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New Light on Primate Evolution

(Ernst Mayr Lecture on 11th November 2003)

Introduction

Over and above its intrinsic interest as a field of biological enquiry, the evolutionary history of primates has attracted particular attention because it provides the zoological context for human evolution. Since Linnaeus formally included humans in the order Primates as a distinctive group of placental mammals, the comparative study of primates (primatology) has become a flourishing and well-established discipline. Excluding tree shrews – commonly classified as primates in earlier literature, but now generally relegated to the separate mammalian order Scandentia – approximately 375 modern primate species can be recognized (Groves, 2005). Partly on grounds of geographical distribution, these extant primates fall into 6 "natural groups": (1) Madagascar lemurs, (2) lorisiforms (lorises and bushbabies), (3) tarsiers, (4) New World monkeys, (5) Old World monkeys, (6) apes and humans (Martin, 1990). The last 3 groups (monkeys, apes and humans) have been collectively labeled "higher primates" to distinguish them from the generally more primitive "prosimians" (lemurs, lorisiforms and tarsiers). An alternative subdivision is to classify lemurs and lorisiforms together as strepsirrhines and tarsiers and higher primates together as haplorhines, reflecting their likely phylogenetic relationships (see Figure 1).

The earliest known undoubted fossil primates date back to the very beginning of the Eocene epoch, approximately 55 million years ago (mya), and all have so far been found exclusively at sites in the northern continents (North America, Europe and Asia). In fact, the first substantial primate fossil from the earliest Eocene – a largely complete skull of *Teilhardina asiatica* – has just been reported from China (Ni et al., 2004). Fossil mammals identified as "archaic primates" (infraorder Plesiadapiformes), predominantly known from the preceding Palaeocene epoch (55–65 mya), have at most only a tenuous connection with the evolution of undoubted "primates of modern aspect" ("euprimates"). As it is generally accepted that Plesiadapiformes
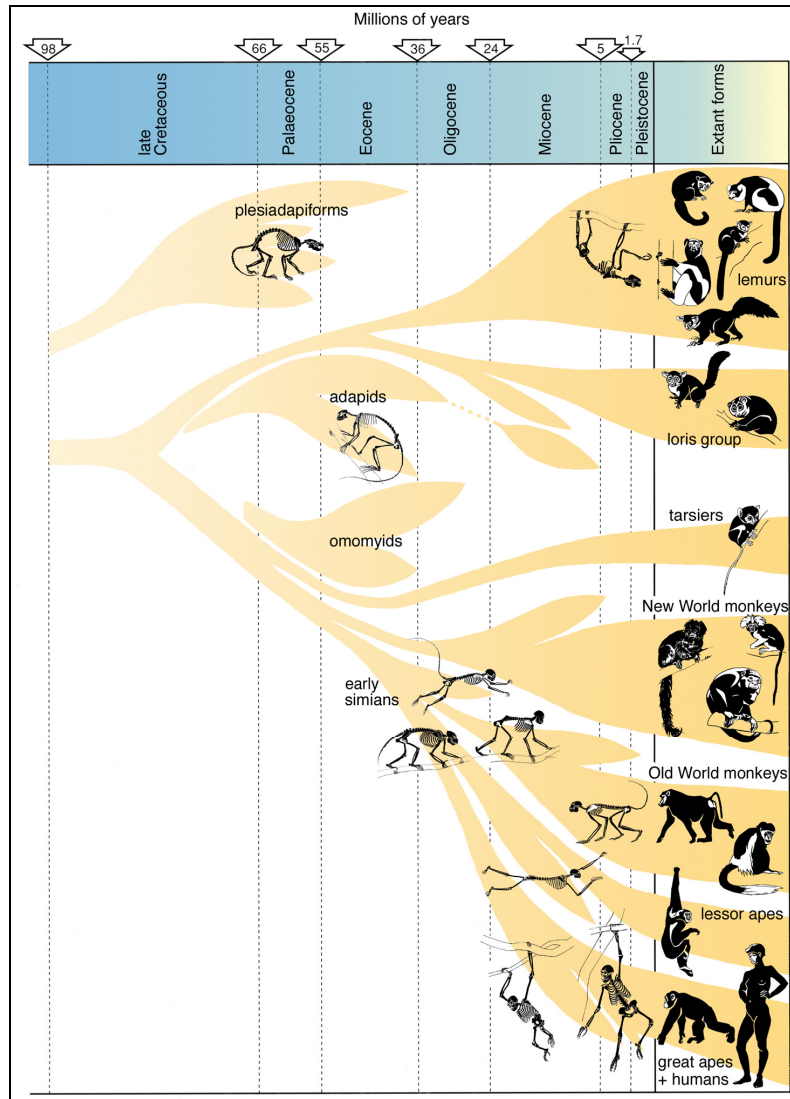
Figure 1

Outline pylogenetic tree for primates (from Martin, 1993), including the plesiadapiform "ar-chaic primates", which are of uncertain affinities, but excluding tree shrews. Note the 6 "nat-ural groups" of living primates and the initial subdivision in the tree between strepsirrhines (lemurs + lorises) and haplorhines (tarsiers + higher primates). In this tree, the age of the last common ancestor of living primates was provisionally indicated as about 85 mya. Original illustration by Lukrezia Bieler-Beerli. Reprinted by permission from *Nature* (Martin, R. D., vol. 363, pp. 223–234) © (1993) Macmillan Journals Limited (http://www.nature. com/).

branched away prior to the common ancestor of euprimates, it is justifiable for present purposes to confine discussion to the evolution of these primates of modern aspect. Fossil euprimates can be crudely divided into early Tertiary forms (largely confined to the Eocene), which have no obvious direct connection with extant primates, and other fossil species that are directly related to one of the modern groups of primates. The latter generally occur from the early Miocene upward, although there are a few exceptional cases dating back to the middle Eocene.

Most early Tertiary primates can be subdivided into "lemur-like" Adapiformes and "tarsier-like" Omomyiformes (Martin, 1990). One widely accepted interpretation is that Adapiformes are linked to strepsirrhine primates while Omomyiformes are linked to haplorhines (e.g. Kay et al., 1997; Fleagle, 1999). However, an alternative interpretation that merits consideration is that the Adapiformes and Omomyiformes together constitute a separate radiation of early primates that had no direct connection to the radiation that led to the array of modern primates (Martin, 1993; Ross, 2003). In a recent survey (Tavaré et al., 2002; Soligo et al., 2006), approximately 400 fossil euprimate species were recognized, documenting various stages of primate evolution over the past 55 my. Broad comparisons of primates, including morphological features of both extant and fossil forms along with chromosomal and molecular evidence for the living species, have led to a gathering consensus with respect to the broad outlines of the phylogenetic tree of primates (Figure 1).

One fundamental issue involved in reconstructing the evolutionary history of primates is inference of the time and location of their origin. With respect to inferred *time* of origin, the standard approach among palaeontologists is encapsulated in the following statement by Simpson (1965, p.19): "[…] 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." In line with this, the mainstream palaeontological interpretation has been that euprimates originated not long before the earliest known fossil forms and certainly no earlier than 65 mya (e.g. see phylogenetic tree in Kay et al., 1997). Indeed, those who have accepted a date as ancient as 65 mya for the origin of primates have generally done so because they included the Palaeocene plesiadapiforms and not because they added 10 my to the time of first appearance of fossil euprimates. However, all such interpretations are based on a direct reading of the fossil record and the underlying assumption that the record is complete enough for this to be reasonable. Evaluation of that assumption and its implications is the central concern of this essay.

In fact, direct reading of the fossil record has often led to the inference that any given group originated in or close to the region that has yielded the earliest known fossil forms. Accordingly, a direct reading of the currently known euprimate fossil record would place the site of origin in the northern continents, as was indeed inferred by some earlier authors. However, this is no longer widely accepted, and most authors now suggest an origin for primates in the southern continents, most commonly in Africa. There has hence been at least a partial retreat from a direct

reading of the fossil record for euprimate origins, with respect to locality if not to time. Yet palaeontologists generally remain reluctant to devote serious attention to the possibility that the known fossil record may also be inadequate as an indicator of the *time* of origin of primates. To some extent, they have been encouraged in this by estimates of the degree of completeness of the mammalian fossil record that have been heavily biased towards unusually rich early Tertiary deposits in North America (Foote et al., 1999; Foote & Sepkoski 1999).

Interpretation of the Fossil Record

The fossil record perforce plays a pivotal rôle in our understanding of the phylogenetic history of living organisms (the "Tree of Life") and has played a prominent, indispensable part in promoting acceptance of the Darwin/Wallace theory of organic evolution. Hypothetical reconstructions of relationships between species can be generated exclusively through analysis of the characteristics of living forms – necessarily so in the case of molecular data. However, fossils provide the only direct evidence of the existence of past organisms and of various morphological features that survive the vagaries of preservation (commonly but not always confined to "hard parts"). Furthermore, for the time being (and possibly forever) the fossil record provides us with the only means of attaching a deep geological timescale to any phylogenetic tree. Successful analyses of "ancient DNA" have so far been limited to special cases that generally do not extend far back into the past (up to a few tens of thousand years as a general rule). In any case, analyses of molecular data, as presently conducted, essentially serve to indicate patterns of branching among lineages and usually tell us little about the characteristics and functioning of past organisms.

