

When, Where and How? Reconstructing a Timeline for Primate Evolution using Molecular and Fossil data

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ABSTRACT: Non-human primates today are found throughout the forests and woodlands of the Old and New World tropics and subtropics, although in earlier phases of primate history, under different climatic regimes, their distribution was even wider. New fossil finds and a growing number of phylogenetic analyses based on nucleotide sequences require constant shifts in our thinking concerning the divergence times of the major primate lineages. Often the insights provided by these two data sources are incongruent with one another, and the source of the disagreement must be sought. In this contribution I summarise current information pertaining to major events in primate evolution stemming from both palaeontology and molecular biology, and review current ideas as to the time and place of the origin of the primate clade.

KEYWORDS: molecular phylogenies, fossils, divergence dates, primate origins.

Non-human primates today are found mainly in the woodlands and forests of the tropical and subtropical regions in South America, Africa, Madagascar and South-east Asia, but in the past they occupied a much wider area of the Earth's surface. Euprimate fossils (i.e., fossils that display the clade-defining traits, e.g. petrosal bulla, postorbital bar) have been recovered from various localities in North America, and throughout the length of South America all the way down to the southernmost tip of Argentina. Primate fossil sites extend from western Europe through to eastern China, and include areas in Africa that are now barren desert. Understanding how they came to occupy their past and current distributions requires a well-supported timescale, and this is an area of primate history that is subject to constant revision as new fossils are discovered and more DNA sequences and ingenious methods of molecular analysis are brought to bear in the calculation of molecular clocks. In this contribution I summarise current knowledge concerning the timing of major events in primate evolution using both of these data sources, and review contemporary thinking as to where the primate clade originated.

One factor needs to be borne in mind with regard to estimating divergence times from molecular data. Because molecular substitution rates are not consistent from one lineage or one gene sequence to another, or even from one nucleotide position to another, they must be calibrated in some way. This is most often done in accordance with the estimated appearance times of the earliest fossils in a given lineage. Two of the most commonly employed calibration points in primate phylogeny are the appearance of the first cercopithecoid fossils, signalling the divergence of apes and monkeys, at 25 Myr, and the first appearance of platyrrhine fossils in South America at 26 Myr. It cannot be stated too strongly that these dates are too recent to record the actual lineage divergence. The probability that the fossil record actually documents the ancestor to any clade is vanishingly small, and these fossil calibration points will always be minimal divergence dates (Eizirik *et al.*, 2001). For example, Yoder and Yang (2000) have estimated the cercopithecoid-hominoid divergence date to be between 30 and 40 Myr, and Arnason *et al.* (1998) predicted it could even be ≥ 50 Myr. Nevertheless, the 25 Myr date continues to be employed (e.g., Page and Godman, 2001; Poux and Douzery, 2004), yielding unrealistically recent dates for the origins of other primate clades.

1. THE ORIGIN OF THE PRIMATE CLADE

The time and place of the origin of the primate clade is controversial. Most palaeontologists (e.g. Gingerich & Uhen, 1994; Alroy, 1999; Benton 1999; Foote *et al.*, 1999) place the origin of the primates, along with those of other extant mammal orders, just after the Cretaceous-Tertiary (K-T) boundary, 65 Myr ago. The most commonly held view is that the mammal radiation was held in check up until the end of the Cretaceous because the potential ecospace was occupied, chiefly by dinosaurs. When the dinosaurs died out during the end-Cretaceous mass extinction event, a host of new ecological opportunities became available to the mammals, which rapidly radiated into the newly freed niches (Easteal, 1999). No undisputed primate fossils are known from sediments older than the K-T boundary. The plesiadapiforms, a group of highly diverse primate-like mammals that were common components of Northern Hemisphere faunas during the Palaeocene and early Eocene, were once referred to as “archaic primates”. Their earliest representative, *Purgatorius*, was recovered during the unearthing of a 65 Myr old *Triceratops* in Montana (Van Valen & Sloan, 1965). Like strepsirrhine primates, plesiadapiforms came in a wide range of body sizes, from < 100 g to > 3 kg, and appear to have followed a diversity of diets, from insects to leaves and seeds, and even gum (Fleagle, 1999). Some were arboreal, while others were apparently terrestrial. However, the concept of plesiadapiforms as pleisomorphic primates has been challenged by fossil discoveries indicating that the living primate suborders, the Strepsirrhini and the Haplorhini, had already begun to diverge from one another in the Palaeocene, around the time that the plesiadapiforms were undergoing their own radiation (Godinot & Mahboubi, 1992). Furthermore, the osteological evidence linking the plesiadapiforms and the primates is no stronger than that linking the primates with the Dermoptera

