

# Primate Origins: Implications of a Cretaceous Ancestry

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## Key Words

Ancestral primates · Body size · Continental drift · Fossil record · Cretaceous/Tertiary boundary · Palaeoclimates · Primate origins

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## Abstract

It has long been accepted that the adaptive radiation of modern placental mammals, like that of modern birds, did not begin until after the Cretaceous/Tertiary (K/T) boundary 65 million years (Ma) ago, following the extinction of the dinosaurs. The first undoubted fossil relatives of modern primates appear in the record 55 Ma ago. However, in agreement with evidence from molecular phylogenies calibrated with dates from denser parts of the fossil record, a statistical analysis of the primate record allowing for major gaps now indicates a Cretaceous origin of euprimates 80–90 Ma ago. If this interpretation is correct, primates overlapped with dinosaurs by some 20 Ma prior to the K/T boundary, and the initial radiation of primates was probably truncated as part of the major extinction event that occurred at the end of the Cretaceous. Following a review of evidence for an early origin of primates, implications of this are discussed with respect to the likely ancestral condition for primates, including a southern continental area of origin and moderately large body size. The known early Tertiary primates are re-interpreted as northern continental offshoots of a 'second wave' of primate evolution.

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## Introduction

Over recent decades, the number of extant primates recognized has been steadily rising. A recent review lists 376 species [Groves, 2005], increased from 356 in a previous review just 4 years earlier [Groves, 2001]. It is generally accepted that these

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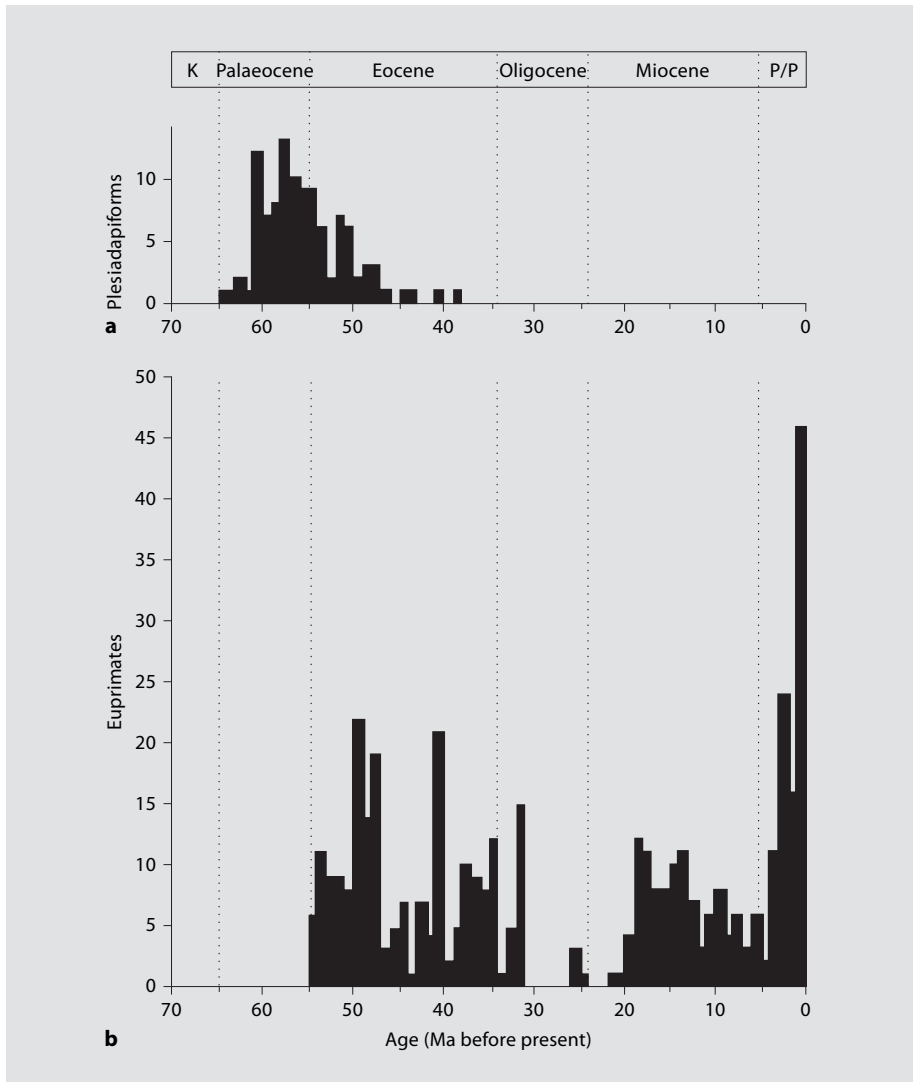
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modern primates belong to 5 'natural groups': (1) lemurs; (2) lorisiforms; (3) tarsiers; (4) platyrrhines (New World monkeys); (5) catarrhines (Old World monkeys, apes and humans). The currently dominant interpretation is that there was an early dichotomy between strepsirrhines (lemurs + lorisiforms) and haplorhines (tarsiers, platyrrhines and catarrhines). Although the affinities of tarsiers are still subject to active debate [Yoder, 2003], the balance of morphological and molecular evidence indicates that they are related to 'higher' primates (platyrrhines + catarrhines) rather than to strepsirrhines [Martin, 1990; Shoshani et al., 1996; Schmitz and Zischler, 2004; Kay et al., 2004].

In seeking to determine the causes behind evolutionary processes in primates and other organisms, the most important step is to establish the context within which specific evolutionary events took place. Accurate contextualization of such events requires knowledge of: (a) the phylogenetic context within which it took place, (b) the chronological context, i.e. when it took place, and (c) the environmental context, i.e. what climatic and other relevant environmental conditions prevailed at that time. With respect to the origins of primates, establishing an accurate chronological context takes on a pivotal role due to the complete absence of any directly relevant fossil evidence [Martin, 1986, 1993; Tavaré et al., 2002; Soligo and Martin, 2006; Soligo et al., 2007].

