

Vicariant Origin of Malagasy Reptiles Supports Late Cretaceous Antarctic Land Bridge

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ABSTRACT: Since the acceptance of Wegener's theory of plate tectonics in the 1960s, continental drift vicariance has been proposed as an explanation for pan-Gondwanan faunal distributions. Given the recognition of historical connections among continents, it no longer was necessary to invoke hypotheses of dispersal across nearly insurmountable barriers. The application of continental drift vicariance theory to Gondwanan floral and faunal distributions provided reasonable explanations for such unusual distributions as that of the southern beech (*Nothofagus*) and chameleons. However, recent studies have demonstrated a significant, if not dominant, role for dispersal in the present-day distributions of these and numerous other "Gondwanan" taxa. The evolutionary histories of three Malagasy groups (boid snakes, podocnemid turtles, and iguanid lizards) commonly have been interpreted as reflecting vicariance because of continental drift associated with the breakup of Gondwana. Bayesian analyses of divergence ages suggest that this pattern is the result of vicariance coincident with the isolation of Madagascar in the Late Cretaceous (~80 million years ago). This represents the first temporal evidence linking the vicariant origin of extant Malagasy vertebrates to a single geologic event. Specifically, our data provide strong, independently corroborated evidence for a contiguous Late Cretaceous Gondwana, exclusive of Africa and connected via Antarctica.

Keywords: Gondwana, vicariance, Boidae, Podocnemidae, Iguanidae, Madagascar.

The biogeographic origins of the endemic Malagasy fauna constitute one of the greatest mysteries of natural history

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and have been the subject of much recent attention focused on whether the primary sources of the island's biodiversity were vicariance or dispersal events (Rage 1988, 2003; Yoder et al. 1996, 2003; Noonan 2000; Vences et al. 2001*a*, 2001*b*; Douady et al. 2002; Raxworthy et al. 2002; Townsend and Larson 2002; Vences 2004). For many years, phylogenetic relationships of Gondwanan groups that include Malagasy members have been interpreted as evidence of a vicariant origin associated with the separation of Indo/Madagascar from Africa (Laurent 1979; Bauer 1993; Murphy and Collier 1997; Farias et al. 1999, 2000; Cracraft 2001; Vences et al. 2001*a*, 2001*b*; Raxworthy et al. 2002; Townsend and Larson 2002; Sparks 2004) or the submersion of an Indo/Madagascar–Antarctic land bridge (Sparks and Smith 2004). However, all biogeographic studies of extant taxa, save one (mantelline frogs; see below), for which the timing of Malagasy origins have been examined (adopting the integrative approach advocated by Donoghue and Moore 2003) suggest dispersal to Madagascar in the Cenozoic (Yoder et al. 1996, 2003; Vences et al. 2001*b*; Douady et al. 2002; Poux et al. 2005) or a Malagasy origin (Raxworthy et al. 2002; Townsend and Larson 2002). These findings coincide with a recent trend of support for dispersal origins in a field where vicariance had been the preferred explanation since the acceptance of continental drift theory in the 1960s (McDowall 2004; Cook and Crisp 2005; de Queiroz 2005; McGlone 2005). On the basis of recent evidence, even the classic examples of Gondwanan vicariant lineages, such as the southern beech tree *Nothofagus* (Knapp et al. 2005), and organisms for which transoceanic dispersal was considered highly unlikely (e.g., amphibians; Vences et al. 2003) have failed to support the hypothesis of continental drift vicariance, instead suggesting that, given sufficient time, even the most improbable dispersal events are possible.

There appears to be a biogeographic revolution afoot whereby the favored (and most frequently supported) explanation of transoceanic distributions has become dispersal (e.g., McDowall 2004; Cook and Crisp 2005; de Queiroz 2005; McGlone 2005). This biogeographic revolution has occurred as the amount of molecular data and

the availability of methods to infer the age of lineages (Thorne et al. 1998; Sanderson 2002; Thorne and Kishino 2002) have increased dramatically. Early molecular-based analyses that relied on the assumption of a molecular clock suggested that divergences of numerous pan-Gondwanan lineages were too recent to be the result of vicariance, yet the questionable assumptions inherent in molecular clock calibrations left the door to vicariance open. However, the advent of relaxed-clock methods has left little doubt as to the role of dispersal in the present-day distributions of flora and fauna. It seems that “wherever we look, ‘cracks’ appear in the ‘only vicariance’ edifice” (McDowall 2004, p. 346) that has dominated biogeography for the last 30+ years. This is not to suggest that dispersal and vicariance are mutually exclusive explanations of biotic distributions, simply that the role of dispersal in structuring biodiversity has until recently been severely underestimated and that of vicariance overestimated. The interplay between these two phenomena in structuring global biodiversity recently was synthesized for 63 plant and animal groups by Sanmartín and Ronquist (2004), who found support for both vicariance and dispersal in many groups, with a particularly strong vicariant signal from the animal data sets.

