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Systematic revision of the avian family Cisticolidae based on a multi-locus phylogeny of all genera

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ABSTRACT

The avian taxon Cisticolidae includes c. 110 species which are distributed throughout the tropical and subtropical parts of the Old World. We estimated the phylogeny of 47 species representing all genera assumed to be part of Cisticolidae based on sequence data from two mitochondrial and two nuclear markers, in total 3495 bp. Bayesian inference and maximum likelihood analyses resulted in a generally well-supported phylogeny which clarified the position of several previously poorly known taxa. The placement of *Drymocichla, Malcorus, Micromacronus, Oreophilais, Phragmacia, Phyllolais*, *Poliolais* and *Urorhipis* in Cisticolidae is corroborated, whereas *Rhopophilus* and *Scotocerca* are removed from Cisticolidae. *Urorhipis* and *Heliolais* are placed in the genus *Prinia* whereas *Prinia burnesii* is shown to be part of Timaliidae, and is placed in the genus *Laticilla*. Although not recovered by all single loci independently, four major clades were identified within Cisticolidae, and one of these is here described as a new taxon (Neomixinae).

1. Introduction

The taxon Cisticolidae was first identified by Sibley and Ahlquist (1990) based on DNA–DNA hybridization data, revealing a previously unanticipated cluster of warbler genera. The speciose genera *Apalis, Cisticola* and *Prinia* comprise the core of the family, which was also considered to include several other genera, most of which are monotypic (Sibley and Monroe, 1990) (Table 1). Several studies confirm that Cisticolidae is a well-defined clade, and have addressed questions that have gradually clarified the phylogenetic position and composition of the clade (Alström et al., 2006, 2011a; Beresford et al., 2005; Cibois et al., 1999; Fregin et al., 2012; Johansson et al., 2008; Nguembock et al., 2007, 2008, 2012; Sefc et al., 2003). Yet, both the circumscription of Cisticolidae as a whole and its position within Sylvioidea (*sensu* Alström et al., 2006 and Fregin et al., 2012) are still insufficiently known. Neither Alström et al. (2006), Nguembock et al. (2007) nor Sefc et al. (2003) obtained topologies containing a well supported sister group of Cisticolidae. The only study that recovered a topology with statistical support for specific sister groups was that of Beresford et al. (2005), which indicated that clades corresponding to Pycnonotidae and Timaliidae (*sensu* Alström et al., 2006) are sisters to Cisticolidae. However, the most comprehensive study of Sylvioidea (Fregin et al., 2012) also failed to resolve the issue, as the position of Cisticolidae as sister to a clade comprising Acrocephalidae, Pnoepygidae, Bernieridae, Donacobiidae and Locustellidae was inferred with poor support.

Among the genera proposed by Sibley and Monroe (1990) to be included in Cisticolidae, several have been confirmed to belong there by recent studies (Table 1; Alström et al., 2006, 2011a; Beresford et al., 2005; Cibois et al., 1999; Fregin et al., 2012; Johansson et al., 2008; Nguembock et al., 2007, 2008, 2012; Sefc et al., 2003), while others have been removed. According to these studies, the genera *Bathmocercus, Eremomela, Neomixis, Orthotomus, Poliolais* and *Scepomycter*, which were placed in Sylviidae by Sibley and Monroe (1990), belong in Cisticolidae. The two monotypic genera *Rhopophilus* and *Scotocerca* exhibit external morphological similarity to *Prinia*, and were placed in Cisticolidae by Sibley and Monroe (1990) based on non-molecular data. However, the former has subsequently been shown to be a babbler (Timaliidae *sensu* Alström et al., 2006, Sylviidae *sensu* Gelang et al., 2009), and the latter to be sister to Cettiidae (Alström et al., 2011a; Fregin et al., 2012).

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Table 1
Previous classifications (left panel) and summary of previous molecular phylogenetic studies (right panel) of taxa included in this study. All taxa that are not part, or have not previously been hypothesized to be part, of the ingroup are excluded. Taxa not analyzed by a particular study are marked NA. Taxa that have not previously been included in a molecular study are marked by ∗.

