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Phylogenetic relationships within Passerida (Aves: Passeriformes): A review and a new molecular phylogeny based on three nuclear intron markers

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ABSTRACT

The avian clade Passerida was first identified based on DNA–DNA hybridization data [C.G. Sibley, J.E. Ahlquist, *Phylogeny and Classification of Birds*, 1990, Yale University Press, New Haven, CT]. Monophyly of the Passerida, with the exception of a few taxa, has later been corroborated in several studies; however, the basal phylogenetic relationships have remained poorly understood. In this paper, we review the current knowledge of the phylogenetic relationships within Passerida and present a new phylogeny based on three nuclear introns (myoglobin intron 2, ornithine decarboxylase introns 6 and 7, as well as β -fibrinogen intron 5). Our findings corroborate recent molecular hypotheses, but also identify several hitherto unrecognized relationships.

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1. Introduction

Of the world's approximately 9600 species of birds, nearly 60% belong to the passerine clade, Passeriformes (Sibley and Monroe, 1990). Compared with other avian groups of comparative age (cf Ericson et al., 2006), no other clade has evolved such great species richness and range of ecological diversification as the passerines. The group is represented in nearly all non-marine habitats and is distributed on all of the continents except Antarctica. In addition, passerines exploit a wide range of food resources, and within this clade many groups have developed morphological specializations for varied diets, including insectivory, (e.g. warblers), nectarivory (e.g. sunbirds), frugivory (e.g. cotingas), granivory (e.g. finches), carnivory (e.g. shrikes), or herbivory (plantcutters), as well as different feeding strategies (e.g. aerial hunting, bark or foliage gleaning and sallying). Most of the anatomical variation within the passerines relates to these differences in foraging and as a result earlier classifications and phylogenetic hypotheses based on morphology do, to a large extent, reflect such functional groups (e.g. Beecher, 1953). Recent molecular-based studies (e.g. Barker et al.,

2004; Beresford et al., 2005; Fuchs et al., 2006; Sibley and Ahlquist, 1990); however, suggest that many of these traditional groups are polyphyletic, and that morphologically similar ecotypes have evolved independently in different parts of the world (Sibley and Ahlquist, 1990).

The first comprehensive molecular study, based on DNA–DNA hybridization data by Charles Sibley and co-workers (summarized in Sibley and Ahlquist, 1990; Sibley and Monroe, 1990) suggested a strikingly different view of the phylogenetic relationships of birds compared to previous phylogenetic hypotheses and classifications based on morphological data; in particular within the passerine birds. However, the DNA–DNA hybridization study met with severe criticism (e.g. Harshman, 1994; Houde, 1987; Mindell, 1992; Sarich et al., 1989) and several relationships suggested by Sibley and Ahlquist (1990) have later been shown to be erroneous (e.g. Barker et al., 2004; Ericson et al., 2002a; Johansson and Ericson, 2003). Nevertheless, the results of Sibley and Ahlquist (1990) have served as the framework for many ecological and comparative phylogenetic studies (e.g. Bennett and Owens, 2002; Fjeldså, 1994; Hawkins et al., 2006; Starck and Ricklefs, 1998). Today, studies based on DNA sequencing have begun to converge on a new passerine topology, which includes features from the DNA–DNA hybridization dendrogram of Sibley and Ahlquist (1990) and traditional classification in addition to several novel relationships. Unfortunately, many areas of conflict and uncertainty remain in

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the passerine tree, and there is a clear need to increase the number of independent loci sequenced, as well as the extent of taxon sampling in order to help resolve difficult nodes.

In this paper, we review recent hypotheses of phylogenetic relationships within in one of the largest clades of passerine birds, the Passerida. In particular, we aim to identify parts of the phylogenetic tree that appear to be robust as well as those parts that remain uncertain. We also present a phylogeny of the Passerida based on data from three nuclear markers (myoglobin intron 2, ornithine decarboxylase (ODC) introns 6 and 7, as well as β -fibrinogen intron 5), in total ~2.3 kb for 90 species. Our primary objective was to examine the basal relationships within Passerida with an emphasis on the early divergences within Sylvioidea, and investigate the phylogenetic position of several taxa of uncertain phylogenetic affinities. In addition, we constructed a phylogeny based on a six-gene dataset (7388 base pairs) for a subset of these taxa in order to examine the effect of increased character sampling on the topology.

1.1. A short overview of passerine phylogenetics

The monophyly of Passeriformes is strongly supported by morphological (Raikow, 1982) as well as molecular data (Cracraft et al., 2004; Johansson et al., 2001), as is the traditional division of the passerines into two major clades, the Oscines and Suboscines. This latter subdivision was based initially on syringeal morphology (Ames, 1971; Müller, 1878), but has also been recovered in several molecular studies (e.g. Ericson et al., 2002a; Irestedt et al., 2001; Lovette and Bermingham, 2000). In addition to these two traditional groups, recent molecular findings (Barker et al., 2002, 2004; Ericson et al., 2002a) suggest that two species endemic to New Zealand, the Rifleman (*Acanthisitta chloris*) and the Rock Wren (*Xenicus gilviventris*) (Acanthisittidae) constitute the sister-group to all other passerines. This finding has had great implications for the understanding of the biogeographic origin of passerine birds (Barker et al., 2004; Edwards and Boles, 2002; Ericson et al., 2003).

Of these three groups, oscines are the most numerous with more than 4500 species. Although the oscines have an almost worldwide distribution, the basal lineages of oscines are primarily distributed in the Australasian region, suggesting that the clade originated within this region (Barker et al., 2002, 2004; Ericson et al., 2002a; Jönsson and Fjeldså, 2006a). Among the several oscine lineages that have spread to other parts of the world, Passerida, with approximately 3500 species, is the largest. This clade was first recognized from DNA–DNA hybridization data (see Sibley and Ahlquist, 1990), and its monophyly has later been supported by analyses of DNA sequence data (Barker et al., 2002, 2004; Ericson et al., 2002a,b), as well as by a unique insertion of one codon in the c-myc gene (Ericson et al., 2000).

Although the general concept of a monophyletic Passerida has been supported by several studies, not all species and clades included in the Passerida by Sibley and Monroe (1990) have been confirmed to be part of this clade (Tables 1 and 2). For instance, DNA sequences from the genes RAG-1 and RAG-2 (Barker et al., 2004) suggest that the New Guinean Crested Berrypecker (*Paramythia montium*—Paramythiidae) as well as the berrypeckers and longbills (*Toxorhamphus*, *Oedistoma*, *Melanocharis*—Melanocharitidae), both placed in the Passerida by Sibley and Monroe (1990), instead form part of two other Oscine clades, the “core Corvoidea” (sensu Barker et al., 2004) and the cnemophiline birds-of-paradise, respectively. Further, some species from Madagascar, for example the four *Newtonia* species (*Newtonia*) and Crossley’s Babbler (*Mystacornis crossleyi*), also appear to be part of the “core Corvoidea” (Cibois et al., 1999, 2001; Yamagishi et al., 2001) rather than members of the Passerida radiation.

Table 1

Clades included in Passerida (sensu Sibley and Monroe 1990) but currently not considered part of that radiation

Taxon		Reference
<i>Toxorhamphus</i>	Melanocharitidae	Barker et al. (2004)
<i>Oedistoma</i>	Melanocharitidae	Barker et al. (2004)
<i>Melanocharis</i>	Melanocharitidae	Barker et al. (2004)
<i>Paramythia</i>	Paramythiidae	Barker et al. (2004)
<i>Erpornis zantholeuca</i> (formerly <i>Yuhina</i>)	Sylviidae, Timaliini	Cibois et al. (2001) and Barker et al. (2004)
<i>Mystacornis crossleyi</i>	Sylviidae, Timaliini	Cibois et al. (1999) and Schulenberg (1993)
<i>Newtonia</i>	Sylviidae, Acrocephalinae	Yamagishi et al. (2001)
<i>Pteruthius</i>	Sylviidae, Timaliini	Reddy and Cracraft (2007)

Table 2

Clades currently considered part of Passerida but not included in that clade in Sibley and Monroe (1990)

Taxon		Reference
<i>Irena</i>	Irenidae	Barker et al. (2002) and Barker et al. (2004)
<i>Chloropsis</i>	Irenidae	Barker et al. (2002) and Barker et al. (2004)
<i>Pseudopodoces humilis</i>	Corvidae, Corvini	James et al. (2003)
<i>Elminia longicauda</i>	Corvidae, Monarchini	Pasquet et al. (2002)
<i>Elminia nigromitrata</i> ^a	Corvidae, Monarchini	Pasquet et al. (2002)
<i>Elminia albonotata</i> ^a	Corvidae, Monarchini	Pasquet et al. (2002)
<i>Erythrocercus</i>	Corvidae, Monarchini	Pasquet et al. (2002)
<i>Culicicapa ceylonensis</i> ^b	Eopsaltriidae	Pasquet et al. (2002) and Barker et al. (2004)
<i>Culicicapa helianthea</i> ^b	Eopsaltriidae	Pasquet et al. (2002)

^a Placed in the genus *Trochocercus* in Sibley and Monroe (1990), but genus shown to be polyphyletic (Pasquet et al. (2002); see also Olson, 1989).

^b Traditionally placed in Muscipapidae (e.g. Watson et al., 1986b) but placed in Eopsaltriidae in Sibley and Monroe (1990), although corrected in Monroe and Sibley (1993).

DNA sequence-based studies have also indicated that several of the taxa that were not included in Passerida by Sibley and Monroe (1990) may in fact be part of this radiation (Table 2). For example, the fairy-bluebirds (*Irena*), leafbirds, (*Chloropsis*), canary-flycatchers (*Culicicapa*) and several species traditionally placed among the monarchine flycatchers (*Erythrocercus* and *Elminia*, including *E. nigromitrata*, and *E. albonotata*) are nested within Passerida (Barker et al., 2004; Pasquet et al., 2002). The Tibetan Ground-Jay (*Pseudopodoces humilis*), which in all previous classifications were placed among the crows (Corvini sensu Sibley and Monroe, 1990), has recently been shown to be a ground-living tit (Paridae) (James et al., 2003).

Sibley and Ahlquist (1990) recognized three clades within Passerida: Muscipapoidea, Sylvioidea, and Passeroidea, with Muscipapoidea basal relative to the other two clades. In the analyses of Sibley and Ahlquist (1990) these clades are; however, separated by very short internodes and subsequent DNA sequence-based studies have not been able to confirm their monophyly (Barker et al., 2002, 2004; Beresford et al., 2005; Ericson and Johansson, 2003; Fuchs et al., 2006). Indeed, if only the highly supported nodes in these molecular studies are considered, Passerida is divided into at least nine clades with uncertain relationships (Fig. 1).

Two of these clades have a taxonomic composition rather similar to Muscipapoidea and Passeroidea (sensu Sibley and Monroe, 1990). Muscipapoidea (sensu Sibley and Monroe, 1990) included dippers (Cinclidae), thrushes (Turdinae), Old World flycatchers and chats (Muscicapinae), starlings and oxpeckers (Sturnini), mimids (Mimini) as well as waxwings, silky-flycatchers and palmchats (Bombycillidae). Monophyly of a clade containing all these groups but Bombycillidae has been supported in several

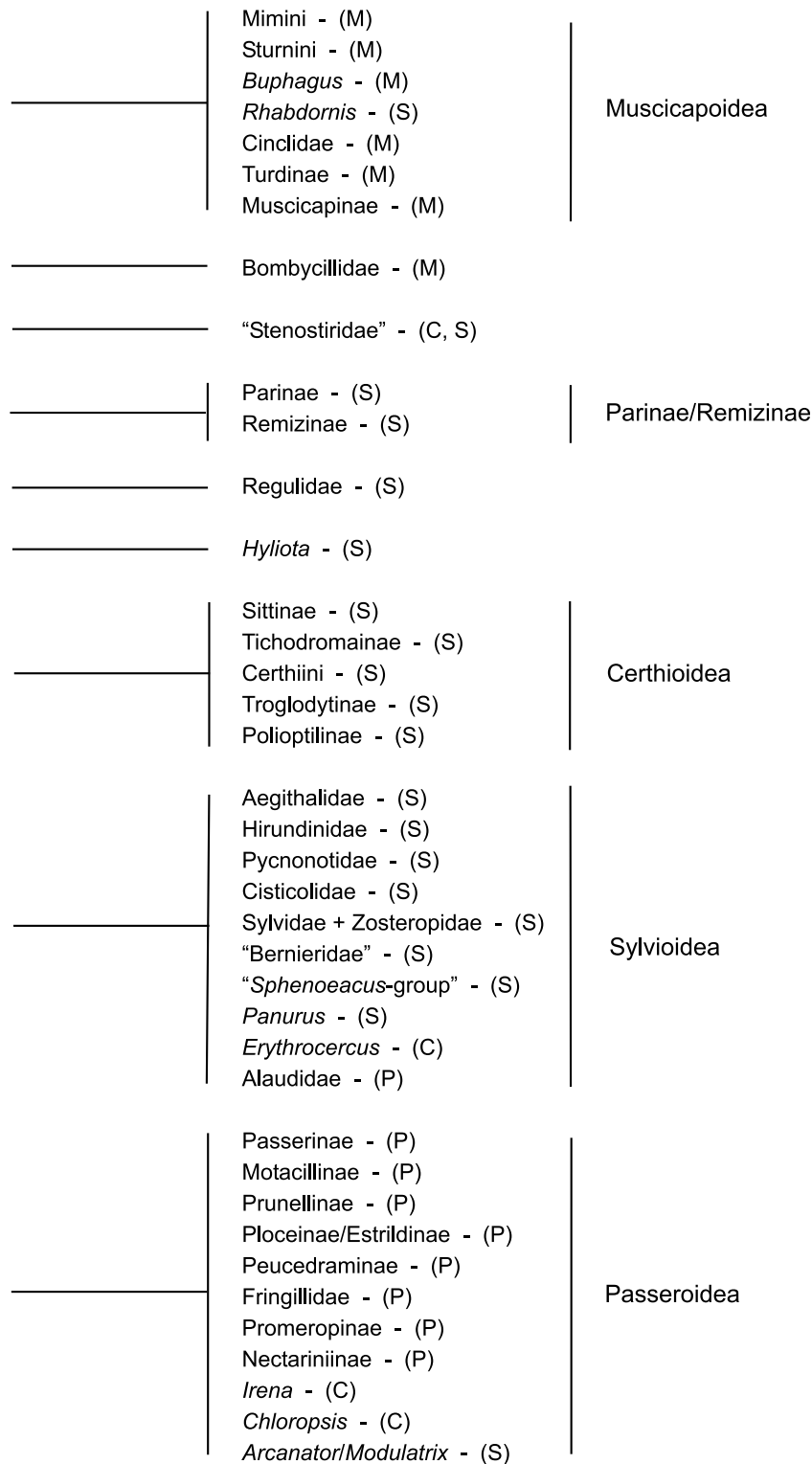


Fig. 1. Currently, recognized relationships among clades in the Passerida based on Sibley and Ahlquist (1990) with changes suggested by recent studies based on DNA sequence data (see text for details). The demarcated clades indicate the terminology we use throughout this manuscript. Letters in parentheses refer to the higher-level clade to which Sibley and Ahlquist (1990) assigned the particular clade: M, Muscicapoidea; S, Sylvioidea; P, Passeroidea, and C, Corvida.