Reliable interpretation of the crucially important fossil record is, however, subject to numerous problems. Many of these derive from the incompleteness of the record, which is manifested in various ways, ranging from the partial preservation of individual specimens (predominance of "fragmentary fossils"), through regional variation in the probability of fossilization, and on to the existence of major gaps in the "Tree of Life". Among many such examples, the problem of incompleteness undoubtedly afflicts the primate fossil record (see Figure 1). On the strepsirrhine side of the primate tree, very few direct fossil relatives of the modern representatives (lemurs and lorisiforms) are known. Until quite recently, the known fossil record for undoubted lorisiforms (with a modern array of at least 28 species; Groves, 2005) extended back only to the early Miocene (about 20 mya) and was limited to 4 genera and 8 species found in East Africa and Pakistan (Phillips & Walker, 2002). The recent discovery in late Eocene deposits in Egypt of fragmentary remains of a relative of bushbabies (*Saharagalago*) and a potential relative of lorises (*Karanisia*) simultaneously doubled the documented geological age of lorisiform primates to about 40 mya and in-

creased the number of known genera by 50 % (Seiffert et al., 2003; Martin, 2003). The very fact that new fossil discoveries can have such a dramatic impact is eloquent testimony to the yawning gaps in our knowledge that still remain. The fossil record for Madagascar lemurs is even less satisfactory, remaining largely undocumented to this day. Apart from an array of subfossil lemurs that died out within the past few thousand years (and were hence really part of the modern fauna), not a single fossil lemur has been discovered in Madagascar. Yet the documented existence of the lorisiforms – the sister group of lemurs – by around 40 mya shows that lemurs must have been in existence since at least that time. For lemurs, we are hence faced with a massive "ghost lineage" that lasted a minimum of 40 my and ultimately led to a modern array of more than 75 species in Madagascar (including the subfossils). An intriguing Oligocene primate *Bugtilemur*, recently discovered in deposits in Pakistan dating back to about 30 mya, has been specifically linked to the dwarf lemur family Cheirogaleidae (Marivaux et al., 2001). This is another dramatic discovery, but it actually raises far more questions than it answers (notably about biogeography) and tells us nothing about the evolution of lemurs within Madagascar.

The haplorhine side of the primate tree is somewhat better documented; but there are still substantial gaps (Figure 1). Even by the most generous interpretation, direct relatives of modern tarsiers (at least 7 species) are limited to one early Miocene species from Thailand, an Oligocene species from Egypt and 2 middle Eocene species from China (Gunnell & Rose, 2002). Higher primates are reliably documented by the late Eocene in Africa, about 40 mya, and more questionably by the middle Eocene in China and South-East Asia (Miller et al., 2005). However, the modern groups of higher primates are unequivocally documented only from the latest Oligocene (for New World monkeys) or from the early Miocene (for Old World monkeys and apes). Moreover, large gaps remain even within these groups. For instance, among the New World monkeys we have yet to find unquestionable fossil relatives of the small-bodied callitrichids (marmosets, tamarins and Goeldi's monkey), which account for 43 of the 128 extant species (i.e. 34 %) and have surely existed as a separate group for at least 30 my. Similarly, among Old World apes not a single direct fossil relative of the 14 species of lesser apes (gibbons) has yet been reliably documented, despite the probable independent existence of this lineage for a comparable period of time.

The existence of extensive gaps in the known fossil record of primates and of other groups of organisms gives rise to major problems in interpretation, both with respect to determining the time of origin of any given lineage and with respect to inferring its geographical site of origin. As indicated above, the standard approach among palaeontologists has been to take the age of the earliest known fossil representative of a given lineage and perhaps add a small increment to allow for the incompleteness of the fossil record. Because the earliest known primates of modern aspect (euprimates) date back only to the basal Eocene (about 55 mya), this common practice leads to an inferred origin for euprimates somewhere in the Palaeocene, around 60 mya. In fact,

similar conclusions have been drawn for various other orders of modern mammals, such as rodents, carnivores, artiodactyls (even-toed ungulates), perissodactyls (odd-toed ungulates), cetaceans (whales and dolphins) and bats. As with primates, the earliest known representatives in all cases date back to no more than 55 mya, and yet they already possess key features of their respective orders. To cite just one example: "Finally, about 50 million years ago, bats first appeared in the fossil record. Because the earliest known fossil bats are so fully adapted to flight and so similar to modern bats, many paleontologists deduce that the founding members of the bat lineage must have lived perhaps as much as ten million years earlier still." (Shipman, 1998, p. 220). This traditional approach has led to widespread recognition of the Tertiary period as the "Age of Mammals", during which a major adaptive radiation led to the modern extensive array of mammal species. Associated with this view is the notion that the dinosaurs ruled the earth until the end of the Cretaceous and that the adaptive radiation of modern mammals was a consequence of the extinction of the dinosaurs. It is now widely, if not universally, accepted that extinction of the dinosaurs and several other groups of organisms was precipitated – or at least heavily influenced – by a giant meteorite impact at the boundary between the Cretaceous and the Tertiary (K/T boundary) about 65 mya. Many investigators see the adaptive radiation of modern mammals as a sequel to the major extinctions at the K/T boundary.

Direct inference of times of origin from the fossil record is subject to 2 problems: (1) If there are substantial gaps in the record, the first known fossil representative is likely to be much younger than the actual first occurrence in the phylogenetic tree. (2) Biases of various kinds in the fossil record influencing preservation and discovery may entail additional error. Regardless of the degree of completeness of the fossil record and of the biases that exist, it is important to recognize that any time of origin inferred directly from a first appearance in the fossil record must be a *minimum* date and that there is no equivalent direct indicator of a maximum date. Furthermore, it should be intuitively obvious that the degree of underestimation of a time of origin based on time of first appearance in the fossil record must increase as the patchiness of that record increases. Given the major gaps in the primate fossil record outlined above, it is only to be expected that a direct reading of that record might lead to serious underestimation of the time of origin of primates and of times of divergence within the primate tree (Martin, 1986, 1990).

A very simple quantitative approach to the problem of incompleteness in the primate fossil record (Martin, 1993) was made by assuming a linear increase in number of species over time and a species survival time of 1 my, equivalent to the average suggested by several studies of the mammalian fossil record. Calculation on this basis indicated that only 3 % of extinct euprimate species have so far been documented, with a huge proportion (97 %) remaining to be discovered. Simulations of trees in which only 3 % of extinct species are known revealed that dating of the time of origin from the first known fossil form would lead to serious underestimation of the actual time of origin. Addition of a roughly estimated correction factor to a date

of 55 mya for the earliest known euprimates led to the inference that ancestral primates actually existed more than 80 mya, which was incorporated into a revised phylogenetic tree for primates (see Figure 1).

This interpretation was challenged soon afterwards by Gingerich & Uhen (1994). Taking the same basic model of a linear expansion in numbers of species between the ancestral primate and the array of modern species, they used a simple calculation to estimate the probability that the common ancestor of primates existed 80 mya, given that all known fossils are confined to the last 55 my. They estimated this probability at the very low figure of 5x10-9. In fact, because many new fossil primate species have been discovered during the intervening decade without increasing the maximum known age beyond 55 mya, the probability according to that mode of calculation is now even lower at $2x10^{-18}$ (Soligo et al., 2006). There are, however, some major flaws in this alternative mode of calculation. Most importantly, although the number of living primate species is initially entered into the calculations, it subsequently drops out and has no influence on the final result, such that any allowance for the degree of incompleteness of the fossil record is ruled out. The probability calculation conducted by Gingerich & Uhen yields the same answer regardless of whether the proportion of primate species documented in the fossil record is 30 %, 3 % (a more likely figure) or 0.3 %. This omission is compounded by the fact that the differential occurrence of fossil primates at different time intervals is also ignored. All fossil euprimate species are lumped together in a single figure. Whereas this might be reasonable if the sampling density of the primate fossil record were high and relatively uniform, it is potentially very misleading if there are major fluctuations in sampling levels over time. This is best illustrated by considering a period of 6 my in the middle of the Oligocene (26–32 mya) for which not a single fossil primate species is yet known. A direct reading of the fossil record would require a precipitous decline in numbers of primate species at about 32 mya, followed by a rapid re-expansion from 26 mya onwards. An alternative interpretation is that, for whatever reason, there has been particularly poor preservation and/or discovery of primates in the middle Oligocene. In fact, the same kind of probability calculation as that used by Gingerich & Uhen (1994) can be applied to assess the likelihood that primates existed during the period 26–32 mya. When this is done for the current figures for euprimate fossil species, the nonsensical answer is obtained that the existence of primates during the middle Oligocene has an even lower probability than the existence of ancestral primates 80 mya, namely 2x10-19 (Tavaré et al., 2002; Soligo et al., 2006). A simple explanation for this is that the calculation made by Gingerich & Uhen (1994) estimates the likelihood of fossil discovery given currently explored sites, rather than the likelihood of existence of past primate species.

