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Extreme Endemic Radiation of the Malagasy Vangas (Aves: Passeriformes)

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Abstract. Phylogenetic relationships of the family Vangidae and representatives of several other passeriform families were inferred from 882 base positions of mitochondrial DNA sequences of 12S and 16S rRNA genes. Results indicated the monophyly of the Vangidae, which includes the genus *Tylas*, hitherto often placed in the family Pycnonotidae. Our results also revealed the Malagasy endemic *Newtonia*, a genus never previously assigned to the Vangidae, to be a member of this family. These results suggest the occurrence of an extensive *in situ* radiation of this family within Madagascar, and that the extant high diversity of this family is not the result of multiple colonizations from outside. The extremely high morphological and ecological diversification of the family seems to have been enhanced through the use and ultimate occupancy of vacant niches in this island.

Key words: 12S rRNA — 16S rRNA — Phylogeny — Passeriformes — Oscines — Vangidae — Madagascar

Introduction

The island of Madagascar lies 400 km off the southeastern coast of Africa and has been isolated from Africa and all other landmasses since at least the end of the Cretaceous, some 80 MY b.p. (Smith et al. 1994). The avifauna of Madagascar, characterized by a high frequency of endemic taxa (52%) (Langrand 1990), clearly reflects this long isolation. The endemic family Vangidae sensu lato consists of 15 species in some 10 genera (Langrand 1990; Goodman et al. 1997) and shows striking ecological and morphological diversifications.

The intra-familial diversity in gross and especially bill morphology (Fig. 1) is so great as to have led to serious taxonomic and phylogenetic confusion (Table 1). Prior to 1932, when Delacour recognized "Vangidés" endemic to Madagascar, the members of the vangas had been assigned to other families, such as the Laniidae. However, Delacour (1932) did not include *Hypositta* and *Tylas* as vangid genera, but placed them in the Sittidae and Pycnonotidae, respectively. Rand (1936) established the family Vangidae, and also assigned *Tylas* to the Pycnonotidae, while recognizing the Eurycerotidae and Hyposittidae monotypic with *Euryceros* and *Hypositta*, respectively. In successive editors of Peter's Checklist of Birds of the World, the Vangidae consisted of 12 species, although *Hypositta* and *Tylas* were considered to be members of the Paridae and Pycnonotidae, respectively (Rand 1960a; Rand and Deignan 1960; Snow 1967; Watson et al. 1986). On the other hand, Dorst (1960c) lumped both *Hypositta* and *Tylas* into the Vangidae. However, because Dorst (1960a, b, c), who argued for the morphological affinity of vangas, did not note which species were compared, and failed to incorporate representatives of other families, recent authors suspected *Tylas* to be a member of the Pycnonotidae or of the Oriolidae, and not the Vangidae (e.g., Howard and Moore 1991; Appert 1994, respectively).

Recently, in his unpublished dissertation, Schulenberg (1995) demonstrated a possible non-monophyly of the

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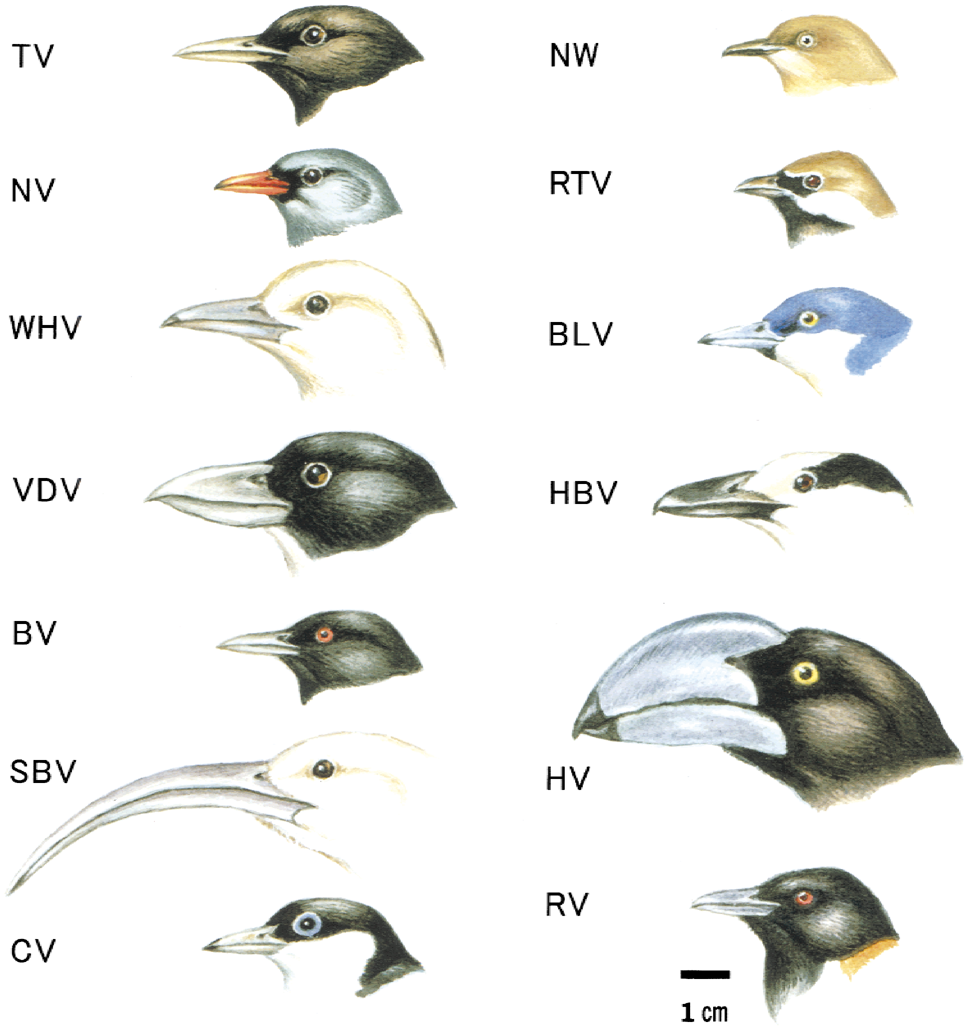