Although the Malagasy Reptilia (primarily boid snakes, podocnemid turtles, and iguanid lizards [B, P, and I]) have long been viewed as key exemplars of Gondwanan vicariance (Laurent 1979; Rage 1988, 2003; Bauer 1993), there has been little analysis regarding their origins and current geographical distributions other than suggestions that observed biogeographic patterns are congruent with (though not exclusively due to) Gondwanan vicariance (Austin 2000; Noonan 2000; Vences et al. 2001a). Other vertebrate groups such as cichlid fishes (Farias et al. 1999, 2000; Vences et al. 2001b; Sparks 2004), aplocheiloid killifishes (Murphy and Collier 1997), and rainbowfishes (Sparks and Smith 2004) also have revealed biogeographic patterns consistent with Gondwanan vicariance. However, these too lack rigorous tests of the temporal framework of early diversification (presumably due in part to a poor fossil record). This is problematic because not only do dispersal scenarios potentially explain these patterns, but also alternative vicariant scenarios have been proposed, yet none of these can be explicitly tested without obtaining divergence time estimates. For example, the observed cichlid/aplocheiloid pattern ([Madagascar + India][South America + Africa]) could be the result of (1) dispersal from an African ancestor to Madagascar/India 90–165 million years ago (mya); (2) fragmentation of a Gondwanan lineage when India/Madagascar separated from Africa (165–130 mya), with subsequent separation of South America/Africa ~100 mya; or (3) a Madagascar/India origin (<165 mya) and dispersal to South America/Africa via the Indo/Malagasy–Antarctic land bridge (as was ap-

parently utilized by rainbowfishes; Sparks and Smith 2004). Regardless of their plausibility, these hypotheses cannot be tested by examination of phylogenetic topology alone.

The endemic Malagasy frog family Mantellidae has been suggested to represent an extant lineage whose origins lie in the separation of Madagascar and India some 88 mya (Bossuyt and Milinkovitch 2001; Roelants et al. 2004). However, the method used to date this lineage is not particularly clear, nor do the results unambiguously support Malagasy vicariance. Roelants et al. (2004) cite the inferred divergence of Rhacophoridae and Mantellidae from Bossuyt and Milinkovitch (2001) as 73.1 ± 19.5 mya, though figure 1 of that article clearly indicates this is the point estimate of the time of diversification of the Mantellidae (i.e., age of the crown group) and not the age of the ancestor of the two families (which was itself used as a fixed calibration point on the basis of the separation of Madagascar and India 87.0–88.2 mya). Using an outside calibration point, the diapsid/synapsid split at 338–310 mya, an age estimate of 53.6–92.6 mya was obtained for the Mantellid/Rhacophorid divergence (Bossuyt and Milinkovitch 2001, note 17). While congruent with Indo/Malagasy vicariance, this timing is also consistent with the putative Paleocene Laurasian land bridge (Rage 1988, 2003) and thus a southward expansion with subsequent isolation. Van der Meijden et al. (2005) also presented data on the divergence time between the Rhacophoridae and Mantellidae, though their estimate also overlaps with the proposed timing of a Laurasian connection (52–100 mya).

Studies of other groups incorporating divergence time estimates have provided strong support for African dispersal-mediated origins of the lemuriform (Yoder et al. 1996; Poux et al. 2005), tenrecid (Douady et al. 2002; Poux et al. 2005), passerine (Beresford et al. 2005), rodent (Poux et al. 2005), and carnivoran (Yoder et al. 2003; Poux et al. 2005) components of the Malagasy fauna and a Malagasy origin with subsequent oceanic dispersal to Africa, India, and various islands for chameleons (Raxworthy et al. 2002; Townsend and Larson 2002). The B, P, and I differ from all of these groups in that they lack living extra-Malagasy, continental, Old World representatives (other than the African boid *Calabaria* that Noonan and Chippindale [2006] demonstrated to be the product of an Africa to Madagascar dispersal event). The geographic distribution of the sister group to the Podocnemidae, the African Pelomedusidae, has fueled further speculation of Gondwanan vicariant origins (Bauer 1993; Noonan 2000). The B, P, and I are found only on Madagascar and the Americas and the B and I on some Pacific Islands. The lack of temporal evidence for vicariant origins of the aforementioned Afrocentric mammalian and avian groups is not surprising, given the ancient age of the Madagascar/Africa

separation. South America and Madagascar, however, appear to have had a much more recent history of connection.

The plate tectonic history of the Gondwanan supercontinent is reasonably well documented on the basis of geophysical data. Separation of Africa from both Madagascar/India in the east (~165 mya; Rabinowitz et al. 1983) and South America in the west (100–120 mya; Hay et al. 1999) resulted in an early isolation of the African landmass. The Madagascar/India subcontinent remained contiguous until their separation in the Late Cretaceous (Hay et al. 1999). However, recent studies indicate that the Madagascar/India subcontinent established and retained faunal exchange capabilities with a contiguous South America/Antarctica/Australia landmass via either the Kerguelen Plateau (Hay et al. 1999) or the Gunnerus Ridge (Case 2002; Case and Krause 2002; fig. 1) until the latter part of the Late Cretaceous (~80 mya; Krause et al. 1997a; Sampson et al. 1998; Buckley et al. 2000; Cooper et al. 2001; Haddrath and Baker 2001; Krause 2001; Case 2002; Case and Krause 2002). This hypothesis suggests the possibility of a more recent, Late Cretaceous, vicariant origin of the Malagasy B, P, and I (~80 mya) than if Indo-Madagascar had remained isolated since its separation from Africa (~165 mya). Alternatively, the lack of such a subaerial connection would suggest three possible origins of the Malagasy B, P, and I: (1) Africa, either 165-million-year-old vicariance or more recent transoceanic dispersal to Madagascar across the Mozambique Channel (Krause et al. 1997b), indicating subsequent African extinction of all three groups; (2) Antarctica, oceanic dispersal from across the Enderby Basin; or (3) Laurasia, latest Cretaceous (~65 mya) connection between Asia, India, Seychelles Plateau, and Madagascar (Rage 1988, 2003).