Genus	Classifications			Phylogenetic studies									
	Sibley and Monroe (1990)	Dickinson (2003)	Ryan et al. (2006)	Cibois et al. (1999)	Sefc et al. (2003)	Beresford et al. (2005)	Alström et al. (2006)	Nguembock et al. (2007)	Nguembock et al. (2008)	Johansson et al. (2008)	Alström et al. (2011a)	Nguembock et al. (2012)	Oliveros et al. (2012)
Apalis	*Apalis*	*Apalis*	*Apalis*	NA	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae
Artisornis	*Orthotomus*	*Artisornis*, incertae sedis	*Artisornis*	NA	NA	NA	NA	Cisticolidae	Cisticolidae	NA	NA	Cisticolidae	Cisticolidae
Bathmocercus	*Bathmocercus*, in Sylviidae	*Bathmocercus* in Sylviidae	*Bathmocercus*	NA	NA	NA	Cisticolidae	Cisticolidae	NA	NA	NA	Cisticolidae	NA
Calamonastes	*Calamonastes*	*Calamonastes*	*Calamonastes*	NA	NA	NA	NA	Cisticolidae	NA	NA	NA	Cisticolidae	NA
Camaroptera	*Camaroptera*	*Camaroptera*	*Camaroptera*	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	NA	NA	Cisticolidae	Cisticolidae
Cisticola	*Cisticola*	*Cisticola*	*Cisticola*	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	NA	NA	NA	Cisticolidae	Cisticolidae
∗*Drymocichla*	*Drymocichla*	*Drymocichla*	*Drymocichla*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Eminia	*Eminia*	*Eminia*	*Eminia*	Cisticolidae	Cisticolidae	Cisticolidae	NA	Cisticolidae	NA	NA	NA	Cisticolidae	NA
Eremomela	*Eremomela*, in Sylviidae	*Eremomela*, in Sylviidae	*Eremomela*, in Sylviidae	NA	NA	NA	NA	NA	NA	Cisticolidae	NA	NA	NA
Euryptila	*Euryptila*	*Euryptila*	*Euryptila*	NA	NA	Cisticolidae	NA	NA	NA	NA	NA	NA	NA
Heliolais	In *Prinia*	*Heliolais*	*Heliolais*	NA	NA	NA	Cisticolidae	NA	NA	NA	NA	NA	Cisticolidae
Hypergerus	*Hypergerus*	*Hypergerus*	*Hypergerus*	Cisticolidae	Cisticolidae	NA	NA	Cisticolidae	NA	NA	NA	Cisticolidae	NA
Incana	*Cisticola*	*Incana*	*Incana*	NA	NA	NA	NA	Cisticolidae	NA	NA	NA	Cisticolidae	NA
∗*Malcorus*	*Malcorus*	*Malcorus*	*Malcorus*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Micromacronus	*Micromacronus*, in Timaliidae	*Micromacronus*, in Timaliidae	Not treated	NA	NA	NA	NA	NA	NA	NA	NA	NA	Cisticolidae
Neomixis	*Neomixis*, in Sylviidae	*Neomixis*, incertae sedis	*Neomixis*	Cisticolidae	NA	NA	NA	Cisticolidae	NA	NA	NA	Cisticolidae	Cisticolidae
Oreolais	*Apalis*	*Apalis*	*Apalis*	NA	NA	NA	NA	Cisticolidae	Cisticolidae	NA	NA	Cisticolidae	NA
∗*Oreophilais*	*Prinia*	*Oreophilais*	*Oreophilais*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Orthotomus	*Orthotomus*, in Sylviidae	*Orthotomus*, incertae sedis	*Orthotomus*	Cisticolidae	NA	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	NA	Cisticolidae	Cisticolidae	Cisticolidae
∗*Phragmacia*	*Prinia*	*Phragmacia*	*Phragmacia*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
∗*Phyllolais*	*Phyllolais*, in Sylviidae	*Phyllolais*	*Phyllolais*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Poliolais	*Phyllolais*, in Sylviidae	*Phyllolais*, incertae sedis	*Poliolais*	NA	NA	NA	NA	NA	NA	NA	NA	Cisticolidae	NA
Prinia	*Prinia*	*Prinia*	*Prinia*	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae	Cisticolidae
Rhopophilus	*Rhopophilus*	*Rhopophilus*	*Rhopophilus*, in Timaliidae[a]	NA	NA	NA	**Timaliidae**	NA	NA	NA	NA	NA	NA
Scepomycter	*Scepomycter*, in Sylviidae	In *Bathmocercus*, in Sylviidae	*Scepomycter*	NA	NA	NA	NA	Cisticolidae	NA	NA	NA	Cisticolidae	NA
Schistolais	*Prinia*	*Schistolais*	*Schistolais*	NA	Cisticolidae	NA	NA	Cisticolidae	Cisticolidae	NA	NA	Cisticolidae	Cisticolidae
Scotocerca	*Scotocerca*	*Scotocerca*	*Scotocerca*	NA	NA	NA	NA	NA	NA	NA	**Sister to Cettiidae**	NA	NA
Spiloptila	*Spiloptila*	*Spiloptila*	*Spiloptila*	NA	NA	NA	Cisticolidae	NA	NA	NA	NA	NA	Cisticolidae
Urolais	*Urolais*	*Urolais*	*Urolais*	NA	NA	NA	NA	NA	Cisticolidae	NA	NA	Cisticolidae	Cisticolidae
∗*Urorhipis*	*Apalis*	*Urorhipis*	*Urorhipis*	NA	NA	NA	NA	NA	NA	NA	NA	NA	

[a] Treated in Collar and Robson (2007).

Nguembock et al. (2007, 2012), who analyzed 15 and 17 cisticolid genera, respectively, using mitochondrial ND2 and nuclear myoglobin intron two sequence data in the first study and also ND3 and ATPase 6 in the second study, are the most complete studies to date. They identified three major clades, of which one is restricted to Madagascar, one to continental Africa, and one represented in Africa, Europe and Asia. The first of these clades comprised a single genus *Neomixis* containing three species.

The second clade identified by Nguembock et al., 2007, 2012, in the latter study comprised eight genera mainly occurring in forested habitats. The genus *Apalis* was shown by Nguembock et al. (2007) to be non-monophyletic, as two species, *Apalis ruwenzorii* and *Apalis pulchra*, were most closely related to *Artisornis metopias*. Nguembock et al. (2008) proposed that the former two species be placed in a newly erected genus *Oreolais*. The two African taxa now placed in *Artisornis* have previously sometimes been placed in *Orthotomus* (e.g. Hall and Moreau, 1970; Watson et al., 1986), but *A. metopias* is not closely related to *Orthotomus* (Fregin et al., 2012; Nguembock et al., 2007, 2008, 2012). The second species in this genus, *A. moreaui*, has not been studied by molecular methods. Also the two genera *Camaroptera* and *Calamonastes* may not be reciprocally monophyletic according to Nguembock et al., 2008, 2012.

In the third of the clades identified by Nguembock et al., 2007, 2012, the genus *Orthotomus* is non-monophyletic, based on the position of *O. sutorius* and *O. atrogularis* in Cisticolidae and *O. cucullatus* outside of that clade. Alström et al. (2006, 2011b) showed that *O. cucullatus* belongs in Cettidae. The latter of these studies included the type of *Orthotomus* (*O. sepium*, Horsfield, 1821), and confirmed that *O. sepium* is part of the same clade as *O. sutorius*, and hence that the name *Orthotomus* should be applied to that clade (and *O. cucullatus* moved to the genus *Phyllergates*). This was corroborated by Sheldon et al. (2012) based on a study including a larger number of *Orthotomus* species. Several African species have by various authors been considered part of the genus *Prinia*, which is part of the third clade, first identified by Nguembock et al. (2007) (e.g. Reichenow, 1907; Rüppell, 1835-1840; Sibley and Monroe, 1990; Watson et al., 1986), but are now placed in their own genera *Artisornis*, *Heliolais, Malcorus, Oreophilais, Phragmacia*, *Schistolais*, *Urolais* and *Urorhipis* (Dickinson, 2003; Ryan et al., 2006). Of these, *Artisornis* and *Urolais* (Nguembock, et al., 2008), *Heliolais* (Alström et al., 2006) and *Schistolais* (Sefc et al., 2003) have been shown to be part of the Cisticolidae clade, while *Malcorus, Oreophilais, Phragmacia* and *Urorhipis* have never been studied by molecular methods. Oliveros et al. (2012) showed that the genus *Micromacronus* was part of the Cisticolidae, but their sample of cisticolids was limited, and no specific sister group was identified.

We here assess the phylogeny of Cisticolidae based on two mitochondrial and two unlinked nuclear loci. We include representatives of all 27 genera treated as part of the family by Sibley and Monroe (1990), Dickinson (2003) and Ryan et al. (2006). Our data include the type species of all of these genera except for *Calamonastes* and *Eremomela.* Representatives of the genera *Drymocichla, Malcorus, Oreophilais, Phragmacia, Phyllolais,* and *Urorhipis* are here for the first time included in a context where their phylogenetic position in the family Cisticolidae can be evaluated based on molecular evidence.