Fig. 1. Sizes, colors, and shapes of bill of vangid species, including *Tylas* and *Newtonia.* (TV): *Tylas eduardi;* (NV): *Hypositta corallirostris;* (WHV): *Leptopterus viridis;* (VDV): *Xenopirostris damii;* (BV): *Oriolia bernieri;* (SBV): *Falculea palliata;* (CV): *L. chabert;* (NW): *Newtonia brunneicauda;* (RTV): *Calicalicus madagascariensis;* (BLV): *L. madagascarinus;* (HBV): *Vanga curvirostris;* (HV): *Euryceros prevostii;* (RV): *Schetba rufa.* Pictures redrawn by K. Kanao from Langrand (1990).

Vangidae. However, his analyses using cytochrome b gene sequence suffered problems of saturation of base substitution. As such, to this point, the familial taxonomic status of several genera remained unclear, and with it, the composition and phylogeny of the Vangidae.

There are three well-known examples of avian adaptive radiation: Galápagos finches, Hawaiian drepanids, and Malagasy vangas. Darwin’s finches, a textbook example of diversification of a single founding population into an array of taxa differentially adapted to diverse environmental niches, consist of 14 species distributed in the Galápagos Islands and the Cocos Islands (e.g., Lack 1947; Grant 1986; Grant and Grant 1989). Hawaiian honeycreepers, consisting of 33 species (James and Olson 1991) distributed in the Hawaiian Islands, also have adapted their bill shapes and colorations (e.g., Amadon 1950; Raikow 1977). In contrast, the radiation of Malagasy vangas may surpass that seen in the Galápagos finches or Hawaiian drepanids. Vangas exceed the finches in terms of number of genera, most of which are monotypic, and diversifications in bill shapes and colorations. The former also exceed the honeycreepers in variations of body size and color. Recently, the collective divergences of these finches and honeycreepers are confirmed based on the molecular data (e.g., Sato et al. 1999; Tarr and Fleischer 1995). The monophyly of Malagasy vangas, however, remained unsolved in the previous studies (see above).

On the basis of DNA sequence data for 12S and 16S ribosomal RNA (rRNA) genes, we show here the occurrence of an extensive endemic radiation of this family within Madagascar.

Materials and Methods

Samples Analyzed. Tissues were obtained from 29 species of 17 families representing Asian, Australian, African, and Malagasy oscines,

Table 1. History of classification of the Vangidae

Vangid genera in the present study	Catalogue of British Museum[a]	Delacour (1932)	Rand (1936)	Peters' checklist[b]	Dorst (1960c)	Milon et al. (1973)	Complete checklist[c]
Calicalicus	Laniidae	—	—	—	—	—	—
Euryceros	Prionopidae	—	Eurycerotidae	—	—	—	—
Falculea	Corvidae	—	—	—	—	—	—
Hypositta	Sittidae	Sittidae	Hypositidae	Paridae	—	—	—
Leptopterus	Laniidae	—	—	—	—	—	—
L. chabert	Prionopidae	—	—	—	—	—	—
Oriolia	Laniidae	—	—	—	—	—	—
Schetba	Laniidae	—	—	—	—	—	—
Tylas	Pycnonotidae[d]	Pycnonotidae	Pycnonotidae	Pycnonotidae	—	—	Pycnonotidae
Vanga	Laniidae	—	—	—	—	—	—
Xenopirostris	Laniidae	—	—	—	—	—	—
Newtonia	Muscicapidae	Muscicapidae	Muscicapidae	Sylviidae		Muscicapidae	Sylviidae

