# 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

daptive radiation is the rapid diversification of a single line-A daptive radiation is the rapid diversities and a series 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 maximumlikelihood 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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**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  $\geq$ 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. 2*B*, 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. 2*B*). 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  $\gamma$  and  $\Delta AIC_{RC}$  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 [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

N. brunneicauda H. corallirostris L chabert P. wardi F prevostii S. rufa curvirostris viridis palliata 0 bernieri х polleni xenopirostris X damii madagascarinus C comorensis M. crosslevi C. madagascariensis . rufocarpalis . eduardi C В 3.0 Speciation events / million years of lineages (log) Number С - PC1 to 4 0 PC1 (Mass axis) (Morphological Disparity) C2 to 4 (B 0.8 0.6 0.4 DTT 0.2

Signifcant Shift in Diversification Rate

Marginal Shift in Diversification Rate

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

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.

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).

**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

N. archboldi

N. fanovanae N. amphichroa 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 Madagascan 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 honey-creepers 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. 24) 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. 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 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 burnin 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-throughtime 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<sub>10</sub>-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  $\gamma$  statistic (21) and  $\Delta AIC_{RC}$  (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  $\gamma$  values indicate a decrease in diversification rates through time, so we tested the observed  $\gamma$  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 diversitydependent 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  $\Delta AIC_{RC}$  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  $\Delta AIC_{RC}$  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  $\beta$  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  $\beta$  should be indistinguishable from zero. Strongly negative  $\beta$  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).

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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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# **Supporting Information**

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0.01

**Fig. S1.** The 50% majority rule consensus tree of Vangidae obtained from the Bayesian analysis of 375 aligned bases of glyceraldehyde-3-phosphodehydrogenase (GAPDH). The appropriate substitution model TIM+ $\Gamma$  was determined with MrModeltest (1), using the Akaike information criterion (AIC) (2, 3). In the Bayesian analysis (4, 5), the Markov chain Monte Carlo (MCMC) was run using Metropolis coupling, with one cold and three heated chains, for 10 million iterations with trees sampled every 500 iterations. Bayesian inference (BI) harmonic mean –In 2962.70. The number of iterations discarded before the posterior probabilities were calculated (i.e., the length of the burn-in period) was graphically estimated using AWTY (6, 7) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity. Maximum-likelihood (ML) analyses were performed using GARLI version 0.95 (8). Five independent analyses (20 million generations) were performed. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications. The score of the best-likelihood tree (–In 2827.81) was within 0.05 likelihood units of the best tree recovered in each of the other four runs, suggesting that the five runs had converged. Bayesian posterior probabilities are indicated above nodes (asterisks indicate posterior probabilities of 1.00), and ML bootstrap values are indicated below nodes. Members of Vangidae are indicated in bold.

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**Fig. S2.** The 50% majority rule consensus tree of Vangidae obtained from the Bayesian analysis of 630 aligned bases of ornithine decarboxylase introns 6 and 7 (ODC). The appropriate substitution model TVM+Γ was determined with MrModeltest (1), using the AIC (2, 3). In the Bayesian analysis (4, 5), the MCMC was run using Metropolis coupling, with one cold and three heated chains, for 10 million iterations with trees sampled every 500 iterations. BI harmonic mean –ln 3606.54. The number of iterations discarded before the posterior probabilities were calculated (i.e., the length of the burn-in period) was graphically estimated using AWTY (6, 7) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity. ML analyses were performed using GARLI version 0.95 (8). Five independent analyses (20 million generations) were performed. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications. The score of the best-likelihood tree (–In 3505.62) was within 0.05 likelihood units of the best tree recovered in each of the other four runs, suggesting that the five runs had converged. Bayesian posterior probabilities are indicated above nodes (asterisks indicate posterior probabilities of 1.00), and ML bootstrap values are indicated below nodes. Members of Vangidae are indicated in bold.

- 1. Nylander JAA (2004) MrModeltest (Uppsala University, Uppsala) (http://www.abc.se/~nylander), Version 2.
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**Fig. S3.** The 50% majority rule consensus tree of Vangidae obtained from the Bayesian analysis of 702 aligned bases of myoglobin intron 2 (Myo). The appropriate substitution model  $K80+\Gamma$  was determined with MrModeltest (1), using the AIC (2, 3). In the Bayesian analysis (4, 5), the MCMC was run using Metropolis coupling, with one cold and three heated chains, for 10 million iterations with trees sampled every 500 iterations. BI harmonic mean –In 4125.66. The number of iterations discarded before the posterior probabilities were calculated (i.e., the length of the burn-in period) was graphically estimated using AWTY (6, 7) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity. ML analyses were performed using GARLI version 0.95 (8). Five independent analyses (20 million generations) were performed. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications. The score of the best-likelihood tree (–In 3992.8146) was within 0.5 likelihood units of the best tree recovered in each of the other four runs, suggesting that the five runs had converged. Bayesian posterior probabilities are indicated above nodes (asterisks indicate posterior probabilities of 1.00) and ML bootstrap values are indicated below nodes. Members of Vangidae are indicated in bold.