Undoubted fossil primates of modern aspect are documented back to the beginning of the Eocene epoch, 55 Ma (million years) ago (fig. 1). They are now widely labelled 'euprimates' to distinguish them from plesiadapiforms ('archaic primates'), which are largely confined to the Palaeocene (55–65 Ma ago), although some representatives survived into the mid-Eocene. Plesiadapiforms may or may not be related to primates [Martin, 1990; Bloch and Boyer, 2002], but regardless of their affinities it is now generally accepted that they diverged prior to the common ancestry of the euprimates. With the possible exceptions of North African *Djebelemur martinezi* [Hartenberger and Marandat, 1992], *Algeripithecus minutus* [Godinot and Mahboubi, 1992] and *Tabelia hammadae* [Godinot and Mahboubi, 1994], euprimates from Early Eocene deposits have so far been found only at sites in the northern continents (North America, Europe and Asia). Although they have primarily been documented from North America and Europe, the earliest substantial euprimate fossil – an almost complete skull of *Teilhardina asiatica* – has recently been reported from China [Ni et al., 2004].

Eocene euprimates, along with a few offshoots surviving into the Miocene, generally have no direct connection with modern primates. For the most part, fossil euprimates that are directly related to one of the 5 natural groups of extant primates first appear in the early Miocene, although there are a few exceptions dating back to the middle Eocene [Miller et al., 2005]. Most Eocene primates can be allocated either to Adapiformes or to Omomyiformes, and many authors [Kay et al., 1997; Fleagle, 1999] link adapiforms to strepsirrhines and omomyiforms to haplorhines. An alternative possibility is, however, that a separate radiation of early primates leading to the adapiforms and omomyiforms was derived from a lineage that diverged prior to the last common ancestor (LCA) of modern primates [Martin, 1993; Ross, 2003; Martin and Ross, 2005]. It has been argued that the close similarity between early Eocene adapiforms and omomyiforms indicates that they cannot be far removed from the LCA of euprimates [Gingerich, 1986; Gebo, 2004]. However, if adapiforms and omomyiforms together represent a separate northern continental radiation of



**Fig. 1.** Chart showing the temporal distribution of archaic primates (plesiadapiforms; **a**) and primates of modern aspect (euprimates; **b**). Plesiadapiforms are largely restricted to the Palaeocene epoch, whereas euprimates abruptly appear in the fossil record at the beginning of the Eocene. Note the approximately 6-Ma gap in the euprimates fossil record in the Oligocene, between 25 and 31 Ma ago.

euprimates, this argument is invalid. The close similarity seen in early representatives of the two groups would simply reflect their relatively recent derivation from a northern continental common ancestor.

The standard interpretation of primate origins [Conroy, 1990; Sussman, 1991; Gebo, 2004] is that living and fossil euprimates are derived from a common ancestor

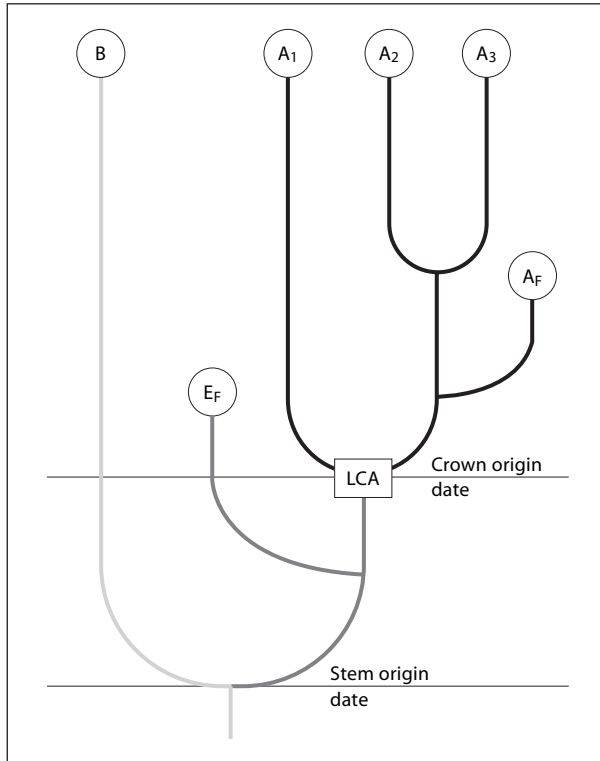
that evolved some time during the Palaeocene, thus postdating the end of the Cretaceous (65 Ma ago). Indeed, the LCA of primates is often placed close to the Cretaceous/Tertiary (K/T) boundary even by those who include the plesiadapiforms as part of their adaptive radiation. Such interpretations reflect the customary palaeontological approach succinctly expressed by Simpson [1965, p. 1]: '... first appearances in the known record are accepted as more nearly objective and basic than opinions as to the time when each group really originated.' It also accords with the traditional interpretation that the emergence and adaptive radiation of modern mammals and birds took place in response to the ecological vacuum opened up by the extinction of dinosaurs at the K/T boundary. According to this view, the evolution of modern mammals and birds is hence confined to the Cenozoic, widely known as the 'Age of Mammals'.

Estimation of divergence times, for which the fossil record provides the only direct guide, is of intrinsic interest in investigating the phylogeny of any group of organisms. Any attempt to link branching events in the primate tree with other factors, such as biogeography, climatic change or the presence and evolution of other groups of organisms, depends upon reliable inference of dates. Reliable inference of divergence times for both mammals and birds is of particular interest precisely because of the timing relative to the K/T boundary 65 Ma ago. With only a few possible exceptions, it remains true that convincing fossil relatives of modern mammals and birds are limited to the Cenozoic. Although fossil relatives of both groups are known from the Cretaceous, the predominant palaeontological view is that those fossils are archaic forms with little or no direct connection to the major radiations after the K/T boundary [Carroll, 1997; Benton, 1999; Foote et al., 1999; Wible et al., 2005]. Among other things, assessment of the potential relevance of continental drift for the origin and diversification of modern orders of mammals and birds depends on the timing of the adaptive radiations of those orders relative to the K/T boundary. If those radiations are essentially confined to the Cenozoic, as in the traditional interpretation, then continental drift can only have had limited relevance. However, if the adaptive radiations of modern mammals and birds began well back in the Cretaceous, continental drift could have played a significant role, and the positions of the southern continents and their relevance to determining contemporary local environments would acquire particular importance [Martin, 1990].

