SEE COMMENTARY

Late Middle Eocene primate from Myanmar and the initial anthropoid colonization of Africa

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Reconstructing the origin and early evolutionary history of anthropoid primates (monkeys, apes, and humans) is a current focus of paleoprimatology. Although earlier hypotheses frequently supported an African origin for anthropoids, recent discoveries of older and phylogenetically more basal fossils in China and Myanmar indicate that the group originated in Asia. Given the Oligocene-Recent history of African anthropoids, the colonization of Africa by early anthropoids hailing from Asia was a decisive event in primate evolution. However, the fossil record has so far failed to constrain the nature and timing of this pivotal event. Here we describe a fossil primate from the late middle Eocene Pondaung Formation of Myanmar, *Afrasia djijidae* gen. et sp. nov., that is remarkably similar to, yet dentally more primitive than, the roughly contemporaneous North African anthropoid *Afrotarsius*. Phylogenetic analysis suggests that *Afrasia* and *Afrotarsius* are sister taxa within a basal anthropoid clade designated as the infraorder Eosimiiformes. Current knowledge of eosimiiform relationships and their distribution through space and time suggests that members of this clade dispersed from Asia to Africa sometime during the middle Eocene, shortly before their first appearance in the African fossil record. Crown anthropoids and their nearest fossil relatives do not appear to be specially related to *Afrotarsius*, suggesting one or more additional episodes of dispersal from Asia to Africa. Hystricognathous rodents, anthracotheres, and possibly other Asian mammal groups seem to have colonized Africa at roughly the same time or shortly after anthropoids gained their first toehold there.

Afrotarsiidae | Eosimiidae | phylogeny | paleobiogeography

The fossil record of early Asian anthropoids has improved rapidly during the last 20 y (1–8). They are currently represented by two different groups, which are usually classified in the families Eosimiidae and Amphipithecidae. Eosimiids are widely considered to be the most basal clade of Anthropoidea currently known (1, 2, 4, 6, 9, 10). The affinities of amphipithecids remain a matter of debate, but most researchers agree that they are more closely related to crown anthropoids than they are to eosimiids (8). Eosimiids appear to be a monophyletic group whose distribution, until recently, was thought to be restricted to China and adjacent parts of southern Asia, with documented records in Myanmar and Pakistan (1, 2, 4, 6, 7). They are best-documented during the middle Eocene of China, where they are currently represented by two genera (*Eosimias* and *Phenacopithecus*) and six species (6). Eosimiids share a unique combination of primitive and derived characters, and all eosimiids discovered to date retain a small body size. Large-scale phylogenetic analyses have consistently identified eosimiids as stem anthropoids (7–11). Only one eosimiid, *Bahinia pondaungensis*, has been reported from the late middle Eocene Pondaung Formation of Myanmar (4). *Bahinia* is larger and morphologically more derived than known Chinese eosimiids, and its molar morphology bridges the gap between the more primitive molars of *Eosimias* and those of later Eocene African anthropoids. The basal anthropoid described here was recovered from the same rock unit as *Bahinia*, but is more similar in size and general morphology to Chinese middle Eocene eosimiids than it is to *Bahinia*. This taxon appears to hold great biogeographic interest, because it is very similar in age, size, and morphology to the early North African anthropoid *Afrotarsius libycus* (Fig. 1), suggesting that *Afrotarsius* is more closely related to the Asian eosimiid radiation than was previously believed (12). This establishes a tight morphological and temporal connection between the early anthropoid faunas of Asia and Africa.

The beginning of anthropoid history in Africa continues to be debated. However, decisive progress has recently been achieved in understanding some of the earliest purported African anthropoids. *Algeripithecus*, which was originally described on the basis of two isolated molars as an early middle Eocene African anthropoid (13), is now recognized as a strepsirrhine, following the discovery of more nearly complete material (14). Other African fossil sites that are older than late middle Eocene, such as the Chambi locality in Tunisia, have so far yielded only strepsirrhine primates (15).

Perhaps the most enigmatic fossil primate currently known from the early Cenozoic of Africa is *Altiatlasius*, from the latest Paleocene of southern Morocco. *Altiatlasius* was initially described as an omomyid (16), but has sometimes been regarded as a very basal anthropoid on the basis of scant morphological evidence (10, 17, 18). The anatomy of *Altiatlasius* remains poorly documented, and the very primitive structure of the teeth that have been assigned to this taxon leave multiple phylogenetic interpretations open, including the possibility that it could be related to toliapinid plesiadapiforms (19). Until more nearly complete and phylogenetically diagnostic specimens of *Altiatlasius* are recovered, its affinities will remain nebulous.