In order to provide a fresh, more reliable perspective on this problem, a novel statistical approach was developed based on a modified χ^2 method (Tavaré et al., 2002). Instead of simple linear expansion in number of species over time, a more biologically realistic logistic model was taken in which 90 % of the modern number of
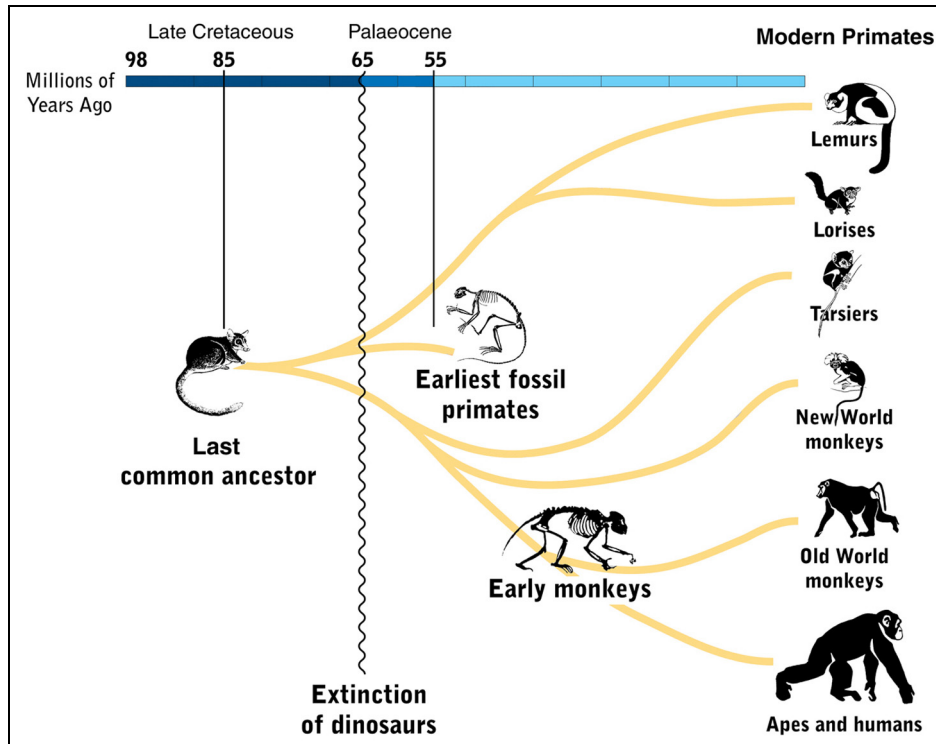
Figure 2
Simplified phylogenetic tree for primates. The last common ancestor that gave rise to modern
primates and all their undoubted fossil relatives (euprimates) is set at approximately 85 mya,
20 mya before the extinction of the dinosaurs at the K/T boundary. The hypothetical recon-
struction of the ancestral primate (drawing by Nancy Klaud) reflects the inference that several
defining features of euprimates (e.g. relatively large, forward-facing eyes; arboreal adapta-
tion including a grasping foot with a divergent big toe) would already have been present at
that stage.

primate species was attained by 49 mya. In other words, the model assumed an initial
relatively rapid expansion of species numbers into the early Eocene, followed by a
phase of slower growth. The modal value for survival of species was set at a higher
value of 2.5 my and permitted to vary with an exponential distribution. It was also
found that effective evaluation of the data required subdivision of the primate fossil
record into relatively narrow time intervals. This was done according to standard
geological subdivisions, with an average interval length of about 4 my. Having set
these basic constraints, stochastically generated trees were repeatedly fitted to the
empirical data for numbers of living and fossil primate species (235 and 395, re-

spectively) that were available at the time of the analysis. (Both figures have since increased.) With each tree, the resulting age of the last common ancestor of modern primates was determined, and the average result obtained was 81.5 mya, with 95 % confidence limits of 72.0–89.6 mya (Tavaré et al., 2002). In fact, an alternative calculation allowing for the possibility that some fossil euprimates branched away prior to the common ancestor of modern primates yields an even earlier date for the common ancestor of euprimates: 85.9 mya, with 95 % confidence limits of 73.3–95.7 mya (Soligo et al., 2006). Hence, this new statistical approach confirms the inference that euprimates originated well back in the Cretaceous, perhaps more than 20 my before the K/T boundary and the extinction of the dinosaurs (Figure 2).

The results reported by Tavaré et al. (2002) and Soligo et al. (2006) are, in fact, based on conservative assumptions, and they are quite robust with respect to modification of any of the parameters. For change in species numbers over time, for instance, replacement of the logistic model with a linear or exponential model leads to a marked increase in the estimated age for the last common ancestor of modern primates. Furthermore, decreasing or increasing the modal survival time for species (e.g. to 2 or 3 my instead of 2.5 my) has very little effect on that estimated age. As it happens, the number of living primate species has recently been revised sharply upwards to about 375 (Groves, 2005), representing a 60 % increase over the figure of 235 species used in the calculations. Although this increase has been offset to some extent by a further increase in the number of recognized fossil primate species, the fact remains that there has necessarily been some resulting decrease in the estimated proportion of fossil primate species discovered to date.

At this juncture, it is important to clarify what is meant by "time of origin" of a particular group of organisms, as there has been some confusion about this. It is necessary to distinguish between the *date of initial divergence* of the target group from its sister group and the subsequent *date of initial diversification* of extant members of the target group from the common ancestor (Figure 3). Either of these dates could be taken as the "time of origin" of a group. The key point is that diversification of the extant members of a target group may take place some time after the founding lineage diverged from the sister group. Accordingly, it might be argued that the primate stem lineage indeed diverged from other placental mammals back in the Cretaceous (the date of initial divergence), but that the date of initial diversification of modern primates (the crown group) did not occur until after the K/T boundary. Hence, it is theoretically possible to claim that early relatives of primates might have existed during the latter part of the Cretaceous, but that they were not recognizable as such because the defining features of primates were not present until the common ancestor of modern primates emerged at a later stage. This argument simply does not apply to the date of 81.5 mya inferred by Tavaré et al. (2002), because the method estimated the date of initial diversification of extant primates (i.e. the date of initial divergence between strepsirrhine and haplorhine primates) and not the date of initial divergence from other placental mammals. In other words, the result indicated that
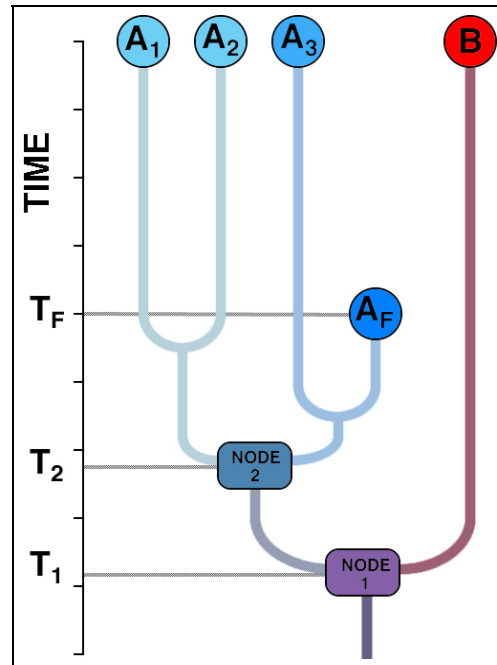
Figure 3

In this schematic phylogenetic tree, the target for consideration is group A, with living re-presentives A_1, A_2 and A_3. The *date of initial divergence* of this target group from its most closely related sister group with living representatives (B) is indicated by node 1 at time T_1. The subsequent *date of initial diversification* of extant members of target group A from their last common ancestor is indicated by node 2 at time T_2. Confusion has arisen because both node 1 and node 2 have been termed the "time of origin", whereas node 2 may be consider-ably younger than node 1. The distinction is important because derived features shared by living representatives of group A may have developed at any point between node 1 and node 2. The first known fossil representative included in group A (A_F), because it possesses some of those shared derived features, yields a *minimum* age for the date of initial diversification of that group (T_F). However, this may be much younger than the actual age if sampling density of the fossil record is poor. Underestimation of the actual date of initial diversification if the age of A_F is taken as a direct indicator will be T_2-T_F, while underestimation of the date of initial divergence will be even greater (T_1-T_F). In this example, the fossil representative A_F diverged after node 2, but it should be noted that fossil relatives of group A may potentially diverge at any stage between node 1 and node 2. It should also be noted that the distinction between date of initial divergence and date of initial diversification matches the distinction between "stem group" and "crown group" now made by palaeontologists (e.g. Archibald, 1999). For A, the stem group consists of the lineage between node 1 and node 2, along with any fossil relatives. The crown group consists of the living representatives (A_1, A_2 and A_3) along with any direct fossil relatives such as A_F. (Illustration modified from Figure 1 of Soligo et al., 2006.)

shared derived features of strepsirrhine and haplorhine primates that were possessed by their last common ancestor were already present well back in the Cretaceous. The clear expectation from this is that any direct fossil relatives of modern euprimates that may be recovered from Cretaceous deposits in the future will possess defining primate features such as relatively large, forward-facing eye-sockets (orbits), a bony bar around the outer margin of each orbit (postorbital bar), formation of the auditory bulla from the petrosal bone and grasping adaptation of the foot with a divergent big toe (Martin, 1990).