With the advent of molecular techniques of phylogenetic inference, reliable estimation of divergence times from the fossil record has become even more important because of the need for an accurate calibration of trees. Molecular data can yield patterns (topologies) but not branching times, so the use of earliest known fossil representatives of individual groups to calibrate nodes in molecular trees has become standard practice. Yet such direct reading of the fossil record requires that the record be complete enough for this to be reasonable. Because of gaps in the fossil record, however, use of the first known fossil representative to infer the age of any given group is potentially unreliable. It is vital to recognize that this approach can yield only a *minimum* estimate for any divergence time and that attempting to set an upper limit with an incomplete fossil record is hazardous. The degree of underestimation of actual divergence times through direct reading of the fossil record will generally increase with decreasing sampling density. The reliable inference of divergence times from fossil evidence hence requires explicit consideration of the effect of gaps.

As there is no convincing fossil evidence for the LCA of euprimates, some increment must obviously be added to the age of the earliest known undoubted fossil representative. With a relatively poor fossil record, the required increment is likely to be large [Martin, 1986, 1990]. The earliest known fossil euprimates are dated at about 55 Ma, but there are undeniable major gaps in the record. Madagascar lemurs (including the recently extinct subfossil species) account for around a quarter of modern primate species, yet not a single fossil relative has so far been found on the island. With the sole exception of Oligocene *Bugtilemur* in Pakistan, tentatively linked to modern dwarf lemurs in the family Cheirogaleidae [Marivaux et al., 2001; but see Seiffert, 2007], the fossil record of Madagascar lemurs remains totally undocumented. If *Bugtilemur* is a cheirogaleid, there is a ghost lineage of at least 30 Ma between this fossil and modern cheirogaleids on Madagascar, and older ghost lineages leading to the other extant families of lemurs. If *Bugtilemur* is not a cheirogaleid but simply an early strepsirrhine, all modern lemurs have a ghost lineage of at least 37 Ma, as fossil members of their sister group (lorisiforms) are now known to date back that far [Martin, 2003; Seiffert et al., 2003, 2005]. Another example of major gaps in the record is provided by the New World monkeys. No convincing relative of marmosets and tamarins (Callitrichidae) has yet been reported, although almost 34% of New World monkeys and more than 11% of extant primates are callitrichids. Undoubted fossil relatives of cebid monkeys indicate that the ghost lineage leading to modern callitrichids extends over at least 20 Ma [McFadden, 1990; Flynn et al., 1995]. It is also noteworthy that there is a gap of several million years in the Oligocene epoch in the primate fossil record as a whole, between the early Oligocene of the Fayum in Egypt and Taqah in Oman, and the late Oligocene deposits of Lothidok, Kenya, and Salla, Bolivia (fig. 1).

Direct reading of the fossil record for any given group can also lead to the questionable inference that its origin is located in or close to the geographical region that has yielded the earliest known fossil representatives. The known late Cretaceous/early Cenozoic fossil record for modern mammals is heavily biased in that northern continents are far better documented than southern regions. Foote et al. [1999] noted the lack of known late Cretaceous mammals in the south (Africa, Australia, Antarctica), at least partly reflecting the fact that recovery of fossil vertebrates is rare at low latitudes and maximal at medium latitudes. In fact, even after the K/T boundary, known Palaeocene mammals generally belong to archaic groups with little or no direct connection to extant groups, as is the case with plesiadapiforms relative to euprimates. Clearly recognizable members of extant orders first appear in the northern continental fossil record at the base of the Eocene, about 55 Ma ago. Transitional forms are generally unknown. This applies not only to euprimates but also to other eutherian groups such as bats and modern hoofed mammals (artiodactyls, perissodactyls). Modern carnivores do not appear in the record until the middle Eocene, but hyaenodontid creodonts (the sister group) do appear 55 Ma ago [Gunnell, 1998; Bowen et al., 2002]. This appearance of modern mammals in the northern continental record coincides with a global increase in temperatures during the late Palaeocene and early Eocene [Wilf and Labandeira, 1999; Zachos et al., 2001; Wing et al., 2005]. It is generally accepted that early Eocene modern mammals must have migrated into the northern continents from elsewhere [Krause and Maas, 1990; Bowen et al., 2002], but convincing fossil evidence for their source area(s) remains elusive.



**Fig. 2.** Illustration of terminological differences regarding divergence times. Species  $A_1$ ,  $A_2$  and  $A_3$  are living members of crown clade A, derived from the LCA.  $A_F$  is the earliest known fossil member of crown clade A (black lines), providing a minimum date for its origin. The stem (dark grey lines) is formed by the lineage connecting the LCA to its divergence from the closest sister group (B), together with any early fossil offshoots such as  $E_F$ . It is crucial to distinguish between the initial divergence separating clades A and B (stem origin date) and the time at which the crown members of clade A began to diverge from the LCA (crown origin date).

### Definition of Divergence Times

In discussing divergence times, it is essential to distinguish between *crown* and *stem* groups [Jefferies, 1979, 1986; Smith and Peterson, 2002]. Modern representatives of any group, together with all fossils derived from their LCA, constitute the crown clade (fig. 2). The stem is formed by the fossil lineage, together with any offshoots, leading to the LCA from the earlier node where the sister group diverged. For any extant species group, the time of divergence of its ancestral stem lineage from the sister group lineage (stem origin date) must be distinguished from the time at which the crown members of that group began to diverge (crown origin date).

The crown origin date is effectively equivalent to the age of the LCA, and it can be assumed that at least some defining features of the crown group had emerged by that stage. The size of the interval between the stem origin and crown origin dates

may vary considerably from group to group. Depending on the aims of the investigator, either the age of the LCA of a crown clade or the divergence date of the stem lineage may be of primary interest. Unfortunately, however, crown origin dates and stem divergence dates have often been confused.

