

Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas

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Adaptive radiation is the rapid diversification of a single lineage into many species that inhabit a variety of environments or use a variety of resources and differ in traits required to exploit these. Why some lineages undergo adaptive radiation is not well-understood, but filling unoccupied ecological space appears to be a common feature. We construct a complete, dated, species-level phylogeny of the endemic Vangidae of Madagascar. This passerine bird radiation represents a classic, but poorly known, avian adaptive radiation. Our results reveal an initial rapid increase in evolutionary lineages and diversification in morphospace after colonizing Madagascar in the late Oligocene some 25 Mya. A subsequent key innovation involving unique bill morphology was associated with a second increase in diversification rates about 10 Mya. The volume of morphospace occupied by contemporary Madagascan vangas is in many aspects as large (shape variation)—or even larger (size variation)—as that of other better-known avian adaptive radiations, including the much younger Galapagos Darwin's finches and Hawaiian honeycreepers. Morphological space bears a close relationship to diet, substrate use, and foraging movements, and thus our results demonstrate the great extent of the evolutionary diversification of the Madagascan vangas.

core corvoidea | island endemism | lineage diversification | passeriformes | phylogenetics

Adaptive radiation is the rapid diversification of a single lineage into many species that inhabit a variety of environments or niches and differ in the morphological and/or physiological traits required to exploit these environments (1–4). Well-known examples of adaptive radiations include Galapagos finches (5), Hawaiian honeycreepers (6), Hawaiian lobeliads (7), and Caribbean anoles (8). Although evolutionary biologists do not understand why some lineages undergo adaptive radiation and others do not, ecological opportunity appears to be a common feature. Opportunity might arise as a new food resource, a mass extinction of competitors and/or predators, and the colonization of new land or environments (4, 9, 10). Adaptive radiation is ultimately the outcome of divergent natural selection arising from occupation of different environments, use of different resources, or resource competition (4). The progressive filling of ecological space, and the accompanying decrease in ecological opportunity, is expected to result in a decrease in rates of diversification and morphological evolution over time (11, 12).

The bird family Vangidae (15 genera, 22 species) is endemic to Madagascar and considered an extraordinary example of adaptive radiation. This is due particularly to the wide range of foraging strategies as well as to the evolution of striking differences in bill morphology that have allowed vangid species to exploit diverse foraging niches (13, 14). However, the evolutionary history of the group remains poorly understood. Previous systematic analyses have not included all members of the group (15–17), and these studies have not investigated morphological traits in a comparative

phylogenetic framework, precluding in-depth ecological and evolutionary interpretations of this enigmatic bird family.

In this study, we present a complete species-level molecular phylogeny of the Madagascan Vangidae, including representatives of all putative close relatives from Africa and Asia (Table S1). Additional African “vanga” species have previously been included in the family Vangidae by some authors, but a recent study has shown that the Madagascan vangas form a distinct monophyletic group (17). We focus on the phylogeny of the endemic Madagascan vangas to test a number of characteristics pertaining to mode and tempo of adaptive radiation in Madagascar with explicit emphasis on physical, ecological, and evolutionary opportunity required for adaptive radiation, in the sense of Simpson (2), to take place. Specifically, we (i) assess the ecological opportunity available when the ancestral vangid arrived in Madagascar, (ii) examine diversification rates through time, (iii) investigate evolutionary rates of morphological diversification (disparity-through-time plot) in combination with examining tree imbalance to locate specific evolutionary transitions (key innovations) that might have increased speciation rates, and, finally, (iv) use a unique statistical approach to investigate a second speciation pulse that coincides with topological imbalance for a subclade exhibiting a marked shift in foraging strategy (key innovation). Specifically, we test whether the diversification dynamics of that subclade are decoupled from the diversity-dependent pattern of the remaining Madagascan vangas.

Results and Discussion

Adaptive Radiation of the Madagascan Vangidae. The maximum-likelihood analyses and Bayesian analyses performed on our concatenated dataset, and on the individual partitions, yielded trees that were topologically congruent for well-supported nodes (Fig. 1A and Figs. S1–S6). Whereas the individual gene trees all found non-Madagascan taxa, the continental “Vangidae” (*Philentoma*, *Bias*, *Hemipus*, *Tephrodornis*, and *Prionops*), nested within the Madagascan Vangidae clade, analyses of the concatenated dataset recovered the Madagascan Vangidae as monophyletic (with low support). A recent analysis of a 13-gene dataset on most vanga species (17) agrees with our more tentative

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Data deposition: The sequences reported in this paper have been deposited in the GenBank database (accession nos. JQ713360–JQ713529); see also Table S1. Vanga morphological data reported in this paper have been deposited in the Dryad database, <http://dx.doi.org/10.5061/dryad.mh2qf615>.