subsequent molecular studies (Barker et al., 2002, 2004; Cibois and Cracraft, 2004; Ericson and Johannson, 2003; Voelker and Spellman, 2004), although this clade appears to also include the three species of Philippine creepers (*Rhabdornis*) (Cibois and Cracraft, 2004; Lovette and Rubenstein, 2007; Zuccon et al., 2006). The placement of Bombycillidae with this group, as suggested by Sibley and Ahlquist (1990), has not been recovered with strong support in

any subsequent study (Barker et al., 2002, 2004; Beresford et al., 2005; Cibois and Cracraft, 2004; Ericson and Johannson, 2003; Fuchs et al., 2006; Voelker and Spellman, 2004). Rather, several of these studies have indicated a more distant relationship, but neither of these alternative placements of the Bombycillidae are strongly supported, and the phylogenetic position of this clade must be considered unresolved within the Passerida. Hereafter

we use the term Muscipoidea for the clade containing: Cinclidae, Turdinae, Muscipapinae, Sturnini, Mimini, and exclude Bombycillidae from this group (Fig. 1).

With a few exceptions, Sibley and Monroe's (1990) circumscription of Passeroidea (Fig. 1) has also been supported by subsequent studies based on DNA sequencing. The berrypeckers and longbills (Paramythiidae and Melanocharitidae), which were placed in Passeroidea by Sibley and Monroe (1990), seemingly are not part of this radiation but rather fall outside the Passerida (see above). The larks (Alaudidae) have also been shown to fall outside the Passeroidea clade, although still within the Passerida radiation (e.g. Barker et al., 2004; Ericson and Johansson, 2003; Sheldon and Gill, 1996). A few clades have also recently been suggested to be part of Passeroidea; for instance Barker et al. (2004) placed the fairy-bluebird (*Irena*) and leafbirds, (*Chloropsis*) as one of the most basal clades in Passeroidea and sister to the Nectariniidae. In addition, the Dapple-throat (*Arcanator orostruthus*) and Spot-throat (*Modulatrix stictigula*), previously placed among babblers (Timalini, Sibley and Monroe (1990), or with the bulbuls and thrushes, respectively (Rand and Deignan, 1960; Ripley, 1964), have now been suggested to have a basal position within the Passeroidea (Barker et al., 2004).

Circumscription of Sylvioidea, the third of the three primary Passerida clades of Sibley and Ahlquist (1990), is more uncertain. Recent DNA sequence-based studies (e.g. Alström et al., 2006; Barker et al., 2004; Ericson and Johansson, 2003; Fuchs et al., 2006) have not been able to confirm monophyly of the Sylvioidea sensu Sibley and Ahlquist (1990). In part, this appears to be a result of poor resolution and low statistical support for the indicated relationships, but could also indicate that some clades included in the Sylvioidea sensu Sibley and Ahlquist (1990), e.g. the titmice and penduline tits (Parinae and Remizinae, respectively), kinglets (Regulidae) and Hyliotas (*Hyliota*), represent deep, isolated lineages within Passerida.

Another group included in the Sylvioidea sensu Sibley and Ahlquist (1990), but whose affinity with that group needs further evaluation, includes the nuthatches (Sittinae), wallcreepers (Tichodrominae), creepers (Certhiini), wrens (Troglodytinae) and gnatcatchers (Poliophtilinae) (e.g. Alström et al., 2006; Barker et al., 2004; Cracraft et al., 2004; Ericson and Johansson, 2003). This clade was also recovered by Sibley and Ahlquist (1990) based on DNA–DNA hybridization analyses but their data suggested that the Black-capped *Donacobius* (*Donacobius atricapillus*) and the Verdin (*Auriparus flaviceps*) also belong to this clade, although this has been challenged in recent sequence-based studies (Alström et al., 2006; Barker, 2004; Gill et al., 2005). In this paper, we refer to this clade (excluding *Donacobius* and *Auriparus*) as Certhioidea (following Cracraft et al., 2004) (Fig. 1).

Given the uncertainties in the phylogenetic placement of several of the clades included in Sylvioidea (sensu Sibley and Monroe, 1990), the term “Sylvioidea” has now become restricted to a much smaller group comprising the “families” (sensu Sibley and Monroe, 1990) Aegithalidae (long-tailed tits), Hirundinidae (swallows), Pycnonotidae (bulbuls), Cisticolidae (African warblers), Zosteropidae (white-eyes), Sylviidae (Old World warblers and babblers) and Alaudidae (larks) (Alström et al., 2006; Beresford et al., 2005; Ericson and Johansson, 2003). However, several studies have demonstrated that few of these “families”, as circumscribed by Sibley and Monroe (1990) are monophyletic (Alström et al., 2006; Beresford et al., 2005; Cibois, 2003; Cibois et al., 2001; Dickinson, 2003; Moyle and Marks, 2006; Nguembock et al., 2007; Sefc et al., 2003). The only exceptions are Hirundinidae and Alaudidae, whose monophyly are well supported by both morphological and molecular data (Mayr, 1958; Sheldon et al., 2005) and Zosteropidae, for which there is currently no molecular data available to confirm or refute the suggested monophyly of this lineage.

No group within Sylvioidea (sensu stricto) poses a greater taxonomic dilemma than the Sylviidae. Recent molecular studies have demonstrated that the various genera included in this “family” are scattered among the other Sylvioidea clades and several species in this group constitute previously unrecognized radiations rather distantly related to other sylvioide taxa. For example, Beresford et al. (2005) identified a clade, informally termed the “*Sphenoeacus*-group”, which includes among others the Cape Grassbird (*Sphenoeacus afer*), Crombecs (*Sylvietta*) and the Rockrunner (*Achaetops pycnopygius*) and suggested that this clade constitutes a relatively basal clade within Sylvioidea. Another recently identified clade with uncertain affinities within the Sylvioidea is the endemic Malagasy “warbler” radiation “Bernieridae” that includes approximately 10 species of sylvioide birds that in earlier classifications were considered to be part of different lineages such as bulbuls, babblers, and Old World warblers (Cibois et al., 1999, 2001; Fjeldså et al., 1999). In addition, the Bearded Reedling (*Panurus biarmicus*), which has generally been placed with parrotbills, the Nicator (*Nicator*), previously considered to be bulbuls (Pycnonotidae) or bush-shrikes (Malaconotidae), and the *Erythrocercus* flycatchers, previously placed with monarchine flycatchers, all apparently constitute isolated branches with uncertain affinities within Sylvioidea (Beresford et al., 2005; Ericson and Johansson, 2003; Fuchs et al., 2006; Pasquet et al., 2002). Alström et al. (2006) proposed a new classification for Sylvioidea (sensu stricto) based on myoglobin and cytochrome *b* sequence data that incorporated some but not all of these changes and divided the traditional Sylviidae into six clades: Cettiidae, Phylloscopidae, Acrocephalidae, Megaluridae, Cisticolidae, and Timaliidae, in addition to the other sylvioide clades (Aegithalidae, Hirundinidae, Pycnonotidae, and Alaudidae).

In addition to Muscipoidea, Passeroidea, Sylvioidea and the other comparably small Passerida clades (Fig. 1), molecular DNA data have identified yet another previously unrecognized clade within Passerida with uncertain phylogenetic affinities (Barker et al., 2004; Beresford et al., 2005; Pasquet et al., 2002). This clade, termed Stenostiridae, contains several species which were previously thought to be monarchine flycatchers and includes the Oriental canary-flycatchers (*Culicicapa*), the African blue-flycatchers (*Elminia*) including the crested-flycatchers *E. nigromitrata* and *E. albonotatus* (Pasquet et al., 2002), and the Fairy-flycatcher (*Stenostira scita*, Beresford et al., 2005).

2. Materials and methods

2.1. Terminology

Scientific names of species follow Dickinson (2003), with the exception of *Modulatrix orostruthus* which we retain in *Arcanator* (see results). The names of higher-level clades follow Sibley and Monroe (1990) with the exceptions as noted in the introduction (see also Fig. 1).

2.2. Taxon sampling and outgroup selection

We sampled representatives of all major clades of Passerida (see Section 1), but aimed to include a broad range of taxa whose systematic position has been disputed in the literature. Our taxon sampling includes the hyliotas, which have recently been suggested to represent a relictual lineage (Fuchs et al., 2006) as well as other problematic taxa including the: Dapple-throat (*A. orostruthus*), the phenetically similar Spotted Thrush Babbler (*Ptyrticus turdinus*), Spot-throat (*M. stictigula*), Grey-chested Thrush Babbler (*Kakamega poliothorax*) (see Jensen and Brøgger-Jensen, 1992) and the sugarbirds (*Promerops* spp.). Furthermore, we included

the Bush Blackcap (*Lioptilus nigricapillus*), Sao Tomé Short-tail (*Amaurocichla bocagii*), Chestnut-capped Flycatcher (*Erythrocerus mccallii*), Karoo Eremomela (*Eremomela gregalis*), and the Brown Emu-tail (*Dromaeocercus brunneus*), all taxa with uncertain affinities. All species included in this study are listed in Table 3.

The Cape Rock-jumper (*Chaetops frenatus*) and Golden Oriole (*Oriolus oriolus*) were included as outgroups and the tree was rooted with the Oriole. The addition of several more distantly related outgroup taxa recovered an identical topology, and all subsequent analyses were performed on the smaller data set.

2.3. Genes and laboratory procedures

Portions of three nuclear genes, myoglobin (MYO), ornithine decarboxylase (ODC), and β -fibrinogen (FIB), were amplified and sequenced for this study; these markers have previously proven useful in resolving phylogenetic relationships among passerine birds (e.g. Ericson and Johansson, 2003; Fjeldså et al., 2003; Fuchs et al., 2004; Irestedt et al., 2006). The sequenced portion of the myoglobin gene is approximately 700 base pairs (bp) and encompassed the complete intron 2, including flanking portions of exons 2 and 3, respectively (Heslewood et al., 1998). The sequenced region of the ODC gene encompassed 700 bp and included the complete introns 6 and 7, along with the intervening exon 7, as well as portions of the flanking exons 6 and 8. The sequenced portion of the β -fibrinogen gene included the complete intron 5 and small pieces of flanking exons for a total of approximately 550 bp.

Laboratory procedures for the extraction, PCR-amplification and sequencing of the nuclear genes followed: Irestedt et al. (2002) and Johansson and Ericson (2005) for Myoglobin intron 2, Allen and Omland (2003) for ODC, and Fuchs et al. (2004) for β -fibrinogen intron 5.

The generated sequences have been deposited in GenBank and the Accession Nos. for all sequences included in this study are given in Table 3.

2.4. Alignment

The sequences were aligned by eye in BioEdit 7.0.1 (Hall, 1999). The alignment of the nuclear introns indicated several instances of insertions and deletions in these sequences, but the sequences could in nearly all cases be unambiguously aligned.

The concatenated alignment of the three-gene segments included 2315 nucleotide positions, excluding a 625 bp insertion in intron 6 of the ODC gene observed in *Motacilla alba* and *A. bocagii*.

All inserted gaps were treated as missing data in the phylogenetic analyses.

2.5. Phylogenetic analysis

Phylogenetic analyses were conducted using three different optimality criteria: (1) parsimony (MP) using PAUP* b10 (Swofford, 2002) with 1000 bootstrap pseudo-replicates, each with three random additions of taxa, (2) maximum likelihood (ML) using the Randomized Axelerated Maximum Likelihood for High Performance Computing (RAxML-VI-HPC) algorithm (Stamatakis, 2006) which enables a general time-reversible (GTR) model (Lanave et al., 1984; Rodríguez et al., 1990; Tavaré, 1986) with Γ -distributed rate variation across sites (four rate categories— Γ_4) (Yang, 1994), and a proportion of invariant sites (I) (Gu et al., 1995) to be estimated for each individual data partition across a concatenated set of sequenced loci with 100 bootstrap pseudo-replicates, and (3) Bayesian Inference (BI) using MrBayes 3.1.1 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003).

