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Out of Asia: Anthropoid Origins and the Colonization of Africa

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Abstract

Anthropoid primates other than humans show a conspicuously disjunct geographic distribution today, inhabiting mostly tropical and subtropical parts of Asia, Africa, and Central and South America. During the latter part of the Eocene, early anthropoids showed a similarly disjunct distribution, although South America and Africa were both island continents then. Attempts to explain the historical biogeography of anthropoids as resulting from vicariance caused by tectonic rifting between South America and Africa conflict with both the chronology and the topology of anthropoid evolution. The only viable hypotheses that remain entail sweepstakes dispersal across marine barriers by early monkeys on natural rafts. Early anthropoids and certain Asian rodent clades seem to have been especially adept at accomplishing sweepstakes dispersal, particularly during the Eocene, although this process has classically been envisioned as highly random and extremely rare. This article identifies and discusses biological and geological factors that make sweepstakes dispersal by certain taxa at given times far less random than previously conceived.

INTRODUCTION

The continuous nature of phylogeny—what Darwin called evolutionary descent with modification—means that closely related sister taxa must have originated in the same place and at the same time. This simple rule establishes tight phylogenetic constraints on attempts to reconstruct when and where higher taxa originated (Norell 1992, Beard 1998a). For many years, the taxon of immediate interest here—Anthropoidea, which includes living monkeys, apes, and humans along with their fossil relatives—was thought to have arisen in Africa, mainly on the basis of early fossil anthropoids that are particularly well documented on that continent (Fleagle & Kay 1987, Holroyd & Maas 1994, Simons 1995, Ciochon & Gunnell 2002, Miller et al. 2005). However, an African origin for Anthropoidea is incompatible with the geographic range of its sister taxon, which consists of extant tarsiers and their close fossil relatives (Beard 2004, 2006). Living tarsiers are restricted to offshore islands in Southeast Asia, and so far fossil tarsiiids are known only from the Asian mainland (Beard et al. 1994, Beard 1998b, Chaimanee et al. 2011, Zijlstra et al. 2013, Ni et al. 2016). The apparent conflict between the Asian distribution of living and fossil tarsiers and the African fossil record of early anthropoids has been reconciled over the past two decades by the discovery of older and phylogenetically basal anthropoid fossils in Asia (Beard et al. 1994, 1996, 2009; Chaimanee et al. 1997, 2012; Jaeger et al. 1999; Gebo et al. 2000; Takai et al. 2001). As a result, the hypothesis that anthropoids originated in Asia, once considered provocative and unlikely, now enjoys a broad consensus among specialists (Beard 2004; Kay et al. 2004; Marivaux et al. 2005a; Seiffert et al. 2005, 2009; Williams et al. 2010; Seiffert 2012).

The fairly recent recognition that anthropoids had to colonize Africa instead of simply originating there transforms how we must think about this aspect of primate evolution. Early African anthropoids should now be considered from the perspective of invasion biology (Vermeij 1996, Holway & Suarez 1999, Kolar & Lodge 2001). Following are pertinent questions: (*a*) When did anthropoids first arrive in Africa, and how did they get there? (*b*) Was the colonization of Africa by early anthropoids phylogenetically simple (i.e., monophyletic) or complicated (i.e., polyphyletic)? (*c*) Were early anthropoids the sole invaders of Africa at that time, or were they part of a larger cohort of alien colonists? (*d*) What impact, if any, did the colonization of Africa have on the subsequent evolution of the anthropoids themselves? And finally, (*e*) how did the colonization of Africa by early anthropoids affect the native mammalian fauna of that continent?

The issue of how early anthropoids initially colonized Africa is inherently linked to tectonic reconstructions of Earth's ancient geography. It is universally accepted that Asia and Africa shared no close geographic connection for most of the Mesozoic and Paleogene, each landmass having been major components of the former northern and southern supercontinents of Laurasia and Gondwana, respectively (Smith et al. 1994, Partridge 2010). On the basis of geological and paleontological data, the tectonic collision between Afro-Arabia and Asia appears to have occurred sometime near the Oligocene–Miocene boundary (roughly 23 Mya) (Kappelman et al. 2003). Because the earliest African anthropoids antedate the collision between Afro-Arabia and Asia by roughly 15 million years, they could not have simply walked across an early Cenozoic land bridge as they dispersed from Asia to Africa.

