



Phylogeny and classification of the avian superfamily Sylvioidea

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Abstract

Sylvioidea is one of the three superfamilies recognized within the largest avian radiation, the parvorder Passerida. In the present study, which is the first taxon-dense analysis of the Sylvioidea based on sequence data (nuclear myoglobin intron II and mitochondrial cytochrome *b* gene), we investigate the interrelationships among the four “sylviooid” clades found by previous workers, as well as the relationships within the largest of these clades. The nuclear and mitochondrial loci estimate basically the same phylogeny, with minor differences in resolution. The trees based on myoglobin and the combined data identify a strongly supported clade that includes the taxa previously allocated to Sylvioidea, except for *Sitta* (nuthatches), *Certhia* (treecreepers), *Parus* (tits), *Remiz* (penduline tits), *Troglodytes* and *Campylorhynchus* (wrens), *Polioptila* (gnatcatchers), and *Regulus* (crests/kinglets); this clade also comprises larks, which have previously been placed in the superfamily Passeroidea. We refer to this clade as Sylvioidea. This clade is further divided into 10 main, well-supported clades, which we suggest form the basis for a revised classification.

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1. Introduction

Molecular data suggest that the oscine passerines had their early evolution in the Australo-Papuan region, from where several groups later dispersed (Barker et al., 2002, 2004; Ericson et al., 2002). Although it seems likely that the group had already evolved by the early Tertiary, dispersal to the Southeast Asian islands and mainland may not have been possible before the Australo-Papuan tectonic plate and smaller terranes in the Indonesian-Philippine region came close to the Eurasian plate, possibly in the late Oligocene and Miocene (Ericson et al., 2003; Hall and Holloway, 1998). The most successful species in the Australo-Papuan region, in terms of num-

ber of descendant species, gave rise to the Passerida sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990), a group that today contains ~75% of all oscine passerine species. Today, members of Passerida occupy all available habitats of the world and inhabit all continents except mainland Antarctica. It is assumed that their ancestor was insectivorous, but a great variety of other feeding specializations took place, and the group now includes a broad diversity of granivores, frugivores, omnivores, and nectar-feeders. The phylogenetic relationships within Passerida have proven difficult to disentangle, possibly due to several cases of rapid radiations within the group. Moreover, widespread and frequent convergences in feeding and locomotory morphology and anatomy have often misled systematists relying on external and internal characters, and the “warbler type,” characterized by a fine pointed bill and a simple arrangement of jaw muscles (Beecher, 1953) cause particular

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problems, as this adaptive type may have been retained, or evolved independently, in several lineages. Genetic analysis has revealed several cases of convergent evolution (e.g., Cibois, 2003a; Cibois et al., 1999; Fjeldså et al., 2003; James et al., 2003; Sibley and Ahlquist, 1990).

From their analyses of DNA–DNA hybridization data, Sibley and Ahlquist (1990) recognized three superfamilies in the parvorder Passerida: Muscipoidea (e.g., waxwings, dippers, thrushes, Old World flycatchers, starlings, and mockingbirds), Sylvioidea (e.g., nuthatches, treecreepers, tits, wrens, crests/kinglets, swallows, bulbuls, babblers, and warblers; Fig. 1 and Table 1), and Passeroidea (e.g., larks, pipits, wagtails, waxbills, weavers, finches, sparrows, cardinals, tanagers, wood-warblers, and icterids). Subsequent studies of DNA sequence data have indicated that both Muscipoidea and Passeroidea, after minor taxonomic adjustments, can be recovered as monophyletic (Barker et al., 2004; Beresford et al., 2005; Cibois and Cracraft, 2004; Ericson and Johansson, 2003; Voelker and Spellman, 2003). However, no subsequent study has suggested monophyly of Sylvioidea sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990).

Few molecular studies have been designed explicitly to investigate higher-level relationships among purportedly sylvioid groups. Exceptions are the studies of babblers by Cibois (2003a) and Malagasy warblers by Cibois et al. (1999), and the more general studies of Barker et al. (2002, 2004), Beresford et al. (2005), Chikuni et al. (1996), Ericson and Johansson (2003), Honda and Yamagishi (2000), and Spicer and Dunipace (2004), all based on DNA sequence data, and the DNA–DNA hybridization studies by Sheldon and Gill (1996). The picture emerging from these studies is that the taxa placed in Sylvioidea by Sibley and Ahlquist (1990) and Sibley and Monroe (1990) fall into four main clades: (1) a “tit–penduline tit clade”; (2) a large and complex “Old World warbler–bulbul–babbler–swallow clade” (containing more than five times as many species as the three others put together); (3) a “nuthatch–tree creeper–gnatcatcher–wren clade”; (4) a “crest/kinglet clade.” Cracraft et al. (2004) termed the third of these clades Certhioidea. The larks, placed in Passeroidea by Sibley and Ahlquist (1990) and Sibley and Monroe (1990), are also “sylvioid” and fall into clade 2. As yet, no study has conclusively resolved the interrelationships between the four “sylvioid” clades.

In their pioneering work on guidelines for a phylogenetic taxonomy, de Queiroz and Gauthier (1990, 1992) took the position that clade names can and should be defined, i.e., a phylogenetic system of definition (PSD). This was subsequently formalized in the PhyloCode, Article 9.4 (Cantino and de Queiroz, 2004). However, phylogenetic studies often differ markedly in taxon sampling, potentially making clade names difficult to compare between studies. As an alternative to the PSD, Härlin (1998) introduced a phylogenetic system of reference (PSR) for naming clades. He argued that a PSD is

not suitable for a historical science based on hypotheses subject to change, and concluded that clades should be *referred to*, not *defined*. Taxon names denote historical individuals, having neither an intension nor a meaning, and the only way to connect a name to an individual is by fixing the reference ostensibly (by pointing it out), an act not considered a definition by Härlin. Furthermore, the assumption that names can be defined, and thus have intension, runs counter to the goal that primacy should be given to naming clades rather than defining names (de Queiroz, 1994). Härlin further argues that definitions suffer from effects such as referring to whatever fits the description, leading to a situation where it is only within the original hypothesis that the taxon name necessarily reflects the views of the systematist. In a system of definition, taxon names, rather than the systematist, determine which part of a tree a name will refer to in an alternative interpretation of the phylogeny. Names can easily lose their intended meaning if a hypothesis changes, potentially giving rise to a plethora of homonyms and synonyms. In contrast, a PSR leaves the door open to modifications of precisely what a name refers to when another than the initial phylogenetic hypothesis is chosen. The use of specifiers is rejected and the entire clade, as presented in a figure, serves as reference to what a name denotes. This favors nomenclatural stability and ensures that the names refer to meaningful natural groups, also within changing hypotheses.

In the present study, we investigate higher-level relationships among the four major “sylvioid” clades by analyzing DNA sequence data obtained from the nuclear myoglobin intron II and mitochondrial cytochrome *b* genes, in total ~1.8kb, for 83 “sylvioid” species. In this first taxon-dense, comprehensive study of “sylvioids” based on sequence data, we also aim to formulate a detailed phylogenetic hypothesis for the largest of the “sylvioid” clades, namely the one comprising the babblers, white-eyes, Old World warblers, bulbuls, swallows, long-tailed tits, and larks (equal to clade B of Ericson and Johansson, 2003), and propose family names under a phylogenetic system of reference (Härlin, 1998; Härlin and Sundberg, 1998).

2. Materials and methods

2.1. Study group

We obtained tissue, blood, and/or feathers from live individuals of representatives for as many different genera as possible within Sylvioidea sensu Sibley and Monroe (1990) (Appendix A). Whenever possible, we included the type species for a genus, as well as samples from main clades discovered in previous intrageneric studies. We used sequences obtained by Ericson and Johansson (2003) for most of the outgroup taxa, which