Close relationships between South American and Indian taxa long have been hypothesized for dinosaurs (Colbert 1981), and a late Cretaceous connection between Madagascar and South America has received biological support recently on the basis of the distributions of fossil crocodyliforms (Buckley et al. 2000), abelisauroid theropod dinosaurs (Sampson et al. 1998), and gondwanatherian mammals (Krause et al. 1997a). Ratite birds are the only extant group for which molecular data and modern systematic methods suggest the existence of a southern land bridge and a vicariant origin of Malagasy/Indian taxa coinciding with the submersion of this bridge in the Late Cretaceous (Cooper et al. 2001; Haddrath and Baker 2001). However, this supposition is based on Tertiary fossils and relationships of an extra-Malagasy taxon (ostrich, a ratite) and the tentative phylogenetic placement of the extinct Malagasy ratite elephant bird. A similar pattern has been reported, though not dated, in rainbowfishes (Sparks and Smith 2004). This scenario suggests a vicariant origin

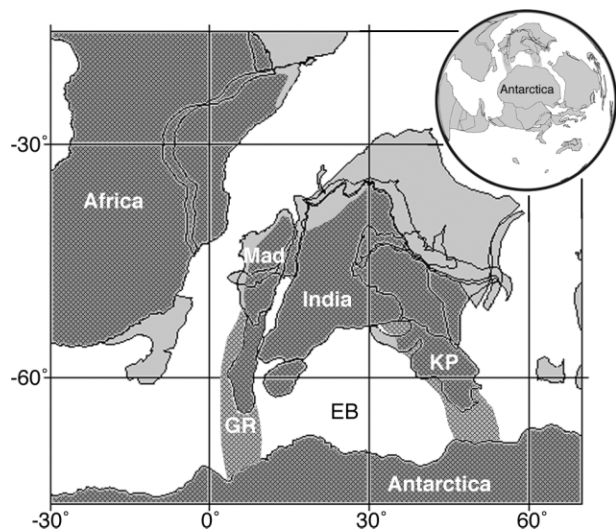


Figure 1: Reconstruction (90 mya) of the Madagascar/India plates illustrating proposed subaerial connections between Madagascar and Antarctica. Dark shading indicates exposed land. Solid lines represent continental margins, with light shading indicating submerged areas. *Mad* = Madagascar, *KP* = Kerguelen Plateau, *GR* = Gunnerus Ridge, *EB* = Enderby Basin. Inset illustrates relative positions of Gondwanan continents at this time. Map from <http://www.odsn.de>; shorelines from Hay et al. (1999) and Case (2002).

of the ostrich and elephant bird coinciding with the submersion of the southern land bridge, subsequent extinction of the elephant bird, and rafting of the ostrich on the Indian subcontinent with subsequent Afro/Arabian dispersal (Cooper et al. 2001) or oceanic dispersal to Africa from Madagascar (Haddrath and Baker 2001).

Material and Methods

Phylogenetic Analysis

For phylogenetic analysis, we used portions of four or five nuclear genes (brain-derived neurotrophic factor precursor [BDNF], neurotrophin-3 [NT-3], recombination activating gene 1 [RAG1], and oocyte maturation factor [*c-mos*, B and I] or proopiomelanocortin [POMC, P]), ornithine decarboxylase [OD, B], and zero to two mitochondrial loci: 12S and 16S for turtles; cytochrome *b* [*cyt-b*] for snakes; available lizard mitochondrial sequences either presented alignment problems [e.g., ND1-CO1] or were incompletely sampled [e.g., 12S, 16S] and were not included). Protocols and primer sequences for amplification of nuclear loci were published by Noonan and Chippindale (2006). All sequences were aligned and edited using Sequencher, version 4.1 (Gene Codes). Phylogenetic analyses were conducted on combined data sets using the

Table 1: Calibration points used in divergence time analysis

Calibration point	Date (mya)	Reference material	Citation
Lizards:			
1. Pleurodont-iguanian split	<230 >165	Lower limit based on early-middle Jurassic <i>Bharatagama</i> (Evans et al. 2002, p. 299); upper limit follows assertion of Evans et al. (2002) that iguanian-scleroglossan dichotomy extends “into early Jurassic or even Late Triassic” and would necessarily predate basal iguanian split	Evans et al. 2002
2. Iguanidae	<180 >25	Earliest definitive pleurodont iguanian (<i>Armandisaurus</i>) with affinities to extant taxa from early Miocene; upper limit based on observations of Evans et al. (2002) and the assumption that the origin of this group does not predate the earliest known Iguaninan in the Jurassic	Norell and de Queiroz 1991; Evans et al. 2002
3. Acrodonta	<180	See 2	Evans et al. 2002
4. Chamaeleonid divergence	>47	Molecular clock	Raxworthy et al. 2002
Snakes:			
5. <i>Epicrates-Eunectes</i> split	>24	Based on Miocene fossils of <i>Eunectes</i> and <i>Pseudoepicrates</i>	Rage 1984
6. <i>Exiliboa-Charina</i> split	>55	Based on Eocene fossils of <i>Dunnophis</i> ; see also appendix and Albino (1996, p. 188) for likely Paleocene record	Rage 1984; Albino 1996
7. Acrochordoidea	>65	Based on Paleocene <i>Nigerophis</i> (Rage 1984, p. 39)	Rage 1984
8. Erycinae	>65	Based on Paleocene <i>Helagras</i> and numerous Eocene taxa (Rage 1984, pp. 23–27); see also appendix and Albino (1996, p. 188)	Rage 1984; Albino 1996
9. Boinae	>55	Based on Eocene Boine <i>Cheilophis</i> (Rage 1984, p. 17; Albino 1993; 1996, p. 188)	Rage 1984; Albino 1996, p. 59
10. Booidea	>75	Based on Cretaceous <i>Dinilysia</i> (Rage 1984, p. 13; Albino 1996, p. 187; 2000, p. 247)	Rage 1984; Albino 1996, 2000
11. <i>Anilius-Tropidophis</i> split	>75	Based on Cretaceous <i>Coniophis</i> (Rage 1984, pp. 12, 66–67); see also appendix	Rage 1984
12. S. A. Boinae	>55	Based on appearance of boine boid and possible erycine material in the early Eocene of Patagonia; see also appendix	Albino 1993, 1996
13. <i>Lichanura-Charina</i> split	>16	Based on Middle Miocene <i>Charina prebottae</i> (Rage 1984, p. 25)	Rage 1984
Turtles:			
14. Cryptodiran-pleurodiran split	>210	Based on Late Triassic <i>Proterochersis</i> and early Jurassic <i>Kayentachelys</i>	Gaffney 1990
15. Podocnemid pelomedusid split	>100	Based on mid-Cretaceous <i>Brasilemys</i> and <i>Araripemys</i>	Gaffney 1990
16. <i>Erymnochelys</i> + <i>Podocnemis</i> clade	>65	Based on early Paleocene cf. <i>Erymnochelys</i> ; see also appendix	Gaffney et al. 2003
17. Chelid-pelomedusoid split	<150 >100	Lower limit based on Late Cretaceous Chelid taxa (references; E. S. Gaffney, personal communication); upper limit assumes the Late Jurassic <i>Platycheilus</i> actually predates the origin of the modern pleurodiria	Gaffney 1990; de la Fuente et al. 2001; de Lapparent de Broin and de la Fuente 2001; de la Fuente 2003
18. <i>Pelomedusa-Pelusios</i> split	>25	Based on the Miocene <i>Pelusios rusingae</i>	Broadley 1981