VICARIANCE, DISPERSAL, AND TIMESCALES

If anthropoids were unable to colonize Africa in the normal way—by walking there—they must have gotten there by some more extraordinary means. Two possibilities exist, neither of which initially seems appealing. The first of these focuses on vicariance—a process whereby organisms

achieve disjunct distributions passively, by having their once broader and contiguous geographic ranges fragmented by tectonic rifting, mountain building, rising sea levels, or other changes to the physical environment. Following the plate tectonic revolution in the earth sciences, numerous evolutionary biologists became fascinated with vicariance as a new and potentially more scientific explanation for the odd geographic distributions that characterize many fossil and modern organisms (de Queiroz 2005, 2014). Anthropoids, which were discontinuously distributed during the Paleogene across Asia, Africa, and South America, have long been a focal point for debate between advocates of vicariance and dispersal in biogeography (Ciochon & Chiarelli 1980, de Queiroz 2014), and this debate has frequently been acrimonious indeed (de Queiroz 2014).

A dominant role for vicariance during early anthropoid evolution has most recently been advocated by Heads (2010), who asserts that anthropoids never colonized Africa, instead having originated there sometime prior to the Early Cretaceous (~130 Mya). Biogeographic reconstructions emphasizing vicariance are forced to hypothesize such an ancient origin for anthropoids so that the evolutionary divergence between platyrrhines (New World monkeys) and catarrhines (Old World monkeys, apes, and humans) can be attributed to rifting between Africa and South America, tectonic activity which commenced then. Multiple problems weigh on such proposals.

Chronology poses the first and most obvious obstacle for reconstructions of early anthropoid evolution that rely on vicariance. The fossil record provides the only direct evidence illuminating the temporal framework for phylogeny, and the oldest fossil anthropoids that are widely accepted as such (Asian eosimiids) date to the middle Eocene (~45 Mya). If one were to accept a strictly vicariant scenario, the first two-thirds of anthropoid evolutionary history have somehow remained invisible to paleontologists, despite the fact that anthropoids must have been widely distributed across South America, Africa, and at least parts of Asia during this interval (employing the biogeographic assumptions that are inherent in vicariance models). By definition, any Early Cretaceous anthropoids that descended from such vicariant ancestors would be members of the anthropoid crown clade (the subset of anthropoids that includes living platyrrhines and catarrhines and any fossils that are descendants of their last common ancestor). As such, identifying their fossils should be straightforward because they would possess the full registry of crown anthropoid synapomorphies. Scholars widely recognize and frequently lament that the fossil record is incomplete, but the level of incompleteness that is required by proponents of early anthropoid vicariance implies some sort of systematic bias that surely demands an explanation. In addition to conflicting with paleontological data, vicariance between New and Old World anthropoids disagrees with molecular estimates of the antiquity of these clades. Recent molecular estimates for the origin of crown anthropoids typically date to the Eocene (Springer et al. 2012, Steiper & Seiffert 2012).

A vicariant origin for African and South American anthropoids is likewise inconsistent with the phylogenetic tree topology describing primate and mammalian relationships. This tree topology rests not merely on the fossil record and morphological data, but also on comprehensive genomic analyses. Theoretically, a tree's topology is independent of estimates of the divergence dates for its major nodes. The chief topological problem for vicariance between early African and South American anthropoids is that anthropoids are hierarchically nested within a series of increasingly inclusive clades that all appear to be rooted in Asia (Beard 2006). The higher-level taxa subsuming Anthropoidea include Haplorhini, Primates, Primatomorpha, Euarchonta, and Euarchontoglires (Beard 2006, Janecka et al. 2007, Springer et al. 2011, Ni et al. 2013). If anthropoids originated on a landmass that encompassed either Africa or South America (or both), one would expect to find their closest living and fossil relatives there, yet this is not the case.

If Early Cretaceous anthropoids existed, they would have faced ecosystems that were completely unlike those they inhabit today. Early Cretaceous floras were not dominated by

angiosperms (Wing & Boucher 1998), and even those angiosperms that were present lacked many of the key ecological attributes of their modern relatives (Feild et al. 2011). The terrestrial vertebrate communities of the Early Cretaceous were also remarkably different from their modern counterparts (Zhou et al. 2003).

Finally, positing that Early Cretaceous anthropoids inhabited the giant landmass spanning Africa and South America fails to eliminate dispersal across expansive marine barriers as a necessary mechanism to account for the known distribution of early fossil anthropoids. By the Early Cretaceous, Asia and Africa/South America were widely separated, and Africa remained isolated from Asia until these continents collided during the middle part of the Cenozoic. Given this paleogeographic context, the Eocene and Oligocene stem anthropoids known from Asia (chiefly eosimiids and amphipithecids) might be explained as resulting from dispersal across the marine Tethyan barrier that separated Asia from Africa, but doing so eliminates the entire *raison d'être* for the vicariance model.

