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 (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
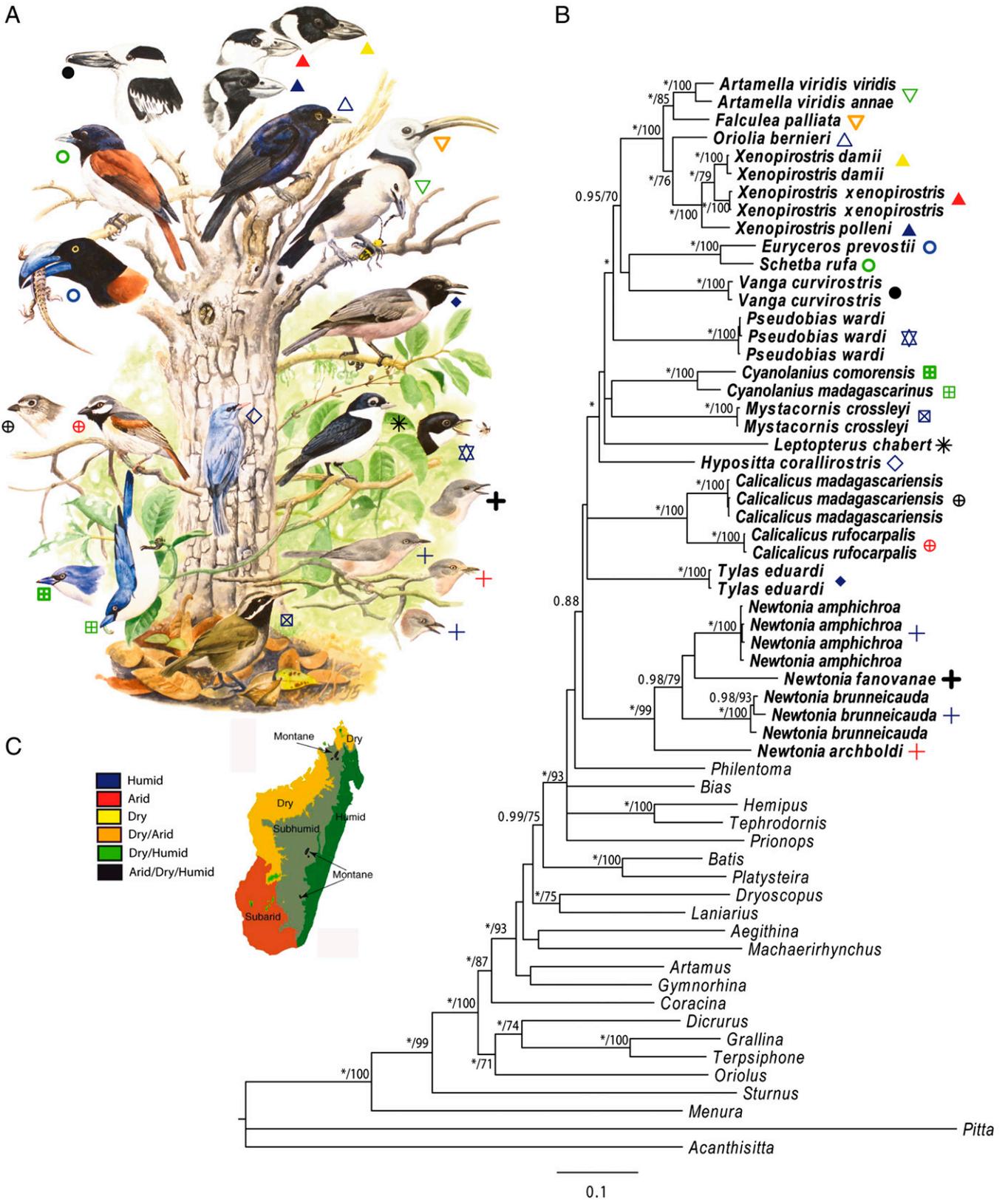
EVOLUTION

