Evolution and biogeography of primates: a new model based on molecular phylogenetics, vicariance and plate tectonics

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The ages of the oldest fossils suggest an origin for primates in the Paleocene (~56 Ma). Fossil-calibrated molecular clock dates give Cretaceous dates (~80–116 Ma). Both these estimates are minimum dates although they are often 'transmogrified' and treated as maximum or absolute dates. Oldest fossils can underestimate ages by tens of millions of years and instead of calibrating the time-course of evolution with a scanty fossil record, the geographical boundaries of the main molecular clades of primates are calibrated here with radiometrically dated tectonic events. This indicates that primates originated when a globally widespread ancestor (early Archonta) differentiated into a northern group (Plesiadapiformes, extinct), a southern group (Primates), and two south-east Asian groups (Dermoptera and Scandentia). The division occurred with the breakup of Pangea in the Early Jurassic and the opening of the central Atlantic (~185 Ma). Within primates, the strepsirrhines and haplorhines diverged with volcanism and buckling on the Lebombo Monocline, a volcanic rifted margin in south-east Africa (Early Jurassic, ~180 Ma). Within strepsirrhines, lorises and galagos (Africa and Asia) and lemurs (Madagascar) diverged with the formation of the Mozambique Channel (Middle Jurassic, ~160 Ma). Within haplorhines, Old World monkeys and New World monkeys diverged with the opening of the Atlantic (Early Cretaceous, ~130 Ma). The main aspects of primate distribution are interpreted as the result of plate tectonics, phylogeny and vicariance, with some subsequent range expansion leading to secondary overlap. Long-distance, trans-oceanic dispersal events are not necessary. The primate ancestral complex was already widespread globally when sea-floor spreading, strike-slip rifting and orogeny fractured and deformed distributions through the Jurassic and Cretaceous, leading to the origin of the modern clades. The model suggests that the topology of the phylogenetic tree reflects a sequence of differentiation in a widespread ancestor rather than a series of dispersal events.

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Introduction

Primates are one of the best-known groups. Birds are well-studied in terms of field observations, but primates have a more extensive fossil record and the molecular phylogeny has been researched in great detail. Primates are widespread in most tropical areas although they are absent from eastern Indonesia and Australasia apart from humans and one introduced species. There are about 400 extant species and they are most diverse in lowland tropical rainforest, including mangrove and freshwater swamp forest. Many species have local distributions and are threatened by habitat loss and commercial hunting, while others are abundant and can be pests for farmers in rural areas.

A great deal is now known about the phylogeny and distributions of the primate clades (Goodman et al. 2005; IUCN, 2008). Nevertheless, there are fundamental disagreements about the group’s evolution, beginning with where and when it originated. The lack of any consensus on this has held up progress in understanding many other aspects of primate evolution.

The basal primate in a phylogenetic sense may be the fossil *Altanius*, from the Eocene of Mongolia, and the oldest primate fossil may be *Altiatlasius*, from the Late Paleocene of Morocco (Fleagle & Gilbert 2006). Still, the interpretation of these fragmentary fossils, in particular their phylogenetic status, is controversial (different interpretations and phylogenies are available for many primate
fossils). Centre-of-origin analyses of the living primates are also inconclusive and the study by Heesy et al. (2006: 420), like others, begins and ends with the unanswered question: ‘On which continent did primates originate?’ Biologists have been debating whether the true centre of origin of primates was in Africa, Asia or America for more than a century and the argument has never been resolved.

The problem of primates’ origin in space is related to the vexed question of their origin in time. While fossil-based dates give an origin for primates in the Paleocene, at ~56 Ma, fossil-calibrated molecular clocks give Cretaceous dates, at ~90 Ma (e.g. Janečka et al. 2007). Despite the fact that both these estimates are minimum dates, in many accounts they are mysteriously ‘transmogrified’ and treated as maximum or absolute dates. The molecular clock dates are not absolute dates, but they are important as they show that fossil-based dates could underestimate ages by tens of millions of years.

Masters (2006: 112) concluded: ‘Where, then, did primates originate, and how did they come to occupy their current distribution? This remains the single most puzzling aspect of primate evolution’. Most reconstructions require one to several over-water dispersal events on vegetation rafts and many authors have raised serious objections to this; Simons (1976, p. 50), for example, was unequivocal: ‘no explanation involving transport across wide reaches of ocean is tenable in accounting for the distribution of any primate...’.

Most writers on biogeography have found the centre of origin concept easy to justify in theory, although in practice they have had difficulty achieving consistent results. For primates, Fleagle & Gilbert (2006) supported Asia as centre of origin, but this was tentative and they considered the issue ‘far from resolved’ (p. 385); Rasmussen (2002) favoured Africa or India; Silcox (2008) suggested Europe; Arnason et al. (2008) proposed South America; Bloch et al. (2007) supported North America (for Primates s.lat.). One multi-author study (Miller et al. 2005, p. 87) epitomized the problem: of the three authors ‘two are more strongly inclined to identify the African origin hypothesis (E.R.M. and G.F.G.) as the clear front runner, the other (R.D.M.) favours the Indo-Madagascar hypothesis’. The primates are already quite well-known and it seems that the more data are accumulated, the more confusing the search for the centre of origin becomes. The origins of the main clades within primates (Table 1) are also obscure. Wright (1997, p. 129) concluded that there is ‘No convincing explanation’ for the origin of the New World monkeys, and that the origins of the primates on Madagascar, the lemurs, are equally ‘enigmatic’.

It is suggested here that the endemism of major clades in Madagascar and America is a valuable clue for deducing the evolution of the group as a whole. The only primates, living or fossil, in Madagascar are lemurs, while the only ones in South and Central America are platyrrhines (Fig. 1). Apart from platyrhine fossils in Patagonia and the Caribbean, neither of the two groups has fossils outside its extant distribution. In a dispersal framework the two groups are considered as separate issues: how did the lemurs and the platyrrhines each migrate to their respective areas and from where? Yet Lehman & Fleagle (2006) made the point that a taxon or a population can occupy an area either because it moved there or because it evolved there. In the vicariance model proposed here, lemurs, platyrrhines and the other groups did not migrate to their respective localities, but instead evolved there, during a single process of differentiation. Each is the local, vicariant representative of a widespread common ancestor. The general methodology and assumptions of vicariance analysis are outlined by Craw et al. (1999) and Heads (in press).

### The main clades of primates

#### Strepsirrhines and haplorhines

The two main primate clades differ in the morphology of the oro-nasal region: in strepsirrhines (‘curled nose’) the nose has a moist, glandular rhinarium like that of a dog and many other mammals, in haplorhines (‘simple nose’) the nose is dry and without a rhinarium. Characters supporting the strepsirrhine-haplorhine split are mainly soft-tissue characters (e.g. the rhinarium and other nasal features) that are seldom preserved in fossils (Gunnell & Rose, 2002: 46).

Haplorhines occur in South America but not Madagascar; strepsirrhines are in Madagascar but not South America (Fig. 1). Haplorhines are widespread in the New and Old World tropics, but are absent, living and fossil, from both Madagascar and Australia/New Guinea (other large clades, such as woodpeckers, are distributed in a similar way). Conversely, no strepsirrhine, living or fossil, has ever been found in South or Central America.

The New World monkeys and the lemurs each have their sister group on mainland Africa and Asia, and haplorhines and strepsirrhines overlap there. Yet the respective distributions of the two main groups within

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**Table 1** The main clades of extant primates (Goodman et al. 2005)

<table>
<thead>
<tr>
<th>Strepsirrhines</th>
<th>Haplorhines</th>
<th>Madagascar</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lemurs</td>
<td>Tarsiens</td>
<td>Mainland Africa and Asia</td>
</tr>
<tr>
<td>Lorises and galagos</td>
<td>Old World monkeys (catarrhines)</td>
<td>SE Asia</td>
</tr>
<tr>
<td>New World monkeys (platyrrhines)</td>
<td></td>
<td>Mainland Africa and Asia</td>
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<td></td>
<td></td>
<td>Tropical America</td>
</tr>
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</table>
Africa are quite different; haplorhines are especially diverse in the west and centre, and occur throughout South Africa, whereas strepsirrhines are diverse in East Africa, and in South Africa do not range west of KwaZulu-Natal. The proportion of strepsirrhine species in local primate faunas declines markedly from East Africa to West Africa, for example from 60% in the Rufiji delta, Tanzania (six strepsirrhine species, four haplorhines; Doody & Hamerlynck 2003) to 14% in the Niger delta/Sanaga River area of Nigeria and Cameroon (six strepsirrhines, 16 haplorhines; Oates et al. 2004) (species are listed in the Appendix).

The distributions of strepsirrhines and haplorhines also differ in southern Asia. Haplorhines have seven subspecies in Sri Lanka and, as might be expected, many more (26) in the much larger India. By contrast, strepsirrhines have three subspecies in Sri Lanka and the same number in all of India, and so they have a higher proportion of their diversity in Sri Lanka than haplorhines do.