The only alternative to vicariance in explaining the distribution of Paleogene anthropoids across parts of Asia, Africa, and South America is dispersal by rafting across marine barriers. Natural rafts of matted vegetation and even large floating islands derived from collapsed river banks are often discharged into adjacent oceans from the mouths of major river systems, especially during flooding events (Houle 1998). Although direct observations of land vertebrates dispersing across marine barriers this way are obviously rare, they do exist (Censky et al. 1998). To account for the known distribution of Paleogene anthropoids, two major episodes of transoceanic dispersal are required: first across Tethys, which enabled early Asian anthropoids to colonize Africa (Chaimanee et al. 2012); and then across the South Atlantic, which allowed the ancestors of modern platyrrhines to colonize South America from Africa (Bond et al. 2015).

WHEN DID ASIAN ANTHROPOIDS COLONIZE AFRICA?

The earliest undoubted African anthropoids come from three sites spanning much of the northern margin of the continent: Bir El Ater in northeastern Algeria (de Bonis et al. 1988), the Dur At-Talah escarpment in central Libya (Jaeger et al. 2010a), and the BQ-2 site in the Fayum Depression of northern Egypt (Seiffert et al. 2005, 2008). All three of these sites have produced specimens of the early parapithecoid anthropoid *Biretia*, which suggests that all three sites are fairly close in age. However, there has been considerable debate regarding the relative ages of these North African sites. Specifically, Jaeger et al. (2010a,b) suggested that the Algerian and Libyan sites of Bir El Ater and Dur At-Talah are slightly older than Egypt's BQ-2, whereas Sallam et al. (2012) suggested that BQ-2 is older than Dur At-Talah. In the absence of direct radiometric dates, attempts to correlate these sites with each other and with global timescales have been limited to assessments of paleomagnetic reversal stratigraphy and biostratigraphy. As recently reviewed by Coster et al. (2015), available biostratigraphic data suggest that all three sites are close in age, probably lying near the middle to late Eocene boundary (~37–38 Mya).

Marivaux et al. (2014a) have recently reported an isolated upper molar described as a new genus and species of primate, *Amamria tunisiensis*, from Djebel el Kébar in central Tunisia. This interesting taxon has been interpreted as being phylogenetically intermediate between primitive eosimiiform anthropoids and more derived simiiform anthropoids. Its age appears to be well established as ~39 Mya (late middle Eocene), potentially ranking it as the oldest known African anthropoid. Unfortunately, because our knowledge of its anatomy is limited to a single upper molar, and because convergence in upper molar morphology between early African anthropoids and adapiforms is now well documented (Tabuce et al. 2009), more nearly complete specimens will be required to validate the affinities of *Amamria*.

Older Eocene sites are known in Africa, primarily in Morocco and Algeria, but these sites have so far yielded only adapiform primates (Tabuce et al. 2009). Current data therefore suggest that anthropoids colonized Africa sometime during the middle Eocene, perhaps only shortly before their first appearance in the fossil record there (Seiffert 2012).

HOW MANY ASIAN ANTHROPOIDS COLONIZED AFRICA?

The simplest examples of biological invasions are those in which invasive taxa are monophyletic, each consisting of single species. On macroevolutionary timescales, such invasions have the potential to trigger evolutionary radiations. Simões et al. (2016) call these types of evolutionary radiations geographic radiations, in recognition of the fact that the radiation is initiated by dispersal of a founding species into a new territory rather than, for example, the acquisition of some key adaptive innovation.

Available data indicate that the colonization of Africa by early Asian anthropoids fails to conform to the simple pattern cited above. Instead, at least two Asian anthropoids are known to have colonized Africa sometime prior to the interval represented by the Eocene sites along the Dur At-Talah escarpment in Libya. One of these Asian anthropoids was a member of the family Afrotarsiidae (Chaimanee et al. 2012). Despite its name, *Afrotarsius* and its close relatives in the family Afrotarsiidae appear to be early anthropoids that, together with Asian eosimiids, comprise the basal anthropoid clade Eosimiiformes (Chaimanee et al. 2012). Chaimanee et al. (2012) suggest that *Afrotarsius libycus* from Dur At-Talah is very closely related to *Afrasia djijidae* from the late middle Eocene of Myanmar (Burma). Furthermore, because Asian *Afrasia* and African *Afrotarsius* are so similar phenetically, Chaimanee et al. (2012) suggest that the colonization of Africa by eosimiiform anthropoids must have occurred only shortly prior to 38 Ma, the inferred age of *Afrotarsius libycus*.