Dash denotes Vangidae. Sources are (a) Gadow (1883) and Sharpe (1877, 1879, 1901); (b) Rand (1960a), Rand and Deignan (1960), Snow (1967) and Watson et al. (1986); (c) Howard and Moore (1990). (d) was listed as Timaliidae in Sharpe (1881).

including all genera of the Vangidae (Table 2). Due to the endangered status of some of the species examined in the present study, most animals were released after the blood sampling, and thus were not collected as voucher specimens.

In his phylogenetic analysis of cytochrome b, Schulenberg (1995), contradictory to results from DNA hybridization data (Sibley and Ahlquist 1990), hypothesized *Laniarius* (Laniidae) to be one of the closest relatives of some vangid taxa, and we selected this genus as an outgroup among non-vangas. Recently, Tuinen et al. (2000) revalued usefulness of the DNA hybridization data (Sibley and Ahlquist 1990) in the gross estimation of avian phylogeny. Even so, however, Tuinen et al. examined only one passeriform taxon, and Honda and Yamagishi (2000) negated Sibley and Ahlquist's (1990) hypothesis in terms of the oscine phylogeny. Judging from the results of Honda and Yamagishi (2000), the phylogenetic relationships within the Oscines still remains unresolved. We therefore incorporated into the analyses all those oscine families, for which tissues were available to us (Table 2). The inclusion of these samples from a wide variety of taxa allows us to predict few errors, if any, in the gross estimation of oscine phylogeny. Taxonomic arrangement followed that of Peters' Check-lists of Birds of the World (Rand 1960a, b; Rand and Deignan 1960; Snow 1967; Watson et al. 1986).

Table 2. Families of the Oscines used in the present analyses

Sample	Family	Assesion nos.
Gallus gallus	Phasianidae[a]	X52392
Coracias caudata	Coraciidae[b]	AF173596
Picoides pubescens	Picidae[c]	AF173562
Tyrannus tyrannus	Tyrannidae[d]	AF173600
Hirundo rustica	Hirundinidae	AB042349, AB042382
Motacilla grandis	Motacillidae	AB042355, AB042388
Hypsipetes madagascariensis	Pycnonotidae	AB042346, AB042379
Tylas eduardi	Pycnonotidae	AB042342, AB042375
Laniarius ferrugineus	Laniidae	AB042365, AB042398
Lanius bucephalus	Laniidae	AB042348, AB042381
Calicalicus madagascariensis	Vangidae	AB042339, AB042372
Schetba rufa	Vangidae	AB042340, AB042373
Vanga curvirostris	Vangidae	AB042336, AB042369
Xenopirostris damii	Vangidae	AB042344, AB042377
Falculea palliata	Vangidae	AB042341, AB042374
Leptopterus viridis	Vangidae	AB042343, AB042376
Leptopterus chabert	Vangidae	AB042335, AB042368
Leptopterus madagascarinus	Vangidae	AB042333, AB042366
Oriolia bernieri	Vangidae	AB042334, AB042367
Euryceros prevostii	Vangidae	AB042337, AB042370
Hypositta corallirostris	Vangidae*	AB042338, AB042371
Copsychus albospecularis	Turdidae	AB042350, AB042383
Leiothrix lutea	Timaliidae	AB042358, AB042391
Phylloscopus coronatus	Sylviidae	AB042354, AB042387
Newtonia brunneicauda	Sylviidae	AB042351, AB042384
Cyanoptila cyanomelana	Muscicapidae	AB042356, AB042389
Parus varius	Paridae	AB042362, AB042395
Sitta europaea	Sittidae	AB042353, AB042386
Emberiza spodocephala	Emberizidae	AB042359, AB042392
Passer montanus	Ploceidae	AB042360, AB042393
Sturnus cineraceus	Sturnidae	AB042352, AB042385
Gymnorhina tibicens	Cracticidae	AB042347, AB042380
Corvus macrorhynchos	Corvidae	AB042345, AB042378

Taxonomic arrangement mainly followed that of Peters' Checklists (e.g., Rand 1960a, b; Rand and Deignan 1960; Snow 1967; Watson et al. 1986). (*) Indicates species assigned to Paridae in this list (Snow 1967). Non-Passeriformes orders are (a) Galliformes; (b) Coraciiformes; and (c) Piciformes, (d) denotes the Suboscines.