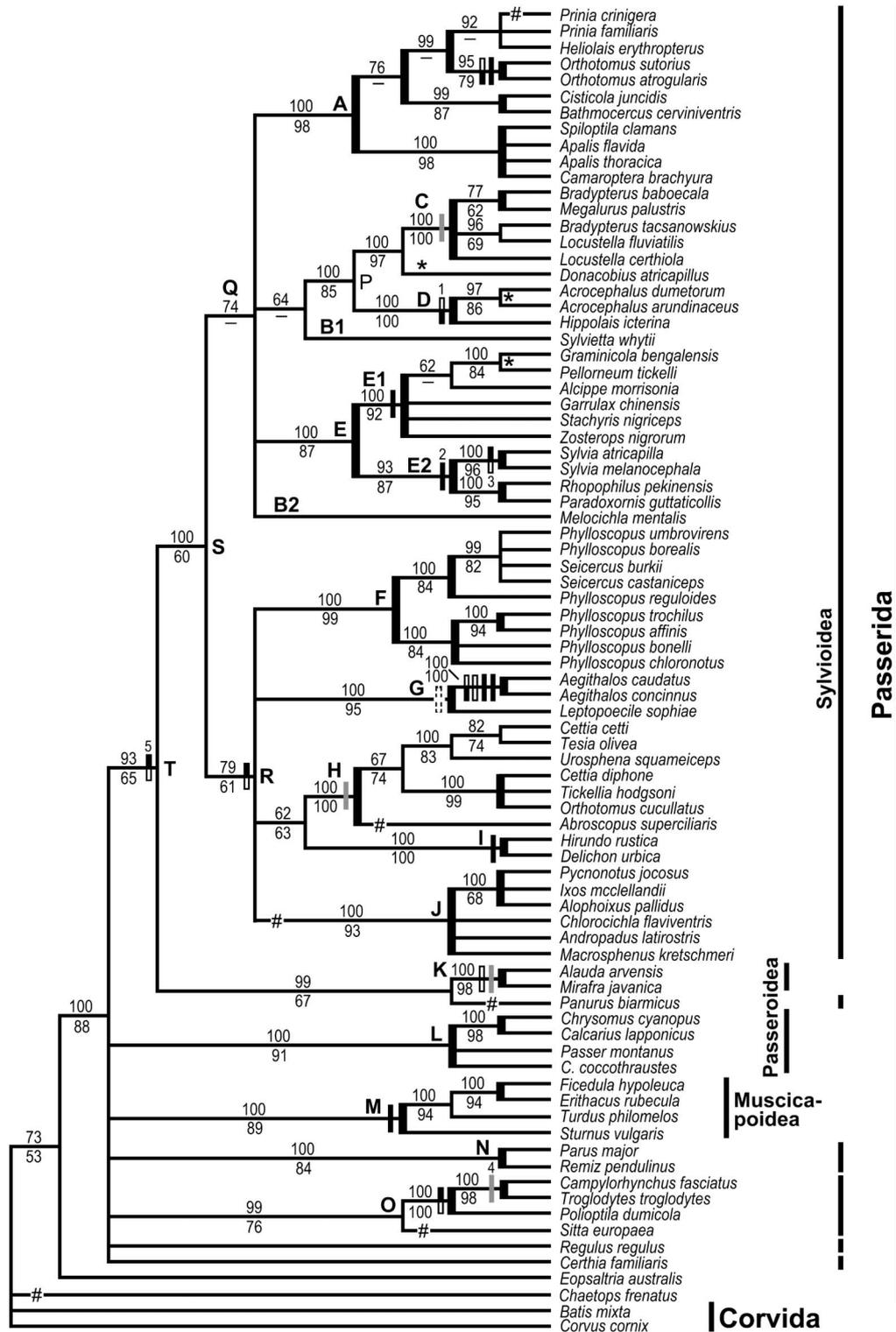


Fig. 1. Relationships among taxa in the superfamily Sylvioidea sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990) and representatives of other main clades within Passerida found in previous studies, rooted by *Corvus* and *Batis*. Estimated by Bayesian analysis of myoglobin intron II sequences (791 bp) under the GTR + Γ model. Posterior probabilities ($\geq 50\%$; 195,000 trees) are indicated above the nodes and parsimony bootstrap values ($\geq 50\%$; 1000 replicates) below the nodes. Synapomorphic indels are indicated by vertical bars: black: 1 bp deletion; black upper half: 2–5 bp deletion; black lower half: 6–9 bp deletion; grey: ≥ 10 bp deletion; unfilled: 1 bp insertion; dashed: 14 bp insertion. All of these indels have a consistency index of 1, except for the ones labeled 1 (also in *Graminicola*), 2 (also in *Andropadus*), 3 (also in *Spiloptila*, *Certhia*), 4 (also in *Sturnus*), and 5 (also shared by *Chaetops*). Clades that agree with the cytochrome *b* tree (Fig. 2) have bold highlights, while incongruent relationships are marked by * ($\geq 95\%$ posterior probabilities and/or $\geq 75\%$ parsimony bootstrap support in both trees) or # (lower support values). The letters denote clades that are discussed in the text.

Table 1

Comparison between the systematics of Sibley and Ahlquist (1990, S&A) and Sibley and Monroe (1990, S&M) (left column) and the results from the present study (right column)

Superfamily Sylvioidea sensu Sibley and Ahlquist (1990), Sibley and Monroe (1990)	Present study
Family Sittidae <i>Sitta</i> * (1)	No support for inclusion in Sylvioidea; part of clade also comprising <i>Troglodytes</i> , <i>Campylorhynchus</i> , <i>Polioptila</i> and <i>Certhia</i> (clade O)
Family Certhiidae Subfamily Certhiinae <i>Certhia</i> * (1) Subfamily Troglodytinae <i>Troglodytes</i> * (1), <i>Campylorhynchus</i> * (1), <i>Donacobius</i> * (1) Subfamily Polioptilinae <i>Polioptila</i> * (1)	No support for inclusion of <i>Certhia</i> , <i>Troglodytes</i> , <i>Campylorhynchus</i> or <i>Polioptila</i> in Sylvioidea; parts of clade also including <i>Sitta</i> (clade O). Close relationship of <i>Troglodytes</i> , <i>Campylorhynchus</i> and <i>Polioptila</i> confirmed, but <i>Donacobius</i> nested within Sylvioidea (sister to clade C/I)
Family Paridae Subfamily Remizinae <i>Remiz</i> * (1) Subfamily Parinae <i>Parus</i> * (1)	Distinctness of taxon and sister relationship between <i>Parus</i> and <i>Remiz</i> confirmed, but no support for inclusion in Sylvioidea (clade N)
Family Aegithalidae <i>Aegithalos</i> * (2)	Distinctness of taxon and inclusion in Sylvioidea confirmed (clade G), but also includes <i>Leptopoecile</i> (in Acrocephalinae according to S&M)
Family Hirundinidae Subfamily Pseudochelidoninae Subfamily Hirundininae <i>Hirundo</i> * (1), <i>Delichon</i> (1)	No taxa from Pseudochelidoninae studied. Distinctness of Hirundininae and inclusion in Sylvioidea confirmed (clade I)
Family Regulidae <i>Regulus</i> * (1)	Position uncertain, but no support for inclusion in Sylvioidea
Family Pycnonotidae <i>Pycnonotus</i> * (1), <i>Andropadus</i> (1), <i>Chlorocichla</i> * (1), <i>Alophoixus</i> (1), <i>Ixos</i> * ^a (1)	Distinctness of taxon and inclusion in Sylvioidea confirmed (clade J), but includes <i>Macrosphenus kretschmeri</i> (in Acrocephalinae according to S&M)
Family Hypocoliidae ^b	Not studied
Family Cisticolidae <i>Cisticola</i> * (1), <i>Heliolais</i> (1), <i>Rhopophilus</i> (1), <i>Prinia</i> * (2), <i>Spiloptila</i> (1), <i>Apalis</i> * (2), <i>Camaroptera</i> * (1)	Distinctness of taxon and inclusion in Sylvioidea confirmed (clade A), but also includes <i>Orthotomus sutorius</i> , <i>O. atrogularis</i> and <i>Bathmocercus</i> (in Acrocephalinae according to S&M), and excludes <i>Rhopophilus</i> (in clade E2)
Family Zosteropidae <i>Zosterops</i> * (1)	Inclusion in Sylvioidea confirmed, but no support for its recognition, since <i>Zosterops</i> is nested within clade E (Sylviinae sensu S&A and S&M)
Family Sylviidae Subfamily Acrocephalinae <i>Tesia</i> (1), <i>Urosphena</i> (1), <i>Cettia</i> (2), <i>Bradypterus</i> (2), <i>Bathmocercus</i> (1), <i>Melocichla</i> * (1), <i>Locustella</i> (2), <i>Acrocephalus</i> * (3), <i>Hippolais</i> * (1), <i>Chloropeta</i> (1), <i>Orthotomus</i> (3), <i>Sylvietta</i> * (1), <i>Macrosphenus</i> (1), <i>Leptopoecile</i> (1), <i>Phylloscopus</i> * (7), <i>Seicercus</i> * (2), <i>Tickellia</i> (1), <i>Abroscopus</i> (1)	Inclusion of Acrocephalinae in Sylvioidea confirmed, but no support for monophyly. <i>Bathmocercus</i> , <i>Orthotomus sutorius</i> , and <i>O. atrogularis</i> are in Cisticolidae (clade A), and <i>Macrosphenus kretschmeri</i> in Pycnonotidae (clade J) sensu S&A and S&M
Subfamily Megalurinae <i>Megalurus</i> * (1), <i>Graminicola</i> (1)	Inclusion of Megalurinae in Sylvioidea confirmed, but no support for the circumscription of S&A and S&M, since <i>Megalurus</i> is nested within clade C (part of Acrocephalinae sensu these authors) and <i>Graminicola</i> within clade E1 (Sylviinae sensu these authors)
Subfamily Garrulacinae <i>Garrulax</i> * (1)	Inclusion of Garrulacinae in Sylvioidea confirmed, but no support for its recognition, since <i>Garrulax</i> is nested within clade E1 (Sylviinae sensu S&A and S&M)
Subfamily Sylviinae Tribe Timaliini <i>Pellorneum</i> * (1), <i>Stachyris</i> * (1), <i>Alcippe</i> (1), <i>Panurus</i> (1), <i>Paradoxornis</i> (1)	Inclusion of Timaliini and Sylviini in Sylvioidea confirmed, but <i>Paradoxornis</i> is in Sylviini sensu S&A and S&M (clade E2), and <i>Panurus</i> is sister to clade K (Alaudidae in superfamily Passeroidea sensu S&A and S&M)
Tribe Sylviini <i>Sylvia</i> * (2)	

The genera in the left column are the ones dealt with in this study; the numbers in parentheses refer to the number of species included; an asterisk means that the genus was studied by DNA–DNA hybridization by Sibley and Ahlquist (1990).