Fig. 1. (*A*) Watercolor by J.F. illustrating the Madagascan vanga species and morphological diversity. From the bottom moving clockwise: *Mystacornis crossleyi*, *Cyanolanius* (two species), *Calicalicus* (two species), *Euryceros*, *Schetba*, *Vanga*, *Xenopirostris* (three species), *Oriolia*, *Falculea*, *Artamella*, *Leptopterus*, and *Newtonia* (four species). (*B*) Bayesian topology of the Vangidae and other closely related core corvoids obtained from the combined dataset of six genes (Myo, ODC, GAPDH, Fib-5 *c*-mos, and ND2). Bayesian posterior probabilities >0.90 (except for the Madagascan vanga clade, pp = 0.88 are indicated to the left of the nodes (asterisks indicate posterior probabilities of 1.00) followed by maximum-likelihood bootstrap values ≥70% from 100 pseudoreplicates. (*C*) Map of Madagascar depicting the main habitat zones.

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*, *Falculea*, *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 lineage-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 non-passerine 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 [*Dicrurus* (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
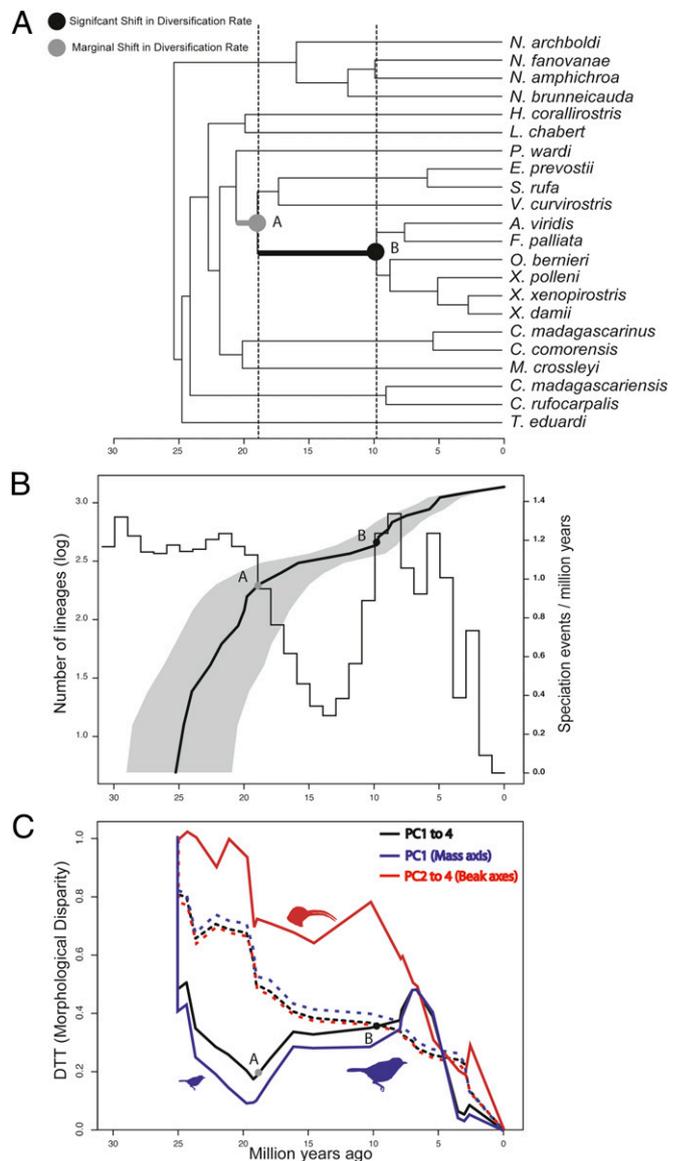

