

Toward an ecophyletic origin of anthropoid primates

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ABSTRACT. The origin of anthropoid primates is examined from an ecomorphological perspective. An appeal is made to address the complexity of the initial anthropoid adaptation head-on, by bringing a variety of analytical approaches to bear and to encourage a move away from reconstructing anthropoid origins by relying on more reductionist phylogenetic methods only. Two major differing approaches to the study of anthropoid origins are reviewed, and an ecomorphological analysis that highlights the evolutionary novelties associated with early anthropoids is presented. The basic question addressed here is, “What makes an anthropoid anthropoid”? That is, how exactly did early anthropoids differ from other contemporary primates? The emphasis is on anthropoid morphology as it is documented in the Paleogene of Africa, the time and place that the earliest known anthropoids occur, because anthropoid origins involved much more than a cladogenic event.

KEYWORDS: Africa, Eurasia, Haplorhine, Strepsirhine, Paleogene, Biogeography, Anthropoid

1. Anthropoid emergence – the power of time, place and ecology

We advocate here for an inclusive ecophyletic view of anthropoid origins that incorporates multiple lines of evidence including phylogeny, biogeography, ecology, and historical contingency. Our purpose is to offer a broad perspective on the key evolutionary novelties involved in anthropoid origins, and to stress the dynamic interplay of intrinsic and extrinsic factors. Here we emphasize the need to investigate anthropoid adaptations at the time and in the place where these novelties developed, because this offers a more accurate reflection of biological reality than does reconstructing anthropoid origins using more reductionist methodologies. This is important because, at its core, the major controversy in the study of anthropoid origins is essentially one of differing approaches. One approach attempts to understand anthropoid origins by working backwards from the present to the past, emphasizing neontological and genetic information, and using extant crown taxa to guide phylogeny reconstruction. The other begins with the fossil record, emphasizing morphology and paleobiogeography, and works from the past up to the present.

2. Morphological features of anthropoids

In order to understand the origin and radiation of anthropoids, one must first be able to recognize what is an anthropoid. Crown clade anthropoids include all monkeys, apes and humans. Based on these living forms it is possible to delineate a suite of uniting morphological features that define this group (Fleagle, 2013), the most important of which is that the eye sits in a fully closed bony socket (Fig. 1). The fact anthropoids have, “full post-orbital closure” is not only a significant reconfiguration of the face and skull away from a more generalized mammalian pattern, it also signals an adaptive enhancement of the visual system that is not present in other primate groups. In addition to post-orbital closure, anthropoids are also characterized by a number of other features, including the loss of the stapedia artery in the middle ear, a tympanic ring (that holds the tympanic membrane or eardrum) that is fused to the lateral wall of the bulla, and some dental features, such as the presence of a true hypocone on upper molars.

3. Anthropoids in phylogenetic perspective

Living primates can be classified in two different ways: gradistically, as prosimian-anthropoid, or cladistically, as strepsirhine-haplorhine. In a prosimian-anthropoid classification, lemurs, lorises and tarsiers are grouped together as prosimians, and monkeys, apes and humans are grouped together as anthropoids. In a strepsirhine-haplorhine classification, lemurs and lorises are classified together as strepsirhines (“wet-nosed”), and tarsiers and anthropoids are classified together as haplorhines (“dry-nosed”) (Fig. 2). We note here that we make only passing reference to the

large radiation of Eocene omomyid and adapiform Euprimates in this analysis – not because they are not important but because their precise phylogenetic position relative to crown primates is difficult to determine.

