Spatial and temporal arrival patterns of Madagascar's vertebrate fauna explained by distance, ocean currents, and ancestor type

Karen E. Samonds[a,1], Laurie R. Godfrey[b], Jason R. Ali[c], Steven M. Goodman[d,e], Miguel Vences[f], Michael R. Sutherland[b], Mitchell T. Irwin[g], and David W. Krause[h]

[a]School of Biomedical Sciences, and [g]School of Biological Sciences, University of Queensland, St. Lucia, Queensland 4072, Australia; [b]Department of Anthropology, University of Massachusetts, Amherst, MA 01003; [c]Department of Earth Sciences, University of Hong Kong, Hong Kong, China; [d]Department of Zoology, Field Museum of Natural History, Chicago, IL 60605; [e]Association Vahatra, BP 3972, Antananarivo 101, Madagascar; [f]Department of Evolutionary Biology, Zoological Institute, Technical University of Braunschweig, 38106 Braunschweig, Germany; and [h]Department of Anatomical Sciences, Stony Brook University, Stony Brook, NY 11794

How, when, and from where Madagascar's vertebrates arrived on the island is poorly known, and a comprehensive explanation for the distribution of its organisms has yet to emerge. We begin to break that impasse by analyzing vertebrate arrival patterns implied by currently existing taxa. For each of 81 clades, we compiled arrival date, source, and ancestor type (obligate freshwater, terrestrial, facultative swimmer, or volant). We analyzed changes in arrival rates, with and without adjusting for clade extinction. Probability of successful transoceanic dispersal is negatively correlated with distance traveled and influenced by ocean currents and ancestor type. Obligate rafters show a decrease in probability of successful transoceanic dispersal from the Paleocene onward, reaching the lowest levels after the mid-Miocene. This finding is consistent with a paleoceanographic model [Ali JR, Huber M (2010) *Nature* 463:653–656] that predicts Early Cenozoic surface currents periodically conducive to rafting or swimming from Africa, followed by a reconfiguration to present-day flow 15–20 million years ago that significantly diminished the ability for transoceanic dispersal to Madagascar from the adjacent mainland.

endemism | phylogenetics | biogeography | evolutionary history | animal distributions

Madagascar's extant vertebrate fauna exhibits high levels of species endemism, yet, for certain groups, is relatively species-poor. Madagascar is also taxonomically imbalanced in that it is not typically "African" (1, 2), as might be expected if most of its ancestors dispersed over a land bridge across the Mozambique Channel or used several intervening islands in a stepping-stone chain facilitated by past lower sea levels (3). Although a few groups appear to be stranded relicts, resulting from Madagascar's shared plate tectonic history with Gondwana (4, 5), for most clades current evidence indicates that the basal stocks arrived after the island was geographically isolated, thus refuting a vicariance model for these organisms.

Currently, the most accepted explanation is that ancestors of most extant Malagasy vertebrate groups rafted, swam, or flew to Madagascar from Africa across the Mozambique Channel during the Cenozoic (6–12). Unfortunately, Madagascar's fossil record of terrestrial vertebrates is restricted to the Late Permian, Triassic, Early–Middle Jurassic, Late Cretaceous (13, 14), and Late Quaternary (extending back only ~80,000 y) (15). As such, this record sheds little light on the critical interval, the Tertiary, when the ancestral stocks of many extant clades are thought to have arrived.

This article analyzes phylogenetic and biogeographic patterns for Quaternary (including extant) Malagasy vertebrate groups within the context of major prevailing geologic and oceanographic conditions throughout the Mesozoic and Cenozoic to provide insights into the mechanisms that resulted in their current existence on the island. We define vertebrate "groups" as Madagascar-endemic clades, each presumed to be descended from a single successful colonization event. Most are families, although other taxonomic ranks (e.g., orders, superfamilies, subfamilies, genera, and species)

are included. We ask whether observed rates of arrival of clade ancestors changed through time and, if so, whether they relate to the position of Madagascar relative to other landmasses, dispersal ability, or geographic source of the colonizers, prevailing ocean currents, or some or all of these factors in combination. We predict that: (*i*) dispersal ability should affect the probability of arrival more in the Cenozoic than the Mesozoic, because only during the last 20–25 Myr of the 185-Myr long Mesozoic, but during the entire Cenozoic, Madagascar was isolated in the Indian Ocean, and any colonizers would have had to arrive via transoceanic dispersal (flying, swimming, or rafting); (*ii*) within the Cenozoic, because of proximity, transoceanic dispersal from Africa should be more common than dispersal from Asia; (*iii*) within the Cenozoic, transoceanic dispersal for obligatory rafters should be more common when surface flows were more conducive to rafting (i.e., during the Paleogene and earliest Neogene (9); and (*iv*) assuming some independence of prevailing winds, storm tracks, and ocean currents, volant species should be less affected by ocean current direction than swimmers and terrestrial rafters. We used two databases to test these predictions. The first database was compiled from the biogeographic literature on extant and recently extinct Malagasy vertebrate clades (Table S1). For each of 81 Late Quaternary vertebrate clades, we established arrival date, source, and ancestor type (obligatory freshwater, terrestrial, facultative swimmer, or volant). The second database incorporated new divergence dates from the recent time-tree analysis by Crottini et al. (16) (see *Materials and Methods* for details). In addition, we collected relevant geological, geophysical, and oceanographic information and used this information to construct the temporal units we wanted to compare.

The number of vertebrate clades present on Madagascar during the Quaternary (excluding those introduced, deliberately or inadvertently, by humans) would have depended on (*i*) vertebrate clade survival across the K–T boundary, (*ii*) rates of colonization during the Cenozoic, and (*iii*) rates of clade extinction. Some vertebrate groups may have successfully colonized Madagascar during the Cenozoic but then succumbed to extinction without being represented in the fossil record. In the absence of fossil evidence, we cannot know the actual rates of clade arrival or extinction through most of the Cenozoic. However, we can test the null hypothesis that background extinction had no effect in shaping the modern (Quaternary) vertebrate assemblage (i.e., there is no relationship between the geological age of clades and their probability of Quaternary representation). If in fact we must reject this null hypothesis, we can still compare arrival rates across time intervals by modeling bound-

ary conditions; that is, the extent to which arrivals that are invisible because of background extinction might influence our inferences. In this article, we do both. We note, however, that most of the comparisons we make are of states (dispersal type, geographic source, colonizer type) within single time intervals, which can be explored without considering missing arrivals and extinctions, and which we do indeed treat without any adjustment for missing data.

Results

The results of our statistical analyses of patterns of colonization are provided in Fig. 1, Tables 1–3, and Tables S2 (our literature-derived database) and S3 [the same database modified to incorporate recent data derived from Crottini et al. (16)]. There is complete concordance between the two, suggesting that our inferences are robust. Specific values reported below pertain to Table S2. None of the results presented in Tables S2 or S3 entail adjustment for missing data.

During most of the Mesozoic (all except the last 20–25 Myr), when transoceanic dispersal was not required for either emigration or immigration, there is no evidence that arrival rates for ancestors that we consider dispersal-advantaged (volant species or facultative swimmers) were higher than those for dispersal-disadvantaged (terrestrial or obligate freshwater species) ancestors. In fact, the opposite is true. In contrast, during the Cenozoic, when transoceanic dispersal was the only mode of arrival, the arrival rate for dispersal-advantaged taxa was more than three times that of dispersal-disadvantaged taxa (0.81/Myr vs. 0.23/Myr; $P < 0.001$) (Table S2). Thus, our first prediction—that dispersal advantage should be more important in the Cenozoic than the Mesozoic—is supported.

Our second prediction—that transoceanic rafting from Africa should be more common than rafting from Asia during the Cenozoic—is also supported. This source difference is highly significant for terrestrial taxa ($P = 0.005$), weakly significant for volant taxa ($P = 0.04$), and nearly significant for facultative swimmers ($P = 0.1$), despite their very low numbers (Table S2). Terrestrial taxa and facultative swimmers arrive from Africa 5–6.5 times more often than from Asia; for volant taxa, arriving from Africa is twice as likely.

Our third prediction—that, during the Cenozoic, obligate rafters (terrestrial taxa) should have arrived in greater numbers when ocean currents were more conducive to rafting, during the Paleogene and earliest Neogene, and that a tipping point should have occurred in the mid-Miocene, coinciding with the shift in ocean surface current direction (1)—is not supported. Contrary to expectations, dispersal-disadvantaged taxa show no significant change in arrival rate from before to after the mid-Miocene ($P = 0.95$). However, dispersal-advantaged taxa show a highly significant increase in arrival rate after the mid-Miocene, when prevailing currents shifted to favor Asia. This shift holds for both facultative swimmers ($P < 0.001$) and volant taxa ($P < 0.001$). Overall arrival rates for taxa from Africa ($P < 0.001$) and Asia ($P = 0.002$) both increase significantly after the shift in current direction. The most

striking difference is not a change in source but a change in colonizer type: volant taxa dominate arrivals after the shift in ocean current ($P < 0.001$) but not before ($P = 0.71$), supporting our fourth prediction that volant species should be less affected by ocean current direction than obligatory rafters (Table S2).

