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A three-dimensional morphometric analysis of the locomotory ecology of Deccanolestes, a eutherian mammal from the Late Cretaceous of India

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A THREE-DIMENSIONAL MORPHOMETRIC ANALYSIS OF THE LOCOMOTORY ECOLOGY OF *DECCANOLESTES*, A EUTHERIAN MAMMAL FROM THE LATE CRETACEOUS OF INDIA

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ABSTRACT—The relationships and ecology of *Deccanolestes*, a eutherian mammal from the Late Cretaceous of India that is known only from isolated dental, mandibular, and postcranial elements, have been a topic of considerable interest and debate. A recent comprehensive phylogenetic analysis has placed this taxon within Adapisoriculidae, a clade of otherwise Paleocene arboreal mammals, but unexpectedly resolved this expanded Adapisoriculidae near the base of the eutherian tree. *Deccanolestes* has been described as having an arboreal or scansorial lifestyle based on its ankle morphology. Here, we present a geometric morphometric study of the astragalus to test hypotheses pertaining to the ecomorphological affinities of *Deccanolestes*. Shape analyses were performed on extant eutherians and marsupials displaying a range of different lifestyles, but predominantly sampling arboreal forms, as well as relevant Cretaceous to Eocene taxa. In addition, we constructed a neighbor-joining tree based on the shape variables to identify similarities among taxa in astragalar morphology. Our results show that Cretaceous and Paleocene taxa, including *Deccanolestes*, cluster most closely and form a separate group distinct from extant mammal clades, including extinct Primates. Strong phylogenetic signal in astragalar morphology among extant taxa, as well as apparent phylogenetic clustering of extant and extinct taxa, complicates a straightforward interpretation of the locomotor ecology of *Deccanolestes*, but our results suggest that the astragalar morphology of *Deccanolestes* has no analogue among the sampled living species. However, this morphology appears prevalent among Cretaceous and Paleocene eutherian mammals.

INTRODUCTION

Known only from isolated dental, mandibular, and postcranial elements, *Deccanolestes* is a genus of eutherian mammals (the clade including placentals and their stem relatives) from the Late Cretaceous intertrappean deposits of India (Prasad and Sahni, 1988). To date, three species of *Deccanolestes* have been described: *D. hislopi* (Prasad and Sahni, 1988), *D. robustus* (Prasad and Godinot, 1994), and *D. narmadensis* (Prasad et al., 2010). The phylogenetic affinities and ecology of *Deccanolestes* remain contentious and are topics of considerable interest due to suggested affinities with Euarchonta (Primates, Dermoptera, and tree shrews) (Prasad and Godinot, 1994; Hooker, 2001; Boyer et al., 2010b). Its location, age, and possible status as a Cretaceous placental mammal make it a key taxon for our understanding of the evolution of Placentalia (Goswami et al., 2011).

Previous studies of this enigmatic taxon were based on poorly preserved specimens and suggested that *Deccanolestes* was a non-placental eutherian (Prasad and Sahni, 1988; Wible et al., 2007), whereas studies focusing on tarsal elements identified it as a potential stem euarchontan (Hooker, 2001; Boyer et al., 2010a; Smith et al., 2010). This latter hypothesis has focused much at-

tention on *Deccanolestes*, because, despite the identification of over 70 Late Cretaceous eutherian species, none have been unambiguously identified as a crown-group placental mammal (although some, such as *Protungulatum* [Archibald et al., 2011], have been suggested as possible placentals). Moreover, recent papers have suggested a close relationship between *Deccanolestes* and the Adapisoriculidae, a clade of apparently arboreal Paleocene mammals from northern Africa and Europe with hypothesized affinities to Eurarchonta or even Primates, based on shared dental (Prasad et al., 2010; De Bast et al., 2012) and postcranial (Boyer et al., 2010b; Smith et al., 2010) characters. Postcrania attributed to Adapisoriculidae have also been suggested to have plesiadapid (Storch, 2008) or primate (Smith et al., 2010) attributes. A third hypothesized affinity for *Deccanolestes* and Adapisoriculidae is to tenrecoid afrosoricids. Seiffert (2010) noted dental and humerus similarities between *Afrodon chleuhi*, *Deccanolestes*, and the Fayum insectivores *Dilambdogale gheerbranti* and *Widanelfarasia bownti*. However, a recent comprehensive phylogenetic analysis of new and better-preserved material of *Deccanolestes* suggested that although *Deccanolestes* is almost certainly an adapisoriculid, this clade is not closely related to Euarchonta, afrosoricids (including tenrecs), or any other clade of placentals, but rather lies near the base of Eutheria (Goswami et al., 2011).

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Deccanolestes has been previously described as possibly having an arboreal lifestyle, based on similarities with arboreal euarchontans in ankle (Godinot and Prasad, 1994; Prasad and Godinot, 1994), as well as in humeral and ulnar morphology (Boyer et al., 2010a, 2010b). Some of the astragalar features that indicate arboreality in *Deccanolestes* as well as arboreal euarchontans include a prominent lateral trochlear crest with distomedial curvature and an extended and rounded navicular facet that is confluent with the sustentacular facet. The calcaneus also bears multiple traits ascribed to arboreality, including an elongated, curved ectal facet, a prominent peroneal tubercle, and a distally extended sustentacular facet (Godinot and Prasad, 1994; Prasad and Godinot, 1994). Yet, no quantitative data or experimental studies exist unambiguously linking these features to an arboreal lifestyle in mammals.

Although many studies have qualitatively examined and compared the morphology of *Deccanolestes* with other mammals, most quantitative analyses have focused exclusively on its phylogenetic relationships. A single quantitative analysis of astragalar morphology has been conducted on *Deccanolestes*, but that study focused on primates and sampled only three non-euarchontans (including *Deccanolestes*) (Boyer et al., 2010b). That study used 20–23 linear and angular measurements and found that *Deccanolestes* clustered with the putative Cretaceous and Paleocene ‘condylarth’ *Protungulatum* (Archibald et al., 2011), as well as some plesiadapids and dermopterans. However, a comprehensive, quantitative, three-dimensional (3D) analysis of tarsal anatomy that samples multiple taxa with hypothesized affinities with *Deccanolestes*, as well as a broad suite of arboreal, scansorial, and terrestrial mammals, in a phylogenetic and ecomorphological framework has yet to be performed. Such an analysis is required to robustly assess if the traits identified as indicating arboreality in *Deccanolestes* are in fact closely associated with this locomotory mode, and to inform on the phylogenetic signal in these traits. We here focus on the astragalus because it possesses many key features that have been suggested to relate to the locomotor ecology and substrate preference of extant mammals. It is thus potentially an informative element for reconstructing the ecology and locomotor behavior of extinct species (Szalay and Decker, 1974; Langdon, 1986; Szalay and Langdon, 1986; Gebo, 1989; Carrano, 1997; Seiffert and Simons, 2001; Youlatos, 2003; Youlatos and Koufos, 2010). Moreover, the astragalus has been used to infer phylogenetic affinities of extinct mammals beyond the specific example of *Deccanolestes* discussed above (Godinot and Dagosto, 1983; Thewissen and Madar, 1999; Salton and Szalay, 2004). However, if the morphology of the astragalus is indeed phylogenetically informative, this potentially complicates the task of using it to make robust inferences on the locomotor ecology of this or other extinct taxa.