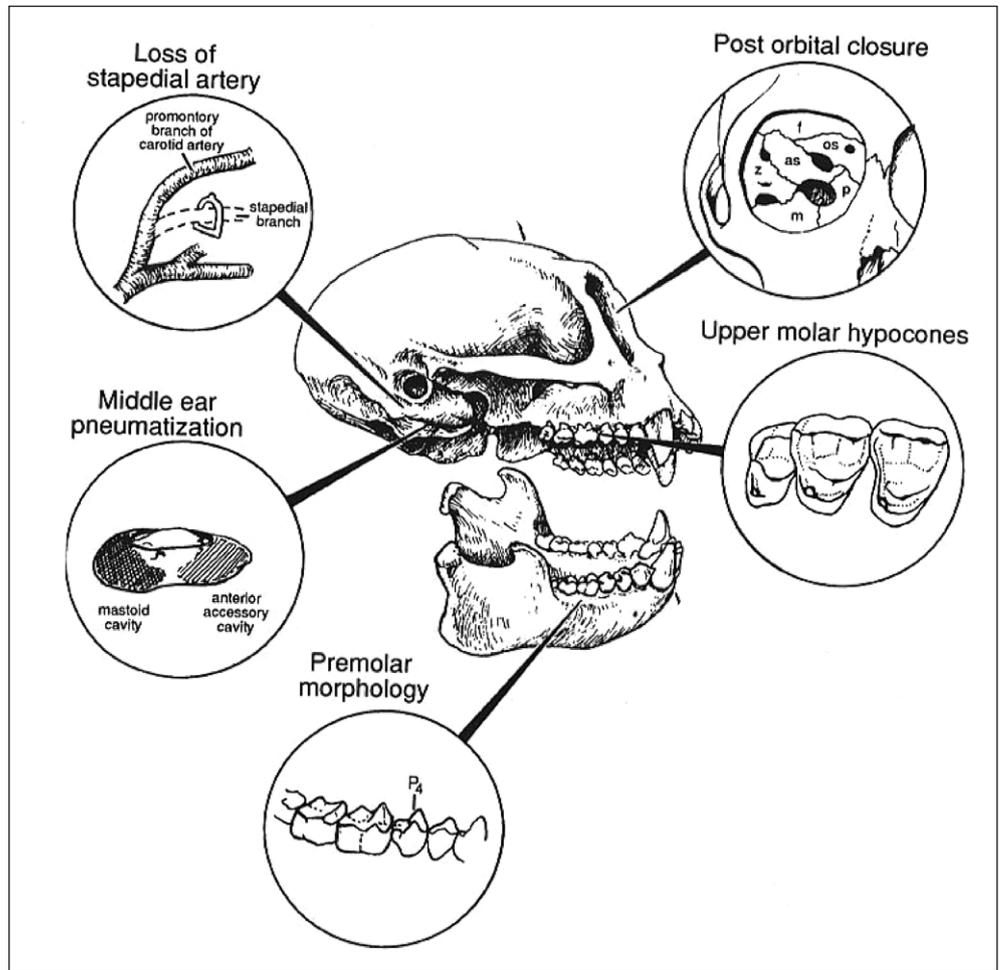
Of these two classificatory arrangements, most researchers consider the strepsirhine-haplorhine division to represent a more accurate reflection of the branching sequence of evolution. Tarsiers and anthropoids share a number of features not seen among lemurs and lorises, including characteristics of the nasal area, orbit, and reproductive system. In addition, DNA analyses (e.g., Springer et al. 2003, 2004, 2012) supports the unity of haplorhines. At the same time though, it is important to note that tarsiers are highly apomorphic and features of the nose, orbit and overall craniogenesis of tarsiers cited as homologies with anthropoids are difficult to assess, because the large numbers of unique features exhibited by tarsiers obscures the true nature of their phylogenetic relationships (reviewed in Miller et al., 2005; Rosenberger and Preuschoft, 2012; Schwartz, 2003, Smith et al., 2013). Nonetheless, neontological and genetic evidence both support the monophyly of haplorhines.

