Has Vicariance or Dispersal Been the Predominant Biogeographic Force in Madagascar? Only Time Will Tell

Anne D. Yoder and Michael D. Nowak

Department of Biology, Duke University, Durham, North Carolina 27708;
email: anne.yoder@duke.edu, mdn3@duke.edu

Key Words

Abstract

Madagascar is one of the world's hottest biodiversity hot spots due to its diverse, endemic, and highly threatened biota. This biota shows a distinct signature of evolution in isolation, both in the high levels of diversity within lineages and in the imbalance of lineages that are represented. For example, chameleon diversity is the highest of any place on Earth, yet there are no salamanders. These biotic enigmas have inspired centuries of speculation relating to the mechanisms by which Madagascar's biota came to reside there. The two most probable causal factors are Gondwanan vicariance and/or Cenozoic dispersal. By reviewing a comprehensive sample of phylogenetic studies of Malagasy biota, we find that the predominant pattern is one of sister group relationships to African taxa. For those studies that include divergence time analysis, we find an overwhelming indication of Cenozoic origins for most Malagasy clades. We conclude that most of the present-day biota of Madagascar is comprised of the descendents of Cenozoic dispersers, predominantly with African origins.

THE KEY TO GONDWANA

To have an interest in the historical biogeography of Madagascar necessitates a thorough understanding of the origins and gradual sundering of Gondwana. When the supercontinent Pangea began to divide into the southern continental landmasses (Gondwana) and northern continental landmasses (Laurasia), approximately 175 Ma, Madagascar was tucked away, deep within Gondwana (Rakotosolofo et al. 1999, Reeves et al. 2002). Very shortly after the division of the southern and northern components of Pangea, Madagascar began the long journey to its current state of remote isolation in the Indian Ocean. Presently, Madagascar is surrounded by a vast oceanic barrier on all sides. It is closest to continental Africa, approximately 400 km to the west, but lies 4000 km from India, 5000 km from Antarctica, and 6000 km from Australia. It is therefore remarkable to consider that each of these landmasses was at one time contiguous with Madagascar. As a consequence of these deep geological relationships, the island's foundations are comprised of ancient continental crust, some of which can be traced back to more than 3200 million Ma (de Wit 2003). Thus, although Madagascar's roughly three-quarter-million km² (about the size of Texas) comprises less than 0.4% of Earth's land surface area, it has existed as an essential constituent of the reconfiguration of the Southern Hemisphere for the past 165 million years.

Initially, Gondwana was a single contiguous supercontinent comprised of what would become Africa, South America, Antarctica, Australia, India, and Madagascar (Figure 1a). Shortly after separating from Laurasia (Figure 1b), rifting between western Gondwana (Africa plus South America) and eastern Gondwana (Madagascar plus India, Antarctica, and Australia) commenced (Briggs 2003) as evidenced by the vast outpourings of the Karoo volcanics (182 ± 1 Ma) (de Wit 2003). From that point, Madagascar and the rest of eastern Gondwana began to drift southward relative to Africa, sliding along the strike-slip fault known as the Davie Ridge (Bassias 1992, Reeves & de Wit 2000). There is a general consensus among geologists that this occurred sometime between 165 and 155 Ma (Agrawal et al. 1992, Briggs 2003, Rabinowitz et al. 1983, Reeves & de Wit 2000, Reeves et al. 2002, Scotese 2000). By 140 Ma (Seward et al. 2004), marine conditions are clearly prevalent along the entirety of Madagascar's west coast. Thus, although separation from Africa began as early as 165 Ma, there was a subsequent period of perhaps 20 million years wherein biotic exchange would have been likely between western and eastern Gondwana. Madagascar reached its current position with respect to Africa by 130–118 Ma (Harland et al. 1990, Rabinowitz et al. 1983, Seward et al. 2004). Although shifts in latitude and relationships to other landmasses remained dynamic for many millions of years subsequent to this positioning, it is certain that Madagascar's present geographic isolation relative to
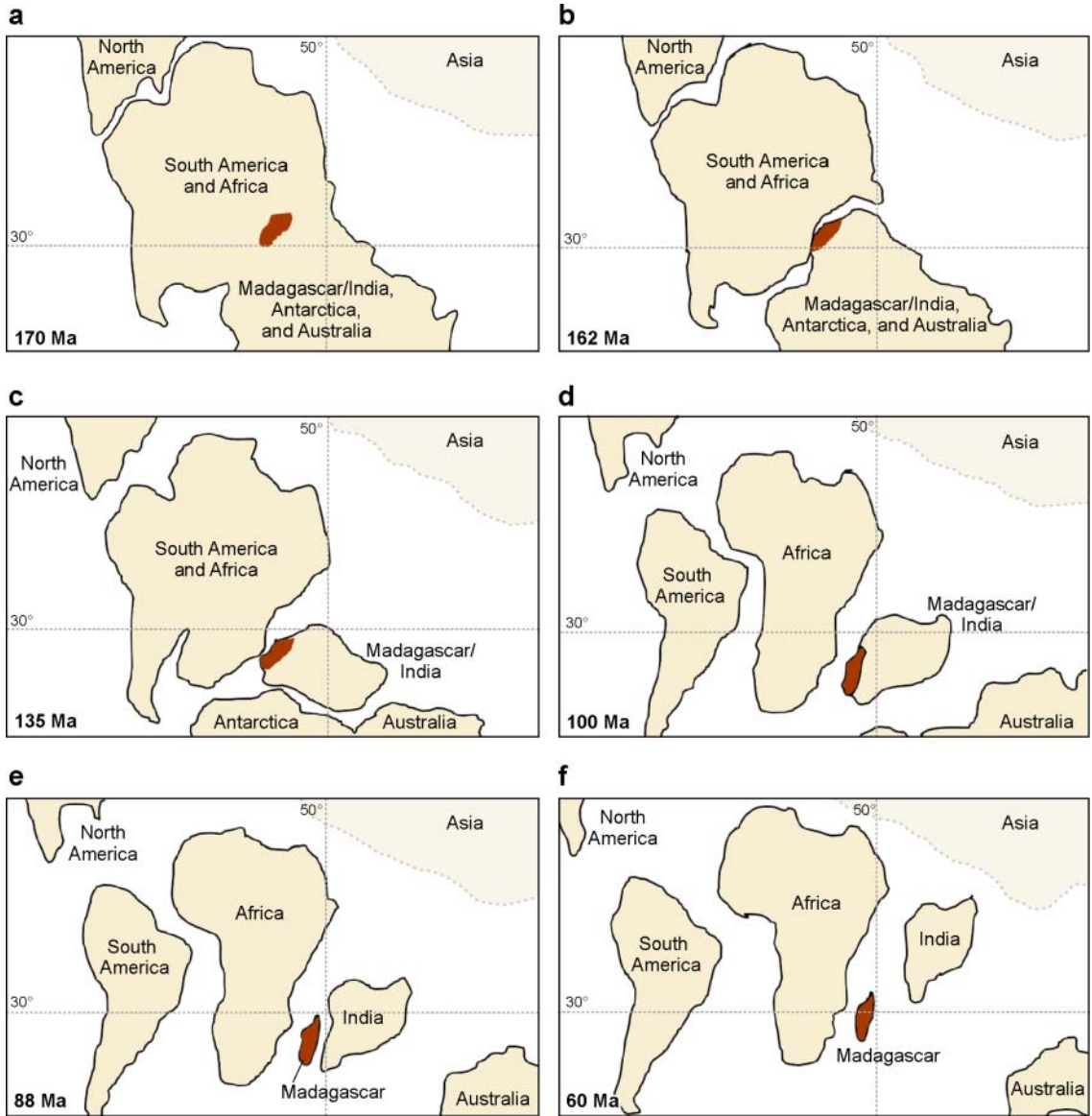
Figure 1

Paleoreconstructions of the breakup of Pangea, and Madagascar's subsequent geographic isolation. Redrawn from (Scotese 2000).

Africa has been stable for at least 118 million years, and probably, considerably longer. Moreover, the Mozambique Channel, separating Madagascar and Africa, is quite deep (3000 m, at the deepest point) and would not have been notably affected by changing sea levels after Madagascar's and Africa's final separation (Krause et al. 1997a).

From this point onward, Madagascar and India remained in close contact, forming the IndoMadagascar subcontinent (Figures 1c & 1d), until the commencement of the northeasterly drift of the Seychelles-Indian block away from Madagascar's eastern margin (Figure 1e). The precise timing of India's separation from Madagascar has been variably dated from 100–95 Ma (Plummer 1996), to 97.6–80.3 Ma (Valsangkar et al. 1981), to 91.2 ± 0.2 Ma (Torsvik et al. 2000), to $87.6 + 0.6$ Ma (Storey et al. 1995). Consensus is emerging, however, that the time of the breakup was correlated with the position of Madagascar over the Marion hot spot. Storey et al. (1995) estimate that the southern tip of Madagascar's east coast was directly over the hot spot by 88 Ma, and it is this date that is most frequently cited in the literature, referencing the final separation of Madagascar and India. This appears to be supported by paleomagnetic data that indicate that the hot spot was beneath Madagascar's central east coast at 118 Ma, and at the south of Madagascar at 88 Ma (Torsvik et al. 1998). Thus, if the timing and position of the hot spot relates to the timing and direction of drifting, then the separation between Madagascar and India may well have occurred over a 30-million-year period, perhaps beginning in the north of Madagascar and progressing to the south (Seward et al. 2004). This is analogous to the model of Madagascar's separation from Africa in that it should be viewed as a prolonged and progressive process, rather than as a sudden event. Clearly, this distinction could potentially have enormous implications for the timing and capacity for biotic exchange between Madagascar and the other key parts of Gondwana. As added complexity, whereas most authorities reconstruct India's position as quite isolated, as it moved northward toward its ultimate collision with Asia in the earliest Eocene (Beck et al. 1995, Zhu et al. 2005) (Figure 1f), others argue that India's lack of a significantly endemic biota indicate that it must have remained within close proximity to other landmasses during its journey (Briggs 1989, 2003).

