

Oldest known euarchontan tarsals and affinities of Paleocene *Purgatorius* to Primates

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Earliest Paleocene *Purgatorius* often is regarded as the geologically oldest primate, but it has been known only from fossilized dentitions since it was first described half a century ago. The dentition of *Purgatorius* is more primitive than those of all known living and fossil primates, leading some researchers to suggest that it lies near the ancestry of all other primates; however, others have questioned its affinities to primates or even to placental mammals. Here we report the first (to our knowledge) nondental remains (tarsal bones) attributed to *Purgatorius* from the same earliest Paleocene deposits that have yielded numerous fossil dentitions of this poorly known mammal. Three independent phylogenetic analyses that incorporate new data from these fossils support primate affinities of *Purgatorius* among euarchontan mammals (primates, treeshrews, and colugos). Astragali and calcanei attributed to *Purgatorius* indicate a mobile ankle typical of arboreal euarchontan mammals generally and of Paleocene and Eocene plesiadapiforms specifically and provide the earliest fossil evidence of arboreality in primates and other euarchontan mammals. Postcranial specializations for arboreality in the earliest primates likely played a key role in the evolutionary success of this mammalian radiation in the Paleocene.

Euarchonta | Primates | Paleocene | paleontology | evolution

Evidence from the fossil record suggests that placental mammals diversified following the Cretaceous–Paleogene (K–Pg) boundary ~66 Mya (1, 2). Among the oldest known placental mammals, the putative primate *Purgatorius* has been documented in the western interior of North America during the first million years after the K–Pg boundary (2–5) to within the first few hundred thousand years of the Paleocene (6). Although the fossil record of *Purgatorius* has been restricted to dentitions long recognized as uniquely similar to those of primates (3, 4), these anatomical data are limited. Some researchers who have preferred to restrict the order Primates to the crown-clade (i.e., Euprimates) have also questioned the primate affinities of *Purgatorius* and other Paleogene plesiadapiforms (reputed stem primates) (e.g., refs 7 and 8). Furthermore, several recent phylogenetic analyses have not supported *Purgatorius* in Primates (9) or even in Placentalia (crown-clade eutherians) (10–12). New evidence supporting *Purgatorius* as the oldest plesiadapiform primate is derived from tarsal bones collected at the late Puercan (Pu3; ~65 Mya) Garbani Channel fauna localities in Garfield County, northeastern Montana. Four decades of fieldwork have resulted in the recovery of hundreds of *Purgatorius* teeth and fragmentary jaws (13). Here we attribute tarsals (astragali and calcanei) to *Purgatorius* based on size and diagnostic euarchontan and plesiadapiform features (Fig. 1 and *SI Appendix*). This taxonomic attribution is supported further by the absence of other euarchontan taxa from the Garbani Channel fauna.

Phylogenetic Analysis

Results from recent broad cladistic analyses that focused on relationships among eutherian mammals do not support primate affinities of *Purgatorius* and instead place *Purgatorius* in a clade

directly outside Placentalia with the contemporary condylarths (archaic ungulates) *Protungulatum* and *Oxyprimus* (10–12). However, the addition of new tarsal data for *Purgatorius* and increased taxon sampling, including a colugo and four plesiadapiforms, using this same matrix, results in a strict consensus tree that supports a monophyletic Euarchonta with Sundatheria (treeshrews and colugos) as the sister group to a fairly unresolved Primates clade that includes *Purgatorius* (Fig. 2A). This result is driven mainly by the addition of euarchontan taxa rather than by new character data for *Purgatorius*, which strongly suggests that the previous support for *Purgatorius* outside Placentalia and Euarchonta is primarily an artifact of taxon sampling (10, 14). To address this issue further, we included the new *Purgatorius* tarsal data in two additional analyses that were designed to evaluate relationships within Euarchonta (15) or more broadly within Euarchontoglires (16). Results from both analyses support *Purgatorius* as the most basal primate (Fig. 2B and C).

