Malagasy Primate Origins: Phylogenies, Fossils, and Biogeographic Reconstructions

Nancy J. Stevens[a]   Christopher P. Heesy[b]

[a]Department of Biomedical Sciences, Ohio University, Athens, Ohio, [b]Department of Anatomy, New York College of Osteopathic Medicine, New York, N.Y., USA

Abstract
The geographic origin of Malagasy primates is a rich source of debate, providing a useful context for understanding effects of differing phylogenetic interpretations upon area of origin reconstructions. This study has evaluated the biogeographic implications of competing primate phylogenies in order to reconstruct the area of origin of Malagasy strepsirhines. The robusticity of biogeographic inference is examined based on sensitivity to tree topology. The results demonstrate extreme vulnerability to both out-group choice and internal tree topology, suggesting caution for area of origin interpretations from phylogenies that exclude fossil taxa. Moreover, even a single taxon can have a powerful effect upon biogeographic interpretations. Perhaps not surprisingly, it is only with greater phylogenetic resolution that a clearer understanding of the biogeographic origins of Malagasy primates will emerge.   Copyright © 2006 S. Karger AG, Basel

Introduction

Madagascar's floral and faunal uniqueness is well documented in the literature, with endemicity in the majority of the island's recorded plants, invertebrates, freshwater fishes, amphibians, reptiles, birds, and mammals [Perrier de la Bathie, 1936; Paulian, 1961; Albignac, 1972; Koechlin, 1972; Tattersall, 1982; Blommers-Schlosser and Blommers, 1984; Wilmé, 1996; Fisher, 1997]. This pattern masks complex ele-

ments of the island's biogeographic history, which likely reflects geographic isolation over tens of millions of years [e.g. Coffin and Rabinowitz, 1987; Storey, 1995; Hay et al., 1999; de Wit, 2003]. For example, some Malagasy taxa appear to share taxonomic affinities with continental African fauna, suggesting dispersal across the Mozambique Channel [Leroy, 1996; Yoder et al., 2003; Vences et al., 2004], whereas other taxa may be more closely related to Asian forms [Eger and Mitchell, 1996; Rage, 1996; but see Thewissen and McKenna, 1992; McKenna, 1995]. In particular, numerous studies have contemplated the biogeographic origins of Malagasy strepsirhine primates [e.g. Wallace, 1876; Simpson, 1940, 1965; Tattersall, 1982; Yoder, 1996a; Martin, 2000; Yoder et al., 2003; Poux et al., 2005; and papers in this volume].

Biogeographic Mechanisms

Two mechanisms often used to explain faunal distributions are habitat vicariance and species dispersal [Pielou, 1979; Pianka, 1994]. Vicariance scenarios rely upon the emergence of barriers to explain faunal distributions, with drift and allopatric speciation resulting from separation of habitats and their resident biota [Pielou, 1979]. Inferences regarding habitat vicariance are strengthened by common speciation patterns in unrelated groups [Myers and Giller, 1988]. For example, hypotheses abound as to the sequence and timing of the breakup of Gondwanan landmasses during the Cretaceous [Coffin and Rabinowitz, 1987; Storey, 1995; McCall, 1997; Hay et al., 1999; de Wit, 2003]. Congruent phylogenetic patterns in different vertebrate clades have been used to test ideas regarding the persistence of connections between certain landmasses or habitats to the exclusion of others [Raxworthy and Nussbaum, 1996a; Krause et al., 1997; Sampson et al., 1998].

But what happens when species distributions do not support a clear pattern of vicariance? For example, although a handful of taxa represent surviving phyletic lines present on Madagascar since the Mesozoic [Leroy, 1996; Schatz, 1996; Le Thomas and Doyle, 1996], continental vicariance likely predated the origin of many vertebrate groups that currently reside on the island [Simpson, 1940; Tattersall, 1982; Vences et al., 2001; Raxworthy et al., 2002; Yoder et al., 2003; but see Hedges et al., 1996; Tavaré et al., 2002]. Some species may have arrived via aerial dispersal from nearby landmasses [e.g. plants: Meve and Liede, 2002; birds: Louette, 1996; insects: Bernardi, 1996], and the presence of temporary land connections has been suggested [McCall, 1997]. Nonetheless, dispersal by rafting and/or island hopping is the dominant explanation for the presence of various mammalian groups [e.g. Simpson, 1940; Yoder, 1996a, b].

Such scenarios often emphasize intrinsic morphological or physiological attributes that permit organisms to disperse. For example, three of the four radiations of mammals that colonized Madagascar have members that are capable of undergoing torpor [Albignac, 1972; Racey and Stephenson, 1996; Warren and Crompton, 1996; but see Mzilikazi et al., this vol., pp. 465–476]. This physiological ability may have conferred an advantage to animals during a rafting dispersal event between landmasses by providing enhanced tolerance of food/water deprivation [Mzilikazi et al., this vol., pp. 465–478]. Dispersal scenarios can be greatly strengthened by refinements of geophysical evidence documenting barriers, land bridges or stepping stones that may have influenced the movements of animals in the past [e.g. de Wit, 2003; Masters et al., this vol., pp. 399–418]. But from which landmass did the Malagasy taxa disperse?

Recent studies have employed an understanding of phylogenetic relationships to provide a context for the interpretation of biogeographical patterns [Raxworthy and Nussbaum, 1994, 1996b; Raxworthy et al., 1998; Beard 1998; Humphries and Parenti, 1999; Stevens and Heesy, 2000; Heesy et al., 2006]. Yet biogeographic interpretations are complicated by the presence of numerous competing phylogenies, often constructed using differing data sets collected on different taxa. Many recent studies have relied on molecular data sets, and are thereby limited to modern and relatively recent taxa [e.g. Yoder et al., 1996]. However, fossils often preserve character states absent in extant taxa [Gauthier et al., 1988; Donoghue et al., 1989; Shoshani et al., 1996], and a similar argument can be made that fossils preserve temporal and geographic data critical for biogeographic reconstructions [Stewart and Disotell, 1998; Heesy et al., 2006]. Today, lemuroids exist only on Madagascar, whereas living non-Malagasy strepsirhines occupy the African continent (galagids and lorisids), as well as Asia (lorisids). In the past, strepsirhines enjoyed an even greater distribution, including Europe and North America [Fleagle, 1999]. Uncertainty regarding Malagasy primate origins is amplified by a relative paucity of fossils from Madagascar and sub-Saharan Africa during the key interval of time suggested for their dispersal [Martin, 2003].

African or Asian Origins of Malagasy Primates
Much of the debate regarding Malagasy primate origins has hinged upon phylogenetic relationships among lorisoids (lorises and galagos), cheirogaleids and lemurids [e.g. Yoder, 1996a, b; Martin, 2000; Roos et al., 2004]. Traditional morphologically based phylogenies emphasized shared cranial and vascular characters supporting a sister taxon relationship between lorisoid and cheirogaleid primates [e.g. Szalay and Katz, 1973; Tattersall and Schwartz, 1974; Cartmill, 1975], implying lemuroid polyphyly or paraphyly. To explain the species distributions we observe today, this arrangement would necessitate successful water crossings to Madagascar by two separate lineages (cheirogaleids and other lemuroids) either separately [Martin, 2000] or via a shared sweepstakes dispersal event. More recent molecular approaches have advocated lemuroid monophyly, requiring just one colonization of Madagascar by a single taxon of continental African strepsirhines [e.g. Yoder et al., 1996; Roos et al., 2004]. Yet lemuroid monophyly does not necessarily imply a simple biogeographic story.