Recent Findings from Molecular Comparisons

The increasing availability of molecular evidence has added a valuable new dimension to phylogenetic reconstruction. In addition to providing abundant, more easily quantifiable information on likely relationships between groups of organisms, such evidence has opened up new possibilities for the inference of divergence times through application of the concept of the "molecular clock" (Easteal et al., 1995; Bromham & Penn, 2003). Although it is now evident that rates of molecular evolution can in fact vary quite markedly between lineages, such that it is necessary to think in terms of "local clocks", the approximate regularity of molecular change is sufficient to permit crude application of the clock concept. However, it should not be overlooked that a molecular clock must be calibrated and that the only method currently available requires use of information from the fossil record to infer the age of at least one node in the tree. Accordingly, if gaps in the fossil record lead to serious underestimation of any divergence date because of direct reliance on first appearance of a fossil relative, that underestimation will have ramifications throughout any molecular tree calibrated with that date. If it is indeed true that the first appearance of a euprimate fossil in the record is considerably younger than the actual age of the last common ancestor of euprimates (55 mya *versus* 81.5 mya or more), and if such underestimation applies throughout the primate record, it follows that calibration of molecular trees using any dates derived from fossil primates is severely misleading. Among other things, this includes inferences regarding the timing of the divergence between African great apes (chimpanzees and gorillas) and humans (e.g. see Arnason et al., 2000).

Accumulating evidence over the past decade from several studies of DNA sequences using a number of calibration dates external to primates has, in fact, confirmed an early date for the initial divergence between primates and other groups of placental mammals (Soligo et al., 2006). In one of the first such studies (Janke et al., 1994) a comparative analysis was conducted using sequence data for a marsupial and several placental mammals. After testing revealed that rates of evolution for 8 mitochondrial genes were compatible with a molecular clock model, a conservative calibration date of 130 mya for the divergence between marsupials and placentals was applied. This

yielded a date of about 93 mya for the divergence between primates and a cluster containing artiodactyls, cetaceans and carnivores. A subsequent study analysed DNA sequence information for both mammals and birds, taking a large sample of 48 nuclear genes with relatively constant rates of change (Hedges et al., 1996). A very early calibration date of 310 mya was used, derived from the well-documented separation between diapsid reptiles (which led to modern reptiles and birds) and synapsid reptiles (which led to mammals – see Figure 4).

Divergence times estimated on this basis were greater than 90 mya for the separation between primates and two other groups of placental mammals (rodents and artiodactyls). In a later publication by the same research team including more species and nuclear DNA sequences (Kumar and Hedges, 1998), it was reported that vertebrate divergence times calibrated in the same way fitted well with most early (Palaeozoic) and late (Tertiary) dates derived from the fossil record, but that considerable gaps were revealed for the Mesozoic (Triassic, Jurassic and Cretaceous). It was inferred that at least 5 modern lineages of placental mammals diverged more than 100 mya and that most orders had diverged by the end of the Cretaceous. In a different approach, a combined analysis of DNA sequences from 3 mitochondrial genes and 2 nuclear genes (Springer et al., 1997) indicated that a group of endemic African mammals (golden moles, elephant shrews, hyraxes, elephants, sea-cows and aardvarks) descended from a specific ancestral stock during the adaptive radiation of the placentals. Using a panel of 9 different calibration dates (including a marsupial/placental split at 130 mya and a ruminant/cetacean split at 60 mya), the mean divergence time between this African group of mammals ("Afrotheria") and other orders of placentals mammals (including primates) was estimated to be about 90 mya. In another key study (Arnason et al., 1996), divergences between various placental mammals, including 7 primate species, were reconstructed using data for complete mitochondrial DNA sequences. The resulting tree was calibrated with a date of 55 mya for the minimum age of the cetacean lineage, yielding an inferred divergence of primates from other orders of placental mammals at about 90 mya. A double calibration based on the fossil record for hoofed mammals was then applied to an expanded dataset (Arnason et al., 1998), taking 60 mya for the divergence between artiodactyls and cetaceans and 50 mya for the divergence within perissodactyls between horses and rhinoceroses. The outcome was an estimate of 95 mya for the time of divergence between primates and hoofed mammals. Given the broad array of DNA sequences and calibration dates used, it is striking that all of these studies consistently indicate that primates diverged from other placental mammals about 90 mya.

Regardless of the reliability of the molecular clock, the ages of some first known representatives of other mammalian groups are simply incompatible with the interpretation that primates diverged only 60-65 mya (Soligo et al., 2006). One clear illustration of this is provided by studies of the relationships of cetaceans (whales and dolphins). It has long been accepted that cetaceans have a sister-group relationship to artiodactyls, but recent molecular evidence has consistently indicated that cetaceans
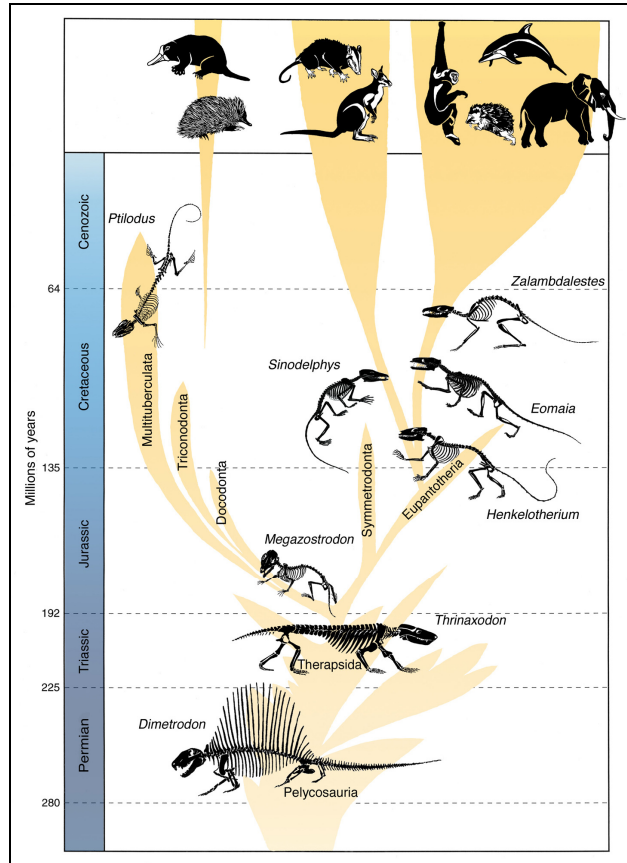
Figure 4

Outline phylogenetic tree for mammals. Fossil mammals, as defined by the possession of a dentary/squamosal jaw hinge, first appear in the record at the Triassic/Jurassic boundary, about 200 mya. They are derived from mammal-like reptiles (synapsids), which diverged from the diapsid reptiles leading to modern reptiles and birds at least 310 mya. For approximately two thirds of their evolutionary history, between the Triassic/Jurassic boundary and the Cretaceous/Tertiary boundary 65 mya, the mammals are very poorly documented in the fossil record, particularly in the southern hemisphere. Modern mammals are divided into 3 groups: monotremes, marsupials and placentals. The monotremes diverged quite early, although they may be more closely related to marsupials and placentals (therian mammals) than indicated here. In any event, the therian mammals undoubtedly shared a later common ancestor, which probably existed at least 130 mya. The closest known fossil relatives of this common ancestor are the eupantotheres, documented by a relatively complete skeleton of *Henkelotherium* (Krebs, 1991). Original illustration by Lukrezia Bieler-Beerli, with the additon of skeletons of the early marsupial *Sinodelphys* (Luo et al., 2003) and of the early placental *Eomaia* (Ji et al., 2002).

are actually nested within artiodactyls as relatives of hippopotamuses. This conclusion, initially indicated by immunological data (Sarich, 1993), is now supported by nuclear gene sequences (Graur & Higgins, 1994; Gatesy, 1997; Gatesy et al., 1996, 1999), by insertions of interspersed elements (retroposons) in the nuclear genome (Nikaido et al., 1999) and by complete mitochondrial DNA sequences (Ursing & Arnason, 1998). The combined evidence supports the following sequence of divergences, from most ancient to most recent, during the evolution of hoofed mammals (ungulates): (1) between perissodactyls and artiodactyls; (2) within artiodactyls between camels+pigs and ruminants+hippos+cetaceans; (3) between ruminants and hippos+cetaceans; (4) between hippos and cetaceans. Given that the first known fossil representative of the cetaceans is dated at 54 mya, it follows that the first of these 4 divergences in ungulate evolution (i.e. between artiodactyls and perissodactyls) must have occurred at a relatively early date and that the separation between ungulates and primates must have taken place even earlier. A date of only 60-65 mya for the divergence of primates from other placental mammals hence seems inherently unlikely. In fact, calibration of a molecular tree with a date of 56.5 mya for the divergence between hippos and cetaceans, while allowing for variation in rates of evolution, yielded a date of 97.6 mya for the divergence between primates and a cluster containing artiodactyls, perissodactyls and carnivores (Huelsenbeck et al., 2000).

