

---

# Phylogeny of babblers (Aves, Passeriformes): major lineages, family limits and classification

MAGNUS GELANG, ALICE CIBOIS, ERIC PASQUET, URBAN OLSSON, PER ALSTRÖM & PER G. P. ERICSON

---

Submitted: 21 July 2008

Accepted: 27 October 2008

doi:10.1111/j.1463-6409.2008.00374.x

Gelang, M. Cibois, A., Pasquet, E., Olsson, U., Alström, P. & Ericson, P. G. P. (2009). Phylogeny of babblers (Aves, Passeriformes): major lineages, family limits and classification. — *Zoologica Scripta*, 38, 225–236.

Babblers, family Timaliidae, have long been subject to debate on systematic position, family limits and internal taxonomy. In this study, we use five molecular regions to estimate the relationships among a large proportion of genera traditionally placed in Timaliidae. We find good support for five main clades within this radiation, and propose a new classification, dividing the babblers into the families Sylviidae and Timaliidae. Within the latter family, four subfamilies are recognized: Zosteropinae, Timaliinae, Pellorneinae and Leiotherichinae. Several taxa, previously not studied with molecular data, are phylogenetically placed within Sylviidae or Timaliidae. This is, however, not the case for the genus *Pnoepyga*, for which we propose the family name Pnoepygidae fam. n.

Corresponding author: Magnus Gelang, Department of vertebrate zoology, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden. E-mail: magnus.gelang@nrm.se  
Magnus Gelang and Per G. P. Ericson, Department of vertebrate zoology, Molecular Systematics Laboratory, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden. E-mails: magnus.gelang@nrm.se; per.ericson@nrm.se

Alice Cibois, Department of Mammalogy and Ornithology, Natural History Museum of Geneva, CP 6434, 1211 Geneva 6, Switzerland. E-mail: alice.cibois@ville-ge.ch

Eric Pasquet, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, UMR5202-CNRS, Case postale 51, 57 Rue Cuvier, F-75231, Paris Cedex 05, France. E-mail: pasquet@mnhn.fr

Urban Olsson, Göteborg University, Department of Zoology, Box 463, SE-405 30, Göteborg, Sweden. E-mail: urban.olsson@zool.gu.se

Per Alström, Swedish Species Information Centre, Swedish University of Agricultural Sciences, Box 7007, SE-75007 Uppsala, Sweden. E-mail: per.alstrom@artdata.slu.se

Magnus Gelang, Department of Zoology, Stockholm University, SE-10691 Stockholm, Sweden

## Introduction

The babblers, which are generally placed in the family Timaliidae (e.g. Cibois 2003a; Alström *et al.* 2006), include about 400 species in more than 60 genera distributed throughout the Australian, Pacific, Eurasian and African regions, with one representative in the New World, the Wrentit *Chamaea fasciata* occurring in North America (Collar & Robson 2007). Morphologically, Timaliidae is defined by its members having unspotted juvenile plumage, usually a single annual moult, scutellated tarsus, presence of rictal bristles, and double humeral fossa. Moreover, the species are generally gregarious, non-migratory and lack seasonal plumages variation. (Sibley & Ahlquist 1990 and references therein). Traditionally, babblers were placed in the 'Old World insectivorous' group, Muscicapidae *sensu* Hartert (1910), Mayr & Amadon (1951) and Deignan (1964), although Beecher (1953) placed most babblers

in Timaliidae, within the superfamily Timalioidea. Based on DNA–DNA hybridization, Sibley & Ahlquist (1990) divided the babblers into the subfamilies Garrulacinae and Sylviinae, and placed them together with warblers (Megalurinae and Acrocephalinae) in the family Sylviidae, as part of the superfamily Sylvioidea. They further divided Sylviinae into three tribes, Timaliini, Chamaeini and Sylviini. They excluded the Australian babblers (i.e. *Garritornis* and *Pomatostomus*) from the typical babblers. Cibois *et al.* (1999, 2001) excluded a number of genera from Timaliidae, such as the Malagasy babblers (e.g. *Neomixis*, *Oxylabes*, *Crossleyia* and *Mystacornis*) and the monotypic genus *Erpornis* (formerly *Yubina zantholeuca*). Cibois (2003a) also excluded *Pteruthius* and *Kakamega*, while including *Zosterops* and *Sylvia*. Several other authors have confirmed the close relationships of *Sylvia* and *Zosterops* to the babblers (Barker *et al.* 2002, 2004; Ericson & Johansson 2003;

Beresford *et al.* 2005; Alström *et al.* 2006). Sibley & Ahlquist (1990) proposed Zosteropidae to be sister to babblers and *Sylvia*.

Until now, Cibois (2003a) has made the only study comprising a broadly represented Timaliidae. According to her phylogeny based on mitochondrial DNA sequence data, six main clades within Timaliidae are recognized. However, the relationships among these clades are generally with poor support. Her results show one clade comprising *Sylvia*, *Pseudoalcippe*, *Paradoxornis*, *Chamaea*, *Chrysomma*, and two representatives of the genus *Alcippe*. This clade is sister to the remaining Timaliidae. Within the main timaliid clade, a clade comprising representatives of the genera *Yubina* and *Zosterops* is sister to the other taxa. A third clade containing *Alcippe poiocephala* and *A. morrisonia* is the sister to two clades, one containing tree- and scimitar babblers (e.g. *Pomatorhinus*, *Stachyris*, *Macronous* and *Timalia*), and one containing jungle- and wren babblers (e.g. *Napothera*, *Malacopteron*, *Pellorneum* and *Illadopsis*). The sister clade to these three clades comprises the song babblers (e.g. *Leiothrix*, *Minla*, *Actinoura* and *Heterophasia*), laughingthrushes (i.e. *Garrulax* and *Babax*) and the genus *Cutia*.

A handful of recent studies concerning Timaliidae systematics have been made based on mitochondrial sequence data. Cibois *et al.* (2002) suggested the genera *Yubina* and *Stachyris* to be paraphyletic with *Zosterops* and the Philippine *Stachyris* nested within *Yubina* (Cibois *et al.* 2002; Cibois 2003a). This was later reconfirmed by Zhang *et al.* (2007). The genus *Alcippe* was revealed by Pasquet *et al.* (2006) to be polyphyletic, and separated into four different clades within Timaliidae, and a taxonomic rearrangement was proposed. Despite the number of recent studies concerning Timaliidae, the major lineages are still vaguely defined phylogenetically and their relationships remain to solve.