(colugos) and Scandentia (tree shrews) (Fleagle, 1999). Thus, while most contemporary primate evolutionists agree to unite all three groups within a clade that includes the primates, the exact order of branching within the clade is contentious. The first undoubted primate fossil hypodigm, *Altiatlasius*, consists of ten isolated teeth recovered from Adrar Mgorn 1 locality in foreland basin deposits of the High Atlas Mountains, and dated at 60 Myr (Sigé *et al.*, 1990).

Studies in molecular biology have posed a major challenge to the palaeontological view of primate origins. Molecular clock estimates suggest that the primate clade diverged from its closest relatives well in advance of the K-T boundary, between 87 – 85 Myr (Eizirik *et al.* 2001; Springer *et al.* 2003; Murphy *et al.* 2004; Yoder & Yang 2004) or even earlier (Arnason *et al.* 1998; Kumar & Hedges 1998). There are three potential solutions to this apparent lack of congruence between palaeontology and molecular biology:

(a) The molecular divergence dates are essentially correct, but genetic divergence was not accompanied by morphological divergence discernible in the fossil record until after the K-T boundary, when new ecological opportunities opened up (Benton, 1999; Foote *et al.*, 1999; Eizirik *et al.*, 2001).

(b) The molecular divergence dates are essentially correct, but the Cretaceous phases of mammalian evolution took place in areas of the globe where there are no Cretaceous deposits, and these lineages suddenly dispersed in the Tertiary (Benton, 1999; Foote *et al.*, 1999); this is the Garden of Eden hypothesis of Foote *et al.* (1999).

(c) The molecular dates are overestimates of the divergence times, because the molecular clock sped up during the initial phases of the Tertiary radiation, as mammals radiated into free ecospace (Benton 1999; Foote *et al.*, 1999).

Statistical estimates of the extent of missing fossil history based on models of fossilization and recovery processes are contradictory in their findings. The model of Foote *et al.* (1999, p. 1310) indicates that “it is unlikely that many modern orders arose much earlier than their oldest fossil records”. Other models are more in line with the molecular data, indicating that the primates diverged approximately 81.5 Myr ago (Martin, 1993; Tavaré *et al.*, 2002).

Finally, a strong signal is emerging from the molecular data showing that the extant mammalian orders did not all radiate around the same time period, as would be suggested by the palaeontological model, but have a well-supported hierarchical pattern (Easteal, 1999). The more basal branches of this hierarchical tree consistently diverge well before the K-T boundary.

2. THE STREPSIRRHINE-HAPLORHINE DIVERGENCE

The most fundamental split in primate biological organisation is reflected in two subordinal divisions: the Strepsirrhini (i.e., the living tooth-combed primates (Infraorder Lemuriformes) and their fossil allies) and the Haplorhini (i.e., the tarsiers, anthropoids, and their fossil allies). The fossil record indicates that this basal divergence oc-

curred during the Palaeocene (65-55 Myr; Sigé *et al.* 1990; Godinot & Mahboubi 1992). Recent phylogenetic analyses (Sieffert *et al.*, 2005; Jaeger and Marivaux 2005) indicate that the oldest known primate, *Altiatlasius* from the Palaeocene of Morocco (Sigé *et al.*, 1990), is a primitive stem anthropoid, as originally suggested by Godinot (1994). Thus, by the time we get our first glimpse of undoubted primates in the fossil record, the haplorhine-strepsirrhine divergence has already occurred. The divergence was certainly well established by the beginning of the Eocene, 55 Myr ago. This was a time of global warming, when moist tropical forests spread across Europe, Asia and North America (Fleagle, 1999), and supported a diverse fauna of euprimates. The vast majority of primate fossils recovered from this epoch have been classified into two distinct, but highly diverse, groups: the Adapiformes, which share several diagnostic characters with the lemuriforms and have hence been allocated to the Suborder Strepsirrhini (Kay *et al.*, 1997; Gebo, 2002), and the Omomyoidea, which have been allied with the extant *Tarsius* and are thus Haplorhini (Kay *et al.*, 1997; Fleagle, 1999).