Description and Comparison of Tarsal Bones

Although previously published cladistic analyses support a close relationship between *Purgatorius* and the condylarth *Protungulatum* (10–12), the tarsals attributed to *Purgatorius* differ considerably from those of *Protungulatum* by having many characteristics of euarchontan mammals that relate to arboreality (Fig. 3). As in other euarchontans, the upper ankle joint of *Purgatorius* is more mobile than that of *Protungulatum*, which has a contact between the fibula and calcaneus that restricts medial–lateral movements at this joint (17). The astragalar trochlea (lateral tibial facet) of *Purgatorius* is relatively longer than that of *Protungulatum*, allowing a greater

Significance

Purgatorius has been considered a plausible ancestor for primates since it was discovered, but this fossil mammal has been known only from teeth and jaw fragments. We attribute to *Purgatorius* the first (to our knowledge) nondental remains (ankle bones) which were discovered in the same ~65-million-year-old deposits as dentitions of this putative primate. This attribution is based mainly on size and unique anatomical specializations known among living euarchontan mammals (primates, treeshrews, colugos) and fossil plesiadapiforms. Results of phylogenetic analyses that incorporate new data from these fossils support *Purgatorius* as the geologically oldest known primate. These recently discovered tarsals have specialized features for mobility and provide the oldest fossil evidence that suggests arboreality played a key role in earliest primate evolution.

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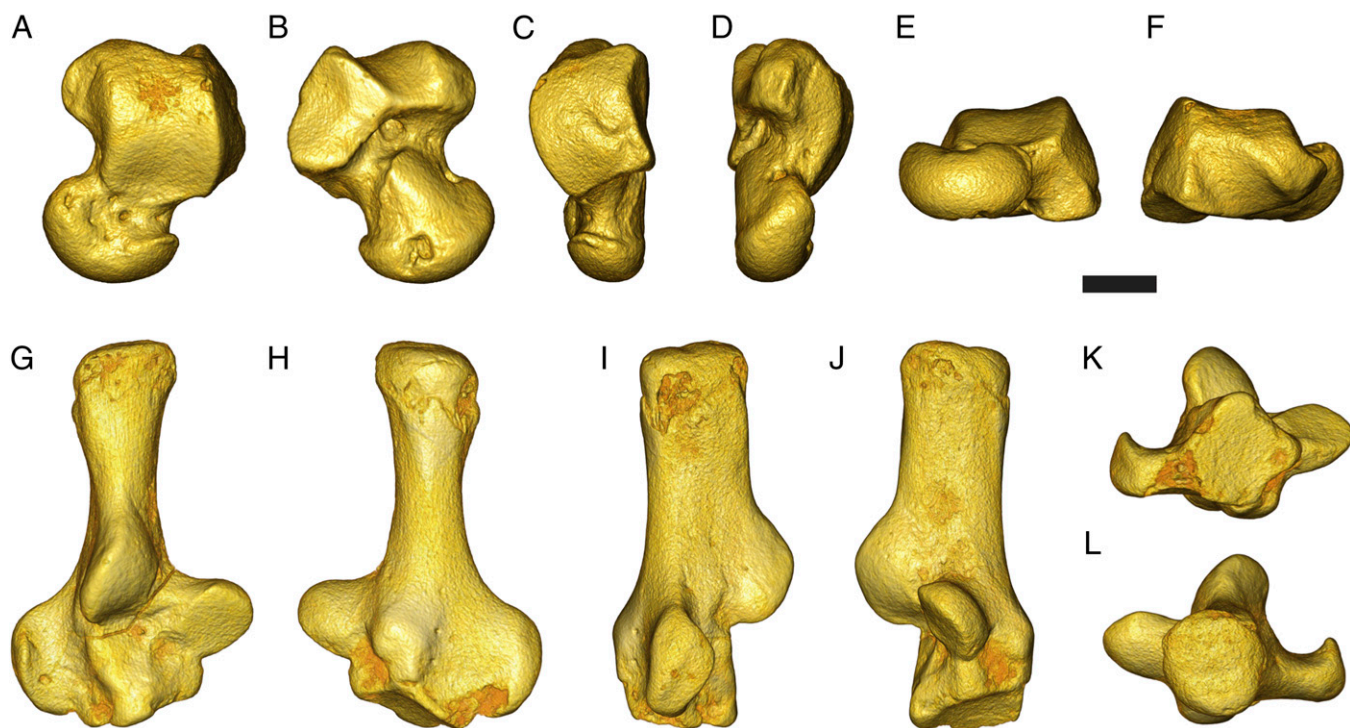


