Evidence for an Asian origin of stem anthropoids

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In PNAS, Chaimanee et al. (1) report a previously undescribed species of primate, *Afrasia,* from the late Middle Eocene of Burma. They identify *Afrasia* as the sister taxon to the African genus *Afrotarsius* but slightly more primitive than it and allied with stem Anthropoidea of south Asia. Anthropoidea is the taxonomic group that today includes New and Old World monkeys, apes, and humans. If upheld, the biogeographic significance of these results is profound: If *Afrasia* and *Afrotarsius* are as closely related as Chaimanee et al. (1) propose, there must have been a late Middle Eocene geographic connection between the primate faunas of Asia and Africa. Further support for intercontinental connections between south Asia and Africa is found among other contemporaneous mammalian groups, including anomaluroid and hystricognathous rodents (2). More provocatively, Chaimanee et al. (1) consider the south Asian late Middle Eocene family Amphipithecidae to be a stem catarrhine clade and suggest that Catarrhini (the group of Old World anthropoids) also originated in south Asia and dispersed to Africa.

A review of fossil evidence lends credence to the phylogenetic and biogeographic scenario of Chaimanee et al. (1). At the same time, it must be acknowledged that gaps in the Paleogene primate fossil record of south Asia and Africa allow for other plausible interpretations. Support for their scenario is not made any stronger by the fact that *Afrasia djijidae* and *Afrotarsius libycus* are known only from a few cheek teeth. For that matter, key anatomical evidence is lacking or incomplete for other Asian stem anthropoids (e.g., in the structure of the posterior wall of the orbit and middle ear) that would make their anthropoid status more certain.

Challenges of Early Anthropoid Phylogeny

The earliest undisputed anthropoids, Proteopithecidae, Parapithecidae, Oligopithecidae, and Propliopithecidae, come from the later Eocene and Early Oligocene of North Africa. They had nearly all the anatomical hallmarks of extant anthropoids, especially resembling living New World monkeys in size, morphology, and reconstructions of their behavior, being frugivorous above-branch arboreal quadrupeds that were highly social and daytime-active with significant reliance on the sense of vision (3–5).

Genetic, embryological, and anatomical evidence demonstrates that the sister group of Anthropoidea is the south Asian tarsier, with the two forming the crown group Haplorhini (6–8). The other clade of extant primates is the lemurs and lorises, called Strepsirrhini. Eocene Holarctic Omomyoidea are generally considered as stem haplorhines, although the precise relationship of omomyoids to tarsiers and anthropoids is uncertain (8). *Tarsius* often is considered to be a relictual omomyoid in south Asia.

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It is generally held that stem anthropoids arose in Asia and that one or several anthropoid groups later migrated to Africa sometime in the Middle or Late Eocene (9). The weight of current fossil evidence supports this Asian origin hypothesis. The earliest member of the tarsier family (Tarsiidae) come from the Middle Eocene of Asia at about 45 Ma (*Xanthorhysis)* (10). Although African late Middle Eocene and Early Oligocene *Afrotarsius* is said by some to be a tarsioid (11, 12), others conclude that is an early anthropoid (13, 14). Stem anthropoids called Eosimiidae first appear in the Asian Middle Eocene at ~45 Ma, and larger-bodied late Middle Eocene Amphipithecidae also are Asian anthropoids and even possibly stem catarrhines (15, 16). Although there are some hints, there is no convincing evidence for the existence of anthropoids in Africa before the late Middle Eocene, ~38 Ma. However, does the (debated) restriction of tarsioids to Asia and the finding that eosimiids first appear in the Middle Eocene of Asia, and only later in Africa, indicate an Asian origin for stem Anthropoidea? Likewise, are amphipithecids stem catarrhines, and if so, did catarrhines have an Asian origin as well?