New Taxon from Pakistan
Marivaux et al. [2001] reported the discovery of a fossil from the Early Oligocene Bugti Hills of Pakistan, suggesting close affinities between this form, *Bugtilemur*, and the modern fat-tailed dwarf lemur, *Cheirogaleus*. The phylogeny based on dental characters presented by Marivaux et al. [2001] generally supports lemuroid monophyly, yet the presence of so derived a cheirogaleid as early as 30 million years ago on the Indian subcontinent implies an ancient divergence between *Cheirogaleus* and other Malagasy lemuroids, and raises questions about the directionality of dispersal events to and from the island of Madagascar [Marivaux et al., 2001]. Deeper divergence times for strepsirhine clades are not entirely controversial, having been suggested by previous molecular work as well as by estimates utilizing statistical approaches to model the completeness of the known fossil record [e.g. Eizirik et al., 2001; Arnason et al., 2002; Tavaré et al., 2002; Yoder and Yang, 2004; but see Godi-

not, this vol., pp. 446–464]. Implications of a 30-million-year-old cheirogaleid in Pakistan for biogeographic reconstructions, however, are far more complicated.

In one scenario, lemuroids may have arisen on continental Africa, dispersed across the Mozambique Channel to Madagascar, and then again traversed a water barrier to reach Pakistan. In another scenario, deeper divergence times may have permitted them to reach and disperse throughout Indo-Madagascar prior to the separation of these landmasses. Martin [2003] has suggested that strepsirhines arose on Indo-Madagascar, with lemuroids and lorisoids diverging as a result of the vicariance of these landmasses. Finally, Marivaux et al. [2001] caution that the presence of a lemur in the Oligocene of Pakistan means we cannot exclude the possibility that lemuroids arose in Asia or Pakistan, dispersing later to Madagascar across the Indian Ocean.

Yet the phylogenetic affinities of *Bugtilemur* are far from resolved [e.g. Seiffert et al., 2003; Godinot, this vol., pp. 446–464]. The analysis by Marivaux et al. [2001] that included adapiform primates rendered the conventional family Cheirogaleidae polyphyletic, joining the *Cheirogaleus-Bugtilemur* clade with lemurids rather than with the group comprised of *Microcebus, Mirza, Phaner* and *Allocebus*. Moreover, this phylogenetic reconstruction supported an untraditional grouping of lorisoids, whereby lorisids were polyphyletic with the inclusion of *Galago*. Their subsequent analysis excluded adapiforms and added additional morphological characters, providing a more conventional phylogenetic arrangement with monophyly observed in lorisids, cheirogaleids and lemuroids [Marivaux et al., 2001], raising questions about why the inclusion of adapiforms destabilized particular clades in analyses based only on this set of dental characters. With respect to adapiforms, lorisoids, and lemuroids, *Bugtilemur* preserves a strikingly derived dentition in lacking upper molar hypocones, a feature shared only with *Cheirogaleus* and forming a basis for their proposed *Bugtilemur-Cheirogaleus* clade. Yet adapiform affinities remain a possibility for *Bugtilemur*, as no specimens retrieved to date have been demonstrated to preserve decisive evidence of tooth comb use, such as microwear generated by the passage of hairs between the teeth during grooming. Moreover, other dental features preserved in *Bugtilemur* may reflect plesiomorphic features problematic for its assignment to so derived a position within the Lemuroidea [Godinot, this vol., pp. 446–464].

Ancient Lorises and Galagos

In 2003, Seiffert et al. reported the first definitive paleontological evidence of crown strepsirhines, recovered from the Late-Middle Eocene Jebel Qatrani Formation of Egypt. *Karanisia* and *Saharagalago* share a number of derived dental features with extant lorisoids including upper molar hypocones [Seiffert et al., 2003]. Moreover, *Karanisia* exhibits alveolar morphology in the anterior mandible consistent with the presence of a tooth comb, an inference confirmed by the presence of microscopic wear grooves on the mesial aspect of the canine [Seiffert et al., 2003]. The phylogenetic analysis presented by Seiffert et al. [2003] placed *Saharagalago* in crown Galagidae, and tentatively allocated *Karanisia* to the Lorisidae as a sister taxon to *Arctocebus*. It should be noted that this analysis recovered an unconventional tarsier-strepsirhine sister grouping to the exclusion of anthropoids, and that subsequent analyses [Seiffert et al., 2005] have placed both taxa in a more basal position among lorisoids. Yet the study remains significant in that *Karanisia* and *Saharagalago* are twice the age of the previously known fossil lorisoids *Komba, Progalago*, and

Mioeuoticus [e.g. Le Gros Clark and Thomas, 1952; Phillips and Walker, 2002]. Recent molecular studies support lorisid monophyly [e.g. Roos et al., 2004], suggesting a divergence between lorisoids and lemuroids well before the Late Eocene [Seiffert et al., 2003], and influencing arguments regarding the age of the Malagasy primate radiation [Roos et al., 2004].

Taken together, recent fossil discoveries from Indo-Pakistan [Marivaux et al., 2001] and continental Africa [Seiffert et al., 2003] call for a closer examination of the biogeographic history of Malagasy strepsirhines, including sensitivity of area of origin reconstructions to out-group choice, in-group topology, and missing fossil data.

Methods

In order to reconstruct the biogeographic area of origin for the Malagasy strepsirhines, this study optimized geographic area onto competing phylogenetic trees using maximum parsimony in MacClade 4.0 [Maddison and Maddison, 2000], reconstructing the most parsimonious sequence of dispersal events to produce the observed distributions of primates. Continents or subcontinents were the minimum geographic unit coded as a trait, an optimization method applied in previous biogeographic analyses [Beard, 1998; Strait and Wood, 1999; Murray, 2001]. For the purposes of this study, continental distribution was treated as an unordered, multistate character, with no constraints on dispersal between landmasses. Hence, taxa could theoretically disperse from South America to Asia. For a given phylogeny, the set of equally most parsimonious solutions to the optimization of a trait was retrieved using the maximum parsimony option in MacClade. Equivocal reconstructions were recovered for nodes and internodes with multiple possible solutions. Equally parsimonious solutions included optimizations favouring parallelisms (ACCTRAN), and reversals (DELTRAN) in addition to all other parsimonious solutions. Because they may not apply to all characters simultaneously, ACCTRAN and DELTRAN do not necessarily demonstrate the most appropriate solution to the evolution of a trait of interest. When node reconstructions were unequivocal, major clades such as the Lemuroidea, Platyrrhini, and Catarrhini were condensed to streamline illustrations.