Most early African anthropoids belong to a different clade—the Simiiformes—that includes crown anthropoids as well as certain fossil taxa (such as Proteopithecidae, Parapithecidae, and Amphipithecidae) that are more closely related to crown anthropoids than they are to eosimiiforms. Strictly speaking, simiiforms did not descend from eosimiiforms, although these clades are sister taxa. Because the only known African eosimiiform appears to be deeply nested within an otherwise Asian eosimiiform radiation (Chaimanee et al. 2012), early African simiiforms such as the parapithecoid *Biretia* and the oligopithecoid *Talabpithecus* must be derived from one or more separate Asian anthropoid clades. How many Asian simiiforms are likely to have colonized Africa?

If Marivaux et al. (2014a) are correct in interpreting the poorly documented *Amamria* from Tunisia as a very basal simiiform, perhaps only one Asian simiiform is necessary to account for the subsequent and expansive radiation of simiiforms in Africa. However, there is ample reason to be skeptical about this scenario, and not merely because of the poor anatomical documentation of *Amamria*. The problem is that various Asian simiiform taxa appear to be nested within a clade containing African and South American simiiforms, rather than being basal to it as one would expect if the simiiform colonization of Africa were monophyletic. For example, phylogenetic analyses of Asian amphipithecids often yield tree topologies in which amphipithecids are more closely related to crown anthropoids than are African parapithecids (Beard et al. 2009, Marivaux et al. 2010, Seiffert 2012, Ni et al. 2013). The poorly documented Oligocene anthropoids from Dera Bugti in Pakistan described by Marivaux et al. (2005a) are even more problematic in this respect. For example, *Bugtipithecus* from the Oligocene of Pakistan was originally interpreted as a late member of the Asian amphipithecoid radiation. However, the recent analysis by Coster et al. (2013) shows that *Bugtipithecus* bears no special relationship to amphipithecids and that it may instead be a crown anthropoid.

Although details remains murky, the picture that seems to be emerging regarding the phylogenetic relationships of early African and Asian simiiforms is that more than one Asian colonist is going to be necessary to account for the African simiiform radiation.

DID OTHER ASIAN MAMMALS COLONIZE AFRICA ALONGSIDE ANTHROPOIDS?

The three main North African sites (Bir El Ater, Dur At-Talah, and BQ-2) yielding early African anthropoids also differ from older Eocene African sites with respect to the fossil rodents that are found there. All three sites have produced fossils of early hystricognath rodents, which are relatives of living African cane rats (*Thryonomys*), dassie rats (*Petromus*), mole-rats (Bathyergidae), and porcupines (Hystricidae), as well as a wide variety of South American caviomorph rodents, including capybaras, chinchillas, and guinea pigs. The widespread hystricognath rodent genus *Protophiomys* has been reported from all three North African sites (Jaeger et al. 1985, 2010b; Sallam et al. 2009), which further suggests that these sites are similar in age. *Protophiomys* has also been reported recently from the same Tunisian late middle Eocene site that yielded the potential anthropoid *Amamria* (Marivaux et al. 2014b). Following their colonization of Africa, hystricognath rodents are typically the most common small mammals encountered in African fossil sites. A broad consensus has emerged that African hystricognaths, like the early African anthropoids with whom these African hystricognaths frequently co-occur, colonized Africa from Asia, having been derived from Asian “baluchimyine” rodents (“baluchimyine” is placed in quotation marks here because this assemblage of Asian rodents is almost certainly not a bona fide clade) (Marivaux et al. 2002; Sallam et al. 2009, 2011; Coster et al. 2010). Indeed, the phylogenetic and biogeographic patterns shown by African and Asian anthropoids and hystricognaths are remarkably similar: Not only do both groups appear suddenly in Africa at the same time (within the current temporal resolution afforded by the African fossil record), but in both cases the African taxa do not appear to be monophyletic with respect to their Asian brethren (suggesting that more than one Asian hystricognath and anthropoid colonized Africa at roughly the same time) (Marivaux et al. 2002, Coster et al. 2010, Sallam et al. 2011).