2. Material and methods

2.1. Study group

In total, we obtained samples or GenBank sequences from 47 taxa representing all 14 genera originally allocated to Cisticolidae by Sibley and Ahlquist (1990); all 21 genera allocated to Cisticolidae (and the four genera *Artisornis, Neomixis, Orthotomus* and *Poliolais* treated as genera *incertae sedis* and placed after Cisticolidae) by Dickinson (2003); and all 26 genera allocated to Cisticolidae by Ryan et al. (2006). In addition, *Oreolais*, *Eremomela* and *Micromacronus*, which were shown by Nguembock et al. (2008), Johansson et al. (2008) and Oliveros et al. (2012), respectively, to be part of Cisticolidae, were included. For taxon names and taxonomy we follow Dickinson (2003). See Tables 1 and 2 and Supplementary Table 1. In addition to these samples, we obtained sequences from GenBank of the mitochondrial nicotinamide dehydrogenase subunit 2 (ND2) and the nuclear myoglobin intron 2 (myo) of 45 additional taxa representing all families in Sylvioidea. Our dataset includes the type species of all putative Cisticolidae genera except *Calamonastes* and *Eremomela*.

2.2. DNA extraction and sequencing

DNA was extracted from blood, feathers or muscle from fresh specimens or toepads from museum specimens using QIA Quick DNEasy Kit (Qiagen, Inc), according to the manufacturer's instructions, but with 20–30 μl 1 M DTT added to the initial incubation step of the extraction of feathers and footpad samples. For 37 taxa for which sequences were not available, we sequenced part of the two mitochondrial genes cytochrome b (cyt *b*) and nicotinamide dehydrogenase subunit 2 (ND2), the nuclear ornithine decarboxylase exon 6 (partial), intron 6, exon 7, intron 7 and exon 8 (partial) (ODC), and the entire nuclear myoglobin intron 2 (myo), although amplification failed in a few cases (Table 2). Eight of the samples were toepads from museum specimens (Table 2).

For fresh samples amplification and sequencing of ND2 followed the protocol of Sorenson et al. (1999); of cyt *b* and myo the protocols described in Olsson et al. (2005); and of ODC the protocols described in Allen and Omland (2003), Friesen et al. (1999). For study skin samples we followed the protocol of Irestedt et al. (2006) for the nuclear loci, while several new primers were designed for the mitochondrial loci (Supplementary Table 2) in order to amplify and sequence the degraded DNA in short overlapping fragments (<250 bp).

2.3. Phylogenetic analyses

Sequences were aligned using MegAlign 4.03 in the DNAstar package (DNAstar Inc.); some manual adjustment was done for the non-coding sequences. For the nuclear loci, heterozygous sites were coded as ambiguous. Trees were estimated by Bayesian inference (BI) using MrBayes 3.2 (Huelsenbeck and Ronquist, 2001, 2005) according to the following: (1) all loci were analyzed separately (single-locus analyses, SLAs). (2) The two mitochondrial loci were concatenated, partitioned by locus (two partitions). (3) The two mitochondrial loci were also partitioned by codon (in total six partitions; cyt *b* and ND2 combined referred to as mitochondrial SLA). (4) All loci were concatenated, partitioned by locus (four partitions). (5) All loci were concatenated, and the two mitochondrial loci were partitioned by codon and the nuclear introns by locus (in total eight partitions). In all analyses of partitoned data, rate multipliers were used to allow different rates for different partitions (Nylander, 2004; Ronquist and Huelsenbeck, 2003). All analyses were run under the best-fit models according to the Bayesian Information Criterion (BIC), calculated in jModeltest (Posada, 2008). For cyt *b* and ND2, the model selected by the BIC was the general time-reversible (GTR) model (Lanave et al., 1984; Tavaré, 1986; Rodríguez et al., 1990), assuming rate variation across sites according to a discrete gamma distribution with four rate categories (Γ; Yang, 1994) and an estimated proportion of invariant sites (*I*; Gu et al., 1995). For myo and ODC, the HKY model (Hasegawa

Table 2
List of species and loci for which original sequence data were produced for this study (in alphabetical order), with geographic origin, museum reference number and GenBank accession number. The *Cisticola guinea* sample is listed as *C. dorsti* by ZMUC (cf Dowsett-Lemaire et al., 2005). Acronyms used: AMNH: American Museum of Natural History, New York, USA; ANSP: Academy of Natural Sciences, Philadelphia, USA; BMNH: Bell Museum, University of Minnesota, Minneapolis, USA; DZUG: Department of Zoology, University of Gothenburg, Gothenburg, Sweden; NRM: Swedish Museum of Natural History, Stockholm, Sweden; UWBM: University of Washington, Burke, Seattle, Washington, USA; VH: Vogelwarte Hiddensee, Germany; ZMUC: Zoological Museum, University of Copenhagen, Copenhagen, Denmark.

