



Multi-locus phylogenetic analysis of Old World chats and flycatchers reveals extensive paraphyly at family, subfamily and genus level (Aves: Muscicapidae)

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ABSTRACT

The chats and flycatchers (Muscicapidae) represent an assemblage of 275 species in 48 genera. Defining natural groups within this assemblage has been challenging because of its high diversity and a paucity of phylogenetically informative morphological characters. We assessed the phylogenetic relationships of 124 species and 34 genera of Muscicapidae, and 20 species of Turdidae, using molecular sequence data from one mitochondrial gene and three nuclear loci, in total 3240 bp. Bayesian and maximum likelihood analyses yielded a well-resolved tree in which nearly all basal nodes were strongly supported. The traditionally defined Muscicapidae, Muscicapinae and Saxicolinae were paraphyletic. Four major clades are recognized in Muscicapidae: Muscicapinae, Niltavinae (new family-group name), Erithacinae and Saxicolinae. Interesting relationships recovered by this analysis include: (i) a clade comprising the 'blue' flycatcher genera *Niltava*, *Cyornis*, *Cyanoptila* and *Eumyias* and some species of *Rhinomyias*; (ii) the position of *Erithacus rubecula* in a clade of otherwise exclusively African species; (iii) a close relationship between the shortwing *Heinrichia calligyna* and the flycatcher *Rhinomyias insignis*; (iv) a sister-relationship between forktails *Enicurus* and whistling thrushes *Myophonus*; and (v) a sister relationship of *Ficedula* and the 'chats' *Monticola*, *Phoenicurus*, *Saxicola* and *Oenanthe*. A high number of traditionally defined genera was found to be paraphyletic or polyphyletic.

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1. Introduction

The chats and Old World flycatchers (Muscicapidae) are a diverse avian taxon, comprising 48 genera and 275 species (Dickinson, 2003; Clements, 2007). Members of this family are widely distributed in the Palearctic, Afrotropical and Indo-Malayan regions, and some species occur in parts of Australasia and the Nearctic. Chats and Old World flycatchers are found in a variety of habitats ranging from primary rainforest to deserts, mountains and arctic tundra. The group includes some of the best studied species of birds, including the European Robin *Erithacus rubecula*, the Common Nightingale *Luscinia megarhynchos* and the European Pied Flycatcher *Ficedula hypoleuca* (Lack, 1965; Cramp, 1988; Lundberg and Alatalo, 1992).

The chats and flycatchers exhibit a broad range of phenotypes, behaviors and lifestyles, and thus offer a rich ground for studies of character evolution. Recurrent phenotypes, such as the combination of a white crown, a dark breast, and an orange or red belly,

are found in several, apparently distantly related genera (*Chaimarornis*, *Thamnolaea*, *Copsychus*, *Phoenicurus*). Polymorphism has been documented in some genera (Mayr and Stresemann, 1950). Several genera include both sexually monomorphic and dimorphic species, whereas others are strictly monomorphic or dimorphic (del Hoyo et al., 2005, 2006). Furthermore, the family includes several speciose genera but also many genera with only one or two species. Thorough phylogenetic analyses are needed to understand the factors that have shaped these patterns of variation and diversity, and to delineate natural taxa.

Until recently, the chats have been combined with the thrushes in a single family (Turdidae), whereas the Old World flycatchers were classified in a separate family Muscicapidae (e.g. Voous, 1977; del Hoyo et al. 2005, 2006). It has been long known that chats and flycatchers show several morphological and behavioral similarities (e.g. Knowlton, 1909; Ripley, 1955; Löhrl and Thaler, 1992). Sibley and Ahlquist's (1990) DNA–DNA hybridization studies suggested that chats and Old World flycatchers are more closely related to each other than to the thrushes. They placed the chats and flycatchers in separate tribes (Saxicolini and Muscicapini) within a newly defined Muscicapinae (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). Other authors have placed the Old

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World flycatchers and chats in separate subfamilies (Dickinson, 2003) and recognized the combined taxon as a family (Muscicapidae; Dickinson, 2003; Clements, 2007).

Subsequent studies using molecular sequence data have shown that the chats and flycatchers (as defined by Sibley and Ahlquist, 1990) do not form reciprocally monophyletic groups (Cibois and Cracraft, 2004; Voelker and Spellman, 2004; Treplin et al., 2008). The most comprehensive study of Muscicapidae relationships recognised two major clades ('Muscicapini' and 'Saxicolini') but did not address phylogenetic relationships within these clades (Voelker and Spellman, 2004). The latter study was based on one nuclear gene (*c-mos*) and two mitochondrial genes (cytochrome *b* and ND2).

Until recently, suprageneric classifications have been inferred on the basis of intuitive assessments of relationships (e.g. Ripley, 1952; Vaurie, 1952, 1953; Irwin and Clancey, 1974; Wolters, 1983). Recent molecular phylogenetic studies have addressed relationships among African forest robins (Beresford, 2003; Voelker et al., 2009), chats and thrushes (Pan et al., 2006a,b) and Asian flycatchers (Lei et al., 2007a,b). A number of molecular phylogenetic studies, mostly based on mitochondrial DNA sequences, involved limited taxon sampling to investigate particular genera, including *Stiphornis* (Beresford and Cracraft, 1999; Schmidt et al., 2008), *Sheppardia* (Roy et al., 2001), *Phoenicurus* (Ertan, 2002, 2006), *Pseudocossyphus* (Goodman and Weigt, 2002), *Erithacus* (Dietzen et al., 2003; Seki, 2006), *Ficedula* (Outlaw and Voelker, 2006), *Oenanthe* (Aliabadian et al., 2007), *Monticola* (Outlaw et al., 2007; Zuccon and Ericson, 2010a), *Saxicola* (Illera et al., 2008; Woog et al., 2008; Zink et al., 2009), *Copsychus* (Sheldon et al., 2009), and *Oenanthe* and *Cercomela* (Outlaw et al., 2010).

The objectives of this study are to assess the phylogenetic relationships of representatives of 34 genera of Muscicapidae using DNA sequences from one mitochondrial and three unlinked nuclear loci, and to identify monophyletic groups for use in taxonomic revision. Our study represents the most comprehensive account of phylogenetic relationships among Muscicapidae so far, both in terms of taxon sampling and number of loci, and provides the basis for a revised classification of Muscicapidae.

2. Methods

2.1. Taxonomic sampling

We include 124 species of Muscicapidae, representing 34 of the 48 genera recognised by Dickinson (2003). We also include 20 species of Turdidae, representing 10 of the 24 genera recognized by Dickinson (2003) (Supplementary Table 1). Our data set does not include representatives of the genera *Chaetops*, *Culicicapa*, *Microeca*, *Newtonia*, *Zeledonia* and *Stenostira*, which have been classified as Old World flycatchers in the past (e.g. Wolters, 1980; Watson et al., 1986; Dickinson, 2003; Clements, 2007), but which have been identified as members of distantly related clades by recent phylogenetic studies (Sibley and Ahlquist, 1990; Lovette and Bermingham, 2002; Beresford et al., 2005). Unless otherwise stated, scientific names follow Dickinson (2003) and English names follow Gill and Donsker (2010).

2.2. DNA extraction, amplification and sequencing

DNA was extracted using QIA Quick DNEasy Kit (Qiagen, Inc.) according to the manufacturer's instructions. We sequenced the mitochondrial cytochrome *b* gene (hereafter *cyt b*), and the nuclear ornithine decarboxylase exon 6 (partial), intron 6, exon 7, intron 7 and exon 8 (partial) (ODC), the entire nuclear myoglobin intron 2 (*myo*), and the complete nuclear lactate dehydrogenase (LDH) in-

tron 3. Amplification and sequencing followed the protocols described in Fregin et al. (2009). The *cyt b* sequence was amplified as one fragment to decrease the risk of amplifying nuclear pseudocopies of the coding gene (e.g., Quinn and White, 1987; Arctander, 1995; Quinn, 1997; Sorenson and Quinn, 1998). No stop codons that would indicate the presence of nuclear pseudogenes (e.g. Sorenson and Quinn, 1998) were found in the coding *cyt b* sequences. The sequences have been deposited in GenBank (accession numbers in Supplementary Table 1).

2.3. Phylogenetic analyses

Sequences were aligned using MegAlign 4.03 in the DNASTAR package (DNASTAR, Inc.); some manual adjustment was necessary for the nuclear sequences. Molecular phylogenies were estimated by Bayesian inference using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). Posterior probabilities (PP) were calculated for *cyt b*, ODC and LDH under a time reversible (GTR) model (Lanave et al., 1984; Tavaré, 1986; Rodríguez et al., 1990), while for *myo* the HKY model (Hasegawa et al., 1985) was used. For all four loci rate variation across sites according to a discrete gamma distribution with four rate categories (G; Yang, 1994) was assumed. For the *cyt b* and ODC data, also with an estimated proportion of invariant sites (I; Gu et al., 1995). The choice of model was determined based on the Akaike Information Criterion (Akaike, 1973) calculated by MrModeltest2 (Nylander, 2004) in conjunction with PAUP* (Swofford, 2001). The sequences from the four loci were analyzed both separately and concatenated. For the concatenated data set, data were divided into four partitions, which were allowed to have partition-specific model parameters (Ronquist and Huelsenbeck, 2003; Nylander et al., 2004). The *cyt b* and ODC sequences were analyzed under the GTR + G + I model. LDH was analyzed under the GTR + G model, while *myo* was analyzed under the HKY + G model. Default priors in MrBayes were used. Four Metropolis-coupled MCMC chains with incremental heating temperature 0.1 were run for 100 million generations, and sampled every 1000 generations. Two runs were run simultaneously, starting from random trees, and the results compared to ascertain that the chains had reached the same target distributions. The first 25% of the generations, long after the chain reached apparent stationarity, were discarded and the posterior probability estimated for the remaining generations. The samples from the stationary phases of the independent runs were pooled to obtain the final results. Maximum likelihood (ML) bootstrapping (1000 replicates) was performed in RAXML v. 7.2.6 (Stamatakis, 2010) on the CIPRES portal (Miller et al., 2009) under the GTR model (unpartitioned). Uncorrected *p* pairwise sequence divergences were calculated in PAUP* (Swofford, 2001).