We examined the role of differing in-group topologies by individually optimizing biogeographic areas onto phylogenies published by Marivaux et al. [2001] and Seiffert et al. [2003]. In addition, we included a composite 'supertree' recently assembled by Heesy et al. [2006], generated by the cladistically based matrix representation using parsimony [Baum, 1992; Ragan, 1992; Purvis, 1995a, b; Bininda-Emonds and Bryant, 1998; Sanderson et al., 1998]. This composite tree of living and fossil primates incorporated information from a broad range of phylogenetic sources, including Fleagle and Kay [1987], Jungers et al. [1991], Beard et al. [1991, 1994], Purvis [1995a], Rose [1995a, b], Begun [1995], Begun and Kordos [1997], Benefit and McCrossin [1997], Horovitz and Meyer [1997], Kay et al. [1997, 1998], Harris and Disotell [1998], Ross et al. [1998], Horovitz [1999], Fleagle [1999], Horovitz and MacPhee [1999], Jaeger et al. [1999], Norejko [1999], Purvis and Webster [1999], Ross [2000], Gebo et al. [2000], and Seiffert et al. [2000]. New fossil taxa, *Bugtilemur, Karanisia* and *Saharagalago,* were inserted in the composite phylogeny following the taxonomic assignments by Marivaux et al. [2001] and Seiffert et al. [2003]. Generic monophyly was assumed for fossil taxa *Eosimias, Archaeolemur, Palaeopropithecus* and *Megaladapis,* with individual species manually inserted as sister taxa. The data matrix is available from the authors on request.

This analysis represents the first examination of Malagasy primate origins to employ character mapping on a phylogeny that comprehensively samples extant and extinct primates at the generic or specific level. Influence of out-group choice upon biogeographic reconstructions was explored by varying out-group combinations to include major continents from which fossil and living primates are known, with equivocal node reconstructions considered irresolvable based on currently available data. The impact of additional fossil finds was explored by experimentally inserting taxa coded from different geographical areas into existing primate clades.
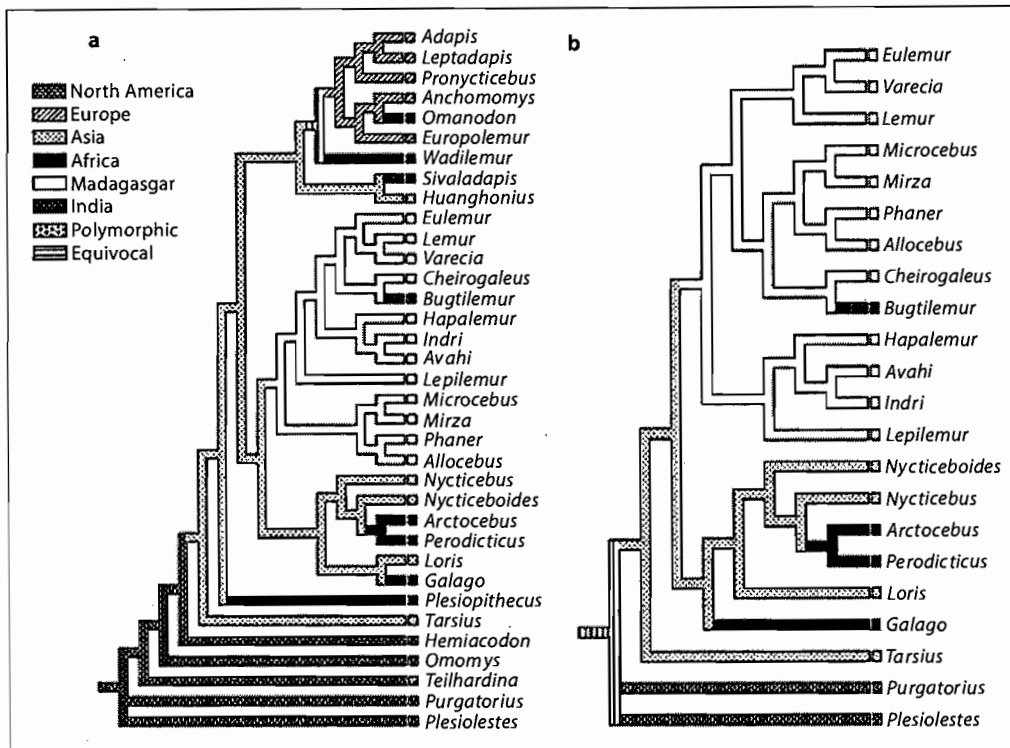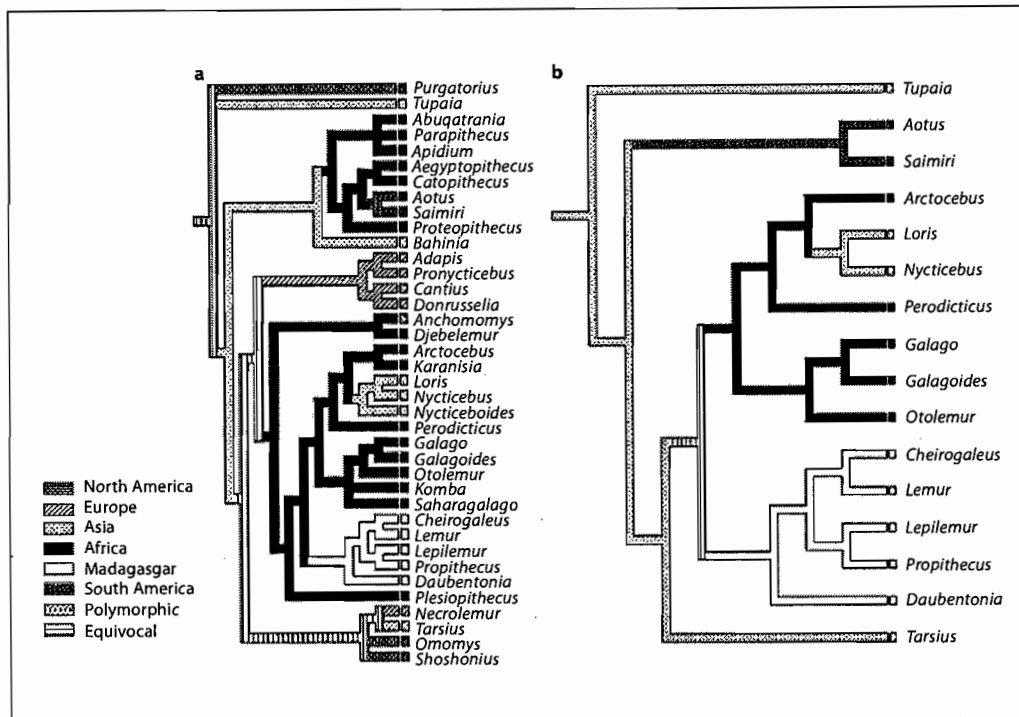
Fig. 1. Biogeographic implications of *Bugtilemur*. **a** Geographic area mapped onto the tree topology published by Marivaux et al. [2001]. This topology retrieves an Asian origin for Malagasy strepsirhines. **b** Geographic area mapped onto the second tree topology published by Marivaux et al. [2001]. Note that this topology omits adapiform primates, and retrieves an Asian area of origin for Malagasy strepsirhines.