Delacour (e.g. 1946, 1950) did extensive work on the taxonomy of Timaliidae, much of which has been confirmed by recent molecular phylogenies. Recently, Collar (2006) proposed a partly revised taxonomy of several Oriental genera and species of Timaliidae.

The inclusion of *Sylvia* in the babbler radiation exemplifies a taxonomic problem, as *Sylvia* is the type genus for Sylviidae Leach, 1820 and well-established for warblers, whereas Timaliidae Vigors & Horsfield 1827 is well-established for babblers, as remarked by Cibois (2003a, 2003b).

We here present a broadly sampled phylogeny of Timaliidae based on DNA sequence data from one mitochondrial and four nuclear loci. Our main aims are to identify the major lineages of the babblers and to better resolve their inter-relationships, based on mitochondrial and nuclear regions. Further, several taxa previously not studied with molecular data are included in this study to add more to the knowledge about the limits and internal relationships of babblers. We also propose changes to the classification.

## Materials and methods

### Study group and laboratory procedures

DNA was obtained from tissue, blood or footpads from 59 species in 46 genera representing Timaliidae, 11 non-timaliid genera representing all except one of the other Sylviidae families or main clades recognized by Alström *et al.* (2006) and Johansson *et al.* (2008), and three representatives of non-sylvioid groups used as outgroups (Table 1). We follow the taxonomy of Dickinson (2003), except for the genera *Alcippe* for which we follow Pasquet *et al.* (2006), and *Rimathorax* and *Napothera* for which we follow Collar (2006).

The laboratory procedures of extraction, amplification and sequencing of three nuclear introns, glyceraldehyde-3-phosphate dehydrogenase intron 11 (GAPDH), myoglobin intron 2 (myoglobin) and ornithine decarboxylase introns 6–7 (ODC), the nuclear protein-coding recombination-activating gene (RAG-1) and the mitochondrial protein-coding gene NADH dehydrogenase II (ND2), followed standard protocols (QiaGene). However, for the material from old study skins we followed Irestedt *et al.* (2006), mainly using hot start touchdown PCR, with three phases of four, four, and finally 32 cycles, with annealing temperatures for each primer combination as shown in electronic supplementary material. For amplification and sequencing of old skins, primers were designed mainly following Irestedt *et al.* (2006), using on-line tools such as Cybergene and Genewalker (available from <www.cybergene.se>), after a by-eye design based on alignments of closely related species. Sequences from four of the taxa without specimen voucher (*Graminicola*, *Rhopophilus*, *Spelaeoris* and *Pnoepyga*) were checked by complementary sequences from study skins, to confirm the identifications. This was also the case for the name-bearing taxa for subfamily names without specimen voucher (*Leiothrix*, *Pellorneum* and *Zosterops*). No unexpected start or stop codons that could indicate the presence of nuclear copies were found in the ND2 sequences.

### Phylogenetic analyses

The sequences were aligned using MegAlign 4.00, DNASTAR package (DNA STAR, Inc.) by the Clustal V algorithm (Higgins *et al.* 1992) with complementary manual adjustments. We estimated the phylogeny by Bayesian inference (BI) using MRBAYES 3.1.1 (Huelsenbeck & Ronquist 2001). To determine evolutionary models implemented in the BI analyses we used MrModeltest2.2 (Nylander 2005) in conjunction with PAUP 4.0b10 (Swofford 2001) with the Akaike Information Criterion (Akaike 1973) applied. For GAPDH, the HKY model (Hasegawa *et al.* 1985) with a gamma-shaped distribution of rates across sites ( $\Gamma$ ) was proposed, for myoglobin the GTR model (Lanave *et al.* 1984; Tavaré 1986; Rodríguez *et al.* 1990) +  $\Gamma$  was proposed. For ND2, ODC and RAG-1 the GTR model +  $\Gamma$  with a proportion of invariable

**Table 1** List of samples used in this study, and GenBank accession numbers of DNA sequences. Samples marked with a are specimen-vouchered samples, b and c are digitally vouchered by photo and sound recording, respectively.