	Origin of samples	Sample numbers	cyt *b*	ND2	ODC	myo
Aegithalos caudatus	Sweden	DZUG 3265	JX869873			
Alauda arvensis	Sweden	DZUG 275		JX869844		
Calamonastes simplex	Tanzania	ZMUC:O6645		JX869845	JX869818	
Camaroptera brevicaudata	Nigeria	DZUG 133		JX869846		
Cisticola carruthersi	Kenya	VH:A1585 (B0736)		JX869847	JX869820	
Cisticola guinea	Nigeria	ZMUC 147281	JX869874	JX869848	JX869821	JX869801
Cisticola exilis	Australia	ANSP 25244	JX869890	JX869849	JX869822	JX869802
Cisticola juncidis	Sardinia, Italy	NRM 20046797		JX869850	JX869819	
Cisticola lais	Tanzania	ZMUC 145468	JX869875	JX869851	JX869823	JX869803
Cisticola nigriloris	Tanzania	ZMUC 139092	JX869876	JX869852	JX869824	JX869804
Copsychus saularis	Bali, Indonesia	DZUG 75		JX869853		
Drymocichla incana[a]	Sudan	NRM 570211	JX869892	JX869854	JX869825	JX869805
Eremomela gregalis	South Africa	VH:B0744		JX869855		
Eremomela pusilla	Nigeria	DZUG 2825		JX869856		
Euryptila subcinnamomea[a]	South Africa	AMNH SKIN 597988	JX869891	JX869857	–	–
Heliolais erythroptera	Nigeria	NRM 20046803		JX869858	JX869826	
Hypergerus atriceps	Nigeria	DZUG 2824	JX869881			
Malcorus pectoralis	South Africa	UWBM 71283	JX869887	JX869859	JX869827	JX869806
Melocichla mentalis	Nigeria	DZUG 3266			JX869828	
Neomixis tenella[a]	Madagascar	ZMUC 27.947			JX869829	
Oreophilais robertsi[a]	Zimbabwe	AMNH SKIN 767551	JX869884	JX869860	JX869830	JX869807
Orthotomus atrogularis	Philippines	ZMUC 117826	JX869882		JX869831	
Orthotomus sepium	Java, Indonesia	DZUG 803		JX869861		
Passer domesticus	Sweden	DZUG 1962			JX869833	JX869809
Phragmacia substriata[a]	South Africa	AMNH SKIN 708625	JX869885	JX869862	JX869834	JX869810
Phyllolais pulchella[a]	Congo	NRM 570212	JX869893	JX869863	JX869835	JX869811
Phylloscopus trochilus	Sweden	DZUG 3189	JX869889		JX869843	JX869817
Poliolais lopezi[a]	Cameroon	NRM 570213	JX869894	JX869864	JX869836	JX869812
Polioptila caerulea	USA	BMNH X7391	JX869886	JX869865	JX869837	JX869813
Prinia atrogularis	India	DZUG 463	JX869877	JX869866	JX869838	JX869814
Prinia bairdii	Tanzania	DZUG 475	JX869878	JX869867		
Prinia burnesii	India	DZUG 464	JX869879	JX869868	JX869839	
Prinia subflava	Kenya	ZMUC 140490	JX869880	JX869869	JX869840	JX869815
Schistolais leucopogon	Kenya	DZUG 1269	JX869888	JX869870	JX869841	
Spiloptila clamans	Mauretania	DZUG 3247		JX869871		
Urorhipis rufifrons[a]	Somalia	NRM 570214	JX869895	JX869872	JX869842	JX869816

[a] Denote toepad samples.

et al., 1985) was chosen by the BIC, plus Γ for myo and $\Gamma + I$ for ODC. Ambiguous base pairs and indels were treated as missing data, but indels were plotted on the trees *a posteriori*. As outgroups, representatives from other sylvioid families were chosen based on the results of Alström et al. (2006), Johansson et al. (2008) and Fregin et al. (2012). Default priors in MrBayes were used. Four Metropolis-coupled MCMC chains with incremental heating temperature 0.1 or 0.05 were run for 5–15 $\times$ 10^6 generations and sampled every 1000 generations. Convergence to the stationary distribution of the single chains was inspected in Tracer 1.5.0 (Rambaut and Drummond, 2009) using a minimum threshold for the effective sample size. The joint likelihood and other parameter values reported large effective sample sizes (>1000). Good mixing of the MCMC and reproducibility was established by multiple runs from independent starting points. Each analysis was run at least twice, and topological convergence was examined by eye and by the average standard deviation of split frequencies (<0.005). The first 25% of the generations were discarded as "burn-in", well after stationarity of chain likelihood values had been established, and the posterior probabilities were calculated from the remaining samples (pooled from the two simultaneous runs).

To establish how well each model fit the data, we calculated Bayes Factors (BF; Newton and Raftery, 1994; Kass and Raftery, 1995) in Tracer 1.5.0 (Rambaut and Drummond, 2009) using the harmonic mean as an approximation of the marginal likelihood of a model.

The concatenated data were also analyzed by maximum likelihood bootstrapping (MLB). MLB was done using RAxML-HPC2 version 7.3.2 (Stamatakis, 2006; Stamatakis et al., 2008) on the Cipres portal (Miller et al., 2010). The data were partitioned as in the BI⩽ (i.e. four and eight partitions, respectively; see above), and as per default GTRCAT was used for the bootstrapping phase, and GTRGAMMA for the final tree inference. 1000 replicates were run.

3. Results

3.1. Sequence characteristics

The combined data set of the concatenated sequences of all four genes (cyt *b*, ND2, myo and ODC) of 92 taxa contained 3495 characters, of which 1590 (45%) were parsimony informative.

The aligned cyt *b* of 81 taxa comprised 1041 characters, of which 481 (46%) were parsimony informative. For 39 sequences the complete target stretch was obtained, while 16 were incomplete at the ends and varied between 995 and 1038 bp in length. 23 sequences lacked longer fragments and were between 823 and 879 characters in length. Three sequences were 307–504 bp in total length.

The aligned ND2 of 91 taxa comprised 1041 characters, of which 623 (60%) were parsimony informative. For 50 sequences the complete target stretch was obtained. 30 sequences were incomplete at

the ends and varied between 1010 and 1038 bps in length. Another nine sequences were between 605 and 935 characters in length.

The length of the nuclear introns varied depending on multiple indels. The aligned ODC of 76 taxa comprised 765 characters, of which 289 (38%) were parsimony informative. For 59 sequences the complete target stretch varying between 659 and 705 bp in length was obtained. 15 sequences were 590–678 bps in length, being incomplete in the ends. Three incomplete sequences were 285–536 bp in length. A total of 18 inferred indel events shared by two or more taxa, as well as several autapomorphic indels were needed to satisfactorily align the ODC sequences.

The aligned myo sequences of 90 taxa comprised 650 characters, of which 235 (36%) were parsimony informative. For 82 sequences the complete target stretch of 514–626 bps in length was obtained. Five sequences were 604–610 bps in length, being incomplete at the beginning. Two sequences that were incomplete both at the beginning and the end were 246 and 261 bp in length, respectively. A total of 14 inferred indel events shared by two or more taxa, as well as several autapomorphic indels, were needed to satisfactorily align the myo sequences.

No unexpected stop codons, indels, or distinct double peaks in the chromatograms that would indicate the presence of nuclear pseudogenes were found in the coding cyt *b* or ND2 sequences. For the toepads, sequencing of several fragments failed, particularly for the nuclear loci.

3.2. Bayes Factor analyses

According to the Bayes Factor (BF) analyses, the more complex models (eight partitions for analyses of all loci and six partitions for analyses of two mitochondrial loci, respectively) were considerably better ($\ln BF > 1400$) than the models with fewer partitions (four for all loci and two for mitochondrial loci, respectively).