Results and Discussion

Impact of Newly Discovered Fossils on Malagasy Primate Origins

When geographic area is mapped onto the taxonomic framework of Marivaux et al. [2001] that included adapiforms, an Asian origin for Malagasy strepsirhines is retrieved (fig. 1a). Marivaux et al. did not discuss their rationale for excluding *Komba* and the modern African galagids, *Otolemur* and *Galagoides*, but these taxa may not have offered further illumination given the traits examined in their study. The taxonomic framework from the analysis of Marivaux et al. that excluded adapiforms also yielded an Asian origin for the Malagasy lemuroid node (fig. 1b).

Mapping geographic area onto the phylogenetic tree of Seiffert et al. [2003], however, yields an African origin for Malagasy strepsirhines (fig. 2a). The role of fossil taxa in recovering an African origin for lemuroids is clearly demonstrated by re-examining the tree topology of Seiffert et al. [2003] with all extinct taxa omitted. The reduced tree recovers an equivocal reconstruction for the area of origin of the Malagasy primate clade (fig. 2b), underscoring the sensitivity of biogeographic reconstruc-

Fig. 2. Biogeographic implications of *Karanisia* and *Saharagalago*. **a** Geographic area mapped onto the tree topology published by Seiffert et al. [2003]. This topology retrieves an African origin for Malagasy strepsirhines. **b** Geographic area mapped onto the tree topology of Seiffert et al. [2003], but with the omission of all extinct taxa. Note that this topology retrieves an equivocal area of origin for Malagasy strepsirhines.

tions to missing data and raising the issue of whether including more Asian fossil taxa might also influence area of origin reconstructions for Malagasy primates.

Visions from a Fuller Tree

Not surprisingly, the examples discussed above suggest that biogeographic reconstructions employing character mapping depend directly on tree topology, with particular sensitivity to missing data. Hence, analyses based on trees including primarily African taxa tend to favour an African origin of Malagasy lemuroids, just as analyses based on trees that emphasize Asian out-groups yield reconstructions favouring an Asian origin. No study to date has examined Malagasy primate origins in light of all available fossil and modern evidence. The remainder of this paper explores the impact of altering both out-group choice and in-group topology on biogeographic reconstructions using a composite tree recently generated by Heesy et al. [2006] that densely samples extant and extinct primates at the generic level.

The effects of out-group choice on biogeographic reconstructions are illustrated in figure 3. Primate out-group variations included Africa, Asia, North America, and Europe, all continents previously debated as an ancestral area for the order Primates
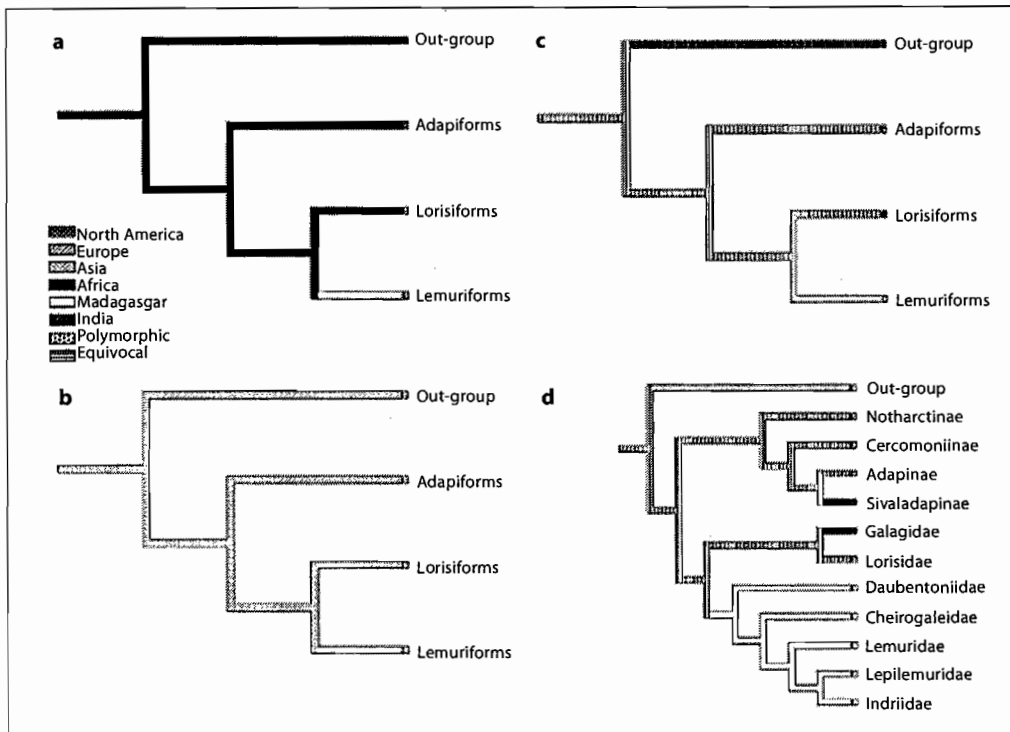
Fig. 3. Effects of out-group choice on biogeographic reconstructions. **a** African primate out-group retrieves an African origin for Malagasy strepsirhines. **b** Asian primate out-group retrieves an Asian Malagasy primate origin. **c** An equivocal reconstruction is retrieved with a North American (pictured) or European primate out-group. **d** Increasing phylogenetic resolution alters the reconstruction to equivocal for the Asian primate out-group.

[e.g. Jacobs, 1980; Gingerich, 1990; Sigé et al., 1990; Gingerich et al., 1991; Kay et al., 1992; Beard, 1993; Rose et al., 1994; Bloch, 2001; Bloch and Boyer, 2002; Silcox, 2002]. Figure 3a illustrates nodes collapsed to the superfamily level with an African primate out-group resulting in the inference of an African origin for Malagasy strep-sirhines. In contrast, North American and European primate out-groups yield an equivocal reconstruction for the area of origin of Malagasy primates (e.g. fig. 3b). An Asian primate out-group implies an Asian origin for lemuroids (fig. 3c). In a less compressed tree, an Asian primate out-group choice reveals an equivocal origin for Malagasy strepsirhines (fig. 3d), demonstrating the role of increased taxonomic resolution for character mapping of biogeographic data.