Fig. 1. Micro-CT scan images of tarsal bones attributed to *Purgatorius* from the late Puercan (Pu3; ~65 Mya) Garbani Channel fauna localities in northeastern Montana. UCMP 197509, left astragalus, and UCMP 197517, right calcaneus, are shown in dorsal (A and G), plantar (B and H), lateral (C and I), medial (D and J), distal (E and K), and proximal (F and L) views, respectively. (Scale bar, 1 mm.) See [SI Appendix](#) for institutional abbreviations.

range of dorsi- and plantarflexion (Fig. 3). The trochlea of *Purgatorius* is medially sloping, is aligned oblique to the long axis of the astragalus, and extends slightly onto the dorsal surface of the

astragalar neck, as is consistent with mammals whose feet abduct during dorsiflexion for climbing on vertical supports (18). The lower ankle joint of *Purgatorius* also is considerably more mobile than that

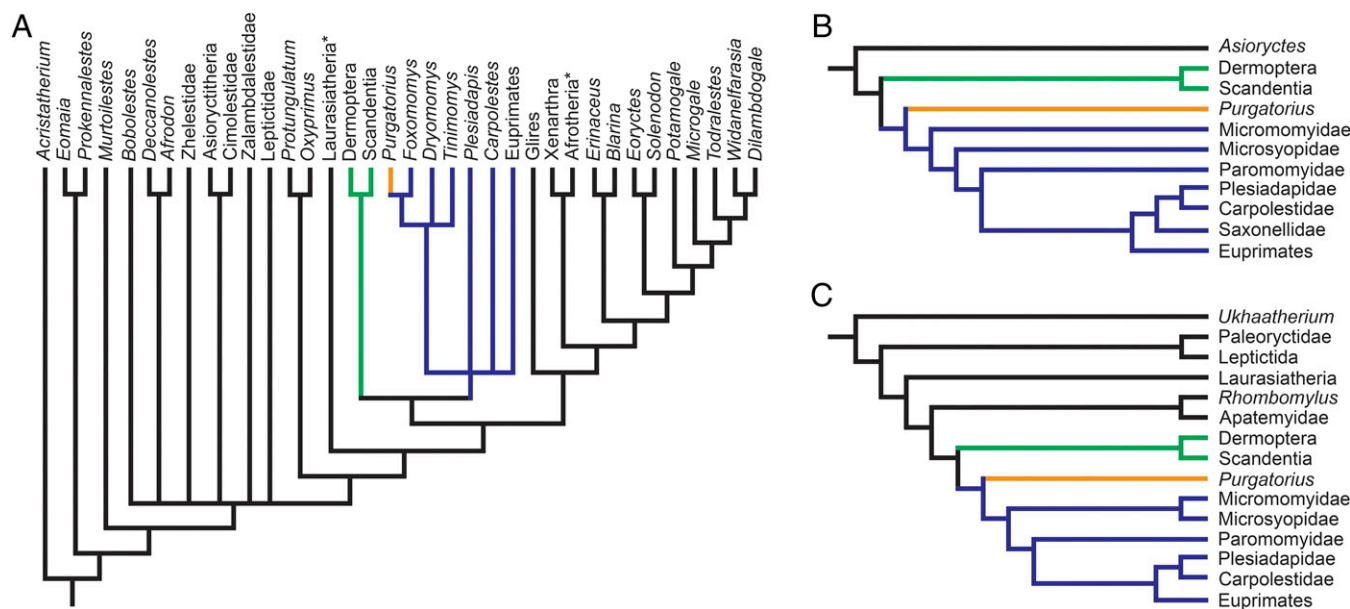


Fig. 2. Hypotheses of evolutionary relationships of *Purgatorius* and other eutherian mammals. (A) Simplified resulting strict consensus cladogram based on data modified from ref. 12, *Purgatorius* tarsals, and five additional euarchontan taxa (colugo *Cynocephalus*, the micromomyid plesiadapiforms *Foxomomys*, *Dryomomys*, and *Tinimomys*, and the carpolestid plesiadapiform *Carpolestes*). Asterisks indicate results from a previously published analysis with Laurasiatheria excluding Eulipotyphla and Afrotheria excluding Afrotheria (12). (B) Simplified resulting single-most-parsimonious cladogram based on data from ref. 15 and *Purgatorius* tarsals. (C) Simplified resulting strict consensus cladogram based on data from ref. 16 and *Purgatorius* tarsals. In all cladograms, Sundatheria is supported and indicated in green, Primates is supported and indicated in violet, and *Purgatorius* is supported as a primate and indicated in orange. See [SI Appendix](#) for methods, full tree topologies, and support values.