The three-gene partitions (MYO, ODC, FIB5) were analyzed both separately and in combination. For the Bayesian analyses the mod-

el of sequence evolution for each partition was selected with the Akaike Information Criterion (Akaike, 1973) calculated in MrModeltest 2.2 (Nylander, 2004). Based on this analysis a GTR + Γ_4 + I model was chosen for ODC and β -fibrinogen intron 5, whereas a GTR + Γ_4 substitution model was chosen for myoglobin intron 2. Default priors were used in all MrBayes analyses. Two independent runs, each with four Metropolis-coupled MCMC chains were run for 10 million generations and sampled every 100 generations. Trees sampled before the chain reached apparent stationarity (burn-in) were discarded and the posterior probabilities for the topology were estimated from the remaining generations. To ascertain whether the chains had reached stationarity we: (1) plotted the log-likelihood values for each run and compared the posterior probabilities among runs, (2) we checked that the average standard deviation of split frequencies had converged towards zero, (3) determined that the potential scale reduction factor approached 1.0 for all parameters and (4) used Tracer v1.4 (Rambaut and Drummond 2007) to determine if the sampling of the posterior distribution had reached an adequate effective sample size.

We also performed additional analyses on a restricted set of taxa (37 ingroup species) that in addition to the myoglobin, ODC and β -fibrinogen sequences included RAG1, RAG2 (Barker et al., 2002, 2004; Beresford et al., 2005), and ND2 sequences (Fuchs et al., 2006 as well as other studies, see Table 2). We included representatives of all major clades of Passerida (as outlined above). Unfortunately, not all taxa are represented by the same species across the different studies, and thus this analysis relies on composite sequences in some cases (Table 4). However, in these cases we have selected species that have been shown to be closely related in other phylogenetic studies or, when this was not possible, we selected congeners in recent classifications. The concatenated alignment of this data set consisted of 7288 bp and was analyzed in a mixed-model analysis in MrBayes 3.1.1, and used a GTR + Γ + I model by gene partition in RAxML-VI-HPC with 100 bootstrap pseudo-replicates. For the Bayesian analyses, we used MrModeltest 2.2 to select an appropriate model of sequence evolution for this six-gene data set, which suggested a GTR + Γ_4 model for myoglobin intron 2 and β -fibrinogen intron 5, and a GTR + Γ_4 + I model for the other four gene regions.

3. Results

3.1. Sequence attributes

The concatenated alignment of the three-gene segments contain 2315 aligned positions: myoglobin 794 base pairs (bp), ODC 803 bp, excluding a 625 bp long insertion in *Motacilla* and *Amaurocichla*, and β -fibrinogen 718 bp. Of these, 1055 bp (318, 380, and 357 bp, respectively) are potentially parsimony informative. Base composition was biased in favor of Adenine and Thymine in all genes (myoglobin: A = 0.28, C = 0.22, G = 0.23, T = 0.26; ODC: A = 0.28, C = 0.17, G = 0.20, T = 0.35; fibrinogen: A = 0.30, C = 0.17, G = 0.21, T = 0.32). A χ^2 test for homogeneity of base frequencies across taxa detected no significant differences for the combined data set ($p = 1.00$) or for the individual data partitions (myoglobin, $p = 1.00$; ODC, $p = 1.00$; β -fibrinogen, $p = 1.00$).

3.2. Phylogenetic relationships

3.2.1. Combined, three-gene data set

The Bayesian analysis resulted in a generally well supported tree (bootstrap > 70%, PP > 0.95; Fig. 2). However, some regions of this tree are poorly resolved, most notably the basal branches in Passerida and several of the basal branches within Sylvioidea (sensu stricto). The bootstrap analysis under the parsimony criterion

Table 3

List of samples (in alphabetical order), with museum voucher numbers and GenBank Accession Nos. Species in bold are also included in the six-gene analysis

Species	Specimen No.	Myo. 2	Reference	ODC	Reference	Fib. 5	Reference
<i>Abroscopus superciliaris</i>	U.O.	DQ008567	4	EU680702	1	EU680620	1
Acrocephalus dumetorum	NRM 569279	AY887682	4	EF625338	1	EF626749	1
Aegithalos caudatus	NRM 976089	AY228281	2	EU680703	1	EU680621	1
<i>Aethopyga flagrans</i>	ZMUC 01346	AY228282	2	EU680704	1	EU680622	1
Alauda arvensis	NRM 966614	AY228284	2	EF625336	6	EF626747	6
<i>Amaurocichla bocagii</i>	Melo GA59729	EU680612	1	EU680700	1	EU680623	1
<i>Amaurocichla bocagii</i>	Melo ST5	EU680613	1	EU680701	1	EU680624	1
<i>Apalis thoracica</i>	ZMUC 05368	DQ008548	4	EU680705	1	EU680625	1
<i>Arachnothera longirostra</i>	NRM 20046985	EU680609	1	EU680706	1	EU680626	1
Arcanator orostruthus	ZMUC 120634	EU680618	1	EU680707	1	EU680627	1
<i>Auriparus flaviceps</i>	FMNH 394359	EU680579	1	EU680708	1	EU680628	1
<i>Bleda syndactyla</i>	ZMUC 119096	EF625276	6	EF625327	6	EF626738	6
Bombycilla garrulus	NRM 986044	AY228286	2	EU680709	1	EU680629	1
<i>Bradypterus mariae</i>	ZMUC 120423	EF625285	6	//		EF626750	6
	ZMUC 119903	//		EF625339	6	//	
<i>Bradypterus victorini</i>	MVZ (uncatalogued)	EU680602	1	EU680710	1	EU680630	1
Catharus guttatus	NRM 20016341	DQ466820	5	EU680712	1	EU680632	1
Certhia familiaris	NRM 976184	DQ466821	5	EU680713	1	EU680633	1
Cettia diphone	ZMUC 117791	EU680584	1	EU680714	1	EU680634	1
<i>Chersomanes albofasciata</i>	MVZ (RSA100)	EU680604	1	EU680716	1	EU680636	1
<i>Chloropsis aurifrons</i>	FMNH 363782	EU680611	1	EU680717	1	EU680637	1
Cinclus cinclus	NRM 20016138	AY228291	2	EU680718	1	EU680638	1
<i>Coccothraustes coccothraustes</i>	NRM 976374	AY228292	2	EU680711	1	EU680631	1
<i>Cryptospiza reichenovii</i>	ZMUC 0785	AY228293	2	EU680719	1	EU680639	1
Culicicapa ceylonensis	NRM 20036793	EU680605	1	EU680720	1	EU680640	1
<i>Delichon urbicum</i>	NRM 976412	DQ008568	4	EU680721	1	EU680641	1
Dicaeum australe	ZMUC 03737	AY228294	2	EU680722	1	EU680642	1
<i>Donacobius atricapilla</i>	NRM 966966	DQ008533	4	EU680723	1	EU680643	1
<i>Dromaeocercus brunneus</i>	FMNH 384749	EU680593	1	EU680724	1	EU680644	1
Elminia albonotata	ZMUC 122624	EU680606	1	EU680725	1	EU680645	1
<i>Eremomela gregalis</i>	MVZ (RSA120)	EU680598	1	EU680726	1	EU680646	1
<i>Erythrocercus mcallii</i>	FMNH 396684	EU680585	1	EU680727	1	EU680647	1
<i>Ficedula hypoleuca</i>	NRM 976132	AY228300	2	EU680728	1	EU680648	1
<i>Garrulax vassali</i>	NRM 20047024	EU680589	1	EU680729	1	EU680649	1
<i>Hartertula flavoviridis</i>	FMNH 438721	EU680597	1	EU680730	1	EU680650	1
<i>Hippolais icterina</i>	NRM 20036451	DQ008531	4	EU680731	1	EU680651	1
Hirundo rustica	NRM 976238	AY064258	3	EF625337	6	EF626748	6
Hylia prasina	ZMUC 119039	EU680583	1	EU680732	1	EU680652	1
<i>Hyltiota flavigaster</i>	FMNH 43959	EU680608	1	EU680733	1	EU680653	1
<i>Illadopsis rufipennis</i>	ZMUC 133229	EU680591	1	EU680734	1	EU680654	1
<i>Irena cyanogastra</i>	ZMUC 119544	EU680610	1	EU680735	1	EU680655	1
<i>Kakamega poliothorax</i>	FMNH 355685	EU680616	1	EU680736	1	EU680656	1
<i>Kakamega poliothorax</i>	FMNH 358054	EU680617	1	EU680737	1	EU680657	1
<i>Leptopoeile sophiae</i>	NRM 20046817	DQ008569	4	EU680738	1	EU680658	1
<i>Lioptilus nigricapillus</i>	DM 38981	EU680586	1	EU680739	1	EU680659	1
<i>Locustella fluviatilis</i>	NRM 20046784	DQ008527	4	EU680740	1	EU680660	1
Macrosphenus flavicans	ZMUC 129975	EF625286	6	EF625340	6	EF626751	6
Megalurus palustris	NRM 20046786	DQ008529	4	EU680741	1	EU680661	1
Mimus saturninus	NRM 966912	AY228304	2	EU680742	1	EU680662	1
Modulatrix stictigula	ZMUC 118848	EU680619	1	EU680743	1	EU680663	1
Motacilla alba	NRM 976193	AY228307	2	EU680699	1	EU680664	1
<i>Nesillas typica</i>	FMNH 384802	EU680592	1	EU680744	1	EU680665	1
<i>Nicator chloris</i>	ZMUC 119452	EU680603	1	EU680745	1	EU680666	1
<i>Panurus biarmicus</i>	NRM 966576	AY228308	2	EU680747	1	EU680668	1
<i>Paradoxornis webbianus</i>	ZMUC 135625	EU680588	1	EU680748	1	EU680669	1
Parus major	NRM 20036752	AY228310	2	EU680749	1	EU680670	1
Passer montanus	NRM 976359	AY228311	2	EF625341	6	EF626752	6
Phylloscopus umbrovirens	ZMUC 120713	AY887721	4	EU680750	1	EU680671	1
<i>Plectrophenax nivalis</i>	NRM 986392	AY228315	2	EU680751	1	EU680672	1
Ploceus capensis	MVZ (RB677)	EU680614	1	EU680752	1	EU680673	1
Polioptila dumicola	NRM 956689	AY228317	2	EU680753	1	EU680674	1
Prinia bairdii	ZMUC 123084	EU680599	1	EU680754	1	EU680675	1
Promerops cafer	MVZ (RB681)	EU680615	1	EU680755	1	EU680676	1
Prunella modularis	NRM 20026243	AY228318	2	EU680756	1	EU680677	1
<i>Psaltriparus minimus</i>	NRM20016337	EU680582	1	EU680757	1	EU680678	1
<i>Pseudoalcippe abyssinica</i>	ZMUC JK10-041104	EU680587	1	EU680758	1	//	
	ZMUC JK11-171004	//		//		EU680679	1
<i>Ptyrticus turdinus</i>	ZMUC 129694	EU680590		EU680759	1	EU680680	1
Pycnonotus barbatus	ZMUC 117636	EF625284	6	EF625335	6	EF626746	6
Regulus calendula	NRM 20016339	EU680580	1	EU680760	1	EU680681	1
<i>Regulus regulus</i>	NRM 20016439	DQ466835	5	EU680761	1	EU680682	1
<i>Remiz pendulinus</i>	ZMUC 01852	AY228319	2	EU680762	1	EU680683	1
<i>Salpornis pilonotus</i>	FMNH 444409	EU680581	1	EU680763	1	EU680684	1
<i>Saltator atricollis</i>	NRM 966978	AY228320	2	EU680764	1	EU680685	1
Sitta europaea	NRM 976163	AY064257	3	EU680765	1	EU680686	1

(continued on next page)

Table 3 (continued)

Species	Specimen No.	Myo. 2	Reference	ODC	Reference	Fib. 5	Reference
<i>Sphenoeacus afer</i>	MVZ (RB660)	EU680601	1	EU680766	1	EU680687	1
<i>Stachyris nigriceps</i>	NRM 947308	AY228321	2	EU680767	1	EU680688	1
<i>Stenostira scita</i>	MVZ (RB661)	EU680607	1	EU680768	1	EU680689	1
<i>Sturnus vulgaris</i>	NRM 966615	AY228322	2	EU680769	1	EU680690	1
<i>Sylvia atricapilla</i>	NRM 976380	AY228323	2	EU680770	1	EU680691	1
<i>Sylvietta leucophrys</i>	ZMUC 123144	EU680600	1	EU680771	1	EU680692	1
<i>Sylvietta whytii</i>	ZMUC 123492	DQ008552	4	EU680772	1	EU680693	1
<i>Thamnornis chloropetoides</i>	FMNH 356699	EU680596	1	EU680773	1	EU680694	1
<i>Tickellia hodgsoni</i>	NRM 20046814	DQ008565	4	EU680774	1	EU680695	1
<i>Troglodytes troglodytes</i>	NRM 986416	AY228325	2	EU680775	1	EU680696	1
<i>Xanthomixis tenebrosus</i>	FMNH 393278	EU680594	1	EU680776	1	EU680697	1
<i>Xanthomixis zosterops</i>	FMNH 393265	EU680595	1	EU680777	1	EU680698	1
Outgroups							
<i>Chaetops frenatus</i>	PFI uncat.	AY228289	2	EU680715	1	EU680635	1
<i>Oriolus oriolus</i>	ZMUC 01376	AY228329	2	EU680746	1	EU680667	1

Abbreviations: DM, Durban Museum, Durban, South Africa; FMNH, Field Museum of Natural History, Chicago, USA; MVZ, Museum of Vertebrate Zoology, University of California, Berkeley, USA; NRM, Swedish Museum of Natural History, Stockholm, Sweden; PFI, Percy FitzPatrick Institute, University of Cape Town, South Africa; ZMUC, Zoological Museum, University of Copenhagen, Copenhagen, Denmark. References: 1, This study; 2, Ericson and Johannson (2003); 3, Ericson et al. (2002b); 4, Alström et al. (2006); 5, Zuccon et al. (2006); 6, Johannson et al. (2007). * Indicates a sequence from another individual.