Of the above predictions, only the third is potentially affected by background clade extinction, because it compares arrival rates over time (rather than within single time intervals). If we make no adjustment for background clade extinction or "invisible" arrivals, we are implicitly assuming that the probability of observing a clade in the Late Quaternary (including the present day) is unrelated to its arrival time (i.e., there is no effect of extinction). However, this assumption can be tested; if the probability of clade extinction at any point in time has not changed significantly over time, then a greater proportion of the clades that arrived early should have also disappeared, resulting in a biased representation of young clades in the Quaternary.

In fact, this prediction holds. A χ^2 test of the relationship between clade age and Quaternary representation confirms our suspicion of an important clade extinction effect, not merely at the K–T boundary, but through the Cenozoic (Table 1). There are highly significant differences in arrival rate through time, and the Quaternary (including extant) fauna has a disproportionate representation of young clades. Again, there is no inferential difference between results derived from our original database ($P < 0.001$), and that modified by Crottini et al. ($P < 0.001$) (Table 1) (16). The apparent increase in arrival rate over time is consistent and striking.

This result implies that we cannot compare arrival rates across time intervals without considering "invisible" arrivals and their implied background extinction rates. We are interested in temporal changes in arrival rates for different vertebrate groups during the Cenozoic; testing our third prediction depends on our ability to decipher them. The simplest "adjustment" that we can make is to assume that the recent past provides a good model for estimating average arrival rates in the more distant past (a uniformitarian assumption), and that the lower apparent arrival rates for the Paleogene and earliest Neogene are artifacts of extinction. Thus, we assume average vertebrate arrival rates of 2.33/Myr throughout the Cenozoic, but we apportion them in each time interval according to observed differences in ancestor type. With the Cenozoic data adjusted in this manner for background extinction bias, an interesting temporal pattern emerges. Specifically, our third prediction (that obligatory rafters arrived in greater numbers when ocean currents were more conducive to rafting) is supported. Terrestrial (dispersal-disadvantaged) species exhibit the strongest temporal shift, having been most likely to arrive in the Paleocene–Eocene (at a rate of 1.33/Myr); that probability decreased during the Oligocene to mid-Miocene (0.85/Myr), and markedly so again during the mid-Miocene to present (0.13/Myr) (Table 2). Dispersal-advantaged taxa (most of which were volant) show the opposite trend, increasing significantly over time (from 1.01 arrivals per million years in the Paleocene–Eocene to 2.20 arrivals per million
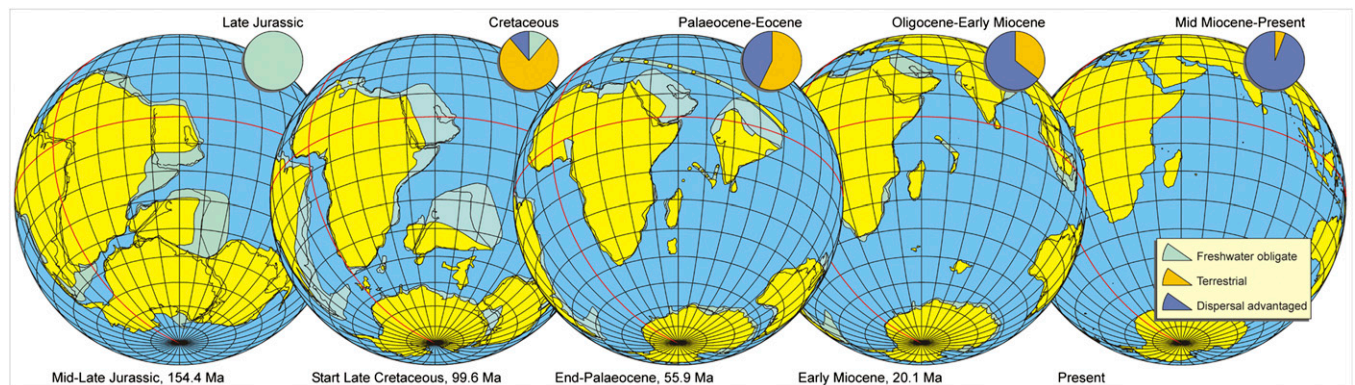

Fig. 1. Maps showing changing landmass configurations and patterns of vertebrate appearance in or colonization of Madagascar by time slice and proportion of dominant colonizer types. These data are observed, unadjusted frequencies, converted to percentages.

Table 1. Observed arrival pattern through time, with values expected under the assumption that arrival rates were, on average, the same through time, and with χ^2 test of the significance of arrival rate differences over time

Epoch	Duration (Myr)	Observed n	Expected n	Arrival rate (arrivals/Myr)	χ^2	n	df	P
Original database								
Mid-Miocene to present	15.0	35	7.1	2.33	136.4	76	4	<0.001
Oligocene to mid-Miocene	18.9	14	8.9	0.74				
Paleocene to Eocene	31.6	14	14.9	0.44				
Cretaceous	80.0	9	37.8	0.11				
Late Jurassic	15.7	4	7.3	0.26				
Crottini et al. database (16)								
Mid-Miocene to present	15.0	33	7.1	2.20	124.3	76	4	<0.001
Oligocene to mid-Miocene	18.9	14	8.9	0.74				
Paleocene to Eocene	31.6	18	14.9	0.57				
Cretaceous	80.0	10	37.8	0.13				
Late Jurassic	15.7	1	7.3	0.06				

Categories were chosen to reflect major geologic and oceanographic conditions.

years in the mid-Miocene to present) (Table 2). Because the shift in ocean current direction made successful arrival of terrestrial species increasingly difficult, the relative proportion of dispersal-advantaged to disadvantaged colonizers increased (Fig. 1).

To test the robustness of this inference, we calculated boundary conditions. We know that our third prediction would hold if the actual average successful colonization rates for vertebrates in the Cenozoic were 2.33/Myr or higher. We tested lower successful colonization rates for the period before the mid-Miocene to determine the point at which significance is lost. Strong significance holds for dispersal-advantaged species regardless of arrival rate. A significant result also holds for dispersal-disadvantaged species as long as the overall successful colonization rate before the mid-Miocene was 1.3/Myr ($P = 0.05$) or higher. In other words, even if the rate of successful vertebrate colonization from the Paleocene to the mid-Miocene was, on average, only 56% (1.3/2.3) of the rate we observe from the mid-Miocene to the present (before human arrival), our third prediction would hold. In fact, given that ocean currents were more conducive to dispersal before the mid-Miocene, it is likely that successful vertebrate colonizations were higher before the mid-Miocene than

afterward; our models are highly conservative. We therefore suggest that our inferences, including confirmation of the third prediction, are robust; they are contextualized in Table 3 (17, 18).

Discussion

Although recent research has defended the importance of dispersal in shaping the faunal composition of Madagascar (7, 19–21), and for animal distributions in general (22–25), this study is unique in rigorously testing these ideas. First, we have shown that dispersal ability affected the probability of arrival more in the Cenozoic than in the Mesozoic, likely because, during the entire Cenozoic, Madagascar was fully isolated physically from other landmasses and all arrivals were, of necessity, via transoceanic dispersal. Second, within the Cenozoic, both before and after the mid-Miocene, Africa was the primary source and Asia (including the Indian subcontinent) the secondary source of colonizers. There is considerable evidence that distance is the most important factor for colonization success for terrestrial dispersers; the much greater distance from Asia to Madagascar was relatively prohibitive. Third, transoceanic dispersal for obligatory rafters during the Cenozoic

Table 2. Arrival pattern during the Cenozoic for dispersal-disadvantaged and dispersal-advantaged taxa, with data adjusted to account for effects of background extinction, assuming average successful colonization rates during the 50.5 Myr before the mid-Miocene comparable to that observed during the past 15 Myr

Type of ancestor	Time interval	Adjusted n for each time interval	Implied arrival rate (per Myr)	Expected proportion for each time interval	Expected n for each time interval	χ^2	n	df	P
Original database									
Dispersal-disadvantaged	Mid-Miocene to present	2	0.13	0.23	13.8	16.3	60	2	<0.001
	Oligocene to mid-Miocene	16	0.85	0.29	17.4				
	Paleocene to Eocene	42	1.33	0.48	28.2				
Dispersal-advantaged	Mid-Miocene to present	33	2.20	0.23	21.4	9.9	93	2	0.007
	Oligocene to mid-Miocene	28	1.48	0.29	27.0				
	Paleocene to Eocene	32	1.01	0.48	44.6				
Crottini et al. database (16)									
Dispersal-disadvantaged	Mid-Miocene to present	1	0.06	0.23	14.3	21.7	62	2	<0.001
	Oligocene to mid-Miocene	15	0.79	0.29	18.0				
	Paleocene to Eocene	46	1.46	0.48	29.8				
Dispersal-advantaged	Mid-Miocene to present	32	2.13	0.23	19.1	15.4	83	2	<0.001
	Oligocene to mid-Miocene	27	1.43	0.29	24.1				
	Paleocene to Eocene	24	0.76	0.48	39.8				

Samonds et al.