Figure 4a depicts the expanded topology of the fossil and modern primate composite tree of Heesy et al. [2006] with resolved nodes compressed. The original analysis excluded *Bugtilemur,* recovering an equivocal area of origin for Malagasy primates [Heesy et al., 2006]. As discussed above, Marivaux et al. [2001] suggested that the presence of a sister taxon to *Cheirogaleus* in Pakistan would have profound implications for Malagasy primate geographic origins. Contrary to this expectation,
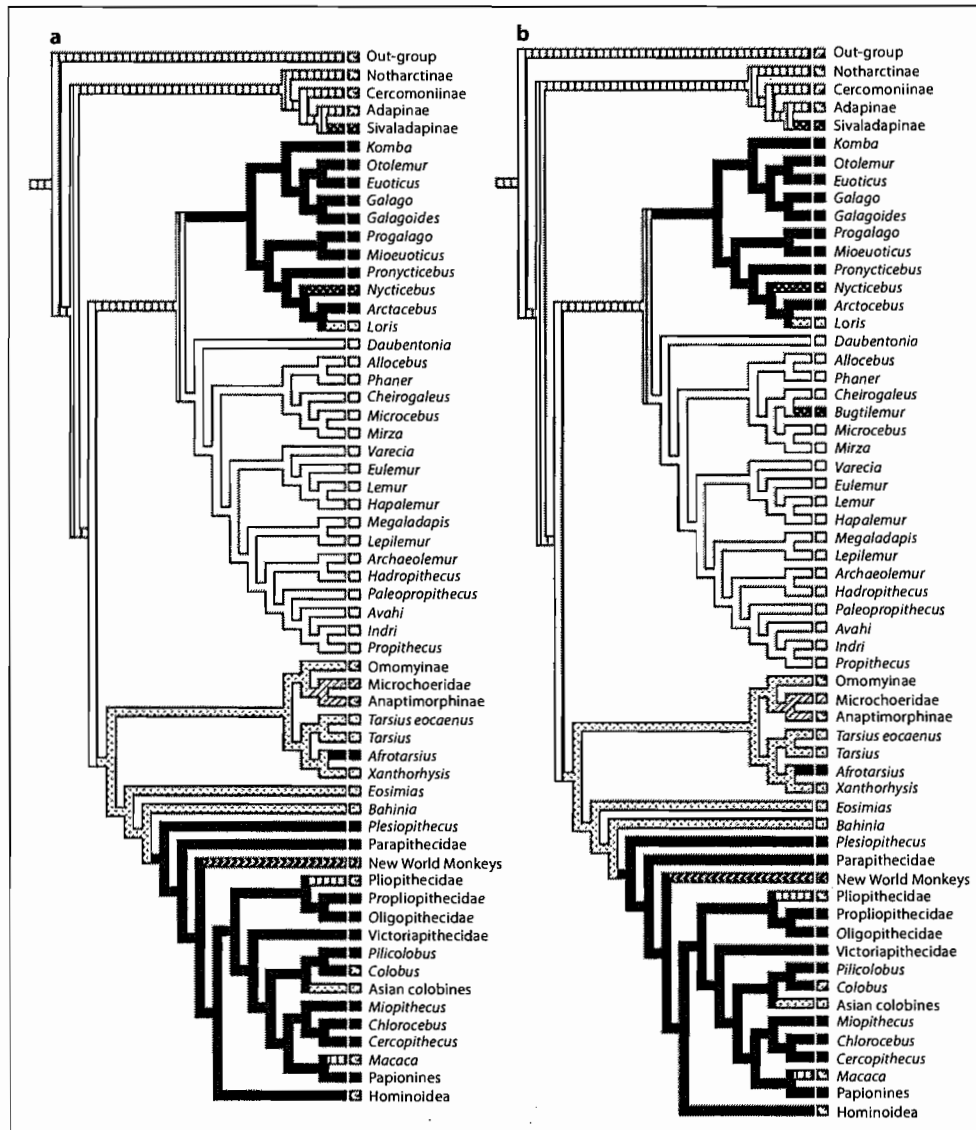
Fig. 4. Biogeographic reconstructions in densely sampled composite phylogeny taken from Heesy et al. [2006]. Shading follows legends in figures 1–3. **a** Equivocal ancestral area reconstruction for Malagasy strepsirhines. **b** Inclusion of *Bugtilemur* does not alter the area of origin reconstruction at the lemuroid node.

(For figure 4c–4d see next page.)
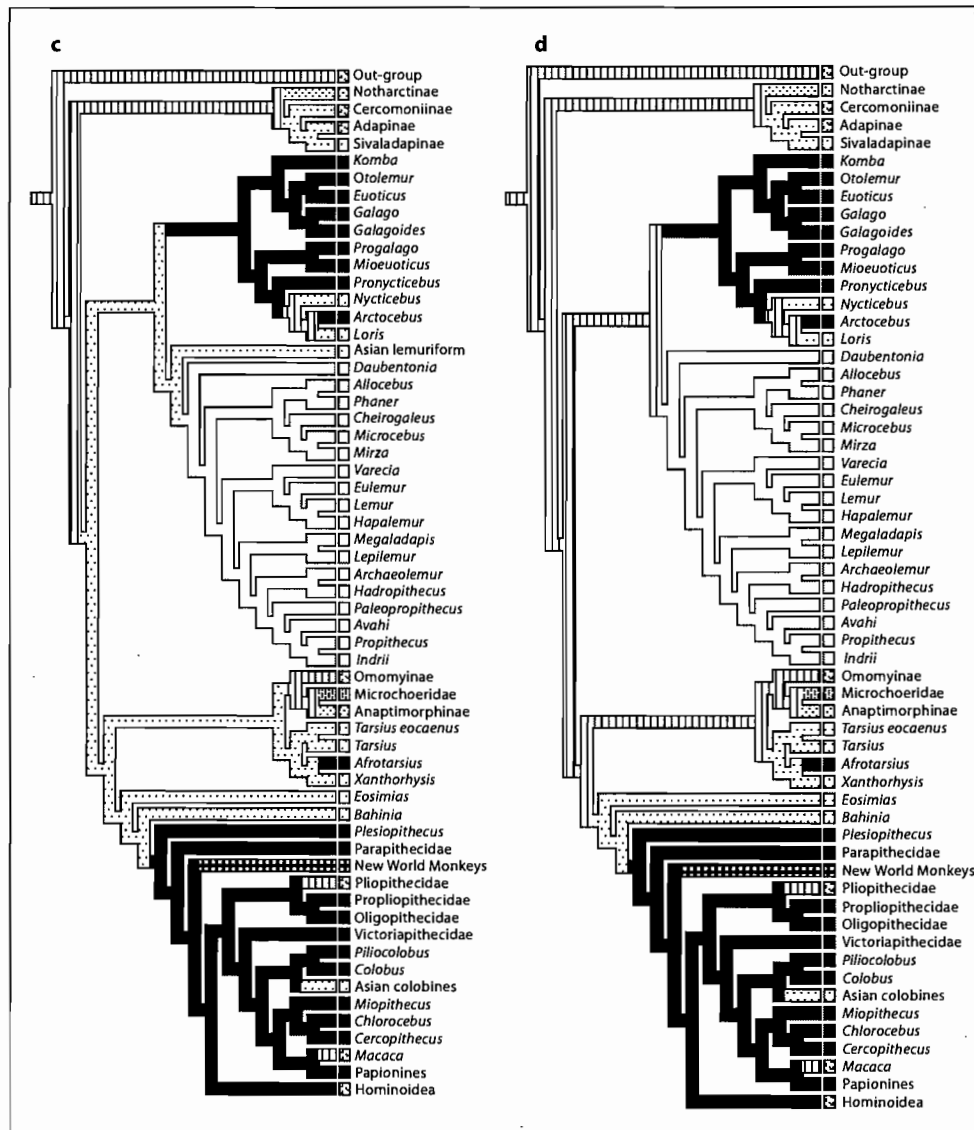
Fig. 4. c An Asian stem lemuriform results in an Asian area of origin reconstruction for Malagasy primates (similarly, an African stem lemuriform results in an African ancestral area reconstruction). **d** An African stem haplorhine yields an African area of origin reconstruction for lemuroids.