Some molecular estimates of the timing of this divergence, based on calibration points external to the primate radiation, are somewhat older than the Palaeocene, i.e., ~ 80 Myr (Arnason *et al.*, 1998), or 77 Myr (Springer *et al.*, 2003; Murphy *et al.*, 2004). The estimations of Porter *et al.* (1997) and Goodman *et al.* (1998), using the 25 Myr calibration point for the cercopithecoid-hominoid divergence, place this event at 63 Myr. Poux and Douzery (2004), using 63 Myr as the date for the emergence of primates, calculate a haplorhine-strepsirrhine split at ≤ 60 Myr. Porter *et al.* (1997) and Goodman *et al.* (1998) further indicate that tarsiers and anthropoids shared a common ancestor 58 Myr ago. All of these dates calculated on the basis of calibration points within the primate clade are too recent from the point of view of the fossil record, and would be scaled back using a more realistic calibration point.

The important fact that emerges from both the palaeontological and molecular picture of early primate evolution, is that the two suborders diverged within a very short time of the origin of the primate clade.

3. THE LEMURIFORM RADIATION

The Infraorder Lemuriformes is made up of two superfamilies: the Lorisioidea (the galagos and lorises of Africa and Asia) and the Lemuroidea (the lemurs of Madagascar).

The lorisoid families appear to have originated in Africa (Yoder *et al.*, 1996; Sieffert *et al.*, 2003) and have a fossil record going back to ~ 40 Myr ago. Sieffert *et al.* (2003) described dental remains from the Fayum Depression that indicate the lorisid and galagid lineages had already diverged by this time, towards the end of the Eocene. More lorisoid material has been recovered from early Miocene deposits (20-15 Myr) of East Africa, testifying to the existence of a lorisoid radiation that did not yet bear the hallmarks of the living lorisoid families (Rasmussen and Nekaris, 1998; Masters *et al.*, 2005). Galagid dental remains discovered recently in Egypt suggest that the defining character of the living family, the molarised P4s, had evolved by 10,000 yr ago (Pickford, pers. comm.).

No fossil lemuroid older than 26,000 yr has yet been found on Madagascar (Simons *et al.*, 1995), making a palaeontological estimate of the timing of the lemuroid radiation very difficult. Molecular investigations have been more productive, and a slew of potential dates has been derived for the lorisoid-lemuroid divergence, as well as for the origins of the mainland and island radiations (Table 1). Most molecular studies have concluded

Authors	Lorisoid-lemuroid divergence	Lemuroid radiation	Lorisoid radiation
Yoder <i>et al.</i> (1996)	≥ 62	≥ 54	≥ 55
Porter <i>et al.</i> (1997)	50.2 – 50.9	41.3 – 47.7	23
Yoder (1997)	61.5 – 61.9	53.7 – 54.1	50.7 – 54.9
Arnason <i>et al.</i> (1998)	~ 68	~ 80	----
Goodman <i>et al.</i> (1998)	50	45	23
Poux and Douzery (2004)	45.4 – 46.7	39.6 – 40.7	13.8 – 14.2
Roos <i>et al.</i> (2004)	61 (50 – 80)	58 (47 – 76)	46 (37 – 60)
Yoder and Yang (2004)	68.5 (61.3 – 75.4)	62 (57.9 – 73.0)	39.1 (38.0 – 41.5)
Poux <i>et al.</i> (2005)	60 (69.6 – 51.6)	50 (58.5 – 41.1)	----

Table 1 – Divergence dates for the lemuriform, lemuroid and lorisoid radiations estimated from nucleotide sequences.