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finding that the Madagascan Vangidae represent a radiation with a single origin, contrary to conclusions based on previous morphological studies (15). We considered these phylogenetic results good evidence for monophyly, so further analyses focused only on the Madagascan Vangidae (henceforth referred to as Vangidae). Systematic relationships at the base of the Vangidae generally had low support, consistent with rapid diversification in the early history of the group (3, 4, 17), although low support values could also simply reflect poor signal in the data. All recognized genera within the family received high support, as did a clade consisting of *Artamella*, *Falcula*, *Oriolia*, and *Xenopirostris*, and a tight link between *Euryceros* and *Schetba*. A chronogram for the Vangidae (Fig. 2A) suggested that the initial radiation started in the Late Oligocene (23 Mya) and that most recognized genera had already appeared by the mid-Miocene (15 Mya). A recent genus-level phylogeny broadly confirms these results (17). Thus, the Vangidae are old compared with other insular adaptive radiations of birds, such as Galapagos finches and Hawaiian honeycreepers, which started diversifying about 4 and 6 Mya, respectively (18, 19).

The line-through-time plot for the Vangidae indicates high diversification rates at the early stage of the radiation (Fig. 2B, bold line), followed by a slowdown roughly between 20 and 10 Mya. Although this diversification pattern agrees with that of Reddy et al. (17) based on their genus-level phylogeny, our species-level phylogeny suggests a subsequent second radiation burst between 10 and 5 Mya, after which diversification rates once again slowed. Accordingly, the number of speciation events per 1-My interval varied widely through time, decreasing initially but with a distinct second peak (Fig. 2B). We investigated this second burst of radiation more closely using a unique method to detect a decoupling of the diversity-dependent dynamics of the innovative clade from the ancestral clade (i.e., key innovation) in combination with morphological data (discussed in the following sections).

Across the whole phylogeny of Madagascan vangas, we found strong support for decreasing diversification rates through time, a pattern that has been termed “diversity dependence” (20). Both the γ and ΔAIC_{RC} statistics (21, 22) rejected constant diversification rates for the maximum clade credibility (MCC) tree under all tested scenarios (Table S2). The significant decrease in diversification rates through time implies the progressive filling of ecological space as the vangid radiation progressed, which is usually seen as a feature of adaptive radiation (4, 11). It also suggests that the Vangidae have reached their “species carrying capacity” or ecological limit (23).

According to Simpson (2), adaptive radiations emerge from three kinds of ecological opportunity: physical, ecological, and evolutionary. The first criterion merely requires that opportunity exists, and indeed the Vangidae evolved on an ecologically diverse island (13). The second criterion requires that opportunities are not limited by competitors or predators, a hypothesis that has not previously been explicitly tested for vangas (e.g., 15–17). The time of arrival to Madagascar of the ancestral vangid 22–29 Mya coincides with the arrival of several potentially competing types of birds and predatory mammals, such as tenrecs, rodents, and carnivores (24, 25). When vangids colonized Madagascar, all groups of present-day mammals, to the exclusion of lemurs, had only recently become established on Madagascar. Although fossil information is lacking, the contemporary avifauna of Madagascar includes two small, ancient endemic clades of nonpasserine birds (Mesitornithidae and *Leptosomus*), and otherwise only groups that arrived after the colonization of the first vangids. The ancestors of endemic nonpasserine radiations such as the couas (Cuculidae: Couinae) and ground rollers (Brachypteraciidae) initially colonized Madagascar in the Miocene (26–28), and most passerine taxa did not arrive until the Plio-Pleistocene [*Dicurus* (29); *Nectarinia* (30); *Zosterops* (31); bulbuls (32)], except for a few groups that arrived in the Miocene [*Foudia* (33); *Coracina* (34)]; possibly Madagascan warblers, Bernieridae (28)]. However, most bird groups are represented by a few, relatively undiversified species. We cannot exclude significant extinction of a previously diverse fauna that might have occupied Madagascar in the Miocene, but given that the