A second highly distinctive group of rodents, the Anomaluroidea—which includes the modern African scaly-tailed flying squirrels—also appears for the first time in Africa at Bir El Ater, Dur At-Talah, and BQ-2. Three genera of anomaluroids are known from these sites, including *Nementchamys* from Bir El Ater (Jaeger et al. 1985), *Kabirmys* from Dur At-Talah and BQ-2 (Sallam et al. 2010b, Coster et al. 2015), and *Shazurus* from BQ-2 (Sallam et al. 2010a). *Nementchamys* and *Kabirmys* are closely related to the only known Asian Eocene anomaluroid, which is *Pondaungimys* from the late middle Eocene of Myanmar (Dawson et al. 2003, Marivaux et al. 2005b), whereas *Shazurus* already bears a highly derived dentition resembling that of modern anomaluroids. Several workers have hypothesized a phylogenetic link between anomaluroids and the only group of rodents known to antedate them in the African fossil record, the Zegdomyidae (Vianey-Liaud et al. 1994; Sallam et al. 2010a,b; Marivaux et al. 2015). However, a wide morphological gulf separates zegdomyids from early anomaluroids, and the few purported synapomorphies that have been proposed to link zegdomyids and anomaluroids are not convincing (Coster et al. 2015). The Asian occurrence of the oldest undoubted anomaluroid, *Pondaungimys*, suggests instead that this clade resembles Hystricognathi and Anthropeidea in having colonized Africa not long prior to the time of Dur At-Talah (Coster et al. 2015).

Given the paleogeographic isolation of Africa during the middle Eocene, it is startling to find that multiple clades of Asian mammals—including two or more anthropoids, two or more hystricognaths, and at least one anomaluroid—appear to have colonized the island continent of

Africa more or less synchronously near the middle to late Eocene boundary. Both before and after this important episode, there is limited evidence for biotic interchange between Asia (or Eurasia) and Africa, right up until the collision between Africa and Asia near the Oligocene–Miocene boundary (Gheerbrant & Rage 2006, Hooker et al. 2008). An important exception to this pattern is provided by anthracotheres, a group of artiodactyls that colonized Africa from Asia slightly later, during the late Eocene. African anthracotheres were semiaquatic, and modern hippopotami are nested within the anthracothere radiation (Lihoreau et al. 2015). Hence, one can easily imagine that the normal rules of dispersal across marine barriers might not have applied so stringently to them.

WAS THE LOTTERY FIXED?

Since the concept of dispersal by terrestrial mammals across expansive marine barriers was first considered in a scientific manner, it has always been viewed as a highly random, extremely infrequent event (Matthew 1915). On macroevolutionary timescales, however, such rare events might well become probable or even likely. Encapsulating these concepts, Simpson (1978) coined the term “sweepstakes dispersal,” which he defined as the “geographic spread of a group of organisms across a barrier, such as an ocean or strait for terrestrial organisms, where the probability of such spread is very small but not zero, analogous to the probability of holding the winning ticket in a sweepstakes” (p. 321).

Positing that multiple taxa of Asian anthropoid primates and hystricognath and anomaluroid rodents colonized Africa at roughly the same time conflicts with these classical ideas about sweepstakes dispersal. Two issues are readily apparent. First, the Asian taxa that succeeded in colonizing Africa were not randomly culled from the broader mammal fauna occupying Asia at that time. Instead, the same Asian mammals—especially anthropoids and hystricognaths—kept winning the jackpot, whereas others (including closely related taxa such as tarsiid primates and multiple other rodent clades) failed to do so (**Figure 1**). Presumably, certain biological attributes that are specific to anthropoids and hystricognaths enhanced their probability of success. Second, the nearly synchronous appearance of all these Asian invaders in the African fossil record indicates that something special must have characterized that particular interval of time.

Biological Factors Bearing on Sweepstakes Dispersal

Assuming that a terrestrial vertebrate is incapable of either swimming or flying across a marine obstacle to colonize a new terrain, its only chance of getting there is by hitching a ride on a natural raft or floating island (Houle 1998, de Queiroz 2014). These potential vessels are not randomly distributed on landscapes. Instead, they are especially prone to form and set sail along the banks of major river systems, particularly during intense flooding events when rivers erode their cutbanks and overflow their channels, carrying flotsam and jetsam downstream and eventually out to sea. Hence, animals that habitually occupy habitats near major river systems have a natural advantage over taxa that prefer habitats farther away from river channels. This type of habitat preference may partly explain the propensity of early hystricognath rodents to excel at sweepstakes dispersal. Extant *Thryonomys* is probably the most ecologically generalized of living African hystricognath rodents, and this taxon prefers marshes and riverbanks, often fleeing to the safety of water when it feels threatened (Nowak & Paradiso 1983). Little is known about the ancient habitat preferences of “baluchimyines” or other basal hystricognaths; however, if they resembled *Thryonomys* in this respect, it would make sense that they are extraordinarily adept at sweepstakes dispersal. Isotopic studies of tooth enamel in early hystricognaths and other contemporary rodent taxa may provide