that the Malagasy lemuriforms are monophyletic, and that the invasion of Madagascar occurred once at some time between the divergence of the superfamilies and the radiation of the Lemuroidea. The lemuroid-lorisoid divergence is estimated to have occurred between 68 (Arnason *et al.*, 1998; Yoder and Yang, 2004) and 50 (Porter *et al.*, 1997; Goodman *et al.*, 1998) Myr ago, while derived ages for the lemuroid radiation range from 62 (Yoder and Yang, 2004) to 40 (Porter *et al.*, 1997; Poux and Douzery, 2004) Myr ago. Arnason and his colleagues have been alone in claiming that the lemuroid radiation began far in advance of the lemuroid invasion of Madagascar, perhaps as early as 80 Myr ago, so that the island was colonised twice by primates: once by the daubentoniids (aye-ayes) and once by the common ancestor of the remaining lemuroids. The lorisoid radiation appears to have been the most difficult to pin down of all the strepsirrhines, with estimates ranging from 55 (Yoder *et al.*, 1996) to 14 (Poux and Douzery, 2004) Myr ago. The fossil record seems to indicate that any date younger than 40 Myr is too recent, casting doubt on several of these estimates. Several molecular studies have also been unable to provide evidence in support of lorisid monophyly to the exclusion of galagids (e.g. see Goodman *et al.*, 1998, Masters *et al.*, 2005), which could indicate that the extant lorisid radiation has deep roots – certainly deeper than the extant galagid radiation.

4. THE ORIGIN AND RADIATION OF THE ANTHROPOIDS

Following the first tantalising glimpse of stem anthropoids in Africa 60 Myr ago, the fossil record is mute until ~ 45 Myr ago, when undoubted early anthropoids existed contemporaneously in North Africa (*Algeripithecus*, Godinot and Mahboubi, 1992) and eastern China (*Eosimias*, Beard *et al.*, 1994). An Eocene tarsier, *Tarsius eocaenus*, was found alongside *Eosimias*, indicating that the tarsier-anthropoid divergence was well established, and making *Tarsius* the longest-lived genus of all primates, living and extinct.

A diverse anthropoid fauna is known from the late Eocene-early Oligocene (37-32 Myr) deposits of the Fayum Depression, Egypt, comprising at least three families: the Parapithecidae, the Propithecidae and the Oligopithecidae. Of these, the parapithecids and oligopithecids have been described as having “a platyrrhine grade of morphological organization that was substantially identical to that of living platyrrhines” (Kay *et al.*, 1997). They also had three premolars, while the Propithecidae had only two, and hence qualify as true catarrhines. Fleagle (1999, p.408) has indicated one late Eocene genus in particular, *Proteopithecus*, is very platyrrhine-like, and shows no specialisations that would preclude it from platyrrhine ancestry. What the Fayum anthropoid assemblage appears to be telling us is that the platyrrhine-catarrhine divergence had occurred by the end of the Eocene (33 Myr), and probably took place in Africa (Takai *et al.*, 2000).

Anthropoids appear for the first time in the South American fossil record in the late Oligocene, 27-26 Myr ago, despite the presence of highly productive fossiliferous deposits of Palaeocene and Eocene age on the continent. The oldest platyrrhine fossil is *Branisella*, which shows several intriguing similarities to *Proteopithecus* in its upper dentition (Takai *et al.*, 2000), and a phyletic relationship has been proposed between them. Where the taxa differ, *Proteopithecus* consistently shows the more ancestral morphology, as befits its greater geological age.

Molecular estimates of the catarrhine-platyrrhine split range from 40 Myr (Goodman *et al.*, 1998) to 48 Myr (Kumar and Hedges, 1998), and even 60 Myr (Arnason *et al.*, 1998), all of which could accord with an African origin. A date of 30 Myr, estimated by Sarich (1970) using immunological distances, is probably too young, since the propithecids are older than this. A more recent immunological study indicated a double invasion of South America by platyrrhines, once by the Cebidae and once by the Atelidae, placing a 52 Myr old date on the emergence of the cebid clade (Bauer and Schreiber, 1997). Platyrrhine paraphyly has not been supported by reconstructions based on sequence data, however (Porter *et al.*, 1997; Goodman *et al.*, 1998), and these studies have yielded a much younger date of *c.* 22 Myr for the cebid-atelid divergence. The true value is likely to lie between these estimates.