3. Results

3.1. Sequence characteristics

We obtained a 1038 bp portion of the coding *cyt b* gene and part of the flanking tRNA-Thr of variable length for 149 taxa. The total length of the aligned sequences comprised 1087 characters. Seven sequences were incomplete, with lengths of 980–1032 bp.

The length of the nuclear introns varied depending on multiple indels (see Fig. S1). For the myoglobin intron a contiguous stretch of 559–677 bp, comprising most of intron 2, was obtained for 134 taxa. Twelve further sequences were used, but did not comprise the entire fragment. The aligned myoglobin sequences comprise 708 characters. A total of 36 inferred indel events were needed to satisfactorily align the myoglobin intron II sequences. Eighteen

of the indels (50%) were shared by two or more taxa, while 18 indels were autapomorphic.

For ODC, sequences were obtained for 136 taxa, comprising part of exon 6, the entire intron 6, exon 7, intron 7, and part of the flanking exon 8. For 100 taxa the complete target stretch of 692–739 contiguous bp was obtained. 36 sequences were incomplete. The aligned sequences contain 818 characters. A total of 53 inferred indel events were needed to satisfactorily align the ODC intron sequences. 31 of the indels (58%) were shared by two or more taxa, while 22 indels were autapomorphic.

The LDH sequences comprised 495–619 bp, mostly intron 3, with an additional 36 bp of the flanking exon 4. About 141 sequences were obtained, of which 131 were complete. The aligned sequences contain 627 characters. A total of 62 inferred indel events were needed to satisfactorily align the LDH intron sequences. 41 of the indels (66%) were shared by two or more taxa, while 21 indels were autapomorphic.

The concatenated dataset contains 3240 characters.

3.2. Phylogeny: deep nodes

The tree based on the concatenated sequences of all loci is shown in Fig. 1. This is the tree hereafter referred to unless otherwise stated. Insertions and deletions in the three nuclear genes are mapped on the multi-locus tree in Supplementary Fig. S1. The single-locus trees are shown in Supplementary Figs. 2–5. The 146 species of Turdidae and Muscicapidae included in this analysis formed a well-supported monophyletic group containing two major clades (A and B). Clade A included 12 species traditionally placed in Turdidae, and *Cochoa viridis*, which is traditionally included in Muscicapidae. All analyses supported *Cochoa* as a member of Turdidae and as the sister-taxon of *Chlamydochaera jefferyi*. The latter relationship was also supported by an insertion and a deletion in both LDH and Myo, and an insertion in ODC (Fig. S1).

Clade B corresponds to Muscicapidae and is well-supported in the multi-locus tree and in all single-locus trees (PP 0.97–1.0), and is further supported by a unique 6-bp insertion in the ODC alignment (Fig. S1). This clade also included all representatives of *Myophonus*, *Alethe*, *Brachypteryx*, *Monticola* and the monotypic *Heinrichia*, which are usually placed in Turdidae (Sibley and Monroe, 1990; Dietzen et al., 2003). Within clade B, a basal subdivision was found between a clade comprising the ‘chat/robin’ and flycatcher genera *Alethe*, *Muscicapa*, *Fraseria*, *Melaenornis*, *Cercotrichas*, *Saxicoloides*, *Trichixos* and *Copsychus* (clade C) and a clade containing all other chats and flycatchers (clade D). Both clades were strongly supported in the multi-locus analysis (PP 1.0 and 0.99, respectively), although clade D was supported only by ODC in the single-locus trees.

Within clade C are two subclades, comprising the ‘robins’ *Cercotrichas*, *Saxicoloides*, *Trichixos*, and *Copsychus* (clade C1; PP 0.93) and the flycatchers *Muscicapa*, *Fraseria* and *Melaenornis* (clade C2; PP 1.0), respectively. The position of *Alethe diademata* within clade C was not strongly supported, and also differed among individual gene trees. Clade C1 (excluding *A. diademata*) was corroborated by two unique (3-bp, 105-bp) deletions in myo (Fig. S1).

Within clade D, several major clades were identified. One of these (clade D1), which was inferred to be sister to the others in clade D, was composed of several genera of ‘blue’ flycatchers (*Cyornis*, *Niltava*, *Eumyias* and *Cyanoptila*), and also included *Ficedula monileger* and three species of *Rhinomyias* (PP 1.0). This clade was strongly supported by the multi-locus dataset, and was recovered by cyt *b* and myo in the single-locus analyses, and was further supported by a 1-bp deletion in the ODC alignment (Fig. S1). Another major group within clade D was a clade of African forest chats, which was supported by analyses of the multi-locus dataset and by two of the single-locus analyses (cyt *b*, myo), and a 1-bp

deletion in the LDH alignment (clade D2; Fig. S1). The European Robin *Erithacus rubecula* was also part of this clade, although its exact position was unresolved.

Clade D3 included a diverse set of flycatchers, shortwings, nightingales and chats and was itself composed of several clades (D3a–i).

- The flycatcher *Rhinomyias insignis*, the shortwing *Heinrichia caliginosa*, two species of *Brachypteryx* shortwings, and five species of *Luscinia* ‘robins’ (*L. brunnea*, *L. cyane*, *L. sibilans*, *L. komadori*, *L. akahige*) formed a clade with high PP (1.0) in the multi-locus tree (clade D3a). However, this clade was rather weakly supported by ML bootstrapping, and was not recovered in any of the single-locus trees.
- Another clade (D3b) was formed by the ‘robins’ *Irania*, three species of *Luscinia* and *Hodgsonius phaenicuroides*. This clade had high PP (0.97) in the multi-locus tree, but was not supported by ML bootstrapping, nor by any of the single-locus analyses.
- The whistling thrushes (*Myophonus*) and fork-tails (*Enicurus*) were identified as sister taxa with strong support in the multi-locus and LDH datasets (clade D3c; PP 1.0), and was further recovered by myo and supported by a 1-bp deletion in the LDH alignment (Fig. S1).
- Eight species of *Luscinia* and *Myiomela leucura* ‘robins’ formed a clade with high PP (0.98) in the multi-locus dataset (clade D3d), although this clade was not supported by ML bootstrapping, and was not recovered in any of the single-locus analyses.
- Eight species of *Ficedula* flycatchers formed a monophyletic group (clade D3e), which had high PP in the multi-locus analysis (1.0), but poor ML bootstrap support, and which was only recovered by cyt *b* in the single-locus analyses. This clade was sister to a clade of ‘chats’, again with high PP but rather low ML support and only inferred by one single-locus analysis (LDH; Fig. S4). The ‘chat’ clade included the redstarts (*Phoenicurus* and allies; clade D3f), rock thrushes (*Monticola*; clade D3g), stonechats (*Saxicola*; clade D3h) and chats, cliff-chats and wheatears (*Myrmecocichla*, *Thamnolaea*, *Campicoloides*, *Oenanthe* and *Cercomela*; clade D3i). All these were strongly supported by the multi-locus data and were recovered in two or three independent single-locus analyses, except clade D3g, which had high PP (1.0) but lower ML bootstrap support (82%) and was only recovered by cyt *b* in the single-locus analyses.

Although the relationships among clades D3a–D3i generally had high PPs, most of them were not recovered by any single-locus analyses and had no or low ML bootstrap support.

3.3. Phylogeny: shallow nodes

Within clade C1, *Cercotrichas podobe*, *C. galactotes*, *C. paena*, *C. hartlaubi* and *C. leucophrys* were more closely related to *Saxicoloides*, *Trichixos* and *Copsychus*, than to *C. coryphaeus*, *C. leucosticta*, *C. quadrivirgata* and *C. barbata*. Although the relationships among *Cercotrichas* inferred in the four single-locus trees differed among loci, all supported the non-monophyly of *Cercotrichas*. *Copsychus saularis* was sister to *Saxicoloides fulicatus*, whereas *C. luzoniensis*, *C. malabaricus indicus* and *C. m. stricklandii* were sister to *Trichixos pyrrhopygus*. *C. malabaricus indicus* and *C. m. stricklandii* were sister taxa but were differentiated in both mitochondrial and nuclear genes, with 2.2% (uncorrected) divergence of cyt *b* (including tRNA-Thr) sequences.

Clade C2 included the flycatcher genera *Muscicapa*, *Melaenornis* and *Fraseria*. The genus *Muscicapa* was represented by 13 of the 23 species recognized by Dickinson (2003). Ten species of *Muscicapa* formed a well-supported monophyletic group (PP 1.0), which