In south-east Asia, strepsirrhines are known east to the Sulu Archipelago, off north-eastern Borneo, and do not occur on the main Philippine islands such as Mindanao. By contrast, haplorhines (macaques and tarsiers) are present on the main Philippine islands and also in Sulawesi. Again, as in Africa and India, strepsirrhines are located on the Indian Ocean side of the region.

Following Matthew (1915), most authors have interpreted the strepsirrhines as older than haplorhines and their distribution in Madagascar and Sri Lanka as ‘marginal’ and relictual. In this evolutionary model strepsirrhines originated in the north and were later pushed out to the margins by the new, more advanced and more competitive haplorhines. While this idea is not accepted here, the differences between the distributions of haplorhines and strepsirrhines are real and important, and could be the result of initial vicariance between the two groups. Madagascar and Sri Lanka may appear to be ‘marginal’ from a north temperate (Holarctic) viewpoint, but in an Indian Ocean or Gondwanan perspective they are central.

**Tarsiers**

Tarsiers (Tarsiiformes s.str.) comprise living *Tarsius* species, in Sumatra, Borneo, Sulawesi and the Philippines, and fossils on mainland SE Asia. There is an Eocene *Tarsius* from Jiansu (near Shanghai) and another tarsiid, *Xanthorhysis*, from Shangxi (near Beijing). The identity of *Afrotarsius* from the Egyptian Oligocene is disputed; it could be a tarsier or an anthropoid (Fleagle & Gilbert 2006).

For many decades the small-brained tarsiers were linked with the small-brained lemurs and lorises as ‘prosimians’, precursors of the large-brained anthropoids or ‘simians’. By contrast, most studies of nuclear DNA place tarsiers with anthropoids, supporting the strepsirrhines and haplorhines as the two main groups of primates, rather than prosimians and anthropoids (Goodman et al. 2005; Schmitz et al. 2005; Matsui et al. 2009). Nevertheless, the position of *Tarsius* remains controversial. Mitochondrial DNA analyses group it with strepsirrhines to give a prosimian clade (Eizirik et al. 2001, 2004; Horner et al. 2007) and it shows a suggestive checker-board pattern of local allopatry (microallopatry) with the only strepsirrhine in its region, *Nycticebus* (Harcourt 1999). One tarsier individual had a strepsirrhine nasal notch on one side and a haplorhine opening on the other side (Simons 2003). The two alternative positions of *Tarsius* are integrative, not exclusive, and may result from retention and incongruent recombination of ancestral characters. Placing tarsiers with either anthropoids or strepsirrhines should not obscure the fundamental differences that tarsiers show from both. Even apart from the huge eyes, each larger than the brain, and the ability to turn the head 180° either way – both features are unique in mammals – *Tarsius* is set apart from...
other primates by its carnivore-like brain, almost totally carnivorous diet, and other characters which make it an unlikely ancestor for anthropoids (Wright et al. 2006). Its biogeography is also distinct as it has populations (and endemic species) further east than all other primates.

Fossil clades of primates: adapiforms and omomyiforms
The extant clades of primates have fossils dating back to the Early Eocene. Two additional groups, adapiforms and omomyiforms, are only known as Cenozoic fossils from the US and Eurasia. Adapiforms were traditionally regarded as Eocene lemurs and omomyiforms as Eocene tarsiers (Matthew 1915), but disagreements with this interpretation have emerged and are discussed below.

Primates and their relatives – the archonta
The term ‘primates’ as used here refers to the order in the narrow sense, excluding the extinct plesiadapiforms (this clade is sometimes referred to as ‘euprimates’, although the new name is not necessary). The orders Primates and Plesiadapiformes, along with two small south-east Asian orders, Dermoptera and Scandentia, make up the super-order Archonta (Fig. 2) (in the premolecular era Archonta included bats; bats are now excluded but, again, there is no need for the new name, euarchonta).

Plesiadapiforms have most of their known diversity in North America where they occur in the US and Canada as far north as Ellesmere Island by northern Greenland; no primate fossils are known this far north. Plesiadapiforms are also known from Europe and China.

Scandentia or tree shrews comprise four Asian genera ranging from Borneo to India and Nepal (not Sri Lanka). Fossils (Asia only) are known back to the Eocene. Dermoptera include two Asian genera of ‘flying lemurs’, Galeopterus in south-east Asia: Thailand, Vietnam, Sumatra, Java and Borneo, and Cynocephalus in the Philippines. The group does not occur in Sulawesi. Extralimital fossils are known from Myanmar and Pakistan (Marivaux et al. 2006). Although Dermoptera and Scandentia are diverse in and around Borneo, neither group occurs in Sulawesi.

More information on these primate sister groups is given in the Appendix. Archonta are widespread globally yet they have never been recorded east of Sulawesi or in parts of western America (western Mexico, Chile), unlike their sister group Glires (rodents and lagomorphs) that has major diversity and endemism in both areas. The groups of Archonta and primates are listed in Table 2.

The topology often given for Archonta is: [Scandentia [Dermoptera (plesiadapiforms, primates)]] although the support is generally weak (Janečka et al. 2007). The four orders are treated here as more or less equivalent clades that were originally allopatric and this is discussed next.

The centre of origin theory of primate evolution
Matthew’s (1915) account of mammalian evolution remains widely accepted as a basic framework. He proposed that: (i) The northern fossil groups of primates and other orders represent ancestors which evolved in the Holarctic (north temperate) centre of origin. (ii) Tropical and southern members of the orders dispersed from the north. (iii) The orders are Cenozoic, as shown by the fossils. (iv) The orders originated on, and dispersed over, a more or less modern arrangement of land and sea.

Many contemporary workers still accept Holarctic centres of origin. For mammals, Gheerbrant & Rage (2006,
p. 224) concluded that ‘all successful and typical African radiations’ have resulted from origins in Laurasia followed by dispersal into Africa. While modern interpretations of primate evolution differ on the location of particular centres, all agree with Matthew (1915) that centres of origin do exist. Beard (2006, p. 439) defended this assumption, arguing that ‘The continuity of phylogenetic descent requires that sister taxa originate in the same place and at the same time’. For example, if we accept that tarsiers and anthropoids are each others’ closest relatives ‘we must also assume that both lineages originated in the same place (since speciation, like politics, is local).’ (Beard 2004: 13–14). Likewise, Godinot & Lapparent de Broin (2003) suggested that because primates have sister groups (Dermoptera and Scandentia) in south-east Asia, this was their centre of origin. In fact, there is no need to assume this. The process may have only involved normal, allopatric (dichopatric) evolution in a global group which divided into the two small clades in south-east Asia, and primates and plesiadapiforms everywhere else. Here there is no centre of origin and no dispersal (i.e. founder speciation), just differentiation in a widespread ancestor around breaks in south-east Asia followed by range expansion and secondary overlap (cf. Heads in press) (Fig. 2).

Beard (2006, p. 439) (cf. Fleagle & Gilbert 2006) suggested that: ‘The order Primates is hierarchically nested within an exclusively Asian branch of the mammalian family tree, suggesting that primates originated in Asia’. This is not quite correct. Dermoptera and Scandentia do not form a clade and primates are not nested in an Asian group; they are nested in an otherwise Asian group. The clade: primates + Dermoptera + Scandentia also occurs in Africa, Madagascar and the Americas. If the fossils are included, in the simplest model the northern plesiadapiforms, the southern primates, and the two south-east Asian orders all originated from an almost global ancestor which divided into the four geographical groups (Fig. 2). While the phylogeny and relative timing indicate that the breaks could have occurred around rifts in the central North Atlantic and Asia/Tethys, this does not mean that primates had a localized ‘centre of origin’ in any of these localities.

Neontologists often assume that a ‘basal group’, such as Scandentia or Dermoptera in Archonta, is ‘primitive’ and occupies the centre of origin of the whole clade. In fact, ‘basal group’ is just a conventional term for a small sister group; the other sister is just as basal (it is the node, rather than any of the clades, which is basal). With respect to fossils, many paleontologists also assume that a basal group – whether defined by phylogeny, stratigraphy, or both – occupies a centre of origin. They read the phylogenetic tree or the stratigraphic sequence as a sequence of dispersal events from a centre of origin, rather than a sequence of differentiation in a widespread ancestor. For example, the omomyid *Teilhardina* is the oldest known primate fossil in Europe and in North America, and also occurs in China. Smith et al. (2006) depicted cartoon figures of omomyids leaping from a centre of origin in China to Europe, and from there to America. Beard’s (2008) figure instead has them leaping from Asia across Beringia to America, and from there to Europe. The two ‘routes’ are interesting alternatives as sequences of differentiation events in a widespread northern ancestor, not as series of dispersal events.