The discussion above has ignored the relative positions and movements of Antarctica and Australia. For the most part, geologists have concluded that Antarctica and Australia began their southward movement away from IndoMadagascar soon after the final separation of the latter from Africa (Briggs 2003), thus implying that terrestrial biotic exchange between these two continents and the remainder of Gondwana would have been impossible after 130 to 125 Ma. Recently, however, numerous investigators are modifying this view. Discovery and analysis of vertebrate fossils from the latest Cretaceous of Madagascar, India, and South America indicate a significant degree of cosmopolitanism among southern Gondwanan biota that can best be explained via terrestrial connections among these landmasses well into the Late Cretaceous. This suggests a subaerial contact between Antarctica and South America in the west, and between Antarctica and IndoMadagascar in the east, apparently existing until circa 80 Ma (Buckley & Brochu 1999; Buckley et al. 2000; Hay et al. 1999; Krause et al. 1997a,b; Sampson et al. 1998, 2001). Two such contacts have been suggested as potential routes for biotic exchange between Madagascar and South America, via Antarctica: the Kerguelen Plateau (KP) and the Gunnerus Ridge (GR) (Figure 2).
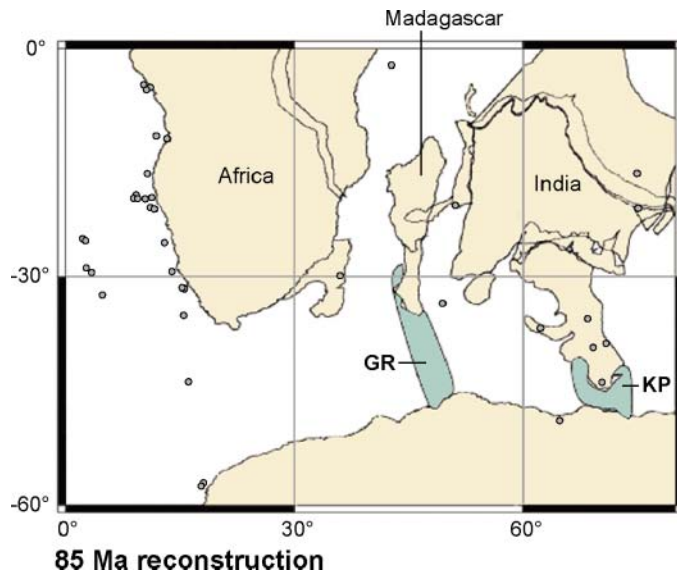
The implication of this biogeographic scenario is surprising because it suggests that the most recent vicariant events between Madagascar and other parts of Gondwana would be with South America, rather than with India, as more established views would have it. Finally, a minority view has argued that Madagascar actually served as a "cul-desac" within southern Gondwana for certain groups such as lemuriform primates, boine snakes, and iguanid lizards that would have arrived there from Laurasia via the Indian subcontinent (Rage 1996, Rage & Jaeger 1995). In this scenario, a terrestrial route existed from Asia to Madagascar via India and the Seychelles Plateau. According to its authors, the "northern hypothesis" need not be incompatible with the aforementioned "southern hypothesis," and indeed, may have been established after the disintegration of the KP and GR (Rage 2003).

Unraveling the historical biogeography of the Malagasy biota necessitates an analysis of many complex factors. The geographic/tectonic position of Madagascar through time must have had a dramatic influence on the past climate and biota on the island. Madagascar's current heterogeneous landscape and climatic profile contain a wealth of information on the historical influences of past climate and the evolution of the island's principle biomes. Although previous vegetation classifications have resulted in much more complex systems, reviewing these in detail is outside of the scope of this review. For this review three biome classifications that emphasize vegetation trends, topography, and climate (Du Puy & Moat 1996, Faramalala 1995, Lowry et al. 1997) are integrated in the classification of Madagascar's six principle biomes (Figure 3).

The current climatological landscape of Madagascar exhibits a remarkable east-west trend in precipitation, which is primarily the result of the orographic effect of the island's eastern mountain range. An evergreen lowland rainforest biome covers the east coast of the island and extends about 100 km inland up the eastern mountains. At
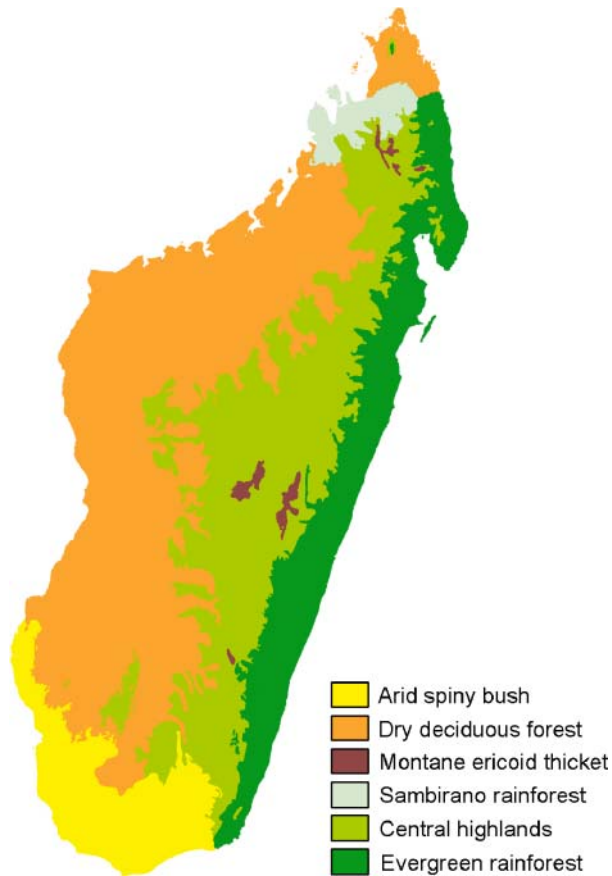
Figure 3

Illustration of biome distributions in Madagascar.

elevations above 800 m and extending well into the island's interior, the rainforest gives way to central highlands, which are dominated by moist montane forest. At higher elevations (i.e., above 2000 m) the central highlands give way to a high elevation thicket dominated by ericoid (Ericaceae) shrubs. On the western half of the island, below 800 m elevation, montane forest shifts to dry deciduous forest dominated by sclerophyllous trees and shrubs. Deforestation and agricultural grazing have heavily impacted both the western dry deciduous forest and the central highlands, and thus very little primary vegetation remains. These regions are now covered in secondary grasslands and are subject to frequent burning. The southwest extent of the dry deciduous forest becomes extremely arid as the influence of the 30-degree latitude subtropical arid belt becomes more pronounced. This region is called the "spiny bush" because of the floral dominance of the near-endemic angiosperm family Didieriaceae. In the extreme northwest, a region of the dry deciduous forest receives heavy seasonal rainfall from Indian monsoonal circulation. This seasonal influx of precipitation has

produced a rainforest biome known as the Sambirano, which is geographically and biologically distinct from the eastern rainforest.

Such ecological heterogeneity within a limited land area begs questions about the sequence of geological and biological events that led to the assembly of these biomes. Most biologists agree that these are important questions, but few have ventured hypotheses. Wells (2003) provides the most detailed model for biome evolution to date. His approach relies heavily on paleogeographic reconstructions and paleoclimatic models, and has broad implications for the biogeographic history of Madagascar and the Southern Hemisphere as a whole. His contribution is of particular importance because it provides distinct hypotheses that can be tested with both geological and biological data. The hypothesis maintains that after Madagascar and India separated at 88 Ma, Madagascar lay within the 30-degree latitude subtropical arid belt and likely experienced a generally dry climate. India probably blocked any easterly influence of moisture from the Proto-Indian Ocean until about the Middle Eocene. In the Late Paleocene/Early Eocene, Madagascar (and Africa) drifted north toward the equator leaving the influence of the 30-degree latitude subtropical arid belt. This led to a significant increase in moisture from the north to the south and was amplified by the clearing of the Indian Ocean such that southeasterly trade winds were hitting the mountains of the Madagascar east coast, thus initiating the orographic precipitation that the eastern rainforest of Madagascar currently experiences. Through the remainder of the Cenozoic, Madagascar was tectonically and climatically rather stable. The last major climatic event to impact the Malagasy biota was the initiation of the Indian monsoons in the Late Miocene (∼8 Ma), perhaps coincident with the rise of the Tibetan Plateau (Rowley & Currie 2006). This then would have been the onset of heavy seasonal rains to the northwestern Sambirano region.

This explicit hypothesis of paleoclimatic history has important implications for the ages of Madagascar's principle biomes. It implies that the arid to seasonally dry biomes are much older than the humid and subhumid biomes. Wells (2003) interpretation is that the dominant biota in Madagascar in the Late Cretaceous and through the Paleocene was similar to the southern arid spiny bush. He envisions the effect of the island's northern drift in the Eocene as constricting the range of the arid spiny bush biome to the absolute south and southwest. Wells (2003) further suggests that current levels of endemism reflect the relative ages of biomes. Assuming that biome endemism is correlated with time, the biomes do show a striking concordance with this model of paleoenvironmental history. It remains for divergence time estimation of the endemic radiations contained within these discrete biomes to serve as an initial test of this complex model of biome evolution.

THE NATURALIST'S PROMISED LAND

It is not from mere curiosity that geologists, biogeographers, and biologists have developed a fascination for Madagascar. Rather, the island presents itself to even the most casual observer as a place of biological wonder. This impression is probably best captured in a quote from the eighteenth-century French naturalist, Philibert Commerson (Teissier 1859):

> May I announce to you that Madagascar is the naturalist's promised land? Nature seems to have retreated there into a private sanctuary, where she could work on different models from any she has used elsewhere. There you meet bizarre and marvelous forms at every step . . . .

