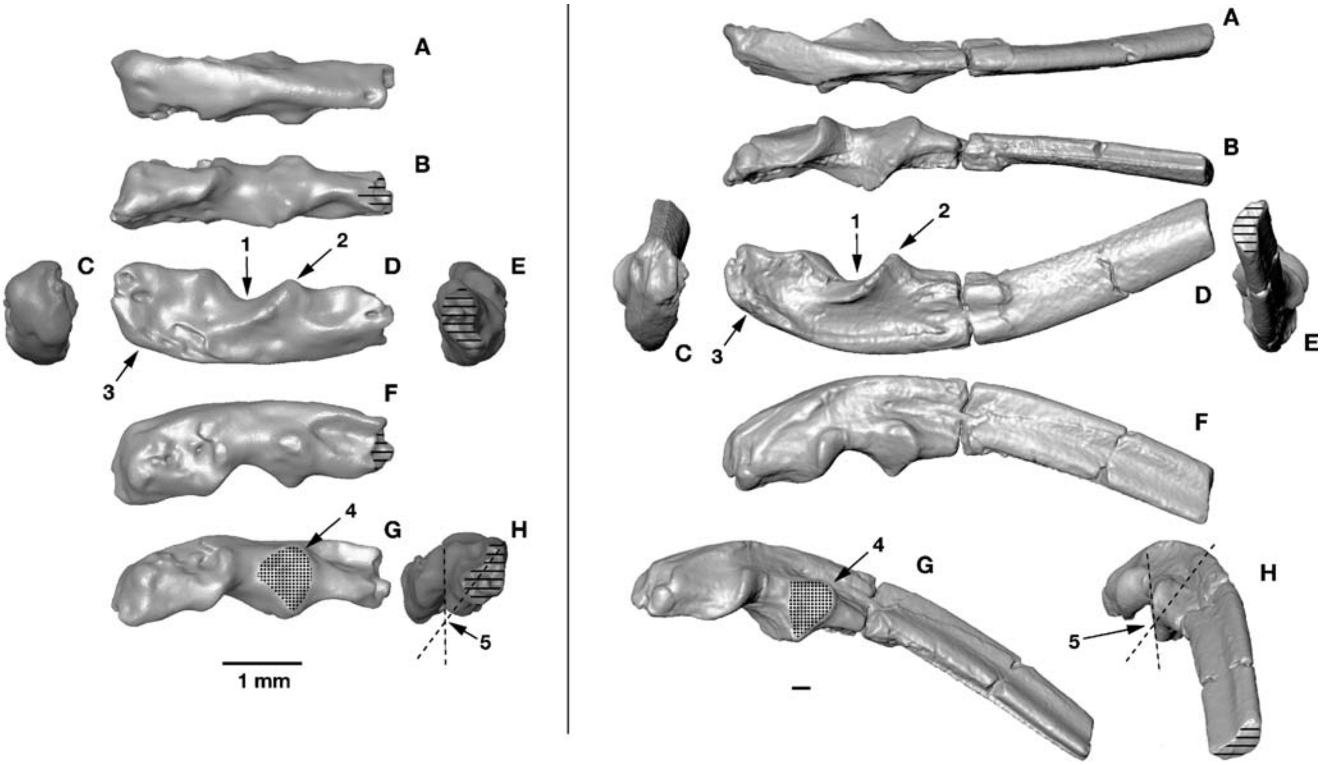

Fig. 6 Left ulna of *D.* cf. *hislopi* (VPL/JU/NKIM/81), at *left*, compared with that of cf. *P. rex* (UM 64588), at *right*. Views: *A* posterior, *B* anterior, *C* proximal, *D* medial, *E* distal, *F* lateral, *G* perpendicular to plane of radial facet, *H* parallel to plane of radial facet. Numbered features: *1* shallow trochlear notch, *2* blunt coronoid process, *3* anteriorly curved olecranon process, *4* broad, flat radial facet, *5* radial facet oriented laterally

as characteristic of euarchontans (Szalay and Lucas 1996); the anteroposterior thickness of its olecranon stays relatively constant along its length (Fig. 6d: *3*).

Humerus principal coordinates analysis

Results of PCOA of six size-standardized measurements of the distal humerus on 41 specimens, representing 20 taxa (Supplementary Tables 1 and 2), parallel the discussion above and show fossil and extant euarchontans (Eu) forming a cluster that excludes *Protungulatum* and *Procerberus* (Bc) (Fig. 7). The humerus of *Deccanolestes* plots between these two clusters in morphospace.