Taxon	Mus. No.	Locality	GAPDH	Myo	ND2	ODC	RAG-1
Ingroup							
<i>Actinodura souliei griseinucha</i>	MNHN 7–13	Vietnam	FJ357853	FJ357924	DQ861971 <sup>1</sup>	FJ358022	FJ358088
<i>Alcippe poioicephala alearis</i>	MNHN 6–74	Umphang, Thailand	FJ357854	FJ357925	DQ861943 <sup>1</sup>	FJ358023	FJ358089
<i>Babax lanceolatus</i> <sup>b</sup>	MNHN 16–6G	Yunnan, China	FJ357855	FJ357926	DQ861979 <sup>1</sup>	FJ358024	FJ358090
<i>Chamaea fasciata</i> <sup>a</sup>	MNHN 8–12	California, USA	FJ357856	FJ357927	DQ861975 <sup>1</sup>	FJ358025	FJ358091
<i>Chrysomma sinense sinense</i>	MNHN 16–3B	Yunnan, China	FJ357857	FJ357928	FJ357986	FJ358026	FJ358092
<i>Cutia nipalensis</i>	MNHN 7–21	Vietnam	FJ357858	FJ357929	DQ861972 <sup>1</sup>	FJ358027	FJ358093
<i>Dumetia hyperythra albogularis</i>	A. Helbig coll.	Mysore, India	FJ357859	FJ357930	FJ357987	FJ358028	FJ358094
<i>Fulvetta vinipectus bietti</i> <sup>b</sup>	MNHN 18–26	NW Yunnan, China	FJ357860	FJ357931	DQ861951 <sup>1</sup>	FJ358029	FJ358095
<i>Gampsorhynchus rufulus</i>	MNHN 4–71	Thailand	FJ357861	FJ357932	DQ861938 <sup>1</sup>	FJ358030	FJ358096
<i>Garrulax erythrocephalus</i>	MNHN 7–20	Vietnam	FJ357862	FJ357933	DQ861987 <sup>1</sup>	FJ358031	FJ358097
<i>Garrulax leucolophus</i>	MNHN 4–6E	Thailand	FJ357863	FJ357934	DQ861939 <sup>1</sup>	FJ358032	FJ358098
<i>Garrulax sannio</i>	MNHN 16–5J	Yunnan, China	FJ357864	FJ357935	DQ861980 <sup>1</sup>	FJ358033	FJ358099
<i>Graminicola b. bengalensis</i>	NRM 20046789	Nepal	FJ357865	DQ008532 <sup>2</sup>	FJ357988	FJ358034	FJ358100
<i>Heleia crassirostris</i> <sup>b,c</sup>	NRM 20086719	Flores, Indonesia	FJ357866	FJ357936	FJ357989	FJ358035	FJ358101
<i>Heterophasia melanoleuca</i>	MNHN 7–26	Vietnam	FJ357867	FJ357937	DQ861974 <sup>1</sup>	FJ358036	FJ358102
<i>Illadopsis cleaveri batesi</i> <sup>a</sup>	MNHN 2–38	Cameroon	FJ357868	FJ357938	DQ861970 <sup>1</sup>	FJ358037	FJ358103
<i>Jabouilleia danjoui</i> <sup>b</sup>	NRM 20047078	Vietnam	FJ357869	FJ357939	FJ357990	FJ358038	FJ358104
<i>Kenopia striata</i> <sup>a</sup>	MNHN 8–95	Sabah, Malaysia	FJ357870	FJ357940	DQ861985 <sup>1</sup>	FJ358039	FJ358105
<i>Kupeornis gilberti</i> <sup>a</sup>	NRM 569566	Cameroon	FJ357871	FJ357941	FJ357991	FJ358040	FJ358106
<i>Leiothrix argentauris</i>	MNHN 8–18	Captive bird	FJ357872	FJ357942	DQ861945 <sup>1</sup>	FJ358041	FJ358107
<i>Liocichla steerii</i> <sup>a</sup>	MNHN 8–98	Taiwan	FJ357873	FJ357943	DQ861986 <sup>1</sup>	FJ358042	FJ358108
<i>Lioparus chrysotis forresti</i>	NRM 20046751	Vietnam	FJ357874	FJ357944	DQ861978 <sup>1</sup>	FJ358043	FJ358109
<i>Lophozosterops javanicus frontalis</i> <sup>b</sup>	NRM 20086720	W Java, Indonesia	FJ357875	FJ357945	FJ357992	FJ358044	FJ358110
<i>Lophozosterops s. superciliosus</i> <sup>b</sup>	NRM 20086721	Flores, Indonesia	FJ357876	FJ357946	FJ357993	FJ358045	FJ358111
<i>Macronous gularis</i> <sup>b</sup>	NRM 20046770	Vietnam	FJ357877	FJ357947	DQ861941 <sup>1</sup>	FJ358046	FJ358112
<i>Malacocincla abbotti</i>	MNHN 4–5I	Thailand	FJ357878	FJ357948	DQ861942 <sup>1</sup>	FJ358047	FJ358113
<i>Minla cyanouoptera sordida</i>	NRM 20046756	Vietnam	FJ357879	FJ357949	FJ357994	FJ358048	FJ358114
<i>Minla ignotincta</i>	MNHN 8–14	Captive bird	FJ357880	FJ357950	FJ357995	FJ358049	FJ358115
<i>Myzornis pyrrhoura</i> <sup>a</sup>	NRM 19838	Sikkim, India	FJ357881	FJ357951	FJ357996	FJ358050	FJ358116
<i>Napothera epilepidota</i>	MNHN 8–82	Vietnam	FJ357882	FJ357952	DQ861983 <sup>1</sup>	FJ358051	FJ358117
<i>Paradoxornis gularis transfluvialis</i> <sup>b</sup>	NRM 20046761	Vietnam	FJ357883	FJ357953	FJ357997	FJ358052	FJ358118
<i>Paradoxornis nipalensis</i>	MNHN 14–22	Yunnan, China	FJ357884	FJ357954	DQ861981 <sup>1</sup>	FJ358053	FJ358119
<i>Paradoxornis verreauxi craddocki</i>	NRM 20046746	Vietnam	FJ357885	FJ357955	FJ357998	FJ358054	FJ358120
<i>Parophasma galinieri</i> <sup>a</sup>	NRM 19783	Addis–Abeba, Ethiopia	FJ357886	FJ357956	FJ357999	FJ358055	FJ358121
<i>Pellorneum ruficeps</i>	MNHN 4–6F	Thailand	FJ357887	FJ357957	DQ861988 <sup>1</sup>	FJ358056	FJ358122
<i>Phyllanthus atripennis bohndorffi</i> <sup>a</sup>	NRM 19787	Beni, Congo	FJ357888	FJ357958	FJ358000	FJ358057	FJ358123
<i>Pnoepyga albiventer albiventer</i> <sup>b,c</sup>	NRM 20086723	Sichuan, China	FJ357889	FJ357959	FJ358001	FJ358058	FJ358124
<i>Pnoepyga pusilla pusilla</i> <sup>b</sup>	NRM 20086724	Yunnan, China	FJ357890	FJ357960	FJ358002	FJ358059	FJ358125
<i>Pomatorhinus ochraceiceps</i> <sup>a</sup>	MNHN 8–47	Laos	FJ357891	FJ357961	FJ358003	FJ358060	FJ358126
<i>Pomatorhinus schisticeps</i>	MNHN 6–73	Thailand	FJ357892	FJ357962	DQ861944 <sup>1</sup>	FJ358061	FJ358127
<i>Ptyrticus turdinus turdinus</i> <sup>a</sup>	NRM 18933	Yambio, Sudan	FJ357893	FJ357963	FJ358004	FJ358062	FJ358128
<i>Rhopophilus pekinensis albosuperciliaris</i> <sup>b</sup>	NRM 20046792	Xinjiang, China	FJ357894	DQ008538 <sup>2</sup>	FJ358005	FJ358063	FJ358129
<i>Rimator pasquieri</i> <sup>a</sup>	NRM 569992	Tonkin, Vietnam	FJ357895	FJ357964	FJ358006	FJ358064	FJ358130
<i>Schoeniparus rufogularis</i> <sup>b</sup>	NRM 20046763	Vietnam	FJ357896	FJ357965	DQ861955 <sup>1</sup>	FJ358065	FJ358131
<i>Speirops lugubris lugubris</i> <sup>a</sup>	NRM 847677	São Thomé island	FJ357897	FJ357966	FJ358007	FJ358066	FJ358132
<i>Spelaeornis chocolatinus</i>	MNHN 14–12	Yunnan, China	FJ357898	FJ357967	DQ861982 <sup>1</sup>	FJ358067	FJ358133
<i>Stachyris chrysaea</i>	MNHN 8–79	Vietnam	FJ357899	FJ357968	FJ358008	FJ358068	FJ358134
<i>Stachyris nigriceps</i>	MNHN 4–6H	Thailand	FJ357900	FJ357969	FJ358009	FJ358069	FJ358135
<i>Stachyris striolata</i>	NRM 20026625	Vietnam	FJ357901	FJ357970	FJ358010	FJ358070	FJ358136
<i>Stachyris whiteheadi</i>	ZMUC 118874	Luzon, The Philippines	FJ357902	FJ357971	FJ358011	FJ358071	FJ358137
<i>Sylvia atricapilla</i>	NRM 976380	Blekinge, Sweden	EF441232 <sup>6</sup>	AY887727 <sup>2</sup>	DQ125994 <sup>4</sup>	EF441254 <sup>6</sup>	AY228038 <sup>3</sup>
<i>Timalia pileolata dictator</i> <sup>a</sup>	NRM 569652	Vietnam	FJ357903	FJ357972	—	FJ358072	FJ358138
<i>Turdinus macrodactyla</i> <sup>b</sup>	NRM 20086722	Bali (market), Indonesia	FJ357904	FJ357973	FJ358012	FJ358073	FJ358139
<i>Turdoides jardineii</i> <sup>a</sup>	MNHN 8–28	Botswana	FJ357905	FJ357974	—	FJ358074	FJ358140