Here, it should be emphasized that all of the molecular studies cited have focussed primarily or exclusively on the time of separation between primates and other groups of placental mammals (i.e. the time of initial divergence in Figure 3). Although the molecular evidence, following calibration with various fossil dates outside the primate tree, consistently indicates that the lineage leading to living primates diverged from other placental mammal lineages about 90 mya, it could be imagined that morphologically recognisable primates did not emerge until 60–65 years ago. Unfortunately, few molecular studies have addressed the question of the age of the last common ancestor of living primates (i.e. the time of initial diversification in Figure 3). However, it is obvious from the short genetic distances involved in that part of the tree that the divergence between strepsirrhine and haplorhine primates must have occurred relatively soon after the primates diverged from other placental mammals. Even if marked variations in rates of molecular evolution can occur, it is highly improbable that the molecular data would be compatible with a divergence between primates and other placental mammals about 90 mya followed by a period of 25–30 my before the common ancestor of euprimates emerged. In one of the few studies that has provided information directly relating to this issue, Arnason et al. (1998) indicated that the split between strepsirrhines and higher primates occurred about 80 mya, some 10–15 my after the primate lineage diverged from other placental mammals. An inferred age of about 80 mya for the initial time of diversification of modern primates fits remarkably well with the age of 81.5 mya estimated by statistical evaluation of the euprimate fossil record allowing for gaps (Tavaré et al., 2002; Soligo et al., 2006).

In a subsequent study, Yoder & Yang (2004) estimated primate divergence dates by applying a Bayesian method permitting variation in rates of molecular evolution to DNA sequences from 4 unlinked genetic loci. Although that study focussed primarily on lemur evolution, several non-primate outgroups were included. Fossil evidence was used to calibrate 8 nodes (4 for primates and 4 for non-primates) with upper and lower bounds, including a range of 63–90 mya for the last common ancestor of strepsirrhines and anthropoids (following Martin 1993; Gingerich & Uhen, 1994; Tavaré et al., 2002). Taking all genetic data together, the age of the ancestral primate node was estimated at 84.9 mya. Two points are of particular interest. First, when the tree was calibrated with a fossil date for just one node, markedly younger divergence dates were obtained. Second, the study by Yoder & Yang (2004) included the early divergence time of 38–42 mya between lorisids and galagids indicated by new fossil evidence (Seiffert et al., 2003). A previous analysis conducted before that information became available had yielded a strikingly concordant divergence time of approximately 40.5 mya (Yang & Yoder, 2003).

In recent years, substantial molecular datasets have been used to generate overall phylogenetic trees for mammals generally, thus clarifying likely relationships among the different orders of placental mammals (Madsen et al., 2001; Murphy et al., 2001a, 2001b). Although various attempts had been made to reconstruct higher-level relationships among mammalian orders using classical morphological evidence (e.g. Novacek, 1992; Novacek & Wyss, 1998), no really convincing picture had resulted. One major finding that has emerged from the new molecular studies is clear confirmation of the existence of the endemic group of African mammals "Afrotheria" identified in previous analyses of DNA sequences (Springer et al., 1997, 1999; Waddell et. al., 1999) and recently supported by analysis of retroposons in the nuclear genome (Nikaido et al., 2003). This is one of 4 supergroups of placental mammals that can now be identified with some confidence: Afrotheria, Euarchontoglires, Laurasiatheria and Xenarthra. Afrotheria as now recognized contains the tenrecs of Madagascar in addition to golden moles, elephant shrews, hyraxes, elephants, sirenians and ardvarks. Although a potential link between hyraxes and elephants had long been suspected, the links with other orders in Afrotheria had not been previously indicated by morphological evidence. Indeed, the inclusion of golden moles and tenrecs splits the long-accepted mammalian order "Insectivora". The supergroup Euarchontoglires includes primates, colugos and tree shrews ("archontans") along with rodents and lagomorphs ("glirans"). Laurasiatheria combines artiodactyls, cetaceans, perissodactyls, carnivores, pangolins, bats and certain "insectivores" (hedgehogs, moles and shrews). The fourth group Xenarthra is a relatively small assemblage restricted to toothless (edentate) mammals currently restricted to South America: anteaters, armadillos, and sloths.

Springer et al. (2003) used a large molecular dataset for representatives of all extant orders of placental mammals, with sequences from 19 nuclear and 3 mitochondrial genes, to estimate basal divergence times. Their method permitted variation in rates

of molecular evolution while applying 9 calibration dates based on first known occurrences in the fossil record (i. e., minimum divergence dates). All results indicated that divergences between placental orders took place in the Cretaceous, whereas diversification within orders took place mainly after the K/T boundary. However, 4 placental orders (Eulipotyphla, Primates, Rodentia, Xenarthra) showed diversification beginning prior to the K/T boundary, the earliest being the initial divergence in primate evolution at 77 mya.

The Broader Context of Mammalian Evolution

The first appearance of mammals in the fossil record (as defined by development of a new jaw hinge between the dentary and squamosal) coincides approximately with the boundary between the Triassic and the Jurassic, approximately 200 mya (Figure 4). They are descendants of the mammal-like reptiles (synapsids), which diverged at least 310 mya from the diapsid reptiles that eventually gave rise to modern reptiles and birds. For approximately two thirds of their evolutionary history, between their first appearance near the Triassic/Jurassic boundary (200 mya) and the K/T boundary (65 mya), the mammals are very poorly documented in the fossil record, particularly for the southern hemisphere. This surely reflects major gaps in the fossil record, as the advanced mammal-like reptiles and the first mammals are particularly well documented in the southern continents. It is inconceivable that the initial stages of mammalian evolution were well under way in the south, but that later developments shifted abruptly and predominantly to the north. Until quite recently, the Jurassic/Cretaceous fossil record of mammals in the southern continents was disappointingly limited to a toothless mandible of *Brancatherulum* from the late Jurassic of Tanzania and Argentinian footprints of similar age attributed to a mammal ("*Ameghenichnus*"). Although the dentition of *Brancatherulum* remains unknown, new research on the deposits from Tanzania has revealed dental remains of 3 other early mammals, a triconodontid, a eupantothere and a haramyid (Heinrich, 1998, 1999). Furthermore, in recent years, the southern continental record has been somewhat expanded by discoveries of fragments of early Cretaceous mammals in Cameroon and Morocco (Brunet et al., 1990; Sigogneau-Russell, 1995), thus confirming that early mammals were indeed present in the southern continents. But the fossil evidence remains exceedingly fragmentary and enormous gaps in the record remain. Despite the inadequacies of the fossil record, it now seems highly probable that the two main groups of modern mammals, marsupials and placentals, diverged early in the Cretaceous at least 125 mya, as fossil mammals of that age identified as a placental (*Eomaia*) and as a marsupial (*Sinodelphys*) have recently been reported from China (Ji et al., 2002; Luo et al., 2003). This, however, means that placentals and marsupials must have existed for at least 60 my prior to the K/T boundary but are very poorly known from the fossil record, particularly for the southern continents.

Although the adaptive radiation of modern placental mammals is comparatively well documented above the K/T boundary, there are still undoubted major gaps not just for primates but also for many other groups. There is, in fact, a systemic problem with respect to the origins of modern placentals in that placental mammals known from the Palaeocene epoch (65–55 mya) generally belong to archaic groups with no clear connection to modern orders. Just as Palaeocene "archaic primates" (Plesiadapiformes) have at the most only a remote connection to euprimates, various other groups of archaic placentals are also of dubious affinities. A case in point is provided by the mesonychians, which were traditionally linked directly to the cetaceans but have been sidelined by new fossil discoveries of early terrestrial relatives of cetaceans (Thewissen et al., 2001). Indeed, it has become clear that a major turnover of the terrestrial mammalian fauna occurred close to the Palaeocene/Eocene boundary, coinciding with an episode of pronounced global warming (Berggren et al., 1998). The warming process at the Paleocene-Eocene boundary (the Late Paleocene Thermal Maximum), which was particularly evident at high latitudes, took about 2 my. During the late Paleocene and early Eocene, Europe, North America and Asia together constituted a single Holarctic biogeographical province with common floristic and faunal elements. The deciduous vegetation that characterized this Holarctic province during the Paleocene was gradually replaced during the early Eocene by markedly different rainforest vegetation, which eventually extended to latitudes as far as 60° north and south of the equator (Wolfe, 1987). In fact, international recognition of the Paleocene/Eocene boundary was initially linked to a more abrupt major turnover in the mammalian fauna characterized by disappearance of archaic groups and immigration by modern placental groups. In Europe, condylarths, adapisoriculid "insectivores", multituberculates and plesiadapiforms declined and were replaced by artiodactyls, perissodactyls, rodents, bats, euprimates and certain other groups. In North America, the transition was accompanied, among other things, by a relatively rapid decline in mesonychians, notungulates and plesiadapiforms, with replacement by artiodactyls, perissodactyls, rodents, insectivores and euprimates. With respect to the new appearances of placental mammal groups in North America, Wing (1998) made the following observation: "These groups do not appear to have mid-Paleocene ancestors in North America, implying that they arrived from a different continent. Several authors have suggested that the late Paleocene-early Eocene mammalian immigrants to North America originated at more tropical latitudes in the Americas, Asia, or Africa (Sloan 1969, Gingerich 1980, 1989, Krause and Maas 1990), and then migrated to middle and high latitudes as global climate warmed in the late Paleocene and early Eocene epochs." As noted by Hooker (1998), the same applies to the comparable faunal turnover that took place in Europe and Asia: "There has been much speculation on the centers of origin of the main mammal groups that appeared essentially synchronously in Europe, North America, and Asia, namely the orders Artiodactyla, Perissodactyla, Primates, and Chiroptera, and the families Hyaenodontidae (Creodonta) and herpetotheriine 'Didelphidae' (Marsupialia). Krause

and Maas (1990) have thoroughly investigated the problem of these origins in a temporally broader study of mammalian immigrants into North America. It is normally accepted that low-latitude areas are involved, in view of the absence of Paleocene representatives in any midlatitude faunas in the northern hemisphere […]." In all cases, however, the ancestors of these immigrating placental mammal groups at the Paleocene/Eocene boundary in the northern hemisphere have yet to be discovered.

