

Primate homeland: forests and the evolution of primates during the Tertiary and Quaternary in Asia

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Abstract Primates evolved in the tropical forests of the Late Paleocene or Early Eocene. The cognitive, locomotor and life-history characteristics that define primates evolved under the equable and generally non-seasonal conditions that distinguish such forests. All primates since have carried the biological imprint of this original association with tropical forests. In Asia, the persistence of tropical forests in Indonesia from the Eocene onward has permitted tarsiers to endure and evolve, while other Eocene primates became extinct on their home continents. Following a disastrous decline in tropical forest distribution and primate diversity at the Late Eocene/Oligocene boundary, forests and primates rebounded during the Late Oligocene and Miocene. The dominant Old World primates of most of the Neogene were hominoids, which inhabited large tracts of woodlands and forests throughout Africa and Eurasia. These relatively large, frugivorous animals were quadrupedal, but many were capable of undertaking bridging postures that allowed them to stretch between arboreal substrates. Hominoids reached the apex of their evolutionary success in the Middle Miocene, then declined—as a result of the slow disappearance of their forest homes—in the Late Miocene, especially after 10 Ma. The extirpation of apes at this time can be traced to their inability to live in more seasonal and open habitats. Old World monkeys originated in forest biomes, but became the dominant primate of the late Neogene because of their ability to live in environments ranging from closed, non-seasonal rainforests to open savannahs and alpine meadows. This adaptability can be traced to their slightly faster life histories and their ability to thrive on a wide range of both high- and low-quality foods.

Key words: rainforests, seasonality, refugia, apes, Old World monkeys

Introduction

The importance of forests, particularly tropical rainforests, in primate evolution has long been recognized. It was not until 1986, however, that the single importance of this relationship was formalized by R.D. Martin in his new definition of primates (Martin, 1986), which started with the words “Primates are typically arboreal inhabitants of tropical and sub-tropical forest ecosystems” (p. 16). Studies of the primate fossil record and of global paleoenvironments have consistently related the early radiation and diversification of the order to the expansion of tropical forest ecosystems of the Early and Middle Eocene. This early association was of profound import in the evolution of primate cognition, locomotion, and life histories. The connection between an arboreal habitat and the evolution of the primate visual system and appendages is often stressed, but the connection between forest ecosystems and primate life histories is rarely made. Simply stated, the presence of widespread tropical forests in the Late Paleocene and Eocene made possible the evolution of some lineages of mammals with ‘slow’ life his-

tory characteristics, i.e. those with small litters, relatively long gestation and weaning periods, and relatively long life spans compared to others mammals of similar size. Primates exhibit these characteristics as well as relatively large brains at every stage of their development (Martin, 1986). The evolution of mammals with these features was made possible because of the phenology of the relatively non-seasonal forests in which they lived, especially because such environments provided year-round supplies of high-quality foods such as large insects, fruits rich in simple sugars, and oil-rich seeds. Under these conditions, primates enjoyed great success as a lineage, and the original association of primates and forests left an indelible imprint on the biology of all subsequent forms.

Forests and Primates of the Early Tertiary

The first confirmed appearance of primates in the fossil record is a contentious matter, but most authorities concur that Late Paleocene-aged specimens attributable to *Decoredon* and *Petrolemur* in China and *Altiaatlasius* warrant this distinction (Hooker, 1998). Paleontological and statistical evidence now suggests that Asia is the likely center of origin for primates, as well as for perissodactyls and artiodactyls (Beard, 1998, 2002; Bowen et al., 2002), but this remains somewhat controversial (Sigé et al., 1990; Simons and Ras-

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mussen, 1994).

The first appearance of primates appears to be tightly coupled to the extremely rapid environmental warming occurring at the Paleocene/Eocene boundary (Alroy et al., 2000; Wing and Harrington, 2001) (Figure 1). The Late Paleocene and Early Eocene witnessed the expansion of humid, multi-stratal forests at low and middle paleolatitudes, due to abundant precipitation, with evergreen rainforests becoming widespread in regions with megathermal temperatures (i.e. with a mean temperature in the coldest month of greater than 18°C, and exhibiting a very low mean annual range of temperatures) (Parrish, 1987; Upchurch and Wolfe, 1987; Morley, 2000). Mammalian faunas of the Early Eocene were dominated by small mammals (generally less than 1 kg), that were semiterrestrial and scansorial with respect to locomotion, and insectivorous or frugivorous in their dietary preferences (Collinson and Hooker, 1987; Gunnell, 1998; Hooker, 1998; Whybrow and Andrews, 2000). The mammals inhabiting Early and Middle Eocene forests were broadly analogous to modern ones, but their community structures emphasized terrestrial frugivores and arboreal insectivores to a much greater extent than do the tropical and subtropical forests of the present day (Jablonski, 2003).