3.3. Single-locus analyses

The trees based on single-locus analyses (hereafter SLAs) varied in resolution. Within Cisticolidae, 100% of the nodes were bifurcating in the combined mitochondrial tree, 68% in the myo tree and 68% in the ODC tree (Supplementary Figs. S1–S3; see also Fig. 2, where gene trees are summarized in pie charts). In the cyt *b* and ND2 gene trees, 83% and 93% of the nodes were bifurcating, respectively (Supplementary Figs. S4 and S5; see also Fig. 2). Although both resolution and clade support varied among these trees, they generally agreed fairly well, and there were few strongly supported topological conflicts. There were only two conflicting reconstructions that received a posterior probability (PP) close to or over 0.95 in different trees: (1) the ODC tree (Supplementary Fig. S3) was in conflict with the other trees (Supplementary Figs. S2, S4 and S5) regarding the position of the members of the *Cisticola* clade, which according to ODC was sister to a clade consisting of *Prinia, Heliolais* and *Urorhipis* with 0.94 posterior probability (PP); and (2) *Garrulax leucolophus* was sister to *Pellorneum ruficeps* and *Prinia burnesii* according to ODC (0.97) (Supplementary Fig. S3), while *Graminicola bengalensis* was sister to these according to myo (1.0), cyt *b* (0.81) and ND2 (0.69) (Supplementary Figs. S2, S4 and S5).

3.4. Concatenated multi-locus analyses

The phylogeny based on the concatenated sequences (Figs. 1 and 2) were overall well supported by our data. The phylogeny was also entirely congruent with the trees obtained by Nguembock et al. (2007, 2012) and Alström et al. (2006). Within Cisticolidae, no polytomies were recovered, and 82% of the nodes received PP $\geqslant$ 0.95.

The inclusiveness of Cisticolidae suggested by the present study differs from those proposed by Sibley and Monroe (1993) and Dickinson (2003) in that three taxa are removed and several added. *Rhopophilus* was placed in Sylviidae *sensu* Fregin et al. (2012); *P. burnesii* was placed in Timaliidae *sensu* Fregin et al. (2012); and *Scotocerca* was placed as sister to Cettiidae *sensu* Fregin et al. (2012). Representatives of the genera *Drymocichla, Malcorus, Oreophilais, Phragmacia, Phyllolais* and *Urorhipis* have not been included in previous studies, and are here all shown to be part of Cisticolidae. The taxa *Artisornis*, *Bathmocercus*, *Eremomela*, *Neomixis*, *Orthotomus* and *Scepomycter*, which were placed in Sylviidae by Sibley and Monroe (1993), are here part of the Cisticolidae clade *sensu* Fregin et al. (2012), in accordance with previous studies (cf. Alström et al., 2006; Beresford et al., 2005; Cibois et al., 1999; Fregin et al., 2012; Johansson et al., 2008; Nguembock et al., 2007, 2008, 2012), except *Neomixis* which was sister to the main Cisticolidae clade in the combined analysis.

The Cisticolidae clade was divided into four well-supported subclades (clades A–D, Fig. 1), although the position of the Philippine *Micromacronus* could not be resolved. Clade A (PP 1.00) (Fig. 1) includes the speciose genera *Apalis* and *Eremomela*, and the genera *Artisornis, Calamonastes, Camaroptera, Drymocichla, Oreolais, Oreophilais, Phragmacia, Phyllolais, Poliolais, Schistolais, Spiloptila,* and *Urolais*. The genus *Apalis* was shown to be polyphyletic by Nguembock et al. (2007, 2008), and the latter study proposed the generic name *Oreolais* for a clade containing *A. pulchra* and *A. ruwenzorii*. In the present study, *A. metopias* was part of the *Oreolais* clade.

Clade B (Fig. 1) contains the speciose genus *Cisticola*, and seven other genera, most of which are monotypic. *Malcorus* and *Euryptila* are part of this clade.

Clade C (Fig. 1) contains the genera *Heliolais, Orthotomus, Prinia* and *Urorhipis*. Monophyly of the genus *Prinia* as circumscribed by Dickinson (2003) was not supported, as *P. burnesii* is removed and the clade including the type of the genus, *Prinia familiaris*, also contains the African *Heliolais erythroptera* and *Urorhipis rufifrons*. Furthermore, the taxa *Oreophilais robertsi, Phragmacia substriata, Schistolais leucopogon* (in clade A, Fig. 1), and *Malcorus pectoralis* (in clade B, Fig. 1), which have previously been placed in *Prinia* (e.g. Watson et al., 1986), are here shown not to be part of the *Prinia* clade.

Clade D (Fig. 1) consists of only three species in the genus *Neomixis*, and is sister to the rest of the Cisticolidae clade in the combined analysis. This was supported by the ND2 gene tree and the mitochondrial and ODC SLAs. In the cyt *b* gene tree and the myo SLA, the position of the *Neomixis* clade was unresolved relative to clades A–C (Fig. 2, S2, S5).

4. Discussion

4.1. Tree topology

The tree based on the concatenated sequences of four loci is overall well supported by our data, and entirely congruent with Nguembock et al. (2007). No strongly supported sister clade to Cisticolidae could be identified. The only previous study that recovered a topology with strong statistical support for specific sister groups is the one by Beresford et al. (2005), which was based on the nuclear RAG-1 and RAG-2. However, the more recent study by Fregin et al. (2012), which included RAG-1 (but not RAG-2) as well as six other markers and a larger number of species, was unable to resolve the exact position of Cisticolidae.

The precise position of *Cisticola* in the phylogeny is somewhat uncertain. Although the support for inclusion of *Cisticola* in clade B (Fig. 1) is high in the concatenated analysis, this is only based