Table 3. Timetable for major changes relevant to the geological and biogeographic history of Madagascar

Date (Myr)	Paleogeographical context	Biogeographic events
8	Increase in intensity of monsoon system.	Ratio of dispersal-advantaged to dispersal-disadvantaged colonizers arriving during the past 15 Myr (but before arrival of humans ~2,500 y ago) is 16:1.
15	Direction of flow of ocean surface waters now no longer conducive to transoceanic dispersal from Africa to Madagascar. Tibetan Plateau reaches current elevation.	
20	At about this time, Madagascar's northern tip begins impinging on the southern equatorial current. It commences a shift in the regional oceanic surface water flow that eventually leads to the modern configuration. It is notable, for it makes Africa to Madagascar over-water dispersal extremely difficult.	From beginning of Oligocene to mid-Miocene, approximately twice as many dispersal-advantaged colonizers arrive as dispersal-disadvantaged taxa. This ratio increases dramatically after shift in prevailing direction of ocean current flow (~20–15 Myr).
23	(Oligocene/Miocene boundary) Monsoon climate of southern Asia and surrounding oceans established.	
35	Indian subcontinent collides with southern Asia, resulting in Himalayan uplift. Abrupt cooling and a major sea-level fall induced by the growth of the ice-sheet on Antarctica marks the Eocene/Oligocene boundary, ~34 Myr.	
40–45	By mid-Eocene, most of Madagascar is north of 30° southern latitude, and thus strongly influenced by the trade winds.	During Paleocene and Eocene (i.e., between 65.5 Myr and 33.9 Myr) dispersal-advantaged and dispersal-disadvantaged colonizers arrive in approximately equal numbers.
57	Northeast corner of India close to southeast Asia.	
65	Ocean separating Indian subcontinent and Madagascar vast. Ocean surface currents conducive to transoceanic transport from Africa to Madagascar (possibly taking ~30 d).	
84	Kerguelen Plateau largely submerged.	Ancestors of some vertebrate groups still represented on Madagascar in Quaternary are believed to have arrived during Cretaceous, between ~145.5 Myr and 65.5 Myr. Major extinction event marks end of Cretaceous. Almost all vertebrate groups in Mesozoic strata of Madagascar are unrepresented in island's Quaternary or extant vertebrate faunas.
88	Madagascar and Indian subcontinent begin separating.	
115–95	Substantial parts of Kerguelen Plateau are emergent, but separated from Indo-Madagascar and Antarctica by deep-water gaps.	
115–112	Any land connection between Madagascar and Antarctica via the Gunnerus Ridge is broken.	
130	Eastern Gondwana begins to breakup with Indo-Madagascar splitting from Antarctica–Australia.	
136	After this time, the spreading between western and eastern Gondwana increases the gap between the two landmasses (it stops at 120–116 Myr).	
165	Western Gondwana (Africa and South America) and Eastern Gondwana (Madagascar, Indian subcontinent, Seychelles, Australia, and Antarctica) begin separating but remain in close proximity.	Some clades of freshwater fish still represented on Madagascar today are believed to have arrived in Late Jurassic, beginning ~161 Myr.

was more common when ocean currents were conducive to rafting. Rafters and swimmers did occasionally colonize Madagascar from Africa against the prevailing current, suggesting some stochasticity in current direction (26, 27); yet, generally, arrivals of terrestrial colonizers were rare after ocean currents in the Mozambique Channel shifted their prevailing direction in the mid-Miocene. Finally, and not unexpectedly, we show that volant species were less affected by ocean current direction than terrestrial species or facultative swimmers; the greater distance from Asia to Madagascar was not prohibitive.

A few additional inferences can be drawn from our data. According to most reconstructions, major freshwater fish groups were well established in Madagascar before the K–T boundary (refs. 28 and 29; but see also ref. 16). The apparent lack of freshwater fish arriving after the Mesozoic underscores a transoceanic dispersal disadvantage far more prohibitive than that which applies to terrestrial (rafting) taxa. It is also possible that the apparent "advantage" for "dispersal-disadvantaged" taxa during the Mesozoic is simply an artifact of persistence; once Madagascar was isolated, these freshwater fish faced no incoming competitors whereas for other groups there was a greater chance of competitive displacement.

Amphibians tend to have low tolerance for marine environments, although salinity tolerance is variable among groups (30), and there is no question that amphibians have crossed marine barriers successfully (21, 31), given their presence on geologically young oceanic islands of volcanic origin (19). However, this understanding does not mean that their mechanism of dispersal would have been swimming. It is far more likely that their ancestors rafted on mats of vegetation, as did terrestrial colonizers.

Facultative swimmers exist in relatively small numbers, suggesting that the ability to swim long distances only rarely confers dispersal advantage. Madagascar's facultative swimmers include large-bodied reptiles (e.g., crocodiles) and mammals (e.g., hippopotamuses). Their arrival rates are considerably lower than those of volant species, and they arrived more often from Africa than from Asia, suggesting that distance restricted their dispersal ability. A true swimming "advantage" may only apply to very large mammals (e.g., hippopotamuses) that can traverse large distances by virtue of their fat reserves (32), and certain semiaquatic reptiles, such as crocodiles or turtles. Hippopotamuses are known to have arrived well before the arrival of humans (33), but nevertheless in the Neogene, presumably by swimming. Crocodiles are also thought to have arrived recently (34, 35), possibly through two independent dispersal events (36). Washed-up elephant remains on Ile Europa, midway in the Mozambique Channel between Africa and Madagascar, may also indicate a nonsuccessful dispersal event (37). These taxa all derive from the nearest major landmass, Africa.

Some researchers have discounted the likelihood of terrestrial rafters surviving on the open seas, citing solar radiation, lack of water and food, and intense fluctuations in temperature that would elevate physiological stress (38). However, Van Duzer's (39) compilation of historic sightings of terrestrial vertebrates on floating islands bears testimony to the relative frequency of such occurrences, and to conditions under which even physiologically challenged species may survive long oceanic transport. In recent history, floating islands (up to 100 m across) have been reported at sea up to 240 km from their places of origination, some housing large, food-bearing trees and freshwater pockets. The frequency of such sightings argues strongly that this mechanism of transport cannot be summarily dismissed (40).

EVOLUTION

Species with the greatest dispersal advantage are volant. Oceanic crossings by birds and bats have been more frequent than crossings by either terrestrial or freshwater vertebrates. Madagascar has 44 recognized bat species, reflecting at least 24 independent colonization events (41); of the eight bat families occurring on the island, only one is endemic. Volant species show relatively low African source bias, suggesting they are not strongly influenced by ocean current direction. Of greater relevance to volant species are prevailing wind direction (42) and the pattern and frequency of storms. Volant taxa of Asian origin may have used stepping stones, such as India, or the Seychelles, Andaman, or Mascarene islands.

Madagascar today experiences easterly on-shore winds, being located squarely within the trade-wind zone (which extends from 30° N to 30° S, ~5° south of Madagascar's current southernmost tip); our best models of Mesozoic and Cenozoic coastlines show that Madagascar was already well within the southeast trade-wind zone by the mid-Eocene, and remained there throughout the rest of the Cenozoic (43) (Fig. 2). Trade winds would have aided the transfer of volant animals from the center or eastern tropical Indian Ocean, including Australia, southeast Asia, and the Indian subcontinent.

In the austral summer, the southwest Indian Ocean region is affected by cyclones and large tropical storms (44, 45) and, as with other similarly situated regions (e.g., Caribbean, Gulf and Atlantic coasts, southeast Asia–northwest Pacific), it would appear that such weather systems can move (and are known to have moved) birds and bats far from their normal distributions, in some cases hundreds of kilometers (46–50). Hence, it is clear that, for flying taxa, distance is not the sole controlling factor.

Other factors likely influenced the dispersal success of birds and bats, including their sociality and reproductive adaptations. The fact that some bats are capable of sperm storage may have given them an increased probability of successfully colonizing and diversifying (51). Animals living in groups, as do many birds and bats, have a greater probability of being carried off with conspecifics, thus increasing the chance of mating and, thereby, successful colonization. An increase in storm frequency likely occurred with the emergence of the monsoon climate of southeast Asia and Madagascar during the past 20 Myr (Table 3) (52). Recent evidence suggests that some

bats are highly capable dispersers; *Mops midas* seems to have repeatedly moved between Africa and Madagascar (53). Finally, changes in the availability of dispersers through time may have also affected changes in dispersal frequency over time; for example, some volant groups (e.g., passerine birds) experienced diversifications after the mid-Miocene (54) that could have increased their subsequent likelihood of colonization.

However, other factors for which we were unable to account may have affected Madagascar's colonization history. Changes through time in the availability of dispersers of different body sizes or physiological adaptations may have affected the probability of successful transoceanic dispersal. Small body size should benefit volant (flying) and terrestrial (rafting) species, but not facultative swimmers, for example.