Note: Additional calibration details are provided in the appendix in the online edition of the *American Naturalist*.

maximum parsimony and maximum likelihood optimality criteria in PAUP* (ver. 4.0b10; Swofford 2001) and Bayesian methods using a Markov chain Monte Carlo approach in MrBayes (ver. 3.01; Huelsenbeck and Ronquist 2001) with a mixed model partitioning approach (Nylander et al. 2004; appropriate likelihood models determined using MODELTEST, ver. 3.06; Posada and Crandall 1998). Clade support for parsimony/likelihood and Bayesian analyses were determined via 1,000 nonparametric bootstrap pseudoreplicates, each with 10 random-taxon-addition replicates, and posterior probability (nchains = 8;

ngenerations (gen) = 5×10^7 ; startingtree = random, burnin = 10^6 gen).

Divergence Time Analysis

Divergence time estimates were obtained using a Bayesian relaxed molecular clock (MULTIDISTRIBUTE package: <http://statgen.ncsu.edu/thorne/multidivtime.html>; programs italicized below; Thorne et al. 1998; Thorne and Kishino 2002) with the B, P, and I constrained by nine, five, and four independent fossil calibrations, respectively

(table 1). First, each of the 15 taxon/locus data sets were analyzed using the program PAML (ver. 3.13; Yang 1997) to determine appropriate nucleotide substitution model parameters. Second, the program *estbranches* was used to estimate branch lengths and the variance-covariance structure of these estimates for all genes. Finally, the application *multidivtime* was used to incorporate the results of *estbranches* and numerous fossil-based calibrations to determine the posterior estimates of clade divergence times ($\text{ngen} = 10^6$) on each data set individually and for the combined data sets of each group. The first appearance of a group in the fossil record was inferred to represent its minimum age. Thus, the majority of calibration points were open-ended minimum ages (e.g., node > 60 mya). Calibration details are detailed in table 1, with additional information (including root node calibration) available in the appendix in the online edition of the *American Naturalist*. For each analysis, one prior and two posterior distributions were obtained. In order to verify that the Markov chain Monte Carlo had reached a stable approximation of the posterior distribution, analyses of combined data sets were run one additional time with $\text{ngen} = 10^7$.

Given that our B, P, and I data sets share three nuclear loci (BDNF, NT-3, RAG1), we conducted an additional dating analysis with a supertree including all three groups and the addition of GenBank sequence data (*Xenopus*, *Gallus*, *Alligator*, and *Mus*) and divergence time calibrations for distant outgroups spanning the synapsid-diapsid divergence 338–288 mya (Graur and Martin 2004) and the avian-crocodylian split 227–242 mya (Reisz and Müller 2004). There has been some concern regarding the influence of the specified prior for the age of the root node on posterior estimates of divergence times. To examine these effects, we conducted additional analyses of the three (B, P, and I) data sets in which we increased and decreased the prior age of the root node (rttm) by 25% as well as conducting runs in which we specified an exceedingly large standard deviation (rttmsd) of this prior by setting rttmsd equal to rttm.

To gauge the accuracy of the fossil calibration points employed in these analyses, we implemented a slightly modified fossil cross-validation analysis modeled after Near and Sanderson (2004) and Near et al. (2005) on the three separate data sets (B, P, and I). Given n calibration points for a particular phylogeny, we conducted n *multidivtime* analyses using only one of the calibration points at a time (fig. 2; for an explanation of the method, see table 2). For nodes on which we placed both upper and lower bounds, we treated these separately, testing the adequacy of each constraint, by running two *multidivtime* analyses. Though the specification of nodal constraints is somewhat different in *multidivtime* and r8s (used by Near and Sanderson [2004] and Near et al. [2005]), our cross-

validation analyses differ from theirs in that our n analyses were conducted with the single calibration point kept as an upper or lower bound rather than a fixed age.