**Table 1** *Continued.*

Taxon	Mus. No.	Locality	GAPDH	Myo	ND2	ODC	RAG-1
<i>Xiphirhynchus s. superciliosus</i> <sup>a</sup>	NRM 569663	Tonkin, Vietnam	FJ357906	FJ357975	FJ358013	FJ358075	FJ358141
<i>Yuhina diademata</i> <sup>b</sup>	MNHN 18–28	Yunnan, China	FJ357907	FJ357976	FJ358014	FJ358076	FJ358142
<i>Yuhina flavicollis rouxi</i> <sup>b</sup>	NRM 20046752	Vietnam	FJ357908	FJ357977	FJ358015	FJ358077	FJ358143
<i>Yuhina gularis gularis</i>	MNHN 7–24	Vietnam	FJ357909	FJ357978	DQ861973 <sup>1</sup>	FJ358078	FJ358144
<i>Zosterops japonica simplex</i> <sup>b</sup>	MNHN 16–6F	Yunnan, China	FJ357910	FJ357979	DQ861968 <sup>1</sup>	FJ358079	FJ358145
Outgroup							
<i>Acrocephalus dumetorum</i>	NRM 569279	Punjab, India	FJ357911	AY887682 <sup>2</sup>	FJ358016	EF625338 <sup>5</sup>	FJ358146
<i>Aegithalos caudatus caudatus</i>	NRM 976089	Uppland, Sweden	FJ357912	AY228281 <sup>3</sup>	AY136588 <sup>10</sup>	EU680703 <sup>11</sup>	AY228001 <sup>3</sup>
<i>Alauda arvensis arvensis</i>	NRM 966614	Sörmland, Sweden	FJ357913	AY228284 <sup>3</sup>	DQ125975 <sup>4</sup>	EF625336 <sup>5</sup>	AY056978 <sup>6</sup>
<i>Corvus corone</i> <sup>a</sup>	MNHN 21–16	France	FJ357914	FJ357980	FJ358017	FJ358080	AY056989 <sup>6</sup>
<i>Donacobius atricapilla atricapilla</i>	NRM 966966	Paraguay	FJ357915	DQ008533 <sup>2</sup>	FJ358018	EU680723 <sup>5</sup>	FJ358147
<i>Hirundo rustica</i>	NRM 973268	Sweden	EF441218 <sup>7</sup>	AY064258 <sup>8</sup>	AY052463 <sup>9</sup>	EF441240 <sup>7</sup>	AY443290 <sup>12</sup>
<i>Lanius collaris</i>	MNHN 2–26	Cameroon	FJ357916	FJ357981	FJ358019	FJ358081	FJ358148
<i>Megalurus palustris toklaio</i>	NRM 20046781	Punjab, India	FJ357917	DQ008529 <sup>2</sup>	FJ358020	EU680741 <sup>11</sup>	AY319988 <sup>13</sup>
<i>Muscicapa striata</i> <sup>a</sup>	MNHN 23–1A	France	FJ357918	FJ357982	DQ861967 <sup>1</sup>	FJ358082	FJ358149
<i>Panurus biarmicus biarmicus</i>	NRM 20026034	Sweden	FJ357919	FJ357983	FJ358021	FJ358083	FJ358150
<i>Phylloscopus collybita abietinus</i>	NRM 20036964	Sweden	FJ357920	DQ125966 <sup>4</sup>	DQ125988 <sup>4</sup>	FJ358084	AY319997 <sup>13</sup>
<i>Prinia bairdii</i>	MNHN 2–45	Cameroon	FJ357921	FJ357984	DQ126000 <sup>4</sup>	FJ358085	FJ358151
<i>Pycnonotus barbatus</i>	MNHN 2–21	Cameroon	FJ357922	FJ357985	DQ402232 <sup>14</sup>	FJ358086	FJ358152
<i>Thamnornis chloropetoides</i> <sup>a</sup>	FMNH 436448	Madagascar	FJ357923	DQ125971 <sup>4</sup>	DQ125995 <sup>4</sup>	FJ358087	AY320004 <sup>13</sup>