Fleagle (1999) acknowledged that many of the key areas for primates have a ‘remarkably meager’ geological record and lack strata that are even potentially fossil-bearing. Nevertheless, he followed Matthew (1915) in accepting a centre of origin/dispersal model for spatial evolution. He also agreed with Matthew’s fossil-based chronology, writing that ‘The evolution of primates, like that of most other groups of modern mammals, has occurred almost totally within the Cenozoic era, the Age of Mammals’... (Fleagle 1999, p. 317). Based on this literal reading of the fossil record, Fleagle & Gilbert (2006: 375) concluded that ‘the evolutionary history of primates seems to have involved a wide range of traditional dispersal mechanisms, including land bridges, chance dispersal over open ocean, and intermediate island hopping’. In Europe, Asia, and America, the oldest primate fossils all ‘appear to be immigrants with no clear ancestors in underlying deposits’ (Fleagle & Gilbert 2006, p. 382). The authors interpreted these absences in the fossil record as a result of real absence and so accepted that they were evidence for dispersal. Instead, the absences could be as a result of normal sampling error in the sparse fossil record of early Cenozoic primates.
**Plesiadapiforms as ancestors**

Whether the main primate clades represent ancestors and descendants of each other or, instead, derivatives of common ancestors, is now being debated more and more. The northern fossil group, the plesiadapiforms, are often regarded as the sister group of the primates (e.g. Janečka et al. 2007) and, traditionally, as the ancestor. On the other hand, Godinot (2006a, p. 85), noting the ‘numerous and contradictory’ hypotheses about relationships in these groups, concluded that plesiadapiforms lie outside the clade Scandentia + primates and are not ancestral to primates. The plesiadapiforms’ sister group may be Dermoptera, rather than primates, or these three may form a trichotomy (Kay et al. 2004). In any case, plesiadapiforms are probably ‘too derived to tell us much about primate evolution’ (Ross 2003; cf. Fleagle 1999; Martin et al. 2007). To summarize, there is no need to interpret the plesiadapiforms as ancestral to primates, even though their oldest fossils are somewhat older (latest Cretaceous/earliest Paleocene vs. later Paleocene). A literal reading of the fossil record would interpret the primates as evolving from the plesiadapiforms and so emerging in the first place from a centre of origin at Garbani Channel, Montana (the location of the oldest plesiadapiform fossil, *Purgatorius*; Clemens 2004); this is not supported here. Instead, the considerable allopatry between the distributions of plesiadapiforms and primates (which is seldom mentioned in the literature) is interpreted a resulting from an original vicariance event.

**Adapiforms and omomyiforms as ancestors**

These two groups are only known as fossils from northern hemisphere countries. Adapiforms are recorded from the Eocene to Miocene of the US, the Mediterranean, and Asia. Omomyiforms are known from the Eocene to Oligocene and have a similar geographic range. For many years adapiforms were regarded as Eocene lemurs, omomyiforms as Eocene tarsiers. These links are now being questioned and the precise relationships of the fossil groups with each other and with the extant groups are the subject of much debate. The fossils show mosaic recombinations of features and there are almost as many different views on the groups’ affinities as there are logical possibilities (Kay et al. 2004). In traditional analyses omomyiforms and adapiforms both appear as paraphyletic complexes with many early offshoots, and modern strepsirrhines arose from within ‘adapiforms’, haplorhines from ‘omomyiforms’ (Matthew 1915, fig. 8; Kay et al. 2004, fig. 7). In other studies (Bajpai et al. 2008) adapiforms are sister to lemuriiforms, and omomyiforms are sister to anthropoids. Other authors have supported an adapiform-anthropoid connection; ‘several interesting similarities’ in upper dentition of the two groups are admitted although cranial and postcranial structure does not show this affinity (Gebo 2002, p. 23). Franzen et al. (2009) hypothesized that a well-preserved adapiform from Germany (*Darwinsius*) and, by implication, the other adapiforms, were haplorhines rather than strepsirrhines. On the other hand, Godinot (2006b) suggested a relationship between early anthropoids and stem lemuriiforms, excluding adapiforms and omomyiforms. He noted that while tarsal characters contradict this, convergences in locomotor adaptations have occurred in other groups.

Ross (2003) pointed out that some omomyiforms and adapiforms are ‘almost indistinguishable’. He suggested they may have nothing directly to do with the origins of haplorhines or strepsirrhines but instead could be an independent radiation and an evolutionary dead end. Anthropoids show marked divergence from basal adapiforms and omomyiforms, and anthropoid fossils may be just as old as these groups (Bajpai et al. 2008), so it is ‘extremely unlikely’ (Ross 2003, p. 199) that anthropoids arose from within them. Martin et al. (2007) interpreted the adapiforms and omomyiforms themselves as early northern ‘offshoots’. They are probably vicariants, not ancestors, of extant clades. In any case, the gaps in the southern hemisphere fossil record mean that adapiforms and omomyiforms may once have been more widespread in the tropics, for example, in the mountains of Gondwana. Eocene adapiforms from Gujarat, India (Rose et al. 2009) may predate the India-Asia collision.

Other groups have been suggested as ‘the ancestor’ of the anthropoids, such as tarsiforms and fossil groups such as eosimiids, although these scenarios are not convincing. As Rasmussen (1994) observed, ‘To many researchers a tarsier-anthropoid clade suggested that anthropoids arose directly from a tarsier-like prosimian’ and the possibility that the two groups may be sisters (or more distant cousins) is often overlooked. Beard (2004, p. 27) pointed out that studies have become ‘fixated on the issue of direct ancestry’ and the ‘ladder paradigm’ of evolution.

Breaking with the ‘search for the ancestor’ approach, Miller et al. (2005, p. 60) presented evidence for a ‘deep time origin of anthropoids’ and argued for ‘an ancient, Gondwanan, non-adapiform, non-omomyiform, non-strepsirrhine, non-tarsiiform origin of anthropoids’. While this proposal is generally viewed as ‘little more than a claim for ignorance regarding the origin of the group’ (Fleagle 1999, p. 421), the idea that the main primate clades are derived from a common ancestor older than them all, rather than one member being the ancestor of the others, may be a valuable step towards understanding anthropoid origins (Fleagle himself gave an ‘agnostic’ dia-
gram of phylogeny for primates, showing five separate groups rather than ancestor-descendant lineages; Fleagle 1999, p. 345).

Ross & Kay (2004, p. 712) also suggested ‘the possibility that extant anthropoids might not be derived from any of the currently known groups of primates’; the tarserianthropoid clade ‘might not have anything to do with omomyiforms… The possibility still remains that the major clades of extant primates (Strepsirrhini, Tarsiiformes and Anthropoidea) are not derived from either adapiforms or omomyiforms and that the latter taxa are completely independent, dead-end radiations of primates…’. Miller et al. (2005, p. 67) probably revealed the mundane truth in suggesting that: ‘the search for an anthropoid ancestor, at least among the adapiforms and omomyiforms, has more to do with the lack of fossils from Paleogene localities on southern continents than with any special features of adapiforms or omomyiforms’.

Centre of origin explanations for the primates of South America
As Fleagle (1999, p. 444) pointed out, ‘The most unsettled question surrounding platyrhine origins is the geographical one: how did platyrhines get to South America?’ Most of the debate has focused on whether North America or Africa was the source and on the possible means of dispersal. Fleagle inferred rafting: ‘regardless of how unlikely rafting may seem, it is presently the only suggested mechanism for transporting terrestrial animals between continents separated by open ocean. If South America was indeed an island continent during the period in question, we must assume that primates rafted from some other continental area. Only a revision of the paleocontinental maps could eliminate the need for rafting in the origin of platyrhines’ (p. 446; italics added). In fact there would be no need for either rafting or changing the maps if primates were older than their oldest fossils and the molecular clock studies discussed below indicate that primates are indeed much older than their fossil record.

Fleagle (1999, p. 447) concluded: ‘At present there is no convincing explanation for the origin of South American monkeys, but dispersal across the South Atlantic from Africa seems to be the least unlikely method’. The question then is: if monkeys were able to raft to America, why were strepsirrhines not able to do the same? Fleagle & Gilbert (2006, p. 395) wrote that rafting across the Atlantic is ‘clearly a chance event, an example of ‘sweepstakes’ dispersal. One can only speculate that by a stroke of good luck anthropoids were able to ‘win’ the sweepstakes while lorises and galagos did not’. The present paper proposes an alternative for platyrhine divergence that does not rely on chance events but on the opening of the Atlantic Ocean.

Centre of origin explanations for the primates of Madagascar
The unsettled question of the American platyrhines and their origin is matched by a similar lack of clarity concerning the primates of the Indian Ocean region. Yoder (1997, p. 13) wrote that ‘One of the most perplexing problems in strepsirrhine evolutionary history is the derivation of a realistic biogeographic model to explain the presence of lemuriforms on the remote island of Madagascar. Because they are the only primates other than humans to have lived there, it is unlikely that the primate clade originated on Madagascar. Thus, the ancestral lemuriform must have come from somewhere else…”’. Conversely, the fact that lemurs are the only primate clade on Madagascar and are not known, living or fossil, from anywhere else could be taken as good evidence that they are autochthonous and formed in situ, as an allopatric vicariant, not by arriving from elsewhere. If lemuriform ancestors (strepsirrhines) did disperse over the sea to Madagascar, it would seem strange that they never colonized America, Australia or New Guinea. Likewise, Masters et al. (2007) observed that monkeys have a far greater chance of dispersing to Madagascar than strepsirrhines, yet there is no evidence that they ever did. Sweepstake dispersal does not account for these particular aspects of the problem or for the overall problem: the great difference between the distributions of strepsirrhines (in Madagascar but not South America) and haplorhines (in South America but not Madagascar).