Fig. 2. (A) BEAST chronogram of the Vangidae pruned to only include one individual per species. (B) Lineage-through-time plot (bold line) with error margins (shaded gray) and speciation events pr million y (thin line). (C) Disparity-through-time plot of PC axes 1–4, PC axis 1 and PC axes 2–4. Average 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

and shape, and explained 14.1% of the total. We then generated disparity-through-time (DTT) plots (Fig. 2C), which partition the contemporary morphological diversity among lineages existing at each time point during the history of the clade (35). Observed morphological disparity among lineages was compared with expected disparity based on simulating a morphological character evolving under a random walk on the phylogenetic tree (35). 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 average disparity in beak morphology is much higher within subclades than expected under Brownian motion, indicating that vangid species within subclades have diversified in beak morphology to the extent that the subclades overlap in beak morphospace (Fig. 2C). In contrast, disparity in all PC axes together, and in the axis reflecting body size in particular, is partitioned among rather than within subclades, suggesting that subclades occupy different parts of the body-size spectrum and that body size has evolved relatively little since its initial diversification among the major clades of Vangidae.

Our results for body size (PC1) therefore concur with adaptive radiation theory: Clades that accumulate species rapidly appear to fill size-dependent ecological space quickly, because subclades evolve to fill different parts of morphospace or adaptive zones (35). Within these adaptive zones of body size occupied by the different subclades, species within subclades subsequently diverged with respect to beak morphology, indicating adaptive differentiation of diet and foraging modes within subclades, to the degree that some species from different subclades occupy the same parts of beak morphospace. Based on an ancestral reconstruction of foraging behavior, Reddy et al. (17) suggested that the diversification of vangas reflected early adaptation to different feeding strategies in the group. The overlap of subclades in beak morphospace and their differentiation in body size shown here suggest a more complex, possibly two-step adaptive process, a hypothesis we investigate in detail in the next section.

Although the ecological space occupied by species of Madagascan vangids has not been characterized directly, one can estimate space filling in comparative analyses by the occupation of morphological space (Fig. 3), which bears a close relationship to diet, substrate use, and foraging movements. Strikingly, the Madagascan radiation has produced nearly the variance in size (PC1) exhibited by passerine birds as a whole, and somewhat more than observed in the Hawaiian honeycreepers and Galapagos finches. Shape variation (PC2–PC6) is less extensive, but is largely outside the range of other passerines on PC5 (bill width/bill depth), the Madagascar species tending to have deep, narrow bills. Thus, the classic island radiations—and the Madagascan vangids are no exception—tend to fill morphological space idiosyncratically and have not achieved the morphological diversity of complete continental passerine avifaunas. Nonetheless, the Madagascan Vangidae species are among the most diverse morphologically of passerine families, which is consistent with rapid diversification in a largely open ecological space.

Two Adaptive Radiations in One. Going beyond previous studies, we show that the high initial speciation rate and subsequent marked slowdown were followed by a second peak in speciation rate in the Late Miocene before diversification again slowed toward the present (Fig. 2B); this second peak in lineage diversification coincided with a marginal second peak in the disparity of bill morphology (Fig. 2C). Simpson's (2) third criterion (evolutionary adaptations) explicitly refers to the consequence of a key innovation, that is, the promotion of diversification by providing access to new ecological space. We suggest that the second peak in diversification might have followed a morphological key innovation within the Vangidae, providing a subclade of vangas new ecological opportunity through changing morphology.