Cercopithecoid fossils have been recovered from early Miocene deposits in Africa, 25-20 Myr old, and they appear to predate the divergence of the living subfamilies, the leaf-eating Colobinae and the cheek-pouched Cercopithecinae. As a result, these fossils are classified in their own subfamily, the Victoriapithecinae (Benefit,

1993; Fleagle, 1999). The fact that these Miocene monkeys are absent from fossil faunas associated with dense forest, and probably preferred more open habitats, has led to the proposal that the cercopithecoid-hominoid divergence occurred as a result of differential adaptation of the two lineages to woodland/savanna and forest habitats, respectively.

As stated above, several molecular phylogeneticists have used this fossil date as a calibration point for the estimation of later divergence dates, although it is likely to be too young (Yoder and Yang, 2000). Hence, Arnason *et al.* (1998), using a calibration point outside the primates, have indicated an age of ≥ 50 Myr for the cercopithecoid-hominoid divergence, and 30 Myr for the Colobinae-Cercopithecinae split. In contrast, Page and Goodman (2001), using the 25 Myr cercopithecoid-hominoid calibration point, have estimated the colobine-cercopithecine split as occurring as recently as 14 Myr ago. Once again, the true value is likely to lie somewhere in between.

5. THE HOMINOID RADIATION

The apes (Superfamily Hominoidea) diversified and dominated the primate faunas of African and Eurasia during the Miocene (23-5 Myr), at a time when monkeys were still relatively rare. Fossils representing 500-1,000 individuals have been recovered from an area spanning Eurasia from Spain to China, and almost the length of Africa from Egypt to Namibia (Fleagle, 1999). The earliest apes are found in Africa, and their radiation appears to have coincided with a period when global temperatures began to increase again after the episode of dramatic cooling that marked the Oligocene epoch. During the early Miocene it is likely that tropical lowland forest covered large tracts of Africa prior to the evolution of the savannas. When the African plate made contact with Eurasia, *c.* 15 Myr ago, apes moved northwards on to that landmass as well.

Given our present state of knowledge, it is not possible to link most fossil apes to particular living taxa. This makes the fossil estimation of hominoid divergences highly problematic. The fossil record of the gibbons (Family Hylobatidae) only extends as far back as the middle Pleistocene of China and Indonesia, but molecular data suggest that they diverged from the great apes at some point between 40 and 14 Myr ago (see Table 2). The 12 Myr old *Sivapithecus* (Kappelman *et al.*, 1991) shows cranial similarities to the living orangutan, but there are postcranial differences which argue against a close relationship between them. The fossil history of African great apes is almost entirely undocumented, with the exception of *Samburupithecus*, a 9.5 Myr old ape the size of a gorilla, from the Samburu Hills in Kenya (Ishida and Pickford, 1997).

A range of dates has been derived from molecular sequence comparisons, and a selection of these is presented in Table 2. The values vary widely, dependent on the calibration points employed. *Sabelanthropus*, the oldest fossil hypodigm claimed for the hominin lineage (Brunet *et al.*, 2002), if the claim is justified, places a minimum limit on the divergence of *Homo* from the great apes of 7-6 Myr.

Authors	Hylobatidae	Pongidae	Gorillini	<i>Homo-Pan</i>
Porter et al. (1997)	21.3	19.6	7.7	7.7
Arnason et al. (1998)	40	30	15 – 17	10 – 13
Goodman et al. (1998)	18	14	7	6
Kumar & Hedges (1998)	14.6 ± 2.8	8.2 ± 0.8	6.7 ± 1.3	5.5 ± 0.2
Yoder & Yang (2000)	----	----	7 – 9	4 – 6
Page & Goodman (2001)	18	14	7	6 – 5

Table 2 – Divergence dates for the hominoid clades estimated from nucleotide sequences.