The oldest undoubted African anthropoids come from three late middle Eocene sites located in Algeria, Libya, and Egypt (10, 12, 20). The most diverse of these early African anthropoid faunas comes from the Dur At-Talah escarpment in central Libya, which appears to date to 38–39 Ma on the basis of magnetostratigraphic,

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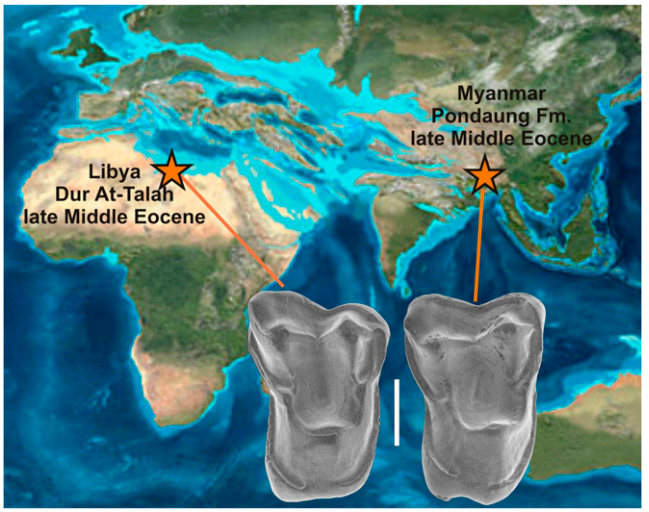

Fig. 1. Striking morphological resemblance between the right upper molars (M^2) of the Asian eosimiiform *Afrasia djijidae* and the contemporaneous African eosimiiform *Afrotarsius libycus* supports an Asia-to-Africa anthropoid dispersal during the middle Eocene. The regions where the two taxa were discovered are positioned on a paleogeographic map of the Old World during the late Eocene (35 Ma) drawn by Ron Blakey (http://www2.nau.edu/rcb7). (Scale bar, 1 mm.)

biostratigraphic, and geological data (12, 21). In addition to *Afrotarsius libycus*, the Dur At-Talah anthropoid fauna also includes the parapithecid *Biretia* (which is also known from penecontemporaneous sites in Algeria and Egypt) and the oligopithecid *Talahpithecus*. Although the late middle Eocene anthropoids from Dur At-Talah are already remarkably diversified, they all retain very small body size. The phylogenetically most problematic anthropoid known from Dur At-Talah, *Afrotarsius libycus*, shares striking dental resemblances with the primate from the Pondaung Formation in Myanmar described here.

Results

Systematic Paleontology. Class Mammalia Linnaeus, 1758; Cohort Placentalia Owen, 1837; Order Primates Linnaeus, 1758; Suborder Anthropoidea Mivart, 1864; Infraorder Eosimiiformes, nov. Family Afrotarsiidae Ginsburg and Mein, 1987; *Afrasia*, gen. nov.

Type Species. *Afrasia djijidae*, gen. et sp. nov.

Etymology. From the intercontinental distribution of eosimiiform primates.

Diagnosis. Small eosimiiform with upper molars nearly identical in size and morphology to those of *Afrotarsius*. Upper molars differ from those of *Afrotarsius* in having slightly more prominent parastyle located farther buccally relative to the paracone. Lower molars differ from those of *Afrotarsius* in having more nearly vertical and cuspidate paraconid that is more lingual in position, slightly reduced entoconid shifted mesially with respect to hypoconid, and less reduced hypoconulid lobe on M_3. Differs from *Eosimias* in having upper molars that are less transverse with wider protocone, smaller parastyle, less extended stylar shelf, and slightly better developed conules, and having lower molars with cristid obliqua joining postvallid farther buccally, stronger and more distal entoconid, more expanded talonid basin, and less reduced hypoconulid lobe on M_3. Smaller than *Phenacopithecus* and *Bahinia*. Further differs from *Phenacopithecus* in having less waisted upper molars with weaker lingual cingulum and M_3 with relatively smaller trigonid. Further differs from *Bahinia* in having upper molars with less bunodont cusps, more extensive stylar shelf, less-developed lingual cingulum, larger trigon basin, stronger conules, and better-developed postmetaconule crista; lower molars with more acute and more nearly vertical cusps and stronger paraconids. Differs from *Phileosimias* by its smaller size, more acute cusps on the upper and lower molars, more reduced conules, more expanded stylar shelf, and less reduced M_3 talonid.