Recent biogeographers have focused more precisely on tabulating the species numbers, phylogenetic diversity, and levels of endemism of Madagascar's biota, finding that the patterns are truly astonishing. For example, 95% of the reptile species, 99% of amphibian species, and 100% of the island's land mammal species (excluding bats) occur nowhere else on Earth. Certain faunas are either poorly represented (e.g., only four orders of terrestrial eutherians are currently represented) or are completely absent (e.g., there are no salamanders, vipers, or varanid lizards), whereas other groups show unrivaled diversity (e.g., chameleons). Of the estimated 12,000 plant species, nearly 10,000 are unique to Madagascar. Moreover, within these endemic groups, the numbers of species can be spectacular. For example, there are at least 50 species of extant primates (suborder Lemuriformes), and when one also includes the more than 16 species of recently extinct subfossil lemurs, the numbers are even more impressive for an island fauna. For perspective, this means that >15% of living primate species are endemic to Madagascar, an island that comprises less than 0.4% of Earth's land surface area. Lizards show even greater levels of diversity, with 346 known species, 314 of which are endemic. As with many of the resident biotic groups, the herpetofauna are as remarkable for what is absent compared to Africa, and to a lesser extent, regions of the western Indian Ocean, as it is for the diversity that is present (Raxworthy 2003). For example, caecilians (Gymnophiones) occur on virtually every southern continent including South America, Africa, India, and even the Seychelles, but not on Madagascar. Worldwide, there are approximately 28 families of frogs, but apparently only 3 of these occur in Madagascar. Within these three families, however, there are more than 300 endemic species, representing nearly 4% of the world's amphibian fauna (Glaw & Vences 2003). This high diversity is even more remarkable given that of the 3 living amphibian clades, only the Anura are represented. Krause (1997a) has succinctly summarized this pattern of spectacular diversity within sporadic phylogenetic lineages as Madagascar's unique signature of "imbalance and endemism."

This pattern of imbalance, endemism, and diversity begs an obvious question: What force or forces have created the pattern? To many, the fact that diversity levels are so high suggest that many groups must have had very long histories in Madagascar, thereby allowing many millions of years for speciation and diversification. Gillespie & Roderick (2002), in an analysis of terrestrial arthropod distributions, distinguish two types of island systems: "Darwinian" islands and "fragment" islands. In the former case, the island will never have been in contact with other biotic reservoirs and is presumed to have an abundant supply of empty ecological niches. On these islands, species numbers will increase at first via colonization, which, over time, will be followed by the formation of neoendemics. According to this model, if isolation persists for vast periods of geological time, the ecological space will eventually be filled via speciation rather than immigration. In the case of fragment islands, Gillespie & Roderick posit that the ecological space will initially be filled due to contact with other

landmasses, but that niches will open up as the fragment island becomes more isolated in a process that they call "relaxation." From this point, speciation among the initial residents will then create paleoendemics that over protracted time periods can result in high levels of endemism. Gillespie & Roderick (2002) place Madagascar squarely within the latter category. In looking at the data, and the patterns of vicariance and dispersal contained therein, we will argue that Madagascar does not comfortably fit into either category but instead shows patterns of neo-endemism that are as strong, if not considerably stronger, than patterns of paleoendemism.

HYPOTHESIS TESTING

Vicariance Versus Dispersal

The sundering of Gondwana over the past 165 million years or so has been a dynamical process. Madagascar's geographic position has been marked by temporal windows wherein biotic exchange would have been facilitated by contact with other landmasses, followed by a long period of progressive geographic isolation. Moreover, the timing and sequence of fragmentation and isolation may at times have been slowly progressive (e.g., Madagascar's long slide south, relative to Africa), or relatively abrupt (e.g., the hypothesized severing of southern connections via Antarctica). Finally, even the most recent conceivable connection to other landmasses via the Kerguelen Plateau at 80 Ma was at best contemporaneous with the temporal origins of major extant clades (e.g., placental mammals), though considerably more ancient than many of the subclades presently extant in Madagascar (e.g., feliform carnivorans). Thus, the present day biota of Madagascar must of necessity be comprised of groups whose presence is best explained by ancient vicariant events, as well as other groups that reached Madagascar via transoceanic dispersal. The challenge for biogeographers, therefore, is to distinguish between these two possibilities.

Prior to modern understanding of continental movements, the default explanation for the presence of biota in remote localities was "oceanic dispersal" (Nelson 1979). The validation of plate tectonics, however, yielded a sea change in the perception of dispersal hypotheses (Wiley 1988). Many researchers began to label dispersal hypotheses as bordering on the "miraculous" (Platnick 1981) or as "pseudoexplanations" (Croizat et al. 1974). Indeed, as de Queiroz (2005) so aptly states the case, biogeographers became "positively contemptuous" of dispersal scenarios. The tide has turned again, however. Numerous studies published within the past few years reveal case after case wherein biotic distributions can only be explained via hypotheses of dispersal (Cook & Crisp 2005, de Queiroz 2005, McDowall 2004, McGlone 2005). Thus, we have reached a state of the art wherein the majority of biogeographers are equally receptive to hypotheses of vicariance and dispersal. The essential question remains, however, of how to distinguish between the two, and with satisfactory degrees of confidence. Area cladograms have typically been employed for demonstrating vicariant distributions. If the phylogenetic history of an organismal group is congruent with the known sequence of vicariant events, then a vicariance scenario is supported (e.g., see Sparks & Smith 2005, Figure 3). Conversely, when phylogenies

reveal lineages from one geographic area deeply nested within clades from another area, dispersal is typically inferred. More recently, temporal information has played a critical evidential role in supporting dispersal hypotheses (e.g., Poux et al. 2005, Yoder et al. 2003).

The assertion that temporal data are necessary for discriminating between vicariance and dispersal hypotheses makes an implicit assumption that divergence ages can be estimated with high degrees of confidence. Unfortunately, the fossil record of Madagascar places a severe handicap on temporal analysis of the Malagasy biota. Most notably, for the Tertiary of Madagascar, terrestrial fossil exposures are virtually nonexistent (Flynn & Wyss 2003, Krause 2003). Although it is true that phylogenetic and coalescent methods for estimating clade ages are growing increasingly sophisticated, they are by no means infallible (Drummond et al. 2006, Kishino et al. 2001, Thorne & Kishino 2002, Thorne et al. 1998, Yang & Rannala 2006), and indeed, should be viewed as rather gross approximations. Nonetheless, if we make the assumption that divergence times can be calculated with confidence, hypothesis discrimination becomes rather tractable. One "only" needs a complete geographic sampling for the clade of interest, a handsome amount of DNA sequence data for both the ingroup and outgroup taxa, and reliable temporal calibrations (e.g., fossils) on several nodes within the phylogeny. But what if an investigator is more ambitious, and actually wants to test for patterns of vicariance and dispersal across an entire biota, such as that of Madagascar? The task becomes daunting.

Not only does one need all of the information described above, one wants it for a global sample encompassing the multitude of taxa that compose a biota, from plants, to invertebrates, to vertebrates. And finally, how does one visualize the summation of so much information and in such a way as to discriminate among the alternate biogeographic hypotheses? Figure 4 makes a first pass at visualizing a very simple null distribution of clade ages for both vicariant and dispersed biota in Madagascar. Here, we model the plants, invertebrates, and vertebrates separately, but visually compare their respective clade ages with respect to their fit to a hypothesized vicariant event. The plants are illustrated in green and are modeled such that 40% of clade ages are compatible with an 80 Ma vicariant event, leaving 60% as hypothesized transoceanic dispersers. The invertebrates are shown in blue, with 60% of clades compatible with an 80 Ma vicariance, and 40% as transoceanic dispersers. Finally, 20% of the vertebrates, illustrated in red, are modeled as vicariants, with 80% as dispersers. We modeled the vicariants to fit a gamma distribution with a shape parameter of two and a scale parameter of seven, and with a zero offset of 75 Ma. This accommodates the assumption that the steep, though not abrupt, left tail of the distribution (corresponding to more recent ages in the distribution) best models the progressive drift of two landmasses over time. Clearly, even in the most abrupt geological timescales, there is considerable time for "filter" dispersal across an ever-widening oceanic barrier. We make no claim that this model actually fits the distribution of clade ages for the biota of Madagascar. Rather, we present this figure as a means for potentially visualizing the distribution of clade ages in such a way as to test for patterns of vicariance versus dispersal in different biotic groups. It will require actual dated phylogenies of Malagasy biota to determine the fit of the data to this potential model.
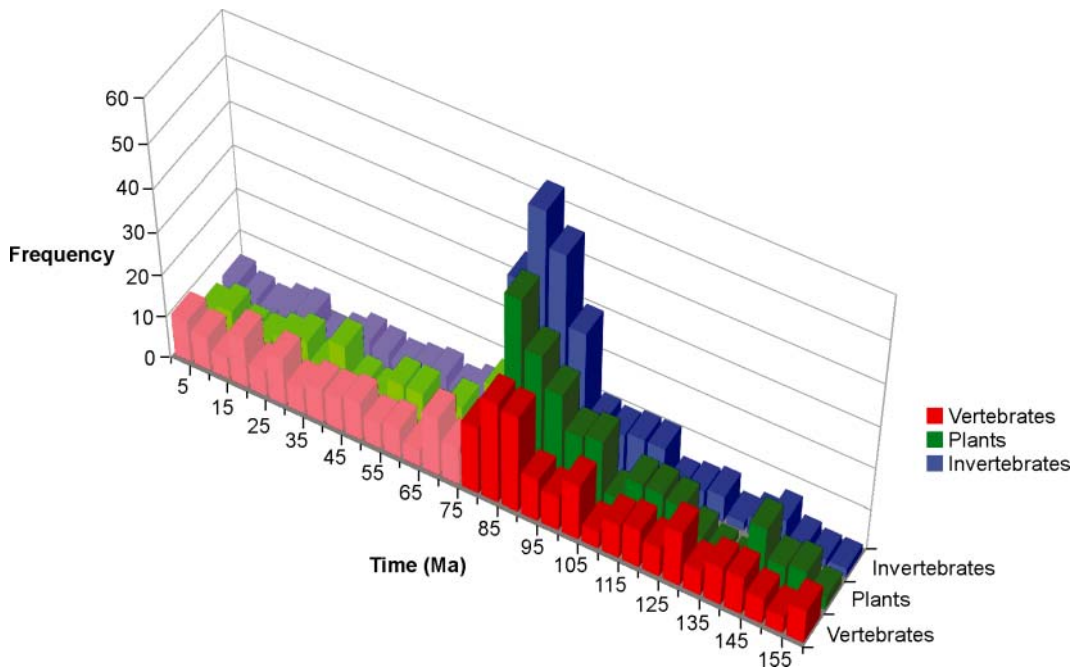
Figure 4

Hypothetical model of divergence dates for plants (*green*), invertebrates (*blue*), and vertebrates (*red*). The 80 Ma mark indicates the most recent plausible vicariance event for Malagasy biota.