^a *Hypsipetes* in Sibley and Ahlquist (1990) and Sibley and Monroe (1990).

^b According to Sibley and Ahlquist “The Hypocoliidae is included in the Sylvioidea, but we lack DNA of *Hypocolius* and do not know its true relationships.

represent the superfamilies Muscipoidea and Passeroidea in the parvorder Passerida sensu Sibley and Monroe (1990) and two basal taxa in the same parvorder, as well as two species from the parvorder Corvida sensu Sibley and Monroe (1990); a few cytochrome *b* sequences were obtained from GenBank (Appendix A).

2.2. DNA extraction and sequencing

Extraction, amplification, and sequencing were done in the same ways as described in Olsson et al. (in press). The sequences are deposited in GenBank (Appendix A).

2.3. Phylogenetic analyses

Sequences were easily aligned, using MegAlign 4.03 in the DNASTAR package (DNASTAR); some manual adjustment was necessary for the myoglobin intron II sequences. Molecular phylogenies were estimated by Bayesian inference using MrBayes 3.0b4 (Huelsenbeck and Ronquist, 2001, 2003). The choice of the model was determined based on the Akaike Information Criterion (Akaike, 1973) and a hierarchical likelihood ratio test (Posada and Crandall, 1998), both calculated in MrModeltest (Nylander, 2004). Posterior probabilities were calculated for myoglobin intron II and cytochrome *b*, both separately and combined. The concatenated myoglobin intron II and cytochrome *b* sequences were divided into two partitions, using rate multipliers to allow different rates for the different partitions (Nylander et al., 2004; Ronquist and Huelsenbeck, 2003). All analyses of the cytochrome *b* dataset were performed under a general time-reversible (GTR) model (Lanave et al., 1984; Rodríguez et al., 1990; Tavaré, 1986), assuming rate variation across sites according to a discrete gamma distribution with four rate categories (Γ_4 ; Yang, 1994) and an estimated proportion of invariant sites (I; Gu et al., 1995), while the myoglobin intron II dataset was analyzed under a GTR + Γ_4 model. Default priors were used. Four Metropolis-coupled MCMC chains were run for $3\text{--}5 \times 10^6$ generations and sampled every 100 generations; the temperature was set to 0.1 in some runs to improve the mixing of the chains, if that was found to be poor at the default temperature 0.2. The first 300,000 generations, before the chain reached apparent stationarity (burn-in), were discarded and the posterior probability was estimated for the remaining generations. Every analysis was repeated three to eight times, starting from random trees, and the results were compared to ascertain that the chains had reached the same target distributions (as suggested by Huelsenbeck et al., 2002). The samples from the stationary phases of the independent runs were pooled to obtain the final results.

Clade support for the unweighted dataset was also assessed by parsimony bootstrapping in PAUP* 4.08b (Swofford, 2001), under the following settings: heuristic

search strategy, starting trees obtained via random stepwise addition, 10 replicates, followed by TBR branch swapping, MulTrees option not in effect (only one tree saved per replicate), gaps treated as missing data, 1000 replicates; 26 parsimony-informative indels in the myoglobin intron II were coded as binary characters (present/absent).

3. Results

3.1. Sequence characteristics

A contiguous 673–734 bp stretch of the myoglobin gene, including the complete intron II and flanking regions of exons 2 (13 bp) and 3 (10 bp), and a 1038 bp portion of the cytochrome *b* gene were obtained for 80 taxa; for a further two, only one region was sequenced (Appendix A). The cytochrome *b* sequence was amplified as one fragment to decrease the risk of amplifying nuclear pseudocopies of the gene (e.g., Arctander, 1995; Quinn, 1997; Quinn and White, 1987; Sorensen and Quinn, 1998). No unexpected stop codons that could indicate the presence of nuclear copies are present in the cytochrome *b* sequences. The aligned myoglobin sequences comprise 791 characters, of which 285 (36%) are parsimony informative, and the aligned cytochrome *b* sequences contain 1038 characters, of which 481 (46.3%) are parsimony informative. The concatenated myoglobin intron II and cytochrome *b* dataset contains 1829 characters, of which 766 (41.9%) are parsimony informative.

A total of 63 inferred indel events were needed to satisfactorily align the myoglobin intron II sequences. A majority of the indels (63%) appeared as autapomorphic deletions of 1 or 2 bp, while 26 indels were shared by two or more taxa. Indels that support the phylogeny are marked in Fig. 1.

3.2. Phylogenetic relationships

3.2.1. Comparison of regions

The trees resulting from the separate analyses of the myoglobin intron and cytochrome *b* gene are shown in Figs. 1 and 2, respectively. The former is overall slightly less resolved than the latter (57 vs. 68% of all nodes), although it is somewhat more resolved basally. There are few topological conflicts between these trees. Only three relationships with posterior probabilities $\geq 95\%$ and/or parsimony bootstrap support $\geq 75\%$ in both the trees are incompatible (marked by * in Figs. 1 and 2). The first one refers to *Acrocephalus* and *Hippolais* (clade D). In the myoglobin tree, the two *Acrocephalus* species are sisters, while in the cytochrome *b* tree *A. dumetorum* is most closely related to *H. icterina*. The support is higher for the first topology. The second case concerns *Donacobius*,

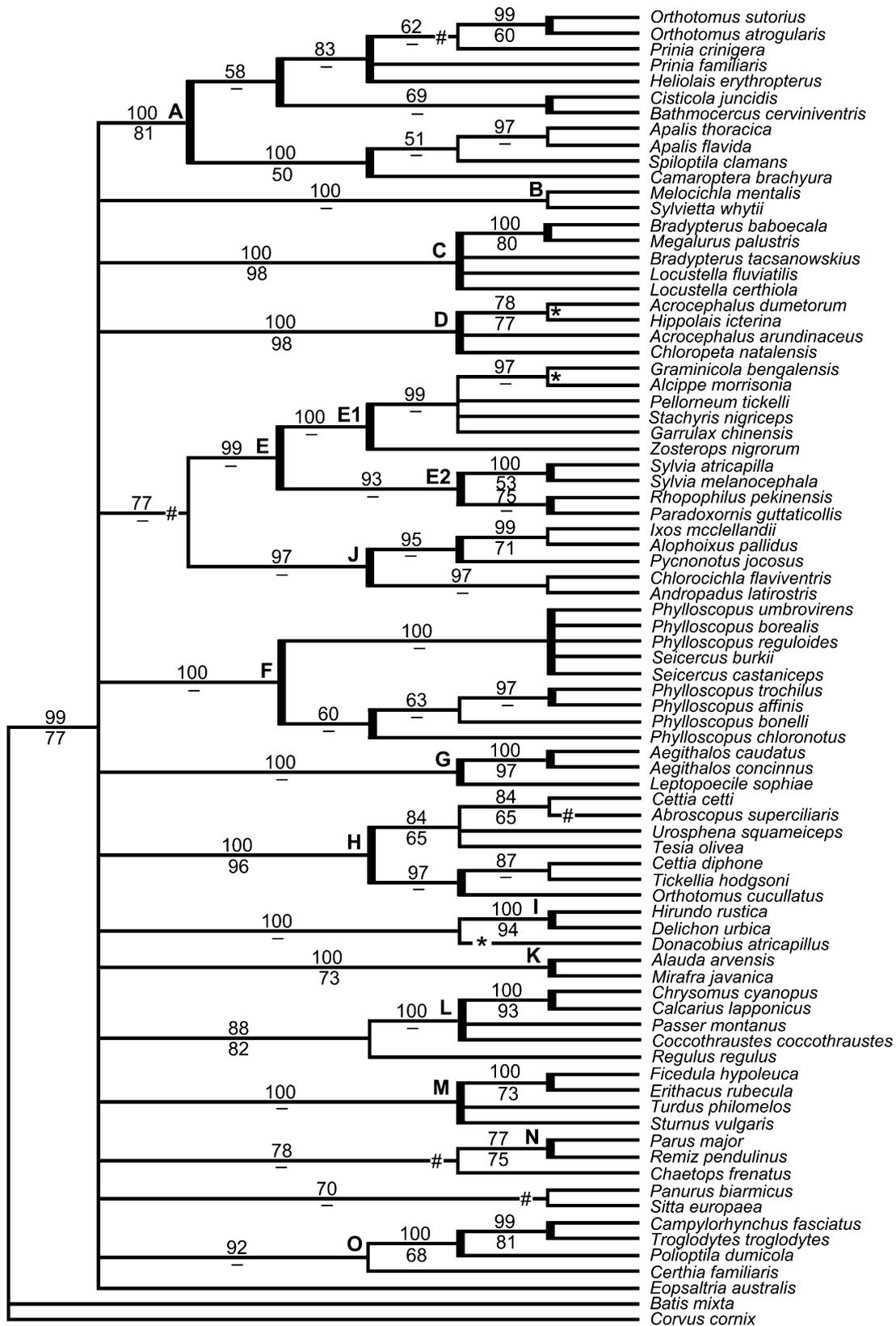


Fig. 2. Relationships of the same taxa as in Figs. 1 and 3, except *Macrosphenus kretschmeri* but including *Chloropeta natalensis*, based on cytochrome *b* sequences (1038 bp) analyzed by Bayesian inference under the GTR + Γ + I model. Posterior probabilities ($\geq 50\%$; 182,000 trees) are indicated above the nodes and parsimony bootstrap values ($\geq 50\%$; 1000 replicates) below the nodes. Clades that agree with the myoglobin intron II tree (Fig. 1) have bold highlights, while incongruent relationships are marked by * ($\geq 95\%$ posterior probabilities and/or $\geq 75\%$ parsimony bootstrap support in both trees) or # (lower support values). The letters denote clades that are discussed in the text.