including *Bugtilemur* as a sister taxon to *Cheirogaleus* does not influence the area of origin reconstruction using this tree topology (fig. 4b). This seems to result from the derived nature of the purported cheirogaleid, causing Marivaux et al. [2001] to nest it deep within the lemuroid clade. Thus, if their phylogenetic assessment is accurate, the taxon does little to clarify the biogeographic origins of this enigmatic group. A similar situation is observed with the addition of fossil lorisoids *Karanisia* and *Saharagalago;* in this case, the inclusion of two important lorisoid out-groups from continental Africa does not alter the equivocal ancestral area reconstruction for lemuroids. Again, it would appear that the crown position of these fossils dampens their impact upon the reconstructed area of origin (but see Seiffert et al., 2005). This should not be taken to imply that fossils are unimportant to biogeographic reconstructions that employ character mapping approaches, but rather that their phylogenetic placement (i.e., position within a given topology) plays the most significant role. Hypothetically, the discovery of a stem sister taxon to lemuroids in Asia would result in the reconstruction of an Asian area of origin for Malagasy primates (fig. 4c), just as an African taxon in the same position would favour an African ancestral area reconstruction. Notably, the discovery of a stem haplorhine from Africa would also imply an African origin for lemuroids (fig. 4d), demonstrating that, depending on its phylogenetic position, even a single new fossil can have a dramatic impact on biogeographic inference.

Pitfalls in Character Mapping Approaches

Although the reconstruction of biogeographic history remains a central topic in studies of vertebrate evolution, this study offers a cautionary note for interpreting areas of origin using phylogenies that do not densely sample the taxa of interest. And as Cunningham et al. [1998] pointed out, parsimony-based character mapping may yield misleading character states when evolutionary rates are rapid and when there is an unequal probability of losses or gains. Large-scale dispersal events may be sporadic and relatively rare, but when they do occur, they have the potential to alter faunal distributions rapidly. Moreover, the probabilities of dispersal are clearly different between various landmasses, and even in different directions between two given landmasses. Differential extinction and the – as yet – low rate of recovery of fossils from many geographic regions provide additional challenges for retrieving meaningful biogeographic reconstructions. Nonetheless, approached with healthy skepticism, character mapping remains a straightforward method for directly assessing biogeographic implications of different phylogenetic tree topologies, offering some degree of improvement over scenario building for understanding the impact of newly discovered fossils on competing ancestral area hypotheses.

References

Albignac R (1972). The Carnivora of Madagascar. In *Biogeography and Ecology in Madagascar* (Battistini R, Richard Vindard G, eds.), pp 667–682. The Hague, Junk.

▶ Arnason U, Adegoke JA, Bodin K, Born EW, Esa YB, Gullberg A, Nilsson M, Short RV, Xu X, Janke A (2002). Mammalian mitogenomic relationships and the root of the eutherian tree. *Proceedings of the National Academy of Sciences, USA* 99: 8151–8156.

▶ Baum BR (1992). Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon* 41: 3–10.

Beard KC (1993). Phylogenetic systematics of the Primatomorpha, with special reference to Dermoptera. In *Mammal Phylogeny: Placentals* (Szalay FS, Novacek MJ, McKenna MC, eds.), pp 129–150. New York, Springer.

Beard KC (1998). East of Eden: Asia as an important center of taxonomic origination in mammalian evolution. *Bulletin of the Carnegie Museum of Natural History* 34: 5–39.

▶ Beard KC, Krishtalka L, Stucky RK (1991). First skulls of the Early Eocene primate *Shoshonius cooperi* and the anthropoid-tarsier dichotomy. *Nature* 349: 64–67.

▶ Beard KC, Qi T, Dawson MR, Wang B, Li C (1994). A diverse new primate fauna from middle Eocene fissure-fillings in southeastern China. *Nature* 368: 604–609.

▶ Begun DR (1995). Late Miocene European orang-utans, gorillas, humans, or none of the above? *Journal of Human Evolution* 29: 169–180.

Begun DR, Kordos L (1997). Phyletic affinities and functional convergence in *Dryopithecus* and other Miocene and living hominids. In *Function, Phylogeny and Fossils. Miocene Hominoid Evolution and Adaptations* (Begun DR, Ward CV, Rose MD, eds.), pp 291–316. New York, Plenum Press.

▶ Benefit BR, McCrossin ML (1997). Earliest known Old World monkey skull. *Nature* 388: 368–371.

Bernardi G (1996). Biogéographie et spéciation des lépidoptères Papilionidae, Pieridae, Danaidae et Acraeidae de Madagascar et des îles voisines. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 491–506. Paris, Editions de l'ORSTOM.

▶ Bininda-Emonds ORP, Bryant HN (1998). Properties of matrix representation with parsimony analyses. *Systematic Biology* 47:497–508.

▶ Bloch JI (2001). New basicrania of Paleocene-Eocene *Ignacius*: re-evaluation of the plesiadapiform-dermopteran link. *American Journal of Physical Anthropology* 116: 184–198.

▶ Bloch JI, Boyer DM (2002). Grasping primate origins. *Science* 298: 1606–1610.

Blommers-Schlosser RMA, Blommers LHM (1984). The amphibians. In *Key Environments: Madagascar* (Jolly A, Oberle P, Albignac R, eds.), pp 89–104. Oxford, Pergamon Press.

Cartmill M (1975). Strepsirhine basicranial structures and the affinities of the Cheirogaleidae. In *Phylogeny of the Primates: A Multidisciplinary Approach* (Luckett WP, Szalay FS, eds.), pp 313–354. New York, Plenum.

Coffin MF, Rabinowitz PD (1987). Reconstruction of Madagascar and Africa: evidence from the Davie Fracture Zone and Western Somali Basin. *Journal of Geophysical Research* 92: 9385–9406.

▶ Cunningham CW, Omland KE, Oakley TH (1998). Reconstructing ancestral character states: a critical reappraisal. *Trends in Ecology and Evolution* 13: 361–366.

▶ De Wit M (2003). Madagascar: heads it's a continent, tails it's an island. *Annual Review of Earth and Planetary Science* 31: 213–248.

▶ Donoghue MJ, Doyle JA, Gauthier J, Kluge AG, Rowe T (1989). The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology and Systematics* 20: 431–460.

Eger JL, Mitchell L (1996). Biogeography of the bats of Madagascar. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 321–328. Paris, Editions de l'ORSTOM.

▶ Eizirik E, Murphy WJ, O'Brien SJ (2001). Molecular dating and biogeography of the early placental mammal radiation. *Journal of Heredity* 92: 212–219.

▶ Fisher BL (1997). Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae). *Journal of Natural History* 31: 269–302.

Fleagle JG (1999). *Primate Adaptation and Evolution*, ed 2. San Diego, Academic Press.

▶ Fleagle JG, Kay RF (1987). The phyletic position of the Parapithecidae. *Journal of Human Evolution* 16: 483–532.

▶ Gauthier J, Kluge AG, Rowe T (1988). Amniote phylogeny and the importance of fossils. *Cladistics* 4: 105–209.