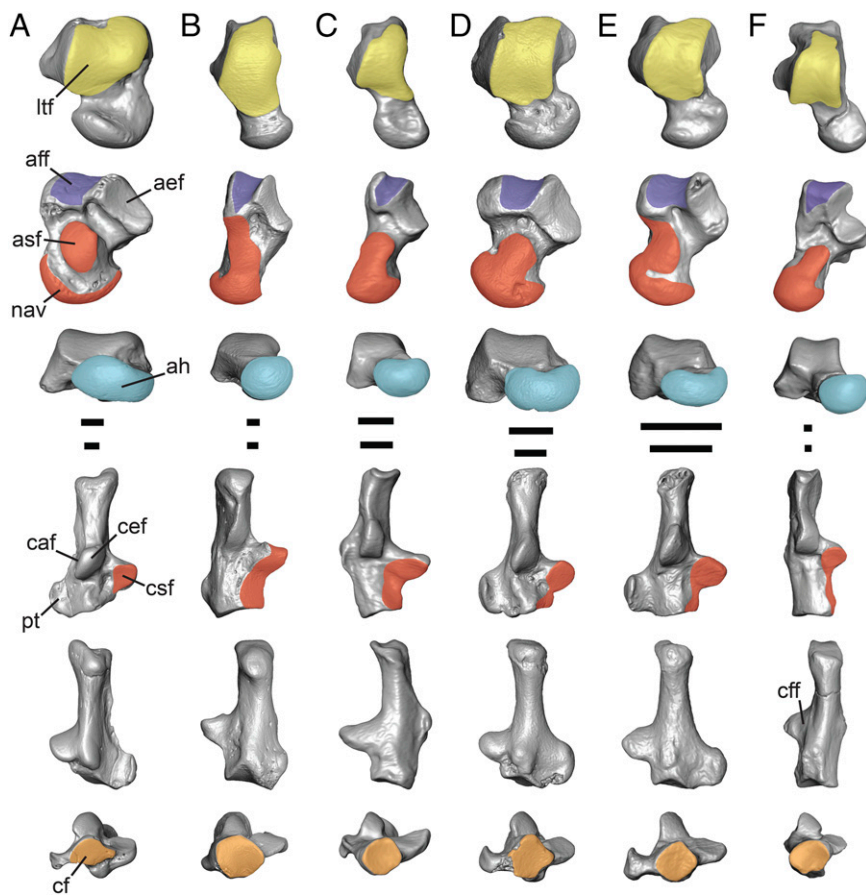


Fig. 3. Comparison of micro-CT scan images of tarsal bones. Columns illustrate tarsals of condylarth *Protungulatum* (A), colugo *Cynocephalus* (B), treeshrew *Ptilocercus* (C), *Purgatorius* (D), the micromomyid plesiadapiform *Dryomomys* (E), and the adapoid euprimate *Notharctus* (F) right astragali (rows 1–3) and calcanei (rows 4–6) in dorsal (rows 1 and 4), plantar (rows 2 and 5), and distal (rows 3 and 6) views, respectively. Some elements are reversed for clarity. (Scale bars: 1 mm.) aef, astragalar ectal facet; aff, astragalar groove for tendon of *musculus flexor fibularis* (violet); ah, astragalar head (blue); asf, astragalar sustentacular facet (red); caf, calcaneal fibular facet; cef, calcaneal ectal facet; cf, calcaneocuboid facet (orange); cff, calcaneal groove for tendon of *musculus flexor fibularis*; csf, calcaneal sustentacular facet (red); ltf, lateral tibial facet (yellow); nav, astragalonavicular facet (red); pt, peroneal tubercle. See [SI Appendix](#) for specimen numbers.

of *Protungulatum*, especially in having increased capacity for movements between the sustentacular facets of the astragalus and calcaneus. *Purgatorius* has a saddle-shaped astragalar ectal facet that articulates with and rotates along a longer, moderately proximodistally aligned calcaneal ectal facet (Fig. 1). This morphology suggests a pronounced capacity for inversion and eversion of the foot, which is supported further by the presence of a well-developed distal calcaneal sustentacular facet and a distally extensive astragalar sustentacular facet that contacts the navicular facet (Fig. 3). These distal articular regions would have come into close contact only during strong inversion of the foot. Such movements are facilitated further at the transverse tarsal joint of *Purgatorius* by the rounded, concave, gliding articulation of the calcaneocuboid facet and its fairly transverse orientation and by the pronounced, rounded navicular facet on the medial side of the astragalar head (Fig. 1). In contrast, *Protungulatum* has a more ovoid, asymmetrical