Inadequate documentation of early placental mammals is hence apparent throughout the fossil record. One striking illustration is provided by the example of the mammalian order containing bats (Chiroptera), which is very diverse and represented by over a thousand extant species. Yet the fossil record for bats is even more limited than that for primates, which include only 376 modern species. The earliest known fossil bats are found in early Eocene deposits of North America, Europe, Africa and Australia (McKenna & Bell, 1997; Simmons & Geisler, 1998). In fact, well-preserved early fossil bats are derived from only two fossil localities, one in North America and one in Europe. The North American bat *Icaronycteris* from the early Eocene Green River Formation was the first to be discovered, and 4 well-preserved specimens have been documented. In Europe, the single site of Messel in southern Germany has yielded a spectacular array of over 100 well-preserved bat skeletons belonging to species of 3 genera (*Archaeonycteris*, *Hassianycteris*, *Palaeochiropteryx*) from early/middle Eocene deposits. At both sites, the bat skeletons already show several diagnostic features associated with the development of flight, and the dimensions of the cochlea indicate initial adaptation for echolocation. Furthermore, examination of traces of stomach contents of some individuals from Messel has revealed scales of moths belonging to families that are currently prominent in bat diets. Indeed, one pregnant individual with 2 late fetuses has been described, suggesting that small litter sizes were already typical for bats at that early stage. Thus, the earliest known bats already possessed many of the features of their modern relatives, but there are no known precursors. Like euprimates, artiodactyls, perissodactyls and rodents, bats appear abruptly in the fossil record of the northern hemisphere with no indication of their origins.

A Rôle for Continental Drift

If the initial divergence and subsequent diversification of various modern groups of placental mammals took place considerably earlier than has been traditionally supposed, namely during the latter half of the Cretaceous rather than during the Palaeocene, this introduces the possibility that continental drift might have played a significant rôle (Martin, 1990). It also increases the likelihood that the southern continents, which have a particularly poor fossil record for the period between 90 and 65 mya, played an important part in the early diversification of placental mammals. If the

initial radiation of placental mammals began during the mid-Cretaceous, about 90 mya, it would have coincided with a period of maximal subdivision of landmasses through a combination of continental drift and extensive formation of epicontinental seas. Such a possibility was explicitly invoked by Kumar & Hedges (1998): "For example, the sudden appearance (in the Early Tertiary fossil record) of mammalian and avian orders, which show large morphological differences, has been taken to imply rapid rates of morphological change at that time. Now, the possibility of 20–70 Myr of prior evolutionary history relaxes that assumption and suggests a greater role for Earth history in the evolution of terrestrial vertebrates." Subsequently, Murphy et al. (2001b) linked the subdivision between their 4 supergroups of placental mammals directly to continental drift. They suggested that Afrotheria (the first group to diverge) became isolated on Africa at an early stage and that Xenarthra originated through isolation in South America. They also proposed that Laurasiatheria and Euarchontoglires became isolated in Laurasia, although it is not evident how this conclusion was reached. (The term "Laurasiatheria" naturally implies some connection with Laurasia, but the association of hoofed mammals, bats, carnivores and certain insectivores with that landmass is by no means as obvious as the inferred connection between Afrotheria and Africa.)

The increasing availability of well-documented reconstructions of past continental positions, including the occurrence of epicontinental seas, has considerably enhanced our ability to explore the biogeographical background to mammalian evolution (e.g. see in particular the PALEOMAP Project – Scotese, 2001). As divergence times for mammals are pushed further back into the past, it seems increasingly likely that the break-up of the southern supercontinent Gondwanaland played some part in their diversification. It seems highly likely, for example, that afrotherian mammals were isolated on Africa at a relatively early stage of the evolution of placental mammals. A key point here is that the primates are not members of Afrotheria, so it now seems improbable that ancestral primates occurred on Africa, as has often been supposed (e.g. Martin, 1990). An alternative possibility is that primates (and perhaps the entire supergroup Euarchontoglires) were isolated on Indo-Madagascar, as hypothesized by Krause and Maas (1990). Given that Madagascar separated from India about 88 mya (Storey, 1995), this could perhaps explain how the lemurs became isolated on Madagascar (Martin, 2000). Derivation of lemurs from a hypothetical ancestral primate stock in Africa was always problematic because Madagascar separated from Africa at such an early stage, at least 130 mya. Briggs (2003) provided the following summary of dates for the rifting history of India during the Mesozoic, prior to its initial collision with Eurasia at about 55–65 mya: (1) separation of Africa and Indo-Madagascar at 158–160 mya; (2) separation of Antarctica and Madagascar+India at about 130 mya; (3) separation of Madagascar and India+Seychelles at 84–96 mya; (4) separation of Seychelles and India at 65 mya. In fact, as part of a general discussion of continental drift, Prothero (1999) suggested that not only primates but also other prominent groups of Tertiary mammals such as artiodactyls and perissodactyls,

which are all undocumented in the northern continental fossil record prior to the Eocene, possibly evolved in India and then entered Eurasia following the collision. (This would mean that Laurasiatheria were isolated on India along with Euarchontoglires.)

It should be noted, however, that Briggs (2003) pointed out that it is generally more difficult to establish longitude, as opposed to latitude, in palaeocontinental reconstructions and suggested that India may have been closer to Africa than has generally been indicated in reconstructions of continental positions during the Mesozoic (e.g. by Scotese, 2001). Some palaeontological evidence indicates exchanges between India and other, supposedly isolated land-masses (e.g. Africa, Eurasia) during the Mesozoic. Moreover, the known fossil record of India lacks the peculiar fauna and flora that would be expected if India had been fully isolated for some 30 million years between its separation from Madagascar and its contact with Eurasia. Whereas the group Afrotheria does not include primates, it does include tenrecs, which is one of the 4 endemic groups of mammals currently present on Madagascar. So some special explanation is in any case necessary for the colonization of Madagascar by tenrecs. It has also been shown that carnivores colonized Madagascar some considerable time after the lemurs (Yoder et al., 2003), so a single, all-embracing explanation of mammalian invasions of Madagascar is clearly ruled out.

Although a proper discussion is beyond the scope of this essay, it is important to note that many of the same arguments apply to the adaptive radiation of modern birds. Because there are similar large gaps in the fossil record, a direct reading of the available evidence would seem to indicate that there was an "explosive" adaptive radiation of modern birds after the K/T boundary, as has traditionally been inferred for mammals (Feduccia, 1995). However, accumulating molecular evidence, combined with biogeographical considerations, has increasingly suggested that the adaptive radiation of modern birds began well before the K/T boundary and that the southern continents played a major part (Cooper & Penny, 1997; Cracraft, 2001; Härlid 1999; Hedges et al., 1996; Kumar & Hedges, 1998; Waddell et al., 1999).

A Tentative Synthesis

The evidence presented in this essay suggests that the diversification of modern primates from a common ancestor, in common with the diversification of many other modern groups of placental mammals, began well back in the Cretaceous. In other words, representatives of many modern placental mammal groups existed long before the extinction of the dinosaurs, although they were not necessarily present in the same places. Given an early date for the diversification of euprimates and other placental mammals, it is highly likely that continental drift played a significant rôle and that the southern continents were of particular importance. There is some reason to believe that the mammalian supergroup including primates (Euarchontoglires),
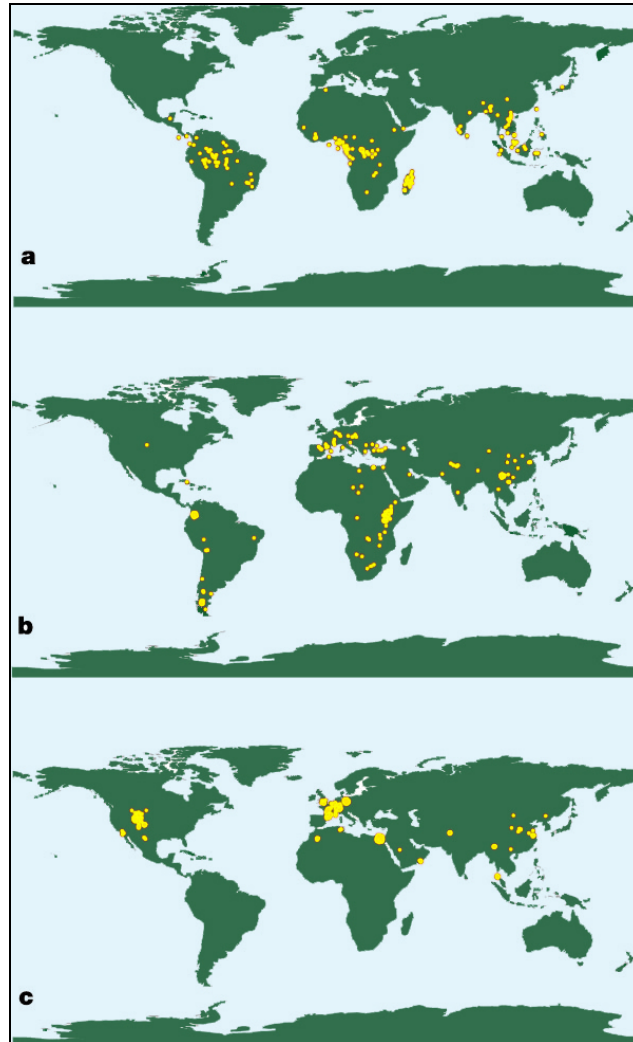
Figure 5

Maps with a present-day continental configuration showing the distributions of (a) modern primates; (b) later Tertiary fossil primates (late Pleistocene to late Oligocene); (c) earlier Tertiary fossil primates (early Oligocene to early Eocene) (from Tavaré et al., 2002). Known earlier Tertiary primates are largely restricted to the northern continents, while extant primates are essentially confined to the southern continents. Later Tertiary primates show an intermediate distribution, with numerous representatives in both northern and southern continents. Reprinted by permission from *Nature* (Tavaré, S., Marshall, C. R., Will, O., Soligo, C. & Martin, R. D., vol. 416, pp. 726–729) © (2002) Macmillan Journals Limited (http://www.nature.com/).

perhaps along with Laurasiatheria, might have been isolated on the drifting landmass of Indo-Madagascar. In light of this possibility, a renewed search for Cretaceous mammals in India might uncover valuable new evidence.