- 1. Nylander JAA (2004) MrModeltest (Uppsala University, Uppsala) (http://www.abc.se/~nylander), Version 2.
- 2. Akaike H (1973) Second International Symposium on Information Theory, eds Petrov BN, Csaki F (Akademiai Kiado, Budapest), pp 276-281.
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- 4. Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
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**Fig. 54.** The 50% majority rule consensus tree of Vangidae obtained from the Bayesian analysis of 623 aligned bases of  $\beta$ -fibrinogen intron 5 (Fib5). The appropriate substitution model TrN+ $\Gamma$  was determined with MrModeltest (1), using the AIC (2, 3). In the Bayesian analysis (4, 5), the MCMC was run using Metropolis coupling, with one cold and three heated chains, for 10 million iterations with trees sampled every 500 iterations. BI harmonic mean –In 3346.42. The number of iterations discarded before the posterior probabilities were calculated (i.e., the length of the burn-in period) was graphically estimated using AWTY (6, 7) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity. ML analyses were performed using GARLI version 0.95 (8). Five independent analyses (20 million generations) were performed. Nodal support was evaluated recovered in each of the other four runs, suggesting that the five runs had converged. Bayesian posterior probabilities are indicated above nodes (asterisks indicate posterior probabilities of 1.00) and ML bootstrap values are indicated below nodes. Members of Vangidae are indicated in bold.

- 1. Nylander JAA (2004) MrModeltest (Uppsala University, Uppsala) (http://www.abc.se/~nylander), Version 2.
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**Fig. 55.** The 50% majority rule consensus tree obtained from the Bayesian analysis of 606 bp of occyte maturation factor Mos (c-mos). The appropriate substitution model TIM+I+F was determined with MrModeltest (1), using the AIC (2, 3). In the Bayesian analysis (4, 5), the MCMC was run using Metropolis coupling, with one cold and three heated chains, for 10 million iterations with trees sampled every 500 iterations. BI harmonic mean –In 2607.89. The number of iterations discarded before the posterior probabilities were calculated (i.e., the length of the burn-in period) was graphically estimated using AWTY (6, 7) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity. ML analyses were performed using GARLI version 0.95 (8). Five independent analyses (20 million generations) were performed. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications. The score of the best-likelihood tree (–In 2461.90) was within 2 likelihood units of the best tree recovered in each of the other four runs. Bayesian posterior probabilities are indicated above nodes (asterisks indicate posterior probabilities of 1.00), and ML bootstrap values are indicated below nodes. Members of Vangidae are indicated in bold.

- 1. Nylander JAA (2004) MrModeltest (Uppsala University, Uppsala) (http://www.abc.se/~nylander), Version 2.
- 2. Akaike H (1973) Second International Symposium on Information Theory, eds Petrov BN, Csaki F (Akademiai Kiado, Budapest), pp 276–281.
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**Fig. S6.** The 50% majority rule consensus tree of Vangidae obtained from the Bayesian analysis of 1,041 aligned bases of NADH dehydrogenase subunit 2 (ND2). The appropriate substitution model GTR+I+F was determined with MrModeltest (1), using the AIC (2, 3). In the Bayesian analysis (4, 5), the MCMC was run using Metropolis coupling, with one cold and three heated chains, for 10 million iterations with trees sampled every 500 iterations. BI harmonic mean –In 18233.41. The number of iterations discarded before the posterior probabilities were calculated (i.e., the length of the burn-in period) was graphically estimated using AWTY (6, 7) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity. ML analyses were performed using GARLI version 0.95 (8). Five independent analyses (20 million generations) were performed. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications. The score of the best-likelihood tree (–In 18347.45) was within 0.5 likelihood units of the best tree recovered in each of the other four runs, suggesting that the five runs had converged. Bayesian posterior probabilities are indicated above nodes (asterisks indicate posterior probabilities of 1.00), and ML bootstrap values are indicated below nodes. Members of Vangidae are indicated in bold.