Afrasia djijidae, sp. nov.

Etymology. Specific name in memory of a young girl from Mogaung village, central Myanmar.

Holotype. NMMP-81, a right M^2 (Fig. 2*A*).

Hypodigm. NMMP-79, a right M_2 (Fig. 2 *C–E*); NMMP-77, a right M_3 (Fig. 2 *F* and *G*); NMMP-85, a right M^1 (Fig. 2*B*).

Type Locality. Nyaungpinle Locality, near Nyaungpinle village, Myaing Township.

Age and Distribution. Late middle Eocene Pondaung Formation, central Myanmar. Dated at ~37 Ma by magnetostratigraphy (22) and fission-track dating (23).

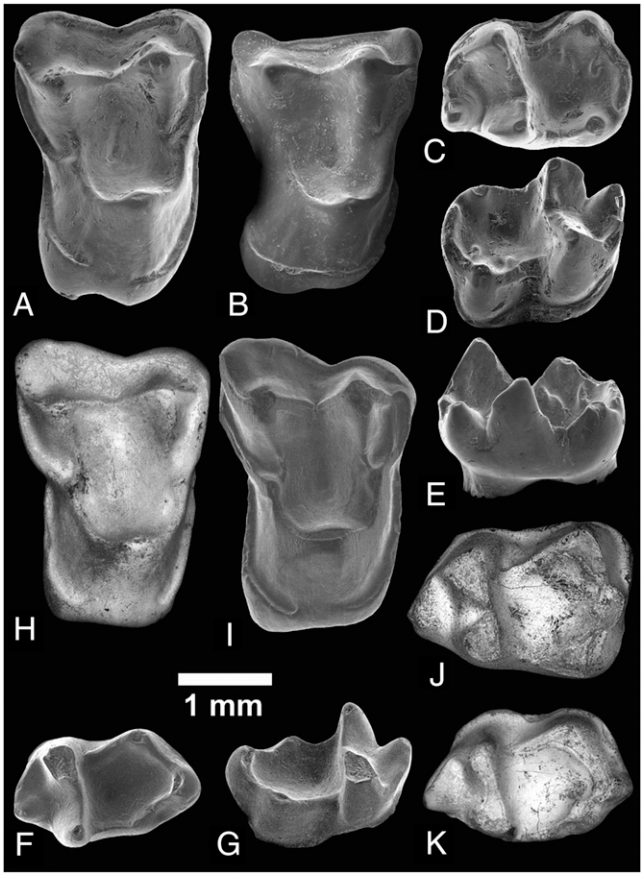

Fig. 2. SEM images of the teeth of *Afrasia djijidae* gen. et sp. nov. (*A–G*) from the Pondaung Formation (Myanmar) and *Afrotarsius libycus* (*H–K*) from Dur At-Talah (Libya). (*A*) Right M^2 (NMMP-81) (holotype) in occlusal view. (*B*) Right M^1 (NMMP-85) in occlusal view. (*C–E*) Right M_2 (NMMP-79) in occlusal (*C*), oblique buccal (*D*), and lingual (*E*) views. (*F* and *G*) Right M_3 (NMMP-77) in occlusal (*F*) and oblique buccal (*G*) views. (*H*) Left M^2 (DT1-33) in occlusal view (mirror image). (*I*) Right M^2 (DT1-34) in occlusal view. (*J*) Left M_2 (DT1-35) (holotype) in occlusal view (mirror image). (*K*) Right M_3 (DT1-36) in occlusal view. (*H–K* pictures are from ref. 12.)

Diagnosis. As for the genus.