To test this hypothesis, we first investigated tree imbalance of the Madagascan vangas, because a significant departure from the appropriate null model (the equal-rates Markov model) should indicate whether lineages within a tree have diversified with different
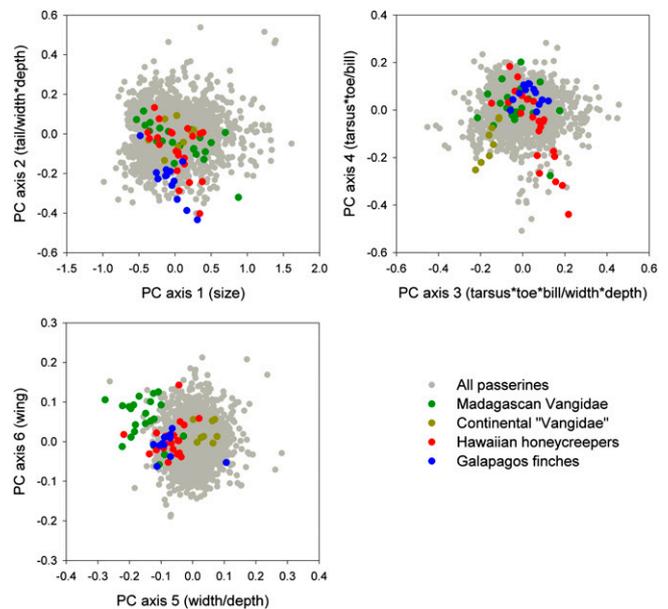

Fig. 3. The morphological distribution of 22 Madagascan vangid species, and 11 continental species in the genera *Philentoma*, *Hemipus*, *Tephrodornis* (Asia), *Prionops*, and *Bias* (Africa), on one size and five shape principal components axes, compared with identical measurements for species in two other monophyletic island passerine bird radiations (Hawaiian honeycreepers and Galapagos finches), against a background of 1,590 additional species of passerine birds sampled globally.

rates (36). The Vangidae phylogeny was significantly more imbalanced than expected under the equal-rates Markov model (MCC tree, $\beta = -1.09$, upper confidence interval limit $= -0.05$), but no single node in the phylogeny showed significant imbalance according to the $\Delta 1$ statistic (37). We did, however, find a significant shift in diversification rate at node B ($P = 0.039$) when applying the relative cladogenesis test, which compares diversification rates for lineages within time slices (38). The clade descending from node B (Fig. 2A) is therefore unusually diverse given diversification rates for the vangids as a whole, and appears to have increased the species carrying capacity for Madagascan vangas. This clade consists of a group of species with strongly divergent bill morphologies: heavy bills for *Xenopirostris* and a long bill for *Falculea* (Fig. 1). The only other species with heavy bills (*Vanga* and *Euryceros*) are found in the sister clade, and it is noteworthy that this clade (node A in Fig. 2A) includes all of the descendants with massive bills, although the diversification rate shift at this node A is only marginally significant (rate cladogenesis test, $P = 0.057$).

To further test the hypothesis of diversification resulting from a key innovation in this subclade, we used the key innovation model of Etienne and Haegeman (39) that is based on the Etienne et al. (40) diversity-dependent birth–death model (where the speciation rate is assumed to be linearly declining with diversity). This key innovation model assumes that diversification is generally diversity-dependent, but key innovations decouple the diversification dynamics of the clade having the key innovation from that of the species lacking it. This decoupling removes the constraint of competition from other species on the innovative lineage, providing the opportunity for rapid radiation. The likelihood approach developed by Etienne and Haegeman (39) for testing this key innovation model also allows for estimating the diversification parameters, including clade-level carrying capacities for the subclade and the main clade (Table S3). We found strong support for a decoupling of diversification dynamics for the subclade descending from node B (the node found to be significantly imbalanced and including species with a divergent bill morphology) from the diversity dependence of the remaining vangids. The fitted parameters for this subclade

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. 2*C*). 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 *Falculea* 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 My $\pm$ 8 SD, and the age of the basal oscine divergence at 63 $\pm$ 2 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 ~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 ΔAIC_{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 ΔAIC_{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 ΔAIC_{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).