Pearson correlation coefficients (Supplementary Table 2) show that PC-1 mainly reflects an increasingly large entepicondyle width (EEC) and trochlea length (TL). PC-2 mainly reflects decreasing trochlea height (TH) and increasing trochlea width (TW). PC-3 reflects increasing capitulum length (CL) and decreasing TW. Although the humerus of *Deccanolestes* overlaps the distribution of euarchontan humeri on both PC-1 and PC-2, the combined presence of a relatively large entepicondyle and deep trochlea (low trochlea shape index, Fig. 5) distinguishes the humeri of *Deccanolestes*, *Protungulatum*, *Procerberus*, and an unidentified arctocyonid from euarchontans of the sample. These are likely to be primitive eutherian features (Szalay and Dagosto 1980).

Discussion

The suite of features observed in the newly discovered humerus and ulnae suggests a habitually flexed elbow joint (Fig. 2), a humeroradial joint that permitted forearm axial mobility, and a humeroulnar joint that functioned in weight-bearing, all hallmarks of a euarchontan-like arboreal lifestyle (Bloch et al. 2007; Szalay and Dagosto 1980; Szalay and Lucas 1996). Therefore, our findings strengthen the hypothesis of Godinot and Prasad (1994) and Prasad and Godinot (1994) that *D. hislopi* was arboreal. Furthermore, as such features are often interpreted as euarchontan synapomorphies (e.g., Silcox et al. 2005), our findings also strengthen the hypothesis that *Deccanolestes* is a euarchontan (e.g., Hooker 2001; Smith et al. 2009). However, the coincidence of arboreal functional features and euarchontan synapomorphies presents a notable possibility of convergence, consistent with the phylogenetic placement in the analyses of Wible et al. (2007).

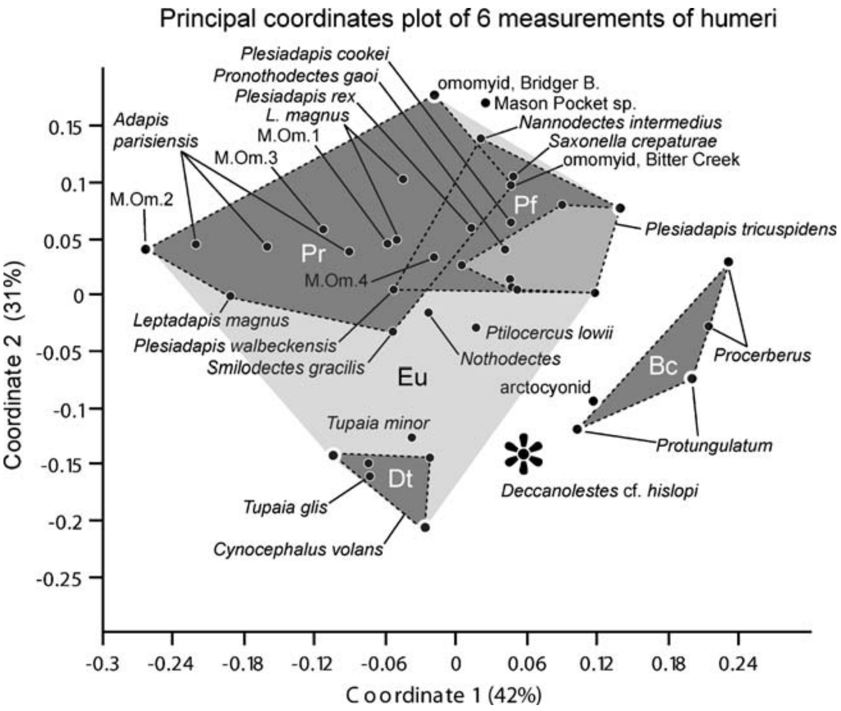

Fig. 7 Results of principal coordinates analysis. Multitoned polygon encompasses definitive euarchontans (*Eu*). Other labeled polygons, some of them overlapping with Eu, include Cretaceous eutherians from Bug Creek Anthills locality (*Bc*), dermopterans (*Dt*), plesiadapiforms (**Pl**), and Euprimates (*Pr*). See Supplementary Table 1 for specimen measurements and Supplementary Table 2 for coordinate correlation coefficients. Microchoerine Omomyid *M.Om*

A major problem with attribution of *Deccanolestes* to Euarchonta had been its plesiomorphic sectorial teeth (Prasad and Sahni 1988; Rana and Wilson 2003). Similarly, the phylogenetic placement of adapisoriculids based on their dentitions has been ambiguous (see review by Smith et al. 2009; Storch 2008). Yet adapisoriculid postcranial bones seem to suggest euarchontan affinities even more strongly than do those of *Deccanolestes*. The possibility that Euarchonta is not united by definitive dental synapomorphies is further suggested by the cladistic topology of Wible et al. (2007), which failed to place a dental taxon, the basal plesiadapiform *Purgatorius*, in Euarchonta or even anywhere within Placentalia. In other words, characters that resolve as primate synapomorphies of *Purgatorius* (e.g., elongate M_3, enlarged M_3 hypoconulid, nannopithex fold on upper molars) in cladistic analyses that include only euarchontans as ingroup taxa (e.g., Bloch et al. 2007) are not especially informative in analyses including more non-euarchontan eutherian taxa that also exhibit such features (e.g., gliroids, Meng et al. 2003) and fewer euarchontans. Many relevant euarchontan postcranial characters are not included in the Wible et al. (2007) matrix, meaning that their phylogenetic significance was not tested by that analysis. However, it now seems that derived tarsal features may link *Deccanolestes* to adapisoriculids phylogenetically and thereby to definitive euarchontans (Smith et al. 2009).