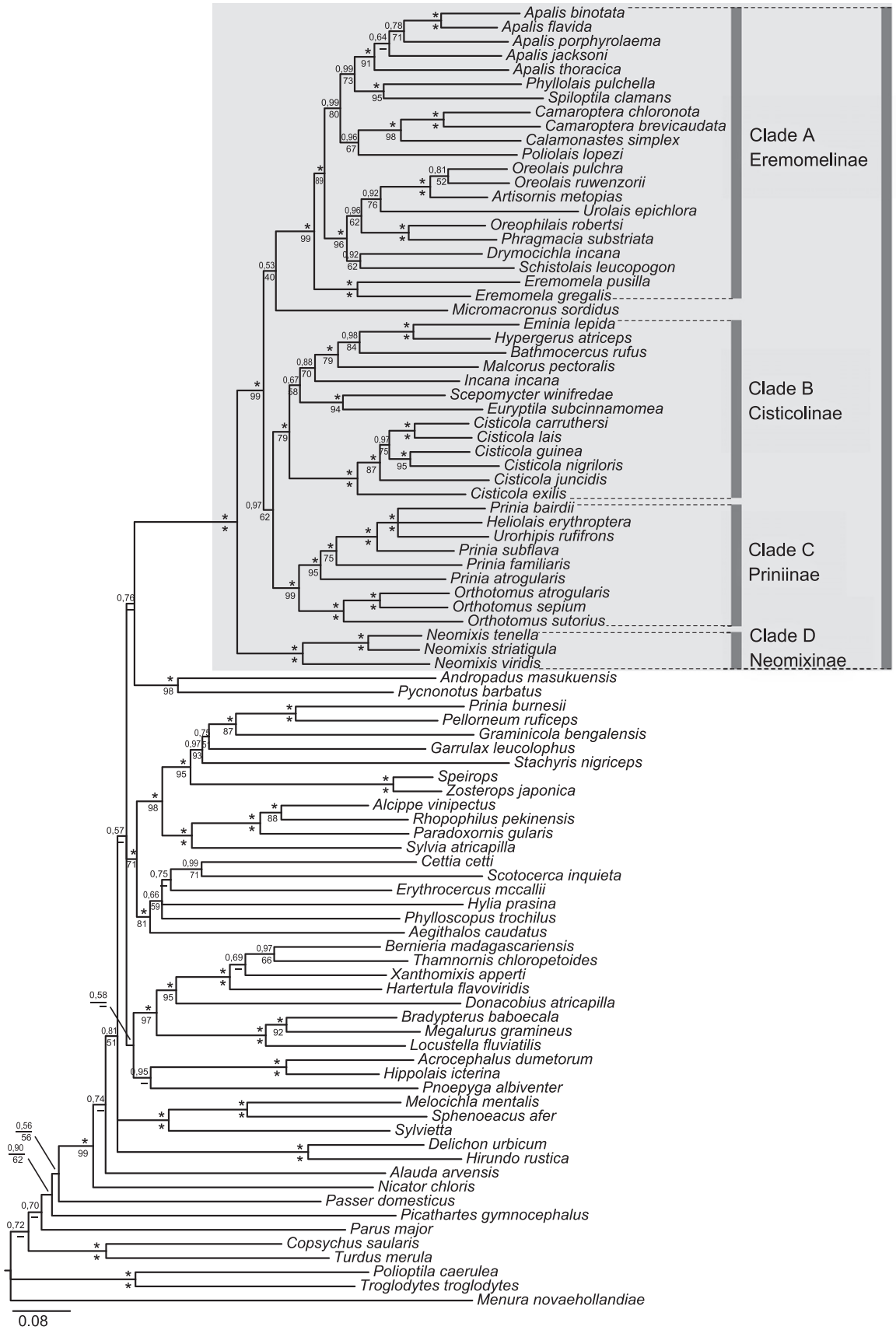

Fig. 1. Phylogeny of Cisticolidae and Sylvioidea outgroup taxa, estimated by Bayesian analysis of concatenated sequences of the mitochondrial cytochrome *b* and ND2 and nuclear myoglobin and ODC introns (in total 3495 bp) in eight partitions. Shaded area delimits Cisticolidae. Values at branches indicate posterior probability (above branches) and maximum likelihood bootstrap values (below branches); * denote posterior probability 1.00 or maximum likelihood bootstrap 100%.

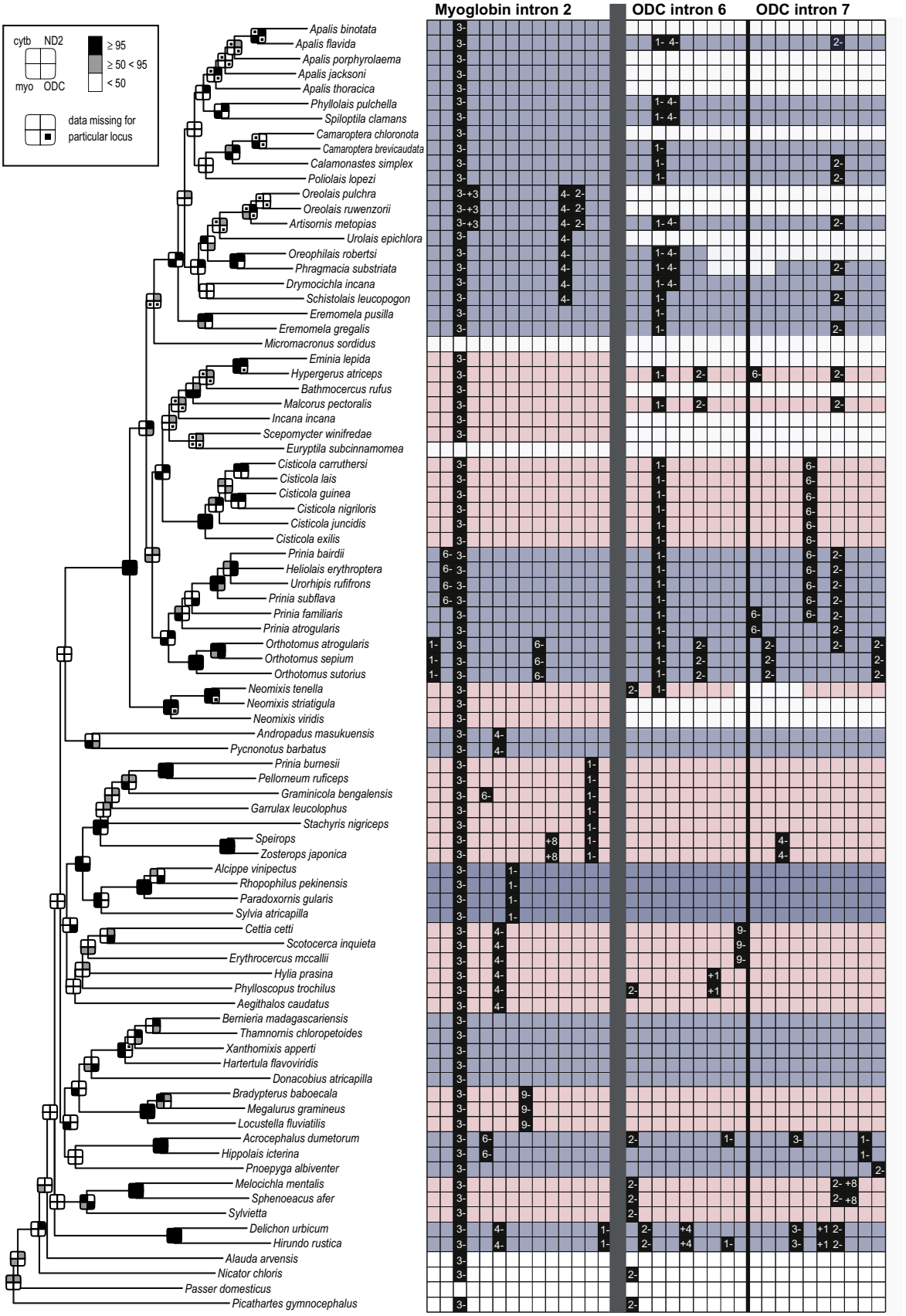

Fig. 2. Same phylogeny as in Fig. 1, with node support from gene tree analyses indicated by pie charts. Indels shared by two or more species are shown on the right. Background color delimits significant clades identified in the phylogeny. Lack of background color in the indel diagram denotes missing sequence data. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