Extraction, Amplification and Sequencing of DNA. The methods of DNA extraction, amplification and sequencing are described in detail elsewhere (Honda et al. 1999a, b). A part (approximately 900 base pairs [bp]) of mitochondrial 12S and 16S rRNA genes were amplified using the polymerase chain reaction (PCR) using primers; the 12S rRNA primers are L1091 (5′-AAACTGGGATTAGATACCCCACTAT-3′) and H1478 (5′-GAGGGTGACGGGCGGTGTGT-3′) (Kocher et al. 1989), and the 16S rRNA primers are L2606 (5′-CTGACCGTGCAAAGGTAGCGTAATCACT-3′) and H3056 (5′-CTCCGGTCTGAACTCAGATCACGTAGG-3′) (Hedges et al. 1993). The numbering system followed the human sequence (Anderson et al. 1981). We also incorporated into the analyses the published data for partial sequences of 12S and 16S rRNAs of several taxa: *Gallus gallus, Coracias caudata, Picoides pubescens* and *Tyrannus tyrannus.* The DNA sequences have been submitted to the DDBJ database, and their accession numbers are given in Table 2.

Phylogenetic Analyses. Alignments for DNA sequences were determined based on maximum nucleotide similarity using CLUSTAL ×

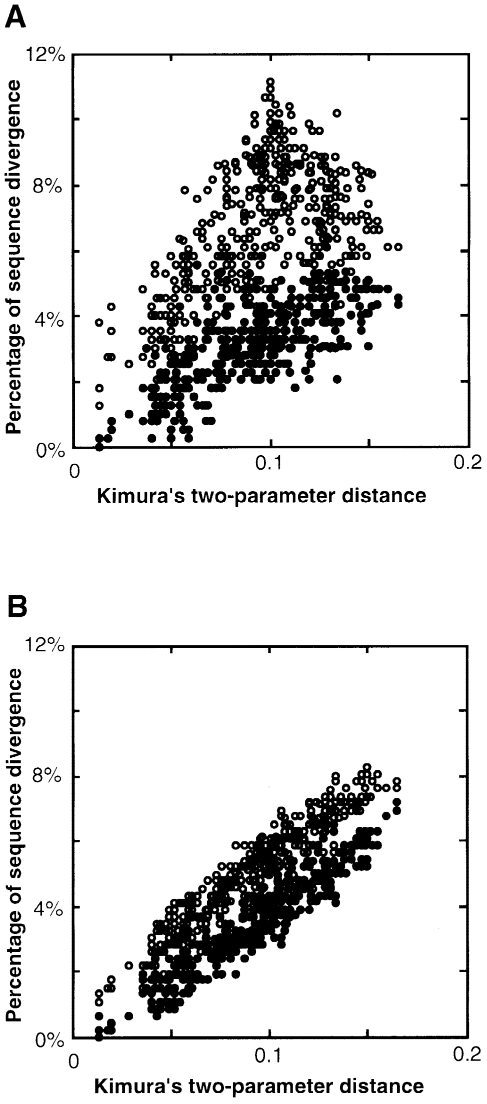


Fig. 2. **(A)** Patterns of nucleotide differences in 12S rRNA genes among taxa. Transitions and transversion differences are plotted against pairwise Kimura's two-parameter distance. Open and closed circles denote transitions and transversions, respectively. **(B)** Transition and transversion differences in 16S rRNA versus pairwise Kimura's two-parameter distance. Open and closed circles denote transitions and transversions, respectively.

1.8 (Thompson et al. 1994) with default gap penalties. The neighbor-joining (NJ) method (Saitou and Nei 1987) was applied to infer relationships among taxa on the basis of a pairwise matrix of the distance from Kimura's (1980) two-parameter model, using CLUSTAL X. The maximum-likelihood (ML) and maximum-parsimony (MP) analyses were also conducted using empirical base frequencies and one category of substitution rates options of PHYLIP 3.54c (Felsenstein 1993) and the heuristic search option of PAUP* 4.0b (Swofford 1998), respectively. In these three analyses, confidences were assessed by bootstrap resamplings (Felsenstein 1985), no bias was assumed between transition and transversion, and gap sites were excluded.

To assess the homogeneity between 12S and 16S rRNA, a partition homogeneity test (Farris et al. 1994) was conducted using PAUP* with heuristic 1,000 bootstrappings. The significance levels were set at $P < 0.01$ to avoid type I errors.