4. Neontological and genetic information

As Rasmussen (1994) discussed, the fact that, among living forms, tarsiers and anthropoids are more closely related to each other than either is to strepsirhines has had a profound influence on what some researchers expect the last common ancestor of tarsiers and anthropoids might have looked like. Researchers influenced by these data (e.g. Le Gros Clark, 1971; Williams et al., 2010a,b) expect that the ancestor of anthropoids was probably tarsier-like or at least shared features that are found in common with living tarsiers and anthropoids. This is partly because tarsiers – being small, nocturnal, still retaining claws on some digits, having flexible ears, etc., are gradistically more primitive than anthropoids with respect to these features, and this means that the tarsier morphology must have “come first” in an evolutionary sense.

However, this kind of reliance on genetic and neontological data is flawed in two important ways. First, ancestral reconstructions predicated on a “direct from the extant to the extinct”, places too great an emphasis on which animals happen to be living today. Certainly there is compelling evidence that among extant primates, tarsiers and anthropoid are more closely related to each other than either is to strepsirhines but this tells us very little about what the last common ancestor of tarsiers and anthropoids was like, especially given the highly apomorphic nature of the living tarsier. Among living forms, hyraxes and elephants are more closely related to each other than either is to anything else, but the last common ancestor of hyraxes and elephants was neither a hyrax nor an elephant, nor some half elephant-half hyrax chimera. To understand how it is that hyraxes and elephants (or tarsiers and anthropoids) are more closely related to each other than either is to anything else living today,

Figure 1. Morphological features uniting Anthropoidea. Modified from Fleagle, 1988.



and what features were present in their last common ancestor, requires evidence from the fossil record.

The second problem is the view of the tarsier as exhibiting a primitive morphology. This kind of logic harks back to the ladder-like Great Chain of Being, in that it adheres to the idea that because tarsiers occupy a lower rung on the gradistic ladder than anthropoids, that tarsiers exhibit some kind of primitive morphology (Le Gros Clark, 1971). That is, that the tarsier morphology must have, “come first” in an evolutionary sense. By this same logic you would propose that apes arose out of monkeys since monkeys occupy a lower rung on the gradistic ladder (see

Martin 1990; Miller et al., 2005). Clearly living tarsiers are highly derived and are autapomorphic in many of the features of the cranium supposedly shared with living anthropoids (e. g. Smith et al., 2013). It is difficult to imagine which, if any, living tarsier features might be found in a basal haplorhine taxon without recourse to the fossil record.

Despite these two procedural caveats, the fact that, among living forms, tarsiers and anthropoids are more closely related to each other than either is to strepsirhines has led some researchers to expect that the last common ancestor of anthropoids and tarsiers was probably tarsier-like in some ways, especially dentally. Some

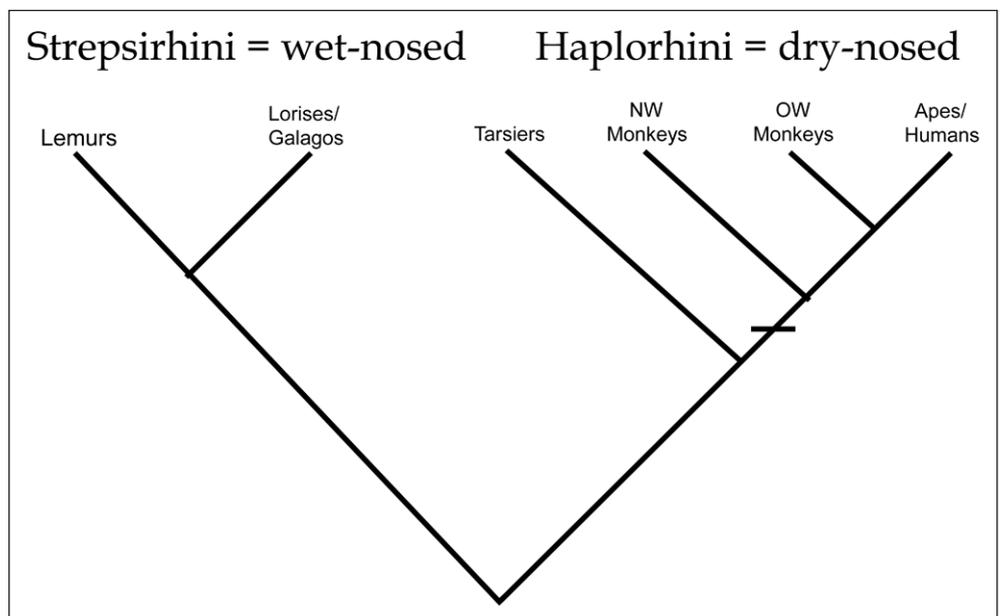


Figure 2. The strepsirhine-haplorhine classification of primates. The black bar indicates the position of early anthropoids.