New sequences were deposited in GenBank under accession numbers AY987964–AY988105. Accession numbers of existing sequences and specimens/tissues, nucleotide substitution models employed, phylogenetic trees for individual genes, and fossil calibration data are available in the appendix.

Results and Discussion

Results of Phylogenetic Analyses

We used sequence data from four or five nuclear loci for each lineage (as well as mitochondrial data for B and P) to determine relationships and quantify the ages of the Malagasy B, P, and I. Extrafamilial outgroups were used to root the trees. Phylogenetic hypotheses resulting from analyses utilizing different optimality criteria (maximum parsimony, maximum likelihood, and Bayesian analysis) did not differ in any relevant respects. In the P and I, the Malagasy + South American taxa formed monophyletic units (fig. 3a, 3c), indicating a close relationship between these geographic areas. The Iguanidae do, however, have a single genus in Fiji (*Brachylophus*) that appears to be nested within the South American clade. This unusual pattern of relationships appears to be the result of dispersal (Sites et al. 1996) and does not negate the hypothesis of a Late Cretaceous vicariant event between the Malagasy and South American (including *Brachylophus*) clades. The relationships within Boidae have recently been presented and discussed in more detail elsewhere (Noonan and Chippindale 2006), and as with iguanids, the Pacific island representatives are more closely related to Neotropical than Malagasy taxa.

Biogeographic Hypotheses

The similar pattern of relationships across diverse taxonomic groups that we demonstrate suggests a common evolutionary history that could be the result of vicariance. We suggest three potential vicariant origins of the Malagasy taxa studied here on the basis of tectonic and paleobiogeographic history: (1) African-Malagasy separation or (2) Malagasy-Antarctic separation (directly [Gunnerus Ridge] or indirectly [Kerguelen Plateau]). These hypotheses would be supported by ages of the Malagasy lineages of ~165 and ~80 mya, respectively, depending on the continental drift scenario chosen. A less popular (3) Laurasian vicariant origin of Malagasy B and I in the late Maastrichtian (~65 mya) has been proposed (Rage 1988, 1996, 2003)

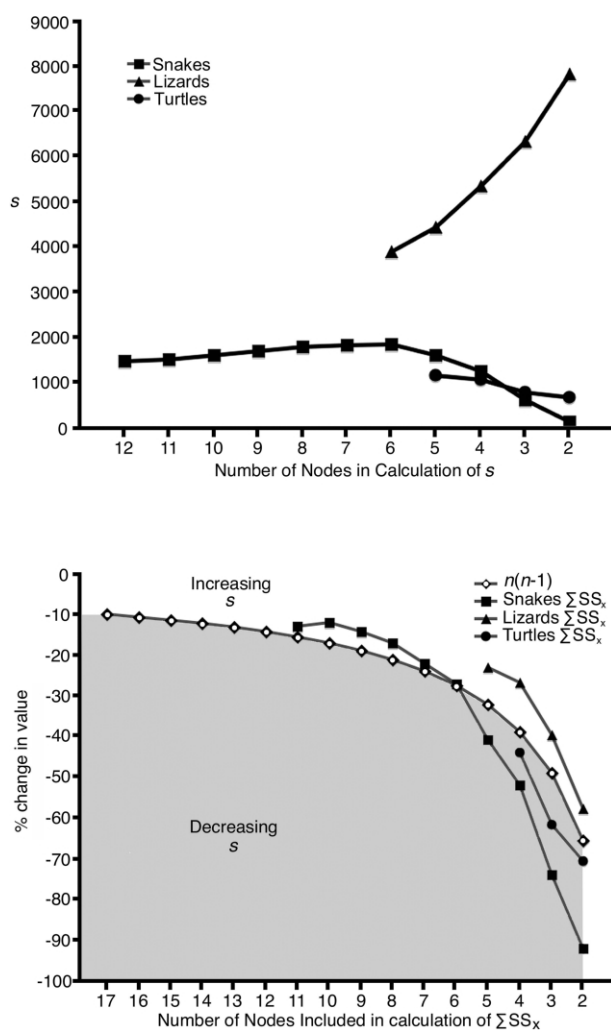


Figure 2: *Top*, plot of s values resulting from sequential removal of fossil calibration points. *Bottom*, illustration of the relationship between ΣSS_x and $n(n-1)$ and their influence on the values of s . Solid points represent the percentage decrease in sequential ΣSS_x values. When calculating values of s , a trend of increasing values will result if the rate of change of ΣSS_x is less than that of $n(n-1)$.

but is poorly supported by geological evidence and the fossil record.

The Mesozoic of Laurasia has produced both acrodont and pleurodont iguanian fossils (Evans et al. 2002), but there is no record of boid snakes, whereas both groups (acrodont iguanians and boid snakes) are known to have been present in South America (B and I; Albino 1996) and India (I; Evans et al. 2002) before the late Cretaceous connection suggested by Rage (1988, 1996, 2003). Additionally, the presence of fossil podocnemid turtles (cf. *Erymnochelys*) in Late Cretaceous formations of Madagascar (Gaffney and Forster 2003) suggests that the Podocnem-

idae already were present on Madagascar at this time. Fossil specimens from the African mainland have been considered allied to or within the genus *Erymnochelys*, though their Oligocene-Pliocene age has little bearing on the question addressed here. Their presence at this late date quite possibly is due to oceanic dispersal from Madagascar, where we know the group to have been present at least 30 million years earlier (for a detailed discussion of the accuracy of identification of this fossil material, see Gaffney and Forster 2003).