THE DATA

The stage is now set for a careful examination of the data. Will the examination of the fossil data (such as they are) and the existing phylogenetic data allow us to distinguish the relative importance that vicariance and transoceanic dispersal have played in generating the biotic communities that presently exist in Madagascar? We believe so, despite the paucity of both data sources. As the sections below on plants, invertebrates, and vertebrates will illustrate, the number of phylogenetic studies devoted largely or strictly to Malagasy biota are few relative to the enormous number of taxa and evolutionary lineages present on the island. Even so, a clear indication emerges.

Phylogenetic Studies—Plants

The Malagasy flora is one of the most distinctive in the world. The most recent estimates of floral endemism are well above 90% at the species level (Goodman & Benstead 2005, Schatz 2000). It is widely agreed that both the vicariance resulting from the breakup of Gondwana and the action of long-distance dispersal were important mechanisms in forming the current levels of Malagasy floral endemism, but there is considerable contention regarding the relative importance of these two mechanisms. The dominant trend among botanists has been to emphasize the influence of Gondwanan vicariance (Grubb 2003, Leroy 1978).

Schatz (1996) was the first to put an emphasis on long-distance dispersal as a mechanism of origin for many elements of the Malagasy flora. He considered the Malagasy flora to be strongly influenced by dispersal from the Australian, Indian, and Southeast Asian floras. Schatz suggests that prevailing easterly winds across the Indian Ocean have fostered a condition in which continuous long-distance dispersal from these regions has been occurring since at least the Early Tertiary. If vicariance is the predominant mechanism underlying the biogeographic history of the Malagasy flora, the evolutionary signature of this vicariance should be significant in our review of phylogenetic studies. Instead, we could find no single phylogenetic study of plants with sufficiently old divergence time estimates (i.e., >80 Ma) to validate hypotheses of Gondwanan vicariance. This result is not surprising in light of the several divergence time analyses suggesting that the majority of angiosperm families with Malagasy elements are relatively young (Anderson et al. 2005, Bremer et al. 2004, Davis et al. 2005, Janssen & Bremer 2004). This is not to say that these vicariant patterns do not exist, but rather they may be relatively rare or expressed at deep taxonomic scales (e.g., familial or ordinal levels).

The most promising groups suggesting a signature of vicariance are those that molecular data place on long branches sister to large, disparate clades. Although none of these groups have been the focus of a detailed analysis of divergence times, they have been largely hypothesized to be relicts that have avoided extinction in the Malagasy flora (Schatz 1996). A few examples include *Takhtajania* (sister to all Winteraceae), *Didymeles* (sister to all Buxales), and *Humbertia* (sister to all Convolvulaceae). Many of the endemic Malagasy families (Didieriaceae, Sarcolaenaceae, Spherosepalaceae, Asteropeiaceae, and Physenaceae) have considerable diversity in Madagascar, and are likely the products either of vicariance or a single, ancient dispersal event. There is evidence for larger fossil distributions for some of these hypothesized relicts. For example, *Didymeles* pollen has been found in Paleocene sediments of Australia and New Zealand, and Sarcolaenaceae pollen has been found in Miocene sediments of South Africa (Schatz 2001). It is unknown whether these fossils represent extinct sister clades or the original home ranges of these groups.

Our review of the literature (Supplemental Table 1, follow the Supplemental Material link from the Annual Reviews home page at http://www.annualreviews.org/) suggests that despite the promise of detecting the signature of vicariance from a very few elements, the importance of dispersal to the assembly of the Malagasy flora cannot be denied. Furthermore, Africa appears by far to be the most important source of floral dispersal to Madagascar. Future divergence time estimates will clarify both the reality of a vicariant signature and the relative antiquity of the Malagasy flora.

Phylogenetic Studies: Invertebrates

Relative to the extraordinary diversity of invertebrates in Madagascar, there is a dearth of phylogenetic studies of these organisms, and for those that have been conducted, virtually all have focused on the insects. No doubt, this deficiency relates to the fact that invertebrate biologists are only beginning to scratch the surface in simply documenting and describing the biota. There are numerous higher-level taxa that are

assumed to be relicts of ancient, pre-Jurassic Gondwanan vicariance, such as crayfish, notonemourine stoneflies, scarabaeine beetles, dipterans, aphids, and araneids (Paulian & Viette 2003), though virtually none of these groups have been subjected to phylogenetic analysis, much less divergence age analysis.

For relatively well-studied groups, such as the ants, hypotheses regarding biogeographic origins can be posed based simply on the distribution of related taxa. In the case of the ants, studies show a much greater affinity of Malagasy taxa to Afrotropical taxa, rather than to Indoasian groups (Fisher 1997, 2003). But with poorly studied groups, even modest phylogenetic analysis can reveal remarkable insights. Based on a study that included a single undescribed Malagasy species in the spider genus *Anelosimus*, investigators found that this species could be grouped within a clade of New World social species. This result provoked an expedition to Madagascar, which then revealed at least five additional periodic species from the initial species locality. When analyzed phylogenetically, the investigators found the Malagasy species to constitute a clade with a sister group relationship to a combined East African plus Americas clade (Agnarsson & Kuntner 2005).

Some studies have posited an explicit hypothesis of vicariant origins, such as a global distribution analysis of the Forficulina (Dermaptera) (Popham 2000). Though not phylogenetic in methodology, the Popham examines their distribution patterns and concludes that their center of origin was Gondwana, in the area that is now northeast Brazil and northwest Africa. From there, these insects are hypothesized to have spread both westward (into the Americas) and eastward to IndoMadagascar. The study also concludes that with the impact of India and Asia, a second center of origin was established for Asia. Presumably, therefore, the presence of the Forficulina in Madagascar represents a classic radiation of paleoendemics. Certainly, this appears reasonable based on distribution analysis but requires phylogenetic study and divergence age estimation for verification.

The most complex biogeographic histories among the invertebrates relate to the butterflies, given our current understanding of Malagasy invertebrate history. In the case of both the swallowtail butterflies (Zakharov et al. 2004) and the satyrine butterflies (Torres et al. 2001), a complex mix of vicariance history and dispersal seems necessary to explain their distribution in Madagascar and other parts of the Old World. In both cases, the researchers have evoked scenarios of Cretaceous vicariance, followed by endemic species radiation within Madagascar and subsequent dispersal from Madagascar to other areas. Certainly, the phylogenies show a strong tendency toward speciation within Madagascar with dispersal radiation from within. Unfortunately, neither study has explicitly addressed the geological timing for these events. The alternatives are that the ancestral Malagasy butterflies were present owing to vicariance, though as we know, this would imply that they existed in Madagascar at least 80 Ma, if not considerably earlier. Either way, it is clear that the subsequent dispersals out of Madagascar occurred sporadically over time, and almost certainly during the Cenozoic, at which time overwater dispersal would have been necessary.

Other invertebrate studies invoking dispersal include a study of the small minnow mayflies (Monaghan et al. 2005) and of fig wasps (Kerdelhue et al. 1999). As with the butterflies, the study of the mayflies also concludes that transoceanic dispersal

between Madagascar and other landmasses occurred multiple times, though the timing of these events is presently obscure. Similarly, the fig wasp study posits long-distance dispersal, though in this case, it appears that dispersal occurred only once, and from Africa to Madagascar. All of these studies inferred dispersal from phylogeny and biogeography alone, given that divergence age estimation has not been an integral part of the investigation. A refreshing example of biogeographic, phylogenetic, and divergence age analysis, however, can be found in a recent study of the allodapine bee genus *Braunsapis* (Fuller et al. 2005). The results are striking and decisive in inferring two transoceanic dispersals, both of which occurred from Africa to Madagascar and within the relatively recent geological past. One is inferred to have occurred 13 Ma, and another much more recently at approximately 3 Ma. Here, it is worth noting that the divergence age estimates are sufficiently distinct that even though estimation errors are possible (if not probable), the relative difference between the two age estimates obviates the possibility that they could have occurred via a single event.

Phylogenetic Studies: Vertebrates

Fishes. Of all the vertebrate taxa to be considered herein, the cichlid fishes of Madagascar represent the most challenging puzzle for differentiating vicariance from dispersal. Despite previous claims that Madagascar's ichthyofauna is notably species poor (Kiener & Richard-Vindard 1972), recent intensive surveys show it to support the expected number of species given the island's land surface area (Sparks & Stiassny 2003). But, despite the abundance of species that potentially offer clues relating to biogeographic history, very few species groups have been the subject of phylogenetic investigation (Sparks & Stiassny 2003). Moreover, of the 14 living groups of freshwater fishes in Madagascar, only one (Ariidae, catfish) is potentially represented in the Cretaceous fossil record (Gottfried et al. 1998). This seems to mirror the pattern for other vertebrates, wherein it appears that there has been a near complete faunal turnover for Malagasy vertebrates, potentially demarcated by the K/T boundary (Krause 2003; Krause et al. 1997a, 1999) and possibly related to a hypothetical bollide impact near Bombay, India, that might have triggered the Deccan volcanism (Negi et al. 1993).

Among the evidence to be marshaled in support of ancient vicariance of the Malagasy freshwater fishes are (*a*) the near-perfect match of area cladograms with the temporal sequence of Gondwanan breakup for rainbow fishes (Bedotiidae), killifishes (Pachypanchax), and cichlids, (*b*) the observation that none of these clades shows a sister group relationship with African lineages, and (*c*) that for 70% of the primary lineages, sister groups are found on former Gondwanan fragments that are now separated from Madagascar by thousands of kilometers of open ocean (Sparks 2004; Sparks & Smith 2004a,b, 2005). Moreover, many of the Malagasy lineages are basal with respect to their relatives found on other landmasses (Sparks & Stiassny 2003). Finally, recent analysis of biogeographic patterns and fossil distributions indicates that the Cichlidae are indeed an ancient radiation with origins deep in the Mesozoic (T.J. Near, submitted).

