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Resolving taxonomic uncertainty and historical biogeographic patterns in *Muscicapa* flycatchers and their allies ☆

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ABSTRACT

Muscicapa flycatchers and their allies (*Bradornis*, *Dioptornis*, *Empidornis*, *Fraseria*, *Myioparus*, *Namibornis*, and *Sigelus*) are widely distributed in Africa, Europe and Asia. This broad distribution and the wide variety of habitats occupied by the group, ranging from arid to tropical forests, presents an interesting opportunity to explore the evolution of biogeographic patterns and habitat associations. Sequence data (up to 3310 base pairs from two mitochondrial and two nuclear genes) were generated for 36 of 42 species which comprise the assemblage. Complementary data from an additional species was retrieved from GenBank, as was an additional gene which was available for 21 of our included taxa. Using model-based phylogenetic methods and molecular clock dating, we constructed a time-calibrated molecular phylogenetic hypothesis for the lineage. Ancestral area reconstructions were performed on the phylogeny using LaGrange and BioGeoBEARS. Our results indicate that *Bradornis*, *Fraseria*, and *Muscicapa* are each non-monophyletic, with the latter being shown to comprise five separate clades each more closely related to other genera. Two new genera (*Chapinia* and *Ripleyia*) are erected to account for these results. *Muscicapa* and allies originated c. 7.4 Ma, most likely in Africa given that their sister lineage is almost entirely from there, and rapidly achieved a Eurasian distribution by c. 7.1 Ma. A second divergence at c. 6.1 Ma resulted in two clades. The first is a largely Eurasian clade that subsequently recolonized Africa, perhaps as the result of the loss of migration. The second is an African clade, and ancestral reconstructions suggest a Congolian (e.g. tropical forest) origin for this clade, with several subsequent diversifications into more arid habitats. This is a unique result, as most tropical forest lineages are confined to that habitat. As with other studies of African bird lineages, Afrotropical forest dynamics appear to have played a significant role in driving diversification in *Muscicapa* and allies, and our results include just the second recorded case of southern to northern African colonization patterns.

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1. Introduction

Higher-level avian systematic relationships have undergone considerable reshuffling over the past few decades, as molecular phylogenetic analyses have made it comparatively easier to resolve homoplasy resulting from convergent evolution (Wake et al., 2011). The overarching result has tended to be more rigorous formulations of relationships, as indicated by consistency of inferred relationships across studies. This rigor is in marked contrast to older taxonomic work which, as pointed out by Sangster et al. (2010), tended to formulate suprageneric classifications based on often misleading assessments of phenotype and morphology, rather than quantitative assessments of relationships.

One example of higher level systematic and considerable taxonomic reshuffling centers on the Muscicapidae (Old World chats and flycatchers). This diverse and speciose assemblage has been the subject of a number of molecular phylogenetic studies that have focused primarily on assigning genera to higher level monophyletic groups. Results of these studies include, or confirm, the removal of chats from Turdidae to Muscicapidae, the separation of chats and flycatchers into tribes within Muscicapidae (Saxicolini and Muscicapini), and the erection of a subfamily (Muscicapinae) to house these tribes (e.g., Cibois and Cracraft, 2004; Voelker and Spellman, 2004; Sangster et al., 2010). Other studies have moved genera between these tribes, and to Saxicolini from Turdinae (e.g., Voelker and Spellman, 2004) and have erected new tribes to accommodate still other monophyletic phylogenetic groups (e.g., Sangster et al., 2010).

Suprageneric relationships are not the only systematic and taxonomic issues in Muscicapidae. For example, in their extensive

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molecular assessment of that family, Sangster et al. (2010) demonstrated that the genus *Melaenornis* (Muscicapini) is not monophyletic, and indeed taxonomic treatments have disagreed on the limits of "*Melaenornis*" by including some taxa from that genus in other genera (e.g., Mayr and Cottrell, 1986; Taylor, 2006; Dickinson and Christidis, 2014). Thus, while we have a better idea of suprageneric relationships in Muscicapidae, we are still working towards assigning species membership to genera with confidence, and the relationships of species within those genera. This has also impacted other types of analyses (e.g., historical biogeography studies) which rely on well-resolved phylogenies to better understand the evolution of the group. Indeed, the intercontinental distribution of Muscicapini, the diversity of habitats collectively occupied by members of the tribe and the presence of migratory behavior in a small subset of species combine to suggest that interesting biogeographic scenarios are likely.

We focus here on the systematics and biogeography of the Muscicapini: Old World chats and flycatchers. This is a diverse assemblage of about 37 species, which collectively have widespread distributions centered in Africa and Eurasia (Taylor, 2006). Our goals are as follows: (1) to resolve the taxonomic issues related to genus-level relationships and genus membership by species, and (2) to assess biogeographic patterns in the group. Based on the distributional patterns of most Muscicapini (as well as the African ancestral area of its sister clade, the Copsychini; Voelker et al., 2014), we expect that: (1) Eurasian taxa will be derived from African ancestors; (2) colonization of Eurasia will be attributable to expansion through the Saudi Peninsula, and not overwater dispersals as we found in Copsychini (Voelker et al., 2014); and (3) gains or losses of migratory behavior by Eurasian taxa will be relevant to explaining intercontinental distribution patterns.

