The phylogenetic affinities of Crossley’s babbler (Mystacornis crossleyi): adding a new niche to the vanga radiation of Madagascar

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Crossley’s babbler (Mystacornis crossleyi) is a passerine endemic to Madagascar. Traditionally, it has been classified as a babbler (Timaliidae), although affinities with warblers and vangas have been suggested. We investigated the phylogenetic affinities of Crossley’s babbler using sequence data from two nuclear introns (myoglobin intron 2 and β-fibrinogen intron 5) and one mitochondrial gene (ND2). We present for the first time (to our knowledge) a molecular phylogeny that confidently places this enigmatic species within the vangas (Vangidae). The inclusion of Crossley’s babbler within the vangas adds another foraging niche—gleaning small invertebrates from the ground—to this already large adaptive radiation of songbirds.

Keywords: Mystacornis crossleyi; Aves; Vangidae; adaptive radiation; Madagascar; molecular phylogeny

1. INTRODUCTION

Madagascar has, in combination with relatively few dispersals, resulted in an avifauna that is characterized by a comparably low species richness coupled with high endemism (Langrand 1990; Hawkins & Goodman 2003). Of the 209 species of birds regularly breeding on Madagascar, approximately 50 per cent are endemic. For songbirds (Passeriformes), this estimate is even greater, with 55 of the approximately 69 species (80%) being endemic (Hawkins & Goodman 2003). Furthermore, these 69 species predominantly belong to one of two large endemic radiations, the Bernieridae and the Vangidae.

The Vangidae represent the larger of these two radiations with at least 17 species; but the taxonomic circumscription of this clade remains uncertain and may include more than 20 species (Schulenberg 2003b). This clade represents one of the more famous examples of adaptive radiations, along with the Galapagos finches and Hawaiian honeycreepers, and shows a remarkable morphological diversification, particularly in bill size and shape. Most of the variation in bill morphology relates to foraging ecology. The vangas are primarily insectivorous, but some species also feed on fruits and a few species regularly take vertebrate prey (Schulenberg 2003b). The vangas have a wide range of foraging strategies, including gleaning off foliage and branches (Callicalicus), trunk gleaning (Hyposita), sallies to foliage and branches (Leptopterus and Vanga), in the air (Pseudobias) and to the ground (Schehba), and probing of trunks (Falcula) (Schulenberg 2003b).

The Bernieridae consist of at least 10 species of warbler-like birds previously classified as members of several different passerine groups (Cibois et al. 2001), including bulbuls, babblers and warblers. The taxonomic delimitation of this clade is poorly understood and may include a few additional species currently of uncertain phylogenetic affinity (Schulenberg 2003a). All species currently assigned to this clade glean for insects but segregate to some extent by diet and by the exploitation of different feeding strata (Schulenberg 2003a). The clade also shows variation in body size and bill shapes, although not as pronounced as in the vangas (Schulenberg 2003a). Other groups of songbirds on Madagascar have seemingly not undergone the same type of adaptive radiations as the vangas and Bernieridae and are represented by only one or two species.

Crossley’s babbler (Mystacornis crossleyi) is endemic to Madagascar and the only member of the genus Mystacornis. It is primarily terrestrial and distributed in the humid forests of the eastern part of the island. It is fairly common where suitable habitat remains, from sea level up to 1800 m (Dee 1986). As with several of the other endemic songbirds on Madagascar, Crossley’s babbler has, as the name implies, traditionally been considered to be a babbler (Timaliidae). However, recent molecular studies have shown that the other ‘babblers’ have erroneously been placed in that clade. Instead, the oxylabes (Oxylabes madagascaensis and Crossleyia xanthophrys) and wedge-tailed Jery (‘Neomixis’ flavoviridis) belong to the Bernieridae (Cibois et al. 2001), a clade which in turn appears to be closely related to the acrocephaline/megalurine warblers in Sylvioidae (sensu stricto; Johansson et al. 2008), and the jeries (Neomixis tenella, Neomixis viridis).
and Neomixis striatigula) appear to be part of another sylvid clade, the cisticolas (Cisticolidae) (Nguembock et al. 2007). This leaves Crossley’s babbler, together with the white-eyes (Zosterops), as the only putative babbler on Madagascar. Although historically associated with the babblers, Mystacornis also bears resemblance to several of the species currently placed in the Bernieridae, particularly Oxylabes. However, molecular
data do not support any of these associations, but rather indicate a position outside the Passerida (Cibois et al. 1999, 2001). Schulenberg (2003b) suggested, based on preliminary data, that Mystacornis might be related to the vangas within the ‘Corvoidea’ radiation (= crown Corvoidea sensu Barker et al. 2004).

We investigate the phylogenetic affinities of Mystacornis using sequence data from two nuclear introns (myoglobin intron 2 and β-fibrinogen intron 5) and one mitochondrial gene (ND2). Our data support a vangid affinity of Mystacornis, which adds yet another feeding niche and behavioural specialization to the vanga radiation.