Strong evidence for vicariance (1, 2, or 3 above) would be a common age, across groups, of origin of the Malagasy lineages. As noted by de Queiroz (2005), though dispersal hypotheses are unfalsifiable, the rejection of plausible vicariant hypotheses supports dispersal by default. Rejection of these three vicariant hypotheses would be supported by intermediate, significantly younger, or variable (across groups) times of origin and would indicate oceanic dispersal (over the Mozambique Channel or Enderby Basin) as the likely origin of the Malagasy lineages.

Assessing the Accuracy of Priors Used in Divergence Time Analysis

Results from analyses investigating the effect of prior age of root node on posterior estimates of divergence time suggest that increasing or decreasing rtm by 25% has only a minimal effect on point estimates and credibility intervals (average ~5% each). Similarly, increasing the standard deviation of this prior ($rtmsd$) by as much as 10 times (to equal rtm) had even less of an effect on posterior point estimates (<2%) and a similar effect on credibility intervals (~5%).

Implementation of Near et al.'s (2005) fossil cross-validation method yielded somewhat unusual results. While this method has not yet been widely applied, initial implementations have provided similar results with sequential removal of decreasingly high SS_x values (see Near et al. 2005 for a description of statistics and methodology), resulting in a decrease in s (see fig. 3 of Near and Sanderson 2004 and fig. 2 of Near et al. 2005). However, similar plots of our three data sets reveal very different patterns of s resulting from the sequential removal of fossil calibration points (fig. 2, *top*). These results illustrate consistently increasing values of s for the lizard data set, decreasing values for the turtles, and a slight, consistent increase followed by a decrease in the snake analysis. While the use of one-tailed F -tests on the n SS_x values from sequential iterations resulted in no significant values (thus no fossils were deemed inconsistent), the variation in patterns of s across analyses suggests a reappraisal of the utility of this method of visualizing the impact of fossil removal.

Near et al. (2005, p. 140) indicate that they "expect s

Table 2: Procedure for successive calculations employed in fossil cross-validation analysis of Near et al. (2005)

Iteration	F_1	F_2	F_3	
First ($n = 3$):				
F_1	NA	$P_{1,2}$ $(P_{1,2} - X_2)^2$	$P_{1,3}$ $(P_{1,3} - X_3)^2$	$\Sigma = SS_{XF_1}$
F_2	$P_{2,1}$ $(P_{2,1} - X_1)^2$	NA	$P_{2,3}$ $(P_{2,3} - X_3)^2$	$\Sigma = SS_{XF_2}$
F_3	$P_{3,1}$ $(P_{3,1} - X_1)^2$	$P_{3,2}$ $(P_{3,2} - X_2)^2$	NA	$\Sigma = SS_{XF_3}$ $s = \Sigma SS_{X(F_1-F_3)}/n(n-1)$
Second ($n = 2$):				
F_1	NA	$P_{1,2}$ $(P_{1,2} - X_2)^2$	Excluded	$\Sigma = SS_{XF_1}$
F_2	$P_{2,1}$ $(P_{2,1} - X_1)^2$	NA	Excluded	$\Sigma = SS_{XF_1}$
F_3	Excluded	Excluded	Excluded	$s = \Sigma SS_{X(F_1-F_2)}/n(n-1)$
Constraint	X_1	X_2	X_3	

Note: F_x represents a node constrained by a calibration point (X_x years). Values in rows represent the posterior estimates ($P_{x \neq x}$) of all other constrained nodes in a divergence time analysis containing only the single calibration point (F_x). Second iteration reflects removal of F_3 from calculations when $SS_{XF_3} > SS_{XF_1}$ and $SS_{XF_3} > SS_{XF_2}$. NA = not applicable.

to incrementally decrease by a small constant amount as fossils are removed if all calibration points are approximately equally accurate.” While relative constancy in the change of s is likely if all fossils are equally accurately identified and dated, the directionality of this change appears to be entirely unrelated to the quality of the fossils in question for our data sets. As illustrated in fig. 2 (*bottom*), it is clear that although accurate fossils may produce a relatively consistent change in the sum of sum of squares (ΣSS_x), the numerator of the equation of s (see plot of lizard data in fig. 2, *top*), if the rate of this change is slower than that of $n(n-1)$, an increase in s is inevitable. For example, in the calculation of s for the lizard data set with six and five fossil calibration points included, the value of $n(n-1)$ decreases by 30% between the two, whereas SS_x decreases by only 22%. Thus, though ΣSS_x is decreasing by a constant amount, and no particular fossil contributes a disproportionate amount to ΣSS_x (average and standard deviation of SS_x values for lizard data set are 19,513 and 3,755 respectively), s actually increases. Thus, we suggest that plotting the rate of change of ΣSS_x relative to $n(n-1)$ may better illustrate the effect of sequential fossil removal than that of s and facilitate the comparison of results across data sets.