The possibility of close affinities between adapisoriculids and *Deccanolestes* gains strength from the latest study of new, well-preserved dental material of *Deccanolestes* recovered from a new intertrappean site, Kisalpuri, in central India (Prasad et al. 2007a, b, 2010). Based on the close similarity of dental morphology of *Deccanolestes* to that of *A. chleuhi* known from the late Paleocene (Thanetian) Adrar Mgorn site, Ouarzazate Basin (Gheerbrant 1988, 1995), and *A. germanicus* from the late Paleocene Walbeck site of Germany (Gheerbrant and Russell 1989; Russell 1964) and in view of the slightly more primitive nature of the teeth of *Deccanolestes* and its older age, Prasad et al. (2010) argue that adapisoriculids were derived from a *Deccanolestes*-like morphotype.

The humerus of *Deccanolestes* seems slightly less “plesiadapiform-like” than those attributed to adapisoriculids in having a larger entepicondyle and a longer trochlea (lower trochlear shape index, Fig. 5). Therefore, if *Deccanolestes* is also a euarchontan, it would appear to be phylogenetically more basal than adapisoriculids known from postcrania. This is concordant with the observations that *Deccanolestes* is from older deposits and has more “primitive” dental features and tarsal morphology than either plesiadapiforms or adapisoriculids.

If *Deccanolestes* is a stem euarchontan, its Late Cretaceous occurrence would be congruent with other aspects of the fossil record suggesting that Euarchonta began to radiate at or near the Cretaceous–Tertiary (KT) boundary (Bloch et al. 2007; Clemens 1974; Van Valen and Sloan 1965). It would also be consistent with many molecular divergence estimates, which indicate the presence of extant euarchontan groups well prior to the occurrence of *Deccanolestes* (Janečka et al. 2007; Springer et al. 2003); these estimates require long ghost lineages for Euprimates, Dermoptera, and

Scandentia. Finally, the occurrence of a stem euarchontan in the Late Cretaceous would be consistent with the conclusion of Wible et al. (2007) that placental mammal groups diverged near the KT boundary. However, their conclusion could be refined: Euarchontan affinities for *Deccanolestes* would indicate that at least some of these divergences *preceded* the KT boundary (i.e., the divergence of Euarchonta from other placental lineages).

From a biogeographic perspective, the presence of *Deccanolestes* in the latest Cretaceous of India is also problematic, whether it is a basal euarchontan, a close relative of adapisoriculids, or both because the most recent comprehensive paleogeographic reconstructions indicate that the Indian subcontinent was physically isolated for most of the Late Cretaceous (beginning 85–90 Ma) and well into the Tertiary, until the Paleocene/Eocene boundary (e.g., Aitchison et al. 2007; Ali and Aitchison 2008; Clyde et al. 2003; Garzanti 2008; Rose et al. 2009; Rowley 1996). It is therefore unclear how euarchontans could have achieved a distribution that includes the Indian subcontinent in the latest Cretaceous as well as North America, Europe, Asia, and Africa by the early Paleocene (Bloch et al. 2007). A vicariant process is unlikely, as it requires the group to have originated more than 160 Ma (prior to the breakup of Gondwana; Ali and Aitchison 2008), which is almost twice as old as even the most extreme molecular divergence estimates for the clade (e.g., Janečka et al. 2007).

Alternatively, dispersal events during the later stages of the Late Cretaceous seem unlikely given that Ali and Aitchison (2008: figs. 9a and 10), in a comprehensive review and evaluation of potential physical and biotic connections of the Indian subcontinent, reconstructed the Indian subcontinent as adrift in the Indian Ocean at this time, separated from Madagascar by some 800–900 km and much further distant than that from the African mainland and Eurasia. At this time, the Indian subcontinent was much larger ("Greater India") and extended an additional 950 km or so further northward, but much if not all of this area, as well as large northwestern and northeastern portions of the subcontinent and much of the Horn of Africa, was likely submerged leaving gaps of over 1,500 km between the "emergent" part of the subcontinent and Afro-Arabia to the west and northwest and Eurasia to the north. Ali and Aitchison (2008, p 158) concluded that in "the very latest Cretaceous, India appears to have reached its maximum level of isolation . . . ringed by a large expanse of ocean" and that "[p]roposals for a connection between the sub-continent and Arabia–Asia by way of the equatorially-located island arc the sub-continent was to collide with in the latest Paleocene seem unlikely."