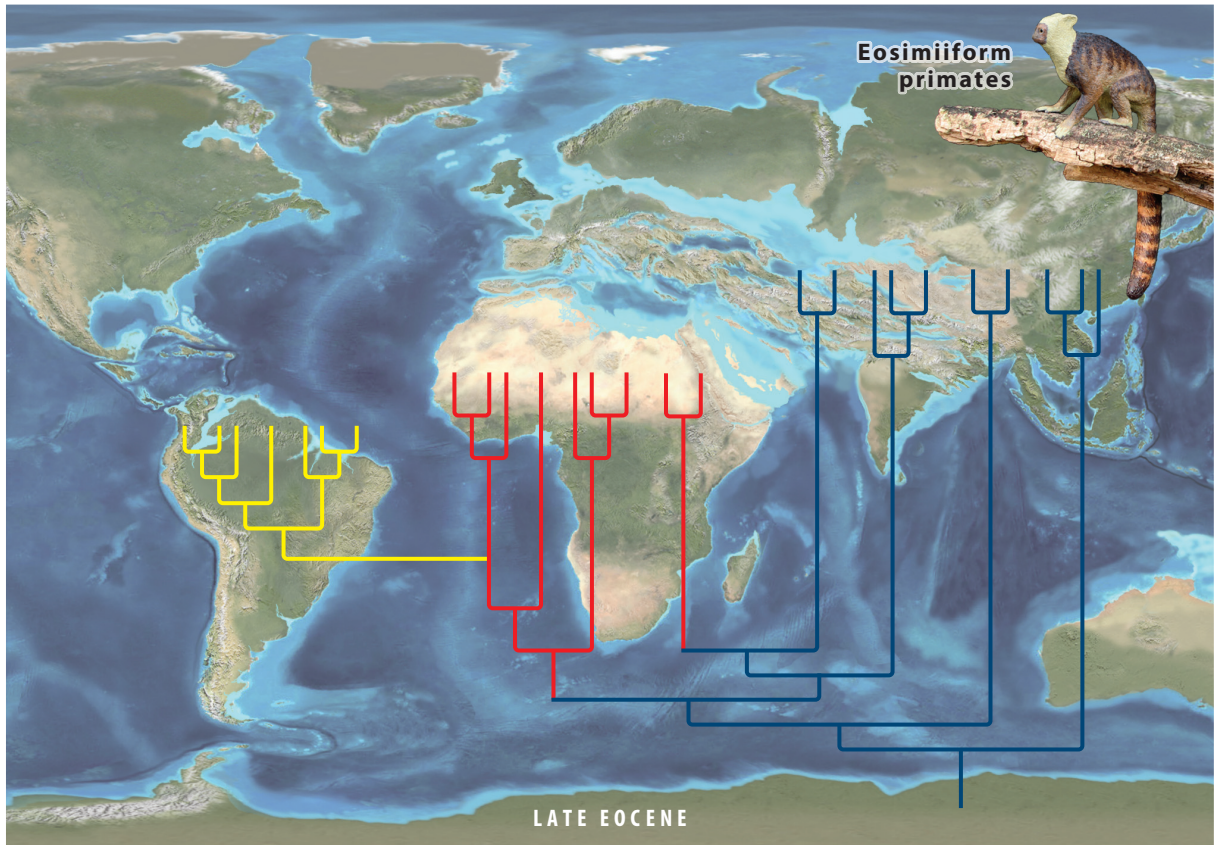


Figure 1

A color-coded and highly schematic phylogenetic tree topology superimposed on a paleogeographic reconstruction for the latter part of the Eocene, illustrating evolutionary and biogeographic patterns discussed in the text. Note that Asian clades (depicted in blue) comprise a paraphyletic basal assemblage of taxa. African clades (depicted in red) are nested within the paraphyletic Asian radiation, indicating a complicated (polyphyletic) colonization of Africa from Asia. A South American clade (depicted in yellow) is the sister group of one of the African clades. The schematic tree topology depicted here is equally applicable to anthropoid primates (including the reconstructed eosimiiform, top left) and hystricognath rodents. In contrast, anomaluroid rodents failed to disperse to South America and may have dispersed only once across Tethys. Paleogeographic map provided courtesy of Dr. Ron Blakey, Colorado Plateau Geosystems, Inc.

a test of this hypothesis. Likewise, the habitat preferences of highly arboreal mammals such as primates and anomaluroid rodents should make them especially prone to sweepstakes dispersal, at least to the extent that they occupy gallery forests and other riparian areas.