which is sister to a clade comprising *Bradypterus*, *Megalurus*, and *Locustella* (clade C) in the myoglobin tree, while it is sister to *Hirundo* and *Delichon* (clade I) in the cytochrome *b* tree. Although both the topologies receive high posterior probabilities, only the myoglobin tree is well supported in the parsimony bootstrap analysis. We obtained the same cytochrome *b* topology when we added a published sequence of *Donacobius* from a different locality (Barker, 2004; not shown). The third case of well-supported incongruence involves the relationships between *Graminicola*, *Pellorneum*, and *Alcippe* (in clade E1). The myoglobin data suggest a sister relationship between the two former, while cytochrome *b* indicates a closer association between the first and the third. Although the posterior probabilities are similar for both the topologies, the bootstrap support is considerably higher for the myoglobin tree. The few other inconsistencies between the myoglobin and cytochrome *b* trees are less well-supported by the data (marked by # in Figs. 1–3).

The tree based on the analyses of the concatenated dataset (Fig. 3) is better resolved (85% of all nodes) than either of the individual gene trees. Several clades receive higher support than in any of the separate analyses, while some of the incongruent ones have lower support values. In the three cases of well-supported incongruence between the myoglobin and cytochrome *b* data, the tree from the combined analysis is compatible with the myoglobin tree, indicating a stronger phylogenetic signal in this dataset in these cases. The combined analysis recovers five clades that are not found in the 50% majority rule consensus trees from the separate analyses of myoglobin and cytochrome *b* (marked by † in Fig. 3), although none of these clades is strongly supported by the data.

3.2.2. Individual clades

The three trees resulting from the analyses of the individual and combined datasets agree on a number of clades within the Sylvioidea sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990) (marked A–J, N, O in Figs. 1–3; Table 1). Clade A is well-supported in all trees, and comprises the mostly Afrotropical and Oriental *Prinia* (prinias) and *Cisticola* (cisticolas), two of the three included species of the Oriental *Orthotomus* (tailorbirds), and the Afrotropical *Apalis* (apalises), *Bathmocercus* (“rufous warblers”) and *Camaroptera* (camaropteras), *Heliolais* (monotypic genus: Red-winged Warbler) and *Spiloptila* (monotypic genus: Cricket Warbler).

Clade B, which comprises the monotypic genus *Melocichla* (Moustached Grass Warbler) and *Sylvietta* (crombecs), receives strong support in the Bayesian analyses of cytochrome *b* and the combined data, but low parsimony bootstrap support in both these analyses, and is not recovered in the myoglobin tree. It is sister to clade A in the combined analysis, with moderate posterior

probability and <50% parsimony bootstrap, while the myoglobin data place only *Sylvietta* in this position, with low support.

Clades C and D are strongly supported in all the trees. The former includes three genera, of which *Megalurus* (grassbirds) has representatives breeding in the Oriental and Australasian regions, *Bradypterus* (“bush warblers”) in the Palearctic, Oriental and Afrotropics, and *Locustella* (grasshopper warblers) in the Palearctic. Clade D comprises the Palearctic, Australasian and Afrotropical *Acrocephalus* (reed warblers), the Palearctic *Hippolais* (“hippolaits warblers”), and the Afrotropical *Chloropeta* (yellow warblers). In the myoglobin and combined trees, the Neotropical monotypic genus *Donacobius* (Black-capped *Donacobius*) is sister to clade C (see above). In the myoglobin and combined data trees, clades C, D, and *Donacobius* together form clade P, which is well-supported in the myoglobin tree, but which has $\leq 50\%$ parsimony bootstrap support in the combined tree. In the cytochrome *b* tree, the interrelations between clades C and D are unresolved, while *Donacobius* is sister to clade I (see above). If the datasets are re-analyzed with *Donacobius* excluded, the resulting myoglobin tree (not shown) is identical to the one including *Donacobius*, whereas the combined data tree (not shown) shows poor support for a sister relation between clades C and D (61% posterior probability; 27,000 trees).

Clade E1 has 100% posterior probability in all analyses and high parsimony bootstrap support in the myoglobin tree, while it receives $\leq 50\%$ bootstrap support in the cytochrome *b* and combined myoglobin/cytochrome *b* trees. It contains representatives of the south Asian genera *Alcippe* (fulvettas), *Pellorneum* (“jungle babblers”), *Stachyris* (“tree babblers”), *Garrulax* (laughing-thrushes), and the monotypic Oriental genus *Graminicola* (Rufous-rumped Grassbird), as well as the Afrotropical, Oriental, and Australasian *Zosterops* (white-eyes). Clade E2 is reasonably well-supported in all analyses except the parsimony bootstrap of the cytochrome *b* data. It comprises the mostly western Palearctic *Sylvia*, the Oriental and south-east Palearctic *Paradoxornis*, and the monotypic east Asian genus *Rhopophilus* (Chinese Hill Warbler). Clades E1 and E2 are sisters, forming clade E, in all analyses, although the support for this relation varies between the trees.

Clade F is strongly supported in all the three trees, and comprises *Phylloscopus* (leaf-warblers) and *Seiurus* (“flycatcher-warblers”). The former genus is widely distributed in the Palearctic and Oriental regions, with a few species occurring in the Afrotropics and Australasia, whereas the latter is restricted to the Orient and south-eastern Palearctic.

The two genera in the well-supported clade G, *Aegithalos* (“long-tailed tits”) and *Leptopoecile* (tit-warblers) are confined to the Palearctic and Oriental regions, and comprise only nine species (Dickinson, 2003).