To assess these issues, we quantitatively compare the shape of the astragalus in *Deccanolestes* to that of several extant and extinct taxa. If *Deccanolestes* is indeed arboreal, as suggested previously, we predict that its astragalar shape will be more similar to that of known arboreal taxa. Nevertheless, astragalar shape could have both phylogenetic and functional components (Bock and von Wahlert, 1965; Szalay 1981a, 1981b, 2000; Szalay and Bock, 1991); consequently, we test whether the shape of the astragalus in extant mammals shows a functional signal when taking into account known phylogenetic relationships for the extant taxa in our study.

MATERIALS AND METHODS

Sample

Thirty-four specimens were used in this study (see Fig. 1 for an illustration of the morphology of the key taxa included). Twenty specimens represent extant placentals (Carnivora, Pri-

mates, Dermoptera, and Scandentia) and marsupials (Didelphimorphia and Diprotodontia) that display ecologies ranging from terrestrial to arboreal. We further included 13 relevant Paleocene and Eocene taxa, including extinct euarchontans such as plesiadapids (*Pronothodectes* and *Plesiadapis*) and early euprimates (Adapidae, Omomyidae, *Catopithecus*), an early ‘condylarth’ (*Protungulatum*), a nyctitherid (*Cryptotopos?*), and two adapisoriculids (*Afrodon* and *Bustylus*), as well as *Deccanolestes hislopi*. Astragali were obtained from the following collections: the American Museum of Natural History Mammalogy and Vertebrate Paleontology departments; the Stony Brook University Museum; the University of Michigan Museum of Paleontology; the ‘Mammifères et Oiseaux’ collection from the Muséum National d’Histoire Naturelle, Paris; the Palaeontology collection of the Natural History Museum, London; the Royal Belgian Institute of Natural Sciences; and the Jammu University Vertebrate Paleontology Laboratory. A complete list of specimens used in the analysis is provided in Table 1.

All the specimens were digitally rendered in order to be able to take landmarks from the surfaces of 3D scans. Scans were acquired using micro-computed tomography (μ CT) scanners or a Breuckmann 3D surface scanner from the Muséum National d’Histoire Naturelle, Paris (white light fringe StereoSCAN^{3D} model with a camera resolution of 1.4 megapixels). Most μ CT scans were taken at Stony Brook University with a Scanco Medical brand scanner (μ CT-40 and vivaCT-75 models at 70 kV; voxel sizes ranging from 10 to 36 μ m). The nyctitherid specimen was scanned at the Natural History Museum, London, using a Metrix X-Tek HMX ST 225 with a voxel size of 3.8 μ m. The adapisoriculid specimens were scanned on Skyscan 1172 (at 49 kV and a voxel size of 11.31 μ m) in the Department of Cell and Developmental Biology, University College London.

Shape Variation Using 3D Geometric Morphometrics

From these scans, we chose a set of 26 landmarks to describe the complex shape of the astragalus (see Fig. 2 and Table 2 for the definition of landmarks). Morphometric data were collected from each scan using the software package Idav Landmark (Wiley et al., 2005).

Shape variation of the sampled astragali was analysed using a 3D geometric morphometric approach. A generalized Procrustes superimposition (Rohlf and Slice, 1990) was performed on the point coordinates using the package Rmorph (Baylac, 2012) in R (R Development Core Team, 2011). Next, we performed a principal component analysis (PCA) on the shape data to evaluate the distribution of species in morphospace. We mapped the phylogeny of extant species by computing internal nodes minimizing the squared parsimony for each PC using the Mtree function in R (Perrard, 2012). The phylogeny used is based on the supertree of Bininda-Emonds et al. (2008) pruned down to include only the taxa included in our analyses. The visualizations of shapes at the extreme of each axis were performed using the Evan toolbox (<http://www.evan.at>) package and are based on 3D thin-plate spline visualizations. These visualizations were obtained by warping the consensus surface model of the full astragalus data set to each extreme of the three primary PC axes by minimizing the bending energy between the consensus and each extreme of the axis (Gunz et al., 2005).

Phenetic Affinities

To evaluate the phenetic affinities (i.e., morphological similarity) of the astragali in our sample, a neighbor-joining tree was constructed using the Euclidean distance of the Procrustes tangent coordinates using the ‘ape’ library in R (Paradis et al., 2012).