The distinction between crown and stem origins connects up with the concept of 'explosive', 'long-fuse' and 'short-fuse' models used by Archibald and Deutschmann [2001] in discussing the timing of the adaptive radiation of modern eutherians relative to the K/T boundary. In the explosive model, both the stem origin dates and the LCAs of modern eutherian orders are set largely or exclusively after the K/T boundary. The explosive and long-fuse models agree in placing the LCAs for modern eutherian orders at or after the K/T boundary, but the long-fuse model differs in invoking extensive stem lineages in the Cretaceous. In the short-fuse model, by contrast, crown origin dates for many eutherian orders are also placed far back in the Cretaceous, quite close to the stem origin dates. With a very long stem lineage leading to the LCA of any modern eutherian order, as is the case in the long-fuse model, initial divergence from other orders is located well back in the Cretaceous, but defining characters of the LCA may only have evolved much later.

### **Molecular Evidence for Early Divergence Times**

Various studies using molecular data have indicated that stem divergences of several modern eutherian orders occurred far back in the Cretaceous, thus agreeing with the long-fuse or short-fuse models but conflicting with the explosive model. Although calibration of molecular trees always requires fossil evidence, these secondarily inferred divergence times are often considerably earlier than the earliest known fossil representatives of the groups that are being investigated. However, if gaps in the fossil record lead to serious underestimation of any divergence date because of direct reliance on the earliest known fossil relative, there will be ramifications throughout any molecular tree calibrated with that date. For euprimates, calibration of molecular data with fossil dates internal to the primate tree often seems to support relatively recent divergence times read directly from the fossil record [Yoder and Yang, 2000; Stauffer et al., 2001; Schrago and Russo, 2003], although this is not always the case [Steiper et al., 2004].

Calibration of eutherian molecular trees with various non-primate dates derived from relatively dense parts of the fossil record commonly indicates early stem divergence of primates from other mammals some time during the middle late Cretaceous [Janke et al., 1994; Arnason et al., 1996, 1998; Hedges et al., 1996; Springer et al., 1997; Kumar and Hedges, 1998; Springer et al., 2003]. Although some analyses of eutherian evolution based on molecular evidence have yielded divergence dates closer to those indicated by direct reading of the fossil record [Douzery et al., 2004; Benton and Ayala, 2003], it must always be borne in mind that calibration dates used in most of these studies are *minimal* dates based on first appearances in the known record. Inference of divergence times in molecular phylogenies also depends on the validity of the 'molecular clock' [Easteal et al., 1995; Bromham and Penny, 2003]. It is now generally recognized that rates of molecular evolution can, in fact, vary substantially between lineages, requiring 'local clocks' rather than a single global clock [Huelsenbeck et al., 2000; Yang and Yoder, 2003]. The inference that primates di-

verged from other mammals about 90 Ma ago has been criticized for this reason, particularly with respect to the very early calibration date of 310 Ma for the split between diapsid and synapsid reptiles used by Hedges et al. [1996] and Kumar and Hedges [1998].

The molecular studies cited thus far are primarily relevant to the time of separation of primates from other eutherian groups (i.e. the stem origin date in fig. 2). Although molecular trees calibrated with various non-primate fossil dates consistently indicate divergence of the lineage leading to extant primates from other eutherian lineages about 90 Ma, it is theoretically possible that morphologically recognizable euprimates first emerged at or after 65 Ma ago. Few molecular studies have directly addressed the age of the LCA of extant primates (i.e. the crown origin date in fig. 2), but it is obvious from the relatively short genetic distances involved that initial divergence from the euprimate LCA (i.e. between strepsirrhines and haplorhines) must have occurred quite soon after the primate stem lineage diverged from other eutherians. Even if rates of molecular evolution vary markedly, the data surely conflict with divergence between primates and other eutherians about 90 Ma followed by up to 30 Ma before the LCA of recognizable euprimates emerged. In one study that directly addressed this issue, Arnason et al. [1998] indicated that the split between strepsirrhines and higher primates occurred about 80 Ma ago, some 10–15 Ma after the primate lineage diverged from other eutherians. It is also worth noting that in a Bayesian approach to estimate the time of origin of Malagasy lemurs, where the primate crown group origin was used as a calibration point with a prior 63–90 Ma, the models mainly converged on a date of about 85 Ma ago for the LCA of living primates [Yoder and Yang, 2004].

During the last few years, substantial molecular data sets have been used to generate overall phylogenetic trees clarifying likely relationships among modern eutherian orders [Madsen et al., 2001; Murphy et al., 2001a, b]. Although reconstruction of higher-level relationships among mammalian orders had been attempted using classical morphological evidence [Novacek and Wyss, 1988; Novacek, 1992], much uncertainty remained. One major novel finding from these large-scale molecular studies has been consistent identification of 4 eutherian superclades: Afrotheria, Euarchontoglires, Laurasiatheria and Xenarthra. The endemic African clade Afrotheria, already indicated by earlier studies of DNA sequences [Springer et al., 1997, 1999; Waddell et al., 1999], has been confirmed by analysis of nuclear retroposons [Nikaido et al., 2003]. Euarchontoglires includes primates, colugos and tree shrews (i.e. 'archontans' without bats) along with rodents and lagomorphs ('glirans'). Laurasiatheria combines artiodactyls, cetaceans, perissodactyls, carnivores, pangolins, bats and eulipotyphlan insectivores (hedgehogs, moles and shrews). Xenarthra is a small assemblage of Neotropical edentates (anteaters, armadillos and sloths). Springer et al. [2003] calibrated 9 scattered nodes in the molecular tree of Murphy et al. [2001b] and applied a dating method allowing differential rates of evolution. It was concluded that stem divergences between eutherian orders generally occurred during the Cretaceous, whereas crown divergences within orders mainly took place around or after the K/T boundary. However, radiation from LCAs that existed prior to the K/T boundary was indicated for Eulipotyphla, Primates (at 77 Ma), Rodentia and Xenarthra.