Nevertheless, our results strongly support the importance of transoceanic dispersal by wind and water as the vehicles whereby most extant vertebrates endemic to Madagascar became established. Prior authors have defended transoceanic dispersal to the island on the basis of the phylogenetic affinities and molecular divergence times of particular taxa (6–9, 19, 20, 22–24, 55). Our argument derives instead from variation in observed colonization patterns: dispersal-advantaged colonizers outnumber dispersal-disadvantaged colonizers during the Cenozoic but not during the Mesozoic; terrestrial species were more likely to arrive when currents were more conducive to transoceanic dispersal; and terrestrial colonizers (unlike volant species) arrived virtually exclusively from the nearest landmass (Africa) during the Cenozoic. Finally, we suggest that the apparent increase in successful colonization rates through the Cenozoic can best be interpreted as an artifact of clade extinction. If we are correct with regard to this latter point, then future discoveries of vertebrate fossils from the Paleogene should include a significant number of clades unrelated to those represented in Madagascar's Mesozoic, subfossil Quaternary, or extant vertebrate faunas.

Materials and Methods

Data reflecting our understanding of the biogeographic history of the extant Malagasy vertebrate fauna and key geological, geophysical, and oceanographic information were compiled from the literature (Table S1). For each of 81 clades represented in the extant or Quaternary "subfossil" fauna, we scored: (*i*) time of arrival (Late Jurassic, Cretaceous, Paleocene–Eocene, Oligocene to early Miocene, mid-Miocene to present) and source area (Gondwana, Indo–Madagascar, Africa, India/southeast Asia, Madagascar); (*ii*) ancestor type (obligate freshwater, terrestrial, facultative swimmer, volant); (*iii*) for Cenozoic arrivals, prevailing ocean current direction at time of arrival, based on paleoceanographic modeling; and (*iv*) dispersal ability (advantaged, disadvantaged). Estimates of time and origin of clade arrival were drawn from the literature, ideally from dated molecular phylogenies combined with cladograms based on standard morphological data that can also integrate fossil taxa. Arrival counts per time interval were converted to observed arrival rates (number/million years), which were analyzed for samples pooled by ancestor type, source, and so forth. We also constructed a second database that incorporated recent divergence dates from the recent time-tree analysis by Crottini et al. (16).

We used the χ^2 function in Minitab v15 to compare observed arrival rates; χ^2 allows the use of a hypothesized set of rates (counts per time interval) to calculate an expected set of counts and compare those to observed rates. We used standard null hypotheses to generate rates driving arrival and compared expected counts dictated by our hypothesized rates to actual observed counts. All such calculations (Tables S2 and S3, on each of the two databases) were executed without adjustments for extinction.

Null hypotheses assuming (*i*) equivalent arrival rates for two "states" or (*ii*) uniform average arrival rates for single states through time, were used to generate expected counts, which we then compared with observed counts. For example, assuming a particular arrival rate for a group of colonizers of a particular type across different periods of time, the expected arrival rates for each period become our total *n* of arrivals divided by the total time, and the expected arrival counts for each period become proportional to the time represented by each period. Alternatively, in comparing, for example, volant and terrestrial colonizations during a single time period, the expected arrival rates under the null hypothesis of no difference by animal type is half the total *n* of arrivals for each animal type, divided by the period. Observed counts are, of course, constrained not merely by our selections (e.g., Cenozoic only) but by missing data (e.g., missing arrival time or missing source for particular colonization events) and thus will not be identical for all tests.
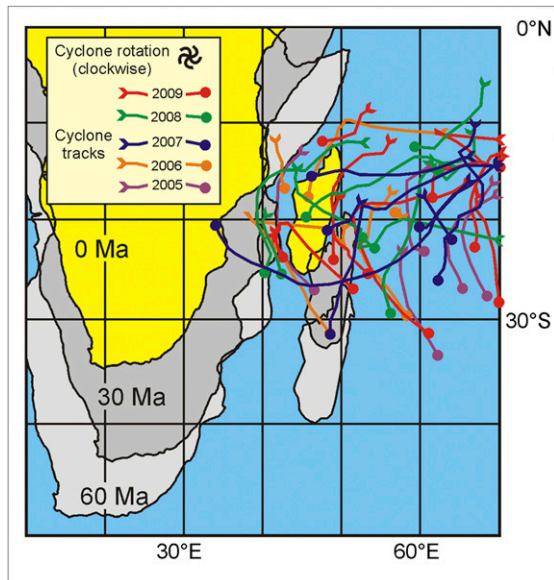
Fig. 2. Map showing the northward drift of Africa and Madagascar from the Paleocene (60 Ma), Oligocene (30 Ma), and present day (0 Ma); Madagascar has moved from outside to within the southerly limit of the southeast trade winds (~30° S). Superimposed on the map are cyclone tracks for 2005–2009, showing the potential influence of tropical storms in aiding transoceanic dispersal ("fishtail" indicates either the initiation point or the position where the storm enters the map area; dot indicates the end point).

When drawing inferences about the past from vertebrate clades represented in the present or very recent past, we should expect undetected background extinctions to bias results. Background extinction rates should not influence tests of whether particular colonizer types were more prevalent than others during a particular time interval, but they may impact inferences regarding temporal changes in arrival rates for particular types. Fortunately, we can apply simple tests to determine whether in fact extinction has played a significant role, and we can apply simple models to make data adjustments that, in effect, "correct" the data for expected missing clade counts. The farther back in time, the more likely the extant counts will be "missing" cases of lineage arrivals and lineage extinctions during that time period. This distinction is important only when comparisons are made of arrival rates over time (our "Prediction 3").

The three time periods of the last 65.5 Myr that we analyzed comprise 31.6, 18.9, and 15 Myr respectively, and yielded 14, 14, and 35 known vertebrate arrivals. We adopted the most recent time period of 15 Myr with its 35 arrivals as our baseline. From this information we infer an average arrival rate of 2.33 successful colonizers per million years. Applied to the whole 65.5 Myr, we estimate a total of 153 successful vertebrate colonizations during the Cenozoic; because we observe only 63 in the extant and recently extinct vertebrate fauna, 90 clades are presumed to have gone extinct.

We then used the arrival-rate discrepancies from 2.33 for the Paleocene to Eocene and the Oligocene to mid-Miocene to allocate the 90 in a 60/30 split. We used the observed animal type (advantaged/disadvantaged) frequencies for each of these time periods to split the added counts into their appropriate cells. Finally, we tested arrival rates lower than 2.33, to determine the rate below which our statistical inferences would change. Higher average arrival rates would not alter our statistical inferences; rather, they would increase our confidence in these inferences.

1. Goodman SM, Benstead JP (2005) Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39:73–77.
2. Reinthal PN, Stiassny MLJ (1991) The freshwater fishes of Madagascar: A study of an endangered fauna with recommendations for a conservation strategy. *Conserv Biol* 5:231–242.
3. McCall RA (1997) Implications of recent geological investigations of the Mozambique Channel for the mammalian colonization of Madagascar. *Proc Biol Sci* 264:663–665.
4. Noonan BP, Chippindale PT (2006) Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic land bridge. *Am Nat* 168:730–741.
5. Gaffney E, Forster C (2003) Side-necked turtle lower jaws (Podocnemididae, Bothremydidae) from the Late Cretaceous Maevarano Formation of Madagascar. *Am Mus Novit* 3397:1–13.
6. Simpson GG (1952) Probabilities of dispersal in geologic time. *Bull Am Mus Nat Hist* 99:163–176.
7. Poux C, et al. (2005) Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Syst Biol* 54:719–730.
8. Yoder AD, Nowak MD (2006) Has vicariance or dispersal been the predominant force in Madagascar? Only time will tell. *Annu Rev Ecol Syst* 37:405–431.
9. Ali JR, Huber M (2010) Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* 463:653–656.
10. Yoder AD, et al. (2003) Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421:734–737.
11. Krause DW (2010) Biogeography: Washed up in Madagascar. *Nature* 463:613–614.
12. Tattersall I (2007) Vicariance vs. dispersal in the origin of the Malagasy modern fauna. *Elwyn Simons A Search for Origins*, eds Fleagle JG, Gilbert CC, Simons EL (Springer, New York), pp 397–408.
13. Krause DW, et al. (2006) Late Cretaceous terrestrial vertebrates from Madagascar: Implications for Latin American biogeography. *Ann Mo Bot Gard* 93:178–208.
14. Flynn JJ, Parrish JM, Rakotosamimanana B, Simpson WF, Wyss AR (1999) A Middle Jurassic mammal from Madagascar. *Nature* 401(6748):57–60.
15. Samonds KE (2007) Late Pleistocene bat fossils from Anjohibe Cave, northwestern Madagascar. *Acta Chiropt* 9(1):39–65.
16. Crottini A, et al. (2012) Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. *Proc Natl Acad Sci USA* 109:5358–5363.
17. Ali JR, Aitchison JC (2009) Kerguelen Plateau and the Late Cretaceous southern-continent bioconnection hypothesis: Tales from a topographical ocean. *J Biogeogr* 36:1778–1784.
18. Ali JR, Krause DW (2011) Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: Refutation of the Gunnerus Ridge causeway hypothesis. *J Biogeogr* 38:1855–1872.
19. Vences M, et al. (2003) Multiple overseas dispersal in amphibians. *Proc Biol Sci* 270:2435–2442.
20. Rocha S, Carretero MA, Vences M, Glaw F, Harris DJ (2006) Deciphering patterns of transoceanic dispersal: The evolutionary origin and biogeography of coastal lizards (*Cryptoblepharus*) in the Western Indian Ocean region. *J Biogeogr* 33(1):13–22.
21. Measey GJ, et al. (2007) Freshwater paths across the ocean: Molecular phylogeny of the frog *Ptychadena newtoni* gives insights into amphibian colonization of oceanic islands. *J Biogeogr* 34(1):7–20.
22. Carranza S, Arnold EN (2003) Investigating the origin of transoceanic distributions: MtDNA shows *Mabuya* lizards (Reptilia, Scincidae) crossed the Atlantic twice. *Syst Biodivers* 1:275–282.
23. de Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol Evol* 20:68–73.
24. Cowie RH, Holland BS (2006) Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. *J Biogeogr* 33:193–198.
25. Heaney LR (2007) Is a new paradigm emerging for oceanic island biogeography? *J Biogeogr* 34:753–757.
26. Wunsch C (2010) Towards understanding the paleocean. *Quat Sci Rev* 29:60–67.
27. Bourjea J, et al. (2007) Phylogeography of the green turtle, *Chelonia mydas*, in the Southwest Indian Ocean. *Mol Ecol* 16:175–186.
28. Sparks JS, Stiassny MLJ (2003) The freshwater fishes of Madagascar: Introduction to the freshwater fishes. *The Natural History of Madagascar*, eds Goodman SM, Benstead JP (Univ of Chicago Press, Chicago), pp 849–863.