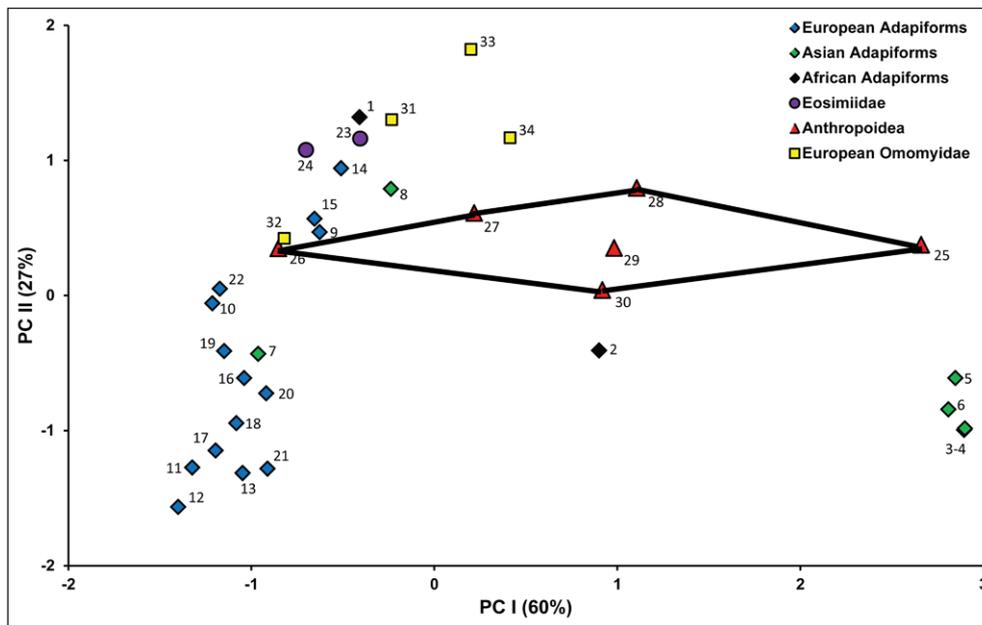


Figure 3. Results of a principal components analysis for thirty-five Old World primate species, based on data derived from Table 1. All variables are related to the size and occlusal morphology of the second lower molar. Blue diamonds = European adapiforms, green diamonds = Asian adapiforms, black diamonds = African adapiforms, purple circles = Eosimiidae, red triangles = Anthropoidea, yellow squares = European Omomyidae.

of these researchers have identified members of the Asian late Middle Eocene (ca. 42 Ma) family Eosimiidae as representing early basal anthropoids, initially based on comparisons with New World fossil primates such as *Neosaimiri*, and later with Asian basal haplorhines (Beard et al., 1994, 1996; Godinot, 1994; Gebo et al. 2001, 2008; Beard & Wang, 2004; Bajpai et al., 2008). All eosimiids are small, weighing somewhere in the 75–280 g range (living tarsiers range from 49–135 g), and their morphology is broadly described as “tarsier-like” (Fleagle, 2013; Rasmussen et al., 1998). Thus, following the logic of a neontological perspective, these animals, that are ancient and tarsier-like but are not true tarsiers must be primitive anthropoids.