Mounting evidence indicating a Cretaceous origin for many modern groups of eutherian mammals is paralleled by similar findings for birds. As with mammals,



the traditional view is that the evolution of modern birds is largely confined to the Cenozoic, with an 'explosive' adaptive radiation of modern birds after the K/T boundary [Feduccia, 1995]. However, several lines of molecular evidence have placed the LCAs of various modern bird groups in the Cretaceous [Hedges et al., 1996; Cooper and Penny, 1997; Waddell et al., 1999]. As with eutherians, reconsideration of the timing of bird evolution in the light of molecular evidence has led to increased emphasis on continental drift and a consequent greater role for the southern continents [Cracraft, 1986, 2001]. In fact, a new fossil find has confirmed the presence of modern birds in Antarctica during the late Cretaceous [Clarke et al., 2005]: *Vegavis* has been identified as a member of waterfowl (Anseriformes), being most closely related to true ducks (Anatidae).

### **Statistical Evidence for an Early Divergence of Primates**

Several recent studies designed to assess the completeness of the mammalian fossil record [Alroy, 1999; Foote et al., 1999, Foote and Sepkoski, 1999] concluded that gaps do not pose a major problem for estimating divergence times and that adaptive radiation of modern eutherians is essentially restricted to the Cenozoic. Alroy [1999] inferred from a statistical analysis of the North American fossil record for mammals that there were fewer species during the latest Cretaceous than during any interval of the Cenozoic and that massive diversification took place during the early Palaeocene. Given that known Cretaceous mammals were generally small and that after the K/T boundary there was a rapid radiation, accompanied by an increasing range of body sizes, he saw the evidence as 'entirely compatible with the existence of a few Cretaceous splits among modern mammal lineages'. But such studies have 2 limitations: (1) attention is focused heavily on the North American mammalian fossil record, which is unusually dense and well documented; (2) analysis is confined to the fossil record, so there is no external check on its completeness. In considering gaps in the record, the relationship between the numbers of living and fossil species is a highly informative input. The array of extant species in the tree can clearly provide some guide to the number of extinct species. Hence, living and fossil species should be considered together when assessing the completeness of the fossil record and inferring divergence times.

Martin [1993] made an initial approach to estimating the age of the euprimate LCA by setting out from the array of approximately 200 living species and 186 fossil species recognized at that time. Two simple assumptions were made: (1) the number of extant primate species was achieved by linear expansion from a single ancestral species; (2) fossil species had a standard survival time of 1 Ma. On this basis, it was calculated that less than 4% of extinct primate species are documented in the known fossil record. Taking this low sampling level into account, it was inferred that the age of the LCA of crown primates was likely to be about 80 Ma ago, some 25 Ma earlier than the first known fossil representatives [Martin, 1993]. This inference was subsequently challenged by Gingerich and Uhen [1994], who used an alternative approach to calculate an extremely low probability ( $p = 5 \times 10^{-9}$ ) for primates to have existed 80 Ma ago. However, although the number of living species is initially entered into that model, it later falls out of the equation. As a result, the model is insensitive to modern species diversity or estimated preservation rates. It is set to return the high-

est probability for the scenario where the age of the LCA is equal to the oldest fossil of that group, thus in effect arguing that the more a scenario differs from a direct reading of the fossil record, the less likely it is to be real. The pitfalls of this approach are demonstrated by applying it to estimating the probability that primates existed during an estimated 6-Ma-long gap in the Oligocene fossil record from which no primates have yet been recovered. Although primates must clearly have existed during that time, calculations using the method of Gingerich and Uhen [1994] returned a probability that was in fact even somewhat lower than that of an 80-Ma LCA of living primates [Soligo et al., 2007]. Even following a recently proposed revision of the age of the later Fayum deposits, which reduced the Oligocene gap to approximately 4 Ma [Seiffert, 2006], the probability for primate life during that time according to the method of Gingerich and Uhen [1994] remains virtually nil at  $2 \times 10^{-13}$ .

Tavaré et al. [2002] subsequently applied a more realistic, novel statistical approach to the problem of inferring the age of the LCA from a patchy fossil record. They determined a most likely age of 81.5 Ma (95% confidence interval: 72.0–89.6 Ma) for the LCA of living primates. They also estimated that no more than 7% of all primate species that have existed are known as fossils. It should be noted that this approach is designed to determine the crown origin time of euprimates (i.e. the date of initial divergence between strepsirrhine and haplorhine primates) and hence excludes the potential argument that early relatives of primates might have existed during the latter part of the Cretaceous but were not recognizable as such because the defining features of primates had not yet emerged. The results obtained indicate that any shared derived features of strepsirrhine and haplorhine primates attributable to their LCA were already present at least 80 Ma ago. This clearly predicts the existence of Cretaceous euprimates possessing defining features such as relatively large, forward-oriented orbits, a postorbital bar along the outer margin of each orbit, formation of the auditory bulla from the petrosal bone and a prehensile foot with a divergent hallux [Martin, 1990] (fig. 3).

It can sometimes be considered moot whether certain early fossil forms attributed to a taxon are basal members of its crown clade or offshoots from its stem lineage. In the case of primates, this applies to early Cenozoic forms in the infraorders Adapiformes and Omomyiformes. Although adapiforms and omomyiforms are widely accepted as members of the crown clade of primates, it has also been suggested that these early Cenozoic fossils may constitute a parallel radiation derived from the stem lineage leading to the LCA of extant primates [Martin, 1993, 2006; Martin and Ross, 2005]. In the analyses reported by Tavaré et al. [2002], adapiforms and omomyiforms were included as members of the primate crown clade. An alternative calculation allowing for the possibility that some fossil euprimates branched away prior to the LCA of extant primates yields an earlier date for the common ancestor of euprimates: 85.9 Ma, with 95% confidence limits of 73.3–95.7 Ma [Soligo et al., 2007].