1. Osborn HF (1902) The law of adaptive radiation. *Am Nat* 36:353–363.
2. Simpson GG (1953) *The Major Features of Evolution* (Columbia Univ Press, New York).
3. Givnish TJ (1997) *Molecular Evolution and Adaptive Radiation*, eds Givnish TJ, Sytsma KJ (Cambridge Univ Press, Cambridge, UK), pp 1–54.
4. Schluter D (2000) *The Ecology of Adaptive Radiation* (Oxford Univ Press, Oxford).
5. Grant PR, Grant BR (2008) *How and Why Species Multiply: The Radiation of Darwin's Finches* (Princeton Univ Press, Princeton, NJ).
6. Pratt HD (2005) *The Hawaiian Honeycreepers: Drepanididae* (Oxford Univ Press, Oxford).
7. Givnish TJ, et al. (2009) Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proc Biol Sci* 276:407–416.
8. Losos JB (2009) *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles* (Univ of California Press, Berkeley, CA).
9. Losos JB, Mahler DL (2010) *Evolution Since Darwin: The First 150 Years*, eds Bell MA, Futuyma DJ, Eanes WF, Levinton JS (Sinauer, Sunderland, MA), pp 381–420.
10. Glor RE (2010) Phylogenetic approaches to the study of adaptive radiation. *Annu Rev Ecol Evol Syst* 41:251–270.
11. Gavrilets S, Vose A (2005) Dynamic patterns of adaptive radiation. *Proc Natl Acad Sci USA* 102:18040–18045.
12. Rabosky DL (2009) Ecological limits on clade diversification in higher taxa. *Am Nat* 173:662–674.
13. Schulenberg TS (2003) *The Natural History of Madagascar*, eds Goodman SM, Benstead JP (Univ of Chicago Press, Chicago), pp 1130–1134.
14. Yamagishi S, Nakamura M (2009) *Handbook of the Birds of the World*, eds del Hoyo J, Elliott A, Christie DA (Lynx Edicions, Barcelona), Vol 14, pp 142–170.
15. Manegold A (2008) Composition and phylogenetic affinities of vangas (Vangidae, oscines, Passeriformes) based on morphological characters. *J Zool Syst Evol Res* 46:267–277.
16. Yamagishi S, Honda M, Eguchi K, Thorstrom R (2001) Extreme endemic radiation of the Malagasy vangas (Aves: Passeriformes). *J Mol Evol* 53(1):39–46.
17. Reddy S, Driskell A, Rabosky DL, Hackett SJ, Schulenberg TS (2012) Diversification and the adaptive radiation of the vangas of Madagascar. *Proc Biol Sci*, 10.1098/rspb.2011.2380.
18. Sato A, et al. (1999) Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proc Natl Acad Sci USA* 96:5101–5106.
19. Lerner HRL, Meyer M, James HF, Hofreiter M, Fleischer RC (2011) Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian honeycreepers. *Curr Biol* 21:1838–1844.
20. Rabosky DL, Lovette IJ (2008) Density-dependent diversification in North American wood warblers. *Proc Biol Sci* 275:2363–2371.
21. Pybus OG, Harvey PH (2000) Testing macro-evolutionary models using incomplete molecular phylogenies. *Proc Biol Sci* 267:2267–2272.
22. Rabosky DL (2006) Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 60:1152–1164.
23. Rabosky DL (2009) Ecological limits and diversification rate: Alternative paradigms to explain the variation in species richness among clades and regions. *Ecol Lett* 12:735–743.
24. 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.
25. Yoder AD, et al. (2003) Single origin of Malagasy Carnivora from an African ancestor. *Nature* 421:734–737.
26. Johnson KP, Goodman SM, Lanyon SM (2000) A phylogenetic study of the Malagasy couas with insights into cuckoo relationships. *Mol Phylogenet Evol* 14:436–444.
27. Kirchman JJ, Hackett SJ, Goodman SM, Bates JM (2001) Phylogeny and systematics of ground rollers (Brachypteraciidae) of Madagascar. *Auk* 118:849–863.
28. Cibois A, Slikas B, Schulenberg TS, Pasquet E (2001) An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. *Evolution* 55:1198–1206.
29. 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(1):158–167.