If the geographical distributions of euprimates over time are examined (Figure 5), it can be seen that earlier Tertiary representatives (32–55 mya) are largely restricted to the northern continents. This contrasts starkly with the distribution of extant primates, which are essentially confined to the southern continents. Fossil primates from later Tertiary deposits (0–26 mya) show an intermediate condition, occurring widely in both northern and southern continents. A direct reading of the fossil record would therefore suggest that primates originated in the northern continents and progressively shifted to the south. However, an alternative interpretation supported by the evidence now available is that primates were prevalent in the northern continents only while there was a period of higher world temperatures during the Eocene. Global cooling ensued around the Eocene-Oligocene boundary, and primates subsequently progressively disappeared from the northern continents. If it was, indeed, the case that the primates initially developed on India during its long period of isolation, then they would have been released into Eurasia at some time between 65 and 55 mya, along with a number of other groups of modern placental mammals. This could explain why no precursors of these modern mammals are present in fossil deposits of the northern continents prior to 55 mya.

In the absence of additional fossil evidence, the alternative reconstruction of primate evolutionary history presented here must, of course, remain speculative. However, that reconstruction represents a testable hypothesis that can be examined in the light of new fossil discoveries in the future. Clearly, whatever the outcome, augmented palaeontological investigation of Cretaceous deposits in India would be of particular interest.

Acknowledgements

view presented in this essay draws heavily on results of our joint research published elsewhere (Tavaré et al., 2002; Soligo et al., 2006).

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References

Archibald, J. D.: Molecular dates and the mammalian radiation. In: Trends in Ecology and Evolution 14 (1999), p. 278.

Arnason, U., Gullberg, A., Burguete, A. S. & A. Janke: Molecular estimates of primate divergences and new hypotheses for primate dispersal and the origin of modern humans. In: Hereditas 133 (2000), pp. 217–228.

Arnason, U., Gullberg, A., Janke, A. & X.-f. Xu: Pattern and timing of evolutionary divergences between hominoids based on analyses of complete mtDNAs. In: Journal of Molecular Evolution 43 (1996), pp. 650–661.

Arnason, U., Gullberg, A. & A. Janke: Molecular timing of primate divergences as estimated by two nonprimate calibration points. In: Journal of Molecular Evolution 47 (1998), pp. 718–727.

Berggren, W. A., Lucas, S. G. & M.-P. Aubry: Late Paleocene-Early Eocene climatic and biotic evolution: an overview. In: Aubry, M.-P., Lucas, S. G. & W. A. Berggren (eds.) Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records, New York: Columbia University Press, 1998, pp. 1–17.

Briggs, J. C.: The biogeographic and tectonic history of India. In: Journal of Biogeography 30 (2003), pp. 381–388.

Bromham, L. & D. Penn: The modern molecular clock. In: Nature Reviews Genetics 4 (2003), pp. 216–224.

Brunet, M., Coppens, Y., Dejax, J., Flynn, L., Heintz, E., Hell, J., Jacobs, L., Jehenne, Y., Mouchelin, G., Pilbeam, D. & J. Sudre: Nouveaux mammifères du Crétacé inférieur du Cameroun, Afrique de l'Ouest. In: Comptes Rendus de l'Académie des Sciences Paris, série II 310 (1990), pp. 1139–1146.

Cooper, A. & D. Penny: Mass survival of birds across the Cretaceous-Tertiary boundary: Molecular evidence. In: Science 275 (1997), pp. 1109–1113.

Cracraft, J.: Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. In: Proceedings of the Royal Society of London B 268 (2001), pp. 459–469.

Easteal, S., Collett, C. & D. Betty: The Mammalian Molecular Clock, Austin, Texas: R. G. Landes, 1995.

Feduccia, A.: Explosive evolution in Tertiary birds and mammals. In: Science 267 (1995), pp. 637–638.

Fleagle, J.G.: Primate Adaptation and Evolution, 2nd edition, Academic Press, New York, 1999.

Foote, M., Hunter, J. P., Janis, C. M. & J. J. Sepkoski: Evolutionary and preservational constraints on origins of biological groups: Divergence times of eutherian mammals. In: Science 283 (1999), pp. 1310–1314.

Foote, M. & J. J. Sepkoski: Absolute measures of the completeness of the fossil record. In: Nature 398 (1999), pp. 415–417.

Gatesy, Y.: More DNA support for a Cetacea/Hippopotamidae clade: the blood-clotting protein gene γ-fibrinogen. In: Molecular Biology and Evolution 14 (1997), pp. 537–543.

Gatesy, Y., Hayashi, C., Cronin, M. A. & P. Arctander: Evidence from milk casein genes that cetaceans are close relatives of hippopotamid artiodactyls. In: Molecular Biology and Evolution 13 (1996), pp. 954–963.

Gatesy, J., Milinkovitch, M., Waddell, V. & M. Stanhope: Stability of cladistic relationships between Cetacea and higher-level artiodactyl taxa. In: Systematic Biology 48 (1999), pp. 6–20.

Gingerich, P. D.: Evolutionary patterns in early Cenozoic mammals. In: Annual Review of Earth and Planetary Sciences 8 (1980), pp. 407–424.

Gingerich, P. D.: New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming: composition and diversity in a rarely sample high-floodplain assemblage. In: University of Michigan Papers in Paleontology 28 (1989), pp. 1–97.

Gingerich, P. D. & M. D. Uhen: Time of origin of primates. In: Journal of Human Evolution 27 (1994), pp. 443–445.

Graur, D. & D. G. Higgins: Molecular evidence for the inclusion of cetaceans within the order Artiodactyla. In: Molecular Biology and Evolution 11 (1994), pp. 357–364.

Groves, C. P.: Order Primates. In: Wilson, D. E. & D. M. Reeder (eds.), Mammal Species of the World: A Taxonomic and Geographic Reference, Volume 1, Baltimore: Johns Hopkins University Press, 2005, pp. 111–184.

Gunnell, G. F. & K. D. Rose: Tarsiiformes: evolutionary history and adaptation. In: Hartwig, W. C. (ed.), The Primate Fossil Record, Cambridge: Cambridge University Press, 2002, pp. 45–82.

Härlid, A.: A New Perspective on Avian Phylogeny: A Study Based on Mitochondrial Genomes, Ph.D. Thesis, Lund University, 1999.

Hedges, S. B., Parker, P. H., Sibley, C. G. & S. Kumar: Continental breakup and the ordinal diversification of birds and mammals. In: Nature 381 (1996), pp. 226–229.

Heinrich, W.-D.: Late Jurassic mammals from Tendaguru, Tanzania, East Africa. In: Journal of Mammalian Evolution 5 (1998), pp. 269–290.

Heinrich, W.-D.: First haramyid (Mammalia, Allotheria) from the Mesozoic of Gondwana. In: Mitteilungen des Museums für Naturkunde Berlin, Geowissenschaften 2 (1999), pp. 159–170.

Hooker, J. J.: Mammalian faunal change across the Paleocene-Eocene transition in Europe. In: Aubry, M.-P., Lucas, S. G. & W. A. Berggren (eds.), Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records, New York: Columbia University Press, 1998, pp. 428–450.

Huelsenbeck, J. P., Larget, B. & D. Swofford: A compound Poisson process for relaxing the molecular clock. In: Genetics 154 (2000), pp. 1879–1892.

Janke, A., Feldmaier-Fuchs, G., Thomas, W. K., von Haeseler, A. & S. Pääbo: The marsupial mitochondrial genome and the evolution of placental mammals. In: Genetics 137 (1994), pp. 243–256 .

Ji, Q., Luo, Z.-Y., Yuan, C.-X., Wible, J. R., Zhang, J.-P. & J. A. Georgi: The earliest known eutherian mammal. In: Nature 416 (2002), pp. 816–822.

Kay, R. F., Ross, C. & B. A. Williams: Anthropoid origins. In: Science 275 (1997), pp. 797–804.

Krause, D. W. & M. C. Maas: The biogeographic origins of late Paleocene-early Eocene mammalian immigrants to the Western Interior of North America. In: Geological Society of America Special Papers 243 (1990), pp. 71–105.