Another potential criticism of the approach taken by Tavaré et al. [2002] is that different identification criteria are used for extant and fossil species. For extant species, for example, the advent of chromosomal and molecular methods has permitted identification of 'cryptic species' that were not immediately apparent from morphological evidence alone. Many (but by no means all) new primate species recorded by Groves [2001, 2005] were identified largely or exclusively using chromosomal or mo-



**Fig. 3.** Hypothetical reconstruction of a Cretaceous common ancestor of euprimates. This reconstruction is based on the inference that the ancestral primate would have had a body mass exceeding 1 kg and would have produced a single, precocial neonate. Other defining features would have been relatively large, forward-oriented eyes and a prehensile foot with a divergent hallux (drawing by Nancy Klaud).

lecular evidence. However, it should also be noted that Alroy [2002] examined historical rates of invalidation and revalidation of named fossil species by applying a 'flux ratio' equation to his data set for 4,861 North American mammal palaeospecies. He came to the conclusion that 24–31% of currently accepted names will eventually prove to be invalid. Hence, for any group of mammals, the number of fossil species that have been recognized from the currently available specimens is likely to decrease rather than increase in the future, thus offsetting any potential overestimation of the number of extant species relative to fossil species in our current data.

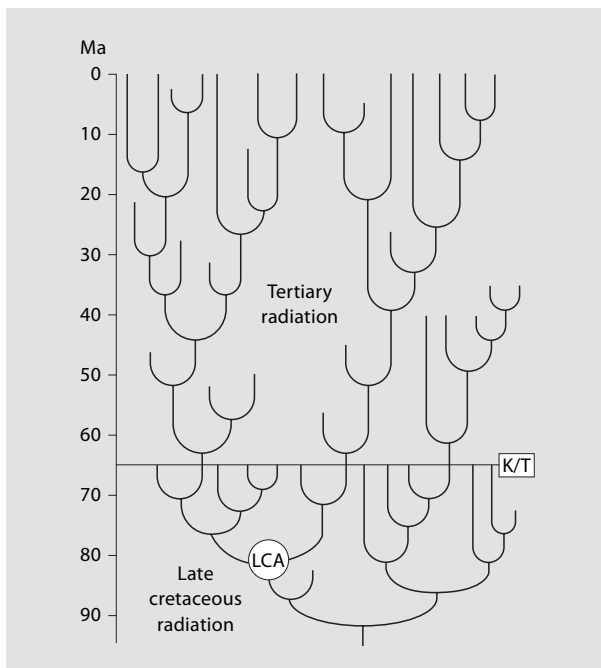
### **Implications of a Cretaceous Origin of Euprimates**

Direct reading of the known fossil record for euprimates without explicit acknowledgement of the effects of substantial gaps can lead to questionable conclusions not only regarding the timing of evolution, but also with respect to the geographical region inhabited by the earliest primates. In fact, these two aspects are closely connected because an earlier, Cretaceous origin for euprimates increases the potential relevance of continental drift and opens up stronger possibilities for a rôle played by the southern continents [Martin, 1990; Hedges et al., 1996; Bowen et al., 2002]. Because the earliest undoubted euprimates are documented from basal Eocene deposits of the northern continents, some authors concluded that they must have originated somewhere within that region [Elliot Smith, 1927]. However, despite the fact that no undoubted basal Eocene euprimates have yet been recorded from the

southern continents, one interpretation that has recently found much favour among primate palaeontologists is that their origin is located in Africa [Gingerich, 1986; Storch, 1986; Martin, 1990; Simons and Rasmussen, 1994; Rose, 1995; Yoder et al., 1996]. Given the modern distribution of primates and the occurrence of undoubted primates in Africa at least from the middle Eocene, this seemed a reasonable possibility prior to the advent of comprehensive molecular phylogenies for eutherian mammals. These in fact indicate that the cluster of endemic African mammals now widely recognized as the superorder Afrotheria does not include primates [Murphy et al., 2001b]. Primates belong instead to the superordinal cluster Euarchontoglires along with dermopterans, tree shrews, rodents and lagomorphs. Although some authors have suggested that the Euarchontoglires originated in Laurasia, there is little convincing evidence to support this interpretation. An alternative interpretation, the 'Indian Ark Hypothesis' following a proposal by Krause and Maas [1990], is that primates and other euarchontoglirans developed on Indo-Madagascar at some time after its separation from Africa [Miller et al., 2005; Martin, 2006].

If it is, indeed, true that the LCA of euprimates was already present somewhere on the southern continents during the Cretaceous around 80–90 Ma ago, a number of additional implications require exploration. In the first place, it is quite likely that – in common with many other groups of organisms around the globe – euprimates would have suffered partial extinction at the K/T boundary. For the well-sampled North American record, Alroy [1999] has estimated that as many as two thirds of all mammal species may have gone extinct at around the K/T boundary. However, evidence from the western interior of North America also suggests that the risk of extinction may not have affected all mammals equally. In eastern Montana, only 9% (1 of 11) of metatherian and 50% (5 of 10) of multituberculate species, but all 6 eutherian species recorded from the latest Cretaceous Hell Creek Formation, were found to have survived into the Cenozoic [Archibald, 1996]. Clearly, more data are needed to assess the potential impact of K/T boundary events on putative primates. Some effect is nevertheless likely and an initial radiation of primates during the latter part of the Cretaceous would then have been followed by partial extinction 65 Ma ago prior to the Tertiary radiation of euprimates that has traditionally been regarded as the exclusive phase of euprimate evolution (fig. 4). Such a two-phase radiation of euprimates would have to be taken into account in any statistical modelling aimed at determining the age of the LCA. Our preliminary work in progress on this issue indicates that the outcome will be an even earlier date for the euprimate LCA.