By Early Eocene times, primates were represented by many species of lemur-like and tarsier-like forms, generally assigned to the superfamilies Adapoidea and Omomyoidea. These primates were among the most common of Early Eocene mammals, comprising an estimated 34 and 45 species, respectively, based on species counts in a well-respected primatology textbook (Fleagle, 1999). By the Middle Eocene, adapoids and omomyoids became less common in North America, but were present in substantial numbers in eastern Asia and Africa, with 38 and 43 total species in each superfamily, respectively.

Among Eocene primates, leaping was a common locomotor specialization, but it was not necessarily practiced in modes identical to those of modern prosimians and tarsiers. The success of leaping as an adaptation of Eocene primates is probably due to the fact that it is an efficient mode of transportation in tropical rainforests (especially within the understory) and that it facilitated the foraging for patchily distributed foods such as insects, fruits, and tree gums (Crompton, 1995; Emmons, 1995). The widespread dependence of Eocene prosimians on leaping specializations was certainly one of the phenomena that led to decline and eventual extinction of most species.

The Middle to Late Eocene witnessed a 15 Myr-long cooling trend, which had disastrous results for many forest-dwelling mammals residing in temperate latitudes. This trend ended with the 'terminal Eocene event' at 33.5 Ma, involving a coincidence of a sudden climatic shift and a major eustatic sea-level fall (Hooker, 2000). The primary consequence of this event for mammals was the dramatic reduction in the extent of tropical forests as a result of the cooling of the climate and increase in the latitudinal temperature gradient (Collinson and Hooker, 1987; Janis, 1993; Hooker, 2000). Here we see, for the first time in primate history, the devastating effects of the first major episode of increased environmental seasonality outside of tropical latitudes. Under these conditions, the many Holarctic adapoids and omomyoids dependent on tropical forest angiosperms and their associated insect communities were stuck without food resources, and without land bridges or other escape routes that would allow them to track the retreat of the rainforests.

In addition to adapoids and omomyoids, true tarsiers are also recognized in the fossil record, beginning in the later part of the Early Eocene, about 45 million years ago. The

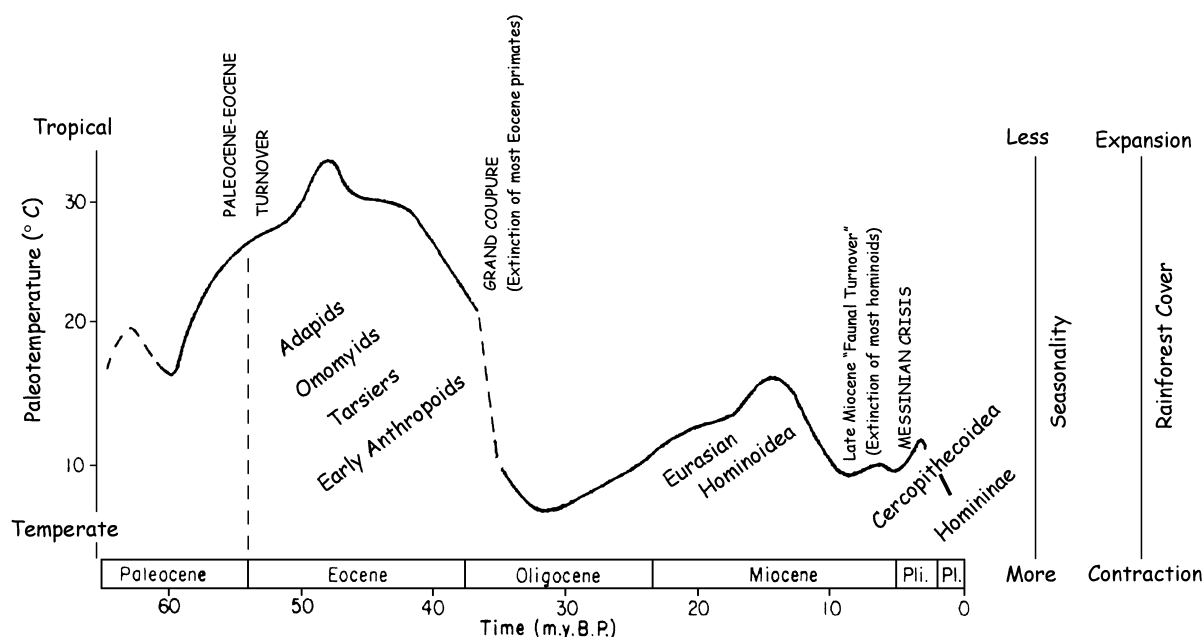


Figure 1. Paleotemperature curve for the Tertiary and Quaternary showing the major episodes of environmental change referred to in the text.