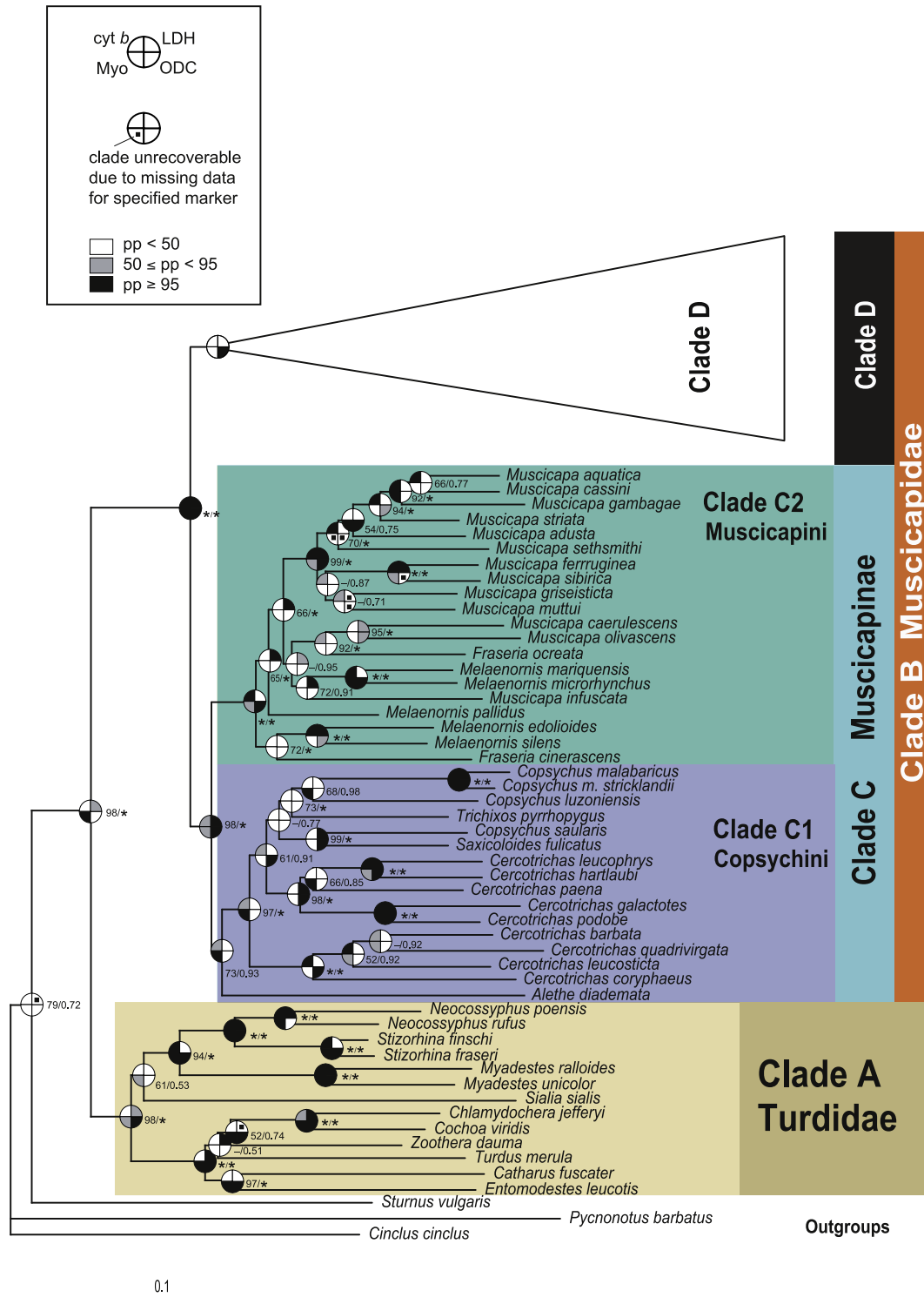


Fig. 1. Relationships of Muscicapidae and Turdidae based on Bayesian analysis of combined mitochondrial cytochrome *b*, and nuclear ODC, myoglobin and LDH intron sequences (3240 bp) divided into two partitions analyzed under the GTR + G + I model (cyt *b* and ODC), one partition analyzed under the GTR + G model (LDH) and one partition analyzed under the HKY + G model (myo). Maximum Likelihood bootstrap values and Bayesian posterior probabilities, respectively, are given for each node. An asterisk denotes a bootstrap value of 100% or a posterior probability of 1.0. A '-' indicates that the node was not recovered by Maximum Likelihood analysis. The pie diagrams indicate support from individual gene trees. The names referring to the marked clades are the ones proposed here.

included a well-supported subclade of mostly African species (*M. sethsmithi*, *M. adusta*, *M. striata*, *M. gambagae*, *M. aquatica*, *M. cassini*), and a poorly-supported clade of four Asian species (*M. ferruginea*, *M. sibirica*, *M. griseicticta*, *M. muttui*). Three other species of *Muscicapa* were placed outside this clade: *M. olivascens* and *M. cae-*

rulescens were sister to *Fraseria ocreata* (PP 1.0), and these in turn were sister to *M. infuscata*, *Melaenornis microrhynchus* and *M. mariquensis* (PP 0.95). *Melaenornis edolioides* and *M. silens* were sister to *Fraseria cinerascens* (PP 1.0) and these three species together were sister to all other species in clade C2. Not all of these

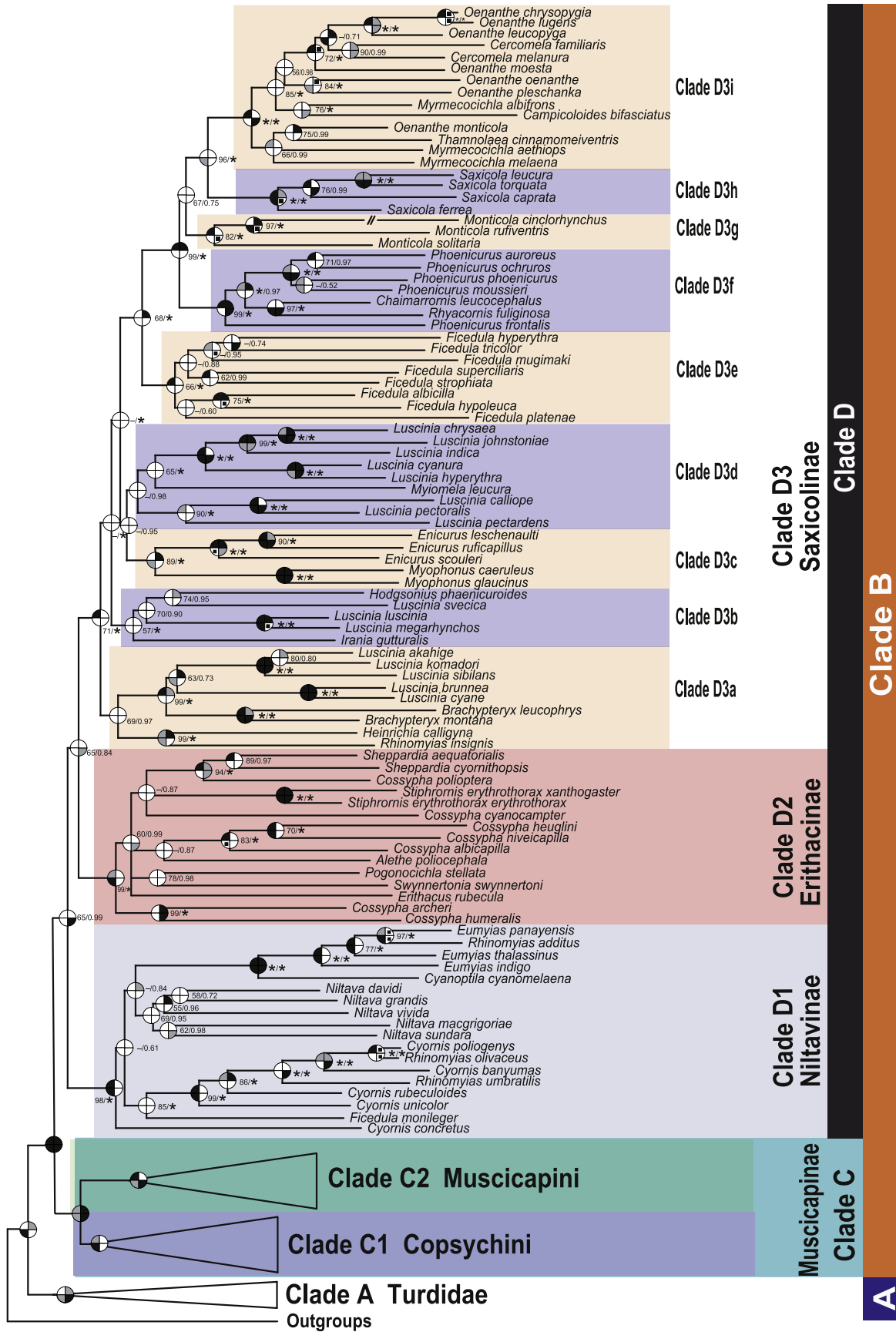


Fig. 1 (continued)

relationships were supported by ML bootstrapping, and the *Melanornis edoloides*–*M. silens*–*F. cinerascens* clade was not recovered in any single-locus analyses.

Within the flycatcher clade D1, two species of *Rhinomyias* were placed as non-sisters within a clade with four species of *Cyornis*. *F. monileger* was sister to this clade, with high PP and reasonably high ML bootstrap support in the multi-locus analysis, but was not inferred by any single-locus analysis. *Cyanoptila cyanomelaena* was the sister species of a clade including three species of *Eumyias* and a third species of *Rhinomyias*, *R. additus*. The clade formed by *Cyanoptila cyanomelaena*, *Eumyias* and *R. additus* was supported in all analyses and further corroborated by a 3-bp insertion in ODC and a 4-bp deletion in LDH (Fig. S1). A clade comprising five species of *Niltava* had moderate PP in the multi-locus analysis, but rather poor ML support, and was not recovered by any single-locus analyses. The position of *C. concretus* within clade D1 could not be resolved.

Clade D2 included the ‘robins’ and chats *A. poliocephala*, *E. rubecula*, *Pogonocichla stellata*, *Swynnertonia swynnertoni* and all species in the genera *Cossypha*, *Sheppardia* and *Stiphornis* that were included in our analysis. This clade is the most poorly resolved of all main clades, and several internal relationships were not recovered in any of the single-locus analyses. The seven species of *Cossypha* were placed at four different positions: (i) *C. arc-heri* and *C. humeralis* formed a strongly supported clade, which was sister to a clade containing all other African forest robins; the latter had high PP (0.99) but low ML support (60%) and was only found in one single-locus analysis; (ii) *C. albicapilla*, *C. nive-icapilla* and *C. heuglini* comprise a well-supported clade (PP 1.0); (iii) *C. polioptera* formed a strongly supported clade with *Sheppardia aequatorialis* and *S. cyornithopsis* (PP 1.0); (iv) *C. cyanocamptor* was not closely related to any of the other species of *Cossypha* in this study, although its exact position could not be resolved. The monotypic genera *Pogonocichla* and *Swynnertonia* were resolved as sister-taxa, with high PP in the multi-locus analysis (0.98) but only moderate ML support (78%) and no support in single-locus analyses. Two distinctive subspecies of *Stiphornis erythro-thorax* included in this study were sisters in all analyses. The exact position of *A. poliocephala* and *E. rubecula* within clade D2 could not be resolved.

Within clade D3a, we recovered a sister relationship of the shortwing *Heinrichia calligyna* and the flycatcher *R. insignis* (PP 1.0). Two species of *Brachypteryx* shortwings formed a strongly supported clade with five species of *Luscinia* (PP 1.0).

Clade D3b included the nightingales *L. luscinia* and *L. megarhynchos* in a strongly supported clade and the ‘robins/chats’ *L. svecica* and *H. phaenicuroides* in a less well corroborated clade (PP 0.95, ML bootstrap 74%; only recovered by LDH in single-locus analyses); these two clades were inferred to be sisters, with poor support. *Irania gutturalis* was sister to these four species in the multi-locus tree, with high PP (1.0) but poor ML bootstrap (57%), and this relationship was not recovered in any of the single-locus trees.