Alternatively, paleontologists and others have argued that the island's freshwater fishes are descended from Cenozoic marine colonizers that are secondarily adapted to freshwater. Myers (1938) classified freshwater fishes into "primary" and "secondary" groups, depending upon the latter's demonstrated tolerance for at least brief periods of saltwater exposure. He placed cichlids in this category. Sparks & Smith (2005) marshal a combination of physiological, life history, and phylogenetic data to reject Myers' division, however, arguing that it is irrelevant to the question of Malagasy fish biogeography. Nonetheless, an explicitly molecular phylogenetic approach using divergence time estimation (Vences et al. 2001) posits a scenario in which the ancestral cichlids were widespread in Africa during the Early Cenozoic. From there, they dispersed to Madagascar and India, with modern cichlids in Africa displacing their ancestral lineages, thereby causing extinction with replacement, but with Malagasy and Indian basal lineages remaining. Though this extinction with replacement hypothesis may appear overly complex and ad hoc, Vences et al. (2001) point out that in Madagascar, cichlids recently introduced from Africa by human agency are replacing the native cichlids with devastating speed and efficiency. As potentially decisive support for the dispersal hypotheses, divergence ages for the Malagasy lineages are shown to be far too recent to be compatible with ancient vicariance (Murray 2001, Vences et al. 2001).

Herpetofauna. Contrary to the situation with the freshwater fishes, there have been quite a few molecular phylogenetic studies conducted on the amphibians and reptiles of Madagascar. In the case of the herpetofauna, the distinction between Cenozoic dispersers and ancient vicariants is fairly clear, and the predominant trend of thought is one of dispersal. Virtually all studies of Madagascar's frogs conclude that their presence in Madagascar is best explained by dispersal, typically from Africa (Vences et al. 2003a, 2004). This runs counter to all traditional hypotheses that argue that amphibian life history and physiology negate the possibility of transoceanic dispersal. Vences et al. (2003b) offer evidence from two endemic species of the genus *Mantellidae* that occur on the island of Mayotte, which is entirely volcanic and surrounded by sea depths of more than 3500 m. Although both species were assumed to have been human introductions from Madagascar, a divergence age analysis reveals that they are far too old to have been the products of human agency. The notable exception to this apparent pattern of Cenozoic transoceanic dispersal in Madagascar's frogs can be found in the analysis of ranid frogs conducted by Bossuyt & Milinkovitch (2001). Their study concludes that ranid origins began on the IndoMadagascar subcontinent, with the retention of ancestral lineages in Madagascar, their extinction in India relating to the formation of the Deccan Traps, and subsequent release into Eurasia upon the collision of India with Asia. Divergence age analysis appears to support the hypothesis, though it should be noted that the primary calibration point applied in the analysis is the 88 Ma separation of Madagascar and India. Thus, one can potentially argue a case of circularity in the derivation of their divergence ages in support of vicariance.

The situation with Madagascar's reptiles is similar in that studies of plated lizards (A. Raselimanana, personal communication; Odierna et al. 2002), colubrid snakes (Nagy et al. 2003), geckos (Austin et al. 2004), tortoises (Caccone et al. 1999),

scincid lizards (Mausfeld et al. 2000), and chameleons (Raxworthy et al. 2002) all show distributions and ages (where calculated) that are most consistent with Cenozoic transoceanic dispersal. Perhaps the most remarkable study in this regard is that of the chameleons, which posits a minimum of five dispersal events among Madagascar, Africa, India, and the Seychelles (Raxworthy et al. 2002). A recent study of the boine snakes, podocnemid turtles, and iguanid lizards comes to quite a different conclusion, however. Using multiple gene loci and Bayesian divergence age analysis (Kishino et al. 2001, Thorne & Kishino 2002, Thorne et al. 1998), along with area cladogram analysis, this study concludes that these three taxa reside in Madagascar owing to a vicariant history (Noonan & Chippendale 2006). The calculation of crown node ages ranging from 76–90 Ma for the Malagasy clades, as well as the geographic distribution of the endemic taxa and their outgroups, is taken as compelling evidence for a protracted connection between South America and Madagascar via Antarctica, as suggested by Hay et al. (1999). The authors decidedly conclude that the data are neither compatible with ancient African/Madagascar vicariance, nor with Cenozoic dispersal.

Birds. Given that birds have the capacity for flight, and are thus assumed to be ready dispersers, it comes as no surprise that all molecular phylogenetic studies of Malagasy birds have concluded that they arrived on Madagascar via dispersal. Detailed studies of vangids (Yamagishi et al. 2001), ground rollers (Kirchman et al. 2001), warblers (Beresford et al. 2005), kingfishers (Marks & Willard 2005), sunbirds (Warren et al. 2003), bulbuls (Warren et al. 2005), kestrels (Groombridge et al. 2002), and asities (Prum 1993) have posited dispersal, typically from Africa. Moreover, for those studies in which divergence ages were determined (Groombridge et al. 2002; Warren et al. 2003, 2005), it appears that several groups and/or species are very recent arrivals (<4 Ma). Again, given flight abilities in birds, it is not terribly surprising that the avifauna of Madagascar might be strictly comprised of Cenozoic transoceanic dispersers. What is surprising, however, has been the discovery that the diversity of Madagascar's avifauna is explained by considerably fewer dispersal events than might be supposed.

This finding is best characterized by the studies of Yamagishi et al. (2001) and Cibois et al. (1999, 2001). In the former case, the researchers found that two genera, *Tylas* and *Newtonia*, both of which had previously been placed in different families, are actually members of the Malagasy Vangidae. Even more remarkably, the latter of the two studies found that 9 of 13 species of Malagasy songbirds belong to a single endemic clade. Prior to these studies, it had been assumed that these species were the product of at least three independent colonizations, rather than the single colonization and subsequent radiation posited by the Cibois et al. (2001) study. Moreover, the diversity of morphologies and ecologies typical of the birds examined by both studies is persuasive evidence of Madagascar's power to generate radiations of neoendemics (sensu, Gillespie & Roderick 2002).

Seemingly, the single exception to scenarios of dispersal for Madagascar's avifauna relates to the recently extinct elephant bird (genus *Aepyornis*). This giant ratite (the largest bird to have ever lived) was one of the many victims of the Holocene megafaunal extinction in Madagascar. Given the consistent agreement between fossil-based (Cracraft 2001) and molecular age estimates (Cooper et al. 2001) for ratite origins in

the Late Cretaceous, many ornithologists have assumed that the elephant bird came to reside in Madagascar via Gondwanan vicariance. Indeed, the molecular phylogenetic age estimates for basal ratites suggest that elephant birds and ostriches may have entered IndoMadagascar via the Kerguelen Plateau, with ostriches eventually arriving in Eurasia via the collision of India and Asia (Cooper et al. 2001).
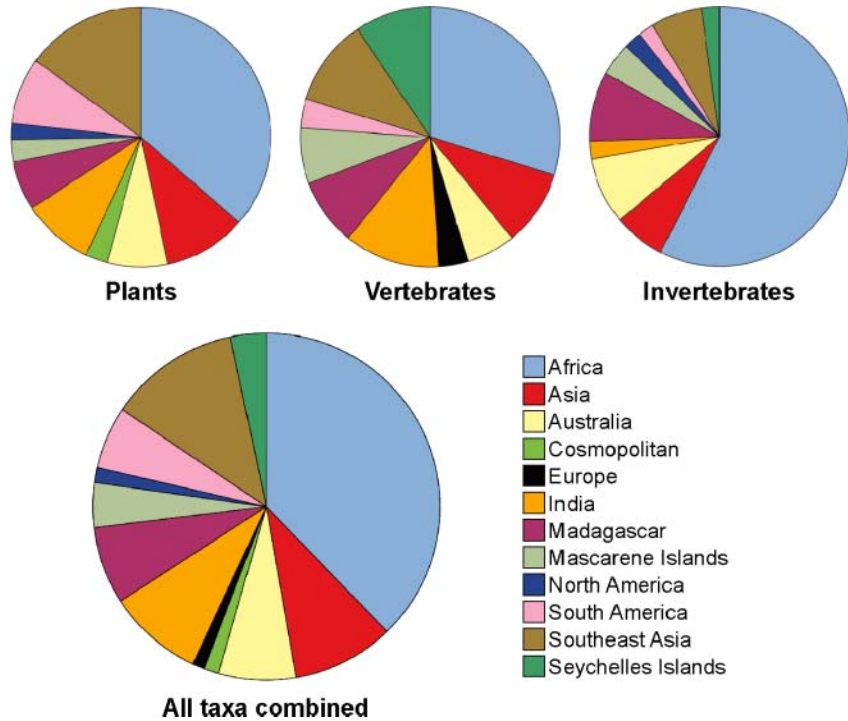
Mammals.   Only four major lineages (classified as Orders) of extant, strictly terrestrial mammals are endemic to Madagascar: the tenrecs (Afrotheria, formerly classified as Insectivora), the lemurs (Order Primates), the nesomyine rodents (Family Muridae), and the carnivorans (Order Carnivora). Madagascar also supports a notable bat fauna, comprised of both micro- and megachiropterans. Of these, only one family, Myzopodidae (the sucker-footed bats), is endemic. With the exception of the bats, all of the terrestrial mammals of Madagascar have been subjected to rigorous molecular phylogenetic analysis, and all groups have had divergence age estimates generated by at least one study. The results of these analyses are strikingly uniform. In all four groups, phylogenetic analysis demonstrated each group to be monophyletic with its sister group found in Africa. These patterns lead to the conclusion that each clade is the product of a single colonization and subsequent radiation of neoendemics within the island. This is true of the lemurs (Goodman et al. 1994; Yoder 1994, 1997; Yoder et al. 1996), rodents (Jansa & Weksler 2004, Poux et al. 2005), tenrecs (Douady et al. 2002, Olson 1999, Olson & Goodman 2003, Poux et al. 2005), and carnivorans (Yoder & Flynn 2003, Yoder et al. 2003). Also, there is a consistent finding among divergence age studies that all crown group ages are post-Mesozoic (Poux et al. 2005; Yang & Yoder 2003; Yoder & Yang 2004; Yoder et al. 1996, 2003), with the oldest estimated age being for the lemurs in the earliest part of the Cenozoic (Yang & Yoder 2003, Yoder & Yang 2004, Yoder et al. 2003). Moreover, a recently published ancient DNA study confirms that the giant subfossil lemurs were members of the same lemuriform clade and are thus descended from the same Cenozoic colonist that produced the extant lemurs (Karanth et al. 2005). The sole molecular phylogenetic study thus far conducted on the bats of Madagascar reveals a slightly different story in finding that the genus *Triaenops* (Family Hipposideridae) is the product of two colonizations of Madagascar, both of which occurred very recently (<1 Ma) (A.L. Russell, J. Ranivo, E.P. Palkovacs, S.M. Goodman, A.D. Yoder, et al., submitted).