on two loci. The cyt *b* tree is largely unresolved, and in the ODC tree *Cisticola* is placed as sister to the *Prinia* clade with moderate support.

4.1.1. Taxonomic implications – taxa not part of Cisticolidae

Prinia burnesii is placed with high support in the family Pellorneidae *sensu* Gill and Donsker (2011) and Fregin et al. (2012). As the type species of *Prinia* (*P. familiaris*) is part of clade B, *P. burnesii* is clearly not part of the genus *Prinia*. We propose that the generic name *Laticilla* is reinstated for this species. *Laticilla* Blyth, 1845 was introduced to replace *Eurycercus* Blyth, 1844, which is a protonym for *P. burnesii*, but this generic name is preoccupied by *Eurycercus* Baird, 1843 which is in current use in Cladocera (Arthropoda).

The monotypic genus *Rhopophilus*, which was previously commonly placed in Cisticolidae (e.g. Dickinson, 2003), has recently been shown to be part of Timaliidae (Alström et al., 2006) and Sylviidae (Gelang et al., 2009), respectively. This discrepancy between these authors is due to different taxonomic treatments of Timaliidae, which was treated as a single family by Alström et al. (2006) but divided into Timaliidae and Sylviidae by Gelang et al. (2009). Note that the use of the name Sylviidae *sensu* Gelang et al. (2009) differs considerably from that of previous authors (e.g. Watson et al., 1986; Sibley and Monroe, 1993; Dickinson, 2003; Ryan et al., 2006).

The monotypic genus *Scotocerca*, which was considered part of Cisticolidae by most previous authors (e.g. Sibley and Monroe, 1990; Dickinson, 2003; Ryan et al., 2006), was shown to be sister to Cettiidae by Alström et al. (2011a) and Fregin et al. (2012), and the latter authors proposed that it be placed in a new family, Scotocercidae.

4.1.2. Major clades in Cisticolidae

Four major clades are strongly supported in the multi-locus phylogeny (PP 1.00). For three of these, family-group names are available and we propose to recognize them taxonomically as follows:

- Eremomelinae Sharpe, 1883. Referred taxa: *Apalis, Artisornis, Calamonastes, Camaroptera, Drymocichla, Eremomela, Oreolais, Oreophilais, Phragmacia Phyllolais, Poliolais, Schistolais, Spiloptila,* and *Urolais* (Clade A, Fig. 1).
- Cisticolinae Sundevall, 1872. Referred taxa: *Bathmocercus, Cisticola, Eminia, Euryptila, Hypergerus, Incana, Malcorus,* and *Scepomycter* (Clade B, Fig. 1).
- Priniinae Roberts, 1922. Referred taxa: *Heliolais, Prinia, Orthotomus* and *Urorhipis* (Clade C, Fig. 1).
- Neomixinae Olsson, Irestedt, Sangster, Ericson and Alström, new subfamily. Type genus: *Neomixis* Sharpe, 1881. Diagnosis: small (10–12 cm) forest warblers; upperparts greenish, underparts yellow. Bill thin and pointed, shorter than tarsus; upper mandible prominently curved; rictal bristles absent. Wing pointed, seldom over 50 mm. Tail slightly rounded, shorter than wing. Legs and feet weak. Sexes similar. For a full description, see Salomonsen (1934). Restricted to Madagascar (Gee, 1986). Referred taxon: *Neomixis* (Clade D, Fig. 1).

The position of *Micromacronus* is unresolved, and future studies including nuclear loci are needed to determine whether the genus belongs in one of the above clades or if recognition at the subfamily level is warranted.

4.1.3. Taxonomic implications – Eremomelinae, Clade A

This clade corresponds to clade B *sensu* Nguembock et al. (2007) and the "Forest warblers cisticolid clade" *sensu* Nguembock et al. (2012). Although there are many exceptions and cases that are ambiguous, species that are part of this clade tend to occur in habitats that are forested or more heavily vegetated than the species in clade C in Nguembock et al. (2007), and the "Open warblers cisticolid clade" in Nguembock et al. (2012) (clades B and C, below).

Johansson et al. (2008) suggested that *Eremomela* was part of Cisticolidae, but their sample of cisticolids was limited. Our combined analyses placed *Eremomela* with high support in clade A. The taxonomy of this clade is complicated and merits further study. The most speciose genus *Apalis* is represented by a small fraction of the species allocated to it, but is still shown to be non-monophyletic. As previously shown by Nguembock et al. (2008), the two species *Apalis pulchra* and *Apalis ruwenzorii* are closely related to *Artisornis metopias*, and not part of the *Apalis* clade (which includes the type species *A. thoracica*), prompting them to erect the generic name *Oreolais* for *pulchra* and *ruwenzorii*. This was also supported in the combined analysis in Nguembock et al. (2012), although the sister relationship between *pulchra* and *ruwenzorii* was only recovered by one of their SLAs (ATPase 6) and contradicted by their ND2 SLA. The present study does not support a sister relationship between *A. pulchra* and *A. ruwenzorii* to the exclusion of *Artisornis*, but neither rejects it. As support for the genus *Oreolais* comes from a small number of loci, further analyses based on additional unlinked nuclear loci are warranted to evaluate its validity. A cautious approach would be to consider these species members of the genus *Artisornis* Friedmann, 1928, in accordance with the rule of priority (ICZN, 1999), though on present evidence (Nguembock et al., 2008, 2012) we tentatively retain *Oreolais*.