fossil record of tarsiers is poor, but clearly records the early origin, persistence, and apparently conservative level of branching evolution in the lineage. All known occurrences of fossil tarsiids are associated with a closed-habitat micro-mammal fauna characteristic of rainforest ecosystems (Jablonski, 2003). Tarsiers appear to have occupied the niche of the small-bodied nocturnal insectivore and carnivore of the tropical rainforest understory, an ecological role that appears to have changed little over the course of over 45 million years (Jablonski, 2003).

Tarsiids have maintained relictual distributions in southeastern Asia long after their close relatives on other continents became extinct, because of the persistence in southeastern Asia of stable, humid multistratal rainforest ecosystems from the earliest Tertiary to the present day. Of all the areas of the Old World once covered by tropical or paratropical rainforest in the Eocene, it is only small, low-latitude areas of Southeast Asia that have retained such forests through the Neogene.

The five recognized species of living tarsiers inhabit parts of Southeast Asia that have been covered with tropical rainforests continuously since the Middle Eocene (Gursky, 1999; Morley, 2000). Land connections between Southeast Asia and mid-latitude Asia since the earliest Tertiary allowed elements of Paleogene Northern Hemisphere rainforests to find refuge in the lower montane forests of Southeast Asia following the mid-Tertiary global climatic deterioration (Morley, 2000). This event has no parallel in other regions (Morley, 2000), and accounts for the fact the rainforests of Southeast Asia more closely resemble the rainforests of the Paleogene than do rainforests elsewhere.

Primates and the Environmental Dramas of the Late Tertiary

The 'terminal Eocene event' brought about a great retraction of tropical rainforests to a narrow belt of continental areas straddling the equator (Janis, 1993; Whybrow and Andrews, 2000). In many present-day temperate regions, a clear trend toward greater seasonality of rainfall and an increase in the mean annual temperature range can be distinguished from the Late Eocene onward, on the basis of fossil pollen and leaf assemblages (Leopold et al., 1992; Wolfe, 1992). These climatic changes led to a great increase, from 34 Ma onward, in areas occupied by 'low biomass vegetation'—dry forests, dry woodlands, wooded grasslands, and grasslands (Behrensmeyer et al., 1992; Leopold et al., 1992; Retallack, 1992b). These environments supported a diversity of mammals that could survive in more seasonal environments, characterized by greater annual fluctuations of rainfall, temperature, and food availability.

The primates of the early Neogene comprised Eocene survivors and a major radiation of new, larger primates, the Anthropoidea. Anthropoids, despite probable origins in Asia in the Middle Eocene (Beard, 1998), became extraordinarily diverse and abundant in the Late Eocene and Early Oligocene of northern Africa and came to dominate the arboreal frugivorous and insectivorous niches (Whybrow and Andrews, 2000). The earliest fossil catarrhines date to the latest Eocene and Early Oligocene and are derived from

deposits representing humid riverine tropical forests and swamp forests close to the southern border of the Tethys Sea (Rasmussen, 2002). These catarrhines, such as *Aegyptopithecus zeuxis* and species of *Propliopithecus*, appear to have been generalized quadrupeds that lacked the locomotor specializations of later catarrhines (Fleagle and Simons, 1978, 1982; Rasmussen, 2002). In their diet and locomotion, the Early Oligocene anthropoids exhibit a range of body sizes and adaptations comparable to those of modern platyrrhines, being mostly frugivorous, insectivorous, and seed-eating, and all arboreal quadrupeds and leapers ranging in approximate size from 5 to 10 kg (Fleagle and Reed, 1999).