Table 4

Species included in the combined, six-gene analysis

Species (This study)	RAG1			RAG2			ND2		
	GenBank	Reference	Species	GenBank	Reference	Species	GenBank	Reference	Species
<i>Acrocephalus dumetorum</i>	AY319972	5	<i>newtoni</i>	AY799825	4	<i>newtoni</i>	DQ125987	6	<i>aedon</i>
<i>Aegithalos caudatus</i>	AY056976	1	<i>iouschensis</i>	AY443103	2	<i>iouschensis</i>	AY136588	7	<i>caudatus</i>
<i>Alauda arvensis</i>	AY056978	1	<i>arvensis</i>	AY443106	2	<i>arvensis</i>	DQ125975	6	<i>arvensis</i>
<i>Arcanator orostruthus</i>	AY443261	2	<i>orostruthus</i>	AY443107	2	<i>orostruthus</i>	DQ125986	6	<i>orostruthus</i>
<i>Bombicilla garrulus</i>	AY056981	1	<i>garrulus</i>	AY443111	2	<i>garrulus</i>	AY329412	8	<i>garrulus</i>
<i>Catharus guttatus</i>	AY443265	2	<i>ustulatus</i>	AY443114	2	<i>ustulatus</i>	AY049524	10	<i>guttatus</i>
<i>Certhia familiaris</i>	AY056983	1	<i>familiaris</i>	AY443115	2	<i>familiaris</i>	DQ466857	11	<i>familiaris</i>
<i>Cettia diphone</i>	AY319977	5	<i>brunnifrons</i>	AY799832	4	<i>brunnifrons</i>	AY382356	12	<i>diphone</i>
<i>Cinclus cinclus</i>	AY056985	1	<i>cinclus</i>	AY443119	2	<i>cinclus</i>	DQ146344	6	<i>cinclus</i>
<i>Culicicapa ceylonensis</i>	AY443279	2	<i>ceylonensis</i>	AY443136	2	<i>ceylonensis</i>	DQ125979	6	<i>ceylonensis</i>
<i>Dicaeum australe</i>	AY443282	2	<i>aeneum</i>	AY443139	2	<i>aeneum</i>	AF290101	14	<i>trigonostigma</i>
<i>Elminia albonotata</i>	AY443338	2	<i>nigromitratus</i>	AY443240	2	<i>nigromitratus</i>	DQ125981	6	<i>albonotata</i>
<i>Hirundo rustica</i>	AY443290	2	<i>rustica</i>	AY443155	2	<i>rustica</i>	DQ176584	17	<i>rustica</i>
<i>Hylia prasina</i>	AY319984	5	<i>prasina</i>	AY799837	4	<i>prasina</i>	AY136606	7	<i>prasina</i>
<i>Macrosphenus flavicans</i>	AY319987	5	<i>flavicans</i>	AY799839	4	<i>flavicans</i>	DQ125997	6	<i>flavicans</i>
<i>Megalurus palustris</i>	AY319988	5	<i>palustris</i>	AY799840	4	<i>palustris</i>	AY382396	14	<i>pryeri</i>
<i>Mimus saturninus</i>	AY057005	1	<i>patagonicus</i>	AY443173	2	<i>patagonicus</i>	AY758198	18	<i>saturninus</i>
<i>Modulatrix stictigula</i>	AY443303	2	<i>stictigula</i>	AY443175	2	<i>stictigula</i>	DQ125985	6	<i>stictigula</i>
<i>Motacilla alba</i>	AY057007	1	<i>cinerea</i>	AY443178	2	<i>cinerea</i>	AF407040	9	<i>alba</i>
<i>Parus major</i>	AY443314	2	<i>major</i>	AY443197	2	<i>major</i>	AY732696	15	<i>major</i>
<i>Passer montanus</i>	AF143738	3	<i>montanus</i>	AY443198	2	<i>montanus</i>	AY030144	19	<i>montanus</i>
<i>Phylloscopus umbrovirens</i>	AY319997	5	<i>collybita</i>	AY799844	4	<i>collybita</i>	DQ125988	6	<i>collybita</i>
<i>Ploceus capensis</i>	AY057022	1	<i>cucullatus</i>	AY443207	2	<i>cucullatus</i>	AF290104	14	<i>cucullatus</i>
<i>Poliophtila dumicola</i>	AY443320	2	<i>caerulea</i>	AY443208	2	<i>caerulea</i>	AY329446	8	<i>caerulea</i>
<i>Prinia bairdii</i>	AY319998	5	<i>bairdii</i>	AY799845	4	<i>bairdii</i>	DQ126000	6	<i>bairdii</i>
<i>Promerops cafer</i>	AY443323	2	<i>cafer</i>	AY443212	2	<i>cafer</i>	DQ125990	6	<i>cafer</i>
<i>Prunella modularis</i>	AY057024	1	<i>collaris</i>	AY443213	2	<i>collaris</i>	AF407038	9	<i>modularis</i>
<i>Pycnonotus barbatus</i>	AY057027	1	<i>barbatus</i>	AY443219	2	<i>barbatus</i>	AF407054	9	<i>barbatus</i>
<i>Regulus calendula</i>	AY057028	1	<i>calendula</i>	AY443220	2	<i>calendula</i>	AY329435	8	<i>calendula</i>
<i>Sitta europaea</i>	AY443332	2	<i>carolinensis</i>	AY443227	2	<i>carolinensis</i>	DQ219775	16	<i>europaea</i>
<i>Sphenoeacus afer</i>	AY799822	4	<i>afer</i>	AY799847	4	<i>afer</i>	DQ125991	6	<i>afer</i>
<i>Stenostira scita</i>	AY799823	4	<i>scita</i>	AY799848	4	<i>scita</i>	DQ125993	6	<i>scita</i>
<i>Sturnus vulgaris</i>	AY057032	1	<i>vulgaris</i>	AY443232	2	<i>vulgaris</i>	AF407048	9	<i>vulgaris</i>
<i>Sylvia atricapilla</i>	AY057033	1	<i>nana</i>	AY443233	2	<i>nana</i>	DQ125994	6	<i>atricapilla</i>
<i>Thamnornis chloropetoides</i>	AY320004	5	<i>chloropetoides</i>	AY799850	4	<i>chloropetoides</i>	DQ125995	6	<i>chloropetoides</i>
<i>Troglodytes troglodytes</i>	AY057038	1	<i>aedon</i>	AY443241	2	<i>aedon</i>	AY460333	13	<i>troglodytes</i>
<i>Chaetops frenatus</i>	AY443266	2	<i>frenatus</i>	AY443116	2	<i>frenatus</i>	DQ125989	6	<i>P. gymnocephalus</i>
<i>Oriolus oriolus</i>	AY443308	2	<i>xanthonotus</i>	AY443185	2	<i>xanthonotus</i>	AY136612	7	<i>auratus</i>

References: 1, Barker et al. (2002); 2, Barker et al. (2004); 3, Groth and Barrowclough, 1999; 4, Beresford et al. (2005); 5, Barker et al., unpublished; 6, Fuchs et al. (2006); 7, Sefc et al. (2003); 8, Voelker and Spellman (2004); 9, Sorenson and Payne, 2001; 10, Winker and Pruett (2006); 11, Zuccon et al. (2006); 12, Drovetski et al. (2004a); 13, Drovetski et al. (2004b); 14, Klicka et al. (2000); 15, Zink (2005); 16, Zink et al. (2006a); 17, Zink et al. (2006b); 18, Barber et al. (2004); 19, Cicero and Johnson (2001).

(MP) resulted in a congruent topology (Fig. 2), although several of the nodes recovered with posterior probabilities less than 0.95 were not recovered in the MP analysis (no search for a most-parsimonious tree was performed and branches with <50% bootstrap support were collapsed). In only two cases, the bootstrap analysis

recovered a sister-group relationship that were not recovered in the Bayesian analysis: the sister-group relationship between *Phylloscopus* and *Hylia* and, between *Irena* and *Chloropsis* was recovered with low support (62% and 61%, respectively). The maximum likelihood (ML) analysis also recovered a topology that was nearly

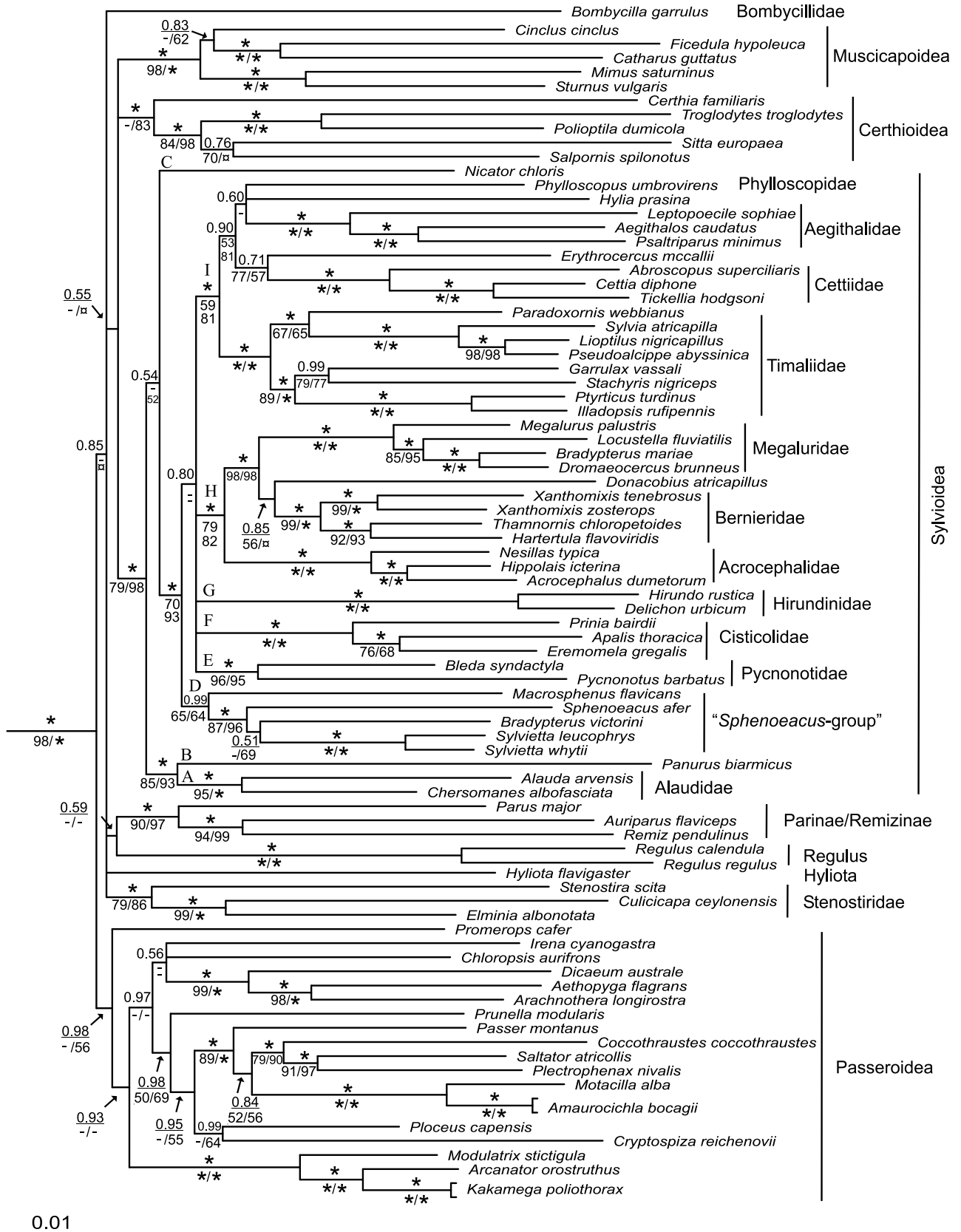


Fig. 2. Bayesian consensus tree of the combined, mixed-model analysis of the three nuclear data partitions: myoglobin intron 2, ODC introns 6 and 7, along with exon 7, and β -fibrinogen intron 5 (total 2315 bp). Numbers above the branches indicate Bayesian posterior probabilities and numbers below bootstrap support under the parsimony optimality criterion and maximum likelihood, respectively. An asterisk * indicates a posterior probability of 1.0 or 100% bootstrap support. \square indicates that the branch was contradicted by an alternative topology (see text for details). The letters A–I denote individual clades identified within the Sylvioidea.

identical to the Bayesian tree, but some conflicts were evident in the most weakly supported regions of the Bayesian tree. These ambiguities relate to the inter-relationships between the major clades of Passerida (as defined in Fig. 1 and Section 1), as well as the relationship of *Donacobius* relative to Bernieridae and Megaluridae, and the placement of *Salpornis* relative to *Sitta* and *Polioptila/Troglodytes* (see below). The nodes that are in conflict between the Bayesian analysis and the ML analysis are indicated in Fig. 2, but the very low bootstrap support for the relationship indicated by the ML analysis, 4–16% for the basal relationships, suggest that this part of the tree should be considered unresolved with the present data. When only nodes with bootstrap support above 50% are considered, only one conflict between the ML analysis and the Bayesian tree is evident, namely the placement of *Salpornis* relative to *Sitta* and *Polioptila/Troglodytes*.

All of the major clades of Passerida (Fig. 1) are recovered with posterior probabilities of over 0.95 (0.98–1.00), and all but Passeroidea have bootstrap support above 70% (83–100%) in the ML analysis (Fig. 2). As indicated above, the relationships of these clades relative to each other are unresolved by all three optimality criteria.