In fact, examination of the relationship between extinction rates and origination rates in the marine fossil record throughout the entire Phanerozoic suggested that biological recovery from extinctions has been characterized by a considerable time lag of about 10 Ma [Kirchner and Weil, 2000]. This effect was reportedly detected not only for major mass extinctions, but also for background extinctions. However, it has now emerged that this long time lag can be attributed to a statistical artefact [Lu et al., 2006]. Ironically, it was found that successful quantitative analysis of the Phanerozoic fossil record to test for covariance between rates of origination and extinction requires explicit reference to the incompleteness of that record. The problem arises because of episodic variation in the probability of preservation of taxa on time scales comparable to the temporal resolution of the data set, which has a stage/substage duration of about 5 Ma. When the data are corrected to allow for incompleteness of the record, significant covariance remains only for the relationship



**Fig. 4.** Schematic illustration of the potential effect of the extinction event at the K/T boundary on primate phylogeny. LCA indicates the last common ancestor of extant primates and their direct fossil relatives. It is likely that an initial radiation of primates during the late Cretaceous was curtailed by the K/T extinction event, to be followed by the major Tertiary radiation that is generally recognized.

between extinctions and originations in immediately subsequent intervals. Lu et al. [2006] therefore concluded: ‘... in general the biosphere’s response to perturbation is immediate geologically and usually short-lived.’ Accordingly, the expectation is that euprimate lineages that survived the K/T extinction event would have radiated relatively rapidly so that the absence of undoubted euprimates from the known Palaeocene record (55–65 Ma ago) cannot be explained by the long lag between extinction and origination invoked by Kirchner and Weil [2000].

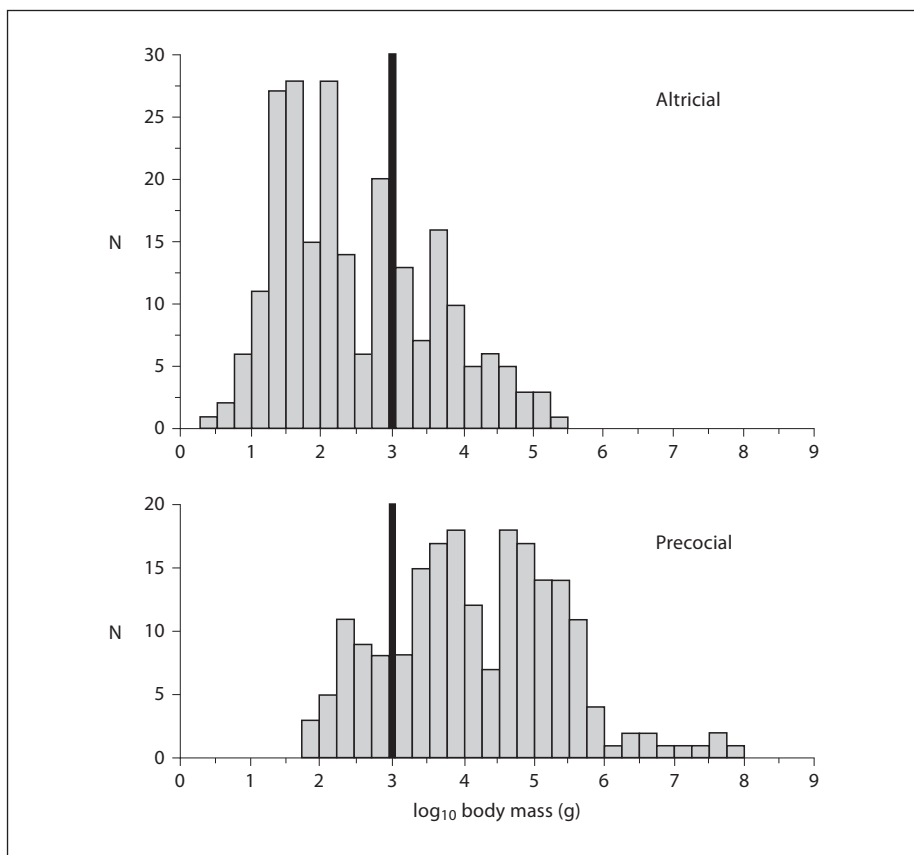
A Cretaceous origin of euprimates also raises new questions with respect to inference of the likely body size and associated ecological characteristics of the LCA [Soligo and Martin, 2006]. For a variety of reasons, it has been widely accepted that the earliest primates were quite small-bodied, weighing no more than 500 g and possibly much less [Dagosto, 1988; Martin, 1990; Cartmill, 1992; Hamrick, 1999; Larson et al., 2000; Gebo, 2004; but see Soligo and Müller, 1999, for an earlier alternative view]. One major reason for the inference that ancestral primates were small-bodied is long-standing acceptance of ‘Cope’s rule’, according to which there has been an inherent trend for body size to increase during the evolution of mammals and various other animal groups [Jablonski, 1996; Alroy, 1998]. Gebo [2004] has recently suggested that the ancestral euprimate was even smaller than proposed by previous

authors, being 'shrew-sized' with a body mass of only 10–15 g. This interpretation was influenced by the small body size of certain early Eocene primates such as *Teilhardina* and *Donrussellia* and, particularly, by the diminutive size of middle Eocene tarsiids and eosimiids from the Shanghuang deposits of China. It has also been emphasized that living primates that have seemingly retained many primitive features (e.g. cheirogaleids, galagids, lorisids and tarsiids) are relatively small, and lesser mouse lemurs (*Microcebus*) have been widely cited as a potential model for ancestral primates. Small body size in the euprimate LCA has been linked to adaptation for activity in a fine-branch environment [Martin, 1990; Sussman, 1991; Cartmill, 1992]. Two main hypotheses, which are not necessarily mutually exclusive, have been proposed to account for the evolution of characteristic visual and locomotor features of primates in the fine-branch niche. One is that the ancestral primate was a visual predator, adapted for predation on insects and other small animals [Cartmill, 1972, 1974a, b]. The second is that ancestral primates evolved in parallel with angiosperm plants, consuming their fruits, flowers and nectar [Sussman and Raven, 1978; Sussman, 1991]. It has also been inferred that ancestral primates were nocturnal in habits [Martin, 1990; Martin and Ross, 2005] and were likely to have been relatively small because modern nocturnal primates are commonly smaller than their diurnal modern relatives. (For a contrary interpretation invoking a diurnal ancestry of primates, see Ni et al. [2005].)