Body size and behavior are additional factors that undoubtedly affect who wins the game of sweepstakes dispersal. Mammals with a small body size will obviously be favored over medium-sized and larger taxa, simply because any given floating island will offer a limited amount of space and other resources to sustain whatever passengers might be riding along. It is unsurprising, then, that early African anthropoids, hystricognaths, and anomaluroids were all small animals (typically much less than 500 g; see Jaeger et al. 2010a,b), increasing the likelihood that genetically viable populations might be transported on floating islands of such finite dimensions. Finally, gregarious social behavior, a trait that characterizes most living anthropoids and is widely ascribed to many early anthropoid taxa (Simons et al. 1999), should enhance a taxon's chances at sweepstakes

dispersal because gregarious taxa will be more likely than solitary forms to strand genetically viable populations on floating islands as they set sail. This notion may explain, in part, the success of early anthropoids at dispersing across Tethys while their sister taxon, the Tarsiiformes, remained behind in Asia.

Geological Factors Bearing on Sweepstakes Dispersal

During the Eocene, the island continent of Afro-Arabia drifted steadily northward toward its impending collision with Asia. All other factors being equal, this tectonic convergence means that the breadth of the Tethyan marine barrier that separated Afro-Arabia from Asia was gradually decreasing over time. However, eustatic sea level dropped precipitously near the Eocene–Oligocene boundary, when continental ice sheets first developed on Antarctica (Katz et al. 2008). Lower eustatic sea level during the early Oligocene should have decreased the width of the marine barrier separating Asia from Afro-Arabia beyond the already reduced dimensions caused by ongoing tectonic convergence. If the width of the marine barrier that separated Asia from Afro-Arabia were the primary factor controlling the probability of sweepstakes dispersal, we should expect greater evidence of successful dispersal during the early Oligocene than during the latter part of the Eocene. Yet as we have seen, the African fossil record supports a significant episode of trans-Tethyan dispersal sometime near the middle to late Eocene boundary, whereas few Eurasian mammals seem to have colonized Africa during the early Oligocene sea level lowstand (a possible exception being the small marsupial *Peratherium africanum*; see Hooker et al. 2008).

Licht et al. (2014) recently provided a host of empirical data and computer simulations of paleoclimatic conditions indicating that the elevated atmospheric $p\text{CO}_2$ during the Eocene instigated monsoonal conditions across southern Asia, despite the absence of high topographic relief related to a fully uplifted Himalaya–Tibetan Plateau. The hyperthermal conditions of the Middle Eocene Climatic Optimum (MECO) (~41 Ma; Bohaty & Zachos 2003) should have corresponded to particularly intense south Asian monsoons. These Eocene monsoons would have subsided during the cooler, drier Oligocene, only to return later in the Miocene, in association with further climate changes and additional uplift of the Tibetan–Himalaya orogen (Licht et al. 2014). Eocene monsoons across southern Asia would have greatly enhanced the likelihood of sweepstakes dispersal because vastly more floating islands would have been launched during Eocene monsoonal flooding events than during the cooler, drier Oligocene. Presumably, the optimal time for sweepstakes dispersal would have been during the MECO, an interval already highlighted by Chaimanee et al. (2012) as possibly corresponding to the initial colonization of Africa by Asian anthropoids.

Local tectonics and associated geomorphological patterns, especially with respect to the development of major river drainages, might also have impacted the likelihood of sweepstakes dispersal. Of relevance to our current discussion, the uplift of the Trans-Himalayan Arc caused by crustal shortening as India was subducted would have produced generally southwesterly drainages in southern and southeastern Asia (Métais et al. 2009, Licht et al. 2013). An important example of this phenomenon is the Katawaz Basin in Pakistan, which corresponds in some ways to a paleo-Indus drainage (Métais et al. 2009). These predominantly southwesterly Asian drainages were optimally oriented to discharge floating islands on a course appropriate for the Afro-Arabian continent.