For Madagascar, Tattersall (2008, p. 405) argued that ‘The strongly filtered nature of the island’s mammal fauna clearly implies some degree of overwater crossing by the founding stocks’. In fact a fauna which includes, for example, the endemic aye-ayes, sloth lemurs, sucker-footed bats, and pseudo-aardvarks is not simply a ‘filtered’ or ‘imbalanced’ version of a ‘normal’ one; it is a distinctive fauna in its own right (cf. Heads 2009). The pseudo-aardvarks (the order Bihymalagasia, extant until about 1000 years ago) are known only from Madagascar and their affinities are unclear (MacPhee 1994). The sucker-footed bats, Myzopoidea, are basal in a worldwide complex comprising Vespertilionidae, Molossidae and others, not minor, low-level derivatives of African clades (Eick et al. 2005). Absence of a Tertiary mammal record in Madagascar probably means that there were also basal taxa, now extinct, in other groups. Tattersall (2008, p. 398) stressed that the Mesozoic fossil record in Madagascar ‘lacks a plausible ancestor’ for the mammals now found there, although this absence may not be significant given the vast gaps in the fossil record of the region. He
also argued that ‘Madagascar has been widely separate from Africa and India since well before the beginning of the Age of Mammals’. In fact the old idea that the Cenozoic was the only Age of Mammals is not quite accurate; dramatic discoveries over the last decade (for example, Hu et al. 2005; Luo & Wiley 2003; Ji et al. 2006) show that Mesozoic mammals and mammaliforms are much more diverse than was thought. Tattersall (2008, p. 398) concluded: ‘It seems certain that dispersal must have been involved…’ for mammals in Madagascar. Nevertheless, given the doubt surrounding the age of lemurs for example, this confidence may not be warranted.

The idea that the Malagasy mammals arrived by over-water dispersal from Africa has been accepted since Victorian times and is often cited as a well-established precedent for chance, ‘sweepstake’ dispersal (Wallace 1876; Simpson 1940; Rabinowitz & Woods 2006; Tattersall 2008). In this model, improbable dispersal events become possible or even probable given enough geological time. Despite its popularity, the possibility of sweepstake dispersal by lemurs had not been examined by scientists familiar with the wide range of relevant factors – geological, oceanographic and meteorological, phylogenetic, ecological and behavioural – until Stankiewicz et al. (2006) carried out a detailed analysis. The study considered a wide range of possible variants, including rafts of vegetation with or without ‘sail effects’ produced by trees on the raft, dispersal by transport of animals in cyclones, and others. The authors concluded that while the rafting theory ‘currently enjoys wide support [it] is not valid at either the theoretical or applied level…’. (p. 221). For example, a raft coming from Africa would drift back to the mainland. Animals would not survive transport by cyclones even if it did happen. The chances of successful dispersal are ‘ludicrously small’ (p. 231) and, in particular, they are ‘so small that even vast tracts of time cannot compensate’ (p. 232).

Torpor or hibernation by heterothermy is observed in two lemur genera and another strepsirrhine, Loris, and it has been suggested that in the Africa-Madagascar crossing ‘entire groups of animals survived the weeks or, even months… without food or water sleeping in a hollow tree while rafting across the sea’ (Kappeler 2000, p. 423). Roos et al. (2004, p. 10653) took this idea seriously and thought it the ‘most plausible’ hypothesis. By contrast, Masters et al. (2007, p. 21) rejected it outright (their paper was titled ‘eyes wide shut’) and concluded that ‘alternative explanations should be sought’ for primates on Madagascar.

A vicariance model for primate evolution
The model given here for the origin of primates (Fig. 2) and their main clades (Fig. 3) begins with vicariance of a widespread ancestor that was already in Africa, Madagascar, Asia and America before the extant clades existed. Long-distance founder dispersal of the modern groups across open ocean is not required. The model is simple and has not been accepted only because the clades are thought to be too young (Cenozoic) and so trans-oceanic dispersal is assumed to have taken place.

The model aims to minimize change in distributions while assuming that groups originated as allopatric vicarians. The chronological calibration is based on the simple biogeographic divisions and associated tectonics at nodes IV (Mozambique Channel) and V (Atlantic Ocean). The dates for node I and III, involving early central Atlantic opening and complex Tethys events, were accepted following the primary calibration. Node II involves a split between haplorhines, mainly in West and Central Africa, and strepsirrhines, mainly in East Africa. Given this geography and the relative timing (earlier than node IV at the Mozambique Channel), a likely explanation is tectonic activity along the Lebombo monocline. This volcanic rifted margin is a great warp running north-south in eastern South Africa, Zimbabwe and Mozambique and is one of the major structures in the region. Rifting here remained incomplete and was a precursor to successful rifting in the Mozambique Channel. The Lebombo monocline is also known as an important biogeographic boundary for taxa in the region (Craw et al. 1999, pp. 77–79).

Node I. Early Jurassic (~185 Ma)
1. Global Archonta ancestor divided into plesiadapiforms in the north, primates in the south and east, and Scandentia and Dermoptera on the terranes that became south-east Asia. The division is correlated with the initial breakup of Pangea, in which the central Atlantic opened and Africa/South America separated from North America. The date (from Veevers 2004) is based on rifting in the Atlas Mountains and mid-ocean ridge basalts on the Canary Islands.

2. Subsequent marginal overlap of plesiadapiforms and primates in the north and complete overlap of Dermoptera, Scandentia and primates in south-east Asia. Correlated with the rotation of Africa-Arabia and its approach to Asia at the Persian Gulf.

Node II. Early Jurassic (~180 Ma)
3. Global primates divided into strepsirrhines, mainly east of the Lebombo Monocline (in Tanzania, Madagascar etc.) and haplorhines west of this line, in South America, Africa (not Madagascar), and Asia (north of the strepsirrhines). Correlated with flexure and volcanism on the Lebombo monocline and final Karoo faulting in east Africa.
4. Partial overlap of haplorhines and strepsirrhines with range expansion of both in central Africa and Asia. Fossil ‘tooth-comb’ primates from Egypt and Oman indicate that the modern distribution of strepsirrhines around the Arabian Peninsula has been reduced through extinction.

At some stage (possibly between 3 and 4) the northern adapiforms may (the phylogeny is debated) have split
from the other, southern strepsirrhines, and the northern omomyiforms may have split from the other, southern haplorhines (possibly around the same time). This could be correlated with Late Jurassic rifting in the Mediterranean. While adapiforms and tooth-comb strepsirrhines have remained vicariant, anthropoids have subsequently expanded their range northward into Europe and Asia (but not north of Mexico), more or less completely overlapping the range of omomyiforms and adapiforms there.

Node III. Early Jurassic (~180 Ma)

5. Haplorhines divided into tarsiers and anthropoids at the same time as, or soon after, the strepsirrhine/haplorhine split. Tarsiers are diverse on Sulawesi (where the only other primate group is the haplorhine Macaca) and also occur east of other primates, with endemic species on eastern Sulawesi islands. This distinct distribution suggests that the tarsiers may have evolved on one or more of the Sulawesi precursor terranes originally located some distance from anthropoids on other Sulawesi terranes. There is current overlap of tarsiers and anthropoids in Sulawesi, Borneo and Sumatra. These three islands are geological composites and tarsiers and anthropoids could have occupied different sets of ‘Sulawesi’, ‘Borneo’ and ‘Sumatra’ terranes long before the modern islands formed as geographic entities.

Up until recently, most reconstructions portrayed eastern Tethys as a wide sea, devoid of any land, between India/Australia (Gondwana) and Asia. But Aitchison et al. (2007) inferred the former presence of two intraoceanic island arc systems between precolission India and Asia and concluded that the ‘Tethys sea ‘was obviously more complex than originally envisaged’ (p. 6). Pre- and proto-primates may have occurred widely throughout the archipelagos formed by these arc terranes and the populations would have been incorporated into Asia during arc-continent accretion.

Node IV. Middle Jurassic (~160 Ma)

6. Strepsirrhines divided into lorises and galagos on mainland Africa and Asia, and lemurs on Madagascar. This is correlated with the opening of the Mozambique Channel and the split of East Gondwana (Madagascar, India, Antarctica and Australia) from West Gondwana (Africa-South America). There was crustal extension between Madagascar and India in the Early Cretaceous, 140–118 Ma, and the two regions separated in the Late Cretaceous (96–84 Ma) (de Wit 2003, fig. 4).