The argument that the LCA of euprimates must have been small because the earliest known fossil primates from the basal Eocene were typically small is another questionable outcome of direct reading of the known fossil record. Indeed, if the LCA of living primates predated the earliest fossil primates by as much as 30 Ma, then direct inference of LCA traits from traits observed in those oldest fossils is dubious. If the LCA of euprimates existed 80–85 Ma ago, the body size of the earliest known fossil representatives aged 55 Ma or less is not directly relevant to the question of the size of ancestral primates. The chronological gap between the hypothesized euprimate LCA and early Eocene fossil relatives leaves room for considerable evolutionary change, particularly if potential effects of the major extinction event at the K/T boundary are taken into account. It is conceivable, for example, that adaptive radiation of primates prior to the K/T boundary generated a range of body sizes but that survival of smaller-bodied species was favoured during the extinction event, thus skewing the body sizes of fossil primates found in the early Tertiary.

In contrast to previous suggestions, Soligo and Martin [2006] have recently concluded from (1) an analysis of change in body mass over time in the primate fossil record, (2) a comparison of body mass distributions of arboreal mammals bearing either claws or nails, and (3) a phylogenetic reconstruction of primate ancestral body mass, that a small-bodied LCA for euprimates is indicated neither by modern species nor by the fossil record. Instead, their results converged on the interpretation that the primate stem lineage was characterized by a significant increase in body mass to around 1 kg or more in the LCA of living primates, at least twice the maximum value of 500 g suggested by Martin [1990] and greatly exceeding the value of 10–15 g proposed by Gebo [2004].

Reproductive biology provides another reason to expect that ancestral primates were unlikely to have been very small. Modern mammals can be divided fairly clearly into altricial mammals, which typically produce large litters of poorly developed neonates after a relatively short gestation period, and precocial mammals, which typ-



**Fig. 5.** Histograms showing body mass distributions for modern altricial and precocial mammals. The vertical grey line indicates a body mass of 1 kg, corresponding to the approximate boundary between the two distributions.

ically produce a single, well-developed neonate after a relatively long gestation period [Martin and MacLarnon, 1985]. One of the defining features of primates is the production of precocial offspring [Martin, 1990]. As was noted by Shea [1987], precocial mammals are generally bigger than altricial mammals, and even modern primates are quite small in comparison to other precocial mammals. The only other small-bodied mammals that commonly produce precocial neonates are bats. Comparison of body mass distributions for large samples of modern altricial and precocial mammals (fig. 5) shows that most altricial mammals have a body mass of less than 1 kg, whereas body mass generally exceeds this value in precocial mammals.

Inference of the body mass of ancestral euprimates is also important with respect to diet. It is now widely accepted that a body mass of 500 g, referred to as 'Kay's threshold', represents the approximate boundary between predominantly insectivorous primates and those that are predominantly folivorous [Kay, 1984; Fleagle, 1999]. It is generally accepted that it would have been difficult for any extinct primates with

an adult size exceeding 350 g to subsist on a primarily insectivorous diet [Kay, 1984]. Gebo [2004] explicitly noted in this context that predominant insectivory would be expected of his postulated shrew-sized ancestral primate with a body mass of 10–15 g. Certainly, the relatively high metabolic rate of such a small-bodied mammal species would require a diet with a high energy content that could be easily digested. However, the prevalent dietary tendency of extant primates is frugivory, and it has long been accepted that in the evolution of the dentition in primates the initial modifications were probably connected with a shift from predominant insectivory to inclusion of an increased proportion of plant food items in the diet [Martin, 1990]. Features of gut morphology such as universal retention of a caecum provide additional support for the interpretation that the LCA of extant primates included a significant proportion of plant food items in its diet [Martin, 1990]. Recent comparative analyses of orbital convergence and brain structure and of ecological correlates of sociality in primates and other mammals have also added support to the notion of a largely frugivorous LCA of euprimates [Barton, 2004; Müller and Soligo, 2005]. A shift towards increased frugivory is, in fact, more readily understandable if the body mass of the LCA of euprimates was 1 kg or more. It has become obvious that reinterpretation of the likely age of the LCA of euprimates has direct ramifications for interpretations of the environmental and ecological context of primate origins.

At this point, it is worth returning to the proposal that the appearance of euprimates in the fossil record paralleled a major radiation of modern angiosperm plants during the Palaeogene [Sussman and Raven, 1978; Sussman, 1991]. On this basis, it was suggested that the major initial adaptations of primates were linked to foraging for various food items on the fine terminal branches of angiosperm trees. This proposal is seemingly threatened by the inference that the LCA of euprimates probably existed 80–85 Ma ago, predating not only the earliest appearance of euprimates in the fossil record by some 30 Ma [Tavaré et al., 2002; Soligo et al., 2007], but also the Palaeogene angiosperm radiation referred to by Sussman [Sussman and Raven, 1978; Sussman, 1991]. However, underestimation of times of origin because of substantial gaps in the fossil record is likely to apply to the emergence and diversification of angiosperms as well, especially with respect to the southern continents. In addition, it is now known that there was a major early diversification of angiosperms at lower latitudes in the mid-Cretaceous, beginning approximately 95 Ma ago [Crane and Lidgard, 1989; Jacobs, 2004]. Angiosperm woods are absent from Cenomanian and older deposits, but are the most common fossils found in younger Cretaceous sediments [Jacobs, 2004], and types of multistratal rainforests are likely to have been established in the northern part of Africa by at least the latest Cretaceous [Morley, 2000; Jacobs, 2004]. It has also been suggested that a trend towards larger fruit size of angiosperms began earlier than previously thought, starting during the late Cretaceous some 85 Ma ago rather than after the K/T boundary [Eriksson et al., 2000]. Hence, the timing of this shift coincides quite well with the inferred shift towards increased consumption of plant food items in the ancestral euprimates. Judging by the currently available data, it is clearly possible that habitats suitable for primates of modern aspect and ecology would have been present on at least some of the southern continents by the time of their suggested origin and initial diversification in the late Cretaceous.



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