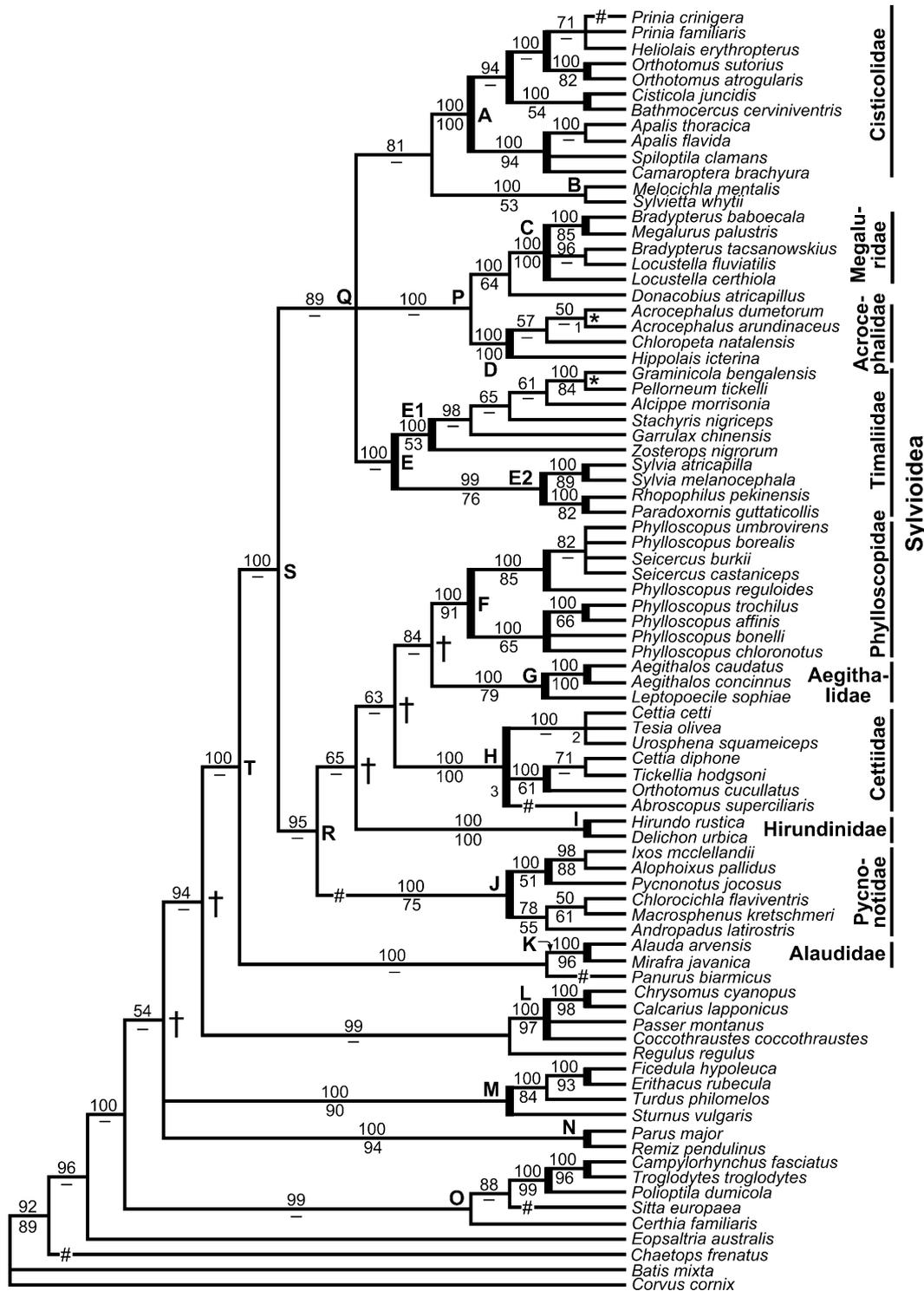


Fig. 3. Relationships of the same taxa as in Figs. 1 and 2, based on combined myoglobin intron II and cytochrome *b* sequences (1829 bp) divided into two partitions analyzed under the GTR + Γ and GTR + Γ + I models, respectively. Posterior probabilities ($\geq 50\%$; 336,000 trees) are indicated above the nodes and parsimony bootstrap values ($\geq 50\%$; 1000 replicates) below the nodes. Clades that agree between the myoglobin and cytochrome *b* trees have bold highlights, while incongruent relationships are marked by * ($\geq 95\%$ posterior probabilities and/or $\geq 75\%$ parsimony bootstrap support in both trees) or # (lower support values). Clades that are not found in either the myoglobin or cytochrome *b* trees are marked by †. The letters denote clades that are discussed in the text. The names referring to the marked clades are the ones proposed here.

Clade H, which is strongly supported in all analyses, contains representatives of the genera *Cettia* (“bush warblers”), *Urosphena* (“bush warblers”), *Tesia* (tesias),

Abroscopus (“flycatcher-warblers”), *Orthotomus cucullatus* (Mountain Tailorbird), and the monotypic genus *Tickellia* (Broad-billed Warbler). These have almost exclusively

Oriental distributions; a few *Cettia* species are found in the southern parts of the Palearctic and in Australasia.

The taxa in the well-supported clade I belong to the speciose and globally distributed group swallows and martins.

Clade J receives high support values in all analyses, except for the parsimony bootstrap of the cytochrome *b* data. It comprises three genera of bulbuls (*Pycnonotus*, *Alophoixus*, *Ixos*) and two greenbulbs (*Chlorocichla*, *Andropadus*) and the only species in the genus *Macrosphenus* (longbills) included in the present study. The genus *Pycnonotus* occurs in the Afrotropical, Oriental, and southern Palearctic regions, *Alophoixus* and *Ixos* in the Orient, and the others in the Afrotropics.

In the myoglobin and combined data trees, clades A–E form clade Q, and clades F–J form clade R, with variable support; clade R is also supported by a 4 bp deletion (Fig. 1). Clades Q and R are sisters, forming clade S. Neither clade Q or clade R is recovered in the cytochrome *b* tree.

Clade K comprises representatives of the lark genera *Alauda* and *Mirafra*, native to the Palearctic and Oriental, and Oriental, Australasian, and Afrotropical regions, respectively. In the myoglobin and combined data trees, this clade is sister to the monotypic Palearctic genus *Panurus* (Bearded Tit/Parrotbill), with high posterior probability but moderate or no parsimony bootstrap support. The lark-*Panurus* clade is sister to clade S, and accordingly to all of clades A–J, with high posterior probability but low or no parsimony bootstrap support; this relation is further supported by a 3 bp deletion (Fig. 1). In contrast, the cytochrome *b* tree places *Panurus* as sister to *Sitta*, with low support.

Parus (tits) and *Remiz* (penduline tits) form a well-supported clade (N) in the trees based on the myoglobin and combined data, respectively, but this grouping receives somewhat lower support in the cytochrome *b* tree. The interrelationships between this clade and the other “sylvioidean” clades are unresolved.

Clade O includes *Troglodytes*, *Campylorhynchus* (wrens), and *Polioptila* (gnatcatchers), with high support. In the combined myoglobin/cytochrome *b* tree, *Sitta* (nuthatches) and *Certhia* (treecreepers) are also part of this clade, although their inclusion is not unanimously supported in the separate analyses of myoglobin and cytochrome *b*. The position of this clade in relation to the other taxa in Sylvioidea sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990) is unresolved.

The relationships of *Regulus* (crests/kinglets) are unresolved in the myoglobin tree, while it is sister to clade L in the cytochrome *b* and combined data trees. The sister relationship to the passeroids has high posterior probability and parsimony bootstrap support in the analyses of the cytochrome *b* and combined myoglobin/cytochrome *b* data, but $\leq 50\%$ bootstrap support in the combined tree.

Our data suggest several cases of non-monophyletic genera: *Bradypterus* and *Locustella* (clade C),

Phylloscopus (clade F), *Cettia* (clade H), and *Orthotomus* (clades A and H).

4. Discussion

4.1. Circumscription of Sylvioidea

Sibley and Ahlquist's (1990) and Sibley and Monroe's (1990) circumscription of Sylvioidea (Fig. 1, Table 1) was disputed by Sheldon and Gill (1996), based on novel DNA–DNA hybridization data. They found a well-supported clade comprising *Criniger* (bulbul), *Hirundo*, *Phylloscopus*, *Stachyris*, *Sylvia*, *Psaltriparus* (monotypic genus: Bushtit), and *Aegithalos*, with *Alauda* as its sister taxon. Sheldon and Gill (1996) also recovered a strongly supported clade with *Sitta*, *Polioptila*, *Certhia*, and *Thryothorus* (wren), and another one including *Parus*, *Auriparus* (monotypic genus: Verdin), *Remiz* and *Anthoscopus* (penduline-tits). However, the interrelationships among these clades, as well as their positions in relation to the muscicapoid and passeroid clades, were unresolved. *Regulus* was placed as the sister to all these. Ericson and Johansson (2003) found almost exactly the same topology as Sheldon and Gill, based on 3.1 kb of *c-myc*, RAG-1, myoglobin intron II, and cytochrome *b* sequence data, although their taxon sampling was slightly different and did not include *Regulus*.

Barker et al.'s (2004) study of RAG-1 and -2 sequences were also partly at variance with the results of Sibley and Ahlquist (1990). They found strong support for a clade including *Zosterops*, *Garrulax*, *Sylvia*, *Cisticola*, *Pycnonotus*, *Aegithalos*, *Hirundo*, and *Alauda* (with the latter being most basal). This was the sister to a well-supported clade comprising *Culicicapa*, *Elminia* (elminias), *Parus* and *Remiz*, although the close relationship between these two clades did not receive unambiguous support by their data. *Certhia* and *Sitta* were firmly united with *Polioptila* and *Troglodytes*, and were sisters to a clade comprising *Regulus* and Muscicapoidae sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990). However, the support for the sister relationship between these two clades, as well as the inclusion of *Regulus*, was low. Beresford et al. (2005), also using RAG-1 and -2 sequence data, was largely in agreement with Barker et al.'s results. Likewise, Voelker and Spellman (2003), who revised Muscicapoidae using combined *c-mos*, cytochrome *b*, and ND2 sequences, found strong support for the exclusion of *Polioptila*, *Regulus*, and *Poecile* (= *Parus*) from a clade containing the sylvioidean taxa *Sylvia*, *Turdoides* (babblers), and *Zosterops*.

Our results agree with Barker et al. (2004), Beresford et al. (2005), Ericson and Johansson (2003), and Sheldon and Gill (1996) in finding a sister relationship between

larks (clade K) and most other Sylvioidea sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990). They also conform with these studies in the lack of support for the inclusion of Sittidae, Certhiidae, Paridae, and Regulidae. On the basis of this evidence, we propose that Sylvioidea refers to clade T in Fig. 3. Future studies will show whether Sylvioidea should include also *Parus*, *Remiz*, *Stenostira* (Fairy Flycatcher), *Culicicapa*, *Elminia* (cf. Barker et al., 2004; Beresford et al., 2005), and other taxa not included here. According to Beresford et al. (2005) and Cibois et al. (1999) the Malagasy genera *Xanthomixis*, *Thamnornis*, *Oxylabes*, *Harterula* and *Cryptosylvicola*, not studied by us, form a clade within Sylvioidea as defined here. Additional taxa and genes will hopefully help resolving the deeper branches, which are generally not very robust in the present analysis, as well as the relationships that disagree between the myoglobin and cytochrome *b* trees, and those that are only supported by one of the regions.