Description. *Afrasia* is a small-sized anthropoid (Table 1) with an estimated body weight of 108 g on the basis of M_2 length and 94 g on the basis of M^1 area using the formulae of Bajpai et al. (24). These body-weight estimates are similar to those obtained for *Eosimias centennicus* by these authors (105 and 88 g, respectively). The known dentition of *Afrasia* generally resembles that of other eosimiiforms, although *Afrasia* is distinctive in having relatively well developed upper-molar conules that give rise to pre- and postconule cristae, variably complete lingual cingula on its upper molars, and a relatively unreduced M_3 talonid. Most notably, the dental morphology of *Afrasia* closely resembles that of *Afrotarsius*, a North African taxon whose affinities have previously been disputed.

The holotype M^2 (Fig. 2*A*) displays a typical eosimiiform morphology that is generally intermediate between that of *Eosimias* and *Bahinia*. Conules are well-expressed and pre- and postconule cristae are well-developed. The stylar shelf is strong and particularly buccal to the metacone, whereas the lingual cingulum is moderately developed and incomplete. Size and most of the morphological characters of the holotype M^2 are identical to those of *Afrotarsius libycus* (Fig. 2 *H* and *I*). Only the location of the parastyle and the mesial development of the stylar shelf distinguish the M^2 of these Asian and African taxa. The parastyle is located more buccally in *Afrasia* than it is in *Afrotarsius*, in which it is located more mesially. The stylar shelf buccal to the paracone is also slightly more extensive in *Afrasia*, yielding a more nearly symmetrical and acutely invaginated ectoflexus than occurs on M^2 in *Afrotarsius*.

M^1 (Fig. 2*B*) is similar to M^2 and differs only by its smaller size, less-invaginated ectoflexus, absence of a distinct postmetaconule crista, and occurrence of a continuous lingual cingulum. Its parastylar area is more rectangular and therefore even more similar to that of M^2 in *Afrotarsius libycus*. Its stylar shelf is narrower, especially buccal to the metacone, than that of M^2 in either the holotype of *Afrasia djijidae* or that of *Afrotarsius libycus*.

M_2 (Fig. 2 *C*–*E*) is identified as to locus on the basis of its trigonid morphology. The three trigonid cusps are discrete, poorly inflated basally, and rather vertical. The paraconid is clearly differentiated from the paracristid, and it occupies a lingual position. However, the trigonid basin is not closed, being open lingually by a deep but narrow valley. In occlusal view, the surface area of the trigonid is quite large compared with the talonid. The metaconid is cuspidate and widely separated from the protoconid. The protocristid is transversely oriented, with a V-shaped profile. The talonid is wider than the trigonid, and the cuspidate entoconid is located directly opposite the larger hypoconid. The hypoconulid is indistinct, being incorporated within the arcuate postcristid, which is separated from the entoconid by a shallow notch. The cristid obliqua is less obliquely oriented than that of *Eosimias*, joining the postvallid near the base of the protoconid. A moderately developed cingulid surrounds the buccal side of the crown. In contrast to those of *Afrotarsius libycus* (Fig. 2*J*), the M_2 trigonid cusps in *Afrasia* are more discrete, being more widely separated at their bases, and the paraconid occupies a more lingual position. The small notch separating the postcristid from the entoconid is absent in *Afrotarsius*, as is the case in most other eosimiiforms, but this feature is also present in *Phileosimias*. The M_2 of *Eosimias* has a narrower talonid and a more obliquely oriented cristid obliqua. Several characters of the M_2 of *Afrasia djijidae* are reminiscent of those of *Phenacopithecus*. However, in the latter Chinese taxon, the cristid obliqua is more obliquely oriented, the entoconid is more mesial in position, and there is no notch separating the postcristid from the entoconid.

M_3 (Fig. 2 *F* and *G*) is characterized by its reduced size versus the anterior molars and by its rather long talonid basin and unreduced hypoconulid lobe. The paraconid is salient and slightly inclined mesially. In its general proportions, M_3 of *Afrasia* more closely resembles that of *Phenacopithecus* than that of other eosimiiforms. It differs from M_3 of *Afrotarsius libycus* (Fig. 2*K*) in having a more elongated hypoconulid lobe and in the relatively mesial position of the entoconid, which is quite distant from the hypoconulid due to the stronger development of its distal lobe. There is a valley between hypoconulid and entoconid but no notch as occurs on M_2.

Eosimias paukkaungensis (25) is documented by an M_3 on a lower jaw fragment and one edentulous lower jaw fragment from the Paukkaung Kyitchaung 2 locality in the Pondaung Formation (25). The size and morphology of M_3 in the holotype of *E. paukkaungensis* are appropriate to pertain to *Bahinia pondaungensis*, particularly with respect to the lingual closure of its trigonid and the relatively central position of its paraconid. Accordingly, we regard *E. paukkaungensis* as a junior subjective synonym of *B. pondaungensis*.