Passeroidea, as defined here (Fig. 1), is recovered with strong support in the Bayesian analysis (posterior probability = 0.98), but is weakly supported by the ML analysis (bootstrap = 56%) and is not recovered in the MP analysis (bootstrap < 50%). This is symptomatic for several of the indicated relationships within Passeroidea which are strongly supported by the Bayesian analysis (PP > 0.95) but are not recovered, or recovered with only weak support, by the MP or ML bootstrap analyses. Nevertheless, the topologies indicated by the three different methods are congruent, and only the position of *Irena* and *Chloropsis* relative to the sunbirds, spiderhunters and flowerpecker clade differs between the analyses (the ML tree suggesting a basal position of *Chloropsis* relative to *Irena* and the sunbird clade, whereas the MP tree places *Chloropsis* and *Irena* sister to each other). However, the support for these alternative topologies is weak (ML bootstrap = 18%, MP bootstrap = 62%), suggesting these three clades form an unresolved trichotomy, as recovered in the Bayesian analysis (Fig. 2). Both the Bayesian and ML analyses place the sugarbirds (*Promerops*) as the sister-group of all other representatives of Passeroidea, although this placement is weakly supported by the Bayesian and ML analyses and unresolved in the parsimony analysis. The Dapple-throat (*A. orostruthus*), Spot-throat (*M. stictigula*), and Grey-chested Thrush Babbler (*K. poliothorax*) are placed in a basal position within Passeroidea by the Bayesian analyses (PP = 0.97, with *Arcanator* and *Kakamega* as sister taxa. The sunbirds, spiderhunters and flowerpeckers (represented by *Aethopyga flagrans*, *Arachnothera longirostra*, and *Dicaeum australe*, respectively) form a monophyletic group and are placed in a clade with the fairy-bluebirds (*Irena cyanigastra*) and leafbirds (*Chloropsis aurifrons*) although with no statistical support (PP = 0.56, ML and MP bootstrap < 50%). The remaining Passeroid species, which include representatives of the accentors, weavers, estrildine finches, sparrows, finches, New World sparrows, and wagtails, form a clade (PP = 0.98, MP bootstrap = 50%, ML bootstrap = 69%) with accentors (*Prunella modularis*) diverging at the base. Within this group there is strong support (including a 625 bp insertion in the ODC) by the Bayesian as well as the MP and ML analyses for placing the enigmatic Sao Tomé Short-tail (*A. bocagii*) with the Motacillidae (represented by *M. alba*).

There is strong support in all analyses for a sister-group relationship between thrushes (Turdinae) and Old World flycatchers (Muscicapinae), represented here by *Ficedula hypoleuca* and *Catharus guttatus*, as well as for a sister-group relationship between starlings (Sturnini—*Sturnus*) and mimids (Mimini—*Mimus*). Both the Bayesian and ML analyses place the dippers (*Cinclus*) as the sis-

ter-group of the thrushes and old world flycatchers although the support is weak (PP = 0.83, ML bootstrap = 62%, MP bootstrap < 50%).

The spotted creeper (*Salpornis spilonotus*) is placed in Certhioidea, together with the tree-creeper, nuthatches and wrens. In the Bayesian analysis, it clusters closer to nuthatches (*Sittinae—Sitta europaea*) than to the morphologically more similar-looking tree-creeper (*Certhiini—Certhia familiaris*). This association is also suggested in the MP analysis. However, the ML analysis places *Salpornis* basal relative to the nuthatches and a clade composed of the gnatcatchers and wrens. Both the association with the nuthatches indicated by the Bayesian and MP analyses or the more basal position indicated by the ML analysis are, however, weakly supported if statistically at all (PP = 0.76, MP bootstrap = 70% vs ML bootstrap = 54%). A sister-group relationship between gnatcatchers (*Polioptilinae—Polioptila dumicola*) and wrens (*Troglodytinae—Troglodytes troglodytes*) is strongly supported by all analyses. In all trees, *Certhia* is recovered in a basal position relative to the other taxa.

Monophyly of Sylvioidea (sensu stricto) is strongly supported (PP = 1.0, MP bootstrap = 79%, ML bootstrap = 98%), but basal relationships are with some notable exceptions, unresolved. In effect, the species included in this analysis form nine clades (denoted A–I in Fig. 2). The Bearded Reedling (*P. biarmicus*; clade B) is placed with high posterior probability and bootstrap support as the sister-group of the larks (represented by *Alauda arvensis* and *Chersomanes albobasata*; clade A). This clade is in turn placed as the sister groups of all other sylvioids (Fig. 2), although low posterior probabilities and lack of bootstrap support for the position leaves the placement of this clade relative to the nicator (*Nicator*; clade C) and remaining sylvioids as unresolved (Fig. 2).

Within this latter clade our analyses identified six primary clades with uncertain inter-relationships. Among these are the bulbuls (Pycnonotidae: *Pycnonotus barbatus* and *Bleda syndactyla*, clade E) and swallows (Hirundinidae: *Hirundo rustica* and *Delichon urbicum*; clade G), as well as the “*Sphenoeacus*-group” (clade D) (Beresford et al., 2005), represented here by the Crombecs (*Sylvietta leucophrys* and *S. whytii*), Yellow Longbill (*Macrosphenus flavicans*) and Victorin’s Scrub-Warbler (*Bradypterus victorini*). Furthermore, the two representatives of the Cisticolidae included (*Apalis thoracica* and *Prinia bairdii*; clade F) constitute a clade, but our analyses suggest that the Eremomelas (*E. gregalis*) also form part of the cisticola radiation.

The remaining sylvioid taxa included in this study fall into two large radiations, (denoted clades H and I in Fig. 2). The first of these two clades (clade I) includes the longtailed tits and bushtits (*Aegithalos* and *Psaltriparus*, respectively), as well as the tit-warbler (*Leptopoeile*), the leaf warblers (*Phylloscopus*), Cettiidae (*Cettia*, *Abroscopus*, and *Tickellia*), the Green Hylia (*Hylia prasina*), the Chestnut-capped Flycatcher (*E. mccallii*), as well as the babblers. Included within the babblers are the African Thrush Babbler (*P. turdinus*), Pale-Breasted Illadopsis (*Illadopsis rufipennis*), African Hill Babbler (*Pseudoalcippe abyssinica*) and Blackcap Mountain-babbler or Bush Blackcap (*L. nigricapillus*), but not the Grey-chested Babbler (*K. poliothorax*), Dapple-throat (*A. orostruthus*) or the Spot-throat (*M. stictigula*), which are placed in Passeroidea.

The second of these large sylvioid clades (clade H) contains among others two clades that correspond to the Megaluridae and Acrocephalidae (sensu Alström et al., 2006). Included with the Megaluridae (represented by *Megalurus palustris*, *Locustella fluviatilis*, and *Bradypterus mariae*) is also the Malagasy Emutail (*D. brunneus*). The Acrocephalidae (sensu Alström et al., 2006) is represented by *Hippolais icterina* and *Acrocephalus dumetorum* in this study, and associated with this clade is also the Madagascar Brush-warbler or Tsikirity (*Nesillas typica*). Included within “clade H” is also another group of Malagasy “warblers” (Bernieridae, rep-

resented by *Thamnornis chloropetoides*, *Hartertula flavoviridis*, *Xanthomixis tenebrosus*, and *X. zosterops* as well as the South American Black-capped *Donacobius* (*D. atricapillus*). Within “clade H” Megaluridae, Berneridae, and the Black-capped *Donacobius* form a strongly supported clade, but the inter-relationships between the three groups differs with different analytical methods. The Bayesian analysis as well as the MP analysis places the Black-capped *Donacobius* with the Malagasy Bernieridae (PP = 0.85, MP bootstrap = 56%), whereas the ML analysis places the *Donacobius* with

Megaluridae (ML bootstrap = 45%). Neither of these alternate topologies are strongly support, suggesting that Bernieridae, Megaluridae, and the *Donacobius* form a polytomy.

3.2.2. Combined, six-gene data set

The topology recovered from the Bayesian analysis of the combined six-gene data set (Fig. 3) is in its general structure similar to the three-gene topology (Fig. 2), but recovers two additional clades. The first of these clades contains

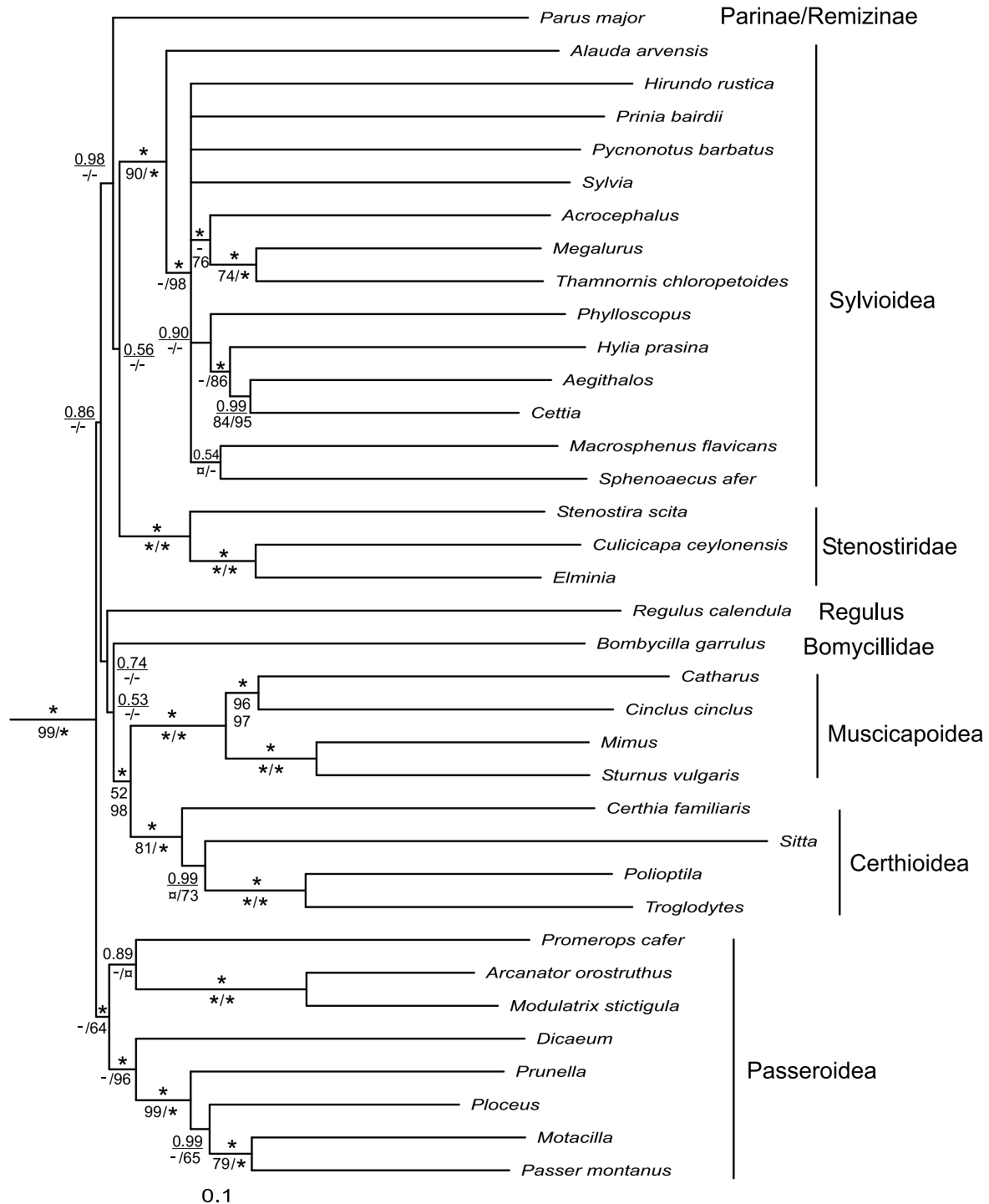


Fig. 3. Bayesian consensus tree of the combined, mixed-model analysis of six data partitions (total 7288 bp): myoglobin intron 2, ODC introns 6 and 7, along with exon 7, β -fibrinogen intron 5, RAG-1, RAG-2, and ND2. Numbers above the branches indicate Bayesian posterior probabilities and numbers below bootstrap support under the parsimony optimality criterion and maximum likelihood, respectively. An asterisk * indicates a posterior probability of 1.0% or 100% bootstrap support. † Denotes a branch in conflict with the maximum likelihood tree (see text for details).

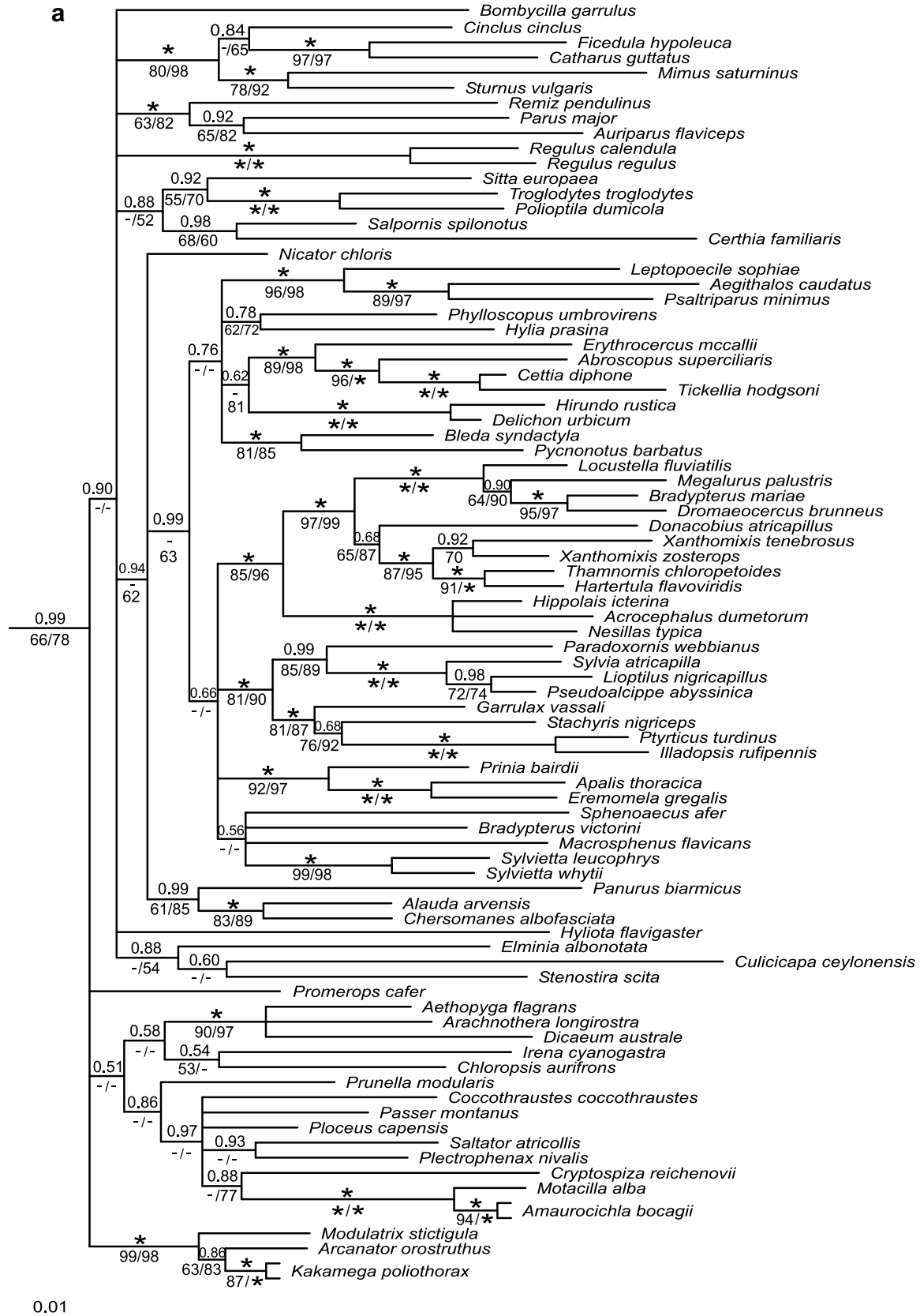


Fig. 4. Bayesian consensus trees from analyses of the individual genes: (a) myoglobin intron 2 (794 bp), (b) ODC introns 6 and 7, and intervening exon 7 (803 bp), (c) β -fibrinogen intron 5 (718 bp). Numbers above the branches indicate Bayesian posterior probabilities and numbers below bootstrap support under the parsimony optimality criterion and maximum likelihood, respectively. An asterisk * indicates a posterior probability of 1.0% or 100% bootstrap support.