29. Gottfried MD, Randriamiaramanana LL, Rabarison JA, Krause DW (1998) Late Cretaceous fish from Madagascar: Implications for Gondwanan biogeography. *J Afr Earth Sci* 27(1A):91–92.
30. Gomez-Mestre I, Tejedo M (2003) Local adaptation of an anuran amphibian to osmotically stressful environments. *Evolution* 57:1889–1899.
31. Myers G (1953) Ability of amphibians to cross sea barriers with special reference to Pacific zoogeography. Proceedings of the 7th Pacific Science Conference of the Pacific Science Association, February 2–March 4, 1949, Auckland and Christchurch, New Zealand, 4:19–27.
32. Durner GM, et al. (2011) Consequences of long-distance swimming and travel over deep-water pack ice for a female polar bear during a year of extreme sea ice retreat. *Polar Biol* 34:975–984.
33. Faure M, Guérin C, Genty D, Gommery D, Ramanivosoa B (2010) Le plus ancien hippopotame fossile (*Hippopotamus laloumena*) de Madagascar (Beloboka, Province de Mahajanga) [The oldest hippopotamus fossil (*Hippopotamus laloumena*) from Madagascar (Beloboka, Mahajanga Province)]. *C R Palevol* 9:155–162.
34. Kuchling G, Lippai C, Behra O (2003) Crocodylidae: *Crocodylus niloticus*, Nile crocodile. *The Natural History of Madagascar*, eds Goodman SM, Benstead JP (Univ of Chicago Press, Chicago), pp 1005–1008.
35. Schmitz A, et al. (2003) Molecular evidence for species level divergence in African Nile crocodiles *Crocodylus niloticus* (Laurenti, 1786). *C R Palevol* 2:703–712.
36. Brochu CA (2003) Phylogenetic approaches toward crocodilian history. *Annu Rev Earth Planet Sci* 31:357–397.
37. Anonymous (1960) Un squelette d'éléphant en épave à l'île Europa [A washed-up elephant skeleton on Europa Island]. *Le Naturaliste malgache* 12:203–204.
38. Kappeler PM (2000) Lemur origins: Rafting by groups of hibernators? *Folia Primatol (Basel)* 71:422–425.
39. Van Duzer C (2004) *Floating Islands: A Global Bibliography* (Cantor Press, Los Altos Hills, CA), p 400.
40. Censky EJ, Hodge K, Dudley J (1998) Over-water dispersal of lizards due to hurricanes. *Nature* 395:556.
41. Goodman SM (2011) *Les chauves-souris de Madagascar [The bats of Madagascar]* (Association Vahatra, Antananarivo), p 129.
42. Weyeneth N, Goodman SM, Appleton B, Woods R, Ruedi M (2011) Wings or winds: Inferring bat migration in a stepping-stone archipelago. *J Evolution Biol* 24:1298–1306.
43. Smith AG, Smith DG, Funnell BM (1994) *Atlas of Mesozoic and Cenozoic Coastlines* (Cambridge Univ Press, Cambridge), p 109.
44. Mavume AF, Rydberg L, Rouault M, Lutjeharms JRE (2009) Climatology and landfall of tropical cyclones in the south-west Indian Ocean. *Western Indian Ocean Journal of Marine Science* 8:15–36.
45. Ash KD, Matyas CJ (2010) The influences of ENSO and the subtropical Indian Ocean Dipole on tropical cyclone trajectories in the southwestern Indian Ocean. *Int J Climatol* 32:41–56.
46. Daniel MJ (1975) First record of an Australian fruit bat (Megachiroptera: Pteropodidae) reaching New Zealand. *NZ J Zool* 2:227–231.
47. Fleming TH, Murray KL (2009) Population and genetic consequences of hurricanes for three species of West Indian phyllostomid bats. *Biotropica* 41:250–256.
48. Heintzelman DS (1961) Kermadic petrel in Pennsylvania. *Wilson Bull* 73:262–267.
49. Hill NP (1945) The 1944 hurricane in New England. *Auk* 62:410–413.
50. Jones RM (1999) Seabirds carried inland by tropical storm Nora. *West Birds* 30:185–192.
51. Crichton EG (2000) Sperm storage and fertilization. *Reproductive Biology of Bats*, ed Crichton EG (Academic Press, London), pp 295–320.
52. Clift PD (2006) Controls on the erosion of Cenozoic Asia and the flux of clastic sediment to the ocean. *Earth Planet Sci Lett* 241:571–590.
53. Ratrimomanarivo FH, Vivian J, Goodman SM (2007) Morphological and molecular assessment of the specific status of *Mops midas* (Chiroptera: Molossidae) from Madagascar and Africa. *Afr Zool* 42:237–253.
54. Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J (2004) Phylogeny and diversification of the largest avian radiation. *Proc Natl Acad Sci USA* 101:11040–11045.
55. 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 Biol Sci* 267:637–649.

EVOLUTION

Supporting Information

Samonds et al. 10.1073/pnas.1113993109

Table S1. Details of arrival and biogeographic context for extant and recently extinct Malagasy vertebrate clades

Taxon (ancestor of)	Class	Time	Source	Type of ancestor	Current direction	Dispersal Ability	References
Cichlidae	Actinopterygii	1 (3)	1 (2)	1	(1) —	1	(1–9)
Bedotiidae	Actinopterygii	1 (3)	1 (3)	1	(1) —	1	(1, 10)
Aplocheilidae	Actinopterygii	2 (3)	4 (3)	1	(1) —	1	(1, 11)
Mugilidae	Actinopterygii	1 (3)	1 (—)	1	(1) —	1	(1, 3)
Clupeidae	Actinopterygii	1	1	1	—	1	(3, 12)
Microhylidae1 (Cophylinae + Scaphiophryninae)	Amphibia	2	—	2	—	1	(13–15)
Microhylidae2 (Dyscophinae)	Amphibia	3	3	2	1	1	(14, 15)
Ptychadenidae	Amphibia	5	2	2	2	1	(16, 17)
Hyperoliidae	Amphibia	4 (3)	2	2	1	1	(1, 18)
Mantellidae	Amphibia	3 (2)	3	2	1 (—)	1	(1, 14, 15, 19–23)
Testudinae	Reptilia	5 (2)	2	3	2 (—)	2	(1, 24)
Podocnemididae	Reptilia	2	1	3	—	2	(25, 26)
Crocodylidae1 (*Crocodylus*)	Reptilia	5	2	3	2	2	(27)
Crocodylidae2 (*Voay*)	Reptilia	5	2	3	2	2	(27, 28)
Chamaeleonidae	Reptilia	3	4	2	1	1	(29)
Gerrhosauridae	Reptilia	2	2	2	—	1	(30)
Opluridae	Reptilia	2	1	2	—	1	(26)
Gekkonidae1*	Reptilia	3	2	2	1	2	(31)
Gekkonidae2†	Reptilia	5	2	2	2	2	(31)
Gekkonidae3‡	Reptilia	5	2	2	2	2	(31)
Scincidae1 (*Trachylepis*)	Reptilia	4	2	2	1	1	(32)
Scincidae2§	Reptilia	4	3	3	1	2	(33)
Scincidae3¶	Reptilia	3	2	2	1	1	(34, 35)
Boidae	Reptilia	2 (3)	1 (2)	2	(1) —	1	(1, 26)
Lamprophiidae1‖	Reptilia	4	2	2	1	1	(36)
Lamprophiidae2 (*Mimophis*)	Reptilia	5 (4)	2	2	2 (1)	1	(1, 36)
Typhlopidae1 (*Typhlops*)	Reptilia	3	1	2	1	1	(37)
Typhlopidae2 (*Xenotyphlops*)	Reptilia	2	1	2	—	1	(37)
Bernieridae	Aves	4	2	4	1	2	(38)
Eurylaimidae	Aves	3	2	4	1	2	(38)
Vangidae1 (*Vanga*)	Aves	4	2	4	1	2	(38)
Vangidae2 (*Artamella, Pseudobias*)	Aves	4	2	4	1	2	(39)
Columbidae1 (*Alectroenas*)	Aves	4	3	4	1	2	(40)
Columbidae2 (*Raphus-Pezophaps*)	Aves	5	3	4	2	2	(40)
Campephagidae	Aves	4	3	4	1	2	(41, 42)
Apodidae	Aves	5	3	4	2	2	(43)
Psittacidae1 (*Agapornis*)	Aves	3	3	4	1	2	(44)
Psittacidae2 (*Psittacula*)	Aves	5	3	4	2	2	(45)
Psittacidae3 (*Coracopsis*)	Aves	3	3	4	1	2	(44, 46)
Pycnonotidae	Aves	5	3	4	2	2	(47)
Strigidae	Aves	5	3	4	2	2	(42)
Sturnidae	Aves	5	3	4	2	2	(48)
Dicruridae	Aves	5	2	4	2	2	(49)
Motacillidae	Aves	5	2	4	2	2	(50)
Nectarinidae1 (*Nectarinia*; *souimanga* clade)	Aves	5	2	4	2	2	(51)
Nectarinidae2 (*Nectarinia*; *notata* clade)	Aves	5	2	4	2	2	(51)
Zosteropidae1 (*Zosterops*; *borbonicus* lineage)	Aves	5	3	4	2	2	(52)
Zosteropidae2 (*Zosterops*; *maderaspatana* lineage)	Aves	5	3	4	2	2	(52)
Mesitornithidae	Aves	2	1	2	—	1	(53)
Aepyornithidae	Aves	2	1	2	—	1	(54, 55)
Lemuroidea	Mammalia	3 (2)	2	2	1 (—)	1	(1, 56–58)