Node V. Early Cretaceous (~130–120 Ma)

7. Anthropoids divided into catarrhines (Old World) and platyrrhines (New World). This is correlated with the opening of the South Atlantic. The South Atlantic rift propagated northward, the Central Atlantic rift (node I) propagated southward, and a transform domain formed between them, separating West Africa and Brazil.

In this model none of the clades has a localized centre of origin. While there has been some range expansion leading to secondary geographic overlap, the main process has been subdivision (vicariance). There is no requirement for any centre of origin, founder speciation or trans-oceanic rafting and the topology of the phylogeny represents a sequence of differentiation in a widespread ancestor, not a radiation by a series of founder dispersal events.

Miller et al. (2005) suggested that plesiadapiforms were likely to have been Laurasian ecological vicarians of primates and this is compatible with the origin of the two clades as phylogenetic and biogeographic vicarians. Marginal overlap of plesiadapiforms and primates in Laurasia, and within primates overlap there of adapiforms/omomyiforms and anthropoids, does not mean there was a centre of origin in the north. Instead it suggests that differentiation and then overlap of Laurasian and Gondwanan groups has taken place in two, more or less distinct phases.

Seiffert et al. (2005) accepted Altiatlasius of the Moroccan Paleocene as the oldest known crown primate and a stem anthropoid. They argued that this implies either immigration into Africa of anthropoid ancestors or ‘the presence of ancient parallel radiations of anthropoids in Asia and Afro-Arabia’. The second alternative (along with a third centre in South America) is compatible with the model presented here.

The pioneer Argentine paleontologist Ameghino (1906) recognized the great diversity of South American fossil mammals, including primates, and saw the region as a centre of origin – a ‘garden of Eden’ – for mammals. This interpretation has been rejected by most North American writers (e.g. Romer 1966), yet McKenna (1980, p. 44) noted that ever since Matthew (1915), Simpson and many other authors have advocated a North American garden of Eden, ‘with nearly Ameghinian fervour’. In a vicariance model, the North Americans and the South Americans are both right. Northern and southern groups of primates both evolved in situ, with anthropoids autochthonous south of the Rio Grande, adapiforms and omomyiforms autochthonous north of there.

**Integrating the primate fossil record and the molecular clock**

A vicariance model explains several aspects of primate evolution better than dispersal models. The only real objec-
tion is that it implies older ages than are generally accepted and so this is discussed here further. Traditional paleontological accounts and also fossil-calibrated molecular clock studies are dependant on the fossil record. Nevertheless, rainforest taxa seldom fossilize and Soligo et al. (2007) stressed the great geographic biases of the mammal record.

Many workers now accept that two sister groups are about the same age. If one of the two groups has much earlier fossils than the other, this implies the second group existed as a ‘ghost lineage’ that has left no record. Analyses based on this concept of cross-calibration have already indicated large gaps in the record (Yoder & Yang 2004; Soligo et al. 2007; Steiper & Young 2008).

**Molecular clock studies show that species are mid-Cenozoic**

Molecular clock studies indicate that mammal species are older than was thought. In particular, the Pleistocene refugium hypothesis has been rejected in many studies on primates such as chimpanzees (*Pan*), guenons (*Cercopithecus*), and spider monkeys (*Ateles*). These indicate that species and even subspecies diverged well before the Pleistocene (Lehman & Fleagle 2006). Divergence between Sumatran and Bornean populations of orangutan (*Pongo*), regarded by different authors as species or subspecies, has been dated with a fossil-calibrated clock at ~10 Ma (Arnason et al. 1996), giving a useful minimum age. Amazon diversity has often been explained as the result of evolution in Pleistocene refugia, but ideas on this are changing. For example, Boubli & Ditchfield (2000) concluded that the platyrrhines *Cacajao calvus* and *Cacajao melanocephalus* s.lat. had already diverged by the Pliocene.

**Cenozoic fossils are already ‘modern’**

Oldest fossils suggest Cenozoic, Holarctic centres of origin for mammal orders (Matthew 1915) and many authors have assumed that primates originated somewhere in the northern continents. Most of the oldest primate fossils are from the basal Eocene of North America, Europe and China. Recent discoveries such as a possible omomyid from the Paleocene of Morocco (*Altiatlasius*) and a possible anthropoid from the basal Eocene of India (*Antbasimias; Bajpai et al. 2008*) change the picture somewhat. But in any case, a literal or ‘direct’ reading of the fossil record always involves ‘the questionable inference that [a group’s] origin is located in or close to the geographical region that has yielded the earliest known fossil representative’ (Martin et al. 2007, p. 281).

In other mammal orders, clearly recognizable bats, artiodactyls and perissodactyls also appear first in the northern continental fossil record, again, at the base of the Eocene. This might be interpreted as a burst of evolution. Nevertheless, in most cases forms transitional to these are unknown, implying the former existence of lineages that have left no record and so the oldest fossil indicates neither the place nor the time of origin. Based on the ‘modern appearance of fossils from Messel in Germany, G. Storch emphasized that ‘Bats were already advanced 49 million years ago [Middle Eocene]. I’m convinced they originated much earlier than you read in textbooks’. (pers. comm., quoted in Hoffmann 2000, p. 48) (cf. Hoo-ker 2001). Likewise, Covert (2002, p. 19) cited the ‘striking similarity’ between Middle Eocene tarsier fossils from China and modern tarsiers. Rossie et al. (2006) described a Middle Eocene Chinese *Tarsius* species from a facial material ‘virtually identical’ (p. 4381) to the corresponding anatomy in living species. They concluded that ‘Virtually modern tarsier-like facial morphology’ (p. 4384), with greatly enlarged orbits and a haplorhine oronasal region, was already present at 45 Ma. Other extant mammal genera with Eocene fossils include the bats *Hipposideros* and *Hipposideros* (M. McKenna pers. comm. in Simons 2003). Fleagle (1999, p. 557) cited *Tarsiùs, Aotus* and *Macaca* as primate genera ‘that seem to have persisted for tens of millions of years with very little change: ..’. In Dermom-tera, the close relative of primates, Marivaux et al. (2006) named a new Oligocene species *Dermotherium chimaera* as it exhibits a ‘mosaic’ recombination of characters seen in the two living species.

At La Venta, central Colombia, Miocene beds (12–14 Ma) have yielded fossil monkeys ‘remarkably similar to modern platyrhines’ and ‘clearly related’ to living *Aotus, Saimiri, Alouatta* and others (Fragaszy et al. 2004, p. 29; cf. Setoguchi & Rosenberger 1987; Rosenberger et al. 2008, p. 99). Fleagle & Kay (1997) concluded that ‘many of the fossil monkeys from La Venta are strikingly similar to modern platyrhines’ (p. 9) and they attributed the ‘modernness’ of the fauna (p. 11) to its ‘relatively late age’.

**Fossil evidence for modern orders in the Mesozoic**

The earliest recognized fossils of the extant mammal orders are from the Eocene or Paleocene and so a literal reading of the fossil record indicates that they originated since the Cretaceous. Extant bird orders were also assumed to be the result of a Cenozoic radiation. This in turn led to the idea that the rise of the mammals and birds was related chronologically and ecologically to the extinction of the dinosaurs. In this interpretation Mesozoic history has no direct relevance to the evolution and biogeography of modern birds and mammals; the Cenozoic is the Age of Birds and the Age of Mammals (Simpson 1937).

The birds are usually interpreted in the same way as the mammals; although the oldest bird fossil, *Archaeopteryx*, is Late Jurassic, the traditional view is that evolution of all
the extant orders (except perhaps the ratites) is confined to the Cenozoic, with an ‘explosive radiation’ after the Cretaceous/Cenozoic boundary. Yet new fossil discoveries, such as a Cretaceous member of the extant order Anseriformes (ducks and geese; Clarke et al. 2005) challenge the idea that the Cenozoic is the only Age of Birds (cf. Wolfson 1948).

In mammals, an Early Cretaceous fossil of Ornithorhynchidae (the platypus family) implies that the platypuses and their sister group echidnas were distinct by then (Rowe et al. 2008). Other Early Cretaceous mammal fossils from Australia include a possible erinaceid (Rich et al. 2001). As indicated above, the known diversity of interesting Mesozoic mammals continues to grow, with the discovery of larger forms that fed on young dinosaurs (Hu et al. 2001). As indicated above, the known diversity of interesting Mesozoic mammals continues to grow, with the discovery of larger forms that fed on young dinosaurs (Hu et al. 2005), a swimming and/or burrowing species with a beaver-like tail (Ji et al. 2006) and a group with digging forelimbs (Luo & Wible 2005).

Molecular clock evidence that modern vertebrate orders are Mesozoic

In addition to the new fossil evidence, another challenge to the idea that the extant orders are Cenozoic comes from molecular clock studies. These have shown that many modern mammal orders, including primates, could have existed tens of millions of years before their first appearance in the fossil record. In contrast with the earliest fossil dates in the Paleogene, molecular clock studies indicated that primates split from the other orders of mammals at 95 Ma in the mid-Cretaceous (Kumar & Hedges 1998). One fossil-calibrated clock study found that all the mammal orders are pre-Cenozoic and cited the ‘increasing difficulty’ of reconciling the clock dates with the Cenozoic explosion model of radiation (Springer et al. 2003).