5. Paleontological evidence

Researchers who are heavily influenced by paleontological evidence tend to take a different stance. Although the incompleteness of the fossil record is well understood, present evidence indicates that undisputed anthropoids are known from Africa at least by the late Eocene (Seiffert, 2012; Seiffert et al., 2005, 2010), while fossil animals identified as tarsiers, or close relatives of tarsiers, are known from early Eocene (Ni et al., 2013) and late middle Eocene sites in Asia (ca. 42) (Beard, 1998; Beard et al. 1994; Chaimanee et al., 2012; Kay 2012), but are currently unknown from deposits in Africa before the late Eocene (Jaeger et al., 2010) unless the two fragmentary primate specimens from Namibia can be confirmed as haplorhines (Pickford et al., 2008).

Family	Genus	Species	Continent	PC I (60%)	PC II (27%)	PC III (10%)
1 Adapidae	<i>Djebelemur</i>	<i>martinezi</i>	Africa	-0,40845	1,3196	0,24086
2 Adapidae	<i>Aframonius</i>	<i>dieides</i>	Africa	0,90074	-0,40701	-1,5356
3 Adapidae	<i>Pondaungia</i>	<i>savagei</i>	Asia	2,8959	-0,99603	0,52191
4 Adapidae	<i>Amphipithecus</i>	<i>mogaungensis</i>	Asia	2,8999	-0,98504	0,51735
5 Adapidae	<i>Pondaungia</i>	<i>cotteri</i>	Asia	2,8485	-0,61106	0,54381
6 Adapidae	<i>Siamopithecus</i>	<i>eocaenus</i>	Asia	2,8093	-0,84342	0,48236
7 Adapidae	<i>Hoanghoni</i>	<i>stehlini</i>	Asia	-0,9624	-0,43192	0,15083
8 Adapidae	<i>Adapoides</i>	<i>trogloodytes</i>	Asia	-0,23625	0,78933	0,12717
9 Adapidae	<i>Donrussellia</i>	<i>gallica</i>	Europe	-0,62662	0,46909	0,37548
10 Adapidae	<i>Cantius</i>	<i>eppi</i>	Europe	-1,2124	-0,057824	0,27043
11 Adapidae	<i>Adapis</i>	<i>reutmeyeri</i>	Europe	-1,3233	-1,2739	0,12957
12 Adapidae	<i>Leptadapis</i>	<i>magnus</i>	Europe	-1,4002	-1,5642	0,090909
13 Adapidae	<i>Caenopithecus</i>	<i>lemuroides</i>	Europe	-1,0472	-1,3142	0,040436
14 Adapidae	<i>Periconodon</i>	<i>huerzeleri</i>	Europe	-0,50882	0,94159	0,16313
15 Adapidae	<i>Adapis</i>	<i>sciureus</i>	Europe	-0,65461	0,56765	0,12446
16 Adapidae	<i>Adapis</i>	<i>sudrei</i>	Europe	-1,0389	-0,61114	0,056717
17 Adapidae	<i>Protoadapis</i>	<i>filholi</i>	Europe	-1,1947	-1,1477	0,0016347
18 Adapidae	<i>Protoadapis</i>	<i>weigelti</i>	Europe	-1,0817	-0,94541	-0,0059908
19 Adapidae	<i>Cantius</i>	<i>savagei</i>	Europe	-1,1486	-0,41133	-0,026706
20 Adapidae	<i>Protoadapis</i>	<i>curvicauspiciens</i>	Europe	-0,91865	-0,72406	-0,11484
21 Adapidae	<i>Cercamoni</i>	<i>brachyrhinchus</i>	Europe	-0,9108	-1,2816	-0,21169
22 Adapidae	<i>Adapis</i>	<i>priscus</i>	Europe	-1,1725	0,048724	-0,17745
23 Eosimiidae	<i>Eosimias</i>	<i>sinensis</i>	Asia	-0,40423	1,1602	0,42329
24 Eosimiidae	<i>Eosimias</i>	<i>centennicus</i>	Asia	-0,70082	1,0761	0,41202
25 Fayum	<i>Serapia</i>	<i>eocaena</i>	Africa	2,6613	0,37532	0,52614
26 Fayum	<i>Arsinoea</i>	<i>callimos</i>	Africa	-0,85203	0,34909	0,38079
27 Fayum	<i>Biretia</i>	<i>megalopsis</i>	Africa	0,21847	0,6102	-0,45806
28 Fayum	<i>Qatrania</i>	<i>wingi</i>	Africa	1,1064	0,79594	-1,0817
29 Fayum	<i>Proteopithecus</i>	<i>sylviae</i>	Africa	0,982	0,35078	-1,3082
30 Fayum	<i>Catopithecus</i>	<i>browni</i>	Africa	0,91833	0,040037	-1,4326
31 Omomyidae	<i>Teilhardina</i>	<i>belgica</i>	Europe	-0,23249	1,3014	0,42731
32 Omomyidae	<i>Necrolemur</i>	<i>antiquus</i>	Europe	-0,81986	0,42276	0,32344
33 Omomyidae	<i>Pseudoloris</i>	<i>parvulus</i>	Europe	0,20099	1,8218	0,17183
34 Omomyidae	<i>Nannopithec</i>	<i>raabi</i>	Europe	0,41386	1,1662	-0,14906