30. Warren BH, Bermingham E, Bowie RCK, 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(1):67–85.
31. 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.
32. Warren BH, Bermingham E, Prys-Jones RP, Thébaud C (2005) Tracking island colonization history and phenotypic shifts in Indian Ocean bulbuls (Hypsipetes: Pycnonotidae). *Biol J Linn Soc Lond* 85:271–287.
33. Prager M, Johansson EIA, Andersson S (2008) A molecular phylogeny of the African widowbirds and bishops, *Euplectes* spp. (Aves: Passeridae: Ploceinae). *Mol Phylogenet Evol* 46:290–302.
34. Jønsson KA, et al. (2010) Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): Transoceanic colonization of Africa from Australo-Papua. *J Biogeogr* 37:1767–1781.
35. Harmon LJ, Schulte JA, II, Larson A, Losos JB (2003) Tempo and mode of evolutionary radiation in iguanian lizards. *Science* 301:961–964.
36. Aldous DJ (2001) Stochastic models and descriptive statistics for phylogenetic trees, from Yule to today. *Stat Sci* 16(1):23–34.
37. Chan KMA, Moore BR (2002) Whole-tree methods for detecting differential diversification rates. *Syst Biol* 51:855–865.
38. Nee S, Mooers AO, Harvey PH (1992) Tempo and mode of evolution revealed from molecular phylogenies. *Proc Natl Acad Sci USA* 89:8322–8326.
39. Etienne RS, Haegeman B (2012) A conceptual and statistical framework for adaptive radiations with a key role for diversity-dependence. *Am Nat*, in press.
40. Etienne RS, et al. (2012) Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. *Proc Biol Sci* 279:1300–1309.
41. Phillimore AB, Price TD (2008) Density-dependent cladogenesis in birds. *PLoS Biol* 6:e71.
42. Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
43. Nylander JAA (2004) MrModeltest (Uppsala University, Uppsala) (http://www.abc.se/~nylander), Version 2.
44. Posada D, Buckley TR (2004) Model selection and model averaging in phylogenetics: Advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Syst Biol* 53:793–808.
45. Nylander JAA, Wilgenbusch JC, Warren DL, Swofford DL (2008) AWTY (are we there yet?): A system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics* 24:581–583.
46. Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD dissertation (Univ of Texas at Austin, Austin, TX).
47. Drummond AJ, Ho SYW, Phillips MJ, Rambaut A (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biol* 4:e88.
48. Drummond AJ, Rambaut A (2007) BEAST (http://beast.bio.ed.ac.uk), Version 1.4.7.
49. Ho SYW (2007) Calibrating molecular estimates of substitution rates and divergence times in birds. *J Avian Biol* 38:409–414.
50. Rambaut A, Drummond AJ (2007) Tracer (http://beast.bio.ed.ac.uk/Tracer), Version 1.4.
51. 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.
52. Weir JT, Schluter D (2008) Calibrating the avian molecular clock. *Mol Ecol* 17:2321–2328.
53. Ricklefs RE, Travis J (1980) A morphological approach to the study of avian community organization. *Auk* 97:321–338.
54. Miles DB, Ricklefs RE, Travis J (1987) Concordance of eco-morphological relationships in three assemblages of passerine birds. *Am Nat* 129:347–364.
55. R Development Core Team (2009) *R: A Language and Environment for Statistical Computing* (R Found for Stat Comput, Vienna).
56. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W (2008) GEIGER: Investigating evolutionary radiations. *Bioinformatics* 24(1):129–131.
57. Rabosky DL (2006) LASER: A maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evol Bioinformatics* 2:247–250.
58. Bortolussi N, Durand E, Blum M, François O (2006) apTreeshape: Statistical analysis of phylogenetic tree shape. *Bioinformatics* 22:363–364.
59. Chan KMA, Moore BR (2005) SYMMETREE: Whole-tree analysis of differential diversification rates. *Bioinformatics* 21:1709–1710.