Taxon (ancestor of)	Class	Time	Source	Type of ancestor	Current direction	Dispersal Ability	References
Eupleridae	Mammalia	4	2	2	1	1	(57, 59)
Nesomyinae	Mammalia	4	2	2	1	1	(57)
Tenrecidae	Mammalia	3	2	2	1	1	(57, 60, 61)
Vespertilionidae1 (*Myotis goudoti*)	Mammalia	5	2	4	2	2	(62, 63)
Vespertilionidae2 (*Scotophilus marovaza*)	Mammalia	5	2	4	2	2	(64)
Vespertilionidae3 (*Scotophilus robustus*)	Mammalia	5	2	4	2	2	(64)
Vespertilionidae4 (*Neoromicia matroka*)	Mammalia	5	2	4	2	2	(65)
Hipposideridae1 (*Hipposideros commersoni*)	Mammalia	5	2	4	2	2	(62, 66)
Hipposideridae2 [*Triaenops* (*T. auritus, T. furculus*)]	Mammalia	5	2	4	2	2	(67)
Hipposideridae3 [*Triaenops* (*T. menamena*)]	Mammalia	5	2	4	2	2	(67)
Myzopodidae	Mammalia	3	—	4	1	2	(62)
Emballonuridae1 (*Emballonura atrata*)	Mammalia	4	—	4	1	2	(62)
Emballonuridae2 (*Coleura* sp. nov.)	Mammalia	4	2	4	1	2	(62, 65)
Emballonuridae3 (*Taphozous mauritianus*)	Mammalia	4	2	4	1	2	(62, 65)
Nycteridae	Mammalia	3	2	4	1	2	(62)
Molossidae1 (*Chaerephon leucogaster*)	Mammalia	5	2	4	2	2	(65, 68)
Molossidae2 (*Chaerephon atsinanana*)	Mammalia	5	2	4	2	2	(65)
Molossidae3 (*Chaerephon jobimena*)	Mammalia	5	2	4	2	2	(65)
Molossidae4 (*Mops leucostigma*)	Mammalia	5	2	4	2	2	(65)
Molossidae5 (*Mops midas*)	Mammalia	5	2	4	2	2	(65)
Molossidae6 (*Mormopterus jugularis*)	Mammalia	—	—	4	—	2	(65)
Molossidae7 (*Otomops madagascariensis*)	Mammalia	—	—	4	—	2	(65)
Molossidae8 (*Tadarida fulminans*)	Mammalia	—	2	4	—	2	(65)
Pteropodidae1 (*Pteropus rufus*)	Mammalia	5	3	4	2	2	(69)
Pteropodidae2 (*Eidolon dupreanum*)	Mammalia	—	2	4	—	2	(62)
Pteropodidae3 (*Rousettus madagascariensis*)	Mammalia	5	—	4	2	2	(65, 70)
Miniopteridae	Mammalia	—	2	4	—	2	(65)
Hippopotamidae1 (*Hippopotamus*)	Mammalia	5	2	3	2	2	(71–73)
Hippopotamidae2 (*Hexaprotodon*)	Mammalia	5	2	3	2	2	(71, 72)
Bibymalagasia	Mammalia	3	2	2	1	1	(74, 75)

Time was scored as: 1, Late Jurassic; 2, Cretaceous; 3, Paleocene–Eocene; 4, Oligocene–early Miocene; 5, mid-Miocene–present. Source was scored as: 1, Gondwana; 2, Africa; 3, Asia/India; 4, Other (Indo-Madagascar or Madagascar). Type of ancestor was scored as: 1, obligate freshwater; 2, terrestrial; 3, facultative swimmer; 4, volant. Ocean current direction at time of arrival was coded as: 1, favoring dispersal from Africa; 2, favoring dispersal from Asia. Dispersal ability was coded as: 1, dispersal-disadvantaged (obligate freshwater or terrestrial); 2, dispersal-advantaged (facultative swimmer or volant). Exceptions to these categorizations of dispersal-advantaged and disadvantaged taxa are provided either parenthetically or in footnotes. Values in parentheses indicate alternate time-tree data proposed by Crottini et al. (1); "—" indicates data missing or unavailable.

*Blaesodactylus, scored as dispersal-advantaged because of saltwater-tolerant hard-shelled eggs, and demonstrated dispersal ability.
†*Hemidactylus mercatorius*, scored as dispersal-advantaged because of saltwater-tolerant hard-shelled eggs, and demonstrated dispersal ability.
‡*Hemidactylus playcephalus*, scored as dispersal-advantaged because of saltwater-tolerant hard-shelled eggs, and demonstrated dispersal ability.
§*Cryptoblepharus*; scored as dispersal-advantaged because they are "semimarine" and have demonstrated dispersal ability.
¶*Amphiglossus, Androngo, Madascincus, Paracontias, Pseudoacontias, Pygomeles, Sirenoscincus, Voeltzkowia.*
‖*Alluaudina, Compsophis, Dromicodryas, Geodipsas, Heteroliodon, Ithycyphus, Langaha, Leioheterodon, Liophidium, Liopholidophis, Madagascarophis, Micropisthodon, Pseudoxyrhopus, Stenophis.*

1. Crottini A, et al. (2012) Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. *Proc Natl Acad Sci USA* 10.1073/pnas.1112487109.
2. Stiassny MLJ (1992) Phylogenetic analysis and the role of systematics in the biodiversity crisis. *Systematics, Ecology and the Biodiversity Crisis*, ed Eldredge N (Columbia Univ Press, New York), pp 109–120.
3. Benstead JP, et al. (2003) Conserving Madagascar's freshwater biodiversity. *Bioscience* 53:1101–1111.
4. Briggs JC (2003) Fishes and birds: Gondwana life rafts reconsidered. *Syst Biol* 52:548–553.