In clade D3d, the ‘robins/chats’ *L. cyanura*, *L. hyperythra*, *L. indica*, *L. chrysaea* and *L. johnstoniae* formed a well-supported clade in nearly all analyses. The relationships among the species in this clade were fully resolved and strongly supported. This clade was sister to *M. leucura* with high PP (1.0), although this relationship was not supported by ML bootstrap or by any of the single-locus analyses. The ‘robins/chats’ *L. pectoralis*, *L. calliope* and *L. pectardens* formed a clade (PP 1.0, ML 90%), which was sister to the previous clade; the inclusion of *L. pectardens* was only inferred by one single-locus analysis (cyt *b*), whereas the sister-relationship between the two others was strongly supported.

None of the relationships among the flycatchers in clade D3e was well supported in both Bayesian and ML analyses.

The ‘redstarts’ (*Chaimarrornis*, *Rhyacornis*, *Phoenicurus*) formed a well-supported clade (clade D3f; PP 1.0), which is corroborated by a 2-bp insertion and a 13-bp deletion in ODC (Fig. S1). *Phoenicurus aureus*, *Ph. ochruros*, *Ph. phoenicurus* and *Ph. moussieri* were more closely related to *Chaimarrornis leucocephalus* and *Rhyacornis fuliginosus* than to *Ph. frontalis*, with strong support (PP 0.97, ML 100%). The sister-relationship between *C. leucocephalus* and *R. fuliginosus* was also strongly supported (PP 1.0, ML 97%).

Clades D3g and D3h, comprising the rock thrushes *Monticola* and chats *Saxicola*, respectively, both displayed well supported internal relationships.

Clade D3i included the chat genera *Myrmecocichla*, *Thamnolaea*, *Campicoloides*, *Oenanthe* and *Cercomela*. *Myrmecocichla albifrons* was more closely related to *Campicoloides bifasciatus* (PP 1.0, ML 76%) than to the two other species of *Myrmecocichla* included in this study, and this sister relationship was corroborated by two deletions in the ODC alignment (Fig. S1). *M. aethiops* and *M. melana* were part of an unresolved trichotomy with *Oenanthe monticola* and *Thamnolaea cinnamomeiventris*. *O. monticola* was not closely related to the other species of *Oenanthe* but instead was sister to *Thamnolaea cinnamomeiventris*, with high PP (0.99) and moderate ML bootstrap support (75%). This relationship was only recovered in one single-locus analysis (LDH), but was corroborated by two 1-bp deletions in LDH (Fig. S1). The two species of *Cercomela* included in this study were nested deeply within *Oenanthe*. Although most of the relationships within this clade have high PPs and high or fairly high ML bootstrap values, they are mostly supported by only one (0–3) single-locus analyses.

4. Discussion

4.1. Higher-level relationships and classification

The flycatchers and chats (Muscicapidae of Dickinson, 2003; Clements, 2007; Muscicapinae of Sibley and Ahlquist, 1990; Sibley and Monroe, 1990) form a large group of morphologically and ecologically diverse taxa, but monophyly of this taxon has been uncertain due to a lack of detailed phylogenetic studies. The analyses conducted in this study corroborate previous suggestions that this taxon is not monophyletic (Voelker and Spellman, 2004; Pan et al., 2006a). Our study provides independent support for the reassignment of *Myophonus*, *Alethe*, *Brachypteryx* and *Monticola* from Turdidae to Muscicapidae, and *Cochoa* from Muscicapidae to Turdidae (Voelker and Spellman, 2004). The results of this study also provide strong evidence that the monotypic genus *Heinrichia* should be transferred from Turdidae to Muscicapidae.

Within Muscicapidae we recovered a basal divergence between clades C and D. These two clades correspond to the Muscicapini and Saxicolini of Cibois and Cracraft (2004) and Voelker and Spellman (2004). Examination of single-locus trees, however, suggests that the strong support for clade D in the multi-locus tree is based entirely on ODC and thus may not reflect the species tree. Nevertheless, the basal split between clades C and D in our study is supported by independent studies reporting the same clades on the basis of RAG1 (Cibois and Cracraft, 2004), combined c-mos, ND2 and cyt *b* for 11 species, and ND2 and cyt *b* for 32 species (Voelker and Spellman, 2004).

In Muscicapidae, three major clades (C, D1 and D2) are strongly supported in the multi-locus tree (PP 1.0, ML > 95%) and are supported by two or more independent loci. One other main clade (D3) has high PP (1.0) but lower ML support (71%) and is only recovered in one single-locus analysis (cyt *b*). We suggest that taxonomic recognition is warranted for these clades and propose to recognize these as subfamilies.

- Muscicapinae (Fleming, 1822). Referred taxa: *Copsychus*, *Trichixos*, *Saxicoloides*, *Cercotrichas*, some species of *Alethe*, *Muscicapa*, *Melaenornis* and *Fraseria* (clade C).
- Niltavinae Sangster, Alström, Forsmark and Olsson, new subfamily and family-group name. Type genus *Niltava* Hodgson, 1837. Referred taxa: *Niltava*, *Cyornis*, *Ficedula monileger*, *Cyanoptila*, *Eumyias*, and some species of *Rhinomyias* (clade D1).
- Erithacinae (G. R. Gray, 1846), new rank. Referred taxa: *Swynertonia*, *Pogonocichla*, *Erithacus*, some species of *Alethe*, *Shepardia*, *Cossypha*, and *Stiphornis* (clade D2).
- Saxicolinae (Vigors, 1825). Referred taxa: *Heinrichia*, some species of *Rhinomyias*, *Brachypteryx*, *Luscinia*, *Irania*, *Hodgsonius*, *Enicurus*, *Myiophonus*, *Myiomela*, *Ficedula*, *Rhyacornis*, *Chaimarrornis*, *Phoenicurus*, *Monticola*, *Campicoloides*, *Saxicola*, *Thamnomalaea*, *Myrmecocichla*, *Oenanthe*, and *Cercomela* (clade D3).

Muscicapinae (as defined here) contains two major clades. One clade comprises the ‘chat/robin’ genera *Cercotrichas*, *Saxicoloides*, *Trichixos*, *Copsychus* and *A. diademata* (clade C1), and the other comprises the flycatcher genera *Muscicapa*, *Melaenornis* and *Fraseria* (clade C2). Although all analyses supported *A. diademata* as a member of Muscicapinae, its position within this clade differed among the four single-locus trees, and its inclusion in clade C1 is not overwhelmingly strongly supported in the multi-locus tree. Excluding *A. diademata*, both clades C1 and C2 are well-supported and we propose to recognise these taxonomically. Our data provide strong evidence that *Ficedula*, *Cyanoptila*, *Cyornis*, *Niltava*, *Eumyias*, and *Rhinomyias* are not part of Muscicapinae but should be transferred to other subfamilies within Muscicapidae.

- Copsychini (Sundevall, 1872), new rank. Referred taxa: *Copsychus*, *Trichixos*, *Saxicoloides*, *Cercotrichas* and, tentatively, *A. diademata* (clade C1).
- Muscicapini (Fleming, 1822). Referred taxa: *Muscicapa*, *Melaenornis* and *Fraseria* (clade C2).

We discuss below, in greater detail, some of our salient findings from a taxonomic perspective.

4.2. Copsychini

The multi-locus tree placed the two species of *Alethe* in distant clades. *A. diademata* was placed in Muscicapinae, although its position is unresolved, whereas *A. poliocephala* was placed in a clade with several other African chats (Erithacinae). Polyphyly of this genus was previously reported by Beresford (2003) on the basis of cyt *b* and β -fibrinogen intron 5 sequences. She erected the new genus *Pseudaethe* for *A. poliocephala* and three other species previously placed in *Alethe*.

The scrub-robins (genus *Cercotrichas*) include 9–10 African species of which two are also found outside Africa. The nine species included in the multi-locus tree formed two well supported groups (both PP 1.0, ML 98–100%). Our analysis indicates that these clades are not sisters and, consequently, that *Cercotrichas* does not represent a monophyletic group. One clade comprises five species (*C. podobe*, *C. galactotes*, *C. paena*, *C. hartlaubi* and *C. leucophrys*), whereas *C. coryphaeus*, *C. leucosticta*, *C. quadrivirgata* and *C. barbata* are sister to a clade comprising the other *Cercotrichas* as well as *Saxicoloides*, *Copsychus* and *Trichixos* (PP 0.91, ML 61%; recovered in two single-locus analyses). These relationships were not predicted by previous classifications. *Cercotrichas* has been subdivided into 2–3 genera by various authors (Vaurie, 1955; Ripley, 1964; Wolters, 1980; del Hoyo et al., 2005), but the composition of these proposed genera differs from the two clades identified in our study. The type species of *Cercotrichas* is *C. podobe*. Therefore, *C. podobe*, *C. galactotes*, *C. paena*, *C. hartlaubi* and *C. leucophrys* will retain the

name *Cercotrichas* (with *Erythropygia* and *Agrobates* as synonyms). The name *Salsolicola* proposed by Oatley (2004) is available for the clade consisting of *C. coryphaeus*, *C. leucosticta*, *C. quadrivirgata* and *C. barbata*. However, our study did not include samples of *C. signata*, which is the type species of *Tychaedon* Richmond, 1917. Therefore, a revision of the genus *Cercotrichas* should await clarification of the phylogenetic position of *C. signata*.

According to our topology, the genus *Copsychus* is paraphyletic. This genus includes 3–4 black/white species (the magpie robins) and four colourful species (the shamas). In our study, the Oriental Magpie-Robin *C. saularis* was more closely related to the Indian Robin *S. fulvicata* than to the shamas. Conversely, the three shamas included in this study, *C. luzoniensis*, *C. malabaricus indicus* and *C. m. stricklandii*, were sister to *Trichixos pyrrhopygus*. Our results suggest alternative classifications of this clade: (1) The generic name *Copsychus* may be restricted to the magpie robins (type species *C. saularis*) and the shamas may be placed in another genus. The name *Kittacincla* Gould, 1836 (type species *C. malabaricus*) is available for the shamas; (2) *T. pyrrhopygus* may be placed in *Kittacincla* or be maintained as a monotypic genus; (3) the magpie robins, shamas and the Indian Robin may be combined in a single genus, for which *Copsychus* Wagler, 1827 is the oldest name. The latter arrangement avoids the recognition of the monotypic genera *Trichixos* and *Saxicoloides* and is preferred here (Table 1).