Primatologists confront a new chronology

Godinot (2006b, p. 458) described the (fossil-calibrated) molecular clock dates for primates as ‘absurd’. This response is understandable from a paleontologist who interprets the record as a literal representation of evolution. Yet this involves transmogrifying minimum dates (‘good’ fossil dates) into maximum dates and to a non-paleontologist this is, if not absurd, somewhat less than completely rational.

While some workers have dismissed the new ideas on the time-course of primate evolution, others have used them as a stimulus to re-examine the primate record and also the methods used to interpret it (Miller et al. 2005; Martin et al. 2007; Soligo et al. 2007). Soligo et al. (2007, p. 30) criticized the ‘common procedure of dating the origin of a group by the earliest known fossil representative, perhaps adding a safety margin of a few million years’.

Instead, as Martin et al. (2007, p. 280) recognized, ‘It is vital to recognize that [using oldest known fossil to infer age] can yield only a minimum estimate…’. The idea of a long time interval between the origin of a group and its initial appearance in the record is not accepted by all researchers. Still, the molecular work and also studies of preservation show that in groups like primates ‘paleontologists are likely to have substantially underestimated the true time of divergence.’ (Miller et al. 2005, p. 67).

Sometimes it seems as if the molecular clock workers do not quite believe their own results and they make genuine efforts to square their ancient dates with the fossil-based chronology. Both molecular workers and paleontologists refer to a molecular date of, say, 100 Ma as ‘incongruent’ or ‘incompatible’ with an oldest-fossil date of, say, 50 Ma. But a difference like this is standard and some difference would always be expected because of the limited rock record available, aspects of preservation and geographic sampling. There is no logical incongruence between these two dates and no special explanation or enquiry is needed. It is quite normal for groups that are known to be ancient through their phylogeny to have no pre-Recent fossil record at all, or for a group with no fossil record to then turn up in, say, the Early Cretaceous (e.g. prosopoid grasshoppers, now known from fossils dated at 110 Ma; Heads 2008).

No other biology-related discipline has escaped the seismic upheavals of the molecular revolution and paleontology will be affected too. While the subject may appear to be immune, as older fossils have no DNA, a new synthesis of molecular phylogeny, developmental genetics and morphology should lead to new ideas on homology and different interpretations of fossil phylogeny. As Szalay & Delson (1979, p. 5) wrote: ‘In a study of primate evolutionary history, it is clear we must concentrate on fossil taxa, but their interpretation is not possible without a firm grasp of extant relatives and other relevant living species’.

For most times and places there is no fossil record and, in agreement with studies on mammals in general (Binninga-Emonds et al. 2007), Soligo et al. (2007, p. 33) concluded that ‘early evolution of the primates has simply remained undocumented [by fossils]’. They indicated undeniable gaps in the record. For example, the extant lemurs make up five of the 13 families of extant primates (Goodman et al. 2005) and have no fossils older than 2800 B.P. (there are no Tertiary mammal fossils in Madagascar; Godinot 2006b). If the other strange lemur families only turned up in, say, the Early Cretaceous (e.g. prosopoid grasshoppers, now known from fossils dated at 110 Ma; Heads 2008).

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Young 2008) and the other lemur families could be older than any of the anthropoid families (Steiper & Young 2008). Thus, the lemur families are all ancient clades with no fossil record.

Many paleontologists have overestimated preservation rates and have even argued that the more a scenario differs from a direct reading of the fossil record, the less likely it is to be real (references in Soligo et al. 2007; Martin et al. 2007). One devout literalist calculated the probability of primates existing at 80 Ma (Late Cretaceous) as one in 200 million! (cited in Soligo et al. 2007). These fundamentalist paleontologists have carefully assessed the completeness of the fossil record but only through analysis of the fossil record itself and Soligo et al. criticized the narrowness and circularity of this approach. They suggested that underlying any direct reading of the primate fossil record is the unstated assumption that most of primate evolution has by now been unearthed and described. Instead, Soligo et al. inferred poor sampling of primates and other mammal orders in the record and concluded that Cretaceous rather than Cenozoic divergence in these orders ‘should now be considered the more likely scenario, in which case the influence of continental drift has probably been considerable’ (Soligo et al. 2007, p. 46). Eizirik et al. (2001) and Arnason et al. (2008) also discussed possible Mesozoic ages for primate clades. They cited Gondwana breakup and referred in general terms to the possibility of vicariance models, although their models still used centres of origin and dispersal.

Critique of the molecular clock: fossil-calibrated clocks give minimum ages only

The idea that fossils only provide a minimum date is cited more and more as an important principle in theory, yet in practice it is often ignored in fossil-calibrated clock analyses. Cross-calibration takes advantage of the fact that one group has a better fossil record than another; for example, ‘Contrary to primates, glires [rodents and lagomorphs] have a very good record’ (Godinot 2006b, p. 459). But what exactly does ‘very good’ mean? The glires record is only being compared with other fossil groups and the ‘very good’ rating does not mean that these fossils give absolute ages. The molecular clock dates were accepted above as more realistic than raw fossil dates. Nevertheless, they are still calibrated with fossils and so are probably too young.

According to Matthew (1915), fossils prove that primates are not old enough to have been affected by major tectonic change. Most modern biologists would agree and observe that fossil-calibrated molecular clocks prove the same thing. In fact, both methods produce fossil-calibrated minimum ages only and cannot rule out earlier ages, only later ones. While Springer et al. (2003) described several shortcomings with previous molecular clock work on mammals, they did not mention the most important one – the use of fossil calibrations. Springer et al. themselves found Late Cretaceous ages (85 Ma) for primates, yet this relied on proposing explicit maximum dates based on the fossils.

It is admitted in theory that fossil-calibrated molecular clocks can only give minimum ages, as with the raw fossil dates they are based on, but in practice the clock dates are usually transmogrified into maximum or absolute dates. All the molecular clock studies of primates have been calibrated using fossils and so all the calculated dates are minimum ages. Despite this, in many studies the dates are presented transmogrified into maximum ages, with statements such as primates evolved at, for example, ~90 Ma It is sometimes suggested that vicariance biogeography ‘is scornful of the significance of the fossil record’ (Cox & Moore 2005, p. 31). This is not correct as vicariance analysis incorporates fossil data where available (cf. Fig. 3C) and uses fossil ages to provide minimum dates. It is not the fossil record that vicariance analysis rejects, only the validity of transmogrification.

Apart from the significance of the fossil dates, it is natural to be sceptical of morphological phylogenies of fossil clades (on which the cross-calibration depends) when, with much better (living) material, morphologists did not retrieve the clades of extant taxa such as Archonta s.str. or Afrotheria. The tendency to regard fossil groups as direct ancestors (stem taxa) will, again, lead to underestimates of age. In any case, many fossil primate clades are known only from fragmentary material so reconstructing the phylogeny is a difficult if not impossible task and the results remain controversial.

Some authors are beginning to acknowledge that molecular clocks calibrated with fossils ‘are not wholly independent tests of fossil evidence.’ (Miller et al. 2005, p. 73; cf. Raauom et al. 2005). Thus, the great value of the clock is not that it gives the right dates (they are still based on fossils) but that it shows the fossil record, as an indication of evolutionary dates, could be wrong by tens of millions of years. Molecular workers try to fit the phylogeny to the fossil dates. Instead, the phylogeny of primates fits easily with the chronological sequence of great rifting events which broke up Pangea and Gondwana at the central-North Atlantic, Tethys, Lebombo monocline, Mozambique Channel, and Atlantic Ocean.

In their perceptive critique, Steiper & Young (2008, p. 180) emphasized that ‘…fossils ‘set’ the molecular clock. Therefore, calibrations can only establish a lower bound… For this reason molecular clock dates are best considered minimum bounds for divergence dates, whether
stated explicitly or implicitly. Because fossil-based calibrations are biased towards younger dates, [fossil-calibrated] molecular clock dates estimated elsewhere in a phylogeny should also tend towards underestimation.

Primatologists sometimes suggest that ‘Molecular divergence date estimates are dependent on calibration points gleaned from the paleontological record’ (Raauw et al. 2005, p. 237) or that the fossil record ‘is our only source of information for calibrating phylogenies’ (Godinot 2006b, p. 455). This is not correct and tectonics offers an alternative which has been used for calibration, more or less successfully, by workers in many other groups (reviewed in Heads 2005; cf. Genner et al. 2007; Azuma et al. 2008). Molecular phylogenies define groups in space and the spatial breaks between the groups are often obvious and clear-cut, as in the primates. These breaks can be correlated with geological history and the radiometric techniques used to date tectonic events are much more reliable than fossil-calibrated molecular clocks.

To summarise, the inferred dates for primate clades using the different methods are:

- *fossils*: Cenozoic, 56 Ma (a minimum date),
- *fossil-calibrated molecular clock*: Cretaceous, 80–120 Ma (a minimum date),
- *tectonics-calibrated molecular biogeography*: Jurassic, 185 Ma (an absolute date).