calcaneocuboid facet that is oriented more obliquely to the long axis of the calcaneus and a less pronounced medial side of the astragalar head, suggesting that *Protungulatum* had less capacity for pedal inversion and used level-oriented foot positions for locomotion on a flat substrate, as do terrestrial quadrupeds (Fig. 3) (17).

Among euarchontans, the tarsals attributed to *Purgatorius* are uniquely similar to those of other plesiadapiforms in having an astragalus with a medially sloping trochlea and a relatively broad

head and a calcaneus with a large peroneal tubercle (Figs. 3 and 4 and [SI Appendix](#)) (18). However, it should be noted that currently euarchontan tarsal comparisons outside Primates are limited to the presumably more derived morphologies of extant colugos and treeshrews, given the paucity of postcranial fossils representing these clades. Unlike the level astragalar trochlea of colugos and the most basally divergent treeshrew *Ptilocercus*, the medially sloping trochlea of *Purgatorius* may have reduced the potential for lateral shear of the tibia on the astragalus when inverted foot postures were used during locomotion on large-diameter supports (Fig. 3). The astragalar head of *Purgatorius* and other plesiadapiforms is broad and ovoid, suggesting frequent use of inverted and everted postures. The large medial aspect of the astragalonavicular facet of *Purgatorius* likely reflects forces frequently transmitted on the medial side of the head during habitual pedal inversion (17), but the more spherical head of colugos, *Ptilocercus*, and many euprimates indicates even greater emphasis on inverted postures in these taxa (Fig. 3). *Purgatorius* also differs from colugos, *Ptilocercus*, and euprimates in having a calcaneus with a much larger and more laterally projecting peroneal tubercle (Fig. 3), which provides more leverage for tendons of peroneal muscles that contribute to eversion (*musculus peroneus longus*) and abduction (*musculus peroneus brevis*) and counterbalance forces that invert the foot (19). The smaller peroneal tubercle in other euarchontans suggests less