6. THE ORIGINS TIMELINE AND PRIMATE BIOGEOGRAPHY

Figure 1 summarises some recent molecular estimates of the ages of the bifurcations of the major primate lineages, along with the data concerning first fossil appearances and some of the other major geological events that have a bearing on the history of the landmasses currently occupied by primates. Virtually all of the land currently making up the tropics and subtropics of the Old and New Worlds was once part of the supercontinent of Gondwana. Approximately 160 Myr ago the supercontinent began to fragment, essentially rupturing into two parts: a western portion made up of South America and Africa, and an eastern portion made up chiefly of India, Madagascar, Antarctica and Australia (Reeves and de Wit, 2000). The separation of Africa and South America began in the south, with the final sundering of West Africa and Brazil occurring *c.* 120 Myr ago. South America and Antarctica remained connected until well into the Palaeogene, with the opening of the Drake Passage occurring at about 30 Myr. Indo-Madagascar maintained a connection with Antarctica by means of the Kerguelen plateau until 90 Myr at the latest (Reeves and de Wit, 2000). Separation between India and Madagascar was completed between 89 and 83 Myr ago, after which India drifted rapidly northwards to join with Asia (Reeves and de Wit, 2000; de Wit, 2003).

What is immediately clear from Figure 1 is that most of these events occurred well before either the molecular or the palaeontological estimates of the origin of the primate clade. The landmasses that make up the current geographic deployment of the primate order are separated from one another by vast stretches of ocean, and have been since the late Cretaceous and earlier. Where, then, did primates originate, and how did they come to occupy their current distribution?

This remains the single most puzzling aspect of primate evolution. Most reconstructions require one to several over-water dispersal events, whereby primates rafted from one landmass to another on mats of vegetation (e.g., Houlen 1999; Yoder *et al.*, 1996). Serious objections have been raised to the idea of rafting primates in terms of the animals' ability to survive an extended period of deprivation and exposure (Simons,