Other taxa can also be compared with *Afrasia*. *Anthrasimias* from the early Eocene of India has been suggested to represent the oldest Asian anthropoid (24). However, the dental characters expected in an eosimiid ancestor differ from those described for *Anthrasimias*. Its upper molars are wide mesiodistally, instead of being transversely elongated like those of eosimiids. Additionally, its stylar shelf is reduced instead of being expansive, its M^1 has an incipient hypocone, and its lower-molar paraconid is crestiform instead of being cuspidate. Because of these important differences from those that would be expected in an early eosimiid, we agree with Rose et al. (26) that *Anthrasimias* is probably an early adapiform.

Similar differences can be cited with *Altiatlasius koulchii* from the late Paleocene of Morocco, at least for its upper molars. In addition, the absence of any connection between the postparaconule crista and premetaconule crista and the main labial cusps in *A. koulchii* represents an additional important difference. The lower molars of *Afrasia* and *Altiatlasius* are fairly similar in general morphology, but the M_3 of *Altiatlasius* remains unknown, limiting the scope of comparisons that can be made between these taxa. Clearly, further material of *Altiatlasius* must be recovered to establish the phylogenetic affinities of this critical fossil.

Table 1. Dental measurements of *Afrasia djijidae* gen. et sp. nov. from several sites of the Pondaung Formation

Specimen	Site	Tooth	MD length (mm)	BL length (mm)
NMMP-81	Nyaungpinle	M^2	2.27	3.35
NMMP-85	Thamingyauk	M^1	2.13	3.06
NMMP-79	Paukkaung Kyitchaung 2	M_2	2.09	1.41
NMMP-77	Nyaungpinle	M_3	2.05	1.27

BL, buccolingual; MD, mesiodistal.

Phylogenetic Analysis. A phylogenetic analysis based on 316 dental, cranial, and postcranial characters (*SI Appendix*) was performed to assess the phylogenetic position of *Afrasia djijidae* and *Afrotarsius libycus*. The data matrix used for this analysis is a simplified version of that of Beard et al. (8), augmented by sampling *Afrasia djijidae* and *Afrotarsius libycus* (*SI Appendix*).

The ingroup includes *Afrasia*, *Afrotarsius*, and 23 selected representatives of the main groups of haplorhines (omomyids, tarsiids, and anthropoids) with sufficiently known morphology (*SI Appendix*). Tarsiids (*Tarsius* and *Xanthorhysis*) were included to test the controversial affinities of *Afrotarsius*, phylogenetic proximity of *Afrotarsius* with tarsiids having been suggested by previous phylogenetic analyses (9, 10, 27) but recently

questioned (12). All of the ingroup taxa are Paleogene with the exception of the early Neogene platyrrhine *Dolichocebus* and the extant *Tarsius*. The Paleogene strepsirrhines *Cantius*, *Adapis*, and *Leptadapis* served as outgroups.

The analysis, run in PAUP 4b10 (28), yielded a single most-parsimonious tree (Fig. 3). In the most-parsimonious tree topology, *Afrotarsius libycus* is not allied with tarsiids, instead being reconstructed as the sister group of *Afrasia djijidae* within the anthropoid clade (node A in Fig. 3). The basal anthropoid affinities for *Afrotarsius* that are advocated here apparently reflect the typically eosimiiform upper-molar morphology recently documented for *Afrotarsius libycus* (12). The lower-molar morphology of *Afrotarsius*, which is all that was known before the discovery of *Afrotarsius libycus*, appears to be phylogenetically less diagnostic because of the convergent acquisition of trenchant cusps and crests as an adaptation for insectivory in both *Afrotarsius* and tarsiids (12). Given the fragmentary nature of the relevant fossils, the *Afrasia* + *Afrotarsius* clade, considered here as the family Afrotarsiidae, is upheld by a surprisingly high level of bootstrap support and a robust Bremer index. Its sister group is an exclusively Asian clade, the Eosimiidae (*Eosimias*, *Phenacopithecus*, and *Bahinia*). Eosimiids and afrotarsiids together comprise a monophyletic group that we designate as the infraorder Eosimiiformes, which constitutes the sister group of all other living and fossil anthropoids. Asian amphipithecids are not closely related to eosimiiforms, being reconstructed as the sister group of a propliopithecid + oligopithecid (i.e., catarrhine) clade, albeit with only weak support in terms of bootstrap values and Bremer index. This result generally agrees with other recent analyses of higher-level primate phylogenetics, in which amphipithecids are reconstructed as either the sister group of the crown anthropoid clade (7, 10) or as being nested within it (8, 11). Hence, although our tree suggests that amphipithecids are more closely related to crown anthropoids than they are to eosimiiforms, there is no current consensus on precisely how amphipithecids are related to catarrhines and platyrrhines. Two other African stem anthropoid families, parapithecids and proteopithecids, are reconstructed as sister taxa, in agreement with several previous analyses (e.g., 7, 9, 27).