4.2. Relationships within Sylvioidea

The present study does not support Sibley and Ahlquist's (1990) and Sibley and Monroe's (1990) classification at the family, subfamily, and tribe levels. Our data identify clades corresponding to their families Cisticolidae (clade A), Aegithalidae (clade G), Hirundinidae (clade I), and Pycnonotidae (clade J), as well as their subfamily Sylviinae (clade E). However, the taxonomic compositions of all of these except I differ from the corresponding groups in Sibley and Ahlquist (1990) and Sibley and Monroe (1990) with respect to at least one genus. Furthermore, our representatives of their family Zosteropidae and subfamilies Acrocephalinae, Megalurinae, and Garrulacinae are either divided into multiple clades with uncertain interrelationships, or nested within one or more of the clades mentioned above. Likewise, the tribes Timaliini and Sylviini are also non-monophyletic according to our results. Our data also disagree with Dickinson's (2003) subfamily Phylloscopinae (comprising *Phylloscopus*, *Seicercus*, *Tickellia*, *Abroscopus*, *Sylvietta*, and others not studied here).

If we collapse the clades with <95% posterior probability and <50% bootstrap support, we obtain a tree with 11 main clades within Sylvioidea (A–K). All of these main clades have $\geq 99\%$ posterior probability in all the three trees, except for clade B. Most of the species in each of these clades have been considered to be closely related based on morphological similarity (e.g., Mayr and Cottrell, 1986; Mayr and Greenway, 1960; Mayr and Paynter, 1964; Morony et al., 1975; Paynter, 1967; Wolters, 1975–1982), and we suggest that these clades form the basis for a revised classification.

Clade A corresponds to Cisticolidae sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990), and our

results support this. Five of the genera in the present study (*Cisticola*, *Prinia*, *Camaroptera*, *Orthotomus*, and *Apalis*), as well as five genera not studied here (*Hypergeus*, *Eminia*, *Schistolais*, *Euryptila* and three species of *Neomixis*), have previously been found to be closely related based on one or more data sets: mitochondrial cytochrome *b* and 16S (Cibois et al., 1999), mitochondrial ND2 and 12S (Sefc et al., 2003), and nuclear RAG-1 and -2 (Beresford et al., 2005). The inclusion in Cisticolidae of *Bathmocercus cerviniventris* (placed in Acrocephalinae by Sibley and Monroe, 1990) and the exclusion of *Rhopophilus* (see below) are well-supported by our data. The evidence for the non-monophyly of *Orthotomus* is strong, since *O. cucullatus* is firmly nested within clade H. However, in the absence of molecular data on the type species of *Orthotomus* (*sepium*), we are unable to decide to which (if any) of these taxa the name *Orthotomus* should be applied. The monotypic genus *Heliolais* was previously synonymised with *Prinia*, but Hall and Moreau (1970) argued, from morphological characteristics, that *Heliolais* ought to be recognized, and that has been followed by most subsequent authors (e.g., Dickinson, 2003; Sibley and Monroe, 1993; Sinclair and Ryan, 2003; Urban et al., 1997). The present study reaffirms the close relationship between these two genera, but does not permit an evaluation of the validity of *Heliolais*.

The species in Sibley and Monroe's (1990) subfamily Acrocephalinae fall into no fewer than eight of the main clades (A, B, C, D, F, G, H, and J) in the present study. Sefc et al. (2003) also failed to find a monophyletic Acrocephalinae. The close relationship between *Melocichla mentalis* and *Sylvietta whytii* found in the cytochrome *b* and combined trees (clade B) is supported by the analysis in Sibley and Ahlquist (1990, Fig. 381, p. 866), which shows *Sylvietta* as sister to *Melocichla* (labeled *S. mentalis*) and *Sphenoecus afer* (though this is not reflected in the linear classification in Sibley and Monroe, 1990). Sibley and Ahlquist (1990) and Sibley and Monroe (1990) place *Melocichla* and *Sylvietta* in the subfamily Sylviinae, while Dickinson (2003) put the former in this subfamily and the latter in Phylloscopinae [not recognized by Sibley and Ahlquist (1990) and Sibley and Monroe (1990)]. Beresford et al. (2005) found a clade comprising *Sylvietta denti*, *Sphenoecus afer*, *Achaetops pycnopygius*, *Bradypterus victorini* and *Macrosphenus flavicans* (the '*Sphenoecus* group'), which was sister to all other Sylvioidea as defined here except for larks. This rather basal position of *Sylvietta* is not contradicted by the present study, if the poorly supported internal nodes in clade S are collapsed. Since clade B is not unanimously well-supported in our analyses, we refrain from assigning a name to it.

We propose that the name Megaluridae refers to clade C of the present study. All taxa in this clade are part of Acrocephalinae sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990), except for *Megalurus*

palustris, which belongs to their subfamily Megalurinae. Beresford et al. (2005) show that *Cincloramphus* and *Schoenicola* are part of this clade. The present study confirms the non-monophyly of *Locustella* and *Bradypterus* found by Drovetski et al. (2004) based on mitochondrial ND2 data. We also demonstrate further evidence of this, since *B. baboecala* is firmly placed as sister to *Megalurus palustris* (latter not studied by Drovetski et al.). We await a more complete study (in preparation) before proposing any taxonomic changes within clade C.

The monotypic genus *Donacobius* was usually placed in the family Mimidae (mimids) (Mayr and Greenway, 1960; Morony et al., 1975; Wolters, 1975–1982), until the American Ornithologists' Union (1983) declared that "recent studies" indicated that it belonged in Troglodytidae. That was also the conclusion reached by Sibley and Ahlquist (1990), based on DNA–DNA hybridization data. However, using cytochrome *b* and β -fibrinogen sequences, Barker (2004) found evidence for an association with *Zosterops* and *Prinia*. The present study confirms Barker's conclusion that *Donacobius* belongs to the Sylvioidea family, as defined here. Its exact position is uncertain, since the myoglobin and cytochrome *b* trees are incongruent. From a biogeographical point of view, the inclusion of *Donacobius* in the Sylvioidea is remarkable, as it is the only member of this group found in South America (south to Paraguay and north-east Argentina; Brewer, 2001; Mayr and Greenway, 1960). Beside larks and swallows, only three other species within Sylvioidea occur naturally in the New World: the monotypic genera *Chamaea* (Wrentit) in Sylviinae (Barhoum and Burns, 2002; Cibois, 2003a; Sibley and Ahlquist, 1982, 1990), and *Psaltriparus* in Aegithalidae (Sibley and Ahlquist, 1990), and *Phylloscopus borealis*. The first two are mainly or entirely confined to western North America, whereas the third has its main distribution in the Palearctic, just reaching western Alaska in the breeding season.

We suggest that the name Acrocephalidae refers to clade D of the present study. All taxa in this clade are part of Acrocephalinae sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990), and their close relationship has been indicated before, based on cytochrome *b* sequences (Helbig and Seibold, 1999) and DNA–DNA hybridization (Sibley and Ahlquist, 1990; only the former two taxa studied). However, our taxon sampling does not permit an evaluation of the possible non-monophyly of *Hippolais* and *Acrocephalus* reported by Leisler et al. (1997) and Helbig and Seibold (1999). Haffer (1991) suggested that *Locustella* and *Acrocephalus* are closely related, but that was disputed by Helbig and Seibold (1999). The present study is not entirely conclusive regarding this relationship. The myoglobin and combined data trees unite clades C and D and *Donacobius* into clade P with high posterior

probability. However, clade P has <50% parsimony bootstrap support in these analyses and <50% posterior probability and parsimony bootstrap in the analyses of cytochrome *b*. Moreover, clade P is very weakly supported in the analyses of the combined dataset when *Donacobius* is excluded.

We suggest that the name Phylloscopidae refers to clade F of the present study. This is a new family name, which has *Phylloscopus* Boie, 1826 as its type genus. Sibley and Ahlquist (1990) and Sibley and Monroe (1990) place *Phylloscopus* and *Seicercus* in Acrocephalinae, while Dickinson (2003), without comment, erects the subfamily Phylloscopinae for these genera, together with *Tickellia*, *Abroscopus*, *Sylvietta*, and others not studied here. The present study strongly corroborates the findings of Olsson et al. (2004, in press) and Päckert et al. (2004) that *Seicercus* is nested within *Phylloscopus*, rendering the latter genus non-monophyletic. As suggested by these authors, the taxonomic implications are that either *Seicercus* be synonymized with *Phylloscopus*, or the complex be split into more than two genera. Although the present study includes samples from all of the main clades found in previous studies (e.g., Olsson et al., 2004, in press; Päckert et al., 2004; Price et al., 1997; Richman and Price, 1992), we prefer to await a more complete study (in preparation) before proposing taxonomic changes.

We propose that the name Cettiidae refers to clade H of the present study. This is a new family name, which has *Cettia* Bonaparte, 1834 as its type genus. All the taxa in this clade are placed in Acrocephalinae by Sibley and Monroe (1990). Although the myoglobin and cytochrome *b* data disagree to some extent regarding the topology of this clade, there is strong evidence that *Cettia* is non-monophyletic. This is surprising, given the striking morphological dissimilarity between *Cettia* and the others, and the morphological homogeneity of *Cettia*. The genera *Tesia*, *Cettia*, and *Urosphena* are usually believed to be near relatives, and so are *Tickellia* and *Abroscopus* (e.g., Dickinson, 2003; Mayr and Cottrell, 1986; Sibley and Monroe, 1990; Wolters, 1975–1982). However, these two groups have not previously been considered to be closely related, and neither of them has been suggested as closely associated with *Orthotomus cucullatus* (e.g., Dickinson, 2003; Inskipp et al., 1996; Mayr and Cottrell, 1986; Sibley and Monroe, 1990; Wolters, 1975–1982). Except for the extraordinarily short-tailed *Tesia olivea*, which has eight rectrices, all of the taxa in clade H have 10 rectrices (personal observations). Here, two of the genera placed in Cisticolidae have 10 rectrices (Urban et al., 1997), while nearly all other passerines have 12 rectrices (Cramp, 1988; Pyle, 1997), including *Orthotomus sutorius* and *O. atrogularis* (personal observations). We await a more complete study (in preparation) before proposing any taxonomic changes.