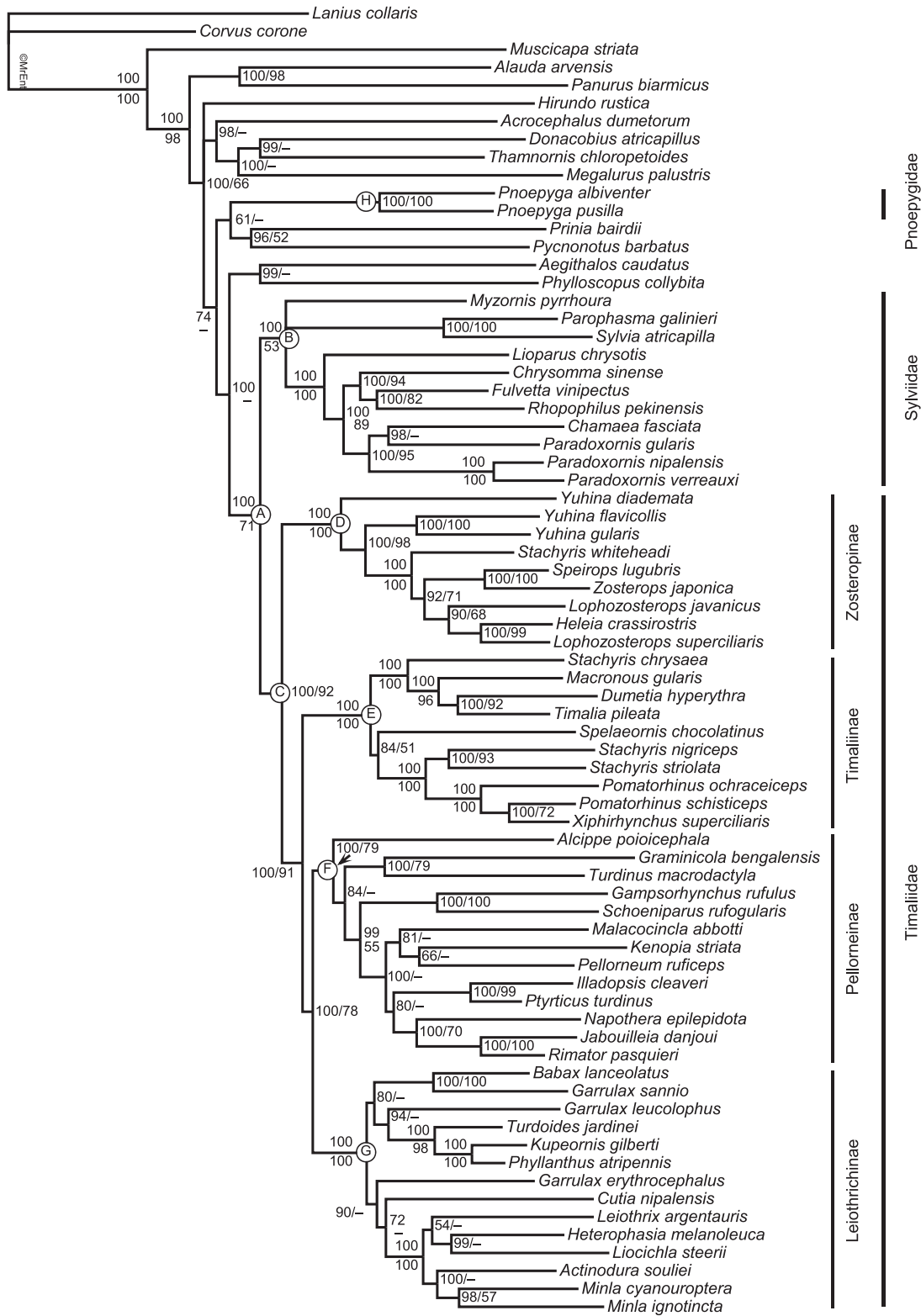
MNHN, Muséum National d'Histoire Naturelle, Paris; NRM, Swedish Museum of Natural History, Stockholm; ZMC, Zoological Museum of Copenhagen. A. Helbig coll., Personal collection of Andreas Helbig; FMNH, Field Museum of Natural History, Chicago. GenBank accession numbers indicated with numbers are from following studies: <sup>1</sup>Pasquet *et al.* (2006); <sup>2</sup>Alström *et al.* (2006); <sup>3</sup>Ericson & Johansson (2003); <sup>4</sup>Fuchs *et al.* (2006); <sup>5</sup>Johansson *et al.* (2007); <sup>6</sup>Barker *et al.* (2002); <sup>7</sup>Jönsson *et al.* (2007); <sup>8</sup>Ericson *et al.* (2002); <sup>9</sup>Wittingham *et al.* (2002); <sup>10</sup>Sevc *et al.* (2003); <sup>11</sup>Johansson *et al.* (2008); <sup>12</sup>Barker *et al.* (2004); <sup>13</sup>Barker *et al.* (unpublished); <sup>14</sup>Moyle & Marks (2006).

sites (I) (Gu *et al.* 1995) were proposed. We estimated phylogenies for all regions in a combined analysis, as well as each region independently. In the combined analysis, the concatenated sequences were partitioned based on the selected substitution models, but the topology was constrained to be the same. Each analysis was started from random trees with four Metropolis-coupled MCMC chains run for five million generations, sampled every 100 generation. The burn-in phase (generally the first 200 000 generations, before the chains had reached the target distributions) was discarded and the posterior probabilities were calculated for the remaining generations. In addition to the BI analysis of the combined data set, we also estimated the phylogeny with Maximum Likelihood (ML) by using TreeFinder [version of January 2008] (Jobb 1997–2008). The ML analysis was performed using the GTR (optimum, empirical) model with the data set analysed as one partition, with default settings and 1000 bootstrap replicates for a 50% consensus tree. All trees were edited using MrEnt 2.0. (Zuccon & Zuccon 2005–2008).

## Results

We obtained a data set of 5925 characters divided in 452 base pairs (bp) of GAPDH, 812 bp of myoglobin, 1023 bp of ND2, 766 bp of ODC and 2872 bp of RAG-1. For *Timalia pileata* and *Turdoides jardineii*, we were not able to obtain any ND2 sequences, and only partial sequences were obtained from the study skins.

According to the combined BI analysis we find good support for a monophyletic babbler radiation (clade A, Fig. 1) containing all ingroup taxa included in this study except the genus *Pnoepyga*. The ML analysis is congruent with the BI analysis, with no topological conflicts (Fig. 1). The babbler clade is sister to a clade containing the genera *Aegithalos* and *Phylloscopus*, with high posterior probability (100%), but unresolved in the ML. Clade A is divided into five subclades (B, D–G), all well-supported (except for moderate ML support for clade A, moderate ML support for the sister relationships of clades F and G, and low ML support for clade B). Clade B, comprising *Sylvia*, *Myzornis*, *Chrysomma*, *Rhopophilus*, *Paradoxornis*, *Chamaea*, etc., is sister to the remaining babblers. The genus *Paradoxornis* is paraphyletic, as *P. gularis* is sister to *C. fasciata*, albeit with no ML support. Two former members of the genus *Alcippe* belong to this clade (*Lioparus chrysotis* and *Fulvetta vimipectus sensu* Pasquet *et al.* 2006). The genera *Sylvia* and *Parophasma* group together and form a trichotomy with *Myzornis* and the rest of the clade. Clade D, containing *Yuhina*, *Stachyris whiteheadi* and Zosteropidae *sensu* Sibley & Ahlquist (1990), is sister to the three remaining clades. In this clade the genera *Lophozosterops* and *Yuhina* prove to be paraphyletic, and *Stachyris whiteheadi* groups with Zosteropidae. Of the three remaining clades, the tree- and scimitar babbler clade (E) is sister to the two remaining clades (F and G). This clade also includes the genus



**Fig. 1** The 50% majority rule consensus tree obtained from the Bayesian analysis of the combined data, with posterior probabilities above and ML bootstrap values below. The letters A–H. refers to comments in the text. Proposed family and subfamily names are shown with vertical lines.