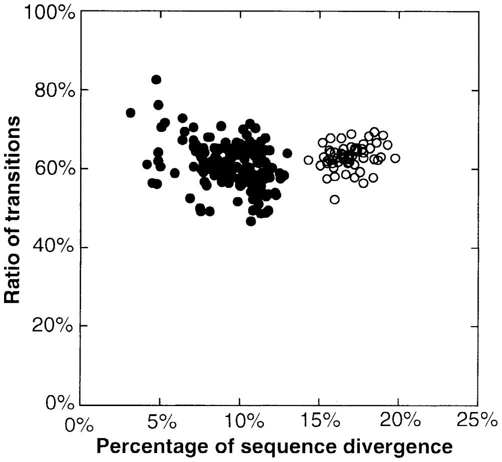


Fig. 3. Percentage of transitions with the variation versus that of sequence divergence for combined data for 12S and 16S rRNA genes. *Vanga curvirostris* was used as a representative of the Vangidae. Open and closed circles denote pairwise comparison of ingroup taxa and outgroup taxa, respectively.

Results

Mitochondrial Sequence Variation

All sequences showed a substantial bias against guanine (G) and thymine (T) on the light strand (A = 28.4–32.3%, C = 25.9–29.7%, G = 19.3–23.2%, T = 19.7–22.1%). Such a bias of guanine can sometimes reflect that condition in mitochondrial genome, and not that in the nuclear integrated copies of mitochondrial genes (e.g., Zhang and Hewitt 1996; Macey et al. 1997). On the other hand, it was reported that frequency of thymine also decreased in the mitochondrial DNA (Cibois et al. 1999; Honda et al. 2000a, b). We were therefore able to interpret these sequences as being those of authentic mitochondrial DNA.

The percentage of transitions and transversions from pairwise comparisons within 12S and 16S rRNAs sequences is plotted against genetic distance in Fig. 2. The percentage of transitions with total sequence is plotted against that of transversions in Fig. 3. Transitions exceeded transversions at low levels of sequence divergence. This agrees with previous studies on animal mitochondrial DNA which reported an initial high (>50%) transition bias which gradually decreases over time (e.g., Hedges et al. 1991; Fuller et al. 1998; Cibois et al. 1999).

The 12S rRNA fragment consisted of 411 total sites, 193 of which were variable. For the 16S rRNA fragment, there were 471 total aligned sites, 178 of which were variable. Inter-familial nucleotide replacements within the Oscines varied from 44 bp (*Emberiza spodocephala* vs. *Passer montanus*) to 113 bp (*Hypositta corallirostris* vs. *Leiothrix lutea*). Intra-familial nucleotide replacements within the Vangidae involved from 11 bp (*Falculea palliata* vs. *Oriolia bernieri*) to 57 bp (*Calicalicus madagascariensis* vs. *Euryceros prevostii*).

The partition homogeneity test revealed no significant heterogeneity between 12S and 16S rRNAs. These results imply that the data sets for two portions of mitochondrial genes are not conflicting, and we therefore analyzed these data as a single set.

Phylogenetic Relationships

The NJ dendrogram derived from aligned sequences is shown in Fig. 4A. The monophyly of the Passeriformes was supported in 73% BP (node 1). The ingroup portion of this dendrogram was divided into two major clusters, one of which was monotypic, consisting of with *Tyrannus* of the suborder Suboscines. The other major cluster, supported in all bootstrap iterations (node 2), contained all oscine families examined here. Within the suborder Oscines, three distinct lineages were supported with high bootstrap values (≥90%). The first lineage consisted of *Parus, Hirundo, Hypsipetes, Phylloscopus,* and *Leiothix* (node 3: 93%), and the second contained *Motacilla, Emberiza, Passer, Sitta, Sturnus, Copsychus,* and *Cyanoptila* (node 4: 92%). The third lineage, consisting of *Corvus, Lanius, Laniarius, Gymnorhina, Tylas, Newtonia,* and all other vangid genera (node 5: 100%), further split to constitute a cluster of vangid genera including *Tylas* and *Newtonia* (node 6: 93%).

In terms of topology of nodes 1–6 at the level of BPs ≥70%, relationships inferred from ML (Fig. 4B) and MP analyses (Fig. 4C) agreed with those expressed in the NJ dendrogram, except for the absence of node 4 in MP. We thus concluded that the recognition of node 4 should not lead to any substantial error in the resultant phylogenetic relationships.