Clade E agrees with Sylviinae sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990), but also includes their Garrulacinae (*Garrulax*) and Zosteropidae (*Zosterops*), well anchored within their tribe Timaliini, as well as *Graminicola* (placed in Megalurinae by Sibley and Monroe, 1990) and *Rhopophilus* (placed in Cisticolidae by Sibley and Monroe, 1990). In addition *Paradoxornis* is in Sibley and Ahlquist's (1990) and Sibley and Monroe's (1990) tribe Sylviini rather than in Timaliini. These results conform with the study of mitochondrial cytochrome *b*, 12S, and 16S data by Cibois (2003a). However, *Graminicola* and *Rhopophilus* were not studied by Cibois, and Sibley and Monroe's placements of these genera were not based on molecular data. The latter authors state that the affinities of *Rhopophilus* are uncertain, and that "B. King (pers. comm.) suggests that it may be timaliine." The close association of the traditional "babblers" (Timaliini and Garrulacinae), *Zosterops* and *Sylvia* has been suggested by several previous studies of mitochondrial and nuclear DNA sequences (e.g., Barker et al., 2002, 2004; Cibois, 2003a; Ericson and Johansson, 2003). *Sylvia* is the type genus of the family Sylviidae, which has undesirable taxonomic implications. Cibois (2003a,b) suggested that if the Timaliidae and several groups of warblers are recognized at the same family level, then Sylviidae Leach, 1820 should be suppressed and the name Timaliidae Vigors and Horsfield, 1827 kept for the babblers and *Sylvia*. We agree with this, and consequently propose that the name Timaliidae refers to clade E of the present study. However, formal suppression of Sylviidae can only be sanctioned by the International Commission on Zoological Nomenclature.

We propose that the name Aegithalidae refers to clade G of the present study. *Aegithalos* and two other monotypic or small genera, but excluding *Leptopoecile*, are usually placed in the family Aegithalidae (e.g., Morony et al., 1975; Paynter, 1967; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990; Wolters, 1975–1982), although Dickinson (2003) put *Leptopoecile* in this family, without any explanation. A close relationship between *Leptopoecile* and *Aegithalos* has been suggested based on mitochondrial 16S sequence data (Sturmbauer et al., 1998).

Clade I is treated as the family Hirundinidae by all previous workers (e.g., Dickinson, 2003; Mayr and Greenway, 1960; Morony et al., 1975; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990; Wolters, 1975–1982), and we support this.

We propose that the name Pycnonotidae refers to clade J of the present study. This is in agreement with most previous authors, except for the inclusion of *Macrosphenus kretschmeri* (e.g., Dickinson, 2003; Mayr and Greenway, 1960; Morony et al., 1975; Sibley and Monroe, 1990; Sibley and Ahlquist, 1990; Wolters, 1975–1982). The taxa in clade J are separated into an African (*Andropadus*, *Chlorocichla*, *Macrosphenus*) and a mainly

Asian (*Pycnonotus*, *Alophoixus*, *Ixos*) clade; the genus *Pycnonotus* is found in both the continents, although there are six times more species in Asia than in Africa (Dickinson, 2003). Pasquet et al. (2001) also found an African and an Asian bulbul radiation, based on mitochondrial 12S and 16S sequence data from a larger number of taxa. With respect to *Macrosphenus kretschmeri*, Urban et al. (1997) state that "it was originally thought to be a bulbul and placed in the monotypic genus *Sua-heliornis*," and that "any placement of *Macrosphenus* remains speculative." Beresford et al. (2005) found *Macrosphenus flavicans* to belong in the "*Sphenoeacus* group", well removed from *M. kretschmeri*. Further studies are required to evaluate the relationships of the other taxa currently in *Macrosphenus*.

We propose that the name Alaudidae refers to clade K of the present study. This family is recognized by all previous authors (e.g., Dickinson, 2003; Mayr and Greenway, 1960; Morony et al., 1975; Sibley and Ahlquist, 1990; Sibley and Monroe, 1990; Wolters, 1975–1982). Earlier, the association between *Panurus* and larks has been highlighted based on the same genetic markers as used herein together with *c-myc* and RAG-1 (Ericson and Johansson, 2003). In the absence of agreement between our different datasets, we do not include *Panurus* in Alaudidae. However, the general belief that *Panurus* is related to *Paradoxornis* [Dickinson, 2003; Mayr and Paynter, 1964; Morony et al., 1975; Wolters, 1975–1982; although Sibley and Monroe (1990) stated that the affinities of *Panurus* are uncertain] is strongly contradicted.

Many more putative Sylvioidea genera remain to be studied, and independent molecular data need to be analyzed, before a robust hypothesis for the Sylvioidea can be formulated. In particular, the deeper branches need to be better resolved.

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Appendix A

List of samples (in alphabetical order), with geographic origin, museum reference number, and GenBank accession number

Taxon	Locality	Regions	Museum No.	GenBank No.
<i>Abroscopus supercilii</i>	Myanmar, Chin	Myo	NMNH B02119	DQ008567
		Cytb		DQ008515
<i>Acrocephalus arundinaceus zarudnyi</i>	China, Xinjiang*	Myo	NRM 20046787	DQ008530
		Cytb		AJ004252
<i>Acrocephalus dumetorum</i>	India, Punjab*	Myo	NRM 569279	AY887682
	Russia?	Cytb	—	AJ004773
<i>Aegithalos caudatus caudatus</i>	Sweden, Uppland	Myo	NRM 976089	AY228281
		Cytb		AY228044
<i>Aegithalos concinnus iredalei</i>	India, West Bengal	Myo	NRM 20046818	DQ008570
		Cytb		DQ008519
<i>Chrysomus (Agelaius) cyanopus cyanopus</i>	Paraguay, Dpto. Presidente Hayes	Myo	NRM 966916	AY228283
		Cytb		AY228046
<i>Alauda arvensis arvensis</i>	Sweden, Sörmland	Myo	NRM 966614	AY228284
		Cytb		AY228047
<i>Alcippe morrisonia schaefferi</i>	Vietnam, Vinh Phuc	Myo	NRM 947309	DQ008535
		Cytb		DQ008483
<i>Alophoixus pallidus annamensis/khmerensis</i>	Vietnam, Quang Tri	Myo	NRM 20046822	DQ008559
		Cytb		DQ008507
<i>Andropadus latirostris latirostris</i>	Uganda	Myo	NRM 20046809	DQ008560
		Cytb		DQ008508
<i>Apalis flavida caniceps</i>	Nigeria	Myo	NRM 20046800	DQ008547
		Cytb		DQ008496
<i>Apalis thoracica griseiceps</i>	Tanzania, Usambara mts.	Myo	ZMUC 05368	DQ008548
		Cytb		DQ008497
<i>Bathmocercus cerviniventris</i>	Tanzania	Myo	NRM	DQ008545
		Cytb	20046798	DQ008494
<i>Batis mixta mixta</i>	Tanzania, Iringa	Myo	ZMUC 02953	DQ011860
		Cytb		DQ011862
<i>Bradypterus baboecala tongensis/transvaalensis</i>	South Africa, Natal	Myo	NRM	DQ008525
		Cytb	20046782	DQ008473
<i>Bradypterus tacsanowskii</i>	China, Hebei*	Myo	NRM	DQ008526
		Cytb	20046783	DQ008474
<i>Camaroptera brachyura pileata</i>	Tanzania, Usambara mts.	Myo	ZMUC 01986	DQ008549
		Cytb		DQ008498
<i>Calcarius lapponicus</i>	Sweden, Torne lappmark	Myo	NRM 976550	AY228287
		Cytb		AY228050
<i>Campylorhynchus fasciatus pallescens</i>	Ecuador, El Oro	Myo	ZMUC O2444	AY228288
		Cytb		AY228051
<i>Chaetops frenatus</i>	South Africa	Myo	—	AY228289
		Cytb		AY228052
<i>Certhia familiaris familiaris</i>	Sweden, Uppland	Myo	NRM 976184	DQ011861
		Cytb		DQ008524
<i>Cettia cetti albiventris</i>	India, Punjab*	Myo	NRM	DQ008561
		Cytb	20046810	DQ008509
<i>Cettia diphone canturians</i>	China, Shaanxi	Myo	NRM	DQ008562
		Cytb	20046811	DQ008510
<i>Chlorocichla flaviventris centralis</i>	Kenya, Arabuko-Sokoke Forest	Myo	ZMUC 01789	AY228290
		Cytb		AY228053
<i>Chloropeta natalensis natalensis</i>	Malawi, Lilongwe	Cytb	NRM 20046802	DQ008523
<i>Cisticola juncidis juncidis</i>	Italy, Sardinia	Myo	NRM	DQ008544
		Cytb	20046797	DQ008493
<i>Coccothraustes coccothraustes coccothraustes</i>	Sweden, Bohuslän	Myo	NRM 976374	AY228292
		Cytb		AY228055
<i>Corvus cornix</i>	Sweden, Uppland	Myo	NRM 986167	AY228327
		Cytb		AY228087
<i>Delichon urbica urbica</i>	Spain, Castilla	Myo	NRM	DQ008568
		Cytb	20046816	DQ008517
<i>Donacobius atricapilla atricapilla</i>	Paraguay, Dpto. Concepcion	Myo	NRM 966966	DQ008533
		Cytb		DQ008481
<i>Eopsaltria australis australis</i>	Australia, Victoria	Myo	MV 1390	AY064732

