

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 editions 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

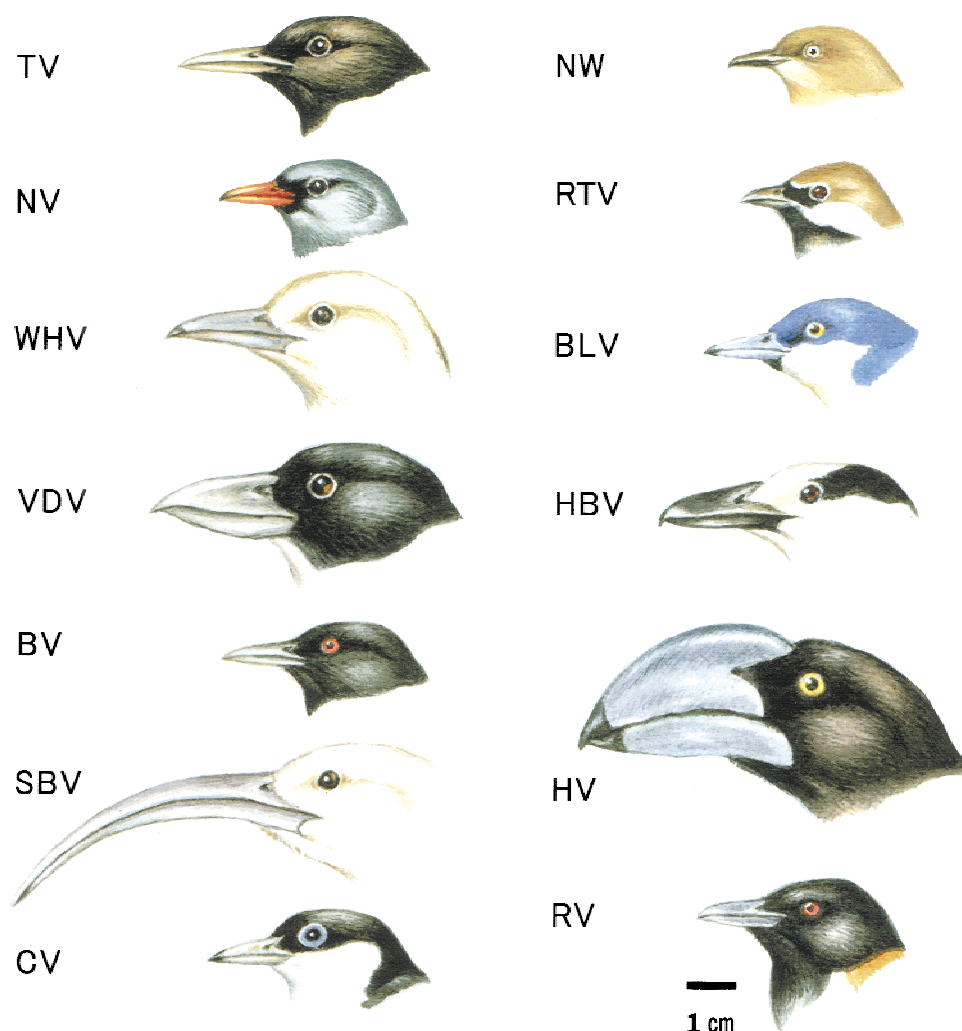


Fig. 1. Sizes, colors, and shapes of bill of vangid species, including *Tylas* and *Newtonia*. (TV): *Tylas eduardi*; (NV): *Hypositta corallirostris*; (WHV): *Leptopterus viridis*; (VDV): *Xenopirostris damii*; (BV): *Oriolia bernieri*; (SBV): *Falculea palliata*; (CV): *L. chaberti*; (NW):

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,