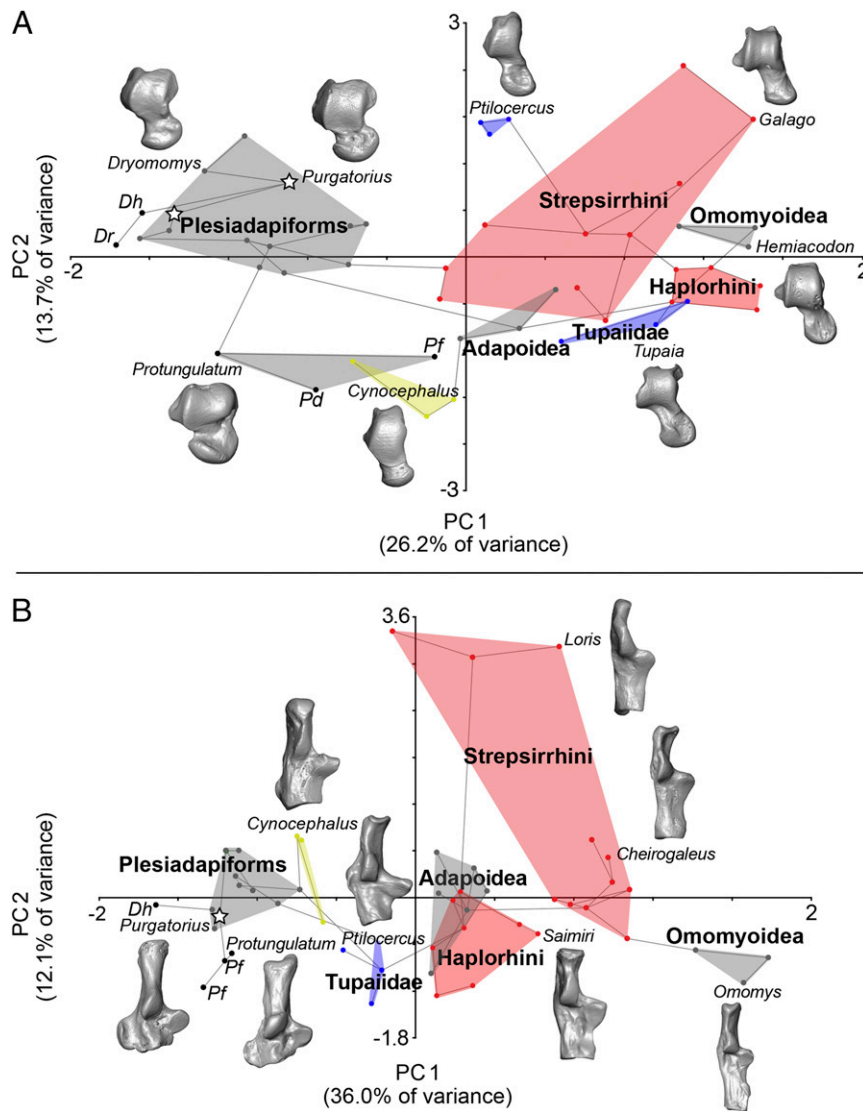


Fig. 4. Results of principal component analysis of 23 astragalar measurements for 34 species (A) and 25 calcaneal measurements for 33 species (B) (SI Appendix). Lines connecting data points reflect a minimum-spanning tree computed from a Euclidean distance matrix. Polygons encompass taxa including living strepsirrhine and haplorhine euprimates (red), treeshrews (blue), and colugos (yellow). Gray polygons encompass fossil groups including adapoid and omomyoid euprimates, plesiadapiforms, and earliest Paleocene mammals *Protungulatum donnae* (Pd) and *Procerberus formicarium* (Pf). Results support tarsals attributed to *Purgatorius* (starred) as a plesiadapiform, which, like *Protungulatum* and Cretaceous *Deccanolestes* (*D. hislopi*, Dh; *D. robustus*, Dr), has tarsal features that may be plesiomorphic, such as a large calcaneal peroneal tubercle. See SI Appendix for eigenvalue, percentage variance, and variable component loadings for each principal component.

emphasis on the peroneal muscles for eversion movements and rotational stability, possibly as a mechanical consequence of the greater degree of distal calcaneal elongation present in these taxa (18, 20).