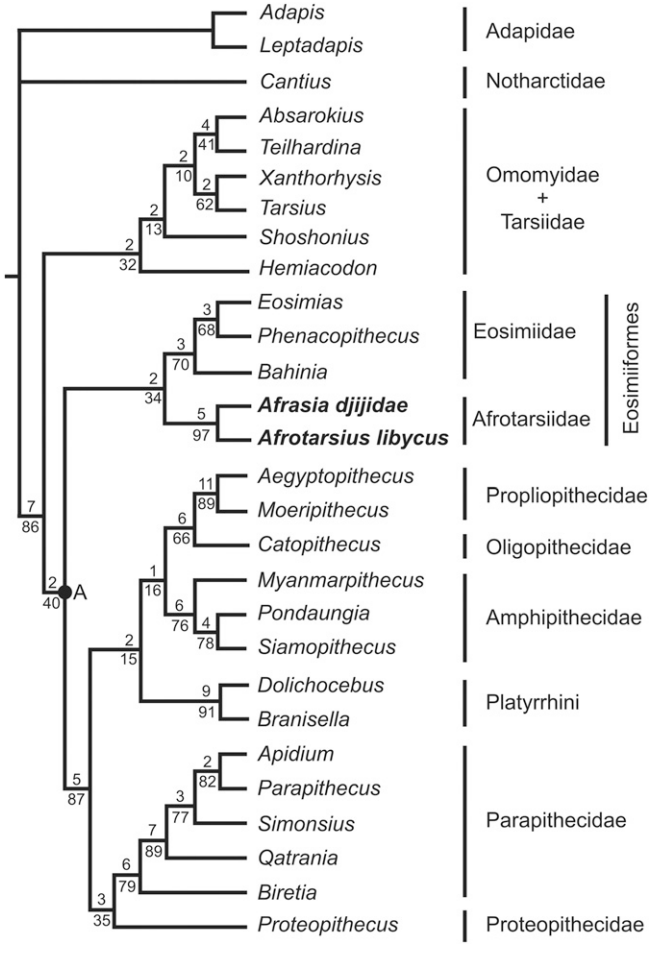

Fig. 3. Cladogram illustrating the phylogenetic positions of *Afrasia djijidae* and *Afrotarsius libycus* within Paleogene anthropoids. Tree length = 1,071 steps; consistency index = 0.422; retention index = 0.534; rescaled consistency index = 0.226. The node lettered A indicates the anthropoid clade. Values above the branches are Bremer indices; values below the branches are bootstrap support (1,000 replications).

Discussion

Afrasia djijidae is a very rare species, currently represented by only four isolated teeth that were recovered during the course of six field seasons by wet-screening several tons of fossiliferous sediment from the Pondaung Formation. Despite the meager sample of *Afrasia* that is now available, this taxon is remarkable in having upper molars that are nearly identical to those of North African *Afrotarsius*. Such close morphological correspondence in early Asian and African anthropoids having the same body size and being more or less contemporaneous in age forges a phylogenetic and biogeographic connection between the eosimiiforms inhabiting Asia and Africa during the middle Eocene. Although the upper molars of *Afrasia* and *Afrotarsius* are tritubercular and therefore relatively primitive, certain details of upper-molar morphology are clearly derived in these animals. For example, the presence of variably developed crests running lingually from the paracone and metacone toward their respective conules (hypoparacrista and hypometacrista, respectively) distinguishes *Afrasia* and *Afrotarsius* from omomyids, *Altiatlasius*, and adapiforms, all of which retain the primitive primate condition in which these upper-molar crests are lacking.