To evaluate these biogeographic hypotheses, we must first have a highly resolved phylogeny of Eocene primates. We are not there yet. Recent comprehensive phylogenetic analyses stemming from virtually the same datasets yield somewhat different cladograms that reflect sensitivity to which taxa are included in the analysis and which sets of analytical assumptions are selected. Pertinent to the biogeographic conclusions of Chaimanee et al. (1), Seiffert et al. (11) conclude that *Afrotarsius chatrathi* [a younger species than the one that Chaimanee et al. (1) describe] is an African tarsioid. If Seiffert et al. (11) are correct, *Afrasia* could be a tarsier relative, and it may be that *Afrasia* documents a dispersal of Asian tarsioids to Africa. Topologies are unstable at the basal nodes of these phylogenetic trees, as indicated by a Bremer support of one or two steps at key nodes of the reconstructed clades (Bremer support is the number of extra steps needed to construct a tree where that clade is no longer present).

The phylogenetic position of later Eocene amphipithecids of Asia also is the subject of considerable debate. Mandibular and dental similarities (17) as well as the structure of an isolated talus (18) suggest amphipithecids are anthropoids. Others allocate a strepsirrhine-like calcaneus and humerus from Burmese sites to amphipithecids and conclude that amphipithecids are strepsirrhines (19). Even accepting the specimen allocations (I do) of Chaimanee et al. (1), the Bremer support for a stem catarrhine placement of amphipithecids is very weak, which perhaps explains why the family has variously been identified as stem anthropoids (11, 20) or placed in an unresolved trichotomy with platyrrhines and catarrhines (16). In any case, in figure 3 in ref. 1, amphipithecids are nested within an otherwise African clade consisting of oligopithecids, propliopithecids, parapithecids, and proteopithecids. Such a topology suggests that amphipithecids migrated out of Africa rather than into it. If catarrhines originated in Asia, their sister group, platyrrhines, must also have done so, which seems unlikely for geographic reasons.

Several other fragmentary fossil remains (isolated teeth) suggest a considerably deeper history for anthropoids in Africa or Asia. Some analyses support the hypothesis that *Altiatlasius* from the late

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See companion article on page 10293.
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Paleocene of North Africa is a stem anthropoid (11, 20, 21), whereas others consider it to be an omomyoid (22) or a plesiadapoid (23). Bajpai et al. (20) proposed that *Anthrasimias* from India is an eosimiid anthropoid extending the Asian fossil record of anthropoids back to the Early Eocene. However, Rose et al. (24) suggested that these isolated teeth could belong to the adapoid *Marcgodinotius*, although admitting that some of the characters of the hypodigm of *Anthrasimias* and also some isolated ankle bones from the same fossil site resemble eosimiids in some respects. Neither *Altiatlasius* nor *Anthrasimias* can be ruled out of contention as a stem anthropoid on the basis of geological age because the proposed date of cladogenesis between anthropoids and tarsiers was early Paleocene or even late Cretaceous (6, 25).

Biogeographic Hypotheses

An Asian origin for stem anthropoids is a plausible scenario based on the present paleontological evidence but is by no means certain. Whether anthropoid primates first differentiated in Africa or Asia remains uncertain because the fossil record of the Paleogene of south Asia and Africa is poorly known and because the Tethys seaway between the two continents was breached by many small mammals during the Paleogene. Irrespective of whether the afrotarsiids *Afrasia* and *Afrotarsius* are related to eosimiids or to tarsioids, the close correspondence between the two genera supports the conclusion that the two are sister taxa and indicates a cross-Tethian dispersal event in the late Middle Eocene. On the other hand, 20 or more million years may separate Asian Middle Eocene stem anthropoids from the date of the last common ancestor of anthropoids and tarsiers. In addition, if either *Altiatlasius* or *Anthrasimias* is a stem anthropoid, repeated primate trans-Tethian dispersal events could have occurred in either direction.

Finally, even if amphipithecids are catarrhines, an Asian origin for Catarrhini seems unlikely because they are nested within an otherwise African clade. Is it not more parsimonious to assume that amphipithecids, if they are catarrhines, had an African origin?