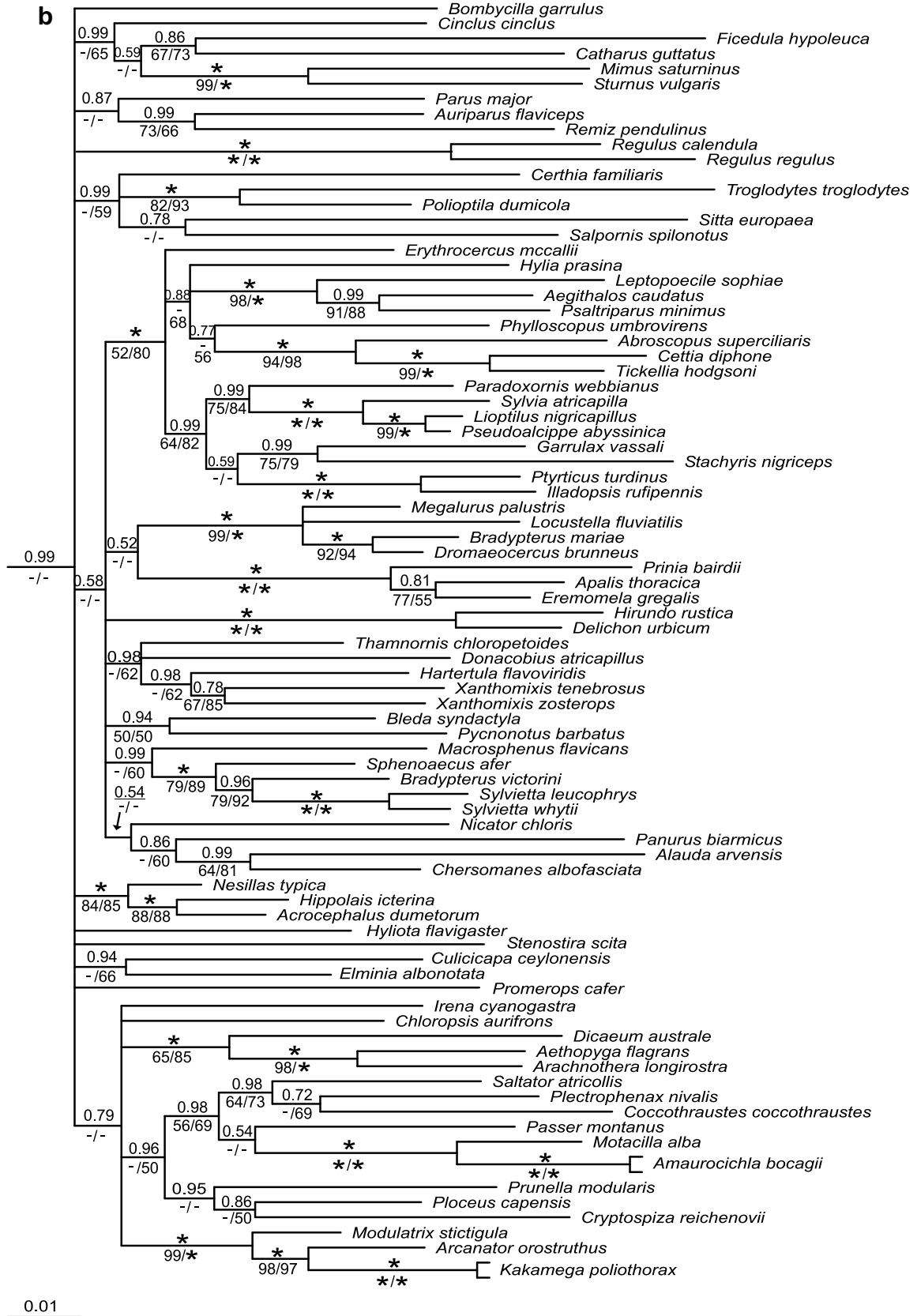


Fig. 4 (continued)

Muscicapoidea and Certhioidea (PP = 1.00, ML bootstrap = 98%, MP bootstrap = 52%). The second clade includes Sylvioidea (sensu stricto), Parinae, Remizinae and Stenostiridae

(PP = 0.98, ML and MP bootstrap < 50%). As in the three-gene topology basal relationships within Sylvioidea are largely unresolved.

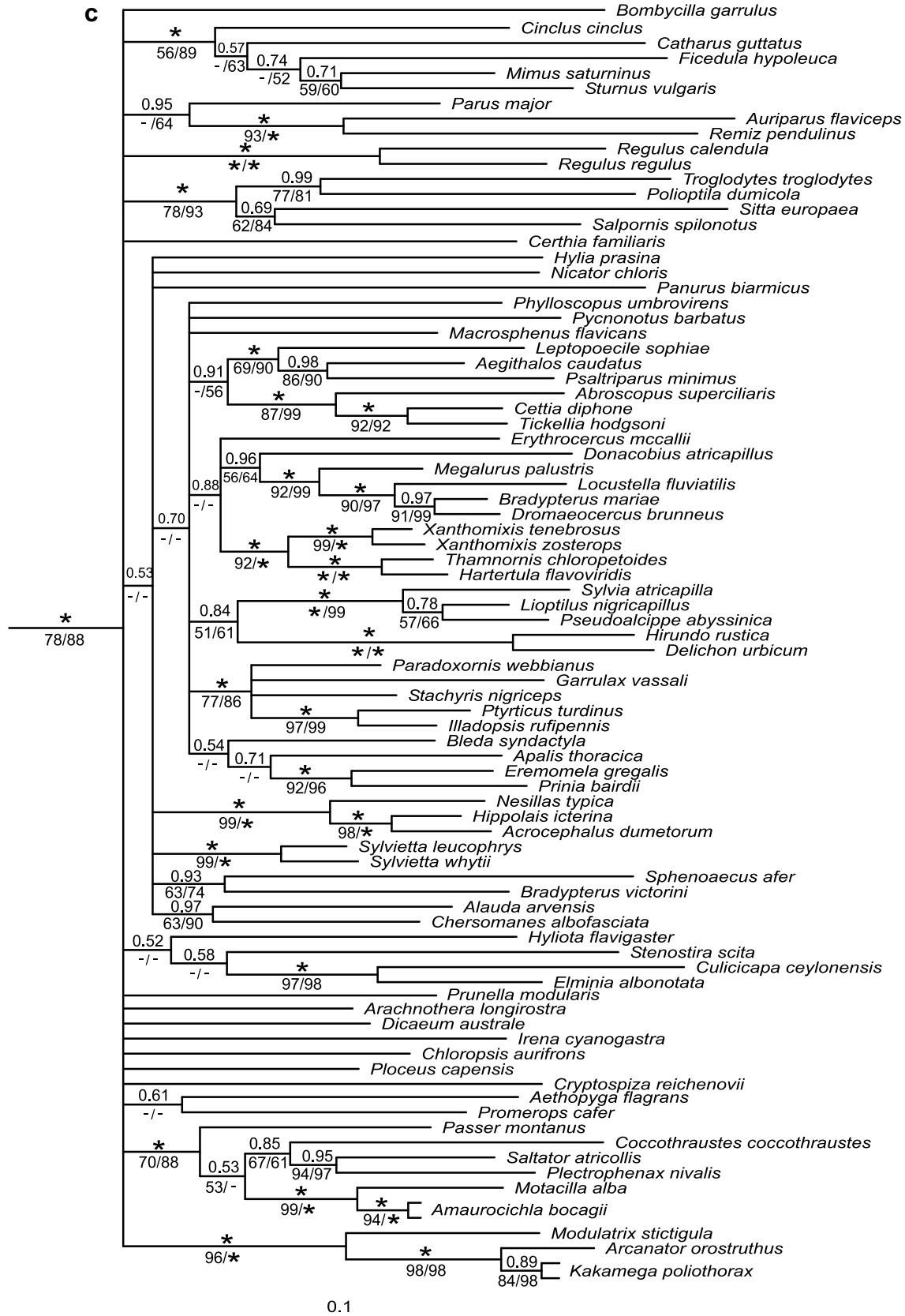


Fig. 4 (continued)

3.2.3. Individual gene trees of myoglobin, ODC, and β -fibrinogen (three-gene data set)

Only 24 branches are identical across all three-gene topologies (Fig. 4). However, most incongruences reflect the poor resolution in the individual gene trees, especially the β -fibrinogen gene tree. Actual conflicts are relatively few, and mostly associated with poorly supported relationships.

The placement of *Cinclus* as sister to the thrushes and Old World flycatchers is only recovered by the Bayesian analysis of the myoglobin intron. In both ODC and β -fibrinogen, *Cinclus* is placed basally in Muscicapoidae, although with low posterior probability. In the MP analyses of the individual genes, the position of *Cinclus* within Muscicapoidae is unresolved. The position of *Salpornis* as the sister of *Sitta*, as indicated by combined analyses, has weak support in the individual gene trees (ODC: PP = 0.78, ML and MP bootstrap < 50%; β -fibrinogen: PP = 0.69, ML bootstrap = 84%, MP bootstrap = 62%), and is strongly contradicted in the myoglobin gene tree where *Salpornis* is placed with *Certhia* (PP = 0.98, ML bootstrap = 60%, MP bootstrap = 68%). ODC and β -fibrinogen also agree in placing *Auriparus* as the sister of *Remiz* (ODC: PP = 0.99, ML bootstrap = 66%, MP bootstrap = 73%; β -fibrinogen: PP = 1.00, ML bootstrap = 100%, MP bootstrap = 93%), in agreement with the combined analyses, whereas *Auriparus* is placed with *Parus* in the myoglobin gene tree (PP = 0.92, ML bootstrap = 82%, MP bootstrap = 65%).

In several instances, a strongly supported relationship in one gene tree is contradicted by a weakly supported relationship in another gene tree. For instance, the relationships between *Megalurus*, *Locustella*, and *Bradypterus/Dromaecocercus* are differently reconstructed in the different gene trees (Fig. 4a–c), and only β -fibrinogen recovers the same topology as in the combined analyses (Fig. 2). Similarly, the recovered association between *Stachyris* and *Garrulax* in the combined analyses (Fig. 2) is supported in only one of the gene trees (ODC: Fig. 4b).

In two cases, conflicts pertain to comparably strongly supported relationships in the different gene trees. The first case relates to the placement of *Eremomela* relative to the cisticolids *Apalis* and *Prinia*. In both the myoglobin (Fig. 4a) and ODC (Fig. 4b) gene trees *Eremomela* is placed as the sister of *Apalis*, (myoglobin: PP = 1.00, ML and MP bootstrap = 100%; ODC: PP = 0.81, ML bootstrap = 55%, MP bootstrap = 77%), which is in agreement with the combined analysis (Fig. 2). However, in the β -fibrinogen gene tree *Eremomela* is placed as the sister of *Prinia* (PP = 1.00, ML bootstrap = 96%, MP bootstrap = 92%), and *Apalis* is placed as sister of these two taxa (Fig. 4c). Secondly, in the myoglobin (Fig. 4a) and β -fibrinogen gene trees (Fig. 4c), *Hartertula* is placed as the sister of *Thamnornis* (PP = 1.00 in both gene trees, ML bootstrap = 100% in both gene trees, MP bootstrap = 91% and 100%, respectively), whereas in the ODC gene tree *Hartertula* is placed as sister to the *Xanthomixis* species in the Bayesian and ML analyses of ODC (PP = 0.98, ML bootstrap = 62%, MP bootstrap < 50%) with *Thamnornis* basal relative to the above taxa.