*Spelaeorthis*, but from our data we are not able to find its exact position in this clade. The genus *Stachyris* is non-monophyletic. The genus *Alcippe sensu* Pasquet *et al.* (2006), and jungle- and wren babblers (except the genera *Spelaeorthis* and *Pnoepyga*) form a clade (F). A former member of *Alcippe* also belongs to this clade (*Schoeniparus rufogularis sensu* Pasquet *et al.* 2006), as do the genera *Graminicola* and *Gampsorbhynchus*. *Ptyrticus* and *Illadopsis* group together, as do *Jabouilleia* and *Rimator*, the two latter as sisters to *Napothera epilepidota*. The laughing-thrush, ground- and song babbler clade (G) is poorly resolved, but with one well-supported clade consisting of song babblers. One clade consists of ground babblers (*Turdoides*) and the two genera *Kupeornis* and *Phyllanthus*, which group together with good support. The genus *Garrulax* is paraphyletic.

From our analysis we are not able to find the exact affinity of the genus *Pnoepyga* (clade H), but it is outside the babbler radiation (clade A) and well within Sylvioidea with high posterior probability. However, the ML analysis is generally unresolved in this part of the Sylvioidea tree.

With some exceptions, the separate gene trees show generally congruent topologies with respect to well-supported clades (Fig. 2). Large parts of the GAPDH tree are unresolved, but there is no conflict in topology with the combined tree. The myoglobin tree is congruent with the combined analyses in placing the clade containing *Paradoxornis*, *Sylvia*, etc. (clade B in Fig. 1) as sister to the remaining Timaliidae. The ND2 tree is congruent with the combined tree in placing the clade containing *Yubina*, *Stachyris whiteheadi* and Zosteropidae as sister to the three 'crown Timaliidae' clades (E–G in Fig. 1). In neither the ODC tree nor the RAG-1 tree are the relationships of the internal clades of Timaliidae supported. In the ND2 tree *Myzornis* falls outside Timaliidae, while *Aegithalos* is sister to *Sylvia* and *Parophasma*, and *Alcippe poiocephala* groups together with *Cutia*. In the ODC tree *Myzornis* groups together with the tree- and scimitar babbler clade (clade E in Fig. 1).

## Discussion

Our results from both BI and ML of the combined data set support the monophyly of the babblers (clade A), with the exclusion of the genus *Pnoepyga*. The genera previously proposed to be moved from other families to Timaliidae, namely *Zosterops* and *Sylvia* (Cibois 2003a; Beresford *et al.* 2005; Alström *et al.* 2006) and *Graminicola* and *Rhopophilus* (Alström *et al.* 2006), are all members of the babbler radiation in our analysis. These results are congruent with the circumscription of Timaliidae according to Cibois (2003a), Alström *et al.* (2006) and Johansson *et al.* (2008). Overall, the relationships among the five main clades within Timaliidae are fully resolved and well-supported. In a few cases, the support differs between the BI and ML analyses. The ML gives moderate support for

clade B as sister to clade C, as well as the sister relationship between clades F and G. The sister relationships of clades D and E–G, and E and F–G are reasonably well-supported by the ML. The BI infers high (100%) posterior probabilities for all these clades. Importantly, the topologies are congruent between the two analyses. The single-locus trees (Fig. 2) are generally congruent in recovering five main clades (except for GAPDH), but the support is generally low. With two exceptions, no incongruence with good support was found between the single-locus trees. In the ODC tree, *Myzornis* is sister to the tree- and scimitar babbler clade with good support, while it is inferred to be outside Timaliidae in the ND2 tree (albeit with weak support). Further, ND2 inferred *Aegithalos* as sister to *Sylvia* and *Parophasma*. Compared to the results of Cibois (2003a), the major lineages are congruent between the studies (*Alcippe* exceptional). However, the topology based on mitochondrial data obtained no, or low support, while we obtained generally strong support with combined mitochondrial and nuclear sequence data.

The genus *Pnoepyga* is consistently found outside of Timaliidae, although we are not able to infer its exact position. This genus is aberrant compared to the babblers in several aspects, such as having non-social behaviours, and morphologically by extremely short tail, and two colour morphs are present for the members of this genus (Collar & Robson 2007).

The members of clade B (Fig. 1) have an African and Eurasian distribution, but are more or less absent from tropical South-east Asia (Dickinson 2003; Collar & Robson 2007). The species typically inhabit drier habitats, such as bushes, grass, bamboo thickets or macchia. *Chamaea fasciata* is exceptional in occurring in dense vegetation of various habitats in North America (Collar & Robson 2007). After years of debate about the systematic affinity of *Chamaea* (Hellmar 1903; Ridgway 1904; Delacour 1946; Mayr 1946; Mayr & Amadon 1951; Mayr & Greenway 1956; Wetmore 1960; Deignan 1964; Mayr & Short 1970; Wolters 1975–82; Voous 1977) several authors have proposed its position in this clade based on molecular data (Sibley 1970; Sibley & Ahlquist 1982, 1990; Cibois 2003a). According to the BI analyses, *Chamaea* is nested within the genus *Paradoxornis* with good support, but more research is required to infer its position. The systematic position of the aberrant, nectar-adapted, monotypic genus *Myzornis* has long puzzled ornithologists, and has not been analysed with molecular data until now. Sharpe (1883, 1903), Oates (1889–90) and Baker (1922) placed it in Liotrichinae, where it was associated with *Chloropsis* and *Aegithina* by Baker (1922). It was placed as *incertae sedis* in Timaliinae by Deignan (1964), and both Delacour (1946) and Rand (1967) placed it close to *Leiothrix*. We find good support for its position in clade B, but we are not able to infer its sister taxon. Nectarivorous feeding behaviour is found in three clades