1. Chaimanee Y, et al. (2012) Late Middle Eocene primate from Myanmar and the initial anthropoid colonization of Africa. *Proc Natl Acad Sci USA* 109:10293–10297.
2. Jaeger J-J, et al. (2010) New rodent assemblages from the Eocene Dur At-Talah escarpment (Sahara of central Libya): Systematic, biochronological, and palaeobiogeographical implications. *Zool J Linn Soc* 160(1):195–213.
3. Kay RF, Simons EL (1980) The ecology of Oligocene African Anthropoidea. *Int J Primatol* 1(1):21–37.
4. Fleagle JG, Kay RF, Simons EL (1980) Sexual dimorphism in early anthropoids. *Nature* 287:328–330.
5. Kirk EC, Kay RF (2004) The evolution of high visual acuity in the Anthropoidea. *Anthropoid Origins: New Visions*, eds Ross CF, Kay RF (Kluwer/Plenum, New York), pp 539–602.
6. Perelman P, et al. (2011) A molecular phylogeny of living primates. *PLoS Genet* 7:e1001342.
7. Martin RD (1990) *Primate Origins and Evolution, a Phylogenetic Reconstruction* (Princeton Univ Press, Princeton).
8. Williams BA, Kay RF, Kirk EC (2010) New perspectives on anthropoid origins. *Proc Natl Acad Sci USA* 107: 4797–4804.
9. Beard KC (2002) Basal anthropoids. *The Primate Fossil Record*, ed Hartwig WC (Cambridge Univ Press, Cambridge, UK), pp 133–150.
10. Beard KC (1998) A new genus of Tarsiidae (Mammalia: Primates) from the middle Eocene of Shanxi Province, China, with notes on the historical biogeography of tarsiers. *Bulletin of the Carnegie Museum of Natural History* 34:260–277.
11. Seiffert ER, et al. (2005) Basal anthropoids from Egypt and the antiquity of Africa's higher primate radiation. *Science* 310:300–304.
12. Simons EL, Bown TM (1985) *Afrotarsius chatrathi*, first tarsiiform primate (?Tarsiidae) from Africa. *Nature* 313:475–477.
13. Jaeger J-J, et al. (2010) Late middle Eocene epoch of Libya yields earliest known radiation of African anthropoids. *Nature* 467:1095–1098.
14. Fleagle JG, Kay RF (1987) The phyletic position of the Parapithecidae. *J Hum Evol* 16:483–532.
15. Beard KC, Wang B, Dawson M, Huang X, Tong Y (1996) Earliest complete dentition of an anthropoid primate from the late middle Eocene of Shanxi Province, China. *Science* 272:82–85.
16. Beard KC, et al. (2009) A new primate from the Eocene Pondaung Formation of Myanmar and the monophyly of Burmese amphipithecids. *Proc Biol Sci* 276: 3285–3294.
17. Kay RF, Williams BA, Ross CF, Takai M, Shigehara N (2004) Anthropoid origins: a phylogenetic analysis. *Anthropoid Origins: New Visions*, eds Ross CF, Kay RF (Kluwer/, Plenum, New York), pp 91–135.
18. Marivaux L, et al. (2003) The anthropoid status of a primate from the late middle Eocene Pondaung Formation (Central Myanmar): Tarsal evidence. *Proc Natl Acad Sci USA* 100:13173–13178.
19. Ciochon RL, Gingerich PD, Gunnell GF, Simons EL (2001) Primate postcrania from the late middle Eocene of Myanmar. *Proc Natl Acad Sci USA* 98:7672–7677.
20. Bajpai S, et al. (2008) The oldest Asian record of Anthropoidea. *Proc Natl Acad Sci USA* 105:11093–11098.
21. Beard KC (2006) Mammalian biogeography and anthropoid origins. *Primate Biogeography*, eds Lehman SM, Fleagle JG (Springer, New York), pp 439–467.
22. Sigé B, Jaeger J-J, Sudre J, Vianey-Liaud M (1990) *Altiatlasius koulchii* n. gen. et sp., primate omomyidé du Paléocène supérieur du Moroc, et les origines des Euprimates. *Paleontographica* 212:1–24.
23. Hooker JJ, Russell DE, Phélizon A (1999) A new family of Plesiadapiformes (Mammalia) from the Old World lower Paleogene. *Palaeontology* 42:377–407.
24. Rose KD, et al. (2009) Early Eocene primates from Gujarat, India. *J Hum Evol* 56:366–404.
25. Steiper ME, Seiffert ER (2012) Evidence for a convergent slowdown in primate molecular rates and its implications for the timing of early primate evolution. *Proc Natl Acad Sci USA* 109:6006–6011.