Nonrandom Sweepstakes Dispersal

It is clear that biological and geological factors can counteract the stochastic elements that are inherent in such unlikely events as sweepstakes dispersal. These factors make it far more likely

that certain taxa will succeed at certain times in dispersing across oceanic barriers, while others consistently fail to do so. Consider, for example, that two of the three major clades of Asian mammals that colonized Africa during the latter part of the Eocene (Anthropoidea and Hystricognathi) were almost immediately able to win the sweepstakes again and disperse across the South Atlantic to colonize South America from Africa (**Figure 1**) (Antoine et al. 2012, Bond et al. 2015). Aside from fully aquatic sirenians (Domning 2001), endemic African afrotheres such as hyracoids, tenrecs, and elephant shrews never won the lottery to South America, despite playing the game for millions of years longer than anthropoids and hystricognaths.

AFTERMATH OF THE ANTHROPOID COLONIZATION OF AFRICA

Regardless of how many Asian anthropoid colonists arrived on the coastline of Afro-Arabia near the middle to late Eocene boundary, it is clear that what followed was a broad, expansive, and highly successful evolutionary radiation. To a large extent, and perhaps completely so, the evolutionary radiation of African anthropoids corresponds to a geographic radiation (Simões et al. 2016). What remains unknown at this stage is whether part of the African anthropoid radiation might also qualify as an adaptive radiation, being contingent on the evolution of one or more key adaptive innovations. Because we remain ignorant of many basic aspects of eosimiiform anatomy and paleobiology, we cannot currently establish whether most or even all the key features comprising the modern anthropoid bauplan were already present in one or more of the Asian anthropoid colonists that reached Africa during the Eocene. If this proves to be true, then the African radiation of early anthropoids was unleashed primarily by geographic, rather than adaptive, factors. Alternatively, it may be that most aspects of the modern anthropoid bauplan evolved in situ in Africa sometime after its colonization by relatively primitive Asian anthropoids. In the latter case, at least part of the African anthropoid radiation would correspond to the narrow definition of an adaptive radiation (Simões et al. 2016). Parenthetically, if key features of the modern anthropoid bauplan evolved only in Africa, this might explain the subsequent success of African anthropoids in comparison with their Asian relatives, which presumably went extinct (Ni et al. 2016).

It is instructive to consider some of the larger patterns evident in the early record of anthropoid evolution in Africa and Asia. Although Africa was colonized by both eosimiiform and simiiform anthropoids hailing from Asia (Chaimanee et al. 2012), only the simiiform anthropoids achieved a successful African radiation. African eosimiiforms seemingly never diversified, and the clade appears to go extinct sometime during the early Oligocene (*Afrotarsius chatrathi* from the upper part of the Fayum sequence in Egypt documents the last known occurrence of the clade in Africa). In contrast, Asian eosimiiforms were reasonably diverse during the middle Eocene (Jaeger et al. 1999, Beard & Wang 2004, Chaimanee et al. 2012), but climatic deterioration across the Eocene–Oligocene transition extracted a particularly heavy toll on Asian anthropoids (Ni et al. 2016).

On the basis of our current understanding of early anthropoid relationships and the documented stratigraphic occurrences of key fossils, it is clear that early African anthropoids—especially simiiform anthropoids—diversified earlier than a literal reading of the fossil record would indicate. For example, Beard et al. (2016) noted that some of the well-known African anthropoid clades that have long been considered to be restricted to the Oligocene, such as parapihthecine parapihthecids and propiophthecid catarrhines, have ghost lineages that extend well back into the Eocene. Were these ghost lineages in fact present in Africa during the Eocene, remaining invisible to paleontology because of their formerly restricted geographic ranges? Or is it possible that the anthropoid colonization of Africa was even more complicated than it now seems? Enhanced geographic sampling of the early record of anthropoid evolution in Africa and Asia will be required to answer these and other questions.

Leveraging their natural predisposition to succeed at sweepstakes dispersal, the colonization of Africa by early Asian anthropoids was hardly the end of the story. Rather, it simply set the stage for the subsequent and very rapid colonization of South America by African anthropoids that had been in residence on that continent for only a short interval of time (Bond et al. 2015) (**Figure 1**). During the early Miocene, Neotropical platyrrhines again demonstrated the prowess of anthropoids at achieving sweepstakes dispersal, becoming the first South American mammals to colonize southern North America millions of years before the establishment of a direct land connection via the isthmus of Panama (Bloch et al. 2016). The remarkable ability of anthropoids to excel at sweepstakes dispersal has therefore laid the foundation and constrained the nature of virtually all major aspects of anthropoid evolution.

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