The tight morphological and temporal correspondence between *Afrasia* and *Afrotarsius* suggests that afrotarsiid anthropoids colonized Africa by dispersing across the Tethys Sea (Fig. 1) sometime during the middle Eocene, only shortly before the first appearance of *Afrotarsius* in the African fossil record. Our estimate of the timing of this dispersal event is based on the strong morphological similarity between *Afrasia* and *Afrotarsius*. If afrotarsiid dispersal had occurred significantly earlier (e.g., during the early Eocene), we would expect greater morphological divergence between *Afrasia* and *Afrotarsius*. Dispersal of afrotarsiids from Asia to Africa (rather than vice versa) is favored because of the hierarchically nested phylogenetic position of *Afrotarsius* within the eosimiiform radiation, which is otherwise an exclusively Asian clade (Fig. 3). This interpretation is also consistent with the prevailing view that the origin of the anthropoid clade, defined as the dichotomy between the anthropoid and tarsier lineages, occurred in Asia (1, 2, 4, 6, 9, 10, 17).

The simplest biogeographic hypothesis that can account for the anthropoid colonization of Africa entails a single successful colonist, such as *Afrotarsius*, dispersing across the Tethyan marine barrier before producing a monophyletic radiation of endemic African anthropoids. However, our current understanding of the evolutionary relationships among early African and Asian anthropoids indicates that the true picture is more complicated. Crown anthropoids and their closest fossil relatives, including African Proteopithecidae and Parapithecidae, appear to be only distantly related to eosimiiforms such as *Afrasia* and *Afrotarsius*. Likewise, Asian amphipithecids appear to be members of this broad assemblage of "higher" anthropoids (7, 8, 10, 11). During the late middle Eocene in both Africa and Asia, eosimiiform anthropoids co-occurred with higher anthropoids (parapithecids and oligopithecids in the case of the Dur At-Talah fauna from

Libya; amphipithecids in the case of the Pondaung fauna from Myanmar). These data suggest that the colonization of Africa by early Asian anthropoids could have involved several clades—an eosimiiform clade that gave rise to *Afrotarsius* and at least one higher anthropoid clade that included the ancestors of Proteopithecidae, Parapithecidae, and crown anthropoids. Both of these clades must have colonized Africa before the late middle Eocene, as demonstrated by the presence of both clades in the Dur At-Talah fauna from central Libya (12). A less likely alternative is that Africa was colonized by a single eosimiiform clade well before the late middle Eocene, providing enough time for the diversity of anthropoids found in the Libyan Dur At-Talah fauna to evolve in situ in Africa.

Three important challenges remain concerning the origin and early evolution of African anthropoids. The first is to achieve tighter constraints on the timing of the initial colonization of Africa by Asian anthropoids, along with the paleogeographic and geodynamic context of this crucial dispersal event. The middle Eocene climate optimum, dated at ~40 Ma (29), is an intriguing candidate to test in this regard, because many intercontinental land mammal exchanges are known to have occurred then, both in North America (1, 30–33) and Europe (34–37). A second challenge is to understand the full taxonomic scope of this intercontinental range extension from Asia to Africa by clarifying the other taxa (in addition to anthropoids, hystricognathous rodents, and anthracotheres) that were involved in this dispersal event. A third challenge is to establish whether eosimiiforms were the only Asian anthropoid primates to disperse to Africa during the early Cenozoic or whether several distinct Asian anthropoid lineages colonized Africa independently. If multiple Asian anthropoid clades colonized Africa, did colonization take place synchronously or in a temporally staggered fashion? Finally, it must be noted that two of the Asian mammal clades (anthropoid primates and hystricognathous rodents) that successfully colonized Africa during the early Cenozoic were able to continue their pattern of intercontinental dispersal across the South Atlantic to invade South America. Recent paleontological discoveries in Peru indicate that (at least) hystricognathous rodents achieved this feat remarkably early, during the middle Eocene (38). It is highly probable that platyrrhine primates followed the same dispersal pathway, but their South American fossil record does not begin until the late Oligocene (39, 40). Therefore, the middle Eocene appears to be a critical interval for the intercontinental dispersal of land mammals, meriting additional fieldwork on all southern continents.

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