Discussion

Sequence Divergence of Oscines

Several studies have demonstrated the usefulness of 16S rRNA gene for avian phylogenetic analyses (e.g., Cibois et al. 1999). In the present study, percentages of transitions and transversions of 12S and 16S rRNAs were increased almost linearly with increasing evolutionary distance (calculated after Kimura 1980), and, although the plots of 16S rRNA (Fig. 2B) seemed to be more regressive than those of 12S rRNA (Fig. 2A), no plateauing or inflection of the curve was observed in these two genes (Fig. 2A, B). These suggest that there are no marked saturation effects in the aligned sequences of 12S and 16S rRNAs (e.g., Miya and Nishida 1998).

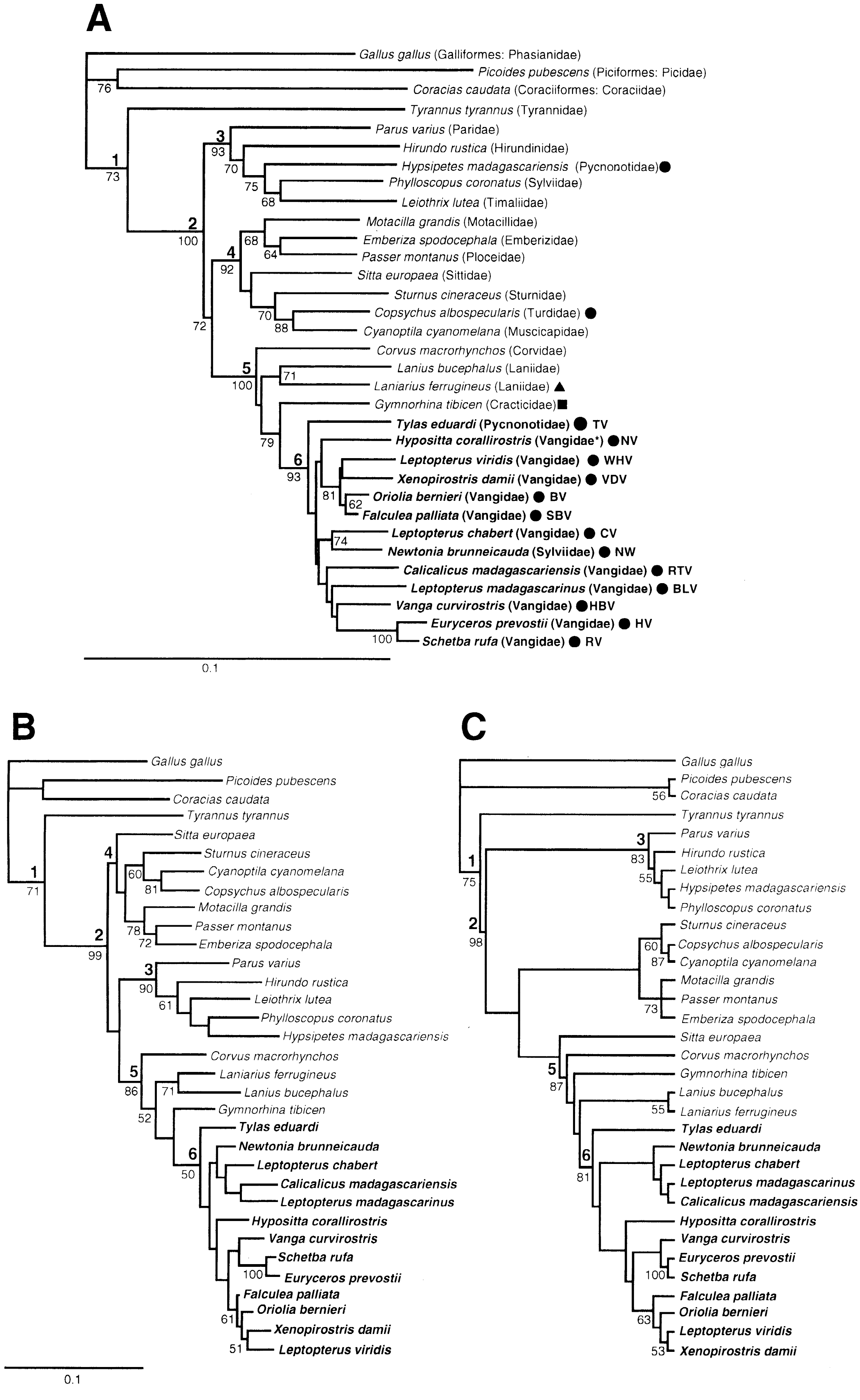
In addition, the scatter plots of transitions ratio against total sequence divergence within ingroup (Fig. 3) did not exhibit a transition plateau (usually corresponding to 40–50% transitions), which is the point where multiple substitutions are occurring at the same site (Brown et al. 1982; Thomas et al. 1989; Hedges et al. 1991). It is unlikely that extreme homoplasies due to multiple hits confounded phylogenetic analyses (e.g., Hedges et al. 1991). Therefore, we think the sequence data for 12S rRNA, as well as those for 16S rRNA, are useful for phylogenetic inference.