- 1. Nylander JAA (2004) MrModeltest (Uppsala University, Uppsala) (http://www.abc.se/~nylander), Version 2.
- 2. Akaike H (1973) Second International Symposium on Information Theory, eds Petrov BN, Csaki F (Akademiai Kiado, Budapest), pp 276–281.
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## Table S1. Taxa and individuals included in the study

PNAS PNAS

Species	Voucher no.	Муо	ODC	GAPDH	Fib5	c-mos	ND2
Madagascan Vangidae							
Artamella viridis viridis F	SMNS D54307	JQ713472	JQ713499	JQ713408			JQ713440
Artamella viridis annae*	MNHN CG 364B	AY816222					AY816229
Calicalicus madagascariensis F	SMNS 114018	JQ713473	JQ713501	JQ713410	JQ713387	JQ713361	JQ713441
Calicalicus madagascariensis F	SMNS 114017	JQ713474	JQ713500	JQ713409	JQ713386	JQ713360	JQ713442
Calicalicus madagascariensis F	SMNS 114019	JQ713475	JQ713502	JQ713411	JQ713388		JQ713443
Calicalicus rufocarpalis T	MNHN 1974-510		JQ713504	JQ713412			JQ713444
Calicalicus rufocarpalis T	MNHN 1974-508	JQ713476	JQ713503	JQ713413			JQ713445
Cyanolanius madagascarinus T	NRM 69993	JQ713477	JQ713505	JQ713414	JQ713389	JQ713362	JQ713446
Cyanolanius comorensis*	MNHN E117	AY529915		DQ406649	AY529983	EF052709	AY529950
Euryceros prevostii T	NRM 71116		JQ713506	JQ713415	JQ713390	JQ713363	JQ713447
Falculea palliata T	NRM 70003		JQ713507	JQ713416		JQ713364	JQ713448
Hypositta corallirostris	NRM 84255	JQ/134/8	JQ/13508	JQ/1341/	JQ/13391	JQ/13365	JQ/13449
Leptopterus chabert 1	NRM 69986	JQ/134/9	JQ/13509	JQ/13418	JQ/13392	JQ/13366	JQ/13450
Mystacornis crossleyi F	SMNS 114028	JQ/13480	JQ/13510	JQ/13419	JQ/13393	JQ/1336/	JQ/13451
Mystacornis crossleyi*	FMINH 345863	FJ1/8361	10742546	10742426	FJ178360	10742272	FJ178356
Newtonia amphichroa F	SMINS 114022	JQ713481	JQ/13516	JQ713426	JQ/1339/	JQ/133/3	JQ713452
Newtonia amphichroa F	SMINS 114025	JQ713482	JQ713511	JQ713420	JQ713394	JQ/13369	JQ713453
Newtonia amphichroa F	SMINS 114026	JQ713483	JQ/13512	JQ713421	JQ713395	JQ/133/0	JQ713454
Newtonia amphichroa F	SMINS 114027	JQ713484	JQ/13513	JQ713422	JQ713396	JQ/133/1	JQ713455
	MINHN 1974-460	10712405	JQ713514	JQ713423		JQ713368	JQ713456
Newtonia brunneicauda I	NRIVI 67967	JQ713485	JQ/1351/	JQ713427		10712272	10712457
	SIVINS 114020	JQ713486	10712515	JQ713424		JQ713372	JQ713457
Newtonia brunneicauda F		JQ713487	10/13515	JQ713425		JQ/133/4	JQ713458
		10712499	10712519	10712429		10712275	JQ713459
Broudobias wardi E		JQ715466	JQ713516	JQ713420	10713308	JQ713375	JQ713460
Pseudobias wardi F		10713/89	10713579	10713429	10713390	10713376	10713467
Pseudobias wardi*		AV520022	JQ713320	DO406642	AV520001	EE052704	AV520068
Schotha rufa T	NRM 70001	10713/190	10713529	10713/31	10713/00	LI 052704	IO713/63
Tylas eduardi E		10713/191	10713522	10713/133	10713/02	10713379	10713464
Tylas eduardi F	SMNS 114023	10713492	10713521	10713432	10713401	10713378	10713465
Vanga curvirostris*	MHNH CG 3644	ΔΥ701505	50715521	DO406640	10+01	ΔΥ056972	ΔΥ701508
Vanga curvirostris T	NRM 69997	10713493	10713523	10713434	10713403	10713380	10713466
Xenonirostris xenonirostris T	MNHN 1994-451	10713494	10713528	10713439	10713407	10713385	10713467
Xenopirostris xenopirostris T	MNHN 1994-449	10713495	10713527	10713438	10713406	10713384	10713468
Xenopirostris damii T	MNHN 1932-3801	JO713496	JO713526	J0713437	JO713404	JO713382	JO713469
Xenopirostris damii T	MNHN 1932-3800	JO713497	JO713525	JO713436		JO713381	JO713470
Xenopirostris polleni T	NRM 69972	JQ713498	JQ713524	JQ713435	JQ713405	JQ713383	JQ713471
Continental Vangidae							
Bias flammulatus*	MNHN CG 1968-1160	AY529927		DQ406652	AY529995		AY529962
Hemipus picatus*	MNHN 33-6A	DQ406637		DQ406647		EF052710	DQ411309
Philentoma velata, pyrhoptera*	LSUMZ B-38542,	AY816221		DQ406667		EF052716	AY816228
	LSUMZ B-38572						
Prionops retzii*	ZMUC 119500	AY529931	EU380457	DQ406654	AY529999	EF052718	AY529966
Tephrodornis pondicerianus*	USNM B2140	EF052762		EF052751		EF052742	EF052689
Other core Corvoidea							
Aegithina tiphia*	AMNH 22963	AY816225		DQ406650		AY056905	AY816232
Artamus cyanopterus*	ZMUC 135911, ANSP10604	DQ406636		DQ406661			DQ096728
Batis poensis*	MNHN CG 1998-783	AY529907	EU272120	DO406665	AY529974	EF052698	AY529941
Coracina melaschistos*	MNHN 6-69	AY529913	FU380423	EF052807	AY529981	EF052702	AY529948
Dicrurus bracteatus/paradiseus*	UWBM 68045, MNHN 5-57	FF052839	EU272113	EF052813	AY529984	EF052735	FF052784
Drvoscopus gambensis*	ZMUC 124320	AY529918		DO406664	AY529986		AY529953
Grallina cvanoleuca*	AMNH LAB 1144	DO084101					DO084074
Gymnorhina tibicen*	MV AC78	AY064741	EU272119	DO406669			AY064756
Laniarius aethiopicus/barbarus*	FMNH 356738, IPMB 16524, ZMUC 116792	AY529920	EF637081		AY529988	EF052705	AY529955
Macharirhynchus flaviventer*	ANWC 39520, KU AM949	FJ821090					DQ084072
Oriolus flavocinctus, xanthornus*	MV 1603, MNHN 4-10D	EF441258	EF441243	EF441221	AY529997	EF052715	GQ901758
Platysteira chalybea, cyanea*	MNHN 3-19, MNHN 02-22	AY529919		DQ406666	AY529998	EF052717	AY529954
Terpsiphone viridis* Passerida	MNHN 2-20	AY529939	EU380458	DQ406641	AY530007	EF052708	AF407058