There is no real conflict between these dates as the first two are estimates of minimum age while the third is an estimate of absolute or maximum age.

As molecular clock studies confirmed, most species in groups such as primates are older than the Pleistocene and are generally mid-Cenozoic, while the mammal orders are not Cenozoic, they are Mesozoic. The total absence of many large groups in the fossil record of the Late Cretaceous–Paleocene is likely to be an artefact, even in groups that were thought to have a ‘very good’ record. With the new clock dates it is now much easier to accept that the fossil record could be misleading about the existence of groups in the Jurassic, identified in this paper as the main period of primate evolution. A vicariance model implies that the fossil-calibrated ages (both molecular and non-molecular) are incorrect if interpreted as absolute ages. The fact that fossil dates only give minimum ages for clades need not constitute a real problem in theory or practice, but it does undermine dispersal models that are based solely on the treatment of fossil dates and their derivatives as maximum dates. This approach has not led to any coherent synthesis of primate evolution, but into a morass of fundamental, unresolved problems about the origins of the group and all its main clades.

Shifting the age of the primates from the Cretaceous to Jurassic may seem a radical step, yet workers in other groups have had to come to terms with much greater changes. Angiosperms have an excellent fossil record, incomparably better than that of primates, and on the basis of the fossils were assumed to be Cretaceous. They are now thought to be much older than this as molecular phylogeny indicates they are basal to ‘extant gymnosperms’, well-known as fossils from the Paleozoic. Botanists are now in the process of re-assessing the identification of fossil pollen from the Triassic and Jurassic (Doyle 2005).

**Using molecular/tectonic biogeography to date clades and assess gaps in the fossil record**

Fossil-calibrated molecular clocks do not provide an independent test of the fossil record and so claims that dates from the molecular studies ‘corroborate’ parts of the fossil record are misleading. By contrast, tectonics-calibrated dates for phylogenetic and biogeographic nodes do provide an independent test of the fossil record. Glazko et al. (2005) dated the Archonta/Glires split at 84–21 Ma. The authors emphasized that the clock was fossil-calibrated and so these are minimum dates. Divergence between Archonta and Glires may have occurred less than 5 million years prior to the origin of primates (Janečka et al. 2007) and so the 121 Ma date for Archonta suggests a (minimum) date of ~116 Ma (Early Cretaceous) for primate divergence (Janecka et al., 2007: Fig. 2, indicated ~86 Ma). It is suggested here that the primates originated at 185 Ma, in the Early Jurassic. The 69 million years difference between the fossil-based minimum date (116 Ma) and the biogeographic estimate (185 Ma) probably reflects the gap in the record of the fossil lineage that Glazko et al. (2005) used to calibrate their clock. As indicated, demonstrable gaps of 100 million years or more exist in the fossil record.

Many modern advocates of fossil-based molecular chronology aim to test vicariance vs. dispersal by transmogrifying minimum, fossil dates into maximum, absolute dates and using a relaxed clock (Poux et al. 2006; Yoder & Nowak 2006). Instead, the clock dates and the fossil record used for the calibration can themselves be tested by assuming vicariance. This seems reasonable; recent evidence from population genetics indicates that while vicariance is likely to be a mode of speciation, there is little or no evidence for founder effect speciation (chance dispersal) (Rundle 2003; Coyne & Orr 2004; Orr 2005).

**Evolution by vicariance and incomplete lineage sorting**

Many studies of primate taxa focus on reconstructing the single ‘ancestral morphotype’ in a group and this assumes a morphologically uniform ancestor. Opposed to this idea
is the fact that incomplete lineage sorting is now well-documented in primates, for example in lemurs (Heckman et al. 2007), colobines (Ting et al. 2008) and hominids (Salem et al. 2003; Caswell et al. 2008). This indicates that the ancestor was already polymorphic before the origin of the taxa under study and that this polymorphism was passed on in the descendants. If the differentiation of the mammal orders and suborders was rapid and if it occurred in ancestral complexes that were widespread and polymorphic, as suggested here for primates, it probably involved retention and recombination of ancestral polymorphism. Relevant examples of incongruent character combinations in morphology include striking similarities in the visual system of primates and fruitbats (Martin 1990; Pettigrew et al. 2008), in the ears of lemurs and bats, in the teeth of some lemurs and those of fruitbats (Kingdon 1974), and in the continuously growing incisors of the basal lemur *Dambouthia* and those of rodents, some marsupials and some Afrotheria. The mammals of Madagascar can be interpreted as a remnant of a former biota based in and around the Indian Ocean and their morphologies represent recombinations from an old pool of early mammalian and pre-mammalian characters.

Retention of ancestral polymorphism is often seen as a problem in the search for the true phylogeny. On the other hand, each incongruent gene tree usually shows a distinct biogeography. Hopefully, former genetic connections may be revealed by searching genetic palimpsests for incomplete lineage sorting. For example, connections between primates in particular regions of north-eastern Brazil and in particular areas of West Africa might be traceable, just as pre-Atlantic shear zones in Brazil can be followed into Nigeria and Cameroon. The unrelated melanic forms *Chiroptes satanas* of north-eastern Brazil (a platyrhine) and *Colobus satanas* of Gabon (a catarrhine) would be interpreted in traditional theory as convergent adaptations; instead there may be a biogeographic and genetic basis to the pattern which predates the platyrhine/catarrhine split.

Primates show many parallel tendencies shared with various other mammals and birds, including binocular vision and a larger brain, and they may have only one morphological synapomorphy (an auditory bulla formed by the petrosal bone; Rasmussen 2002). This could easily be a parallelism too and a direct ancestor, by definition without the character, would be difficult to identify. Although the extant primates (and extant mammals) are monophyletic with respect to other extant groups, it is not certain that this is the case with respect to the many fossil groups. Apart from only having a single morphological synapomorphy, primates are unique among mammal orders in that both the extreme types of placentation (non-invasive epitheliochorial and highly invasive haemochorial) are present in a single order (Martin 2008). Strepsirrhines have the former, haplorhines (and also Dermoptera) the latter.

If parallelism is as universal as molecular phylogenies indicate, the strange extant mammals of southern Africa and Madagascar – lemurs, aardvarks, pseudo-aardvarks and many others – may be related to evolution in Gondwana and the Karoo basin of southern and east Africa. This interpretation predicts a wide range of morphology in Mesozoic mammaliaforms, for example. The Karoo fossils are a remarkable sample of the transition from ‘reptile-like’ early mammals to true mammals. Unfortunately, sedimentation in the Karoo beds ended with the vast flood-basalt eruptions of the mid-Jurassic; after this there is an almost continuous gap of 120 million years in the mammalian fossil record of Africa that extends through much of the Jurassic and all the Cretaceous. This ‘surely represents an enormous omission in our knowledge of mammalian evolution rather than real absence of mammals from Africa’ (Miller et al. 2005). Even in the Karoo there will be many groups still unsampled (or misidentified) and these may include pre- and proto-primates.

*Molecular clock studies and the biogeography of Madagascar*

Masters et al. (2006, p. 400) described the origin of the Madagascar vertebrates as ‘one of the most tantalizing enigmas facing biogeographers… Simpson’s (1940) prediction that sweepstake dispersal events should occur at random intervals is not borne out by the mammal data. According to the molecular divergence dates estimated by Poux et al. (2005), sweepstakes dispersal events seem to have occurred very early in the history of a clade, and never again’. Masters et al. (2006, p. 414) suggested a reconsideration of the geophysical and molecular data is needed to address the ‘apparent paradoxes’ and this data is the basis of the model presented here.

Yoder & Nowak (2006) gave a thorough review of the molecular clock literature on Malagasy taxa. In every study of plants the fossil-calibrated clocks dated the Madagascar clades as younger than 80 Ma and so they were all attributed to post-Gondwana dispersal, none to vicariance. With a single exception, studies of animal taxa showed the same result. All molecular dating studies of Malagasy invertebrates, reptiles and mammals have concluded in favour of dispersal, as the inferred (fossil-calibrated) divergence times were post-Mesozoic. The only sequenced group whose presence on Madagascar has been attributed to vicariance are the cichlids, freshwater fishes. Molecular dating studies of this group (Sparks 2004; Sparks & Smith 2004) avoided the use of fossil calibrations completely.
Instead, the vicariant distributions of the two main molecular clades: Madagascar-Africa-South America, and Madagascar-India-Sri Lanka, were correlated with tectonics – the opening of the Mozambique Channel – and this was used as a calibration (the same method is used here for primates). So although Yoder & Nowak (2006, p. 416) concluded by stating that the importance of dispersal ‘cannot be denied’, really the only thing the cited studies show is the importance of the calibration method. Recent molecular studies on cichlids have continued to use the rifting of Gondwana rather than the fossil record to calibrate molecular phylogenies (the oldest fossil is Eocene), and this has produced some intriguing results (Genner et al. 2007; Azuma et al. 2008).