▶ Gebo DL, Dagosto M, Beard KC, Qi T (2000). The smallest primates. *Journal of Human Evolution* 38: 585–594.

▶ Gingerich PD (1990). African dawn for primates. *Nature* 346: 411.

▶ Gingerich PD, Dashzeveg D, Russell DE (1991). Dentition and systematic relationships of *Altanius orlovi* (Mammalia, Primates) from the Early Eocene of Mongolia. *Geobios* 24: 637–646.

► Harris EE, Disotell TR (1998). Nuclear gene trees and the phylogenetic relationships of the mangabeys (Primates: Papionini). *Molecular Biology and Evolution* 15: 892–900.

Hay WW, DeConto RM, Wold CN, Wilson KM, Voigt S, Schulz M, Wold AR, Dullo WC, Ronov AB, Balukhovsky AN, Söding E (1999). Alternative global Cretaceous paleogeography. In *Evolution of the Cretaceous Ocean-Climate System* (Barrera E, Johnson CC, eds.), pp 1–47. Boulder, Special Papers of the Geological Society of America.

► Hedges SB, Parker PH, Sibley CG, Kumar S (1996). Continental breakup and the ordinal diversification of birds and mammals. *Nature* 381: 226–229.

Heesy CP, Stevens NJ, Samonds KE (2006). Biogeographic origins of primate higher taxa. In *Primate Biogeography* (Fleagle JG, Lehman S, eds.), pp 419–437. New York, Kluwer.

Horovitz I (1999). A phylogenetic study of living and fossil platyrrhines. *American Museum Novitates* 3269: 1–40.

► Horovitz I, MacPhee RDE (1999). The quaternary Cuban platyrrhine *Paralouatta varonai* and the origin of Antillean monkeys. *Journal of Human Evolution* 36: 33–68.

Horovitz I, Meyer A (1997). Evolutionary trends in the ecology of New World monkeys inferred from a combined phylogenetic analysis of nuclear, mitochondrial, and morphological data. In *Molecular Evolution and Adaptive Radiation* (Givnish TC, Sytsma KC, eds.), pp. 189–224. Cambridge, Cambridge University Press.

Humphries CJ, Parenti LR (1999). *Cladistic Biogeography: Interpreting Patterns of Plant and Animal Distributions*, ed 2. Oxford, Oxford University Press.

Jacobs LL (1980). Siwalik fossil tree shrews. In *Comparative Biology and Evolutionary Relationships of Tree Shrews* (Luckett WP, ed.), pp 205–216. New York, Plenum Press.

► Jaeger J-J, Thein T, Benammi M, Chaimanee Y, Soe AN, Lwin T, Tun T, Wai S, Ducrocq S (1999). A new primate from the middle Eocene of Myanmar and the Asian early origin of anthropoids. *Science* 286: 528–530.

► Jungers WL, Godfrey LR, Simons EL, Chatrath PS, Rakotosamimanana B (1991). Phylogenetic and functional affinities of *Babakotia* (Primates), a fossil lemur from northern Madagascar. *Proceedings of the National Academy of Sciences, USA* 88: 9082–9086.

► Kay RF, Johnson D, Meldrum DJ (1998). A new pitheciin primate from the middle Miocene of Argentina. *American Journal of Primatology* 45: 317–336.

► Kay RF, Ross C, Williams BA (1997). Anthropoid origins. *Science* 275: 797–804.

► Kay RF, Thewissen JGM, Yoder AD (1992). Cranial anatomy of *Ignacius graybullianus* and the affinities of the Plesiadapiformes. *American Journal of Physical Anthropology* 89: 477–498.

Koechlin J (1972). Flora and vegetation of Madagascar. In *Biogeography and Ecology in Madagascar* (Battistini R, Richard-Vindard G, eds.), pp 145–190. The Hague, Junk.

► Krause DW, Prasad GVR, von Koenigswald W, Sahni A, Grine FE (1997). Cosmopolitanism among Gondwanan Late Cretaceous mammals. *Nature* 390: 504–507.

Le Gros Clark WE, Thomas DP (1952). The Miocene lemuroids of East Africa. In *Fossil Mammals of Africa*, vol 5. London, British Museum of Natural History.

Leroy J-F (1996). Biogéographie: quelques grands faits relatifs à la flore angiospermienne malgache. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 59–71. Paris, Éditions de l'ORSTOM.

Le Thomas A, Doyle JA (1996). Geographic relationships of Malagasy Annonaceae. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 85–94. Paris, Éditions de l'ORSTOM.

Louette M (1996). Biogéographie, origine et évolution des oiseaux aux Comores. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 337–348. Paris, Éditions de l'ORSTOM.

Maddison DR, Maddison WP (2000). *MacClade 4: Analysis of Phylogeny and Character Evolution.* Version 4.0. Sunderland, Sinauer Associates.

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

► Martin RD (2000). Origins, diversity and relationships of lemurs. *International Journal of Primatology* 6: 1021–1049.

► Martin RD (2003). Combing the primate record. *Nature* 422: 388–391.

McCall RA (1997). Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. *Proceedings of the Royal Society of London, B* 364: 663–665.

► McKenna MC (1995). The mobile Indian raft: a reply to Rage and Jaeger. *Systematic Biology* 44: 265–271.

► Meve U, Liede S (2002). Floristic exchange between mainland Africa and Madagascar: case studies in Apocynaceae-Asclepiadoideae. *Journal of Biogeography* 29: 865–873.

► Murray AM (2001). The fossil record and biogeography of the Cichlidae (Actinopterygii: Labroidei). *Biological Journal of the Linnean Society* 74: 517–532.

Myers AA, Giller PS (1988). *Analytical Biogeography. An Integrated Approach to the Study of Animal and Plant Distributions.* London, Chapman & Hall.

Norejko J (1999). *Comparative Myology of Archontan Mammals*. MS thesis, State University of New York, Stony Brook.

Paulian R (1961). *La Zoogéographie de Madagascar et des Iles Voisines*. Antananarivo, L'Institut de Récherche Scientifique Tananarive-Tsimbazaza.

Perrier de la Bathie H (1936). *Biogéographie des Plantes de Madagascar*. Paris, Société d'Editions Géographiques, Maritimes et Coloniales.

Phillips AM, Walker A (2002). Fossil lorisoids. In *Fossil Primates* (Hartwig WC, ed.) pp. 83–95. Cambridge, Cambridge University Press.

Pianka ER (1994). *Evolutionary Ecology*. New York, HarperCollins College Publishers.

Pielou EC (1979). *Biogeography*. New Jersey, Wiley Interscience.

► Poux C, Madsen O, Marquard E, Vieites DR, de Jong WW, Vences M (2005). Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores and rodents as inferred by nuclear genes. *Systematic Biology* 54: 719–730.

► Purvis A (1995a). A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London* 348:405–421.

► Purvis A (1995b). A modification to Baum and Ragan's method for combining phylogenetic trees. *Systematic Biology* 44:251–255.

Purvis A, Webster AJ (1999). Phylogenetically independent comparisons and primate phylogeny. In *Comparative Primate Socioecology* (Lee PC, ed.), pp 44–70. New York, Cambridge University Press.