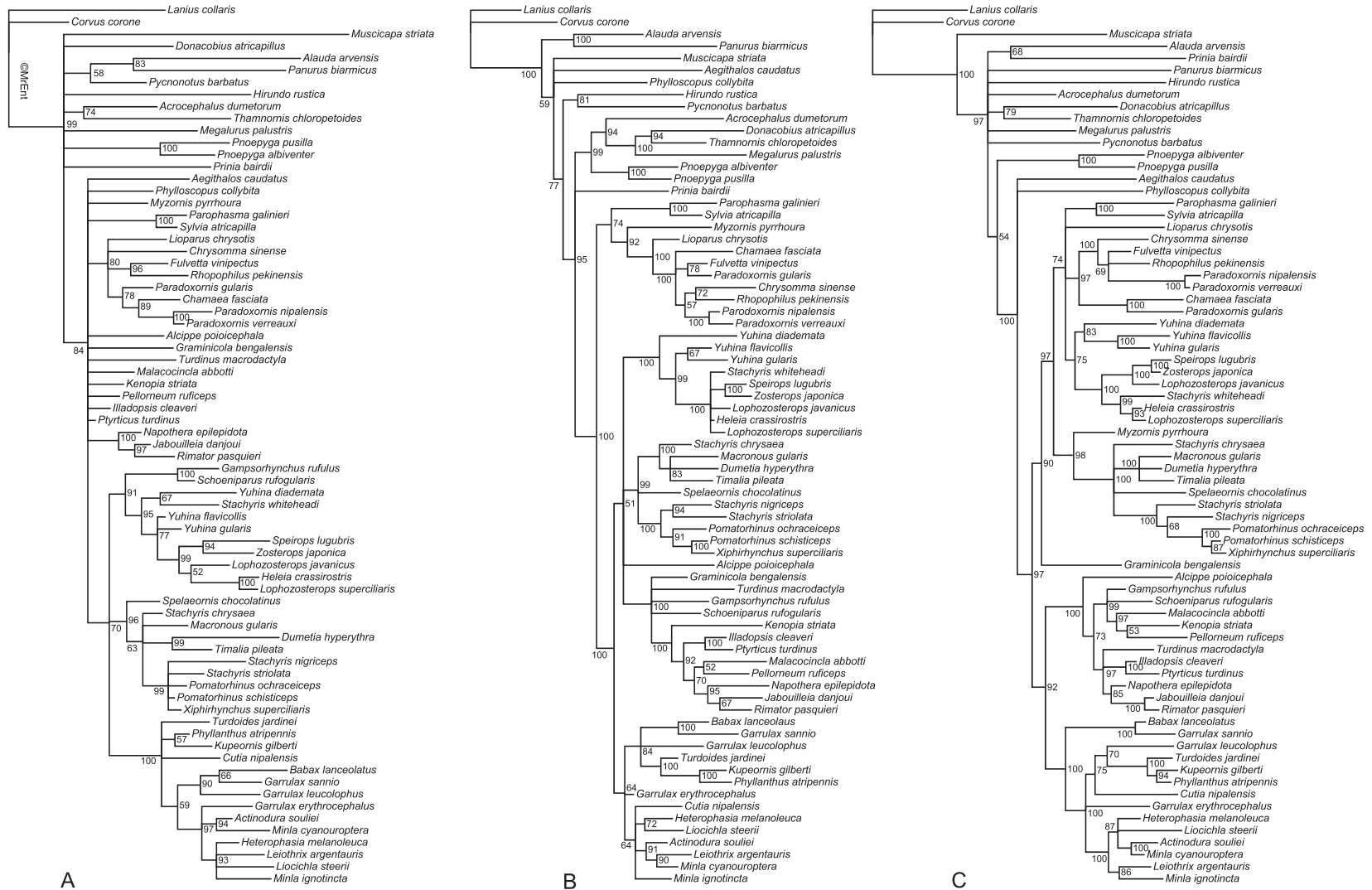


Fig. 2 A–E. Single-locus trees from the Bayesian phylogenetic analyses. —A. GAPDH; —B. Myoglobin; —C. ODC; —D. ND2; —E. RAG-1.

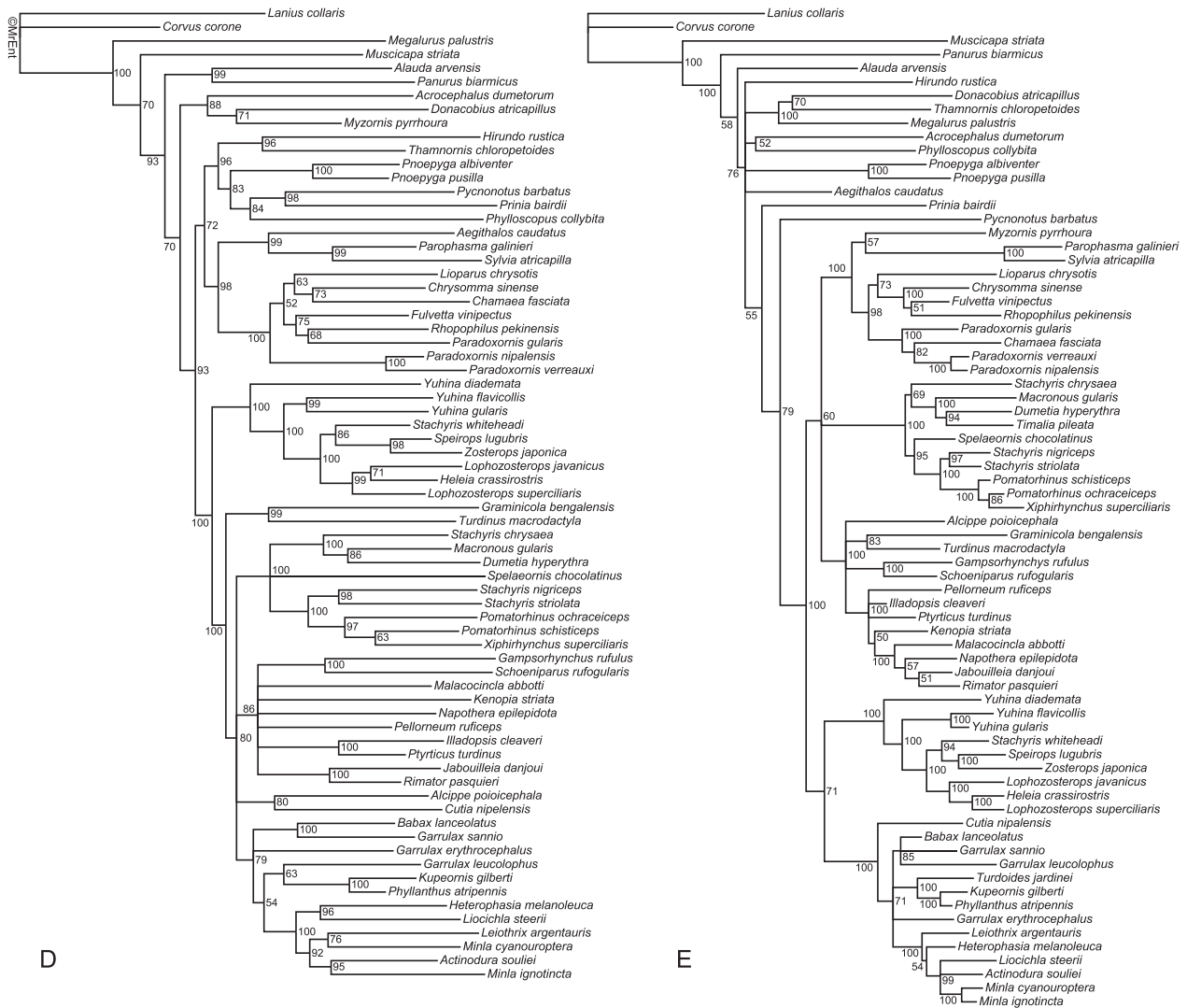


Fig. 2 Continued.