Table 1. Data from 35 Old World primates used to generate the principal components analysis.

However, the divergence of tarsiers and anthropoids is thought to have occurred somewhere in the range of 50 to 60 Ma based on both paleontological and molecular evidence (Seiffert, 2012; Springer et al., 2012; Ni et al., 2013). The presence of a ~55 million year old tarsiiiform in China (Ni et al., 2013) still leaves a minimum of 15 million years of anthropoid evolution (since anthropoids are the sister group to tarsiers) missing from the fossil record. In the absence of more information about the earliest phases of haplorhine evolution it is relevant to note that the earliest fossil evidence for a true strepsirhine primate, representing the sister group to haplorhines, is from the late Eocene of Africa (Seiffert et al., 2003), if not before (if aziibiids are strepsirhines; Tabuce et al., 2009). Hence, researchers working from the fossil record up tend to support the position that Africa may have been the source of strepsirhine evolution with dispersal generating to other landmasses from there (Yoder et al., 1996; Yoder & Nowak, 2006, but see Marivaux et al., 2001). Therefore, although the first known tarsier relatives are known from Asia, the fossil record seems to indicate that the first known anthropoids are from Africa, and the hypothesis that anthropoids are an African radiation is bolstered by the presence in Africa of the sister group to haplorhines – the lemurs and lorises.

6. Ecomorphology

At this point it is profitable to ask “what makes an anthropoid an anthropoid? How can an anthropoid be recognized other than as a node on a branching diagram? How exactly did the early anthropoids differ from contemporary primates, i.e., what was the evolutionary novelty that characterized early anthropoids? And what do the morphological features observed in early anthropoids indicate about the initial phases of the anthropoid radiation?”

Ecomorphological analyses show that Fayum anthropoids were adaptively distinct from other contemporary African and Eurasian primates (see also Seiffert, 2012). Figure 3 presents results of a principal components analysis for thirty-five Old World primate species. The data set includes twenty-three adapiforms, four omomyids, six Fayum anthropoids, and two eosimiids. All variables included in the analysis were features related to the size and occlusal morphology of the second lower molar (Table 1). The first two principal components account for 87% of the variation in this study. The first principal component encompasses 60% of the variance and is essentially an overall assessment of m2 crown topology, sorting species along a dietary shearing-to-crushing gradient. The second principal component accounts for 27% of the variance and sorted the data by m2 size. We use m2 size area here as a proxy for body weight, since m2 size in primates is correlated with body weight at an r^2 of $>.95$ (Gingerich & Smith, 1984). The third principal component accounts for ca. 10% percent of the variance and sorted taxa by relative paracristid and cristid oblique development.