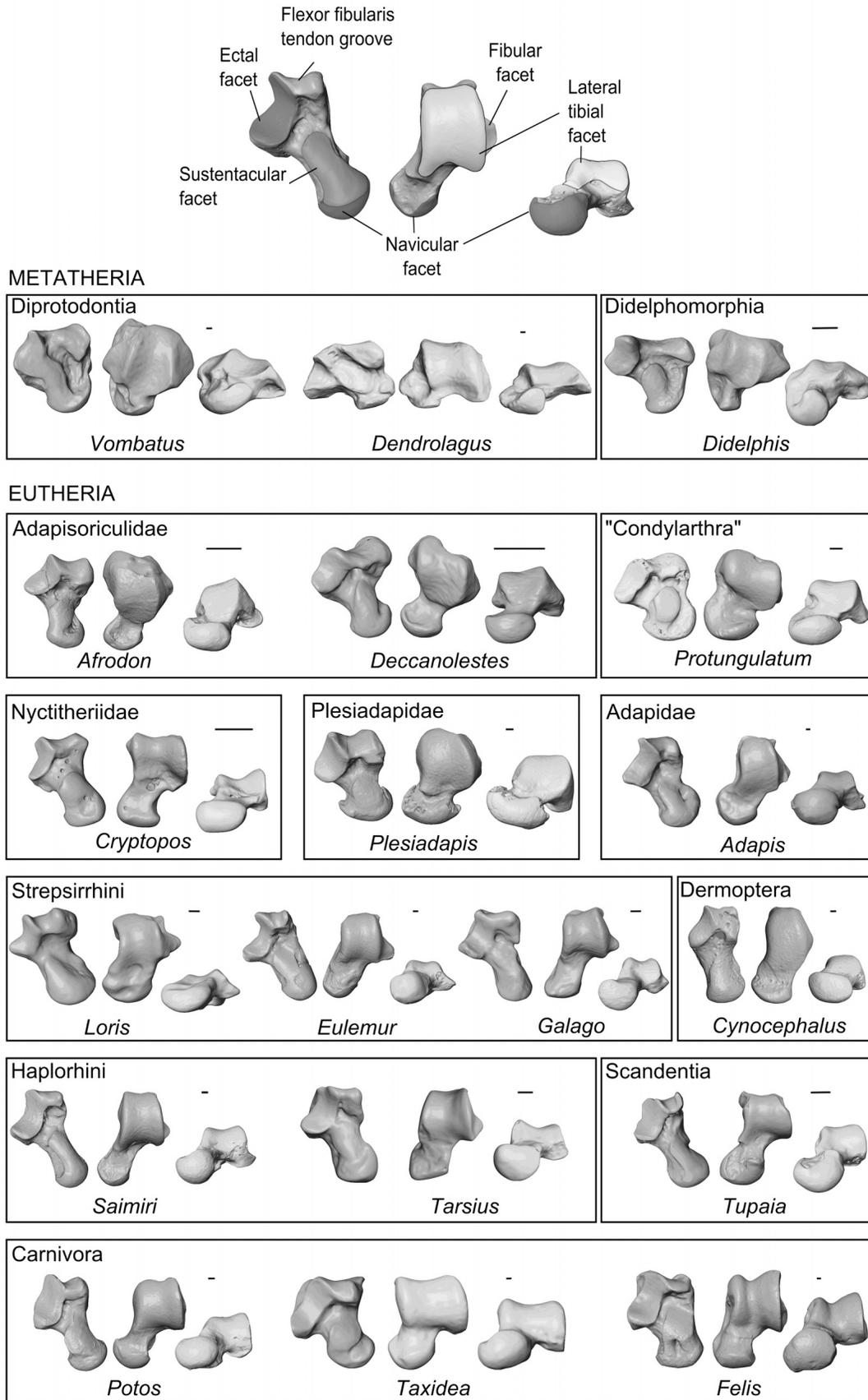


FIGURE 1. Detailed anatomical rendering of the astragalus of *Cebus* and 3D scans of the key taxa included in our data set. Scale bars equal 1 mm.

TABLE 1. Details of specimens used in analyses.

Taxon	Specimen
METATHERIA	
Didelphomorpha	
<i>Didelphis virginiana</i>	MNHN CG 1997-108
<i>Didelphis marsupialis</i>	MNHN CG 2003-15
Diprotodontia	
<i>Vombatus ursinus</i>	MNHN CG 1972-148
<i>Dendrolagus inustus</i>	MNHN CG 1930-484
EUTHERIA	
Adapisoriculidae	
† <i>Afrodon</i> , n. sp.	IRSNB M1981, O1
† <i>Bustylus marandati</i>	IRSNB M1979, N1
† <i>Deccanolestes hislopi</i>	VPL/JU/NKIM/52
‘Condylarthra’	
† <i>Protungulatum donnae</i>	AMNH 118260
Leptictimorph?	
†Unnamed leptictimorph	YPM uncataloged
Nyctitheriidae	
† <i>Cryptopos</i> ?	NHMUK M.60095
Carnivora	
<i>Felis silvestris</i>	MNCN 21536
<i>Taxidea taxus</i>	NMB 9783
<i>Ailurus fulgens</i>	MNHN CG 1999-26
<i>Martes foina</i>	Personal collection
<i>Potos flavus</i>	MNHN CG 1995-957
Euarchonta?	
† <i>Pronothodectes gaoi</i>	UALVP 49120
Scandentia	
<i>Tupaia glis</i>	SBU uncataloged
Dermoptera	
<i>Cynocephalus volans</i>	YPM 963
Plesiadapidae	
† <i>Plesiadapis cookei</i>	UM 87990
† <i>Plesiadapis rex</i>	UM 94816
Euprimates	
Omomyidae	
† <i>Hemiacodon gracilis</i>	AMNH 12613
Adapidae	
† <i>Notharctus</i> sp.	AMNH 11474
† <i>Leptadapis magnus</i>	NMB OE 496
† <i>Adapis</i> sp.	AMNH 111935
Strepsirrhini	
<i>Galago moholi</i>	HTB 747
<i>Loris tardigradus</i>	HTB 750
<i>Cheirogaleus medius</i>	DPC-0142
<i>Eulemur fulvus</i>	DPC-095
† <i>Otolemur crassicaudatus</i>	SBU 1163
Haplorhini	
<i>Callithrix pygmaea</i>	SBU uncataloged
<i>Tarsius syrichta</i>	DPC-0127
<i>Saguinus oedipus</i>	SBU NSg6
<i>Saimiri sciureus</i>	SBU uncataloged
† <i>Catopithecus browni</i>	DPC-22844

† indicates fossil specimen. **Abbreviations:** **AMNH**, American Museum of Natural History, New York; **DPC**, Duke Lemur Center Division of Fossil Primates, Durham, North Carolina; **HTB**, Cleveland Museum of Natural History, Hamann-Todd non-human primates osteological collection, Cleveland, Ohio; **IRSNB**, Royal Belgian Institute of Natural Sciences, Brussels; **MNHN CG**, Muséum national d’Histoire Naturelle Catalogue Générale, Paris; **NHMUK**, The Natural History Museum, London; **NMB**, Natuhistorisches Museum Basel, Basel; **SBU**, Stony Brook University, Stony Brook, New York; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta; **UM**, University of Michigan, Ann Arbor, Michigan; **VPL/JU/NKIM**, Vertebrate Palaeontology Laboratory, University of Jammu, Naskal intertrappean mammal catalogue numbers; **YPM**, Yale Peabody Museum, New Haven, Connecticut.

We used the eight first principal components (PCs), which combined represent more than 76% of the overall variation in the data set, to construct the neighbor-joining tree. Selection of the number of significant axis used to construct this tree was per-

formed using the broken-stick criterion of the ‘RBiodiversity’ library in R (Kindt, 2012).