As discussed, fossil-based ‘molecular’ clocks can only give maximum, absolute ages by transmogrification of minimum ages and this is seen in a clock study of the Malagasy mammal orders by Poux et al. (2005). The authors found that lemurs and their African sister group diverged first (at 60 Ma), followed by equivalent Africa/Madagascar splits in tenrecs, carnivorans, and then rodents. The clock calculations were calibrated using six ‘well-established’ (p. 721) fossil dates which were transmogrified into maximum dates; Poux et al. assigned minimum and maximum dates for five fossil clades and a minimum date for a sixth. The primate radiation was assigned a minimum age of 63 Ma and a maximum of 90 Ma. This is not logical. If even one maximum date was well-established for any taxon, analysis would be much more straightforward, but there are no maximum dates in the mammalian fossil record. In a similar study, Poux et al. (2006) again used transmogrified data and inferred young dates for trans-Atlantic disjunctions in primates and in hystricomorph rodents. Based on this, they accepted trans-Atlantic rafting.

Yoder et al. (2003) and Poux et al. (2005) concluded that the different degrees of differentiation shown between the Malagasy mammals and their mainland sister groups indicate different times of divergence and hence colonization. Instead, in a vicariance model different degrees of difference reflect prior aspects of genome architecture. Molecular clock analyses that rely on degree of difference suggest that every endemic clade in Madagascar is the result of a separate event, unrelated to any other, and that community-wide vicariance has played no role. This method will reach the same conclusion for any biogeographic pattern, as all patterns include clades of different rank. Vicariance in the orders of mammals in Madagascar suggests instead that their spatial differentiation has resulted from exposure to the same earth history and that the different degree of differentiation in each of the four is not related to time.

The primates are closely related to the rodents and the biogeography of this larger group, with about 40% of all mammal species, is relevant. The trans-Atlantic disjunctions have already been mentioned. Rodents have three primary clades and each occurs in America, Africa and Asia (Horner et al. 2007). Despite this overlap, there are significant differences among the three clades, especially with respect to Madagascar:

- Hysticomorpha (porcupines, the basal group): east to Borneo (cf. strepsirrhines); not in Madagascar.
- Sciuromorpha (squirrels): east to Sulawesi (cf. haplorhines); not in Madagascar.
- Myomorpha (rats): east to Australasia, with a diverse clade in Madagascar.

Many authors have commented on the surprising absence of the first two groups, especially the otherwise widespread squirrels, from Madagascar and Australasia; the same pattern occurs in haplorhines. The distribution of the rodents is different from that of the primates, and yet the main phylogenetic/biogeographic breaks (nodes) are the same: Atlantic Ocean, Mozambique Channel, Makassar Strait (Wallace’s line) and the Banda/Molucca Sea, east of Sulawesi.

Horner et al. (2007) suggested that rodents diverged from lagomorphs and that the three main rodent clades diverged from each other at around 60 Ma (a minimum date), with all this evolution taking place within just 3.1 million years. A similar ‘early, rapid’ differentiation is accepted here for the main primate clades; the proposed age of the groups is much older than has been thought, although the time involved in their differentiation may be much less.

Conclusions

Traditional, fossil-based models and the new fossil-calibrated molecular clocks both support an origin of primates after the Early Cretaceous, in which case the group would be too young to have been affected by Pangea-Gondwana breakup. Both models infer dispersal over a more or less modern geography. The problem is that dispersal models all leave many, serious problems unresolved; for example, how did primates cross the major barriers of the Atlantic Ocean and Mozambique Channel? And if they could disperse across, why did this only happen once, early on, in each case? Why are New World monkeys sister to the Old World monkeys, not deeply nested within them, as a dispersal model would predict? How could primates disperse across the Atlantic and Mozambique Channel when they have never crossed the stretch of sea (Salu Timpaa Strait, 20 km wide) that separates Sulawesi from eastern Indonesia and Australasia? Studies have focused on means of dispersal and island-hopping, but these may not be relevant. Most
primates have excellent powers of movement, running, climbing and leaping on cliffs and trees. Some Old World primates, such as *Nasalis* and *Macaca*, are well-known to be strong swimmers; in America, *Aotus* has been observed swimming in the wild (Eisenberg et al. 2000) and ‘all neotropical forms can probably swim to some extent’ (Eisenberg et al. 2000, p. 231). Many primates undertake extensive annual migrations through different forest types (e.g. several Amazon species; Barnett & Brandon-Jones 1997; Boubli et al. 2008). On the other hand primate species also exhibit strong philopatry and maintain strict geographic limits. The problem lies in dove-tailing the excellent potential powers of movement with the observed strong phylogenetic differences among the primate faunas of the different regions. The platyrhines in South and central America, and the lemurs in Madagascar both show a complete lack of geographic overlap with any other group. This, together with the widespread overlap of nearly all genera *within* South America, Africa and Asia, indicates that while there has been no trans-oceanic dispersal (as expected from their observed ecology) there have been phases of mobilism on the continents leading to overlap of the genera by normal range extension. Within most genera nearly all the species are allopatric, indicating a later phase of immobilism and differentiation.

In centre of origin/dispersal theory, the distribution of a group develops *after* its origin in phylogeny, as a separate process – range expansion from the centre of origin. In vicariance, distribution is produced by the phylogeny and so distribution and phylogeny develop at the same time. This means the distribution can be informative about the phylogeny and *vice versa*. When considering the biogeography of any taxon, traditional biogeography looks for a centre of origin, usually somewhere within the current range. Instead, a vicariance analysis looks for the break between the group and its sister. The main problem is not explaining how each individual group managed to migrate to its own area, it is explaining how and why migration ceased and the rifts between the groups formed, i.e. how an originally widespread group could break up and evolve different members in different areas. The mechanism suggested here is earth history/plate tectonics.

Rose (1995, p. 170) noticed that ‘Conjecture about the place of origin of both primates and anthropoids seems to change with each new discovery – a sure indication that existing evidence is simply insufficient’. Instead, the situation (unchanged since 1995) could indicate that there is no centre of origin and that primates originated as a southern vicariant of plesiadapiforms, while anthropoids developed as a western vicariant of tarsiers.

Critical analyses of sweepstake dispersal (Stankiewicz et al. 2006; Masters et al. 2007), new interpretations of the fossil record and phylogeny (Miller et al. 2005; Martin et al. 2007; Soligo et al. 2007) and molecular clock studies indicating a much older, Mesozoic chronology (Glazko et al. 2005) together represent a major break with Matthew’s (1915) centre of origin/dispersal model of primate evolution. The new work is instead compatible with a vicariance model in which the spatial distribution of molecular clades is correlated with radiometrically dated tectonics. This approach combines the best of molecular biology and hard-rock geology, and avoids the problems of fossil calibration. In the new chronology, fossils are used to give minimum ages only and dates are not transmogrified. While the method gives dates that are older than those accepted in fossil-based clock scenarios, many clock studies (and fossils themselves) have already demonstrated massive gaps in the fossil record.

Yoder & Yang (2004, p. 768) concluded their fossil-calibrated molecular clock study by writing that ‘The initial radiation of lemuriform primates... is estimated to have occurred approximately 62 Ma, near the onset of the Tertiary. This is a surprisingly ancient date, as it precedes the appearance of euprimates in the global fossil record. Indeed, if we were to base our judgements of primate antiquity on a strict interpretation of the known fossil record, this estimate of lemuriform antiquity would be considered incredible. Instead, increasing numbers of primatologists and palaeontologists concur that the fossil record is far too scant and ‘frighteningly incomplete’ (Fleagle 2002) to impose strict limits on our interpretation of the temporal context for primate evolution’ [italics added]. This reasoning is correct and important, and the argument should be extended to a critique of fossil-calibrated molecular clock dates. If workers have already dismissed the fossil record as a basis for chronology, as Yoder & Yang (2004, p. 768) have in accepting the ‘surprisingly ancient’ dates for lemons, tens of millions years older than the oldest fossil, it would be logical to take one more step and not base clock dates on fossils at all. It makes sense to avoid staking the entire chronological analysis on a ‘frighteningly’ scant record, when the distinctive biogeography of molecular clades and accurate radiometric dates can be used instead (cf. Genner et al. 2007; Azuma et al. 2008).

Geographic distribution is not just another character. It may seem fluid and ephemeral compared with the morphological distinctions, yet distribution now appears to have a special phylogenetic significance. Many molecular studies have shown that groups based on traditional morphological homologies are misleading and that phylogeny correlates instead with geographic distribution; distribution has turned out to be the ‘character of characters’ for molecular phylogeny in general. If Cenozoic fossil-based
clock dates are replaced with Mesozoic dates based on tectonics and molecular clade distribution it should be possible to move beyond the legacy of Matthewian zoogeography: paradoxes and enigmas, endless, fruitless debate about centres of origin, and reliance on theoretical processes of dispersal that in practice have proved to be unfeasible.

References


**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Supplementary notes on groups.

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