## Table S1. Cont.

DNAC DNAC

Species	Voucher no.	Муо	ODC GAPDH		Fib5	c-mos	ND2	
Sturnus vulgaris*	NRM 966615, NRM 20046688	AY228322	EF441253	EF441231	EU680690 AY0569		EU551975	
Basal oscines								
Menura novaehollandiae*	MV F722, unvouchered	AY064744	EF441242	DQ406670		AY056934	NC_007883	
Suboscines								
Pitta versicolor, guajana*		DQ786002	DQ785966	DQ785927	EF501826	AY056952	EF501927	
Outgroup								
Acanthisitta chloris*	NRM 569989, unvouchered	EU726212	EU726220	EU726202	GQ140172	HM159194	AY325307	

AMNH, American Museum of Natural History (New York, United States); ANSP, Academy of Natural Science (Philadelphia, United States); ANWC, Australian National Wildlife Collection (Canberra, Australia); FMNH, Field Museum of Natural History (Chicago, United States); IPMB, Institut für Pharmazie und Molekulare Biotechnologie, Heidelberg University (Germany); KU, University of Kansas (Lawrence, United States); LSUMZ, Museum of Natural Science, Louisiana State University (Baton Rouge, United States); MNHN, Muséum National d'Histoire Naturelle (Paris, France); MV, Museum Victoria, Melbourne, Australia; NRM, Naturhistoriska Riksmuseet (Stockholm, Sweden); SMNS, Staatliches Museum für Naturkunde (Stuttgart, Germany); USNM, United States National Museum (Washington, DC, United States); UWBM, Burke Museum, University of Washington (Seattle, United States); ZMUC, Zoological Museum, University of Copenhagen (Denmark). F, sequenced from fresh material; T, sequenced from toe pads. \*Sequence downloaded from GenBank.