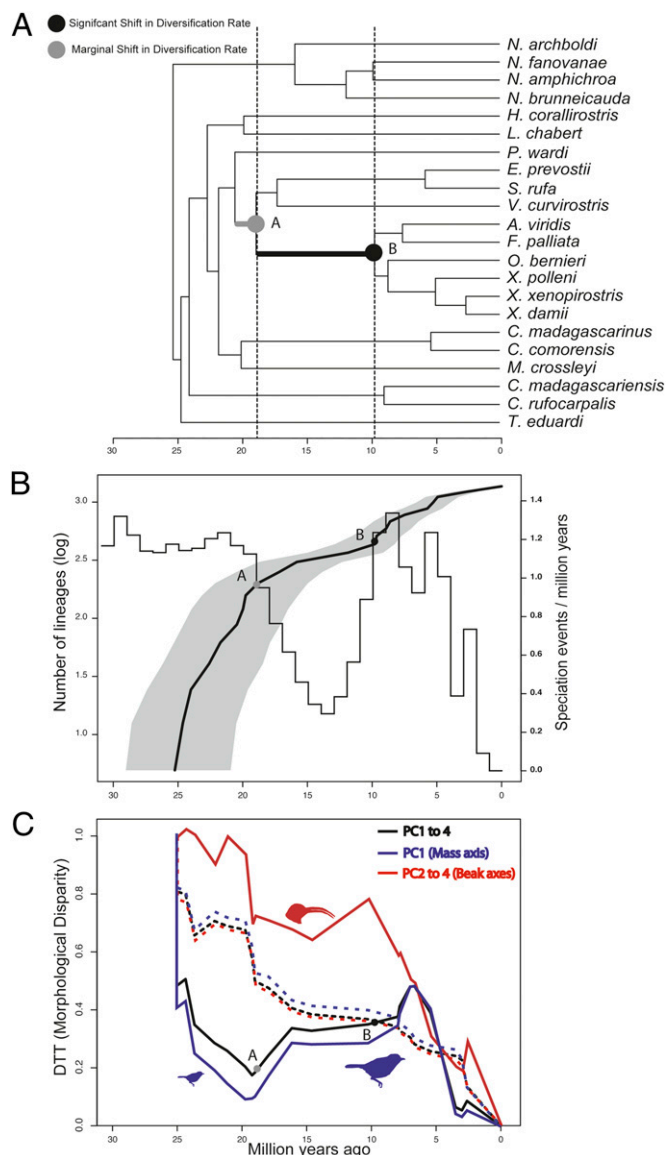


Fig. 2. (A) BEAST chronogram of the Vangidae pruned to only include one individual per species. (B) Lineage-through-time plot (bold line) with error margins (shaded gray) and speciation events per million y (thin line). (C) Disparity-through-time plot of PC axes 1–4, PC axis 1 and PC axes 2–4. Average extant disparity at a given point in time is the average disparity of subclades whose ancestral lineages were present at that time relative to the disparity of the entire taxon. The higher the value of relative disparity, the greater the average volume of morphological space occupied by subclades relative to the morphological disparity of the taxon as a whole. The dotted line shows mean simulated disparity under a Brownian-motion model (35).

present fauna is depauperate compared with ecologically similar continental areas, the first vangid ancestor likely arrived on an island with abundant physical and ecological opportunity.

Morphological Diversification. Simpson’s (2) third criterion refers to the appearance of novel evolutionary adaptations. To trace the connection between morphological adaptation and diversification, we examined seven morphological traits (wing length, tail length, tarsus length, middle toe length, and the length, width, and depth of the culmen measured at the base). In a principal components (PC) analysis, the first axis (PC1) was linked to size and explained 81.6% of the total variance. The other prominent axes (PC2–PC4) were related to shape variation, particularly with respect to bill size

included the same initial speciation rate and extinction rate, but a different “clade carrying capacity.” Thus, the accumulation of lineages through time provides support for the Madagascan vangas as two radiations in one, with a subclade increasing the ecological species limit as a whole about 10 Mya, although both radiations have apparently reached their ecological limits at present. Vangid congeners are largely allopatric and ecomorphologically similar and, as such, may not count fully in an adaptive radiation. However, the decoupling of diversification dynamics for the subclade descending from node B was significant, even when treating the species within each of the genera *Newtonia*, *Xenopirostris*, *Calicalicus*, and *Cyanolanius* as single taxa.