5. Chakrabarty P (2004) Cichlid biogeography: Comment and review. *Fish Fish* 5:97–119.
6. Sparks JS, Smith WL (2004) Phylogeny and biogeography of cichlid fishes (Teleostei: Perciformes: Cichlidae). *Cladistics* 20:501–517.
7. Sparks JS, Smith WL (2005) Freshwater fishes, dispersal ability, and nonevidence: "Gondwana life rafts" to the rescue. *Syst Biol* 54:158–165.
8. Azuma Y, Kumazawa Y, Miya M, Mabuchi K, Nishida M (2008) Mitogenomic evaluation of the historical biogeography of cichlids toward reliable dating of teleostean divergences. *BMC Evol Biol* 8:215.
9. Sparks JS (2004) Molecular phylogeny and biogeography of the Malagasy and South Asian cichlids (Teleostei: Perciformes: Cichlidae). *Mol Phylogenet Evol* 30:599–614.
10. Sparks JS, Smith WL (2004) Phylogeny and biogeography of the Malagasy and Australasian rainbowfishes (Teleostei: Melanotaenioidei): Gondwanan vicariance and evolution in freshwater. *Mol Phylogenet Evol* 33:719–734.
11. Murphy WJ, Collier GE (1997) A molecular phylogeny for aplocheiloid fishes (Atherinomorpha, Cyprinodontiformes): The role of vicariance and the origins of annualism. *Mol Biol Evol* 14:790–799.
12. Stiassny MLJ (2002) Revision of *Sauvagella* Bertin (Clupeidae; Pellonulinae; Ehiravini) with a description of a new species from the freshwaters of Madagascar and diagnosis of the Ehiravini. *Copeia* 2002(1):67–76.
13. van der Meijden A, Vences M, Hoegg S, Meyer A (2005) A previously unrecognized radiation of ranid frogs in Southern Africa revealed by nuclear and mitochondrial DNA sequences. *Mol Phylogenet Evol* 37:674–685.
14. van der Meijden A, et al. (2007) Nuclear gene phylogeny of narrow-mouthed toads (Family: Microhylidae) and a discussion of competing hypotheses concerning their biogeographical origins. *Mol Phylogenet Evol* 44:1017–1030.
15. Van Bocxlaer I, Roelants K, Biju SD, Nagaraju J, Bossuyt F (2006) Late Cretaceous Vicariance in Gondwanan Amphibians. *PLoS ONE* 1(1):e74.
16. Vences M, et al. (2004) Phylogeography of *Ptychadena mascareniensis* suggests transoceanic dispersal in a widespread African-Malagasy frog lineage. *J Biogeogr* 31:593–601.
17. Measey GJ, et al. (2007) Freshwater paths across the ocean: Molecular phylogeny of the frog *Ptychadena newtoni* gives insights into amphibian colonization of oceanic islands. *J Biogeogr* 34(1):7–20.
18. Vences M, Kosuch J, Glaw F, Bohme W, Veith M (2003) Molecular phylogeny of hyperoliid treefrogs: Biogeographic origin of Malagasy and Seychellean taxa and re-analysis of familial paraphyly. *J Zool Sys Evol Res* 41:205–215.
19. Vences MJ, Glaw F (2001) When molecules claim for taxonomic changes: New proposals on the classification of Old World treefrogs. *Spixiana* 24:85–92.
20. Vences M, et al. (2003) Multiple overseas dispersal in amphibians. *Proc Biol Sci* 270:2435–2442.
21. Bossuyt F, Milinkovitch MC (2001) Amphibians as indicators of early tertiary "out-of-India" dispersal of vertebrates. *Science* 292:93–95.
22. Bossuyt F, Brown RM, Hillis DM, Cannatella DC, Milinkovitch MC (2006) Phylogeny and biogeography of a cosmopolitan frog radiation: Late cretaceous diversification resulted in continent-scale endemism in the family ranidae. *Syst Biol* 55:579–594.
23. Kurabayashi A, et al. (2008) Phylogeny, recombination, and mechanisms of stepwise mitochondrial genome reorganization in mantellid frogs from Madagascar. *Mol Biol Evol* 25:874–891.
24. Palkovacs EP, Gerlach J, Caccone A (2002) The evolutionary origin of Indian Ocean tortoises (*Dipsochelys*). *Mol Phylogenet Evol* 24:216–227.
25. Noonan B (2000) Does the phylogeny of pelomedusoid turtles reflect vicariane due to continental drift? *J Biogeogr* 27:1245–1249.
26. Noonan BP, Chippindale PT (2006) Vicariant origin of malagasy reptiles supports late cretaceous antarctic land bridge. *Am Nat* 168:730–741.
27. Brochu CA (2007) Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. *Zool J Linn Soc* 150:835–863.
28. Bickelmann C, Klein N (2009) The late Pleistocene horned crocodile *Voay robustus* (Grandidier & Vaillant, 1872) from Madagascar in the Museum für Naturkunde Berlin. *Fossil Record* 12:13–21.
29. Raxworthy C, Forstner M, Nussbaum R (2002) Chameleon radiation by oceanic dispersal. *Nature* 415:784–787.
30. Raselimanana AP, Noonan B, Karanth KP, Gauthier J, Yoder AD (2009) Phylogeny and evolution of Malagasy plated lizards. *Mol Phylogenet Evol* 50:336–344.
31. Vences M, et al. (2004) Natural colonization or introduction? Phylogeographical relationships and morphological differentiation of house geckos (*Hemidactylus*) from Madagascar. *Biol J Linn Soc Lond* 83:115–130.
32. 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.
33. Rocha S, Carretero MA, Vences M, Glaw F, Harris DJ (2006) Deciphering patterns of transoceanic dispersal: The evolutionary origin and biogeography of coastal lizards (*Cryptoblepharus*) in the Western Indian Ocean region. *J Biogeogr* 33(1):13–22.
34. Brandley MC, Huelsenbeck JP, Wiens JJ (2008) Rates and patterns in the evolution of snake-like body form in squamate reptiles: Evidence for repeated re-evolution of lost digits and long-term persistence of intermediate body forms. *Evolution* 62:2042–2064.
35. Crottini A, et al. (2009) A multilocus phylogeny of Malagasy scincid lizards elucidates the relationships of the fossorial genera *Androngo* and *Cryptoscincus*. *Mol Phylogenet Evol* 53:345–350.
36. Nagy ZT, Joger U, Wink M, Glaw F, Vences M (2003) Multiple colonization of Madagascar and Socotra by colubrid snakes: Evidence from nuclear and mitochondrial gene phylogenies. *Proc Biol Sci* 270:2613–2621.
37. Vidal N, et al. (2010) Blindsnake evolutionary tree reveals long history on Gondwana. *Biol Lett* 6:558–561.
38. Beresford P, Barker FK, Ryan PG, Crowe TM (2005) African endemics span the tree of songbirds (Passeri): Molecular systematics of several evolutionary 'enigmas'. *Proc Biol Sci* 272:849–858.
39. Fuchs J, Fjeldsa J, Pasquet E (2006) An ancient African radiation of corvoid birds (Aves: Passeriformes) detected by mitochondrial and nuclear sequence data. *Zool Scr* 35:375–385.
40. Shapiro B, et al. (2002) Flight of the dodo. *Science* 295:1683.
41. Fuchs J, Cruaud C, Couloux A, Pasquet E (2007) Complex biogeographic history of the cuckoo-shrikes and allies (Passeriformes: Campephagidae) revealed by mitochondrial and nuclear sequence data. *Mol Phylogenet Evol* 44:138–153.
42. Fuchs J, et al. (2008) Tracing the colonization history of the Indian Ocean scops-owls (Strigiformes: Otus) with further insight into the spatio-temporal origin of the Malagasy avifauna. *BMC Evol Biol* 8:197.
43. Johnson K, Clayton D (1999) Swiftlets on islands: Genetics and phylogeny of the Seychelles and Mascarene swiftlets. *Phelsuma* 7:9–13.
44. Schweizer M, Seehausen O, Güntert M, Hertwig ST (2010) The evolutionary diversification of parrots supports a taxon pulse model with multiple trans-oceanic dispersal events and local radiations. *Mol Phylogenet Evol* 54:984–994.
45. Groombridge JJ, Jones CG, Nichols RA, Carlton M, Bruford MW (2004) Molecular phylogeny and morphological change in the Psittacula parakeets. *Mol Phylogenet Evol* 31:96–108.
46. Wright TF, et al. (2008) A multilocus molecular phylogeny of the parrots (Psittaciformes): Support for a Gondwanan origin during the cretaceous. *Mol Biol Evol* 25:2141–2156.
47. 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 Lond* 85:271–287.
48. Zuccon D, Cibois A, Pasquet E, Ericson PGP (2006) Nuclear and mitochondrial sequence data reveal the major lineages of starlings, mynas and related taxa. *Mol Phylogenet Evol* 41:333–344.
49. Pasquet E, Pons JM, Fuchs J, Cruaud C, Bretagnolle V (2007) Evolutionary history and biogeography of the drongos (Dicruridae), a tropical Old World clade of corvoid passerines. *Mol Phylogenet Evol* 45:158–167.
50. Voelker G (2002) Systematics and historical biogeography of wagtails: Dispersal versus vicariance revisited. *Condor* 104:725–739.
51. Warren BH, Bermingham E, Bowie RC, Prys-Jones RP, Thébaud C (2003) Molecular phylogeography reveals island colonization history and diversification of western Indian Ocean sunbirds (*Nectarinia:* Nectariniidae). *Mol Phylogenet Evol* 29:67–85.
52. Warren BH, Bermingham E, Prys-Jones RP, Thébaud C (2006) Immigration, species radiation and extinction in a highly diverse songbird lineage: White-eyes on Indian Ocean islands. *Mol Ecol* 15:3769–3786.
53. Cracraft J (2001) Avian evolution, Gondwana biogeography and the Cretaceous-Tertiary mass extinction event. *Proc Biol Sci* 268:459–469.
54. Cooper A, et al. (2001) Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature* 409:704–707.
55. Bourdon E, de Ricqles A, Cubo J (2009) A new Transantarctic relationship: Morphological evidence for a Rheidae–Dromaiidae–Casuariidae clade (Aves, Palaeognathae, Ratitae). *Zool J Linn Soc* 156:641–663.
56. Yoder AD, Yang ZH (2004) Divergence dates for Malagasy lemurs estimated from multiple gene loci: Geological and evolutionary context. *Mol Ecol* 13:757–773.
57. Poux C, et al. (2005) Asynchronous colonization of Madagascar by the four endemic clades of primates, tenrecs, carnivores, and rodents as inferred from nuclear genes. *Syst Biol* 54:719–730.
58. Horvath JE, et al. (2008) Development and application of a phylogenomic toolkit: Resolving the evolutionary history of Madagascar's lemurs. *Genome Res* 18:489–499.
59. Yoder AD, et al. (2003) Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421:734–737.
60. 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* 22:357–363.