Nonetheless, there is biotic evidence for connections or dispersal between the Indian subcontinent and Eurasia around the latest Cretaceous (e.g., Bhatia et al. 1990; Khosla et al. 2004; Prasad and Rage 1995; Prasad et al. 2007b; Sahni et al. 1982). Furthermore, if adapisoriculids are closely related to *Deccanolestes*, then the presence of adapisoriculids in Africa (Gheerbrant 1988, 1995) and Europe (Gheerbrant and Russell 1989, 1991; Smith et al. 2009; Storch 2008) during the Paleocene suggests a dispersal event between the Indian subcontinent and northeastern Africa by this time or earlier (Prasad et al. 2010). There are also similarities among the Late Cretaceous vertebrate faunas of India, Madagascar, and South America, although there is currently no evidence for eutherian dispersals between India and these landmasses at that time (e.g., Krause et al. 2006). The phylogenetic conclusions of Prasad et al. (2010) and previous suggestions of close affinities between Late Cretaceous Laurasian and Indian eutherians (e.g., Khosla et al. 2004; Prasad et al. 2007b) could be taken to suggest that eutherian mammals dispersed from Laurasia to India and then to Africa. However, the Late Cretaceous of Africa is not yet sampled for fossil eutherians, and the discovery of more basal taxa there could eventually suggest a different pattern of dispersal (e.g., Gheerbrant and Rage 2006; Prasad et al. 2010). Acknowledging all of this, Eurasia, the Indian subcontinent, and Africa are among the most likely places of origin for Euarchonta.

Despite fossil evidence from the latest Cretaceous of the Indian subcontinent for biotic connections of some form with Eurasia and Africa, there is a lack of such evidence for the Paleocene, as the fossil record of Paleocene terrestrial mammals from the Indian subcontinent is nonexistent. Therefore, there is no fossil evidence to directly contradict or support paleogeographic reconstructions of isolation at this time. Krause and Maas (1990) hypothesized that the isolated Indian subcontinent was a "Noah's Ark" (sensu McKenna 1973), carrying the basal stocks of several modern orders of mammals that then disembarked and dispersed throughout Laurasia when the Indian subcontinent "docked" at or near the Paleocene/Eocene boundary. Such a hypothesis has been entertained by others for various plant and animal taxa (e.g., Bossuyt and Milinkovitch 2001; Conti et al. 2002; Cooper et al. 2001; Erickson et al. 2002; Gower et al. 2002; Kumazawa and Nishida 2000; Macey et al. 2000; Morley and Dick 2003; Murphy and Collier 1997; Prasad et al. 2007b; Whatley and Bajpai 2006). Ultimately, it is important to have pre-Eocene fossil evidence from the Indian subcontinent for the existence of any group of animals hypothesized to have originated on the subcontinent prior to its docking with Asia. If *Deccanolestes* is a stem euarchontan, its presence on the Indian subcontinent since at least the latest Cretaceous is consistent with the hypothesis of an Indian origin for the extant euarchontan orders. This hypothesis is attractive for Euarchonta as it would help explain why definitive members of its extant orders appear in the fossil record no earlier than the early Eocene (Scandentia (Tong 1988), Dermoptera (Marivaux et al. 2006), Euprimates (e.g., Smith et al. 2006)). However, the hypothesis for an Indian origin of Dermoptera is contradicted if evidence that Laurasian Paleocene plagiomenids are stem dermopterans is accepted (Bloch et al. 2007). An Indian origin of Euprimates is contradicted by evidence that Laurasian Paleocene plesiadapiforms are stem primates (e.g., Bloch et al. 2007; Janečka et al. 2007) and that *Altiatlasius*, from the late Paleocene of Morocco, is a euprimate (Gheerbrant et al. 1998; Godinot 1994; Sigé et al. 1990).

We do not currently have a solution that accounts for this discrepant information; in light of the spotty Late Cretaceous and Paleocene fossil record in many key areas and the uncertain nature of paleogeographic reconstructions involving the Indian subcontinent and surrounding landmasses, the number of possible scenarios are plentiful and we can only appeal to future discoveries and analyses to narrow it. While the new postcranial elements present important information on *Deccanolestes*, we recognize that extensive phylogenetic analyses must be undertaken to more rigorously evaluate the tentative hypothesis that *Deccanolestes* and adapisoriculids are closely related to each other and that one or both are stem euarchontan mammals. Furthermore, from a paleontological perspective, discovery of additional remains of *Deccanolestes* and other Late Cretaceous and Paleocene mammals from Africa and the Indian subcontinent will be important for understanding the pattern of origin and diversification of euarchontans and other groups of placental mammals.

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