Micromomyids are the most primitive plesiadapiforms known from skeletons (Fig. 2 B and C) and have been reconstructed as being most similar to *Ptilocercus* among extant mammals (15). Thus it is significant that *Purgatorius*, which has teeth very similar to those of primitive micromomyids (21, 22), also shares with that group unique tarsal features including a slightly grooved astragalar trochlea with a relatively high medial ridge and a fairly consistent mediolateral width (Fig. 3), whereas other stem primates have a flat and more medially sloping trochlea that is widest distally. *Purgatorius* and micromomyids also are most similar in tarsal features related to the tendon of *musculus flexor (digitorum) fibularis*, which contributes to digital flexion and plantarflexion of the foot and is important for pedal grasping.

These taxa have a very large and mediolaterally wide *flexor fibularis* groove on the astragalus (Fig. 3), as is consistent with the large origination areas indicating sizeable flexor muscles on the tibia and fibula of micromomyids (23). However, the corresponding groove for the tendon of *flexor fibularis* on the plantar aspect of the calcaneal sustentaculum is shallow in *Purgatorius* and micromomyids, as it is in treeshrews and colugos (Fig. 3). The presence of a deep *flexor fibularis* groove on the calcaneal sustentaculum has been considered a synapomorphy for primates related to stronger hallucal grasping, whereas this muscle has been considered to play a less active role in treeshrews and colugos (18). In fact, a deep *flexor fibularis* groove is present on the calcaneus of euprimates and more derived plesiadapiforms (including paromomyids and plesiadapoids). The combination of a large groove for the tendon of the *flexor fibularis* on the astragalus and absence of a deep groove on the calcaneus in *Purgatorius* and micromomyids may be a primitive retention in

these taxa. Similar characteristics are present in *Protungulatum* and the Cretaceous eutherian *Deccanolestes*, whose affinities lie well outside the Euarchonta (Fig. 2).

Discussion

The evolution of diagnostic euprimate traits associated with grasping, leaping, and an enhanced visual system has long been thought to relate in part to arboreality (24), although substrate preferences of our earliest primate ancestors have been less clear. Certain features of euprimates, such as grasping hands and feet, already had evolved to various degrees among plesiadapiforms (15, 20, 23, 25–28). Nearly all plesiadapiform species are known only from fossil dentitions, and the several known partial skeletons belong to fairly derived and relatively late-occurring members of their respective clades (23). Based on ecological inferences from the shape of the skull and teeth, it has been suggested that arboreality and herbivory evolved independently in plesiadapiforms and euprimates following their divergence from a ground-dwelling, insectivorous ancestor (29). However, tarsals of *Purgatorius* reported here indicate instead that arboreality was characteristic of the oldest and most primitive known stem primate. *Purgatorius* is more primitive than other plesiadapiforms and euprimates in retaining three lower incisors, four lower premolars, and molars with taller trigonids and more acute cusps that likely reflect an omnivorous diet that included a large proportion of insects (3, 13). Like the dentition (3, 4), the tarsals of *Purgatorius* reflect a plesiomorphic state that is sufficiently primitive to have given rise to the more derived morphologies present in all later primates.

The major radiation of angiosperms in the Late Cretaceous continued throughout the earliest Paleocene and dominated megaflores in the North American western interior (30, 31). Within this context, the immigration of *Purgatorius* represents the infusion of a unique arboreal mammal into North America during the first million years following the K–Pg boundary (32). Increased size of seeds and fruits is correlated with increases in the proportions of animal-dispersed taxa during this time (33) and would have provided an arboreal and omnivorous primate such as *Purgatorius* with angiosperm products including fruits, flowers, and associated insect pollinators (15, 34–36). Therefore, the postcranial specializations for arboreality documented in *Purgatorius* would have allowed this animal to access resources that were not directly available to many contemporary terrestrial mammals, such as *Protungulatum*. The fossil record provides a direct test to evaluate adaptive scenarios, however incremental (8), and future recovery and analysis of early euarchontan fossils will continue to improve our understanding of primate origins. The previously unidentified fossils of *Purgatorius* described here suggest that the divergence of primates from other mammals was not a dramatic event. Instead, the beginning of primate evolutionary history likely involved subtle changes in the postcranial skeleton that allowed easier navigation and improved access to food resources in an arboreal setting.