61. Poux C, Madsen O, Glos J, de Jong WW, Vences M (2008) Molecular phylogeny and divergence times of Malagasy tenrecs: Influence of data partitioning and taxon sampling on dating analyses. *BMC Evol Biol* 8:102.
62. Teeling EC, et al. (2005) A molecular phylogeny for bats illuminates biogeography and the fossil record. *Science* 307:580–584.
63. Stadelmann B, Jacobs D, Schoeman C, Ruedi M (2004) Phylogeny of African *Myotis* bats (Chiroptera, Vespertilionidae) inferred from cytochrome b sequences. *Acta Chiropt* 6:177–192.
64. Trujillo RG, Patton JC, Schlitter DA, Bickham JW (2009) Molecular phylogenetics of the bat genus *Scotophilus* (Chiroptera: Vespertilionidae): Perspectives from paternally and maternally inherited genomes. *J Mammal* 90:548–560.
65. Goodman SM (2011) *Les chauves-souris de Madagascar* [The bats of Madagascar] (Association Vahatra, Antananarivo), p 129.
66. Hand S, Kirsch J (1998) A southern origin for the Hipposideridae (Microchiroptera)?: Evidence from the Australian fossil record. *Bat Biology and Conservation*, eds Kunz T, Racey P (Smithsonian Institution, Washington, DC), pp 72–90.
67. Russell AL, Goodman SM, Cox MP (2008) Coalescent analyses support multiple mainland-to-island dispersals in the evolution of Malagasy Triaenops bats (Chiroptera: Hipposideridae). *J Biogeogr* 35:995–1003.
68. Jones KE, Bininda-Emonds ORP, Gittleman JL (2005) Bats, clocks, and rocks: Diversification patterns in Chiroptera. *Evolution* 59:2243–2255.
69. O'Brien J (2009) Multiple colonisations of the western Indian Ocean by *Pteropus* fruit bats (Megachiroptera: Pteropodidae): The furthest islands were colonised first. *Mol Phylogenet Evol* 51:294–303.
70. Goodman SM, Chan L, Nowak M, Yoder A (2010) Phylogeny and biogeography of western Indian Ocean *Rousettus* (Chiroptera: Pteropodidae). *J Mammal* 91:593–606.
71. Stuenes S (1989) Taxonomy, habits and relationships of the sub-fossil Madagascan hippopotamuses, *Hippopotamus lemerlei* and *H. madagascariensis. J Vertebr Paleontol* 9:241–268.
72. Boisserie J-R (2005) The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): A review based on morphology and cladistic analysis. *Zool J Linn Soc* 143(1):1–26.
73. Faure M, Guérin C, Genty D, Gommery D, Ramanivosoa B (2010) Le plus ancien hippopotame fossile (*Hippopotamus laloumena*) de Madagascar (Belobaka, Province de Mahajanga) [The oldest hippopotamus fossil (*Hippopotamus laloumena*) from Madagascar (Belobaka, Mahajanga Province)]. *C R Palevol* 9:155–162.
74. MacPhee RDE (1994) Morphology, adaptations, and relationships of *Plesiorycteropus*, and a diagnosis of a new order of eutherian mammals. *Bull Am Mus Nat Hist* 220:1–214.
75. Asher R, Novacek M, Geisler J (2003) Relationships of endemic African mammals and their fossil relatives based on morphology and molecular evidence. *J Mamm Evol* 10(1-2):131–194.

Table S2. Original database

Condition (state 1/state 2)	State 1 observed *n*	State 2 observed *n*	State 1 observed rate of arrival per Myr	State 2 observed rate of arrival per Myr	Expected arrival rate (per Myr) for both states	χ^2	*n*	*df*	*P*
Prediction 1: Era by dispersal type									
Mesozoic (advantaged/ disadvantaged)	1	12	0.01	0.13	0.07	9.3	13	1	0.002
Cenozoic (advantaged/ disadvantaged)	53	15	0.81	0.23	0.52	21.2	68	1	<0.001
Prediction 2: Colonizer type by source (Cenozoic only)									
Terrestrial (arriving from Africa/Asia)	13	2	0.20	0.03	0.11	8.1	15	1	0.005
Facultative swimmers (arriving from Africa/Asia)	5	1	0.08	0.02	0.05	2.7	6	1	0.10 NS
Volant (arriving from Africa/Asia)	26	13	0.40	0.20	0.30	4.3	39	1	0.04
Prediction 3: Colonizer type by current and source by current (Cenozoic only)									
Terrestrial (currents favor Africa/Asia)	14	4	0.28	0.27	0.28	0.005	18	1	0.95 NS
Facultative swimmers (currents favor Africa/Asia)	1	5	0.02	0.33	0.09	12.4	6	1	<0.001
Volant (currents favor Africa/Asia)	13	26	0.26	1.73	0.60	42.3	39	1	<0.001
From Africa (currents favor Africa/Asia)	16	25	0.32	1.67	0.63	33.7	41	1	<0.001
From Asia (currents favor Africa/Asia)	7	9	0.14	0.60	0.24	10.1	16	1	0.002
Prediction 4: Current by dispersal type (Cenozoic only)									
When currents favor Africa (disadvantaged/advantaged)	13	15	0.26	0.30	0.28	0.14	28	1	0.71 NS
When currents favor Asia (disadvantaged/advantaged)	2	33	0.13	2.2	1.17	27.5	35	1	<0.001

The χ^2 tests of the significance of differences between observed counts and counts expected on the basis of null hypotheses of equivalent arrival rates for two states, or constant arrival rate over time for a single state, as specified. Observed counts are raw numbers, unadjusted for extinction. Dispersal type is as follows: advantaged: volant (flying), facultative swimmer (walking/swimming) or otherwise tolerant of transoceanic crossing; disadvantaged: terrestrial (walking/rafting) or obligate freshwater (swimming only, intolerant of salt water). Source: Africa vs. Asia (including India); other sources are not included. Colonizer type (in Cenozoic): terrestrial, facultative swimmer, volant. Current direction (in Cenozoic): favoring dispersal from Africa, or from Asia.

Table S3. Modified database, incorporating values from Crottini et al. (1)

Condition (state 1/state 2)	State 1 observed n	State 2 observed n	State 1 observed rate of arrival per Myr	State 2 observed rate of arrival per Myr	Expected arrival rate (per Myr) for both states	χ^2	n	df	P
Prediction 1: Era by dispersal type									
Mesozoic (advantaged/ disadvantaged)	2	9	0.02	0.09	0.05	4.5	11	1	0.035
Cenozoic (advantaged/ disadvantaged)	52	18	0.79	0.27	0.53	16.5	70	1	<0.001
Prediction 2: Colonizer type by source (Cenozoic only)									
Terrestrial (arriving from Africa/Asia)	14	1	0.21	0.02	0.11	11.3	15	1	0.001
Facultative swimmers (arriving from Africa/Asia)	4	1	0.06	0.02	0.04	1.8	5	1	0.18 NS
Volant (arriving from Africa/Asia)	26	13	0.40	0.20	0.30	4.3	39	1	0.04
Prediction 3: Colonizer type by current and source by current (Cenozoic only)									
Terrestrial (currents favor Africa/Asia)	14	3	0.28	0.20	0.26	0.27	17	1	0.61 NS
Facultative swimmers (currents favor Africa/Asia)	1	4	0.02	0.27	0.08	9.2	5	1	0.002
Volant (currents favor Africa/Asia)	13	26	0.26	1.73	0.60	42.3	39	1	<0.001
From Africa (currents favor Africa/Asia)	19	23	0.38	1.53	0.64	24.1	42	1	<0.001
From Asia (currents favor Africa/Asia)	8	9	0.16	0.60	0.26	8.7	17	1	0.003
Prediction 4: Current by dispersal type (Cenozoic only)									
When currents favor Africa (disadvantaged/advantaged)	17	15	0.34	0.30	0.32	0.13	32	1	0.72 NS
When currents favor Asia (disadvantaged/advantaged)	1	32	0.07	2.13	1.07	29.1	33	1	<0.001

The χ^2 tests of the significance of differences between observed counts and counts expected on the basis of null hypotheses of equivalent arrival rates for two states, or constant arrival rate over time for a single state, as specified. Observed counts are raw numbers, unadjusted for extinction. Dispersal type is as follows: advantaged: volant (flying), facultative swimmer (walking/swimming) or otherwise tolerant of transoceanic crossing; disadvantaged: terrestrial (walking/rafting) or obligate freshwater (swimming only, intolerant of salt water). Source: Africa vs. Asia (including India); other sources are not included. Colonizer type (in Cenozoic): terrestrial, facultative swimmer, volant. Current direction (in Cenozoic): favoring dispersal from Africa or from Asia.

1. Crottini A, et al. (2012) Vertebrate time-tree elucidates the biogeographic pattern of a major biotic change around the K–T boundary in Madagascar. *Proc Natl Acad Sci USA*, 10.1073/pnas.1112487109.