Divergence Time Analyses

Estimates of ages for Malagasy lineages resulting from analyses of individual genes provide a modest range of divergence times (72–95 mya; table 3). Analyses of the

combined gene data sets, which have been shown to provide more accurate estimates of divergence times than single genes alone (Yang and Yoder 2003), demonstrate a common, Late Cretaceous (76–90 mya) origin of the Malagasy B, P, and I (fig. 4). Analysis of the tree containing all taxa and additional outgroups (not shown) also supports this timing of events, with the Malagasy lineages of the B, P, and I dating to 75, 80, and 67 mya, respectively. This indicates that dispersal origins for these groups are highly unlikely. However, the origin of the Malagasy B, P, and I does not appear to be the result of a vicariant event coinciding with the separation of Madagascar from Africa (~165 mya) nor a late Maastrichtian Laurasian connection (~65 mya). The supertree analysis and the 95% credibility intervals of the individual locus analyses of the iguanid data set are not inconsistent with the Laurasian hypothesis, but we emphasize the antiquity of the combined locus estimate (90 mya) and the exclusion of the Laurasian connection from the 95% credibility interval of this analysis (fig. 4). The similarity in ages of the Malagasy B, P, and I lineages strongly indicates that these three groups were isolated by a common event in the Late Cretaceous. Our results support a vicariant origin coinciding with the isolation of Madagascar from a contiguous post-African Gondwana ~80 mya (Hay et al. 1999; Case 2002; Case and Krause 2002). The role of drift vicariance in the diversification of these lineages also is supported by the observed divergence time between the Podocnemidae and the African Pelomedusidae (123 mya, 95% credibility interval = 105–144 mya) that coincides with current es-

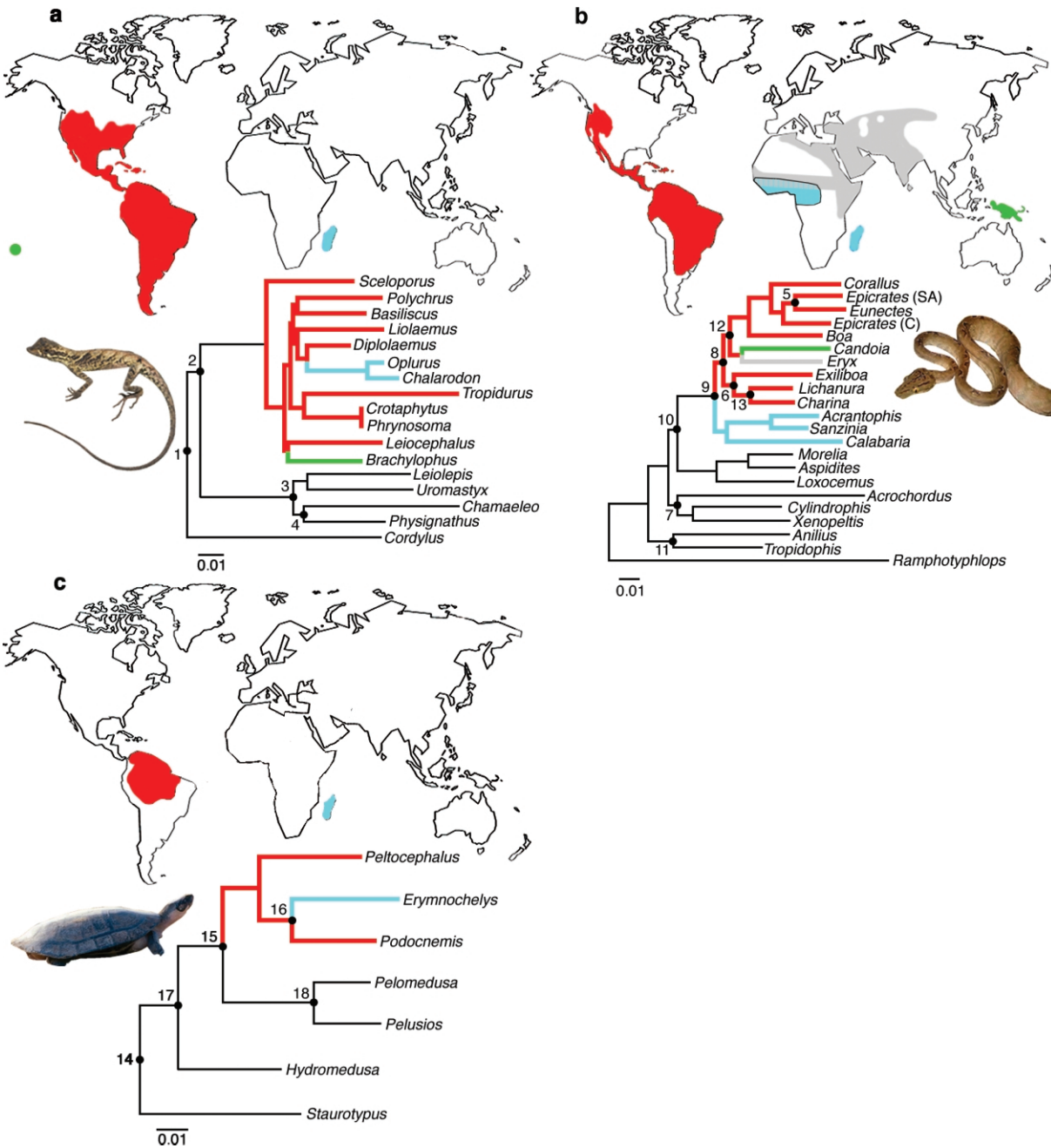


Figure 3: Geographic distribution and inferred phylogenetic relationships of (a) Iguanidae (pleurodont iguanians), (b) Boinae (including the Ungaliophiidae and erycine genera *Eryx*, *Charina*, *Calabaria*, and *Lichanura*), and (c) Podocnemidae. Thick branches indicate clade of interest (boid snakes, podocnemid turtles, and iguanid lizards), with color corresponding to shaded geographic distributions. Thin black branches indicate outgroup taxa included in analysis. Circles indicate location of calibration points used in dating analyses; numbers correspond to calibration points detailed in table 1.

timates of the timing of South American/African separation. These findings provide a stark contrast to previous inferences of the origins of extant Malagasy vertebrates, nearly all of which date to the Cenozoic (fig. 4).