The second speciation burst therefore constitutes a significant second radiation, probably due to a key innovation. Our results show that it is consistent with species within subclade B partitioning beak morphospace, as indicated by the second peak in the PC axes 2–4 around 10 Mya (Fig. 2C). However, it is not only the design of the bill that matters but also the way it is put to use. Members of clade B exhibit unusual adaptations in foraging behavior (cf. 17). All members are probers, and *Xenopirostris*, *Oriolia*, and *Artamella* species strip bark off trees to search for food underneath, whereas *Falcula* has evolved a long decurved bill, which it uses to retrieve prey items hidden underneath the bark or in deep crevices. This “woodcreeper” key innovation may have been so advantageous that the clade was able to radiate significantly, even after the vangids as a whole had reached an ecological limit signified by a decreasing diversification rate. We propose that this key innovation at node B caused a second adaptive radiation in a clade that had already diversified adaptively, with each genus within clade B filling a slightly different foraging niche.

In conclusion, phylogenetic diversification rates combined with morphological trait measurements demonstrate that the Vangidae constitute a textbook example of an adaptive radiation with a complex history of ecological innovation. The adaptation of bill shapes for different foraging techniques may have partitioned the ecological space among subclades and driven diversification in Madagascan vangas, comparable in scope to other bird radiations (i.e., Galapagos finches, Hawaiian honeycreepers). The strong evidence we show for decreasing diversification rates over time may be interpreted as a sign of progressive niche filling, which would be expected for an adaptive radiation (4, 11, 41). In addition, our results suggest that a key innovation in beak shape supportive of novel woodcreeper foraging behaviors within the family created a second adaptive radiation with a second burst of speciation.

Materials and Methods

Taxon Sampling and Phylogenetic Analyses. We sequenced six genes (four nuclear introns, one nuclear coding region, and one mitochondrial gene, in total 3,977 bp) for all 22 putative members of the Vangidae. In the phylogenetic analyses, we included a number of African and Asian species that have been demonstrated to be closely related to the Vangidae (Table S1). We used MrBayes version 3.1.2 (42) to estimate phylogenetic relationships. Substitution models were determined with MrModeltest version 2.0 (43), using the Akaike information criterion (AIC) (44). In the analyses of individual genes, four Metropolis-coupled Markov chain Monte Carlo (MCMC) simulations, one cold and three heated, were run for 20 million iterations with trees sampled every 500 iterations. For the combined analysis, the MCMC was run for 50 million iterations. The burn-in and convergence diagnostics were graphically assessed using AWTY (45). Maximum-likelihood analyses were performed using GARLI version 0.95 (46). Five independent analyses (50 million generations) were performed, and nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications.

Dating Analyses. We used BEAST version 1.5 (47, 48) to estimate the divergence dates within Vangidae; we assigned the best-fitting model, as estimated by MrModeltest version 2.0 (43), to each of the partitions. We assumed a Yule speciation process for the tree prior and an uncorrelated log-normal distribution for the molecular clock model (49). We used default prior distributions for all other parameters and ran MCMC chains for 50

million generations. We used the program Tracer (50) to assess convergence diagnostics.

To obtain absolute diversification times, we relied on two previously published age estimates within the Passeriformes (the age of Acanthisittidae versus other passerines at $76 \text{ My} \pm 8 \text{ SD}$, and the age of the basal oscine divergence at $63 \pm 2 \text{ SD}$) generated by Barker et al. (51) based on three different approaches. The confidence intervals for our calibration points represent averages, with 95% confidence intervals including the most extreme ages in the study.

The use of secondary calibration points is associated with substantial error margins. To further corroborate the absolute dating estimates, we assessed the molecular rate of evolution (corrected pairwise distances) for the mitochondrial marker (ND2) for nodes younger than 12 My, which has been demonstrated to maintain a rate of evolution of $\sim 2\%$ per My (52). The two dating approaches produced congruent results.

Morphology. To examine the history of morphological variation, we measured 1–21 individuals (in total 264 individuals) of each of 22 species of vangas from museum collections around the world (deposited in Dryad; <http://dx.doi.org/10.5061/dryad.mh2qf615>). The characters examined (wing length, tail, tarsus, and middle toe, and the length, width, and depth of the culmen measured at the base) are believed to represent various aspects of adaptation to differences in habitat use and foraging strategies (53, 54). All values were log-transformed, and a principal components analysis [prcomp command in R version 2.10.1 (55)] was used to reduce dimensionality of our dataset and to account for correlations among characters due to overall body size.