Krebs, B.: Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupantotheria, Mammalia) aus dem Oberen Jura von Portugal. In: Berliner geowissenschaftliche Abhandlungen 133 (1991), pp. 1–121.

Kumar, S. & S. B. Hedges: A molecular timescale for vertebrate evolution. In: Nature 392 (1998), pp. 917–920.

Luo, Z.-X., Ji, Q., Wible, J. R. & C.-X.Yuan: An early Cretaceous tribosphenic mammal and metatherian evolution. In: Science 302 (2003), pp. 1934–1940.

Madsen, O., Scally, M., Douady, C. J., Kao, D. J., Debry, R. W., Adkins, R., Amrine, H. M., Stanhope, M. J., de Jong, W. W. & M. S. Springer: Parallel adaptive radiations in two major clades of placental mammals. In: Nature 409 (2001), pp. 610–614.

Marivaux, L., Welcomme, J. L., Antoine, P.-O., Métais, G., Baloch, I. M., Benammi, M., Chaimanee, Y., Ducrocq, S. & J.-J. Jaeger: A fossil lemur from the Oligocene of Pakistan. In: Science 294 (2001), pp. 587–591.

Martin, R. D.: Primates: a definition. In: Wood, B. A., Martin, L. B. & P. Andrews (eds.), Major Topics in Primate and Human Evolution, Cambridge: Cambridge University Press, 1986, pp. 1–31.

Martin, R. D.: Primate Origins and Evolution: A Phylogenetic Reconstruction, New Jersey: Princeton University Press, 1990.

Martin, R. D.: Primate origins: plugging the gaps. In: Nature 363 (1993), pp. 223–234.

Martin, R. D.: Origins, diversity and relationships of lemurs. In: International Journal of Primatology 21 (2000), pp. 1021–1049.

Martin, R. D.: Palaeontology: Combing the primate record. In: Nature 422 (2003), p. 388.

McKenna, M. C. & S. K. Bell: Classification of Mammals Above the Species Level, New York: Columbia University Press, 1997.

Miller, E. R., Gunnell, G. F. & R. D. Martin: Deep time and the search for anthropoid origins. In: Yearbook of Physical Anthropology 48 (2005), pp. 60–95.

Murphy, W. J., Eizirik, E., Johnson, W. E., Zhang, Y.-P., Ryder, O. A. & S. J. O'Brien: Molecular phylogenetics and the origins of placental mammals. In: Nature 409 (2001a), pp. 614–618.

Murphy, W. J., Eizirik, E., O'Brien, S. J., Madsen, O., Scally, M., Douady, C. J., Teeling, E., Ryder, A. O., Stanhope, M. J., de Jong, W. W. & M. S. Springer: Resolution of the early placental mammal radiation using Bayesian phylogenetics. In: Science 294 (2001b), pp. 2348–2351.

Ni, X., Wang, Y., Hu, Y. & C. Li: A euprimate skull from the early Eocene of China. In: Nature 427 (2004), pp. 65–68.

Nikaido, M., Nishihara, H., Hukumoto, Y. & N. Okada: Ancient SINEs from African endemic mammals. In: Molecular Biology and Evolution 20 (2003), pp. 522–527.

Nikaido, M., Rooney, A. P. & N. Okada: Phylogenetic relationships among certartiodactyls based on insertions of short and long interspersed elements: Hippopotamuses are the

closest extant relatives of whales. In: Proceedings of the National Academy of Sciences, USA 96 (1999), pp. 10261–10266.

Novacek, M. J.: Mammalian phylogeny: Shaking the tree. In: Nature 356 (1992), pp. 121–125.

Novacek, M. J. & A. R. Wyss: Higher-level relationships of the recent eutherian orders: Morphological evidence. In: Cladistics 2 (1988), pp. 257–287.

Phillips, E. M. & A. C. Walker: Fossil lorisoids. In: Hartwig, W. C. (ed.), The Primate Fossil Record, Cambridge: Cambridge University Press, 2002, pp. 83–95.

Prothero, D. R.: Plate tectonics and continental drift. In: Singer, R. (ed.), Encyclopedia of Paleontology, Chicago: Fitzroy Dearborn, 1999, pp. 940–943.

Ross, C. F.: Review of "The Primate Fossil Record": Edited by Walter C. Hartwig. In: Journal of Human Evolution 45 (2003), pp. 195–201.

Sarich, V. M.: Mammalian systematics: twenty-five years among their albumins and transferrins. In: Szalay, F. S., Novacek, M. J. & M. C. McKenna (eds.), Mammal Phylogeny. Volume 1: Placentals, Berlin: Springer-Verlag, 1993, pp. 103–114.

Scotese, C. R.: Atlas of Earth History. PALEOMAP Project, Arlington, Texas, 2001 (website: http://www.scotese.com).

Seiffert, E. R., Simons, E. L. & Y. Attia: Fossil evidence for an ancient divergence of lorises and galagos. In: Nature 422 (2003), pp. 421–424.

Shipman, P.: Taking Wing: *Archaeopteryx* and the Evolution of Bird Flight, London: Weidenfeld & Nicolson (1998).

Sigogneau-Russell, D.: Further data and reflexions on the tribosphenid mammals (Tribotheria) from the Early Cretaceous of Morocco. In: Bulletin du Muséum National d'Histoire naturelle de Paris, 4. série (C) 16 (1995), pp. 291–312.

Simmons, N. B. & J. H. Geisler: Phylogenetic relationships of *Icaronycteris*, *Archaeonycteris*, *Hassianycteris*, and *Palaeochiropteryx* to extant bat lineages, with comments on the evolution of echolocation and foraging strategies in Microchiroptera. In: Bulletin of the American Museum of Natural History 235 (1998), 1–182.

Simpson, G. G.: The Geography of Evolution, Philadelphia: Chilton Books, 1965.

Sloan, R. E.: Cretaceous and Paleocene terrestrial communities in western North America. In: Yochelson, E. L. (ed.), Proceedings of the North American Palaeontological Convention 1, Lawrence: Allen Press, 1969, pp. 427–453.

Soligo, C., Will, O., Tavaré, S., Marshall, C. R. & R. D. Martin: New light on the dates of primate origins and divergence. In: Ravosa, M. J. & M. Dagosto (eds.), Primate Origins: Adaptations and Evolution, New York: Springer, 2006, pp. 29–49.

Springer, M. S., Amrine, H. M., Burk, A. & M. J. Stanhope: Additional support for Afrotheria and Paenungulata, the performance of mitochondrial versus nuclear genes, and the impact of data partitions with heterogeneous base composition. In: Systematic Biology 48 (1999), pp. 65–75.

Springer, M. S., Cleven, G. C., Madsen, O., de Jong, W. W., Waddell, V. G., Amrine, H. M. & M. J. Stanhope: Endemic African mammals shake the phylogenetic tree. In: Nature 388 (1997), pp. 61–64.

Springer, M. S., Murphy, W. J., Eizirik, E. & S. J. O'Brien: Placental mammal diversification and the Cretaceous-Tertiary boundary. In: Proceedings of the National Academy of Sciences U.S.A. 100 (2003), pp. 1056–1061.

Storey, M.: Timing of hot spot-related volcanism and the breakup of Madagascar and India. In: Science 267 (1995), pp. 852–855.

Tavaré, S., Marshall, C. R., Will, O., Soligo, C. & R. D. Martin: Using the fossil record to estimate the age of the last common ancestor of extant primates. In: Nature 416 (2002), pp. 726–729.

Thewissen, J. G. M., Williams, E. M., Roe, L. J. & S. T. Hussain: Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. In: Nature 413 (2001), pp. 277–281.

Ursing, B. M. & U. Arnason: Analyses of mitochondrial genomes strongly support a hippopotamus-whale clade. In: Proceedings of the Royal Society, London B 265 (1998), pp. 2251–2255.

Waddell, P. J., Cao, Y., Hasegawa, M. & D. P. Mindell: Assessing the Cretaceous superordinal divergence times within birds and placental mammals by using whole mitochondrial protein sequences and an extended statistical framework. In: Systematic Biology 48 (1999), pp. 119–137.

Wing, S. L.: Late Paleocene-Early Eocene floral and climatic change in the Bighorn Basin, Wyoming. In: Aubry, M.-P., Lucas, S. G. & W. A. Berggren (eds.), Late Paleocene-Early Eocene Climatic and Biotic Events in the Marine and Terrestrial Records, New York: Columbia University Press, 1998, pp. 380–400.

Wolfe, J. A.: Distribution of major vegetational types during the Tertiary. In: Sundquist, E. T. & W. S. Broecker (eds.), The Carbon Cycle and Atmospheric CO_2: Natural Variations, Archean and Present, Washington, D. C.: American Geophysical Union, 1987, pp. 357–375.

Yang, Z. H. & A. D. Yoder: Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. In: Systematic Biology 52 (2003), pp. 705–716.

Yoder, A. D., Burns, M. M., Zehr, S., Delefosse, T., Veron, G., Goodman, S. M. & J. J. Flynn: Single origin of Malagasy Carnivora from an African ancestor. In: Nature 421 (2003), pp. 734–737.

Yoder, A. D. & Z. H. Yang: Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. In: Molecular Ecology 13 (2004), pp. 757–773.