# Table S2. Testing for constant diversification rates in the Vangidae using the $\gamma$ and $\Delta AIC_{RC}$ statistics

Tree simulations	γ ΜCC	95th percentile	∆AIC <sub>RC</sub> MCC	95th percentile
Observed	-2.9313		11.4694	
100% known	0.0002***	0.0006***	0.0008***	0.0034**
75% known	0.0006***	0.0026**	0.0012**	0.0052**
50% known	0.0004***	0.0022**	0.0034**	0.0106*
25% known	0.0072**	0.0198*	0.0094**	0.0280*

The observed values of the two measures are given for the maximum clade credibility (MCC) tree. Other values are *P* values for the MCC tree and the 95th percentile of a random sample (1,000 trees) from the posterior distribution of trees. These *P* values were generated from simulated null distributions, where 5,000 trees were simulated for each assumed total species number, going from all species known (100%) to only 25% of species known. \*\*\**P* < 0.001, \*\**P* < 0.05.

Table S3.	Comparison of va	rious birth-death	models o	f diversification:	constant-rate	models (C	CR), models	with a	n overall	shift	in
speciation	rate, extinction rate	e, or carrying capa	city (SR), a	and key innovation	on models (KI)						

	$\lambda_1$	μ1	<i>K</i> <sub>1</sub>	$\lambda_2$	μ2	<i>K</i> <sub>2</sub>	Ts	∆AIC
Pure-birth (CR1)	0.06	0 (fixed)	$\infty$ (fixed)	_	_	_		23.8
Birth–death (CR2)	0.06	0.00	$\infty$ (fixed)	_	_	_	_	21.8
Pure-birth with shift in speciation rate (SR1)	0.27	0 (fixed)	$\infty$ (fixed)	0.04	0 (fixed)	$\infty$ (fixed)	19.77	13.9
Diversity-dependent speciation without extinction (CR3)	0.20	0 (fixed)	22.57	_	_	_	_	12.0
Diversity-dependent speciation with diversity-independent extinction (CR4)	0.57	0.04	21.34	_	—	—	—	12.5
Diversity-dependent speciation with diversity-independent extinction with shift in carrying capacity (SR2)	0.46	0.00	12.56	$\lambda_1$	μ1	21.84	9.77	3.26
Diversity-dependent speciation with diversity-independent extinction and key innovation, with two clades having the same parameters (KI1)	0.23	0.00	16.00	$\lambda_1$	μ <sub>1</sub>	Κ1	9.77	6.61
Diversity-dependent speciation with diversity-independent extinction and key innovation, with two clades having different carrying capacities (KI2)	0.62	0.02	15.53	$\lambda_1$	μ1	5.81	9.77	0
Diversity-dependent speciation with diversity-independent extinction and key innovation, with two clades having different carrying capacities and different extinction rates (KI3)	0.60	0.02	15.51	$\lambda_1$	0.00	5.65	9.77	1.72
Diversity-dependent speciation with diversity-independent extinction and key innovation, with two clades having different carrying capacities and different speciation rates (KI4)	0.57	0.02	15.42	1.15	μ1	5.41	9.77	1.36
Diversity-dependent speciation with diversity-independent extinction and key innovation, with two clades having different parameters (KI5)	0.55	0.02	15.51	1.98	0.06	5.62	9.77	2.90

All models with diversity-dependent diversification have a linearly declining speciation rate with diversity (1). For the SR models,  $\lambda_2$ ,  $\mu_2$ , and  $K_2$  refer to the parameters after the shift, whereas for KI models they refer to the parameters of the innovative subclade.  $T_s$  is the time of the shift and refers to the timing of the shift (in SR models) or the key innovation event (KI), which in the latter case was confined between 18.8 and 9.65 Mya.  $\Delta$ AlC denotes the differences in AlC values, the lowest value (0) being the best model. Technical note: The SR1 model differs from the Yule2rate model as implemented in the LASER package (2) in that the shift time can be anywhere; it need not be at a branching point. In this case, it is just after a branching point. For the SR2 model, the shift is just before the branching point. —, not applicable.

1. Etienne RS, et al. (2012) Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record. Proc Biol Sci 279:1300-1309.

2. Rabosky DL (2006) LASER: A maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. Evol Bioinformatics 2:247-250.

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