Phylogenetic Signal

To estimate the phylogenetic signal in astragalar shape for extant taxa, we used a randomization test following the method of Blomberg et al. (2003). A K-statistic was calculated for the first three PCs of our sample of living species using the ‘picante’ library in R (Kembel et al., 2010). Because the phylogenetic affinities of many of the extinct taxa in our data set are still contentious, we excluded them from the analysis of phylogenetic signal. The K-statistic is a simple comparison of the phylogenetic signal observed in our shape data relative to the phylogenetic signal observed for a trait under Brownian motion on a given phylogeny (topology and branch lengths). In order to calculate this K-statistic, we used a phylogeny that corresponded to the subset of our sample of living species pruned from the supertree provided in Bininda-Emonds et al. (2008). The higher the K-value is, the stronger the phylogenetic signal. A K-value of 1 corresponds to character evolution under Brownian motion and indicates some degree of phylogenetic signal. A K-value greater than 1 indicates a strong phylogenetic signal, which means that traits are conserved within the phylogeny. Conversely, a K-value close to 0 means that phylogenetic signal is weak, indicating large amounts of morphological convergence.

Influence of Locomotion on Astragalar Shape

Because species share some part of their evolutionary history, they cannot be treated as independent data points. Thus, we conducted these analyses in a phylogenetic framework (Felsenstein, 1985; Harvey and Pagel, 1991). We used only living species using the phylogeny of Bininda-Emonds et al. (2008) pruned down to contain only the taxa included in our study. To test whether locomotor ecology influences the shape of the astragalus, we performed a phylogenetic multivariate analysis of variance (MANOVA) (Garland et al., 1993) on the first eight principal components, which together explain 76% of the shape variation observed in our sample of astragali. We used the *phy.manova* function in the R package ‘geiger’ (Harmon et al., 2008) for our analysis. To test whether animals with different locomotor ecologies differed significantly in shape, simulations of new shape variables on the tree were performed. First, we used the Wilks statistic as a multivariate test to estimate the F-value in our original MANOVA. Next, we ran 1000 simulations to create an empirical null distribution against which the F-value from the original data could be compared. We considered differences among categories to be significant if the original P-value was higher than the P_{95} -value derived from the empirical simulated distribution.

RESULTS

Shape Variation Using 3D Geometric Morphometrics

The first three PC axes accounted for 53.78% of the total shape variation. The distribution of the different taxa on PC1 (Fig. 3A) shows all extant placentals and extinct Euprimates falling on the negative part of the axis, whereas marsupials defined the positive end of the axis. Interestingly, all of the Cretaceous and Paleogene eutherians, including the nyctitherid, Adapisoriculidae (including *Deccanolestes*), Plesiadapidae, and *Leptictis*, fall in between these two groups, with *Protungulatum* invading marsupial space.

Shape changes associated with PC1 (Fig. 4) illustrate that marsupials and Cretaceous eutherians have a more robust astragalus with a relatively short neck and a relatively short and large sustentacular facet, a relatively large flexor fibularis tendon groove

TABLE 2. Definition of the landmarks used for geometric morphometrics analyses.

Landmark	Definition
1	Most proximomedial point of the ectal facet
2	Point of maximum of curvature of the ectal facet between landmarks 1 and 3
3	Most distomedial point of the ectal facet
4	Most distolateral point of the ectal facet
5	Most proximolateral point of the ectal facet between landmarks 5 and 1
6	Point of maximum of concavity between landmarks 5 and 1
7	Tip of the protuberance distomedial of the flexor fibularis tendon groove
8	Point of maximum of concavity between landmarks 7 and 9
9	Tip of the protuberance proximomedial of the flexor fibularis tendon groove
10	Most proximolateral point of the sustentacular facet
11	Most proximal point of the sustentacular facet
12	Most proximomedial point of the sustentacular facet
13	Most distomedial point of the sustentacular facet
14	Most proximomedial point of the navicular facet
15	Point of maximum of concavity of the dorsal side of the navicular facet between landmarks 14 and 16
16	Most proximolateral point of the navicular facet
17	Most distolateral point of the sustentacular facet
18	Most distomedial point of the medial ridge of the lateral tibial facet
19	Point of maximum of concavity between landmarks 18 and 20
20	Most distolateral point of the lateral ridge of the lateral tibial facet
21	Point of maximum of convexity of the lateral ridge of the lateral tibial facet
22	Most proximolateral point of the lateral ridge of the lateral tibial facet
23	Most proximomedial point of the medial ridge of the lateral tibial facet
24	Point of maximum of convexity of the medial ridge of the lateral tibial facet
25	Most proximolateral point of the ectal facet
26	Tip of the navicular facet

Landmark numbers correspond to those indicated on Figure 2.

in comparison with the ectal facet which is relatively short, a relatively large and short lateral tibial facet, and a relatively larger navicular facet. In contrast, most eutherians, including all placentals, displayed (Fig. 4) a more gracile astragalus with a rel-

atively long neck bearing a relatively long and thin sustentacular facet, a relatively narrow flexor fibularis tendon groove in comparison with the ectal facet being relatively large, a relatively high and narrow lateral tibial facet, and a relatively small navicular facet. The shape of the astragalus of *Deccanolestes* is more similar to that of Metatheria and closer to *Protungulatum*, Adapisoriculidae, and Plesiadapidae than to living Placentalia, as suggested by the shape variation on this axis.

Principal component 2 (Fig. 3) separated *Dendrolagus*, terrestrial and fossorial carnivorans, and *Leptictis* on the negative end, from Dermoptera, Strepsirrhini, Adapidae, Adapisoriculidae, and Plesiadapidae on the positive end. The other marsupials, arboreal and some terrestrial carnivorans, tree shrews, catarrhine primates, the nyctither, and *Protungulatum* fell in an intermediate position on PC2. Shape changes associated with PC2 (Fig. 4) indicated that *Dendrolagus* and the terrestrial carnivorans defining the negative end of the axis are characterized by lateral tibial facet relatively large, a robust neck, and a relatively shorter and broader ectal facet in comparison with the flexor fibularis tendon groove, which itself is relatively more elongated and flat and points more proximodistally. In contrast, the positive end of PC2 represents an astragalus shape with a relatively thin lateral tibial facet, a relatively gracile neck, and a larger ectal facet in comparison with the flexor fibularis tendon groove, which itself is relatively narrow. On this axis, *Deccanolestes* was characterized by an astragalus shape similar to that of Plesiadapidae, Adapidae, Strepsirrhini, and other Adapisoriculidae.