(continued on next page)

Appendix A (continued)

Taxon	Locality	Regions	Museum No.	GenBank No.
<i>Erithacus rubecula rubecula</i>	Sweden, Blekinge	Cytb	NRM 976377	AY064273
		Myo		AY228296
<i>Ficedula hypoleuca hypoleuca</i>	Sweden, Blekinge	Cytb	NRM 976132	AY228058
		Myo		AY228300
<i>Garrulax chinensis chinensis</i>	Hong Kong	Cytb	NRM	AY228062
		Myo		DQ008536
<i>Graminicola bengalensis</i>	Nepal	Cytb	20046790	DQ008484
		Myo	NRM	DQ008532
<i>Heliolais erythropterus erythropterus</i>	Nigeri	Cytb	20046789	DQ008480
		Myo	NRM	DQ008550
<i>Hirundo rustica rustica</i>	Sweden, Uppland	Cytb	20046803	DQ008499
		Myo	NRM 976238	AY064258
<i>Hippolais icterina</i>	Sweden, Öland	Cytb	NRM	DQ008516
		Myo		DQ008531
<i>Ixos maclellandii tickelli</i>	Thailand, Chiang Mai	Cytb	20046788	DQ008479
		Myo	NRM	DQ008558
<i>Leptopoeile sophiae obscura</i>	China, Qinghai	Cytb	20046796	DQ008506
		Myo	NRM	DQ008569
<i>Locustella certhiola ssp.</i>	China, Hebei*	Cytb	20046817	DQ008518
		Myo	NRM	DQ008528
<i>Locustella fluviatilis</i>	Kenya*	Cytb	20046785	DQ008476
		Myo	NRM	DQ008527
<i>Macrosphenus kretschmeri kretschmeri</i>	Tanzania, Usambara mts.	Cytb	20046784	DQ008475
		Myo	ZMUC 03883	DQ008574
<i>Megalurus palustris toklaio</i>	India, Punjab	Cytb	NRM	DQ008529
		Myo	20046786	DQ008477
<i>Melocichla mentalis mentalis</i>	Nigeria	Cytb	NRM	DQ008551
		Myo	20046804	DQ008500
<i>Mirafra javanica williamsoni</i>	Thailand, Ayuthaya	Cytb	NRM	DQ008571
		Myo	20046819	DQ008520
<i>Orthotomus atrogularis nitidus</i>	Vietnam, Quang Tri	Cytb	NRM	DQ008543
		Myo	20046821	DQ008492
<i>Orthotomus cucullatus cucullatus</i>	Indonesia, Sumatra	Cytb	NRM	DQ008566
		Myo	20046815	DQ008514
<i>Orthotomus sutorius inexpectatus</i>	Thailand, Chiang Mai	Cytb	NRM	DQ008542
		Myo	20046795	DQ008491
<i>Panurus biarmicus biarmicus</i>	Sweden, Närke	Cytb	NRM 966576	AY228308
		Myo	AY228070	
<i>Paradoxornis guttaticollis</i>	Vietnam, Yen Bou	Cytb	NRM	DQ008539
		Myo	20046750	DQ008488
<i>Parus major major</i>	Sweden, Uppland	Cytb	NRM 956363	AY228310
		Myo	AY228072	
<i>Passer montanus montanus</i>	Sweden, Uppland	Cytb	NRM 976359	AY228311
		Myo	AY228073	
<i>Pellorneum tickelli fulvum</i>	Vietnam, Ha Tinh	Cytb	NRM	DQ008534
		Myo	20026653	DQ008482
<i>Phylloscopus affinis</i>	Pakistan, NW Frontier Prov.	Cytb	NRM	DQ008555
		Myo	20046807	DQ008503
<i>Phylloscopus bonelli</i>	Morocco*	Cytb	NRM	DQ008554
		Myo	20046806	Z73485
<i>Phylloscopus borealis borealis</i>	China, Hebei*	Cytb	NRM	AY887685
		Myo	20036962	AY635052
<i>Phylloscopus chloronotus simlaensis</i>	Pakistan NW Frontier Prov.	Cytb	NRM	DQ008556
		Myo	20046808	DQ008504
<i>Phylloscopus reguloides reguloides</i>	India, West Bengal	Cytb	NRM	AY887710
		Myo	20036996	AY656235
<i>Phylloscopus trochilus trochilus</i>	Sweden, Västergötland	Cytb	NRM	AY887719
		Myo	20037010	
<i>Phylloscopus umbrovirens fugglescouchmani</i>	Sweden	Cytb	—	Z73492
		Myo	ZMUC 120713	AY887721
<i>Poliophtila dumicola dumicola</i>	Tanzania, Uluguru mts.	Cytb	AY635062	
		Myo	NRM 956689	AY228317

Appendix A (continued)

Taxon	Locality	Regions	Museum No.	GenBank No.
<i>Prinia familiaris</i>	Chaco	Cytb		AY228079
	Indonesia, Java	Myo	NRM 20046794	DQ008541
<i>Prinia crinigera catharia</i>	Myanmar, Chin	Cytb		DQ008490
		Myo	NRM	DQ008540
<i>Pycnonotus jocosus pattani</i>	Vietnam, Quang Tri	Cytb	20046793	DQ008489
		Myo	NRM	DQ008557
		Cytb	20046820	DQ008505
<i>Regulus regulus regulus</i>	Sweden, Uppland	Myo	NRM	DQ008572
		Cytb	20016439	DQ008521
<i>Remiz pendulinus pendulinus</i>	Sweden	Myo	—	AY228319
		Cytb		AY228081
<i>Rhopophilus pekinensis albosuperciliaris</i>	China, Xinjiang	Myo	NRM	DQ008538
		Cytb	20046792	DQ008487
		Myo	NRM	DQ008553
<i>Seicercus burkii</i>	India, West Bengal	Cytb	20046805	AY635065
		Myo	NRM 569288	AY887724
<i>Seicercus castaniceps castaniceps</i>	Myanmar, Chin	Cytb		AY887680
		Myo	NRM 976163	AY064257
<i>Sitta europaea europaea</i>	Sweden, Uppland	Cytb		AF378102
		Myo	NRM	DQ008546
<i>Spiloptila clamans</i>	Mauritania	Cytb	20046799	DQ008495
		Myo	NRM 947308	AY228321
<i>Stachyris nigriceps yunnanensis</i>	Vietnam, Vinh Phuc	Cytb		DQ008485
		Myo	NRM 966615	AY228322
		Cytb		AF378103
<i>Sturnus vulgaris vulgaris</i>	Sweden, Sörmland	Myo	NRM 976380	AY887727
		Cytb	—	Z73494
<i>Sylvia atricapilla atricapilla</i>	Sweden, Blekinge	Myo		DQ008537
	Germany	Cytb		DQ008486
<i>Sylvia melanocephala melanocephala</i>	Italy, Sardinia	Myo	NRM	DQ008537
		Cytb	20046791	DQ008486
<i>Sylvietta whytii whytii</i>	Tanzania, Iringa	Myo	ZMUC 123492	DQ008552
		Cytb		DQ008501
<i>Tesia olivea</i>	China, Yunnan	Myo	NRM	DQ008564
		Cytb	20046813	DQ008512
<i>Tickellia hodgsoni</i>	India, West Bengal	Myo	NRM	DQ008565
		Cytb	20046814	DQ008513
<i>Troglodytes troglodytes troglodytes</i>	Sweden, Öland	Myo	NRM 986416	AY228325
		Cytb		AY228084
<i>Turdus philomelos philomelos</i>	Sweden, Dalsland	Myo	NRM	DQ008573
		Cytb	20046801	DQ008522
<i>Urosphena squameiceps squameicepslussurianus</i>	China, Hebei*	Myo	NRM	DQ008563
		Cytb	20046812	DQ008511
<i>Zosterops nigrorum ssp.</i>	Philippines, Isabella	Myo	ZMUC O2663	AY228326
		Cytb		AY228326

Samples collected outside the breeding areas are marked by an asterisk in the Locality column. AMNH: American Museum of Natural History, New York, USA; MV: Museum Victoria, Melbourne, Australia; NMNH: National Museum of Natural History, Washington, DC, USA; NRM: Swedish Museum of Natural History, Stockholm, Sweden; ZMUC: Zoological Museum of the University of Copenhagen, Copenhagen, Denmark.

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