3.3. Phylogenetically informative “indels”

Excluding singletons and indels only found in single taxa, approximately 40 indel events were identified in the concatenated data. Most of these indels give further support to already well established groups in the phylogeny, for instance the two representatives of Hirundinidae (*Hirundo* and *Delichon*) share several indels, as do the two representatives of Alaudidae (*Alauda* and *Chersomanes*), and also the two species of *Regulus* included in our study. Mapped onto the phylogeny in Fig. 2 various indel events support the clades referred to as Megaluridae, Aegithalidae, Cettiidae, Acrocephalidae, as well as Sylvioidea (sensu stricto) and Passeroidea. Other groups supported by indels include *Troglodytes*

and *Polioptila*, *Sylvia*, *Lioptilus* and *Pseudoalcippe*, *Ptyrticus*, and *Illadopsis*, as well as *Auriparus* and *Remiz*. In some cases, indels give additional support to more controversial groupings, such as a deletion of nine bp in intron 6 of the ODC gene of Cettiidae and *Erythrocercus* and an insertion of 6 bp in the same intron in Alaudidae and *Panurus*. *Amaurocichla* and *Motacilla* share two indels; a deletion of 14 bp in myoglobin intron 2 and an insertion of 625 bp in ODC intron 6. *Arcanator* and *Kakamega* share a comparably large deletion of 279 bp in the β -fibrinogen gene. Within Certhioidea, *Sitta*, *Polioptila*, *Troglodytes*, and *Salpornis* share a unique insertion of 4 bp in β -fibrinogen that is not found in *Certhia* or in any other of the species included in this study. A few indels do not corroborate the indicated phylogeny in Fig. 2. For instance, Aegithalidae, Cettiidae, *Phylloscopus*, *Hylia*, *Erythrocercus*, Hirundinidae, and Pycnonotidae share a 4 bp deletion in myoglobin, but the group is not indicated as monophyletic in the recovered topology in Fig. 2. An additional five indel events are incongruent with the recovered topology. The first of these indels is a 2 bp deletion in the myoglobin gene found in *Certhia* as well as in the babblers *Pseudoalcippe*, *Sylvia*, and *Lioptilus*. The next two apparently non-homologous indels are found in ODC intron 7; the first of these are found in *Bombycilla*, *Salpornis*, *Dicaeum*, *Irena*, and *Promerops*, the second in the representatives of Muscicapoidae, *Leptopoecile*, *Stenostira*, and *Modulatrix*. Both these indel events in ODC are deletions, 3 and 17 bp long, respectively. However, these two cases represent two of the very few instances where the placement of the indel is ambiguous, and in both cases there are two alternative placements for the deletions relative to the other sequences. The last two of the apparently non-homologous indels are found in β -fibrinogen. The first of these is a deletion of 9 bp in *Chersomanes* (but not *Alauda*) and *Eremomela*, whereas the second, a deletion of 10 bp would support a sister-group relationship between *Eremomela* and *Prinia* to the exclusion of *Apalis*. This latter deletion is contradicted by an insertion of 14 bp in β -fibrinogen in *Eremomela* and *Apalis* (but not *Prinia*) that is congruent with the topology in Fig. 2.

4. Discussion

Although Passerida constitutes the dominant group of passerines in the northern hemisphere, the origin and early diversification of the oscine passerines in Australasia suggests that the now worldwide distributed Passerida originated from an ancestral species that dispersed from the Australasian region (Barker et al., 2002; Ericson et al., 2002a, 2003; Fuchs et al., 2006), possibly in the Eocene (Barker et al., 2004). Two alternative routes for dispersal out of the Australasian region have been suggested, one across the islands on the Sunda Shelf to Asia (Barker et al., 2004; Ericson et al., 2002a), the other across now submerged plateaus in the Indian Ocean to Africa (Fuchs et al., 2006; Jønsson and Fjeldså, 2006a).

The present-day proximity between the Australasian region and southeast Asia would seem to suggest a dispersal route over the Indo-Malayan Archipelago and subsequent colonization of the rest of the world via Asia (Barker et al., 2002, 2004; Ericson et al., 2002a, 2003). Barker et al. (2004) estimated from molecular clock analyses of RAG-1 and RAG-2 sequence data that this dispersal took place approximately 45 million years ago (mya). An alternative dispersal scenario has, however, been suggested based on the observation that several African lineages appear to have a basal position within Passerida (Fuchs et al., 2006; Jønsson and Fjeldså, 2006a) suggesting that Africa, rather than Asia, may have been the first stop for at least some lineages. At 45 mya, Australia was situated much further south than today (Hall, 2002) and a possible connection between Australia and Africa is thought to have existed

across the Indian Ocean via the now submerged Kerguelen, Crozet and Broken Ridge plateaus (Fuchs et al., 2006; Jönsson and Fjeldså, 2006a; see also Schwarz et al., 2006), although it remains uncertain to what extent these plateaus were above water at that time.

The former of these two dispersal hypotheses of the passerines thus builds on the present geographical proximity between Australia and Asia, whereas the latter is an inference from the observation that several basal Passerida lineages are represented in Africa. Both hypotheses suffer from incomplete knowledge of the basal phylogenetic relationships within the Passerida radiation. In order to discriminate between these two biogeographical hypotheses and to establish a well supported hypothesis for the world-wide expansion of passerines, it is necessary to resolve the basal relationships within the Passerida and establish the ancestral distribution of the constituent clades.

In this study, we have used sequences from three nuclear introns to examine the primary lineages within Passerida. Although the majority of the relationships recovered within the Passerida receive strong support in both the Bayesian and ML bootstrap analyses in this study (Fig. 2), some parts of the topology are characterized by short internodes and no or low statistical support. One of these parts is the basal divergences in Passerida, which in effect consists of a polytomy composed of nine clades (Bombycillidae, *Hyliota*, Muscicapoidae, Certhioidea, Sylvioidea, Paridae, *Regulus*, Stenostiridae, and Passeroidea). Even with the addition of the two nuclear protein-coding genes RAG-1 and RAG-2, as well as the mitochondrial ND2 for a subset of the taxa (Fig. 3, total 7288 bp), basal relationships remain uncertain. However, both the Bayesian and maximum likelihood analyses of this ~7.2 KB data set identify two clades with strong support (PP = 1.0, ML bootstrap = 98%); one containing Certhioidea and Muscicapoidae, the other containing Sylvioidea, Stenostiridae, and Parinae/Remizinae.

4.1. Bombycillidae

The Bombycillidae, a species poor group whose phylogenetic placement relative to other groups of passerines has remained problematic (reviewed in Sibley and Ahlquist, 1990). In addition to the waxwings (*Bombycilla*) included in this study, this group also contains the Palmchat (*Dulus dominicus*), silky-flycatchers (*Ptilonys*, *Phainopepla*, and *Phainoptila*) (Sibley and Monroe, 1990), and possibly the Grey Hypocolius (*Hypocolius ampelinus*), which has often been associated with this group based on plumage patterns and behavior (Porter and Aspinall, 2005). The UPGMA clustering of DNA–DNA hybridization data (Sibley and Ahlquist, 1990) suggested a sister-group relationship between Bombycillidae and Muscicapoidae (*sensu stricto*), but with ambiguous support (Sibley and Ahlquist, 1990, p. 630). In DNA sequence-based studies (Barker et al., 2002, 2004; Beresford et al., 2005; Cibois and Cracraft, 2004; Ericson and Johansson, 2003; Fuchs et al., 2006; Voelker and Spellman, 2004) the placement of Bombycillidae as the sister-group of Muscicapoidae has remained unresolved, although at least two studies have indicated a putative relationship between these two clades (Barker et al., 2004; Beresford et al., 2005; see also Jönsson and Fjeldså, 2006b).

4.2. *Regulus* and *Hyliota*

The placement of the kinglets (*Regulus*) remains unresolved in both the three- and six-gene analyses. Traditionally, kinglets have been associated with various groups of warblers that today are considered part of the Sylvioidea radiation. Recent molecular studies have not been able to confirm such an association, and the kinglets constantly fall outside the Sylvioidea in an unresolved position relative to other clades in the Passerida (Alström et al., 2006; Barker 2004). The African *Hyliotas* (*Hyliota*) are usually associated

with warbler-like birds currently placed in Sylvioidea, but affinities with flycatchers and bushshrikes have been suggested (see Fuchs et al., 2006). Although the exact phylogenetic position of the *hyliotas* remains unresolved (Fig. 2), this study supports the result of Fuchs et al. (2006) by placing the *hyliotas* outside the Sylvioidea radiation although within Passerida.

4.3. Muscicapoidae

Within Muscicapoidae the thrushes (Turdinae) and Old World flycatchers (Muscicapinae) are placed as sister-groups, as are starlings (Sturnini) and mimids (Mimini), and both clades are recovered with high posterior probabilities (1.0) and bootstrap support (ML and MP 100%) in our analyses. Both these sister-group relationships have been supported in other molecular analyses, including DNA–DNA hybridization data (Sibley and Ahlquist, 1990) and DNA sequence-based studies (Barker et al., 2004; Cibois and Cracraft, 2004; but see Voelker and Spellman, 2004). The placement of the dippers (*Cinclus*) relative to the above mentioned clades remain unresolved (Fig. 2). Previous studies (Cibois and Cracraft, 2004; Sibley and Ahlquist, 1990; Voelker and Spellman, 2004) have yielded incongruent results regarding the phylogenetic position of *Cinclus* within the Muscicapoidae and the indicated position of the dippers as the sister taxon of the thrushes and flycatchers by the combined three-gene analysis in this study has weak support (Fig. 2). However, the addition of RAG-1, RAG-2, and ND2 sequence data seems to strengthen this hypothesis, as an association with the thrushes (no representative of Muscicapinae was included) is strongly supported by the Bayesian, likelihood and parsimony analyses (Fig. 3).

Recent molecular studies have revealed that Muscicapinae and Turdinae (as circumscribed in Sibley and Monroe, 1990) are not monophyletic (Voelker and Spellman, 2004). Furthermore the Sturnini apparently includes the Philippine creepers (*Rhabdornis*), but not the oxpeckers (*Buphagus*) (Cibois and Cracraft, 2004; Lovette and Rubenstein, 2007; Zuccon et al., 2006); the latter forming a basal branch relative to the starling/mimid clade.

4.4. Certhioidea

This clade is strongly supported by the Bayesian and maximum likelihood analyses of the combined data set (PP = 1.0, ML bootstrap = 83%) and is recovered in two of the three individual gene trees (myoglobin and ODC). The parsimony analyses and the Bayesian analysis of the β -fibrinogen intron do not contradict this association, but in these analyses *Certhia* is placed as unresolved relative to the other taxa. There is strong support in all data partitions for a sister-group relationships between the gnatcatchers (Poliophtilinae) and wrens (Troglodytinae). Furthermore, the placement of the Spotted Creeper (*S. spilonotus*) within Certhioidea is strongly supported by both the Bayesian and parsimony analyses, but its inter-relationship with the tree-creepers (Certhiini) and nuthatches (Sittinae) is uncertain. However, the position of *Salpornis* within Certhioidea differs between the analytical methods, but in none of the analyses is *Salpornis* placed as sister to the tree-creepers (Certhiinae) as traditionally assumed (Greenway, 1967). In the Bayesian and MP analyses of the combined three-gene data set *Salpornis* is placed as the sister-group of the nuthatches (Sittidae), whereas the ML analysis place it as the sister of the *Sitta* and the gnatcatcher/wren clade, although support for either arrangement is low (PP = 0.76, MP bootstrap = 70%, ML bootstrap = 54%). There is also some disagreement among the different gene trees for the placement of *Salpornis*. Both the ODC and β -fibrinogen support the placement of *Salpornis* as sister to *Sitta* with no statistical support (PP = 0.78 and 0.69, respectively), whereas there is relative strong support in the myoglobin data set for plac-

ing *Salpornis* with the tree-creepers (PP = 0.98, MP bootstrap = 68%). Interestingly, *Salpornis* shares with *Sitta*, *Poliophtila* and *Troglodytes* a unique insertion of 4 bp in β -fibrinogen that is not found in *Certhia* or in any of the other species included in this study, corroborating the topology in Fig. 2. The DNA–DNA hybridization study by Sibley and Ahlquist (1990) placed the Spotted Creeper with the tree-creepers in agreement with previous classifications and external morphology. However, in their hybridization experiments that used *Salpornis* as a tracer they included only a tree-creeper (*C. familiaris*) and no representative of the nuthatches for comparison (Sibley and Ahlquist, 1990, Fig. 269).

4.5. Passeroidea

In agreement with Barker et al. (2004), our data support the inclusion of the Dapple-throat (*A. orostruthus*) and Spot-throat (*M. stictigula*) from the Eastern Arc Mountains of Tanzania as a basal clade within Passeroidea. In addition to these two species our data also support the suggestion by Jensen and Brøgger-Jensen (1992) that the Grey-chested Babbler (*K. poliothorax*) from the Central African and Cameroon montane forests may be part of this assemblage. *Kakamega* is placed as the sister-group of *Arcanator* in our analyses (Fig. 2), which is further supported by a shared deletion of approximately 300 bp in the β -fibrinogen gene in the two species. Our data also indicate a basal position of the sugarbirds (*Promerops*) relative to all other passeroids, challenging the topological arrangements suggested by Barker et al. (2004), in which this taxon is placed as the sister of the *Arcanator*/*Modulatrix* clade, and by Sibley and Ahlquist (1990), in which *Promerops* is placed with the sunbird/spiderhunter/flowerpecker clade (Nectariniinae). All these groups, as well as the fairy bluebirds (*Irena*) and leafbirds (*Chloropsis*), constitute basal branches within Passeroidea (see also Barker et al., 2004). Interestingly, all these basal lineages are slender-billed nectarivores or insectivores, morphologically similar to certain sylvioid groups. Even the accentors (*Prunella*), which apparently form a basal clade in the “core Passeroidea”, have slender bills. However, within “core Passeroidea”, most other species, with some exceptions, have finch and sparrow-like bill morphology, associated with a shift to a primarily granivorous diet. The recovered topology within the “core Passeroidea” in our combined three-gene analysis (Fig. 2) is identical to the topology recovered by Barker et al. (2004).