Principal component 3 (Fig. 3) separated the nyctither, Adapisoriculidae (including *Deccanolestes*), *Protungulatum*, Plesiadapidae, Scandentia, and Carnivora from all euprimates (which form a tight cluster) and marsupials. The shape changes associated with PC3 (Fig. 4) show that marsupials and euprimates are characterized by a neck with a sustentacular facet pointing more laterally relative to the body, a relatively higher lateral fibular facet with a medial ridge inserted more distally, a proximodistally thinner ectal facet, and a relatively shorter navicular facet. In contrast, the other taxa display a neck with a sustentacular facet oriented perpendicular to the body, a relatively shorter lateral fibular facet with a medial ridge inserted more proximally, a proximodistally broader ectal facet, and a relatively high navicular facet. On this axis, *Deccanolestes* was characterized by an astragalus shape similar to that of *Protungulatum*, *Tupaia*, and the other Adapisoriculidae.

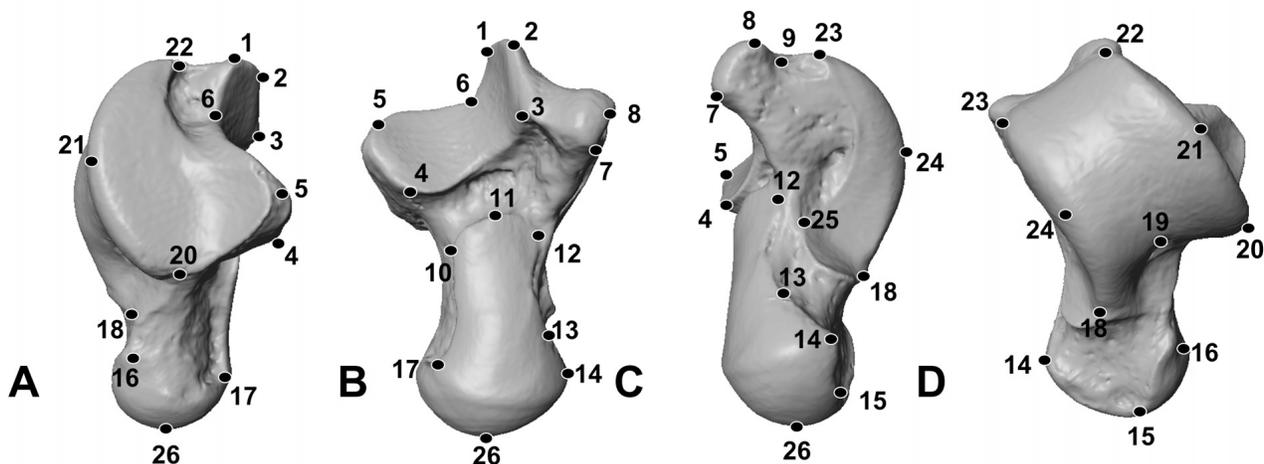


FIGURE 2. Landmarks used to quantify shape variation on the astragalus, illustrated on the astragalus of *Cebus* in **A**, lateral view; **B**, ventral view; **C**, medial view; **D**, dorsal view. Black dots represent landmarks.

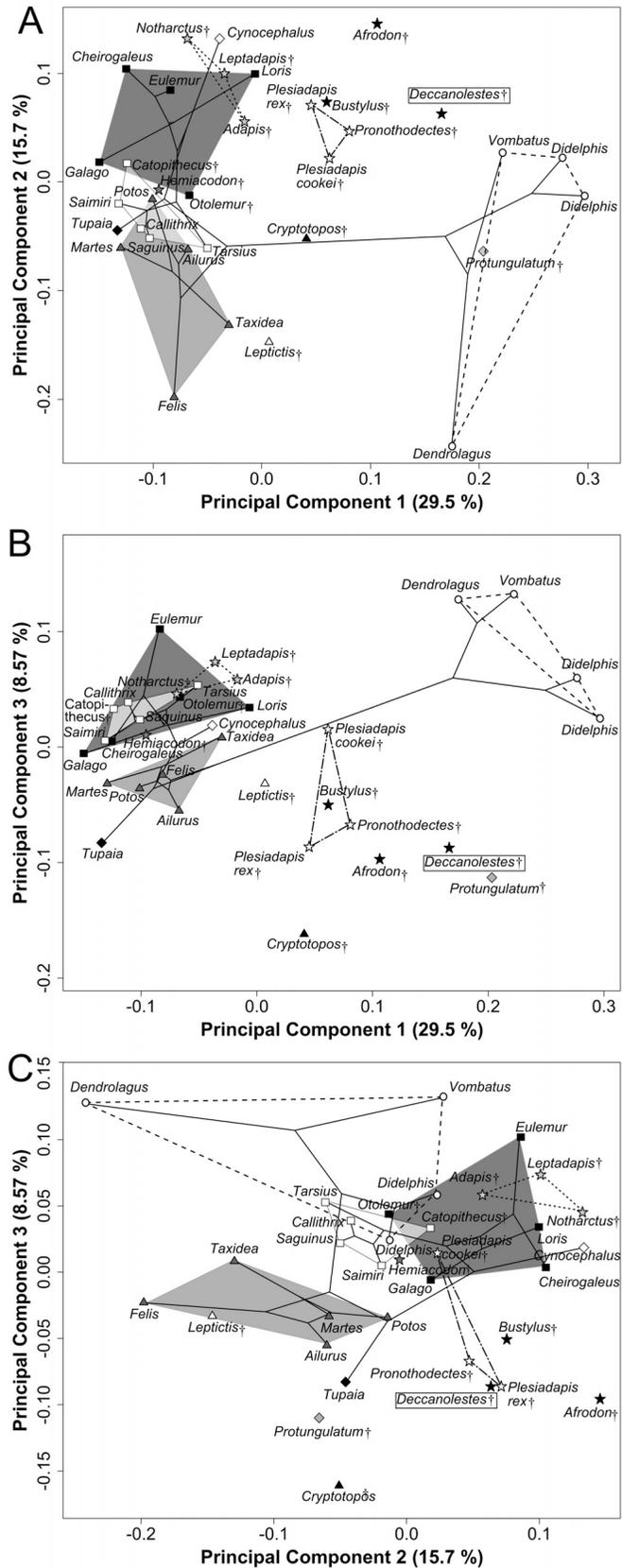


FIGURE 3. Results of the principal component analysis performed on the morphometric data for the astragalus, with the phylogeny of living taxa mapped onto their distribution. **A**, PCs 1 and 2; **B**, PCs 1 and 3; **C**, PCs 2 and 3. Symbols are as follows: † indicates fossil specimens; light gray triangles and polygons, Carnivora; dark gray squares and polygons, Strepsirrhini; white squares and polygons, Haplorhini; white circles and dashed line polygon, Metatheria; black diamond, Scandentia; white diamond, Dermoptera; light gray stars and dotted polygon, Adapidae; white stars and dash + dotted polygon, Plesiadapidae; black stars, Adapisoriculidae; black triangles, Nyctitheriidae; white triangle, *Leptictis*; dark gray stars, Omomyidae; light gray diamonds, 'Condylarthra.'