The taxonomic status of the White-crowned Shama *Copsychus m. stricklandii* has been controversial. Most authors recognise *stricklandii* as a species based on its white crown and sympatry with *C. m. suavis* in Sabah and Sarawak, Malaysia, and Kalimantan Timur, Borneo (Inskipp et al., 1996; Sheldon et al., 2001; Mann,

Table 1

Recommended taxonomic changes based on the results of the present study. Species listed in brackets were not included in this study (see main text for discussion).

| Dickinson (2003) | Recommended taxonomy | Comment |
|---------------------------------------|-----------------------------------|---------|
| <i>Alethe poliocephala</i> | <i>Pseudaethe poliocephala</i> | (1) |
| <i>Saxicoloides fulvicatus</i> | <i>Copsychus fulvicatus</i> | |
| <i>Trichixos pyrrhopygus</i> | <i>Copsychus pyrrhopygus</i> | |
| <i>Rhinomyias umbratilis</i> | <i>Cyornis umbratilis</i> | |
| <i>Rhinomyias olivaceus</i> | <i>Cyornis olivaceus</i> | |
| <i>Rhinomyias additus</i> | <i>Eumyias additus</i> | |
| <i>Rhinomyias insignis</i> | <i>Vauriella insignis</i> | |
| (<i>Rhinomyias goodfellowi</i>) | (<i>Vauriella goodfellowi</i>) | |
| (<i>Rhinomyias gularis</i>) | (<i>Vauriella gularis</i>) | |
| (<i>Rhinomyias albigularis</i>) | (<i>Vauriella albigularis</i>) | |
| <i>Ficedula monileger</i> | <i>Anthipes monileger</i> | (2) |
| <i>Luscinia brunnea</i> | <i>Larvivora brunnea</i> | |
| <i>Luscinia cyane</i> | <i>Larvivora cyane</i> | |
| (<i>Luscinia ruficeps</i>) | (<i>Larvivora ruficeps</i>) | |
| <i>Luscinia akahige</i> | <i>Larvivora akahige</i> | |
| <i>Luscinia komadori</i> | <i>Larvivora komadori</i> | |
| <i>Luscinia sibilans</i> | <i>Larvivora sibilans</i> | |
| <i>Hodgsonius phaenicuroides</i> | <i>Luscinia phaenicuroides</i> | |
| <i>Luscinia calliope</i> | <i>Calliope calliope</i> | |
| <i>Luscinia pectoralis</i> | <i>Calliope pectoralis</i> | |
| <i>Luscinia pectardens</i> | <i>Calliope pectardens</i> | |
| (<i>Luscinia obscura</i>) | (<i>Calliope obscura</i>) | |
| <i>Luscinia chrysaes</i> | <i>Tarsiger chrysaes</i> | |
| <i>Luscinia cyanura</i> | <i>Tarsiger cyanurus</i> | |
| <i>Luscinia hyperythra</i> | <i>Tarsiger hyperythrus</i> | |
| <i>Luscinia indica</i> | <i>Tarsiger indicus</i> | |
| <i>Luscinia johnstoniae</i> | <i>Tarsiger johnstoniae</i> | |
| <i>Chaimarrornis leucocephalus</i> | <i>Phoenicurus leucocephalus</i> | |
| <i>Rhyacornis fuliginosa</i> | <i>Phoenicurus fuliginosus</i> | |
| (<i>Rhyacornis bicolor</i>) | (<i>Phoenicurus bicolor</i>) | |
| All species of <i>Cercomela</i> | <i>Oenanthe</i> | |
| All species of <i>Myrmecocichla</i> | <i>Oenanthe</i> | |
| <i>Thamnomalaea cinnamomeiventris</i> | <i>Oenanthe cinnamomeiventris</i> | |
| <i>Campicoloides bifasciatus</i> | <i>Oenanthe bifasciata</i> | |

(1) Previously suggested by Beresford (2003), who also placed *A. fuellebornei*, *A. poliophrys* and *A. cholensis* in *Pseudaethe*; (2) previously suggested by Outlaw and Voelker (2006), who also placed *Ficedula solitaria* in *Anthipes*.

2008). Possible hybrids have been reported from two localities in Sabah and Kalimantan Timur, and this has been interpreted as evidence that *stricklandii* is conspecific with *C. malabaricus* (Smythies, 1957; Collar, 2004). Our *cyt b* sequences of *stricklandii* and *C. malabaricus* differ by 2.2%, a level similar to or exceeding that observed in several species pairs (e.g. Johnson and Cicero, 2004). Our molecular evidence in combination with previously reported differences in plumage and sympatric breeding indicates that the inclusion of *stricklandii* as a subspecies of *C. malabaricus* (e.g. Dickinson, 2003; del Hoyo et al., 2005) may be premature and that further research is warranted.

4.3. *Muscicapini*

The genera *Muscicapa*, *Melaenornis* and *Fraseria* form a well-supported clade. Previous authors have expanded the genus *Muscicapa* to include the genera *Ficedula*, *Cyornis*, *Cyanoptila* (Hartert, 1907; Delacour and Mayr, 1945; Delacour, 1946), *Niltava* (Delacour, 1946) or *Eumyias* (Vaurie, 1953; Watson et al., 1986). However, our data do not support a close relationship between *Muscicapa* and these genera, and place *Ficedula* in Saxicolinae (as circumscribed here) and *Cyornis*, *Cyanoptila*, *Eumyias* and *Niltava* in Niltavinae (as circumscribed here). This finding corroborates and extends a previous study which found that *Ficedula* and *Cyornis* are more closely related to ‘chats’ (Saxicolini) than to other ‘flycatchers’, including *Muscicapa* (Voelker and Spellman, 2004). Our study also does not support a close relationship between *Muscicapa* and *Rhinomyias*, as suggested by Delacour and Mayr (1945) and Wolters (1950).

Our results suggest that *Muscicapa*, *Melaenornis* and *Fraseria* are not monophyletic. Three species of *Muscicapa* were more closely related to species classified in *Melaenornis* and *Fraseria* than to other species of *Muscicapa*: *M. olivascens* and *M. caerulescens* were sister to *Fraseria ocreata*, and *M. infuscata* was sister to *Melaenornis mariquensis*.

The genus *Melaenornis* is a morphologically heterogeneous group of 12 species. It has recently been subdivided into 3–4 genera based on differences in overall plumage color and pattern (e.g. Sinclair and Ryan, 2003; del Hoyo et al., 2006). We include representatives of three of these putative genera: *Bradornis* (*M. mariquensis*, *M. microrhynchus*, *M. pallidus*), *Sigelus* (*M. silens*) and *Melaenornis* (*M. edolioides*). Our study also included both species of *Fraseria*, which are sometimes subsumed in *Melaenornis* (e.g. Watson et al., 1986). Our results suggest that neither the two ‘traditional’ classifications nor the proposed reclassifications accurately reflect their relationships, although most of the relationships are not convincingly well supported. *Melaenornis* (sensu Dickinson, 2003) is not monophyletic because *M. edolioides* and *M. silens*, *M. pallidus*, and *M. mariquensis* and *M. microrhynchus* were each more closely related to species classified in other genera than to each other. An expanded *Melaenornis* (sensu Watson et al., 1986), which includes the two species of *Fraseria*, also does not form a clade. Recognition of *Bradornis* (sensu Sinclair and Ryan, 2003; del Hoyo et al., 2006) is contra-indicated by the non-sister relationship of *M. mariquensis*/*M. microrhynchus* and *M. pallidus* in our study.

The two species of *Fraseria* were distantly related in most of our analyses, which is surprising given their similarities in size, shape, plumage coloration, plumage pattern and geographic distribution (del Hoyo et al., 2006). However, LDH (Fig. S4) is the only locus that strongly contradicts a close relationship between *F. ocreata* and *F. cinerascens*, and monophyly of *Fraseria* is not contradicted by two single-locus trees (ODC (Fig. S3), Myo (Fig. S5)). Therefore, our evidence for non-monophyly of *Fraseria* must be regarded as tentative. In any case, these results indicate that a comprehensive revision of the genera *Muscicapa*, *Melaenornis* and *Fraseria* is warranted.

4.4. Blue flycatchers and polyphyly of *Rhinomyias*

The flycatcher clade here referred to as Niltavinae, containing the genera *Niltava*, *Cyornis*, *Eumyias*, *Cyanoptila* (monotypic), *Ficedula monileger*, and three species of *Rhinomyias*, is well supported. In these genera, except *F. monileger* and *Rhinomyias*, males of most or all species (*Niltava*, *Cyornis*, *Cyanoptila*) or both sexes (*Eumyias*) have blue upperparts.

The genus *Cyornis* was separated from *Niltava* by Parkes (1965, 1971), but this has not been universally adopted (e.g. Morony et al., 1975; Watson et al., 1986; Howard and Moore, 1991). Our study suggests that *Niltava* is more closely related to *Eumyias* and *Cyanoptila* than to *Cyornis*, although the support for this was poor. Vaurie (1953) previously noted similarities of *Eumyias* and *Niltava* in proportions. A sister-relationship between *Cyanoptila* and *Eumyias* is strongly supported by all analyses. Monophyly of *Niltava* had high PP in the multi-locus analysis, although it was not inferred by any single-locus analysis, and the relationships among the species were supported by 0–1 single-locus analyses each. However, the morphological similarity between the species (del Hoyo et al., 2006) adds further support to the correctness of this clade.

Cyornis includes 17 species of which five were included in the present study. Our data suggest that *Cyornis* does not constitute a monophyletic group of species due to the inclusion of two species of *Rhinomyias*. The position of *Cyornis concretus* was unresolved.

Our study included four of the eleven species of the Asian genus *Rhinomyias*. In all analyses, *Rhinomyias* was polyphyletic. Three species were included in Niltavinae (*R. umbratilis*, *R. olivaceus*, *R. additus*) and one in Saxicolinae (*R. insignis*, discussed in paragraph 4.6). The placement of the brown-backed *R. umbratilis* and *R. olivaceus* within a clade of blue-backed *Cyornis* flycatchers, and *R. additus* within *Eumyias*, are novel. The lack of blue plumage coloration in *R. umbratilis*, *R. olivaceus* and *R. additus*, and in *F. monileger*, may represent apomorphic losses of blue coloration. However, the relative positions of these species within *Cyornis* and *Eumyias* varied among different analyses, and therefore the exact relationships should be considered uncertain. Our study included the type species of *Rhinomyias* (*R. umbratilis*). Given the strong support for its inclusion in the *Cyornis* clade, we recommend that *Rhinomyias* Sharpe, 1879 is placed in the synonymy of *Cyornis* Blyth, 1843. *R. additus* should be placed in the genus *Eumyias*.