The end of the Oligocene and beginning of the Miocene, about 23 Ma, marks the first appearance of hominoids (apes *sensu lato*) and Old World monkeys. During the Early Miocene, climates became warmer and considerably drier, with the establishment of a steeper latitudinal thermal gradient (Kennett, 1985; Behrensmeyer et al., 1992). This trend was associated with major orogenic events, which resulted in the formation of the Rocky Mountains, Andes, and Himalayas (Janis, 1993). The Early Miocene witnessed a return of global climatic equability, although not to Early Eocene levels. This was reflected in an increase in the distribution of tropical rainforests (Morley, 2000), flanking paratropical forests and subtropical woodlands, and the emergence of chaparral or thorn scrub on the western sides of continents (Janis, 1993).

The catarrhines of the Early Miocene are mostly of modern aspect, with most thought to be stem hominoids (e.g. Harrison, 2002). The early apes comprise a mixture of pronograde arboreal quadrupeds (unlike modern apes) such as *Griphopithecus* and arboreal suspensory feeders such as *Oreopithecus* more reminiscent of modern hominoids (Begun, 2002; Pilbeam, 2002). Their body sizes were in the approximate range of 5–20 kg (Fleagle and Reed, 1999). The early Old World monkeys such as *Victoriapithecus* were terrestrial and smaller, ranging in body size from 3 to 5 kg (Benefit and McCrossin, 2002). The habitats in which most of these catarrhines lived were forested and are best described as subtropical woodlands. These woodlands were probably structurally unlike equatorial forests (Andrews et al., 1997; Harrison, 2002; Pilbeam, 2002), with larger physical gaps between trees, fewer epiphytes and lianas, and a thinner canopy (Parker, 1995). In these habitats, one of the most significant adaptations made by many apes (especially *Pliopithecus* and *Oreopithecus*) involved the evolution of bridging postures, which permitted the animals to cross gaps in the forest canopy and to harvest foods in the terminal branches of trees without recourse to leaping or coming to the ground. This adaptation has been interpreted as one promoting the harvesting of widely separated, high-quality food items (Chivers, 1991; Andrews et al., 1997).

Catarrhine fossils of the Miocene derive mostly from what are thought to have been subtropical woodland habitats that had a moderately seasonal pattern of rainfall and a moderate range of annual mean temperatures (Morley, 2000). These habitats exhibited a moderate level of seasonality with respect to the productivity of potential catarrhine foods such as fruits, seeds, and young leaves. Most species of Miocene apes appear to have enjoyed mostly frugivorous diets similar

to those of living apes (Ungar and Kay, 1995). Miocene apes exhibited prolonged life histories (Kelley, 1997, 2002), which are compatible with stable environments with predictable levels of resource productivity (Jablonski et al., 2000).

The most widespread distributions and highest levels of diversity of ape species were attained when Miocene forests (including subtropical woodlands) reached their maximum distributions, approximately 12–17 Ma (Bernor, 1983; Jablonski et al., 2000). Old World monkey species were still uncommon elements of forest faunas at this time (Jablonski and Kelley, 1997; Jablonski and Whitfort, 1999; Benefit and McCrossin, 2002). Thus, under the relatively equable regimes of Early Miocene, the most successful catarrhines were apes. Despite being selective feeders, obligate tree-dwellers (as a result of their postural and locomotor specializations), and exhibiting a slow life history, they survived and diversified.

The climatic deterioration at the end of the Miocene and its effects on mammalian evolution have been studied in great detail (e.g. Quade et al., 1989; Retallack, 1992a; Cerling et al., 1993; Retallack et al., 1995; Barry et al., 2002). Beginning 13 Ma, temperatures began a consistent decline that persisted through the Pliocene. This is associated with a retreat of tropical floras and the expansion of temperate deciduous tress, grasses, composites, and herbaceous dicots (Behrensmeyer et al., 1992). Environmental change accelerated from 10 Ma onward, as a result of increasing continental fragmentation due to plate tectonic movements and to mountain-building. These events, in concert with extensive migrations of fauna between Africa and Eurasia, brought about what has been referred to as the Late Miocene 'faunal turnover'. In Asia, paleoecological evidence points also to a clear shift to a drier and more seasonal climate, especially after 9.2 Ma, and the appearance of open woodlands or grassy woodlands as early as 7.4 Ma (Barry et al., 2002).