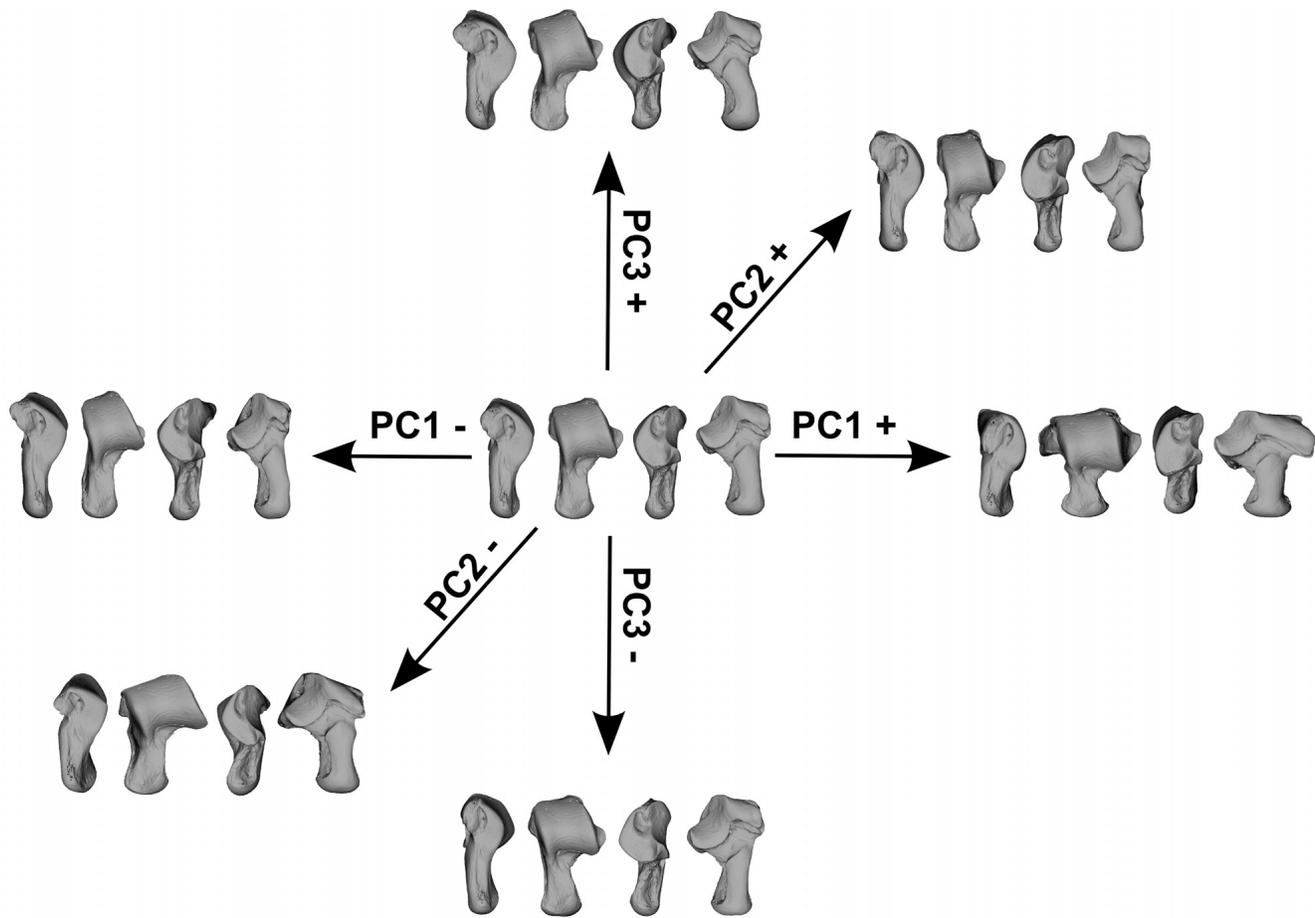


FIGURE 4. Shape changes associated with each principal component axis. Shapes correspond to the positive and negative extreme of each axis.

Phenetic Affinities

On the neighbor-joining tree (Fig. 5), three distinct clusters can be distinguished. The first group is composed of marsupials (Didelphimorphia and Diprotodontia), *Deccanolestes*, and *Protungulatum*. The second group is composed of Adapidae, Plesiadapidae, and Plesiadapidae. The third group includes the nyctitheres, Dermoptera, Strepsirrhini, *Leptictis*, Omomyidae, Haplorhini, Scandentia, and Carnivora. Based on the neighbor-joining tree, *Deccanolestes* is morphologically (phenetically) most similar to *Protungulatum* and the marsupials, followed by Plesiadapidae, Adapidae, and others Adapisoriculidae.

Phylogenetic Signal

Table 3 shows the values of the K-statistic and its significance levels. The K-statistic calculated for the first principal component is higher than 1 (close to 3), which indicates a strong phylogenetic signal in the shape of the astragalus. The K-statistic is lower than 1 for the other principal components, although it approaches 1 for PC2 (0.77). The randomization test showed a significant phylogenetic signal for the first two principal components of shape variation for the astragalus, which combined represent 45.2% of the total variation in the data set.

Influence of Locomotion on Astragalus Shape

A standard and a phylogenetic MANOVA were performed on the first eight principal components, representing 76% of the to-

tal shape variation in the data set. Although results of the standard MANOVA were significant, the results of the phylogenetic MANOVA were not (MANOVA: Wilks $\lambda = 0.11$, $F_{2,17} = 2.5$, $P < 0.01$; MANOVA: $P_{\text{phy}} = 0.11$). These results indicate that although the shape of the astragalus is different for animals with different locomotor ecologies, these results no longer hold when phylogeny is taken into account. Thus, the ecological/functional signal present in the astragalus shape is nested within phylogenetic clades.