Figure 3 demonstrates that the earliest known African anthropoids occupied a different adaptive space than most other contemporary Old World primates. The first principal component shows that the majority of the Fayum anthropoids (*Catopithecus*, *Proteopithecus*, *Biretia*, and *Qatrania*) fall in the “moderate crushing” ecomorphospace. Exceptions to this are the enigmatic *Arsinoea* (Family incertae sedis) which has greater shearing capability than most other Fayum primates, and the parapithecoid *Serapia* which exhibits an extreme crushing ability, rivaling that of the much larger-bodied Asian Eocene primates *Pondaungia*, *Amphipithecus* and *Siamopithecus*.

The distribution along the second principal components axis shows that African Eocene anthropoids are of moderate body size relative to their contemporaries, overlapping with the small end of the range for adapiforms and the large end for omomyids. The fact that African anthropoids are about the same body size as many other contemporary primates but are ecologically distinct is important because it demonstrates that it is not body size that is the driving force behind the distinction of Fayum anthropoids. Because body size is such a critical component of an animal’s life history and ecology (Eisenberg, 1981; Damuth & MacFadden, 1990), it might be expected that development of a divergent adaptation would be related to a difference in body size. Instead, however, one of the key adaptive features of early Fayum

anthropoids seems to lie in their greater dental crushing potential in conjunction with small body size.

The third principal component accounts for only about 10% of variance and reflects the relative development of the paracristid and cristid oblique. *Serapia* has a short and poorly developed cristid oblique and essentially is similar to Pondaung amphipithecids in this feature. *Arsinoea* also falls out separately from the other Fayum anthropoids based mostly on a better developed paracristid in combination with a moderate cristid oblique. The other Fayum anthropoids all have short paracristids and relatively well developed cristid oblique and occupy unique ecomorphospace as was the case for the first principal component.

7. An emergence scenario

Incorporation of information about the adaptations, age and geographic distribution of early anthropoids allows development of an adaptive scenario of anthropoid emergence. Evidence from the fossil record indicates that recognizable anthropoids were present in Africa by ca. 38 Ma (Seiffert et al., 2005, 2010), and these animals were united by their unique postorbital closure and occupation of an arboreal and mostly fruit-eating niche (Kirk & Simons, 2001). It is clear that within this adaptive complex, frontation of orbits and the development of stereoscopic color vision played a large role (Ross, 2000; Dominy, 2004; Kirk & Kay, 2004)

It has become widely accepted that molecular and morphological phylogenies converge to support an origin for primates that is rooted in Laurasian Euarctontoglires (Springer et al., 2003, 2004, 2012; Bloch et al. 2007; Godinot, 2007). Given this starting point, one way to reconcile the Eurasian origin of primates with an early divergence date of ~60 Ma for the haplorhine-strepsirhine split, the distribution of tarsier-like primates in Eurasia (42 Ma), and Africa (38 Ma), and the presence of anthropoids and strepsirhines in Africa by 38 Ma, is to propose that the ultimate cladogenic source of African primates was a Eurasian stem primate that reached the African continent early in the Paleogene. The idea that the progenitor of African primates likely arrived in Africa from Eurasia is neither new nor particularly controversial (Colbert, 1937; Ba Maw et al., 1979; Gingerich, 1980). However, the African fossil record prior to 40 Ma is equivocal. The only African primate recovered prior to 40 million years is the enigmatic *Altitasius*, which has been variously recognized as an omomyid euprimate (Sigé et al., 1990), a plesiadapiform primate (Hooker et al., 1999), or as a possible basal anthropoid (Godinot, 1994, 2010; Beard, 2004; Seiffert et al., 2005; Bajpai et al., 2008).