Materials and Methods

Regression Analysis. To assess whether tarsals described here (SI Appendix, Table S1) are of a size consistent with their attribution to the *Purgatorius* dental sample from the Garbani Channel fauna (SI Appendix, Fig. S1), least squares linear regression analyses were run in Microsoft Excel to evaluate the scaling relationship between the natural log area of the second lower

molar and astragalar tibial trochlea width, as well as between the natural log second lower molar area and calcaneal cuboid facet area for euarchontan mammals. Skeletal elements from a sample of 60 dentally associated skeletons of euarchontans including extant taxa and fossil plesiadapiforms were microCT scanned, and digital reconstructions were measured using Avizo 6 software (SI Appendix, Table S2). The 95% confidence limits on the prediction interval of tooth size from postcranial element dimensions were generated using equation 17.29 of ref. 37. Dimensions from isolated tarsals and teeth of *Purgatorius* (SI Appendix, Table S3) then were plotted on the resulting regression equations (SI Appendix, Fig. S2).

Principal Component Analysis. To evaluate our qualitative observations that the tarsals attributed to *Purgatorius* are generally similar to those of euarchontan mammals and are specifically similar to those of plesiadapiforms, we ran principal component analysis on the correlation matrix derived from 18 linear and 5 angular astragalar measurements (SI Appendix, Fig. S3A) following ref. 38 for 48 individuals representing 34 species (SI Appendix, Table S4) and 19 linear and 6 angular calcaneal measurements (SI Appendix, Fig. S3B) following ref. 39 for 54 individuals representing 33 species (SI Appendix, Table S5). Additionally, we ran a cluster analysis using the correlation matrix as our similarity metric and using the paired group method for linking cases. All analyses were run using PAST v. 2.16 (40). All linear measurements were size-standardized using the geometric mean of a subset of the measures. Angular measurements are reported in degrees but were analyzed in radians. The expanded taxonomic sample includes Puercan mammals, fossil plesiadapiforms and euprimates, and extant euarchontans (SI Appendix, Tables S4 and S5). All tarsals were microCT scanned, and digital reconstructions were created and measured using Avizo 6 software. Eigenvalue, percentage variance, and variable component loadings were recorded for each principal component (SI Appendix, Tables S6 and S7).

Phylogenetic Analysis. Cladistic analysis using maximum parsimony was performed in TNT (41) on three revised character matrices (12, 15, 16). Four plesiadapiforms, one colugo, and new *Purgatorius* tarsal data were added to the character matrix of ref. 12, and new *Purgatorius* tarsal data were added to the character matrices of refs. 15 and 16. In all analyses, New Technology Search was used to obtain the stabilized consensus five times, and resulting most parsimonious trees (MPTs) were used as starting trees in a Traditional Heuristic Search that was carried out using tree bisection reconnection (TBR). All resulting MPTs were used to obtain a strict consensus, and, following the methods of ref. 12, the Pruned Trees function was used to identify the least stable taxa, which were removed using the Prune Taxa function if large polytomies were present. The Tree Filter function was used to delete longer trees and duplicate MPTs. Bremer branch supports were calculated using the Traditional Search option (10 replicates per run with TBR enforced) from 50,000 suboptimal trees up to 10 steps longer than the most parsimonious tree. See SI Appendix for more detailed methodology, list of specimens analyzed, and specific modifications to character matrices (SI Appendix, Tables S8–S10).

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