Cretaceous Vicariance of Gondwanan Reptiles

Our results raise obvious questions regarding the absence of extant B, P, and I from India and Australia. The fossil

Table 3: Bayesian estimates of divergence age of Malagasy reptiles

Group and genes (total bp)	Age (mya)
Podocnemidae:	
12S (399)	79 (65–106)
16S (345)	88 (66–122)
NTF3 (580)	85 (66–120)
POMC (521)	91 (67–123)
RAG1 (862)	92 (67–127)
BDNF (717)	81 (66–115)
Six fragments combined	76 (66–96)
Boidae:	
cyt <i>b</i> (1,099)	81 (69–96)
OD (659)	85 (69–104)
CMOS (570)	86 (69–106)
NTF3 (515)	88 (70–108)
BDNF (729)	89 (71–109)
RAG1 (854)	83 (68–101)
Six fragments combined	77 (68–89)
Iguanidae:	
NTF3 (543)	81 (40–130)
BDNF (732)	95 (49–146)
RAG1 (875)	85 (56–123)
CMOS (535)	72 (37–118)
Four fragments combined	90 (67–118)

Note: Numbers in parentheses following age estimates represent 95% confidence intervals.

record indicates that iguanids and the extinct sister group to podocnemids (Bothremydidae; Gaffney et al. 2003) were formerly present in India. Iguanid fossils are extremely rare, but the family is known from the Jurassic of India (Evans et al. 2002). The novel phylogenetic hypothesis of the Boidae presented here suggests that the genus *Eryx* represents the modern Boidae in India and is supported by the Paleocene appearance of erycines in the Laurasian fossil record (Rage 1984). Interestingly, the geographic distribution and relationship to Neotropical taxa of *Eryx* closely mirror the biogeographic history suggested for ratite birds (Cooper et al. 2001). The absence of extant P and I in India may be related to the extensive Deccan Traps volcanism (~66 mya; Officer et al. 1987) associated with the rapid movement of the Indian plate northward. The dissimilarity of the Australian paleofauna from that of the rest of Gondwana is not unique to the B, P, and I (e.g., titanosaurid [Rage 1988] and abelisaurid [Sampson et al. 1998] dinosaurs). The lack of shared faunas between greater Gondwana and Australia may be real (reasons for this have been proposed by Janis 1993), yet the lack of a Late Cretaceous Australian fossil record precludes the conclusion of true absence.

Despite numerous investigations of the evolutionary origins of Malagasy vertebrates, ours is the first study to provide strong, quantitative support for a Gondwanan vic-

ariant origin of any extant Malagasy vertebrate group by falsifying alternative hypotheses of vicariance and dispersal. This evolutionary and biogeographic pattern is independently corroborated by three divergent reptilian lineages. Previous research has suggested a Late Cretaceous subaerial connection between South America and Madagascar/India on the basis of inferred relationships of fossil taxa (Krause et al. 1997a; Sampson et al. 1998; Buckley et al. 2000; Case 2002; Case and Krause 2002; Rage 2003) or the relationships of extra-Malagasy taxa (e.g., ostrich; Cooper et al. 2001; Haddrath and Baker 2001). Our results support the existence of a Late Cretaceous land bridge between Madagascar/India and South America/Antarctica. Furthermore, the submergence of this subaerial connection ~80 mya appears to have resulted in a vicariant origin for the ancestors of living boid snakes, podocnemid turtles, and iguanid lizards of Madagascar.

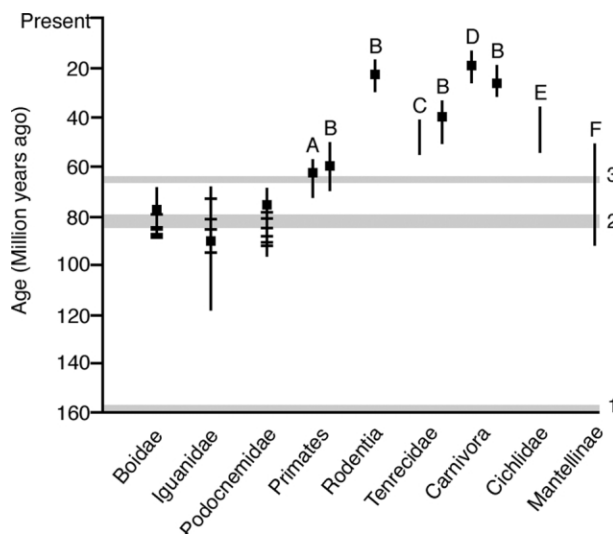


Figure 4: Comparison of estimates of age of Malagasy lineages from this and other studies (A, Yoder et al. 1996; B, Poux et al. 2005; C, Douady et al. 2002; D, Yoder et al. 2003; E, Vences et al. 2001b; F, Bossuyt and Milinkovitch 2001) to proposed vicariant hypotheses: (1) African vicariance, (2) Kerguelen/Gunnerus Ridge vicariance, (3) Laurasian vicariance. Graphical representation of hypotheses 1 and 2 and hypothesis 3 are intended to indicate the latest and earliest possible physical Malagasy connection, respectively. Squares indicate Bayesian posterior age estimates of combined-data analyses, and small horizontal lines represent estimates based on analyses of individual genes. Vertical lines indicate 95% credibility intervals of combined-data analyses for the boid snakes, podocnemid turtles, and iguanid lizards. Estimates of the age of the Cichlidae and Tenrecidae are based on a molecular clock (Vences et al. 2001b; Douady et al. 2002). Estimated age of the Mantellidae represents mean \pm SD of the only estimate obtained by not constraining the node of interest (Mantellidae/Rhacophoridae).

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