Our study provides strong support for the placement of *Ficedula monileger* in Niltavinae. A previous study based on mitochondrial DNA data has shown that this species is not part of the *Ficedula* clade (Outlaw and Voelker, 2006), although its true affinities have remained unclear until now. Outlaw and Voelker (2006) placed *F. monileger*, and the morphologically very similar *F. solitaris*, in the genus *Anthipes*. This arrangement is tentatively supported by our results, with the caveat that the position of *Cyornis concretus* could not be resolved. Future studies based on denser sampling of *Cyornis* should determine the exact position of *F. monileger* and *F. solitaris* relative to *Cyornis*.

4.5. African forest robins and European Robin

Our analyses provide strong support for a clade of African chats (clade D2). This clade is roughly equivalent to the ‘African forest robin assemblage’ of Irwin and Clancey (1974), but also includes the European Robin *E. rubecula*, as previously also found by Voelker et al. (2009) based exclusively on mitochondrial DNA. Ripley (1952, 1964) had already suggested a close relationship between *E. rubecula* and several African chats (*Pogonocichla*, *Stiphornis*, *Sheppardia*), but his expanded genus *Erithacus* also included the nightingales, ‘rubythroats’ and ‘bush robins’ (*Luscinia*), which are here shown to be only distantly related to *E. rubecula*. More recent classifications have suggested a close relationship between *E. rube-*

cula and the Palearctic nightingales, 'rubythroats' and 'bush robins' (e.g. Howard and Moore, 1991), or the Japanese Robin *L. akahige* and Ryukyu Robin *L. komadori* (Sibley and Monroe, 1990; Clements, 2007).

The Swynnerton's Robin *S. swynnertonii* and White-starred Robin *Pogonochila stellata* have been combined in a single genus (White, 1962; Ripley, 1964), but are currently placed in two monotypic genera on the basis of differences in tail pattern and plumage sequence (Irwin and Clancey, 1974). Our multi-locus tree recovered *Swynnertonia* and *Pogonochila* as sister taxa, with strong support in the multi-locus tree but not in any of the single-locus analyses. We therefore recommend that these taxa are maintained in separate genera until their relationships are better supported.

The genus level classification of the akalats (*Sheppardia*) and robin-chats (*Cossypha*) has long puzzled taxonomists. A large number of alternative arrangements have been proposed in studies based on non-cladistic analyses of morphological characters (Ripley, 1952, 1964; White, 1962; Hall and Moreau, 1970; Irwin and Clancey, 1974; Wolters, 1980, 1983; Jensen, 1989). Based on mitochondrial and nuclear DNA data, Beresford (2003) subsumed several species of *Cossypha* in *Sheppardia*. However, that revision was problematic due to low bootstrap support and conflicts between analyses based on nuclear DNA data and combined nuclear and mitochondrial data. A second molecular study based on mitochondrial data only, placed one species of *Cossypha* in *Sheppardia* and three other species of *Cossypha* in the genus '*Callene*', but did not provide details on other genera of African forest robins (Voelker et al., 2009). Furthermore, because Voelker et al. (2009) did not include *Cinclidium frontale*, which is the type species of *Callene* Blyth, 1847, it remains unclear if this genus is correctly named. Analysis of our multi-locus data set strongly suggests that *Cossypha* (sensu Dickinson, 2003) is not monophyletic. Species classified in *Cossypha* were placed in three different positions: (i) *C. archeri* and *C. humeralis* were sister to all other African forest robins; (ii) *C. albicapilla*, *C. niveicapilla* and *C. heuglini* were sister to *A. poliocephala*; (iii) *C. polioptera* formed a clade with *S. aequatorialis* and *S. cyornithopsis*; and (iv) *C. cyanocampter* was part of an unresolved polytomy with *Stiphornis* and the previous clade. The relationships among the clades containing *Cossypha* were poorly supported. However, the third clade is strongly supported, which provides independent support for the placement of *C. polioptera* in the genus *Sheppardia* (cf. Voelker et al., 2009).

Since many internal nodes are insufficiently corroborated (due to poor support, or lack of corroboration from independent loci) more data are needed before a comprehensive taxonomic review can be undertaken. However, our data do suggest that the present classification of akalats and robin-chats does not accurately reflect their relationships.

4.6. Shortwings and White-browed Jungle Flycatcher

We recovered a sister relationship of the Great Shortwing *H. caligyna* and the White-browed Jungle Flycatcher *R. insignis*. This relationship, which was strongly supported, was unexpected because these two genera have long been classified in separate (sub)families (Ripley, 1964; Watson et al., 1986; Dickinson (2003)). *Heinrichia*, the other shortwing genus *Brachypteryx* and *R. insignis* are dwellers of the undergrowth (Coates and Bishop, 1997; del Hoyo et al., 2006), and members of these three genera also have relatively short wings (Coates and Bishop, 1997). *Heinrichia* is sometimes merged with *Brachypteryx* (Ripley, 1964), but this is not supported by our study. Our finding of a non-sister-relationship between *Heinrichia* and *Brachypteryx* supports the continued recognition of *Heinrichia*.

The evidence for polyphyly of *Rhinomyias* indicates that a taxonomic revision is warranted. Both Vaurie (1952) and Wolters

(1980) noted that *R. insignis*, *R. goodfellowi*, *R. gularis* and *R. albigularis* stand out among *Rhinomyias* in several traits. Compared to other species of *Rhinomyias*, these four taxa are characterized by stocky proportions, a much larger bill and a strongly-marked head pattern. In addition, these species forage in the undergrowth whereas other species of *Rhinomyias* forage in the tree canopy (e.g. del Hoyo et al., 2006). Wolters (1980) has proposed the new genus name *Vauriella* for these species, with *R. insignis* as the type species. Although our study included only one of these species, a close relationship among these four species has long been accepted and all four have been included in a single species (Vaurie, 1952). Based on our results, we suggest that the genus *Vauriella* is reinstated for *R. insignis* and, tentatively, *R. goodfellowi*, *R. gularis* and *R. albigularis*. However, in view of the four-way polyphyly of *Rhinomyias* in our study, and a previous study which reported *R. goodfellowi* to be sister to *Melaenornis pallidus* (Cibois and Cracraft, 2004), a comprehensive study of the species currently included in *Rhinomyias* is clearly warranted.

4.7. Polyphyly of *Luscinia*

The genus *Luscinia* is a morphologically diverse group of nightingales, 'robins' and 'chats'. The relationships, limits and validity of this genus have been problematic since the late 19th century (Seeböhm, 1881). Some authors have placed all species of *Luscinia* (sensu Dickinson, 2003), along with the African genera *Sheppardia* and *Stiphornis*, in the genus *Erithacus* (Ripley, 1964). Others have split *Luscinia* (sensu Dickinson, 2003) into two genera and placed five species in the genus *Tarsiger* (e.g. Sibley and Monroe, 1990; Clements, 2007). Wolters (1980) included only two species in the genus *Luscinia* (*L. luscinia*, *L. megarhynchos*) and placed all other species in eight different genera (Wolters, 1980). Our study included 16 of the 18 currently recognised species of *Luscinia*. Our results indicated that (i) there is no support for a close relationship between any of the species of *Luscinia* and the European Robin *E. rubecula* or the African robin genera *Sheppardia* and *Stiphornis*, and (ii) *Luscinia* is a polyphyletic group of species, which consists of four separate clades.

L. brunnea, *L. cyane*, *L. sibilans*, *L. akahige* and *L. komadori* form a weakly supported clade, which is sister to *Brachypteryx* (well supported). The relationships (*L. brunnea*, *L. cyane*), and (*L. sibilans*, (*L. akahige*, *L. komadori*)) are strongly supported. *L. akahige* and *L. komadori* are sometimes placed in the genus *Erithacus*, presumably based on morphological similarity (e.g. Sibley and Monroe, 1990; Clements, 2007), which is hence refuted here. Our results support a previous study of mitochondrial DNA which suggested that *L. akahige* and *L. komadori* are more closely related to species traditionally included in *Luscinia* than to *E. rubecula* (Seki, 2006).

H. phaenicuroides, *L. svecica*, *L. luscinia* and *L. megarhynchos* form a clade which is sister to *Irania gutturalis* in the multi-locus tree (PP 1.0). However, this result must be regarded as tentative in view of the lack of strong support from our single-locus analyses. *Hodgsonius* and *Irania* have not been included in any previous phylogenetic analysis and their phylogenetic position has been unclear. In most classifications, *H. phaenicuroides* is listed near the redstarts (Ripley, 1964; Wolters, 1980). The sister relationship of *H. phaenicuroides* and *L. svecica* is therefore surprising. The close relationship of *I. gutturalis* to the 'true' nightingales *Luscinia* (as defined here) has been predicted by classifications that placed the two genera next to each other in a linear sequence (e.g. Wolters, 1980). The sister relationship of *L. luscinia* and *L. megarhynchos* was expected based on their similarity in plumage and songs (e.g. Cramp, 1988).

L. pectoralis, *L. calliope* and *L. pectardens* form a well-supported clade, although the exact position of this clade was poorly resolved. A close relationship between the two rubythroats, *L. pectoralis* and *L. calliope*, has long been suspected based on their distinctive

plumage patterns. A close relationship of the rubythroats and the Firethroat *L. pectardens* has not been predicted by previous classifications, which have placed *L. pectardens* near *L. brunnea* (Wolters, 1980; Dickinson, 2003).

L. cyanura, *L. hyperythra*, *L. indica*, *L. chrysaea* and *L. johnstoniae* form a well-supported clade. These species are often placed in the genus *Tarsiger* (Voous, 1977; Cramp, 1988; Sibley and Monroe, 1990; Inskipp et al., 1996; Clements, 2007), although monophyly of this group has long been controversial. For instance, Sharpe (1901, 1903) accepted only a single species of *Tarsiger* (*T. chrysaeus*), which he placed in the family Muscicapidae, and classified the other three species that were known at the time (*L. hyperythra*, *L. cyanura*, *L. indica*) in the family Turdidae under the generic name *lanthia*. Howard and Moore (1991) restricted the genus *Tarsiger* to *L. cyanura* and *L. chrysaea* and placed *L. hyperythra*, *L. johnstoniae* and *L. indica* in *Eriothacus*.