2. MATERIAL AND METHODS

(a) Taxon sampling

We compared DNA sequences of M. crossleyi with 51 species of passerines, using a meliphagid (Leaden Honeyeater Ptiloprora species included (as well as GenBank accession numbers) is detailed in table 1 of the electronic supplementary material.

Laboratory procedures for the extraction, PCR amplification and sequencing of the nuclear genes follows Irestedt et al. (2002), Fuchs et al. (2004), and Johansson & Ericson (2005). Mitochondrial ND2 was amplified with primers L5219 Met and H6313 Trp (Sorenson et al. 1999). The concatenated alignment of the three gene segments included 2369 nucleotide positions (myoglobin: 676 bp; β-fibrinogen intron 5: 659 bp; ND2: 1034 bp). All gaps were treated as missing data in the phylogenetic analyses.

(b) Phylogenetic analyses

Phylogenetic relationships were estimated using Bayesian inference in MrBayes v. 3.1.1 (Ronquist & Huelsenbeck 2003). The three gene partitions were analysed separately and in a combined mixed-model analysis. The model of sequence evolution for each partition was selected with the Akaike information criterion (Akaike 1973) calculated in MrModeltest v. 2.2 (Nylander 2004).

The general time-reversible (GTR) model with gamma-distributed invariant sites (I) was chosen for ND2, whereas GTR+4 was used for each of the nuclear gene segments (myoglobin and β-fibrinogen intron 5). Default priors were used in all MrBayes analyses. Two independent runs, each with four Metropolis-coupled Markov chain Monte Carlo chains, were run for 5 million generations and sampled every 100 generations. At the end of the run, the standard deviation of split frequencies was less than 0.01. Trees sampled before the chain reached stationarity were discarded.

Node support was also evaluated under the parsimony optimality criterion with a non-parametric bootstrap analysis in PAUP* v. 4.0.b10 (Swofford 2002), as well as with maximum likelihood (ML) using RAxML-VI-HPC (Stamatakis 2006). For the ML analyses, a GTR+4 model was used for each gene region and support was estimated with 100 bootstrap pseudo-replicates, whereas the parsimony analysis was performed with 1000 bootstrap pseudo-replicates, each with 10 random additions of taxa.

3. RESULTS AND DISCUSSION

The combined mixed-model analysis of the three-gene dataset strongly suggested a corvid affinity for Mystacornis, with no support for an association with the babblers or members of the Bernieridae (figure 1). Instead, there is strong support for placing Mystacornis as yet another member of the vanga radiation, as Mystacornis is placed as sister to Pseudobius, with Cyanolanitis basal relative to them. The vangas, including Mystacornis, are placed with strong support in a clade together with the African helmetshrikes (Prionops) and the flycatcher-shrikes (Megabates flammulatus and Bias musculus; see also Fuchs et al. 2004). This clade may also include the Asian woodshrikes (Tephrodornis), flycatcher-shrikes (Hemipus) and philetornas (Philetornis) (Moyle et al. 2006). A corvid affinity of Mystacornis is supported in all gene trees, and both the nuclear β-fibrinogen intron 5 and mitochondrial ND2 place Mystacornis in the vanga clade (see figures 2 and 3 of the electronic supplementary material). Myoglobin is inconclusive in this regard, but places Mystacornis in a polytomy together with the vangas, helmetshrikes, batises (Batis and Platysteira) and a clade with the bushshrikes and allies (malacoenotids) (see figure 1 of the electronic supplementary material).

Based on patterns of the jaw musculature, Beecher (1953) proposed that Mystacornis might be a vanga. However, this suggestion had little impact on later classifications and Mystacornis remained placed among babblers despite very little evidence for this association. The vangid affinity of Mystacornis leaves the white-eyes as the only representatives of the babbler radiation on Madagascar.

The addition of Mystacornis to the vanga clade adds more than just another species to this radiation. Mystacornis is primarily an understorey bird, only taking wing when threatened or during territorial fights (Langrand 1990; T. S. Schulenberg 1989–1995, personal observation). Despite the remarkable adaptive radiation among the vangas, Mystacornis is the only vanga species that forages on the ground, primarily by gleaning small invertebrates from either the ground or low vegetation. Three genera of vangas exclusively forage by gleaning vegetation, and six other genera frequently employ this foraging behaviour. Interestingly, some observations suggest that Mystacornis also probes dead wood on the forest floor (Goodman, in Schulenberg 2003b); probing of woody substrates is another frequently employed foraging strategy of vangas, especially in species with the most derived bill morphologies (e.g. Falculea, Xenopirostris). Samples used in this study were provided by the Field Museum of Natural History, Swedish Museum of Natural History and Zoological Museum, University of Copenhagen. This research was supported by grants from the Department of Science and Technology (South Africa) to R.C.K.B. and from Magn. Bergvalls Stiftelse to U.S.J.


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