Summary of Emergent Patterns in the Data

The data presented above point to two generalities: (*a*) that there are numerous endemic clades of Malagasy taxa whose closest sister group relationships are to African taxa, and (*b*) that there appears to be an overwhelming indication of Cenozoic dispersal. Figures 5 and 6 summarize these data and confirm the impression. Figure 5 illustrates the fact that nearly half of Malagasy plants, invertebrates, and vertebrates studied show sister group relationships to African taxa. Moreover, the consideration of outgroup nodes (data available in Supplemental Table 1) suggests that the majority of lineages ancestral to Malagasy endemics had their origins in Africa. Finally, Figure 6 shows that for those groups in which divergence ages have been estimated,

Plants   **Vertebrates**   **Invertebrates**

All taxa combined

- Africa
- Asia
- Australia
- Cosmopolitan
- Europe
- India
- Madagascar
- Mascarene Islands
- North America
- South America
- Southeast Asia
- Seychelles Islands

the vast majority of both crown and stem ages fall within the Cenozoic. The inescapable inference therefore is that the living biota is predominantly comprised of neoendemics that have evolved from transoceanic dispersers. Certainly, this strains credulity for some (e.g., Stankiewicz et al. 2006), especially given our knowledge of Madagascar's extreme and long-standing isolation. Moreover, the number of studies, relative to the number of endemic taxa, is paltry and we must therefore proceed with caution in drawing our conclusions.

It is not a novel observation to view the living Malagasy biota as "immigrants" (Krause 2003, Krause et al. 1997a, Simpson 1952). Indeed, Simpson (1952), in disputing hypotheses of landbridge connections between Madagascar and other landmasses, pointed out that the very limited representation of mammalian taxa in Madagascar is a definitive indication that the probability of colonization must have been "exceedingly low." It is here that one must revisit the impression that transoceanic dispersal hypotheses border on the "miraculous" (Platnick 1981). Since Simpson's time, landbridge hypotheses have continued to be invoked (e.g., McCall 1997), though they have not received empirical support (e.g., Poux et al. 2005, Yoder et al. 2003). Thus, rafting remains as the predominant explanation, at least for the vertebrates extant terrestrial mammals. Though there is compelling evidence that there may once have been two small subaerial exposures in the Mozambique Channel during the Miocene that could have broken the trip from Africa into three north to south stages of 295,
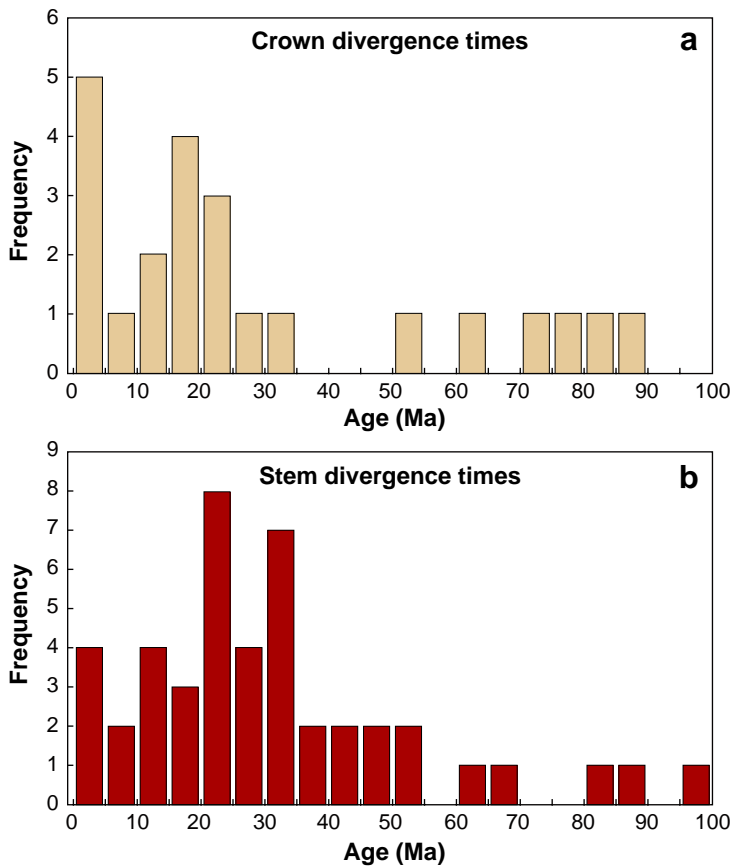
210, and 125 km, and in the direction of the prevailing currents (Bassias 1992, Krause
et al. 1997a, Malod et al. 1991), this would have been for a limited geological period,
and would still have required long sea voyages as well as multiple and improbable
colonizations.

Perhaps a more useful model can be drawn from present-day phenomena. Krause
(1997a) reviews contemporary reports of floating "islands" of vegetation, often with
standing trees and mammalian inhabitants, observed in remote oceanic locations,
tens and hundreds of kilometers from land (Carlquist 1965, King 1962, Millot
1953). Certainly, there have been numerous empirical reports of transoceanic dis-
persal in lizards during recent history (Calsbeek & Smith 2003, Carranza et al. 2000,
Censky et al. 1998). Add to this evidence the likelihood that the ancestors of today's
Malagasy mammals were either hibernators, or had other physiological capacities for
reduced metabolic demands (Kappeler 2000), and the "miraculous" becomes slightly
more routine. Finally, given their less stringent life history attributes, credulity is
far less strained by hypotheses of long-distance dispersal in plants and invertebrates
(Barnes et al. 2006, Cowie & Holland 2006, Monaghan et al. 2005, Thiel & Gutow
2005). Given the data on hand, and the remarkable consistency of the trend across

evolutionary lineages, we must consider the following to be the most credible hypothesis for the time being: Madagascar is an island primarily comprised of neoendemics that are the descendents of Cenozoic waif dispersers.

LITERATURE CITED

Agnarsson I, Kuntner M. 2005. Madagascar: an unexpected hot spot of social *Anelosimus* spider diversity (Araneae: Theidiidae). *Syst. Entomol.* 30:575–92

Agrawal PK, Pandey OP, Negi JG. 1992. Madagascar: a continental fragment of the paleo-super Dharwar craton of India. *Geology* 20:543–46

Anderson CL, Bremer K, Friis EM. 2005. Dating phylogenetically basal eudicots using *rbcL* sequences and multiple fossil reference points. *Am. J. Bot.* 92:1737–48

Austin JJ, Arnold EN, Jones CG. 2004. Reconstructing an island radiation using ancient and recent DNA: the extinct and living day geckos (Phelsuma) of the Mascarene islands. *Mol. Phylogenet. Evol.* 31:109–22

Barnes DKA, Hodgson DA, Convey P, Allen CS, Clarke A. 2006. Incursion and excursion of Antarctic biota: past, present and future. *Glob. Ecol. Biogeogr.* 15:121–42

Bassias Y. 1992. Petrological and geochemical investigation of rocks from the Davie Fracture Zone (Mozambique Channel) and some tectonic implications. *J. Afr. Earth Sci.* 15:321–39

Beck RA, Burbank DW, Sercombe WJ, Riley GW, Barndt JK, et al. 1995. Stratigraphic evidence for an early collision between northwest India and Asia. *Nature* 373:55–58

Beresford P, Barker FK, Ryan PG, Crowe TM. 2005. African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary 'enigmas.' *Proc. R. Soc. London Ser. B.* 272:849–58

Bossuyt F, Milinkovitch MC. 2001. Amphibians as indicators of early tertiary "out-of-India" dispersal of vertebrates. *Science* 292:93–95

Bremer K, Friis EM, Bremer B. 2004. Molecular phylogenetic dating of asterid flowering plants shows Early Cretaceous diversification. *Syst. Biol.* 53:469–505

Briggs JC. 1989. The historic biogeography of India isolation or contact? *Syst. Zool.* 38:322–32

Briggs JC. 2003. The biogeographic and tectonic history of India. *J. Biogeogr.* 30:381–88

Buckley GA, Brochu CA. 1999. An enigmatic new crocodile from the Upper Cretaceous of Madagascar. In *Cretaceous Fossil Vertebrates*, ed. D Unwin, pp. 147–55. London: Paleontol. Assoc.

Buckley GA, Brochu CA, Krause DW, Pol D. 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature* 405:941–44

Caccone A, Amato G, Gratry OC, Behler J, Powell JR. 1999. A molecular phylogeny of four endangered Madagascar tortoises based on MtDNA sequences. *Mol. Phylogenet. Evol.* 12:1–9

Calsbeek R, Smith TB. 2003. Ocean currents mediate evolution in island lizards. *Nature* 426:552–55

Carlquist S. 1965. *Island Life*. Garden City, NY: Nat. Hist. Press

Carranza S, Arnold EN, Mateo JA, López-Jurado LF. 2000. Long-distance colonization and radiation in gekkonid lizards, *Tarentola* (Reptilia: Gekkonidae), revealed by mitochondrial DNA sequences. *Proc. R. Soc. London Ser. B* 267:637–49

Case JA. 2002. A new biogeographic model for dispersal of Late Cretaceous vertebrates into Madagascar and India. *J. Vertebr. Paleontol.* 22(Suppl. 3):42A

Censky EJ, Hodge K, Dudley J. 1998. Over-water dispersal of lizards due to hurricanes. *Nature* 395:556

Cibois A, Pasquet E, Schulenberg TS. 1999. Molecular systematics of the Malagasy babblers (Passeriformes: timaliidae) and warblers (Passeriformes: sylviidae), based on cytochrome *b* and 16S rRNA sequences. *Mol. Phylogenet. Evol.* 13:581–95

Cibois A, Slikas B, Schulenberg TS, Pasquet E. 2001. An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. *Evol. Int. J. Org. Evol.* 55:1198–1206