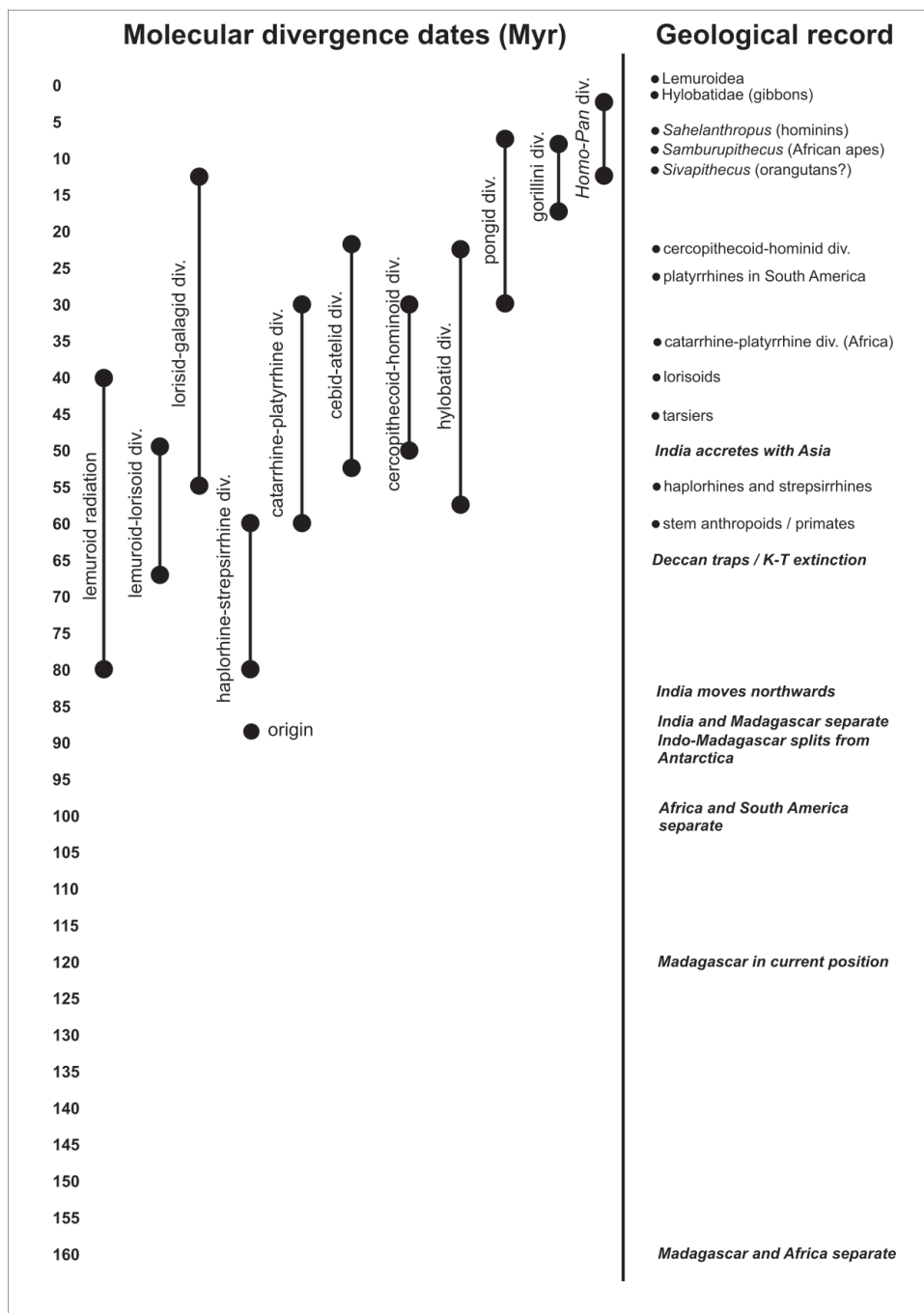


Figure 1 – Molecular estimates of the ages of the bifurcations of the major primate lineages, along with the data concerning first fossil appearances and other major geological events.

1976). The situation is particularly difficult to understand in the case of the invasion of Madagascar from Africa, for this appears to have occurred in defiance of current and wind directions (Masters *et al.*, 1995; Stankiewicz *et al.*, 2005). Nevertheless, in the absence of any more feasible alternative, these scenarios remain popular among primate evolutionists.

Africa was traditionally considered the birthplace of the primate clade, chiefly because the oldest primate fossils had been found there (Gingerich, 1990; Sigé *et al.*, 1990). It was also proposed as the place of origin for the anthropoid (Godinot and Mahboubi 1992; Godinot, 1994) and lemuriform (Yoder *et al.*, 1996; Sieffert *et al.*, 2003; Roos *et al.*, 2004) radiations. However, the observation that the primates do not form part of the clade of endemic African mammals (Eizirik *et al.*, 2001; Springer *et al.*, 2003; Murphy *et al.*, 2004), along with the fact that the sister taxa to the primates (Scandentia, Dermoptera, Plesiadapiformes) have apparently never been present on the African continent (Beard, 1998), have shifted attention from Africa to Asia as the source continent. All three of the sister taxa mentioned above either still occur in Asia, or did so in the distant past. However, Asia was isolated from other landmasses by considerable stretches of water until well after the primate radiation had begun. Until *c.* 55 Myr ago, Europe and Asia were separated by the Obik Sea (Smith *et al.*, 1994; Ni *et al.*, 2004), and for *Altiatlasius* to have inhabited Morocco 60 Myr ago, its ancestors must have crossed the not insubstantial Tethys Ocean that divided Africa from Eurasia (Smith *et al.*, 1994). At approximately this time, the lemuriform ancestors, too, would have had to make the journey not only to Africa, but to Madagascar as well. Either our early primate ancestors were extremely keen seafarers, or there is an important aspect of the puzzle missing.

Krause and Maas (1990) and Martin (2003) have suggested that primates originated either on India when it was adrift in the Indian Ocean, or on Indo-Madagascar when it was still a single landmass. The problem with both of these scenarios is that India docked with Asia only *c.* 50 Myr ago (Rowley, 1998), which makes it difficult to understand how primates might have arrived in North Africa by 60 Myr ago. A possible land bridge caused by the Deccan traps may account for this problem (de Wit, 2003; Masters *et al.*, 2005; Masters and de Wit under revision), but the fact that the primate sister groups have never been found on Madagascar needs to be explained for this model to be feasible.

Despite the phenomenal growth in molecular and fossil data that has occurred in recent years, major aspects of early primate evolution remain a mystery. The answer is surely out there, and as we continue to pick away at the traces and clues that have been left behind in karyotypes, molecular sequences and the fossil-bearing strata of the vast unexplored parts of the world, we must as surely find it.

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