Endemic Radiation of Vangas

Our findings overturn existing beliefs concerning the phylogeny of the Vangidae and the composition of its members. Notably, our results (Fig. 4) unambiguously indicate the monophyly of the Vangidae, and also clearly show that *Tylas* and several other species which have occasionally been assigned to the Pycnonotidae (bulbuls) or other families are actually vangid taxa. Our results also indicate the Malagasy endemic genus *Newtonia* to be a member of the Vangidae. This is especially surprising because this genus has hitherto been assigned to the Sylviidae (warblers) or to the Muscicapidae (flycatchers), but never to the Vangidae (see Table 1), although Olson (1989) noted the anatomical similarities between *Tylas* and *Newtonia.*

Previous taxonomic studies that addressed morphological similarities among vangas examined only *Dryoscopus* (Laniidae) as a representative of closely related taxa, and did not incorporate other families (Dorst 1960a,b,c). Although these studies have often been referred to as evidence for the monophyly of the Vangidae and the closest affinity between vangid genera and *Dryoscopus*, they failed to provide any substantial support for the monophyly and sister taxa of this family, neither taxonomically nor phylogenetically. A more recent study of vangid phylogeny which examined sequence variations in the mitochondrial cytochrome b gene did not support the monophyly of this family (Schulenberg 1995). He went so far as to interpret such a result as multiple colonizations, i.e., the Vangidae as a nonmonophyletic taxon. However, his interpretation will be misleading because the data are inherently flawed by the saturation of base substitution in the samples. In contrast, the present results suggest that the sequence variations in 12S and 16S rRNA genes are useful, not saturated (see above). We thus consider our results to provide substantial support for the validity of the family Vangidae, although we could not completely negate inclusions of other oscine taxa within the vangid cluster.

The diversity of the Vangidae (including *Tylas* and *Newtonia*) in Madagascar seems to have occurred through an endemic radiation, and not through multiple colonizations from outside. This radiation involved high morphological and ecological diversifications, which many previous authors interpreted as taxonomic differences between the Vangidae and other families: Pycnonotidae, Muscicapidae, Sylviidae, Prionopidae (helmet shrikes), Sittidae (nuthatches), Corvidae (crows), Sturni-


A
Gallus gallus (Galliformes: Phasianidae)
Picoides pubescens (Piciformes: Picidae)
76
Coracias caudata (Coraciiformes: Coraciidae)
Tyrannus tyrannus (Tyrannidae)
3
93
Parus varius (Paridae)
Hirundo rustica (Hirundinidae)
70
Hypsipetes madagascariensis (Pycnonotidae) ●
75
Phylloscopus coronatus (Sylviidae)
68
Leiothrix lutea (Timaliidae)
1
73
2
100
Motacilla grandis (Motacillidae)
68
Emberiza spodocephala (Emberizidae)
64
Passer montanus (Ploceidae)
4
92
Sitta europaea (Sittidae)
Sturnus cineraceus (Sturnidae)
70
Copsychus albospecularis (Turdidae) ●
88
Cyanoptila cyanomelana (Muscicapidae)
72
Corvus macrorhynchos (Corvidae)
5
100
Lanius bucephalus (Laniidae)
71
Laniarius ferrugineus (Laniidae) ▲
Gymnorhina tibicen (Cracticidae) ■
79
Tylas eduardi (Pycnonotidae) ● TV
Hypositta corallirostris (Vangidae*) ● NV
6
93
Leptopterus viridis (Vangidae) ● WHV
Xenopirostris damii (Vangidae) ● VDV
81
Oriolia bernieri (Vangidae) ● BV
62
Falculea palliata (Vangidae) ● SBV
Leptopterus chabert (Vangidae) ● CV
74
Newtonia brunneicauda (Sylviidae) ● NW
Calicalicus madagascariensis (Vangidae) ● RTV
Leptopterus madagascarinus (Vangidae) ● BLV
Vanga curvirostris (Vangidae) ● HBV
Euryceros prevostii (Vangidae) ● HV
100
Schetba rufa (Vangidae) ● RV
0.1
B
Gallus gallus
Picoides pubescens
Coracias caudata
Tyrannus tyrannus
Sitta europaea
4
Sturnus cineraceus
60
Cyanoptila cyanomelana
81
Copsychus albospecularis
1
71
Motacilla grandis
78
Passer montanus
72
Emberiza spodocephala
2
99
3
90
Parus varius
Hirundo rustica
61
Leiothrix lutea
Phylloscopus coronatus
Hypsipetes madagascariensis
Corvus macrorhynchos
5
86
Laniarius ferrugineus
71
Lanius bucephalus
52
Gymnorhina tibicen
Tylas eduardi
6
50
Newtonia brunneicauda
Leptopterus chabert
Calicalicus madagascariensis
Leptopterus madagascarinus
Hypositta corallirostris
Vanga curvirostris
Schetba rufa
100
Euryceros prevostii
Falculea palliata
Oriolia bernieri
61
Xenopirostris damii
51
Leptopterus viridis
0.1
C
Gallus gallus
Picoides pubescens
56
Coracias caudata
Tyrannus tyrannus
3
83
Parus varius
Hirundo rustica
Leiothrix lutea
55
Hypsipetes madagascariensis
Phylloscopus coronatus
1
75
2
98
Sturnus cineraceus
60
Copsychus albospecularis
87
Cyanoptila cyanomelana
Motacilla grandis
Passer montanus
73
Emberiza spodocephala
Sitta europaea
5
87
Corvus macrorhynchos
Gymnorhina tibicen
Lanius bucephalus
55
Laniarius ferrugineus
Tylas eduardi
6
81
Newtonia brunneicauda
Leptopterus chabert
Leptopterus madagascarinus
Calicalicus madagascariensis
Hypositta corallirostris
Vanga curvirostris
Euryceros prevostii
100
Schetba rufa
Falculea palliata
Oriolia bernieri
63
Leptopterus viridis
53
Xenopirostris damii