Oreophilais robertsi and *P. substriata* have been included in *Prinia* by various authors (e.g. Watson et al., 1986), but are here shown to be sisters to the *Urolais* and *Artisornis/Oreolais* clade. As *Oreophilais* and *Phragmacia* are themselves sisters, a valid taxonomic option is to place them in the same genus, with priority for *Phragmacia* Brooke and Dean, 1990. However, for lack of morphological or behavioral traits uniting them, we propose that *O. robertsi* and *P. substriata* are kept in monotypic genera for the time being.

The genera *Camaroptera* and *Calamonastes* form a monophyletic group, and may be in need of taxonomic revision (cf. Hall and Moreau, 1970; Dowsett and Forbes-Watson, 1993). However, this will require a denser taxon sampling than is included here, and should include the type species of *Calamonastes* (*C. fasciolatus*), which is missing for our dataset. There is good support for *Calamonastes* being part of the same clade as *Camaroptera* according to all the SLAs except ODC.

The clade comprising *Artisornis, Oreolais*, *Drymocichla, Phragmacia, Oreophilais, Schistolais* and *Urolais* is strongly supported in the multi-locus dataset and receives further support from a synapomorphic indel in the myoglobin alignment. Morphologically, this clade is supported by a reduced number of rectrices compared to the remainder of clade A (10 as compared to 12; but this trait is also shared with other genera in Cisticolidae, e.g. *Bathmocercus*, *Malcorus*, *Poliolais*, *Phyllolais* and some *Prinia*). As all these genera are monotypic, except *Oreolais, Schistolais* and *Artisornis* which contain two species each, a case can be made to place all species in this clade in a single genus, for which *Drymocichla* Hartlaub, 1881 would have priority. However, as the taxa that are part of this clade are morphologically diverse, we recommend that the current taxonomy is left unchanged.

4.1.4. Taxonomic implications – Cisticolinae, Clade B

This clade together with Clade C of this study correspond to a subclade in clade C in Nguembock et al. (2007) and to the "Open warblers cisticolid clade" in Nguembock et al. (2012). The topology of this clade is congruent with previous studies (Nguembock et al., 2007; Bowie et al., 2009), but *Malcorus pectoralis* and *Euryptila subcinnamomea* are added. The taxa in this clade are morphologically

Table 3
Recommended taxonomic changes compared to Dickinson (2003) and Sibley and Monroe (1990), based on the results of the present study.

	Recommended taxonomy	Comment
Artisornis, *incertae sedis*	in Cisticolidae	
Bathmocercus, in Sylviidae *sensu* Sibley and Monroe (1990)	in Cisticolidae	
Eremomela, in Sylviidae, *sensu* Sibley and Monroe (1990)	in Cisticolidae	
Heliolais erythroptera	*Prinia erythroptera*	
Micromacronus	in Cisticolidae	
Neomixis, *incertae sedis*	in Cisticolidae	
Orthotomus, *incertae sedis*	in Cisticolidae	
Poliolais, *incertae sedis*	in Cisticolidae	
Prinia burnesii, in Cisticolidae	*Laticilla burnesii,* in Timaliidae *sensu* Fregin et al. (2012)	
Rhopophilus, in Cisticolidae	in Sylviidae, *sensu* Fregin et al. (2012)	(1)
Scepomycter, in Sylviidae, *sensu* Sibley and Monroe (1993)	in Cisticolidae	
Scotocerca, in Cisticolidae	sister to Cettiidae, *sensu* Fregin et al. (2012)	(2)
Urorhipis rufifrons	*Prinia rufifrons*	(3)

(1) Previously shown by Alström et al. (2006) and Gelang et al. (2009). (2) Previously shown by Alström et al. (2011a). (3) Placed in *Spiloptila* by Dowsett and Forbes-Watson (1993).

and ecologically diverse, and although most genera are monotypic, we see no practical gain in merging any of them. The predominantly African genus *Cisticola* differs markedly from the other genera in this clade in being one of the most speciose of all avian genera (45 species, Dickinson, 2003).

4.1.5. Taxonomic implications – Priniinae, Clade C

This clade together with Clade B of this study correspond to a subclade in clade C in Nguembock et al. (2007) and to the "Open warblers cisticolid clade" in Nguembock et al. (2012). The clade is divided into two subclades, one containing the Asian *Orthotomus* and the other comprising the Asian and African *Prinia* and the African *Heliolais* and *Urorhipis*. The type of *Orthotomus* (*O. sepium*, Horsfield, 1821) is part of the Asian *Orthotomus* clade, thus determining the correct use of this generic name (corroborated by Alström et al., 2011b; Sheldon et al., 2012). Several taxa (*Artisornis, Malcorus, Oreophilais, Phragmacia, Prinia burnesii, Schistolais*, *Urolais*) that have previously been included in *Prinia* by various authors (e.g. Reichenow, 1907; Rüppell, 1835–1840; Sibley and Monroe, 1990; Watson et al., 1986) are here shown not to be part of the *Prinia* clade. On the other hand, *H. erythroptera* and *U. rufifrons* are firmly anchored in the *Prinia* clade, as was previously shown for the former by Alström et al. (2006) by a smaller number of taxa and loci. We propose that these two species are included in *Prinia,* under the names *Prinia erythroptera* and *Prinia rufifrons*, respectively (Table 3).

4.1.6. Taxonomic implications – Neomixinae, Clade D

This clade corresponds to clade A in Nguembock et al. (2007) and to the "Basal cisticolid clade" in Nguembock et al. (2012). The exact position of this clade must be regarded as somewhat uncertain. Two of the SLAs (ND2 and ODC) support a specific (sister) relationship with the remainder of Cisticolidae. A sister relationship of *Neomixis* to other Cisticolidae was previously found by Cibois et al. (1999) and Nguembock et al. (2007). Nevertheless, both its position as part of the Cisticolidae clade and monophyly of *Neomixis* are strongly supported. *Hartertula flavoviridis*, which has previously been included in *Neomixis* (e.g. Mayr and Paynter, 1964) is here part of the Bernieridae clade, consistent with previous molecular studies (Alström et al., 2011c, their Supplementary Fig. 2; Cibois et al., 1999, 2001; Fregin et al., 2012).

5. Future perspectives

The members of Cisticolidae are found in most terrestrial habitats, ranging from rainforest to wetlands or semi-desert. The clade consists of a mixture of monotypic genera with restricted distributions and several speciose genera (e.g. *Apalis*, *Cisticola, Eremomela, Prinia*), containing both restricted-range species and species with wide ranges. This mixture of relict species and proliferating genera suggests several bursts of adaptive radiation. Analysis of these patterns could provide valuable insights into the speciation process.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2012.11.004.

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