Surprisingly, the Sao Tomé Short-tail (*A. bocagii*; two individuals sequenced) appears to be associated with the Motacillidae (here represented by *M. alba*) with strong support in all gene trees. This species has been placed as an aberrant member of the longbills (*Macrosphenus*) in Sylvioidea, but its phylogenetic association with this group has been uncertain. This rather poorly known species is endemic to Sao Tomé Island on the West African coast and is restricted to forest streams on the island. It is a nondescript bird with a long thin bill and short abraded tail. The apparent close relationship between *Amaurocichla* and *Motacilla* is unexpected as *Amaurocichla* is morphologically very similar to the African Longbills, albeit smaller, and bears little resemblance to other members of the Motacillidae although in conformity with these it is mainly terrestrial and is usually described as having a typical pipit-like gait (Urban et al., 1997).

4.6. Sylvioidea (sensu stricto)

The monophyly of this clade is strongly supported (PP = 1.00, ML bootstrap = 98%, MP bootstrap = 79%) and the topology is in general agreement with the results of Beresford et al. (2005) based on RAG-1 and RAG-2 sequences. Larks are placed as the most basal branch in both studies, a position also recovered by Fuchs et al. (2006) and Alström et al. (2006). In agreement with the latter

two studies, the Bearded Reedling (*P. biarmicus*) is placed as the sister clade of the lark radiation, a position which is further supported by a shared insertion of 5 bp in intron 6 of ODC in these two groups. The position of the nicator (*Nicator*) as the next branch in the tree (Fig. 2) is also in agreement with the results of Beresford et al. (2005), although we have no statistical support for this relationship in our study (PP = 0.54), and in essence the nicators form a basal trichotomy with the larks/Bearded Reedling clade and the remaining sylvioids. Within the remaining sylvioids, the earliest split separates the “*Sphenoecus*-group” from the other sylvioids, in agreement with the results of Beresford et al. (2005), although levels of support remain weak. Nevertheless, despite the poor support for the early branching within Sylvioidea, the congruence between the topology recovered in this study and that recovered in the study by Beresford et al. (2005) based on independent nuclear DNA data sets, does lend stronger support to this hypothesis.

The “*Sphenoecus*-group” is seemingly an all-African radiation and consists of at least the African crombecs (*Sylvietta*), longbills (*Macrosphenus*), Victorin’s Scrub-Warbler (*B. victorini*), the Grassbird (*S. afer*) and the Rockrunner (*A. pycnopygius*) (Beresford et al., 2005), and possibly also the Moustached Grass Warbler (*Melocichla mentalis*, Alström et al., 2006, their clade B).

The remaining part of the sylvioid clade, “core Sylvioidea”, is composed of species included in the “families” Hirundinidae, Pycnonotidae, Cisticolidae, Aegithalidae, Sylviidae, and Zosteropidae in Sibley and Monroe (1990). However, in agreement with several other recent sequence-based studies (e.g. Alström et al., 2006; Beresford et al., 2005; Fuchs et al., 2006) our data suggest that this classification, and the phylogeny based on DNA–DNA hybridization data (Sibley and Ahlquist, 1990) underlying this classification may not reflect the phylogenetic relationships within this complex. In particular, Sylviidae (sensu Sibley and Monroe, 1990) appears to be composed of several distantly related groups that are nested among the other clades. Our results are more in line with the proposed classification by Alström et al. (2006), although the indicated inter-relationships between these clades do in some cases differ. In the following discussion, we generally follow the classification of Alström et al. (2006), but also identify some additional clades not indicated in their study (Fig. 2).

Taxonomic delimitation of clades in the “core Sylvioidea” remains poorly understood. At present only Hirundinidae appears to be a well supported monophyletic clade (Mayr, 1958; Sheldon et al., 2005), although recent studies have reduced the numbers of species with uncertain affinities. For instance, several taxa previously placed among the bulbuls, e.g. *Nicator*, the Malagasy tetrakas (formerly *Phyllastrephus*, but now *Bernieria* and *Xanthomixis*), *Tylas vanga* (*Tylas eduardi*), and the Dapple-throat (*A. orostruthus*) have been shown to fall outside the Sylvioidea (Barker et al., 2004; Beresford et al., 2005; Cibois et al., 2001; Schulenberg, 1993; Yamagishi et al., 2001, see also Fig. 2). Further, our data suggests that the Blackcap Mountain-babbler (*L. nigricapillus*) is not related to bulbuls (contra Fry et al., 2000), but is instead a babbler (Fig. 2). Within the Pycnonotidae, the phylogenetic affinities of the Malia (*Malia grata*) and the Black-collared Bulbul (*Neolestes*), often associated with the bulbul radiation (e.g. Sibley and Monroe, 1990), still need to be verified. Recent studies (Alström et al., 2006; Beresford et al., 2005; Nguembock et al., 2007; Sefc et al., 2003; Sibley and Monroe, 1990) have also led to a better understanding of the Cisticolidae, although the boundaries of this clade remain uncertain as only a few taxa potentially associated with that group have been included in phylogenetic studies. For example, our study suggests that the Eremomelas (*Eremomela*) are part of the cisticolid radiation.

Megaluridae (sensu Alström et al., 2006) includes at least members of the genera *Megalurus*, *Bradypterus* (excluding *B. victorini*),

and *Locustella*, and our study also supports the inclusion of the Malagasy Emu-tail (*D. brunneus*) in this clade. The Megaluridae may also include the *Schoenicola* grassbirds and Australian song-larks *Cinchoramphus* (see Beresford et al., 2005). Another clade, apparently closely related to Megaluridae, is Acrocephalidae (Fig. 2, see also Alström et al., 2006; Beresford et al., 2005) and our study strongly supports the inclusion of another endemic Malagasy warbler, the Tsikiry (*N. typica*), within the Acrocephalidae. Associated with Megaluridae and Acrocephalidae is another endemic Malagasy radiation, Bernieridae, here represented by *X. tenebrosus*, *X. zosterops*, *T. chloropetoides*, and *H. flavoviridis*. In addition, this clade also includes *Cryptosylvicola randrianasoloi*, *Crossleyia xanthophrys*, *Oxylabes madagascariensis*, *Berniera madagascariensis*, *Xanthomixis apperti*, and *X. cinereiceps* (Cibois et al., 1999, 2001). Bernieridae is placed with strong support together with the megalurine warblers and the Black-capped Donacobius, although the sister-group relationship between the Black-capped Donacobius and Bernieridae is only weakly supported. It should be noted that our study did not include the many Indopacific taxa possibly associated with the megalurine and acrocephaline warblers.

In agreement with Alström et al. (2006), our study supports the inclusion of the tit-warblers (*Leptopoecile*) within Aegithalidae (see also Dickinson, 2003). In addition, Aegithalidae appears to be associated with *Cettia* warblers (Cettiidae sensu Alström et al., 2006), the Green Hylia (*H. prasina*), Chestnut-capped Flycatcher (*E. mccallii*) and *Phylloscopus* warblers. Although only recovered with little to no support (PP = 0.90, ML bootstrap = 81%, MP bootstrap = 53%), a similar clade was also recovered in the studies by Beresford et al. (2005) and Alström et al. (2006), although differences in taxon sampling do not make the studies fully comparable. All three studies do agree on the association of Aegithalidae with the *Cettia* warblers, and Beresford et al. (2005) also placed *Hylia* within this clade. However, in their tree, *Phylloscopus* is placed in an unresolved position relative to these other taxa and other sylvioid lineages. Alström et al. (2006) did not include *Hylia* in their analysis, but with weak support, *Phylloscopus* was associated with Aegithalidae and Cettiidae. Included with *Phylloscopus* were also the *Seicercus* warblers and Alström et al. (2006) proposed the name Phylloscopidae for this clade. The circumscribed taxonomic composition of Phylloscopidae sensu Alström et al. (2006) differs from the Phylloscopinae delimited by Dickinson (2003), which also included *Tickellia*, *Sylvietta*, *Abrascopus*, *Eremomela*, and *Graueria*. Our results confirm the findings of Alström et al. (2006) in that *Tickellia*, *Sylvietta*, and *Abrascopus*, are not closely related to *Phylloscopus*, and we demonstrate in this study that *Eremomela* is part of the Cisticolidae. In the myoglobin gene tree (Fig. 4A), *Hylia* is recovered as the sister-group of *Phylloscopus* (Phylloscopidae). This association is not recovered in any other of the gene trees and is only recovered with low support by the parsimony analysis of the combined data set (bootstrap = 62%).

The Chestnut-capped Flycatcher (*E. mccallii*), which has previously been associated with the Monarchine flycatchers (Sibley and Monroe, 1990; Watson et al., 1986a) and recently suggested to have a sylvioid affinity (Pasquet et al., 2002), is found to be associated with the *Cettia* warblers (Cettiidae) and long-tailed tits (Aegithalidae), although the exact position within this group is unresolved. This clade may also include the Tit-Hylia (*Pholidornis rufiae*), which was suggested to be closely related to the Green Hylia (Sefc et al., 2003). This clade also includes the Asian Mountain Tailorbird (*Orthotomus cucullatus*) (Fuchs et al. 2006).

The taxonomic delimitation of the babbler clade has historically been difficult and recent molecular findings have suggested that several taxa previously placed among the babblers, for example: *Oxylabes*, *Crossleyia*, *Mystacornis*, *Neomixis*, *Hartertula*, *Erpornis*, *Rhabdornis*, *Pteruthius*, *Arcanator*, and *Modulatrix* are part of other

avian radiations (e.g. Barker et al., 2004; Cibois, 2003; Cibois and Cracraft, 2004; Cibois et al., 1999, 2001; Reddy and Cracraft, 2007; Sibley and Ahlquist, 1990). The placement of the *Sylvia* warblers and the wren-tit (*Chamaea fasciata*) among the babblers, as first suggested by Sibley and Ahlquist (1990), has been confirmed in several studies (e.g. Barhoum and Burns, 2002; Cibois, 2003), but these studies also suggest that the white-eyes (Zosteropidae) and laughing-thrushes (*Garrulax* and *Liocichla*) are nested within the babbler radiation, contrary to the findings of Sibley and Ahlquist (1990). In addition, it has recently been suggested that the Rufous-rumped Grassbird (*Graminicola bengalensis*) and White-browed Chinese Warbler (*Rhopophilus pekinensis*) are part of the babbler radiation (Alström et al., 2006).

Our study confirm the findings of Barker et al (2004) and places the Dapple-throat (*A. orostruthus*) and Spot-throat (*M. stictigula*) within the Passeroidea along with another presumed babbler, the Grey-chested Babbler (*K. poliothorax*) (Fig. 2). However, the Spotted Thrush Babbler (*P. turdinus*), rather similar to *Arcanator* by plumage pattern, is a babbler, placed near *Illadopsis*. The Bush Blackcap (*L. nigricapillus*), whose systematic position among babblers have been disputed because of its behavior, ecology and bulbul-like shape is also placed within the babblers, close to the African Hill Babbler (*P. abyssinica*) and the *Sylvia* “warblers”.

The Bayesian analyses place Timaliidae together with Aegithalidae, Cettiidae, Phylloscopidae, the Green Hylia (*H. prasina*) and Chestnut-capped Flycatcher (*E. mccallii*) (clade “I”, Fig. 2). This placement of the babblers is strongly supported by the Bayesian analysis (PP = 1.00) and receives moderate support in the bootstrap analyses (ML bootstrap = 81%; MP bootstrap = 59%) and is not supported in the studies of Beresford et al. (2005) and Alström et al. (2006). In addition, a deletion of 4 bp in intron 2 of the myoglobin gene in *Phylloscopus*, *Hylia*, *Erythrocerus*, Cettiidae, Aegithalidae, Hirundinidae, and Pycnonotidae, but not in the Timaliidae, suggests an alternative association (as noted by Alström et al., 2006, though *Hylia* and *Erythrocerus* were not studied). Whether this deletion is homologous in these taxa is difficult to evaluate, for instance, a 3 bp deletion in the same region in *Eremomela* (placed in the Cisticolidae in our study) suggests that this could be a labile region, but the taxonomic distribution of this deletion is congruent with the topology recovered by Alström et al. (2006) based on myoglobin intron 2 and cytochrome b (see also Fig. 4A).

4.7. Delimitation of Passerida

With the recent updates of taxonomic composition (Table 1 and 2), the circumscription of Passerida appears rather well-defined. However, two clades not included in the Passerida of Sibley and Monroe (1990), but tentatively associated with this group in some recent studies (e.g. Barker et al., 2004; Beresford et al., 2005; Ericson and Johansson, 2003) are the Picathartidae and Petroicidae (Eopsaltridae sensu Sibley and Monroe 1990, but see Bock, 1994). The existence of Picathartidae as a deep lineage was first suggested based on DNA–DNA hybridization data (Sibley and Ahlquist, 1990) and was proposed to include the rock-jumpers (*C. frenatus* and *Chaetops aurantius*) and rock-fowl (*Picathartes gymnocephalus* and *P. oreas*). The clade could; however, not be placed relative to other passerine groups by the DNA–DNA hybridization data and was omitted from the UPGMA tree. Later studies have confirmed a close relationship between the rock-jumpers of southern Africa and the rock-fowl of West Africa (Barker et al., 2004; Ericson and Johansson, 2003), but also the Malaysian Railbabbler (*Eupetes macrocerus*) has recently been suggested to be part of this clade (Jönsson et al., 2007). Based on sequences from four genes (c-myc, RAG-1, myoglobin intron 2, and cytochrome b), Ericson and Johansson (2003) placed the Picathartidae as the sister-group of Passerida, and Petroicidae basal relative to these groups. This position of Picathartidae

was also supported by a one codon insertion in the *c-myc* gene present in Passerida and Picathartidae, but not in Petroicidae or any other passerine examined (Ericson and Johansson, 2003). Contrary to these findings, Barker et al (2004) suggest a sister-group relationship between Passerida and Petroicidae to the exclusion of Picathartidae (analyses based on RAG-1 and RAG-2 sequences; but see Irestedt and Ohlson 2008).

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