To assess correlation between speciation events and morphological evolution within the Vangidae, we applied the morphological disparity-through-time procedure (35). DTT analyses simulate morphological disparity under a model of Brownian motion and compare this simulation to the observed phenotypic disparity among and within subclades relative to total disparity at all time bins in a phylogeny. DTT was computed using the average squared Euclidean distances implemented in the GEIGER package for R (56). The morphological disparity index was computed to assess whether disparity within lineages was less than or greater than the median expectations of the null model.

Madagascan morphological diversification was compared with the Passeriformes as a whole based on a principal components analysis calculated from the covariance matrix of seven \log_{10} -transformed variables measured on 1,612 species broadly sampled, including all 22 species of Madagascan Vangidae and 11 continental species in the genera *Philentoma*, *Hemipus*, *Tephrodornis* (Asia), *Prionops*, and *Bias* (Africa). (Inquiries concerning these data should be directed to R.E.R.)

Analyses of Diversification Rates and Tree Imbalance. We used two statistical measures to test for constant diversification rates in the phylogeny of Vangidae: the γ statistic (21) and $\Delta\text{AIC}_{\text{RC}}$ (22). One thousand trees were randomly sampled from the posterior distribution of the dating analysis, disregarding the burn-in, to take uncertainty in phylogenetic reconstruction into account. All diversification rate analyses were carried out on the MCC tree and those 1,000 posterior trees. Multiple sequences, outgroups, and continental vangas were deleted from the trees, so that each Madagascan vanga species was represented by only one tip. Analyses were run in R version 2.10.1 (55) and its contributed package LASER (57).

We used LASER to generate four sets of null distributions for each of our statistics, by simulating 5,000 trees under the pure-birth model (constant speciation rate, no extinction), for each set. Because our phylogenetic reconstructions included all 22 known species, we did not have to account for unsampled species (e.g., 17, 20). The first set of trees was simulated to grow from the root until the tip number reached 22, which assumes that 100% of the vanga species are known. We then simulated trees under each of the assumptions that 75%, 50%, and 25% of vanga species are known, and subsequently deleted tips at random until the simulated trees contained 22 tips. This procedure takes into account undescribed or extinct species, assuming that these are missing at random in the phylogeny (20, 21).

Strongly negative γ values indicate a decrease in diversification rates through time, so we tested the observed γ values against the four sets of null simulations with one-tailed tests (21). We fitted five diversification models to our trees in a maximum-likelihood framework (22), two of which had constant diversification rates through time (the pure-birth model and a birth–death model with constant, above-zero speciation and extinction rates) and three of which were rate-variable models (models of diversity-dependent diversification with logistic and exponential growth rates, and a modified pure-birth model with one switch between two constant

speciation rates). To avoid inflation of type I error rates, the $\Delta\text{AIC}_{\text{RC}}$ statistic is then the difference in AIC values of the best rate-variable model and the best rate-constant one, so we tested for significantly positive $\Delta\text{AIC}_{\text{RC}}$ values with one-tailed tests (22).

Furthermore, we assessed whether diversification rates have been equal throughout the evolutionary history of the Vangidae (i.e., the MCC tree). We computed the β parameter with the R package apTreeshape (58), which compares nodal imbalance throughout the phylogeny to the equal-rates Markov model (36). Under this null model, every node should have an equal chance of diversification, and β should be indistinguishable from zero. Strongly negative β values indicate strong imbalance, whereas strongly positive values indicate unusual balance; both cases imply that diversification rates may have varied through time and/or between clades.

Two approaches to identify nodes with unusually high numbers of descendants (i.e., unusually species-rich clades) were used: the $\Delta 1$ statistic, which considers topological information only (37, 59), and the relative cladogenesis test, which tests lineages within time slices along the whole phylogeny for differences in the number of descendants (38). These were calculated in R with the packages GEIGER (56) and apTreeshape (58).

Finally, we used a novel likelihood approach developed by Etienne and Haegeman (39) to detect whether and where a key innovation may have occurred. A key innovation is defined here as a decoupling of the diversity-dependent dynamics of the innovative clade from the ancestral clade. This decoupling only makes sense when diversification is diversity-dependent, because then it matters which species contribute to the diversity dependence. We compared models with an overall (i.e., anywhere in the phylogeny) rate shift between branching time A and branching time B and key innovation models where the subclade originates from node B but the key innovation itself may have happened anywhere between node A and node B. We used the AIC to differentiate between the models (39).

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