For primates, the most important consequence of the gradual but inexorable increase in environmental seasonality beginning in the Late Miocene was the steady and dramatic decline in the distribution of suitable forest habitats, affecting most especially the belt of subtropical woodland inhabited by the apes of Eurasia (Bernor, 1983; Fortelius et al., 1996). For most apes, the environmental deterioration of the Late Miocene meant extinction and the consequent collapse of diversity in a major primate clade. The strong dependence of apes on forest habitats of low seasonality was related to their slow life histories, their mostly frugivorous 'high-quality' diets, and modes of posture and locomotion that precluded easy terrestriality in more open habitats (Jablonski et al., 2000).

The Late Miocene was not a time of decline for all primate lineages. During this period, the Old World monkeys (superfamily Cercopithecoidea) and a single lineage of apes, the hominins (subfamily Homininae) started on a long path toward ecological dominance. The success of these groups can be traced to their possession of exaptations that turned into excellent adaptations for the drier and more seasonal environments of the latest Tertiary and Quaternary. Because of limitations of space, only the evolution of the Old World monkeys in relation to waning and waxing forest environ-

ments will be discussed here.

The success of Old World monkeys can be linked to their possession of life history, dietary and locomotor characteristics that are distinct from those of apes. The life history parameters of cercopithecoids are characterized by an earlier age for onset of reproduction, shorter gestation times, shorter weaning periods, and short interbirth intervals. Compared to apes, Old World monkeys thus exhibit an overall capacity for a much higher intrinsic rate of increase of population and an ability to time their breeding and birth schedules in highly seasonal habitats (Jablonski et al., 2000). With respect to diet, monkeys are more eclectic feeders than apes and can subsist on generally lower-quality foods, when quality is defined in terms of easily realized energy yield (Temerin and Cant, 1983; Wrangham et al., 1998; Jablonski et al., 2000). Colobine monkeys are worthy of special note here because their capacity for fermentation of cellulose and hemicellulose through the action of bacterial symbionts living in the forestomach allows them to partake of vegetation that contains significant amounts of fiber and toxic secondary compounds or antifeedants, which tend to deter many herbivores (Bauchop, 1978; Wrangham et al., 1998).

The design of the locomotor apparatus in Old World monkeys has also worked to their evolutionary advantage. Most Old World monkeys have remained generalized quadrupeds that can generally move comfortably in the trees or on the ground through open or closed environments. This afforded them an adaptive flexibility that most apes (especially those in Asia) lacked, and that was of great importance in the more open environments of the Late Tertiary and Quaternary.

The life history, dietary, and locomotor characteristics that permitted Old World monkeys to undergo tremendous diversification and range expansion in the Late Miocene continued to work well for the group during the Pliocene and Pleistocene, periods associated with rapidly alternating periods of expansion and contraction of Afrotropical, lowland, and subtropical forests (Eeley and Lawes, 1999; Jablonski et al., 2000). Only under the extreme seasonal conditions and dramatically fluctuating climates of the latest Pleistocene were monkey species driven to extinction or into more salubrious forest refugia (Jablonski et al., 2000).

Conclusions

For roughly the first third of their known evolutionary history, from about 50 to 33 Ma, primates lived in equable tropical and paratropical forests. Primates evolved their defining characteristics in such habitats, and from that time onward, primates have borne the 'biological imprint' of their association with relatively non-seasonal forests. Since the Eocene, increasing fragmentation of continents, changes in atmospheric and oceanic circulation, and major mountain-building events have created profound changes in global climate. Long periods of climatic equability, such as those witnessed during the Early and Middle Eocene, have been supplanted by less stable regimes, characterized in general by heightened seasonality of temperature and rainfall. The 'terminal Eocene event' extirpated most of the world's primate fauna, except for those forms like tarsiers, lemurs, and lorises, which survived in the relict rainforests and other lowland

forests of Asia and Africa. The next major period of primate diversification occurred in the Early Miocene, beginning about 20 Ma, primarily involved early hominoids (apes). These animals were primarily frugivorous and mostly agile tree climbers. This radiation came slowly to an end under the drier conditions of the Late Miocene. Most apes became extinct at this time, because of the constraints of their slow life histories, their dependence on year-round supplies of high-quality foods such as fruits, and modes of locomotion that precluded their safe and efficient progression on the ground in more open environments.

The last major group of nonhuman primates to undergo major periods of diversification and range expansion were the Old World monkeys, who did so beginning under the strongly seasonal conditions of the terminal Miocene, 6–7 Ma. Monkeys succeeded where apes failed by establishing a pattern of somewhat faster life histories, an ability to survive on eclectic, often low-quality diets, and the retention of an unspecialized quadrupedal locomotor habitus.

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