DISCUSSION

The astragalus is often considered to be a functionally informative structure, and it is commonly used in paleoecological studies due to its excellent preservation (Szalay and Decker, 1974; Langdon, 1986; Szalay and Langdon, 1986; Gebo, 1989; Carrano, 1997; Seiffert and Simons, 2001; Youlatos, 2003; Youlatos and Koufos, 2010). However, the precise relationship between astragalus morphology and its role in locomotion remains poorly understood, in part due to the lack of comparative, experimental studies on the functional role of this bone during locomotion. Here, we attempted to elucidate the locomotor ecology of the enigmatic Cretaceous Indian eutherian *Deccanolestes* using a 3D morphometric comparison with extant and extinct mammals representing locomotor modes ranging from terrestrial to arboreal. Our results suggest that the astragalus shape of *Deccanolestes* displays no real analogue among the living species sampled here. Although some parts of its morphology converge on marsupials,

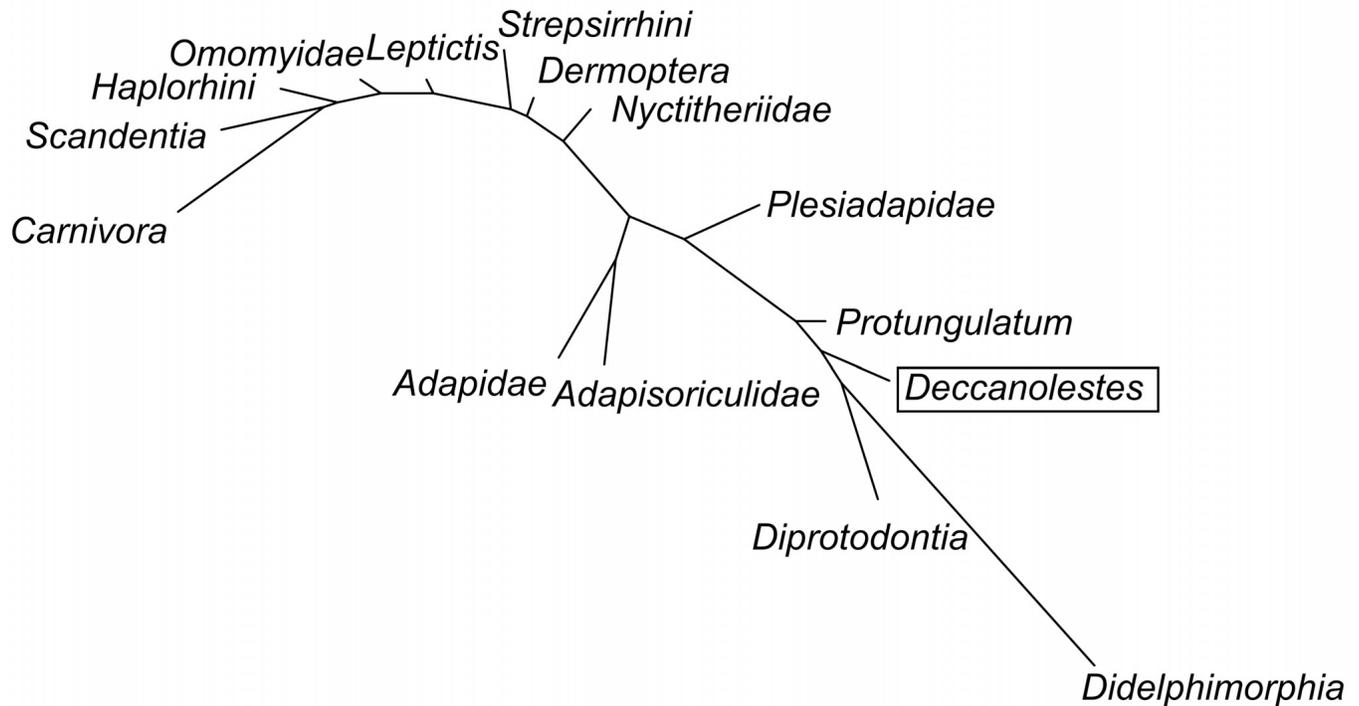


FIGURE 5. Phenetic affinities among taxa. The neighbor-joining tree was calculated using the Euclidean distances of the tangent scores of the first eight PC axes.

Deccanolestes is more similar in shape to extinct Cretaceous and Paleocene eutherian mammals, particularly *Protungulatum* but also *Adapisoriculidae* and *Plesiadapidae*. This similarity of tarsal morphology of *Deccanolestes* with *Protungulatum* was previously suggested by Szalay (1984, 2006). Interestingly, he argued that last common ancestor of eutherians and metatherians was more terrestrial and rather *Protungulatum*-like. Although *Deccanolestes* had not been discovered at the time, Szalay (1984) previously showed that the astragalar morphology of early eutherians is not represented among living forms. Thus, the interpretation of form and function of the early eutherians, as well as reconstruction of their locomotor habits, may not be easily derived from comparisons with extant taxa, a result that is further supported by this analysis of *Deccanolestes*.

The results presented here are broadly consistent with the analysis of astragalar length measurements conducted by Boyer et al. (2010b) in finding broad similarities between *Deccanolestes*, *Plesiadapidae*, and the early 'condylarth' *Protungulatum*. However, in contrast to the results of Boyer et al. (2010b) and Smith et al. (2010), our results show it to be distinct from the dermopteran *Cynocephalus*. We also demonstrate quantitatively that the astragalus of *Deccanolestes* is similar in its overall shape

to that of the *Adapisoriculidae* *Bustylus* and *Afrodon*, as Smith et al. (2010) suggested previously based on qualitative comparisons.

Based on the results of the principal component analysis, it appears that the overall shape of the astragalus as captured by our landmarks does not reflect the lifestyle or locomotor mode in extant samples in a straightforward manner. For example in our data set, the positive and negative ends of PC1 were defined by arboreal taxa (*Didelphis* at the positive end and *Galago* at the negative), but terrestrial taxa, such as *Martes* and *Vombatus*, also fell near the ends of this axis. Part of this variation may be due to variation in the mechanisms of hind foot inversion across mammals, with marked differences between eutherians and some groups of marsupials, including didelphids (Jenkins and McClearn, 1984). On PC2 (Fig. 3A), the most terrestrial carnivorans, *Felis* and *Taxidea*, are situated on the negative part of the axis. In contrast, the inverse pattern was observed for marsupials, with the most terrestrial species situated towards the positive part of PC2 and the most arboreal ones towards the negative side, nearest the most terrestrial placental. Moreover, (Fig. 3B) arboreal and terrestrial species of Carnivora clustered closely on PC3, with no evident differentiation of any taxa based on locomotory modes. However, this result may partly be due to the fact that the astragalar shape of carnivorans and other living placentals are more similar to each other in both form and function than either are to marsupials. Difference in locomotor style appears to drive the distribution of living species of eutherians on PC2 and PC3 (Fig. 3C). Indeed, a trend from terrestrial to arboreal species is evident along the PC2 for the extant placentals, especially for the carnivorans. Interestingly, the distribution in morphospace of the carnivoran taxa in our study is similar to that obtained previously by Polly (2008).

Based on our results, the variables that appear to be driving the major axes are the shape of the lateral tibial facet, the

TABLE 3. Results of K-statistics calculated for the first three principal components and their associated P-values.