M. leucura was sister to *L. cyanura*, *L. hyperythra*, *L. indica*, *L. chrysaea* and *L. johnstoniae* in the multi-locus tree with strong support, but this relationship was not supported by any of the single-locus analyses, and should therefore be considered uncertain. *M. leucura* has been considered closely related to *M. diana* (e.g. Dickinson, 2003) and both species have been included in the genus *Cinclidium* together with *C. frontale* (e.g. Ripley, 1964). Since our study did not include these two species, we cannot comment on the taxonomic validity of *Myiomela* and *Cinclidium*.

The polyphyly of the genus *Luscinia* warrants a revision of its generic limits. We suggest that *Luscinia* (sensu Dickinson, 2003) should be reassigned to at least four genera.

- *Larvivora* Hodgson, 1837 may be reinstated for *L. brunnea*, *L. cyane*, *L. sibilans*, *L. komadori* and *L. akahige*. Alternatively, *Larvivora* Hodgson, 1837 may be restricted to *L. brunnea* and *L. cyane*, and the name *Icoturus* Stejneger, 1886 may be used for *L. sibilans*, *L. komadori* and *L. akahige*. Our study did not include *L. ruficeps*. We tentatively place this species in *Larvivora* based on the similarity of its structure, song and behaviour to those of *L. brunnea* and *L. cyane* (G. Sangster, P. Alström, U. Olsson unpubl. data).
- We tentatively restrict *Luscinia* Forster, 1817 to *L. svecica*, *H. phaenicuroides*, *L. luscinia* and *L. megarhynchos*, in spite of the insufficient support for the monophyly of this genus. We retain *Irania* as a monotypic genus for *I. gutturalis*. Additional data are needed to corroborate these results.
- *Calliope* Gould, 1836 is available for *L. pectoralis*, *L. calliope* and *L. pectardens*. We also tentatively place *L. obscura* in this genus based on its plumage similarity to *L. pectardens* (Goodwin and Vaurie, 1956; Ripley, 1958; del Hoyo et al., 2005).
- *Tarsiger* Hodgson, 1845 is the traditional name for *L. cyanura*, *L. hyperythra*, *L. indica*, *L. chrysaea*, *L. johnstoniae* (e.g. Voous, 1977; Cramp, 1988; Sibley and Monroe, 1990; Inskipp et al., 1996; Clements, 2007) and should be reinstated for these species. According to our results, the five species of *Tarsiger* form a well-supported monophyletic group. A breakup of *Tarsiger* into three genera, as proposed by Wolters (1980) is not warranted.

4.8. Whistling thrushes and forktails

A close relationship of the whistling thrushes *Myophonus* and forktails *Enicurus* has not been previously suspected, but is strongly supported in the multi-locus tree. Both genera have a strictly southern Asian distribution and range south to Borneo and Java. The two groups are both found, in particular, near forested mountain streams, but have highly divergent plumage patterns, coloration and structure. The seven species of *Myophonus* are fairly large 'thrushes' with elaborate songs and a rather dark plumage dominated by shiny blue colors (del Hoyo et al., 2005), including

bright ultraviolet plumage patches (Andersson, 1996). The seven species of *Enicurus* have boldly patterned black and white plumages and elongated, deeply forked tails and simple piercing vocalizations (similar to calls of *Myophonus*) (del Hoyo et al., 2005). The finding of a sister-group relationship of these two divergent genera offers interesting avenues for studies of the relative roles of ecology (e.g. habitat) and sexual selection in driving the evolution of morphological and acoustic signals.

4.9. *Ficedula* flycatchers and terrestrial chats

The *Ficedula* flycatchers (clade D3e) and the 'chats' *Chaimarrornis*, *Rhyacornis*, *Phoenicurus*, *Monticola*, *Saxicola*, *Cercomela*, *Oenanthe*, *Campicoloides* and *Myrmecocichla* (clades D3f-i) represent two major radiations.

Our analysis of the combined data set included 8 species of *Ficedula*, which formed a monophyletic group, with the exception of *F. monileger*. As noted above, *F. monileger* turned up in a clade with *Cyornis*, *Eumyias* and *Niltava*. Monophyly of *Ficedula* (excluding *F. monileger*) was recovered with high PP but poor ML support in the multi-locus tree and was only inferred by one single-locus analysis (cyt *b*). The phylogenetic relationships among *Ficedula* species have previously been studied by Outlaw and Voelker (2006) using mitochondrial DNA sequences. In common with Outlaw and Voelker's (2006) study, several basal relationships among *Ficedula* were poorly supported in our analysis.

Our analyses of the multi-locus data set recovered a strongly supported clade of 7 species of redstarts. The White-capped Redstart *Chaimarrornis leucocephalus* and Plumbeous Water Redstart *Rhyacornis fuliginosa* were recovered as sisters, and were nested in *Phoenicurus*, which renders the latter paraphyletic. This finding is consistent with a previous study based on cyt *b* data, which demonstrated paraphyly of *Phoenicurus* (Pan et al., 2006a). The phylogeny obtained here indicates that *Chaimarrornis* and *Rhyacornis* (which includes a second species, *R. bicolor*, not included in this study) should be included in *Phoenicurus*. Alternatively, if *Chaimarrornis* and *Rhyacornis* are retained as monotypic genera, *P. frontalis* and *P. schisticeps* (latter not included here, but sister to *P. frontalis* in Pan et al., 2006a) should be placed in a separate genus, for which the name *Phoenicuropsis* Wolters, 1980 is available.

The genus *Oenanthe* is not monophyletic in our analyses. The two species of *Cercomela* included in this study were part of a clade consisting of six species of *Oenanthe*. Tye (1989a,b) expressed the view that *Oenanthe* may not be monophyletic, and noted that some species of *Oenanthe* appear closer to *Cercomela* whereas others may be closer to *Myrmecocichla*. Our study, and that of an independent study based on mitochondrial DNA (Outlaw et al., 2010), support this view.

The Mountain Wheatear *O. monticola* of southern Africa did not cluster with the other species of *Oenanthe* but was placed as the sister taxon of *Thamnolaea cinnamomeiventris* within a strongly supported clade with *M. aethiops* and *M. melaena*. Based on gross morphology, Tye (1989a) speculated that *O. monticola* might be more closely related to *Myrmecocichla* than to other *Oenanthe*. Others have underscored the distinctiveness of *O. monticola* by placing it in a monotypic genus *Dromolaea* (e.g. Wolters, 1980).

The three species of *Myrmecocichla* included in our study did not comprise a monophyletic group. *M. albifrons* formed a sister-relationship with *C. bifasciatus*, whereas *M. aethiops* and *M. melaena* were sister to *O. monticola* and *T. cinnamomeiventris*. Wolters (1980) proposed to subdivide the genus *Myrmecocichla* into two genera: *Myrmecocichla* (including *M. nigra*, *M. aethiops*, *M. formicivora*, *M. tholloni*) and *Pentholaea* (including *M. melaena*, *M. albifrons*, *M. arnotti*). However, monophyly of 'Pentholaea' is not supported by our results because *M. albifrons* and *M. melaena* were not closely related in our study.

Table 2

Comparison between the Dickinson (2003) classification of Turdidae and Muscicapidae and the classification proposed in this study. Numbers after generic names in the first column refer to species sampled in this study/species recognized by Dickinson (2003).