dae (starlings), Laniidae (shrikes) or other monotypic families, most of which were distantly located from the Vangidae in nodes 3 and 4 (Fig. 4).

Interestingly, our data also suggest that some passeriform families have independently dispersed into Madagascar, whereas others [e.g., Picidae (woodpeckers) of Piciformes, Sittidae, Paridae and Laniidae] have never reached this island. The absence of these latter families seems to have left various niches vacant and available to the Vangidae (Yamagishi and Eguchi 1996). For example, *Hypositta* climbs along trunks like a nuthatch or treecreeper (Certhiidae), whereas *Xenopirostris* digs and *Falculea* probes, woodpecker-like, into tree trunks for wood-boring insects. This ecological diversity of vangas is most likely to have increased through the utilization of vacant niches normally occupied by other families (Yamagishi and Eguchi 1996). The extreme diversity of vangid bill shapes (Fig. 1) seems to have been enhanced as a functional adaptation to changes of foraging behavior related to the use and ultimate occupancy of these vacant niches.

Phylogenetic Relationships of the Oscines

Honda and Yamagishi (2000), based on DNA sequence data, indicate the presence of at least three phylogenetic lineages within the Oscines. The inclusion of additional taxa in the present study confirms these lineages, which may be referred to as the Sylviid Group (node 3), the Muscicapid Group (node 4), and the Corvid Group (node 5). Each of the groups seems to constitute three independent evolutionary lineages within the Oscines, although the number and size of samples examined in the present study are too small to draw any definite conclusion.

In the present study, we demonstrated that the Vangidae is a member of the Corvid Group (as depicted in Fig. 4). Unfortunately, however, our analyses failed to infer interfamilial detailed relationships within those three groups. Further analyses are necessary to reveal the phylogenetic relationships and to revise the systematics within the Oscines.

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Fig. 4. **(A)** Neighbor-joining (NJ) dendrogram derived from distance matrix from 12S and 16S rRNA sequence data. Numbers beneath branches are bootstrap proportions (BP) in the 1,000 replications (<50% are omitted). Nodes with bold numbers are identical to ML and MP analyses. Circles, triangles, and rectangles indicate Malagasy, African, and Australian taxa, respectively. (*) Indicates species assigned to the Paridae in Peters’ Check-lists (Snow 1967). Members placed within the Vangidae in the present study are indicated in boldface. See Fig. 1 for the abbreviations of vangid species. Bar equals 0.1 of Kimura’s two-parameter distance. **(B)** Maximum-likelihood (ML) dendrogram (ln likelihood = −8,141). Branches without BP values were not supported in >50% of the 100 replicates. All branches were supported as significantly positive ($P < 0.01$). Bar equals 0.1 unit. **(C)** Maximum parsimony (MP) cladogram using the heuristic option (1,337 steps, 255 bp informative under the condition of parsimony, consistency index = 0.41, homoplasy index = 0.59, retention index = 0.50). Branches without BP values were not supported in >50% of the 1,000 replicates.

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