A more controversial proposition than a Eurasian origin for members of the order Primates is that there is a direct link between Asian eosimiids and African anthropoids, and that the African anthropoid radiation was the result of eosimiid immigration into Africa (Beard, 2004). The major issues with this are two-fold. First, Asian eosimiids are represented primarily by dental material and also some foot bones, but no unequivocal cranial evidence is known so it is unclear whether eosimiids possess any key anthropoid features (e.g. postorbital closure, stapedia artery pathway, bulla structure). Certainly the development of characteristic anthropoid features must have arisen in a mosaic fashion, so it would not be expected that stem forms would possess the entire suite. However, the lack of any cranial evidence for eosimiids makes the connection to African anthropoids tenuous. This is important because the emergence of anthropoids was not simply a cladogenic event. Initial bouts of cladogenesis probably produced a fair number of stem primate taxa, but it was a coalescence of factors including their presence in Africa at a propitious time, and with a particular range of attributes, that led one of these lineages to produce the modern anthropoid radiation.

Second, an Asian origin hypothesis paints with a very broad brush in emphasizing anthropoids arriving in Africa and filling an empty niche, a proposal whose details are out of synch with studies of plant energetics. “When the first Asian anthropoids arrived in Africa, they encountered a bountiful continent that was surprisingly free of potential competitors. The vast majority of the resident mammals were afrotheres. This left the ecological niche at which primates excel – that of the arboreal mammalian

frugivore and insectivore – largely if not completely vacant” (Beard, 2004: 272). We find this “low-hanging fruit” proposition, i.e., that the anthropoid niche was largely open upon arrival, to be not fully considered. Investment in reproduction imposes considerable cost on a plant and no plant will invest energy in producing fruit if a dispersal mechanism is not already available (Cody, 1966; Fenner and Thompson, 2005). In addition, many large mammals not technically designated as “frugivores” are known to disperse sizable quantities of fruits and seeds (Bodmer, 1989, 1991; Dinerstein, 1989; Janzen & Martin, 1982). Indeed it is highly likely that many afrotherians not traditionally classified as “frugivorous” animals such as *Palaeomastodon*, *Phiomia*, and *Arsinoitherium*, as well as some bats, birds, rodents and hyraxes (Rasmussen, 1989) all utilized fruits. Hence, the idea that the success of the anthropoid radiation was due to a frugivorous niche being open when anthropoids arrived in Africa is doubtful in light of ecological principles.

A more nuanced ecophyletic view would suggest that members of the African anthropoid lineage developed unique behavioral and morphological features that allowed them to successfully occupy the small-bodied frugivore adaptive space. Within this framework, the origin of anthropoids was the result of a stochastic (non-predictable) coalescence of factors, including the arrival of primitive primates in the right place (Africa) at the right time (the Paleogene), with a particular range of biological potential which permitted development of their signature suite of features. It is important to note that none of this information is accessible by interpreting nodes on a cladogram.

8. Summary

It was not simply a cladogenic event that produced the emergence of anthropoids. The origin of anthropoids – in either a temporal, geographic or morphological sense – is not predictable from a branching diagram depicting sister group relationships of living taxa. Certainly, cladogenesis was responsible for producing a number of stem primate and stem anthropoid taxa, but it was a coalescence of factors including their presence in Africa at a particular time, and with a given range of biological potential that led one of these lineages to produce the anthropoid radiation. Empirical evidence including the temporal and geographic contexts in which anthropoids are found, early anthropoid paleobiology, morphological and molecular phylogenetic information, all indicate that a small frugivore-insectivore stem primate likely emigrated from Eurasia to Africa in the early Paleogene, and that at least by the late Eocene, anthropoids were wide-spread in Africa, and were a fundamentally different kind of primate than were their contemporaries. With their characteristic postorbital closure, early anthropoids were likely processing visual information in a different manner from primates elsewhere, and anthropoids were exploiting a small to medium body-sized frugivore niche in a unique way as indicated by ecomorphological analysis.

The circumstances that combined to produce the anthropoid radiation were singular. Therefore it is only by combining all available empirical evidence in an ecophyletic framework that it becomes possible to achieve a fuller and more nuanced understanding of anthropoid emergence. Dependence only on reductionist methodologies seldom allows access to the complexity of biological adaptation. After all, the goal is to understand the complexity of anthropoid emergence, not to reduce that complexity so that it can be understood.

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