| Dickinson (2003) Genus | This study Genus | Higher taxon |
|-----------------------------------|-----------------------|--|
| Turdidae | | |
| <i>Neocossyphus</i> (2/2) | <i>Neocossyphus</i> | Turdidae |
| <i>Stizorhina</i> (2/2) | <i>Stizorhina</i> | Turdidae |
| <i>Myophonus</i> (2/7) | <i>Myophonus</i> | Muscicapidae: Saxicolinae |
| <i>Geomalía</i> (0/1) | – | – |
| <i>Zoothera</i> (1/32) | <i>Zoothera</i> | Turdidae |
| <i>Ixoreus</i> (0/1) | – | – |
| <i>Ridgwayia</i> (0/1) | – | – |
| <i>Cataponera</i> (0/1) | – | – |
| <i>Sialia</i> (1/3) | <i>Sialia</i> | Turdidae |
| <i>Myadestes</i> (2/13) | <i>Myadestes</i> | Turdidae |
| <i>Cichlopsis</i> (0/1) | – | – |
| <i>Catharus</i> (1/12) | <i>Catharus</i> | Turdidae |
| <i>Hylodichla</i> (0/1) | – | – |
| <i>Entomodestes</i> (1/2) | <i>Entomodestes</i> | Turdidae |
| <i>Platycichla</i> (0/2) | – | – |
| <i>Psophocichla</i> (0/1) | – | – |
| <i>Turdus</i> (1/65) | <i>Turdus</i> | Turdidae |
| <i>Nesocichla</i> (0/1) | – | – |
| <i>Cichlherminia</i> (0/1) | – | – |
| <i>Cochoa</i> (1/4) | <i>Cochoa</i> | Turdidae |
| <i>Chlamydochaera</i> (1/1) | <i>Chlamydochaera</i> | Turdidae |
| <i>Brachypteryx</i> (2/5) | <i>Brachypteryx</i> | Muscicapidae: Saxicolinae |
| <i>Heinrichia</i> (1/1) | <i>Heinrichia</i> | Muscicapidae: Saxicolinae |
| <i>Alethe</i> (2/5) | <i>Alethe</i> | Muscicapidae: Muscipapinae: Copsychini |
| | <i>Pseudalethe</i> | Muscicapidae: Erithacinae |
| Muscicapidae: Saxicolinae | | |
| <i>Pogonocichla</i> (1/1) | <i>Pogonocichla</i> | Muscicapidae: Erithacinae |
| <i>Swynnertonia</i> (1/1) | <i>Swynnertonia</i> | Muscicapidae: Erithacinae |
| <i>Stiphornis</i> (2/2) | <i>Stiphornis</i> | Muscicapidae: Erithacinae |
| <i>Sheppardia</i> (2/8) | <i>Sheppardia</i> | Muscicapidae: Erithacinae |
| <i>Erithacus</i> (1/1) | <i>Erithacus</i> | Muscicapidae: Erithacinae |
| <i>Luscinia</i> (16/18) | <i>Luscinia</i> | Muscicapidae: Saxicolinae |
| | <i>Larvivora</i> | Muscicapidae: Saxicolinae |
| | <i>Calliope</i> | Muscicapidae: Saxicolinae |
| | <i>Tarsiger</i> | Muscicapidae: Saxicolinae |
| <i>Irania</i> (1/1) | <i>Irania</i> | Muscicapidae: Saxicolinae |
| <i>Cossyphula</i> (0/1) | – | – |
| <i>Cossypha</i> (7/14) | <i>Cossypha</i> | Muscicapidae: Erithacinae |
| <i>Xenocopsychus</i> (0/1) | – | – |
| <i>Cichladusa</i> (0/3) | – | – |
| <i>Cercotrichas</i> (9/10) | <i>Cercotrichas</i> | Muscicapidae: Muscipapinae: Copsychini |
| <i>Namibornis</i> (0/1) | – | – |
| <i>Copsychus</i> (3/7) | <i>Copsychus</i> | Muscicapidae: Muscipapinae: Copsychini |
| <i>Trichixos</i> (1/1) | <i>Copsychus</i> | Muscicapidae: Muscipapinae: Copsychini |
| <i>Saxicoloides</i> (1/1) | <i>Copsychus</i> | Muscicapidae: Muscipapinae: Copsychini |
| <i>Phoenicurus</i> (5/11) | <i>Phoenicurus</i> | Muscicapidae: Saxicolinae |
| <i>Hodgsonius</i> (1/1) | <i>Luscinia</i> | Muscicapidae: Saxicolinae |
| <i>Rhyacornis</i> (1/2) | <i>Phoenicurus</i> | Muscicapidae: Saxicolinae |
| <i>Chaimarornis</i> (1/1) | <i>Phoenicurus</i> | Muscicapidae: Saxicolinae |
| <i>Myiomela</i> (1/2) | <i>Myiomela</i> | Muscicapidae: Saxicolinae |
| <i>Cinclidium</i> (0/1) | – | – |
| <i>Grandala</i> (0/1) | – | – |
| <i>Enicurus</i> (3/7) | <i>Enicurus</i> | Muscicapidae: Saxicolinae |
| <i>Saxicola</i> (4/10) | <i>Saxicola</i> | Muscicapidae: Saxicolinae |
| <i>Campicoloides</i> (1/1) | <i>Oenanthe</i> | Muscicapidae: Saxicolinae |
| <i>Oenanthe</i> (7/22) | <i>Oenanthe</i> | Muscicapidae: Saxicolinae |
| <i>Cercomela</i> (2/9) | <i>Oenanthe</i> | Muscicapidae: Saxicolinae |
| <i>Myrmecocichla</i> (3/7) | <i>Oenanthe</i> | Muscicapidae: Saxicolinae |
| <i>Thamnolaea</i> (1/2) | <i>Oenanthe</i> | Muscicapidae: Saxicolinae |
| <i>Pinarornis</i> (0/1) | – | – |
| <i>Monticola</i> (3/10) | <i>Monticola</i> | Muscicapidae: Saxicolinae |
| <i>Pseudocossyphus</i> (0/2) | – | – |
| Muscicapidae: Muscipapinae | | |
| <i>Fraseria</i> (2/2) | <i>Fraseria</i> | Muscicapidae: Muscipapinae: Muscipapini |

Table 2 (continued)

| Dickinson (2003) Genus | This study Genus | Higher taxon |
|---------------------------|---------------------|--|
| <i>Melaenornis</i> (5/12) | <i>Melaenornis</i> | Muscicapidae: Muscipapinae: Muscipapini |
| <i>Empidonis</i> (0/1) | – | – |
| <i>Rhinomyias</i> (4/11) | <i>Cyornis</i> | Muscicapidae: Niltavinae |
| | <i>Eumyias</i> | Muscicapidae: Niltavinae |
| | <i>Vauriella</i> | Muscicapidae: Saxicolinae |
| <i>Muscicapa</i> (13/23) | <i>Muscicapa</i> | Muscicapidae: Muscipapinae |
| <i>Myioparus</i> (0/2) | – | – |
| <i>Stenostira</i> (0/1) | – | – |
| <i>Humblotia</i> (0/1) | – | – |
| <i>Ficedula</i> (9/29) | <i>Ficedula</i> | Muscicapidae: Saxicolinae |
| | <i>Anthipes</i> | Muscicapidae: Niltavinae |
| <i>Cyanoptila</i> (1/1) | <i>Cyanoptila</i> | Muscicapidae: Niltavinae |
| <i>Eumyias</i> (3/5) | <i>Eumyias</i> | Muscicapidae: Niltavinae |
| <i>Cyornis</i> (5/17) | <i>Cyornis</i> | Muscicapidae: Niltavinae |
| <i>Niltava</i> (5/6) | <i>Niltava</i> | Muscicapidae: Niltavinae |
| <i>Muscicapella</i> (0/1) | – | – |
| <i>Culicicapa</i> (0/2) | – | – |

Thamnolaea is sometimes subsumed in *Myrmecocichla* (Sibley and Monroe, 1990; Howard and Moore, 1991). As noted above, our data support a close relationship of *Thamnolaea* with some species of *Myrmecocichla*.

The taxonomic position of Buff-streaked Chat *C. bifasciatus*, endemic to southern Africa, has long puzzled taxonomists. Various authors have placed this species in *Myrmecocichla* (Seebohm, 1881), *Oenanthe* (Ripley, 1964), *Saxicola* (Tye, 1989a) or in the monotypic genus *Campicoloides* (Wolters, 1980; Dickinson, 2003). Our data suggest that it is not closely related to *Saxicola* but is part of a well-supported clade with *Oenanthe*, *Myrmecocichla* and *Thamnolaea*, as the sister taxon of *M. albifrons*. Illera et al. (2008) had previously noted, on the basis of *cyt b* data, that the Buff-streaked Chat does not belong in *Saxicola* but could not resolve its exact position due to limitations of taxon sampling.

The paraphyly of *Oenanthe* and *Myrmecocichla* indicates that the current classification of these chats does not accurately reflect their relationships. Our study sampled only two species of *Cercomela* but this included the type species, *C. melanura*. To maintain *Cercomela* as a genus would require the subdivision of *Oenanthe* into at least three genera. To avoid unnecessary proliferation of generic names, we recommend that *Cercomela* Bonaparte, 1856 be included in *Oenanthe* Vieillot, 1816. The genus *Oenanthe* (including *Cercomela*) may be expanded slightly to include *M. albifrons* and *C. bifasciatus*. A second genus would include the species *O. monticola*, *M. aethiops*, *M. melaena* and both species of *Thamnolaea*. However, because our study did not include *M. formicivora*, which is the type species of *Myrmecocichla*, it is unclear whether *Myrmecocichla* Cabanis, 1850 or *Thamnolaea* Cabanis, 1850 is the appropriate name for this genus. The second alternative, which we prefer, is to place *C. bifasciatus* and all species of *Myrmecocichla* and *Thamnolaea* in *Oenanthe* Vieillot, 1816. This arrangement acknowledges the lack of strong morphological differences between traditional *Oenanthe* and *Myrmecocichla*, and between *Myrmecocichla* and *Thamnolaea*.

On the basis of a less extensive molecular data set (the mitochondrial *cyt b* and ND2) but more extensive sampling of *Oenanthe* and *Cercomela*, Outlaw et al. (2010) recently confirmed that both *Oenanthe* and *Cercomela* are paraphyletic. They argued that, whereas *Cercomela* should be included in *Oenanthe*, some species traditionally included in *Cercomela* should be transferred to two newly revived genera. Their study did not include *Oenanthe monticola* (type species of *Dromolaea* Cabanis, 1851) and did not specify which species of *Myrmecocichla* (which our study indicates is paraphyletic) were sampled. As a result, it is unclear whether the new

genera proposed by Outlaw et al. (2010) are adequately delimited and correctly named.

5. Conclusions

This study takes a large step towards resolving the relationships among birds in the Muscicapidae. Our analyses include more than 70% of the genera and close to 50% of the species of Muscicapidae, and use one mitochondrial and three unlinked nuclear loci (in total 3240 bp of aligned sequences) to infer the relationships of these. Our study clarifies a number of long-standing taxonomic problems and identifies several well-supported major clades. In addition, our study adds strength to a number of hypotheses suggested in previous studies (e.g. Beresford, 2003; Cibois and Cracraft, 2004; Voelker and Spellman, 2004; Outlaw and Voelker, 2006; Pan et al., 2006a; Seki, 2006; Outlaw et al., 2010). To let taxonomy reflect the evolutionary relationships within Muscicapidae, revisions are warranted at several taxonomic levels (see Table 2). A major outcome of the present study is that no less than 13 of the 21 (62%) of the genera (sensu Dickinson, 2003) of which we included more than one species was non-monophyletic (15 of 24 [63%] if our redefined Muscicapidae is used). Our results, and those of previous studies which have reported non-monophyly in several additional genera (e.g. *Monticola* (Goodman and Weigt, 2002), *Sheppardia* (Beresford, 2003), *Cercomela* (Outlaw et al., 2010), *Thamnolea* (Zuccon and Ericson, 2010a)), indicate that traditional, non-cladistic analysis of plumage patterns, which appear to be highly susceptible to selective pressure, has provided a misleading account of the diversity and evolutionary history of the chats and Old World flycatchers. The high levels of non-monophyly reported in our study suggest the need for dense taxon sampling in future phylogenetic analyses. In the meantime, the broad taxonomic scope and generally strong support for our phylogenetic hypothesis of Muscicapidae means that it is of potentially great value to future comparative studies of the behaviour, life-history and ecology of this diverse group.

Note added in proof

After the completion of this manuscript, an independent study of the relationships among chats and flycatchers was published by Zuccon and Ericson (2010b). Their study was based on one mitochondrial and four nuclear loci (3553 bp) and 68 ingroup species. The phylogenetic relationships among the major clades identified in our paper are fully supported by Zuccon and Ericson (2010b), and vice versa. The congruence between these two studies adds strength to the taxonomic revisions proposed in our paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ymp.2010.07.008.

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