Cook LG, Crisp MD. 2005. Directional asymmetry of long-distance dispersal and colonization could mislead reconstructions of biogeography. *J. Biogeogr.* 32:741–54

Cooper A, Lalueza-Fox C, Anderson S, Rambaut A, Austin J, et al. 2001. Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature* 409:704–7

Cowie RH, Holland BS. 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *J. Biogeogr.* 33:193–98

Cracraft J. 2001. Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proc. R. Soc. London Ser. B.* 268:459–69

Croizat L, Nelson G, Rosen DE. 1974. Centers of origin and related concepts. *Syst. Zool.* 23:265–87

Davis CC, Webb CO, Wurdack KJ, Jaramillo CA, Donoghue MJ. 2005. Explosive radiation of Malpighiales supports a mid-Cretaceous origin of modern tropical rain forests. *Am. Nat.* 165:E36–65

de Queiroz A. 2005. The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol. Evol.* 20:68–73

de Wit MJ. 2003. Madagascar: Heads it's a continent, tails its an island. *Annu. Rev. Earth Planet. Sci.* 31:213–48

Douady CJ, Catzeflis F, Kao DJ, Springer MS, Stanhope MJ. 2002. Molecular evidence for the monophyly of tenrecidae (mammalia) and the timing of the colonization of Madagascar by Malagasy Tenrecs. *Mol. Phylogenet. Evol.* 22:357–63

Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PLOS Biol.* 4:e88

Du Puy DJ, Moat J. 1996. A refined classification of the vegetation types of Madagascar, and their current distribution. See Lourenço 1996, pp. 205–18

Faramalala MH. 1995. Formations végétales et domaine forestier de Madagascar. Washington, DC: Conserv. Int., map

Fisher BL. 1997. Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae). *J. Nat. Hist.* 31:269–302

Fisher BL. 2003. Formicidae, ants. See Goodman & Benstead 2003, pp. 811–19

Flynn JJ, Wyss AR. 2003. Mesozoic terrestrial vertebrate faunas: the early history of Madagascar's vertebrate diversity. See Goodman & Benstead 2003, pp. 34–40

Fuller S, Schwarz M, Tierney S. 2005. Phylogenetics of the allopadine bee genus Braunsapis: historical biogeography and long-range dispersal over water. *J. Biogeogr.* 32:2135–44

Gillespie RG, Roderick GK. 2002. Arthropods on islands: colonization, speciation, and conservation. *Annu. Rev. Entomol.* 47:595–632

Glaw F, Vences M. 2003. Introduction to the amphibians. See Goodman & Benstead 2003, pp. 883–98

Goodman M, Bailey WJ, Hayasaka K, Stanhope MJ, Slightom J, Czelusniak J. 1994. Molecular evidence on primate phylogeny from DNA sequences. *Am. J. Phys. Anthropol.* 94:3–24

Goodman SM, Benstead JP, eds. 2003. *The Natural History of Madagascar.* Chicago: Univ. Chicago Press, 1709 pp.

Goodman SM, Benstead JP. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39:1–5

Goodman SM, Patterson BD. 1997. *Natural Change and Human Impact in Madagascar.* Washington, DC: Smithson. Inst. Press, 432 pp.

Gottfried MD, Randriamiarimana LL, Rabarison JA, Krause DW. 1998. Late Cretaceous fish from Madagascar: implications for Gondwanan biogeography. *J. Afr. Earth Sci.* 27:91–92

Groombridge JJ, Jones CG, Bayes MK, van Zyl AJ, Carrillo J, et al. 2002. A molecular phylogeny of African kestrels with reference to divergence across the Indian Ocean. *Mol. Phylogenet. Evol.* 25:267–77

Grubb PJ. 2003. Interpreting some outstanding features of the flora and vegetation of Madagascar. *Perspect. Plant Ecol. Evol. Syst.* 6:125–46

Harland WB, Armstrong RL, Cox AV, Craig LE, Smith AG, Smith DG. 1990. *A Geological Time Scale.* Cambridge: Cambridge Univ. Press. 263 pp.

Hay WW, DeConto RM, Wold CN, Wilson KM, Voigt S, et al. 1999. Alternative global Cretaceous paleogeography. In *Evolution of the Cretaceous Ocean Climate System*, ed. E Barrera, CC Johnson, pp. 1–47. Geol. Soc. Am. Spec. Pap., Boulder, CO

Jansa SA, Weksler M. 2004. Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. *Mol. Phylogenet. Evol.* 31:256–76

Janssen T, Bremer K. 2004. The age of major monocot groups inferred from 800+ *rbcL* sequences. *Botan. J. Linn. Soc.* 146:385–98

Kappeler PM. 2000. Lemur origins: rafting by groups of hibernators? *Folia Primatol.* 71:422–25

Karanth KP, Delefosse T, Rakotosamimanana B, Parsons TJ, Yoder AD. 2005. Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. *Proc. Natl. Acad. Sci. USA* 102:5090–95

Kerdelhue C, Le Clainche I, Rasplus JY. 1999. Molecular phylogeny of the Ceratosolen species pollinating Ficus of the subgenus Sycomorus sensu stricto: biogeographical history and origins of the species-specificity breakdown cases. *Mol. Phylogenet. Evol.* 11:401–14

Kiener A, Richard-Vindard G. 1972. Fishes of the continental waters of Madagascar. In *Biogeography and Ecology in Madagascar*, ed. R Battistini, G Richard-Vindard, pp. 477–99. The Hague: W. Junk

King W. 1962. The occurence of rafts for dispersal of land animals into the West Indies. *Q. J. Fla. Acad. Sci.* 45–52

Kirchman JJ, Hackett SJ, Goodman SM, Bates JM. 2001. Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. *Auk* 118:849–63

Kishino H, Thorne JL, Bruno WJ. 2001. Performance of a divergence time estimation method under a probabilistic model of rate evolution. *Mol. Biol. Evol.* 18:352–61

Krause DW. 2003. Late Cretaceous vertebrates of Madagascar: a window into Gondwanan biogeography at the end of the age of dinosaurs. See Goodman & Benstead 2003, pp. 40–47

Krause DW, Hartman JH, Wells NA. 1997a. Late Cretaceous vertebrates from Madagascar: implications for biotic change in deep time. See Goodman & Patterson 1997, pp. 3–43

Krause DW, Prasad GVR, von Koenigswald W, Sahni A, Grine FE. 1997b. Cosmopolitanism among Gondwanan Late Cretaceous mammals. *Nature* 390:504–7

Krause DW, Rogers RR, Forster CA, Hartman JH, Buckley GA, Sampson SD. 1999. The Late Cretaceous vertebrate fauna of Madagascar: implications for Gondwanan paleobiogeography. *GSA Today* 9:1–7

Leroy JF. 1978. Composition, origin, and affinities of the Madagascan vascular flora. *Ann. Mo. Bot. Gard.* 65:535–89

Lourenço WR. 1996. *Biogéographie de Madagascar*. Paris: Ed. ORSTOM, 588 pp.

Lowry PPI, Schatz GE, Phillipson PB. 1997. The classification of natural and anthropogenic vegetation in Madagascar. See Goodman & Patterson 1997, pp. 93–123

Malod JA, Mougenot S, Raillard S, Maillard A. 1991. Novelles constraintes sur la cinematique de Madagascar: les structures de la chaine Davie. *C. R. Acad. Sci. (Paris), Ser. 2* 312:1639–46

Marks BD, Willard DE. 2005. Phylogenetic relationships of the Madagascar pygmy kingfisher (Ispidina madagascariensis). *Auk* 122:1271–80

Mausfeld P, Vences M, Schmitz A, Veith M. 2000. First data on the molecular phylogeography of scincid lizards of the genus Mabuya. *Mol. Phylogenet. Evol.* 17:11–14

McCall R. 1997. Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. *Proc. R. Soc. London Ser. B* 264:663–65

McDowall RM. 2004. What biogeography is: a place for process. *J. Biogeogr.* 31:345–51

McGlone MS. 2005. Goodbye Gondwana. *J. Biogeogr.* 32:739–40

Millot J. 1953. Le continent de Gondwana et les méthodes de raisonnement de la biogéographie classique. *Ann. Sci. Nat. Zool. (Sér. 11)* 15:185–219

Monaghan MT, Gattolliat JL, Sartori M, Elouard JM, James H, et al. 2005. Trans-oceanic and endemic origins of the small minnow mayflies (Ephemeroptera, Baetidae) of Madagascar. *Proc. R. Soc. B* 272:1829–36

Murray AM. 2001. The fossil record and biogeography of the Cichlidae (Actinoptery-gii: Labroidei). *Biol. J. Linn. Soc.* 74:517–32

Myers GS. 1938. Fresh-water fishes and West Indian zoogeography. *Annu. Rep. Smith-son. Inst.* 1937:339–64

Nagy ZT, Joger U, Wink M, Glaw F, Vences M. 2003. Multiple colonization of Madagascar and Socotra by colubrid snakes: evidence from nuclear and mito-chondrial gene phylogenies. *Proc. R. Soc. B* 270:2613–21

Negi JG, Agrawal PK, Pandey OP, Singh AP. 1993. A possible K-T boundary bolide impact site offshore near Bombay and triggering of rapid Deccan volcanism. *Phys. Earth Planet. Inter.* 76:189–97

Nelson G. 1979. From Candolle to Croizat: comments on the history of biogeogra-phy. *J. Hist. Biogeogr.* 11:269–305

Noonan B, Chippendale PT. 2006. Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic landbridge. *Am. Nat.* In press

Odierna G, Canapa A, Andreone F, Aprea G, Barucca M, et al. 2002. A phylogenetic analysis of cordyliformes (Reptilia: Squamata): comparison of molecular and karyological data. *Mol. Phylogenet. Evol.* 23:37–42

Olson LE. 1999. *Systematics, evolution, and biogeography of Madagascar's Tenrecs (Mammalia: Tenrecidae)* PhD thesis. Univ. Chicago

Olson LE, Goodman SM. 2003. Phylogeny and biogeography of Madagascar's tenrecs (Lipotyphla, Tenrecidae). See Goodman & Benstead 2003, pp. 1235–42

Paulian R, Viette P. 2003. An introduction to the terrestrial and freshwater inverte-brates. See Goodman & Benstead 2003, pp. 503–11