Variable	K	P
Principal component 1	2.96	0.0009
Principal component 2	0.77	0.003
Principal component 3	0.46	0.21

Principal components showing significant phylogenetic signal ($\alpha < 0.05$) are indicated in bold.

fibular surface, the navicular facet, and the relative proportion of the ectal facet in comparison with the flexor fibularis tendon groove. These traits effectively distinguish between the different groups of mammals included in our analysis: marsupials, the fossil eutherians (including extinct placentals), and the extant placentals. Interestingly, these characters that differentiate placentals, marsupials, and fossil eutherians closely resemble those previously suggested by Szalay (e.g., 1977, 1984, 2006) and Szalay and Sargis (2006). Among the characters that have been used to assign astragali to an arboreal lifestyle, the extended and rounded navicular facet confluent with the sustentacular facet seems to be a particularly important one (although confluence is occasionally observed in terrestrial taxa, such as the guinea pig, *Cavia*, and the navicular facet is not always rounded in arboreal/scansorial taxa, such as the tree squirrel *Sciurus*). Unfortunately, the fusion of these two structures is impossible to quantify using our landmark-based geometric morphometric analysis. The fibular surface and navicular facet have both also been suggested to be related to arboreality (Godinot and Prasad, 1994; Prasad and Godinot, 1994). Yet, in our analyses, changes in the shape of these two articular surfaces appear to distinguish between phylogenetic groups rather than reflecting arboreality. The results of our analysis of phylogenetic signal demonstrated that the shape of the astragalus in our sample contains strong phylogenetic signal (Table 3). This suggests that astragalar shape may be less informative with respect to ecology and locomotor behavior in mammals. This result is also supported by the MANOVA and phylogenetic MANOVA performed on the extant species included in our data set, which showed that phylogeny drives the observed relationship between shape and locomotor ecology and suggests that changes in morphology are nested within clades. Explicit biomechanical studies may be one worthwhile avenue for future study that could generate a priori predictions against which observed patterns of morphological variation can be tested.

Although it may be tempting to interpret these results phylogenetically, the purpose of this phenetic analysis was to assess the utility of astragalar morphology to elucidate the locomotor ecology of extinct taxa. Furthermore, as noted above, some of the discrete characters that are important in previous phylogenetic analyses of these taxa cannot be captured with 3D landmarks, and some of the key characters of interest involve the relationship of the astragalus to the calcaneum, rather than astragalar traits in isolation. Although there is strong clustering of well-resolved phylogenetic groups on some components, there are also clear temporal groupings. For example, Eocene to extant placentals cluster separately to Cretaceous and Paleocene eutherians, even though the latter group includes taxa more closely related to extant placentals than to the other Cretaceous and Paleocene taxa. These temporal groupings suggest that eutherian sympleiomorphies, as well as synapomorphies of placental clades and convergences related to locomotory ecology, all are influencing the distribution of taxa in astragalar morphospace.

Overall, these results suggest that because the astragalus carries significant phylogenetic signal, astragalar shape cannot be interpreted in simply ecological or functional terms. Of course, strong phylogenetic signal does not necessarily invalidate the possibility that astragalar morphology also carries significant ecological signal; however, this ecological signal appears to be clade-specific and does not suggest an overall phenotype linked to arboreality across mammals. Another complicating factor is that arboreality is a broad grouping, which remains difficult to define due to large variation in the degree of arboreality or scansoriality across mammals. Clearly, functional constraints and subsequent morphological changes in tarsal elements will be influenced by the type of substrate used by an animal and its locomotor behavior. For example, animals that use narrow branches versus the trunk to move upon can be expected to show different morphologies, as has been demonstrated for

Caribbean *Anolis* lizards (Mattingly and Jayne, 2004; Losos, 2009). Moreover, whether an animal is jumping from branch to branch, running along branches, or climbing on vertical broad substrates such as tree trunks will affect its morphology.

In interpreting the functional morphology of the astragalus, it is also important to note that functional capacities may not equal behavioral repertoires (Bock and Von Wahlert, 1965; Jenkins and McClearn, 1984; Oxnard et al., 1990; Boyer and Bloch, 2008). As elegantly explained by Jenkins and McClearn (1984), small body size in terrestrial habitats is likely to select for many of the same features as arboreality selects for in larger mammals. This is due to the fact that even sticks, small rocks, and leaf litter present relatively large-scale 3D obstacles that must be climbed over and around for a small ambulatory mammal. This puts a demand on the capacity for rotational mobility in the limb joints. For example, tenrecs are mainly generalized terrestrialists; however, most if not all have a distally extended sustentacular facet on the calcaneus (see figures in Salton and Szalay, 2004), which is usually associated with arboreal behaviors that require mobility at the lower ankle joint (Szalay and Decker, 1974). On the other hand, *Echinops*, the most arboreally committed tenrec (Salton and Szalay, 2004; Salton and Sargis, 2009), does appear to differ from its brethren in having by far the least trochleated (flattest) lateral tibial facet. All other taxa have much more substantial grooves on the trochlea, which limits the mobility of the upper ankle joint to flexion and extension. Thus, the flattened un-trochleated lateral tibial facet of *Deccanolestes* may in fact be telling us that it is indeed slightly more focused on arboreal substrates than the average tenrec (but maybe not much more). Future studies comparing *Deccanolestes* with a broader range of mammals, rather than focusing on arboreal taxa as we have here, may provide important additional data on the ecology of *Deccanolestes*, although the strong phylogenetic signal observed for astragalar morphology here, coupled with the lack of a close relationship between *Deccanolestes* and any extant mammal clade (Goswami et al., 2011), will continue to be a complicating factor in deciphering the precise ecology of this enigmatic mammal.

More exhaustive sampling within species and among taxonomic groups, better resolution in the definition of habitat categories, and further quantitative studies on the morphology of the astragalus, ideally including surface analyses, are needed to better understand the ecological signal contained within the morphology of this bone. Our data suggest that the astragalar morphology of *Deccanolestes* and other adapisoriculids is unambiguously different from any arboreal mammal sampled, or any other extant mammal included in our analysis, suggesting that its precise ecology may not be represented in the modern biota. This result supports the descriptions of early eutherian ankle morphology previously made (Szalay 1977, 1984, 2006; Szalay and Sargis, 2006), and places *Deccanolestes* in the form-function milieu of other early eutherians, rather than among modern placentals. Incorporating data from more than a single element and a broader ecological range will be crucial to improving reconstructions and interpretations of this animal's lifestyle and locomotor mode, yet such studies await further fossil discoveries from the Cretaceous of India and other relevant localities.

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