2. Material and methods

2.1. Taxon sampling and sequencing

Primarily following Dickinson and Christidis (2014; exceptions noted below) our analyses included 37 Muscicapini species representing the following genera: *Muscicapa* (19 of 23 species), *Melaenornis* (3/4), *Myioparus* (2/2), *Namibornis* (1/1), *Dioptrornis* (3/3; all considered *Melaenornis* by Dickson and Christidis), *Empidornis* (1/1), *Fraseria* (2/2), *Sigelus* (1/1) and *Bradornis* (4/4) (Supplementary Table S1). We note here that the last five of these genera, until recently, have been considered *Melaenornis* (e.g., Mayr and Cottrell, 1986; Taylor, 2006), but that genus has been rendered non-monophyletic in a recent molecular systematic study (Sangster et al., 2010), which included a subset of the Muscicapini species ($n = 21$) included here as part of our broader sampling. Zuccon and Ericson (2010) similarly found *Melaenornis* to be non-monophyletic, but included just nine Muscicapini species. We did not include the monotypic *Humblotia*, which Dickinson and Christidis (2014) place as a Muscicapini species (but see Jønsson and Fjeldså, 2006), but we did include *Namibornis*, which is not a member of Copsychini (see Mayr and Cottrell, 1986, and results below) as previously suggested. As outgroup taxa, we included a suite of *Erythropygia* and *Copsychus* species which, as members of Copsychini, form the sister clade to Muscicapini (Sangster et al., 2010; Voelker et al., 2014).

Whole genomic DNA was extracted from tissue or toepads using the DNeasy tissue extraction kit (Qiagen, Valencia, CA, USA). We used the polymerase chain reaction (PCR) to amplify the mitochondrial cytochrome-*b* (CYB) and NADH dehydrogenase subunit 2 (ND2) genes, as well as the autosomal nuclear Myoglobin (MB intron 2) and Beta-Fibrinogen (FGB intron 5) genes. Standard primers and reaction conditions were employed. PCR products were cleaned with ExoSAP-IT (Affymetrix, Santa Clara, CA, USA). Sanger sequencing was performed at the Beckman Coulter Genomics facility (Danvers, MA, USA). The mtDNA sequences were aligned using Sequencher v. 4.9 (Gene Codes Corporation, Ann Arbor, MI, USA). Introns were aligned using MAFFT (Katoh, 2013).

2.2. Phylogenetic analyses and divergence dating

To determine the best-fit model(s) for the mitochondrial (mtDNA) sequence data, we assessed three alternate partitioning schemes, each of which relied on appropriate partition models derived from MrModelTest (Nylander, 2004). In our first partitioning scheme (two partitions) the ND2 and CYB genes were unlinked. In the second (four partitions), first and second codon positions were linked for ND2, linked for CYB, and third codon positions for each gene were treated as independent partitions. In the third scheme (six partitions), each codon position was unlinked across both genes. For each mixed-model partition scheme, we used MRBAYES (Huelsenbeck and Ronquist, 2001) to initiate two runs of four Markov-chain Monte Carlo (MCMC) chains of 5,000,000 generations, each starting from a random tree and sampling every 100 generations. Each run resulted in 50,000 trees and converged on the same topology. The first 5000 trees from each analysis were removed as "burn-in", and the remaining 90,000 trees were used to generate a majority rule consensus tree. Bayes factors were computed using the harmonic means of the likelihoods calculated from the *sump* command within MRBAYES. A difference of 2 ln Bayes factor >10 was used as the minimum value to discriminate between mixed-model partitioning schemes (Brandley et al., 2005; Brown and Lemmon, 2007), and the six partition scheme was identified as the best-fit to the mitochondrial data. We then used the six-partition mtDNA scheme in combination with the nuclear gene data. Best-fit models for nuclear data were also derived from MrModelTest analyses. This combined analysis set each nuclear gene and each mtDNA codon position as unlinked in two runs of four MCMC chains in MRBAYES as described above.

We also incorporated best fit models for each gene in BEAST 2.0 (Drummond et al., 2006, 2012) to reconstruct a tree using all loci, and simultaneously estimated divergence times across all species. We employed a lineage substitution rate of 0.014 per lineage/million years for CYB using a relaxed, uncorrelated lognormal clock. This substitution rate translates to 2.8% per million years, and is generally applicable to the CYB gene in songbirds (Weir and Schluter, 2008; Lerner et al., 2011). We used a rate of 0.029 per lineage/million years for ND2 (Lerner et al., 2011). We applied a slightly broader prior (0.002) for FGB than the 0.0017 rate used by Lerner et al. (2011), to reflect the greater variation of rates among introns. We applied the same 0.002 rate to MB. Standard deviations for the mitochondrial genes (CYB: 0.001; ND2: 0.0025) followed Lerner et al. (2011), while we used a 0.002 standard deviation for the introns. A Yule process speciation prior was implemented in each analysis. Two separate MCMC analyses were run for 10,000,000 generations with parameters sampled every 1000 steps, with a conservative 20% burn-in. Independent runs were combined using LogCombiner v.1.6.1 (Drummond et al., 2012). Tracer v.1.5 (Rambault and Drummond, 2007) was used to measure the effective sample size of each (all >200) and calculate the mean and upper and lower bounds of the 95% highest posterior density interval (95% HPD) for divergence times. Tree topologies were assessed using TreeAnnotator v.1.7 (Rambault and Drummond, 2007; Drummond et al., 2012) and FigTree v.1.3.1 (Rambault, 2008). Finally, we also performed the above analyses on a five gene dataset. These analyses included the ODC1 gene from 21 ingroup taxa for which data was available on GenBank. Nexus trees of both datasets are available as Supplementary material in the online version.

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