Racey PA, Stephenson PJ (1996). Reproductive and energetic differentiation of the Tenrecidae of Madagascar. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 307–319. Paris, Editions de l'ORSTOM.

► Ragan MA (1992). Phylogenetic inference based on matrix representation of trees. *Molecular Phylogenetic and Evolution* 1: 53–58.

Rage J-C (1996). Le peuplement animal de Madagascar: une composante venue de Laurasie est-elle envisageable? In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 27–35. Paris, Editions de l'ORSTOM.

► Raxworthy CJ, Nussbaum RA (1994). A rainforest survey of amphibians, reptiles and small mammals at Montagne D'Ambre, Madagascar. *Biological Conservation* 69: 65–73.

Raxworthy CJ, Nussbaum RA (1996a). Patterns of endemism for terrestrial vertebrates in eastern Madagascar. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 369–384. Paris, Editions de l'ORSTOM.

Raxworthy CJ, Nussbaum RA (1996b). Amphibians and reptiles of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: a study of elevational distribution and regional endemicity. *Fieldiana: Zoology* 85: 158–170.

Raxworthy CJ, Andreone F, Nussbaum RA, Rabibisoa N, Randriamahazo H (1998). Amphibians and reptiles of the Anjanaharibe-Sud Massif, Madagascar: elevational distribution and regional endemicity. *Fieldiana: Zoology* 90: 79–92.

► Raxworthy CJ, Forstner MRJ, Nussbaum RA (2002). Chameleon radiation by oceanic dispersal. *Nature* 415: 784–787.

► Roos C, Schmitz J, Zischler H (2004). Primate jumping genes elucidate strepsirrhine phylogeny. *Proceedings of the National Academy of Sciences, USA* 101: 10650–10654.

► Rose KD (1995a). The earliest primates. *Evolutionary Anthropology* 3:159–173.

► Rose KD (1995b). Anterior dentition and relationships of the early Eocene omomyids *Arapahovius advena* and *Teilhardina demissa*, sp. nov. *Journal of Human Evolution* 28: 231–244.

Rose KD, Godinot M, Bown TM (1994). The early radiation of Euprimates and the initial diversification of Omomyidae. In *Anthropoid Origins* (Fleagle JG, Kay RF, eds.), pp 1–28. New York, Plenum Press.

► Ross CF (2000). Into the light: the origin of Anthropoidea. *Annual Review of Anthropology* 29: 147–194.

► Ross C, Williams B, Kay RF (1998). Phylogenetic analysis of anthropoid relationships. *Journal of Human Evolution* 35: 221–306.

► Sampson SD, Witmer LM, Forster CA, Krause DW, O'Connor PM, Dodson P, Ravoavy F (1998). Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science* 280: 1048–1051.

► Sanderson MJ, Purvis A, Henze C (1998). Phylogenetic supertrees: assembling the trees of life. *Trends in Ecology and Evolution* 13: 105–109.

Schatz GE (1996). Malagasy/Indo-Australo-Malesian phytogeographic connections. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 73–83. Paris, Editions de l'ORSTOM.

► Seiffert ER, Simons EL, Attia Y (2003). Fossil evidence for an ancient divergence of lorises and galagos. *Nature* 422: 421–424.

▶Seiffert ER, Simons EL, Fleagle JG (2000). Anthropoid humeri from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences, USA* 97: 10062–10067.

▶Seiffert ER, Simons EL, Ryan TM, Attia Y (2005). Additional remains of *Wadilemur elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the National Academy of Sciences, USA* 102: 11396–11401.

▶Shoshani J, Groves CP, Simons EL, Gunnell GF (1996). Primate phylogeny: morphological vs molecular results. *Molecular Phylogenetics and Evolution* 5: 102–154.

Sigé B, Jaeger J-J, Sudre J, Vianey-Liaud M (1990). *Altiatlasius koulchii* n. gen. et sp., primate omomyidé du Paléocène supérieur du Maroc, et les origines des euprimates. *Palaeontographica A* 214: 31–56.

Silcox M (2002). The phylogeny and taxonomy of plesiadapiformes. *American Journal of Physical Anthropology* Suppl 34:141–142.

Simpson GG (1940). Mammals and land bridges. *Journal of the Washington Academy of Sciences* 30: 137–163.

Simpson GG (1965). *The Geography of Evolution*. New York, Capricorn Books.

Stevens NJ, Heesy CP (2000). Biogeographic origins of primate higher taxa. *Journal of Vertebrate Paleontology* 20(suppl 3): 71A.

▶Stewart C-B, Disotell TR (1998). Primate evolution – in and out of Africa. *Current Biology* 8: R582–R588.

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

▶Strait DS, Wood BA (1999). Early hominid biogeography. *Proceedings of the National Academy of Sciences, USA* 96: 9196–9200.

Szalay FS, Katz CC (1973). Phylogeny of lemurs, galagos, and lorises. *Folia Primatologica* 19: 88–103.

Tattersall I (1982). *The Primates of Madagascar*. New York, Columbia University Press.

Tattersall I, Schwartz J (1974). Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). *Anthropological Papers of the American Museum of Natural History* 52: 139–192.

▶Tavaré S, Marshall CR, Will O, Soligo C, Martin RD (2002). Using the fossil record to estimate the age of the last common ancestor of extant primates. *Nature* 416: 726–729.

▶Thewissen JGM, McKenna MC (1992). Paleobiogeography of Indo-Pakistan: a response to Briggs, Patterson, and Owen. *Systematic Biology* 41: 248–251.

▶Vences M, Freyhof J, Sonnenberg R, Kosuch J, Veith M (2001). Reconciling fossils and molecules: Cenozoic divergence of cichlid fishes and the biogeography of Madagascar. *Journal of Biogeography* 28: 1091–1099.

▶Vences M, Kosuch J, Rodel M-O, Lotters S, Channing A, Glaw F, Bohme W (2004). Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. *Journal of Biogeography* 31: 593–601.

Wallace AR (1876). *The Geographical Distribution of Animals: With a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface*. London, MacMillan & Co.

Warren RD, Crompton RH (1996). Lazy leapers: energetics, phylogenetic inertia and the locomotor differentiation of the Malagasy primates. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 259–266. Paris, Editions de l'ORSTOM.

Wilmé L (1996). Composition and characteristics of bird communities in Madagascar. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 349–362. Paris, Editions de l'ORSTOM.

▶Yoder AD (1996a). Back to the future: a synthesis of strepsirhine systematics. *Evolutionary Anthropology*, 6: 11–22.

Yoder AD (1996b). The use of phylogeny for reconstructing lemuriform biogeography. In *Biogéographie de Madagascar* (Lourenço WR, ed.), pp 245–258. Paris, Editions de l'ORSTOM.

▶Yoder AD, Yang Z (2004). Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Molecular Ecology* 13: 757–773.

▶Yoder AD, Burns MM, Zehr S, Delefosse T, Veron G, Goodman SM, Flynn JJ (2003). Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421: 734–737.

▶Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R (1996). Ancient single origin for Malagasy primates. *Proceedings of the National Academy of Sciences, USA* 93: 5122–5126.