Platnick NI. 1981. The progression rule or progress beyond the rules in biogeogra-phy. In *Vicariance Biogeography: a Critique*, ed. G Nelson, DE Rosen, pp. 144–50. New York: Columbia Univ. Press

Plummer PS. 1996. The Amirante Ridge/trough complex: response to rotational transform rift/drift between Seychelles and Madagascar. *Terra Nova* 8:34–47

Popham EJ. 2000. The geographical distribution of the Dermaptera (Insecta) with reference to continental drift. *J. Nat. Hist.* 34:2007–27

Poux C, Madsen O, Marquard E, Vieites DR, de Jong WW, Vences M. 2005. Asyn-chronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Syst. Biol.* 54:719–30

Prum RO. 1993. Phylogeny, biogeography, and evolution of the broadbills (Eurylaimidae) and asities (Philepittidae) based on morphology. *Auk* 110:304–24

Rabinowitz PD, Coffin MF, Falvey D. 1983. The separation of Madagascar and Africa. *Science* 220:67–69

Rage JC. 1996. Le peuplement animal de Madagascar: une comosante venue de Laurasie est-elle envisageable? See Lourenço 1996, pp. 27–35

Rage JC. 2003. Relationships of the Malagasy fauna during the Late Cretaceous: northern or southern routes? *Acta Palaeontol. Pol.* 48:661–62

Rage JC, Jaeger JJ. 1995. The sinking Indian raft: a response to Thewissen and McKenna. *Syst. Biol.* 44:260–64

Rakotosolofo NA, Torsvik TH, Ashwal LD, Eide EA, de Wit MJ. 1999. The Karoo Supergroup revisited and Madagascar-Africa fits. *J. Afr. Earth Sci.* 29:135–51

Raxworthy CJ. 2003. Introduction to the reptiles. See Goodman & Benstead 2003, pp. 934–49

Raxworthy CJ, Forstner MR, Nussbaum RA. 2002. Chameleon radiation by oceanic dispersal. *Nature* 415:784–87

Reeves CV, de Wit M. 2000. Making ends meet in Gondwana: retracing the transforms of the Indian Ocean and reconnecting shear zones. *Terra Nova* 12:272–80

Reeves CV, Sahu BK, de Wit M. 2002. A re-examination of the paleo-position of Africa's eastern neighbours in Gondwana. *J. Afr. Earth Sci.* 34:101–8

Rowley DB, Currie BS. 2006. Palaeo-altimetry of the late Eocene to Miocene Lunpola basin, central Tibet. *Nature* 439:677–81

Sampson SD, Carrano MT, Forster CA. 2001. A bizzare predatory dinosaur from the late Cretaceous of Madagascar. *Nature* 409:504–6

Sampson SD, Witmer LM, Forster CA, Krause DW, O'Connor PM, et al. 1998. Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. *Science* 280:1048–51

Schatz GE. 1996. Malagasy/Indo-australo-malesian phytogeographic connections. See Lourenço 1996, pp. 73–84

Schatz GE. 2000. Endemism in the Malagasy tree flora. In *Diversity and Endemism in Madagascar*, ed. WR Lourenço, SM Goodman, pp. 1–9. Paris: Mém. Soc. Biogéogr.

Schatz GE. 2001. *Generic Tree Flora of Madagascar*. Cumbria, UK: Kew, 490 pp.

Scotese CR. 2000. *PALEOMAP Project: Earth History* (paleogeographic maps). Dept. Geol., Univ. Texas, Arlington

Seward D, Grujic D, Schreurs G. 2004. An insight into the breakup of Gondwana: identifying events through low-temperature thermochronology from the basement rocks of Madagascar. *Tectonics* 23:C3007

Simpson GG. 1952. Probabilities of dispersal in geologic time. *Bull. Am. Mus. Nat. Hist.* 99:163–76

Sparks JS. 2004. Molecular phylogeny and biogeography of the Malagasy and South Asian cichlids (Teleostei: Perciformes: Cichlidae). *Mol. Phylogenet. Evol.* 30:599–614

Sparks JS, Smith WL. 2004a. Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). *Cladistics* 20:501–17

Sparks JS, Smith WL. 2004b. Phylogeny and biogeography of the Malagasy and Australasian rainbowfishes (Teleostei: Melanotaenioidei): Gondwanan vicariance and evolution in freshwater. *Mol. Phylogenet. Evol.* 33:719–34

Sparks JS, Smith WL. 2005. Freshwater fishes, dispersal ability, and nonevidence: "Gondwana life rafts" to the rescue. *Syst. Biol.* 54:158–65

Sparks JS, Stiassny MLJ. 2003. Introduction to the freshwater fishes. See Goodman & Benstead 2003, pp. 849–63

Stankiewicz J, Thiart C, Masters JC, de Wit MJ. 2006. Did lemurs have sweepstake tickets? An exploration of Simpson's model for the colonization of Madagascar by mammals. *J. Biogeogr.* 33:221–35

Storey M, Mahoney JJ, Saunders AD, Duncan RA, Kelley SP, Coffin MF. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science* 267:852–55

Teissier O. 1859. Unpublished letters of Philibert Commerson. *Bull. Soc. Sci. Arts Belles-Lett. Toulon*, pp. 265–75

Thiel M, Gutow L. 2005. The ecology of rafting in the marine environment. II. The rafting organisms and community. *Oceanogr. Mar. Biol.* 43:279–418

Thorne JL, Kishino H. 2002. Divergence time and evolutionary rate estimation with multilocus data. *Syst. Biol.* 51:689–702

Thorne JL, Kishino H, Painter IS. 1998. Estimating the rate of evolution of the rate of evolution. *Mol. Biol. Evol.* 15:1647–57

Torres E, Lees DC, Vane-Wright RI, Kremen C, Leonard JA, Wayne RK. 2001. Examining monophyly in a large radiation of Madagascan butterflies (Lepidoptera: Satyrinae: Mycalesina) based on mitochondrial DNA data. *Mol. Phylogenet. Evol.* 20:460–73

Torsvik TH, Tucker RD, Ashwal LD, Carter LM, Jamtveit B, et al. 2000. Late Cretaceous India-Madagascar fit and timing of break-up related magmatism. *Terra Nova* 12:220–25

Torsvik TH, Tucker RD, Ashwal LD, Eide EA, Rakotosolofo NA. 1998. Late Cretaceous magmatism in Madagascar: paleomagnetic evidence for a stationary Marion hot spot. *Earth Planet. Sci. Lett.* 164:221–32

Valsangkar AB, Radhakrishnamurty K, Subbarao KV, Beckinsale RD. 1981. Paleomagnetism and potassium-argon age studies of acid igneous rocks from the St. Mary Islands. *Mem. Geol. Soc. India* 3:265–76

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. *J. Biogeogr.* 28:1091–99

Vences M, Kosuch J, Glaw F, Bohme W, Veith M. 2003a. Molecular phylogeny of hyperoliid treefrogs: biogeographic origin of Malagasy and Seychellean taxa. *J. Zool. Syst. Evol. Res.* 41:205–15

Vences M, Kosuch J, Rodel MO, Lotters S, Channing A, et al. 2004. Phylogeography of Ptychadena mascareniensis suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. *J. Biogeogr.* 31:593–601

Vences M, Vieites DR, Glaw F, Brinkmann H, Kosuch J, et al. 2003b. Multiple overseas dispersal in amphibians. *Proc. R. Soc. London Ser. B* 270:2435–42

Warren BH, Bermingham E, Bowie RCK, Prys-Jones RP, Thebaud C. 2003. Molecular phylogeography reveals island colonization history and diversification of western Indian Ocean sunbirds (Nectarinia: Nectariniidae). *Mol. Phylogenet. Evol.* 29:67–85

Warren BH, Bermingham E, Prys-Jones RP, Thebaud C. 2005. Tracking island colonization history and phenotypic shifts in Indian Ocean bulbuls (Hypsipetes: Pycnonotidae). *Biol. J. Linn. Soc.* 85:271–87

Wells NA. 2003. Some hypotheses on the Mesozoic and Cenozoic paleoenvironmental history of Madagascar. See Goodman & Benstead 2003, pp. 16–34

Wiley EO. 1988. Vicariance biogeography. *Annu. Rev. Ecol. Syst.* 19:513–42

Yamagishi S, Honda M, Eguchi K, Thorstrom R. 2001. Extreme endemic radiation of the Malagasy vangas (Aves: Passeriformes). *J. Mol. Evol.* 53:39–46

Yang Z, Rannala B. 2006. Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Mol. Biol. Evol.* 23:212–26

Yang Z, Yoder AD. 2003. Comparison of likelihood and Bayesian methods for estimating divergence times using multiple gene loci and calibration points, with application to a radiation of cute-looking mouse lemur species. *Syst. Biol.* 52:705–16

Yoder AD. 1994. Relative position of the Cheirogaleidae in strepsirhine phylogeny: a comparison of morphological and molecular methods and results. *Am. J. Phys. Anthropol.* 94:25–46

Yoder AD. 1997. Back to the future: a synthesis of strepsirrhine systematics. *Evol. Anthropol.* 6:11–22

Yoder AD, Burns MM, Zehr S, Delefosse T, Veron G, et al. 2003. Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421:734–37

Yoder AD, Cartmill M, Ruvolo M, Smith K, Vilgalys R. 1996. Ancient single origin of Malagasy primates. *Proc. Natl. Acad. Sci. USA* 93:5122–26

Yoder AD, Flynn JJ. 2003. Origin of Malagasy Carnivora. See Goodman & Benstead 2003, pp. 1253–56

Yoder AD, Yang Z. 2004. Divergence dates for Malagasy lemurs estimated from multiple gene loci: geological and evolutionary context. *Mol. Ecol.* 13:757–73

Zakharov EV, Smith CR, Lees DC, Cameron A, Vane-Wright RI, Sperling FAH, 2004. Independent gene phylogenies and morphology demonstrate a Malagasy origin for a wide-ranging group of swallowtail butterflies. *Evolution* 58:2763–82

Zhu B, Kidd WSF, Rowley DB, Currie BS, Shafique N. 2005. Age of initiation of the India-Asia collision in the east-central Himalaya. *J. Geol.* 113:265–85

Contents

Indexes