within the babbler radiation (clade B, *Myzornis*; clade D, *Yuhina* and *Zosterops*; clade G, *Heterophasia* (Rand 1967; Collar & Robson 2007)). We find *Parophasma* as sister to *Sylvia*, according to our taxon sampling. Until now, *Parophasma* has not been studied with molecular data, and no certain affinity has been proposed for this taxon, but relationships to *Lioparus*, *Kupeornis* or the Old World warblers has been proposed (Collar & Robson 2007). *Rhopophilus* was placed in Cisticolidae by Sibley & Monroe (1990), but this was not based on molecular data. However, it was included in Timaliidae, in a clade with *Sylvia* and *Paradoxornis*, by Alström *et al.* (2006) based on myoglobin and cytochrome *b* sequence data, and that is corroborated here. The close affinity of *Lioparus chrysotis* and *Fulvetta vinipectus* to other taxa in clade B has previously been shown by Pasquet *et al.* (2006).

Clade D comprises yuhinas, *Zosteropidae sensu* Sibley & Ahlquist (1990) and one representative of the Philippine *Stachyris* babblers. This clade is distributed over much of the Asian, Pacific, Australasian and African regions (Dickinson 2003). The members of this clade generally inhabit tropical and subtropical forests and semiopen habitats. Unlike most other babblers, members of both *Zosterops* and *Yuhina* are adapted to nectar-feeding (cf. *Myzornis*) (Rand 1967). As previously shown (Zhang *et al.* 2007), and corroborated here, the Philippine *Stachyris* babblers are sisters to *Zosteropidae sensu* Sibley & Ahlquist (1990), and these are nested within the paraphyletic *Yuhina*. We confirm the inclusion of *Zosterops* and additional members of *Zosteropidae* in the babbler radiation. Until now, the genera *Lophozosterops* and *Heleia* have not been analysed using molecular data, and based on



our analyses they are closely related to *Zosterops*, *Speirops* and the Philippine *Stachyris* babblers.

The tree- and scimitar babblers of clade E are confined to South, East and South-east Asia, where they typically are found in the undergrowth or close to the ground of tropical or subtropical forests, forest edge and bamboo growth (MacKinnon & Phillipps 1999; Robson 2000; Collar & Robson 2007). The position of *Spelaornis* in this clade, and the paraphyly of *Stachyris* and *Pomatorhinus* are congruent with the results of Cibois *et al.* (2002) and Cibois (2003a). Until now, no molecular data has been available for *Dumetia*, and in our analyses we infer its sister relationship to *Timalia*. Much of this clade corresponds to the tribe Timaliini by Delacour (1946, 1950), except the genera *Pomatorhinus* and *Xiphirhynchus* which were associated with wren babblers in the tribe Pomatorhinini, and the non-timaliid genus *Neomixis*.

Clade F is found in understorey close to, or on, the ground in Africa, South & South-east Asia. Alström *et al.* (2006) showed that *Graminicola* is a babbler and sister to *Pellorneum* according to their taxon sampling, while our results suggest that it is sister to *Turdinus macrodactyla*. A denser taxon sampling is needed to infer its exact position. *Graminicola* is aberrant in relation to the remaining taxa of clade E by inhabiting wet grasslands and reeds (Grimmet *et al.* 1998; Collar & Robson 2007). Wren babblers (including *Pnoepyga* and *Spelaornis*) were treated as members of Pomatorhinini by Delacour (1946, 1950).

Clade G is distributed over large parts of Africa and South, East and South-east Asia. The members of this clade typically inhabit forested habitats except the *Turdoides* ground babblers, which generally inhabit dry areas with scattered bushes (Collar & Robson 2007). The systematic affinities of *Kupeornis* and *Phyllanthus* as sister to *Turdoides*, in our analyses, show that these genera either are *Turdoides* taxa adapted to an arboreal life, or arboreal sisters to the exceptional *Turdoides*. A detailed study of clade G with dense taxon sampling will clarify this question. No previous study has employed molecular data to elucidate the relationships of these genera, and their systematic affinity has been proposed close to *Lioptilus*, or to *Turdoides* (Collar & Robson 2007). *Phyllanthus* was included in Turdoidini by Delacour (1946, 1950).

#### Taxonomic implications

Oates (1889–1890) used Crateropodidae Swainson 1832, and Liotrichidae Swainson 1832 for babblers, while Baker (1922) fused the two and used Timaliidae Vigors & Horsfield 1827 after *Crateropus* was synonymized with *Turdoides* Cretzschmar 1827. Sibley & Monroe (1990) used Sylviidae for babblers and warblers combined, and placed babblers in Garrulacinae and Sylviinae (tribes Timaliini and Chamaeini). However, the genus *Sylvia* was shown to be part of the babblers, and Sylviidae Leach, 1820 therefore became paraphyletic (Cibois

2003a; Beresford *et al.* 2005; Alström *et al.* 2006). Zosteropidae Bonaparte 1853 does not have priority over Sylviidae Leach, 1820 or Timaliidae Vigors & Horsfield 1827. Since the name Timaliidae is well-established for babblers, while Sylviidae is as well-established for warblers, Cibois (2003b) suggested the possibility of suppressing Sylviidae if these taxa are united in the same family, because most of the species in this clade are babblers and not warblers. Such action would lead to less confusion than if Timaliidae was synonymized with Sylviidae. However, formal suppression of Sylviidae can only be authorized by the International Commission on Zoological Nomenclature (ICZN), and because Sylviidae is valid, we find it appropriate to divide the babbler radiation (clade A) into two families, Sylviidae and Timaliidae. Several names potentially referring to clade B have been proposed (e.g. Sylviidae Leach 1820; Paradoxornithidae Horsfield & Moore 1854; Chamaeidae Baird 1858). Delacour (1946) used Chamaeini Baird 1858 for most of the members except *Sylvia*, while Sibley & Monroe (1990) included parrotbills in Timaliini Vigors & Horsfield 1827, and *Sylvia* in Sylviini Leach 1821. We propose Sylviidae Leach, 1820 based on *Sylvia*, to refer to clade B by priority. We propose Timaliidae Vigors & Horsfield 1827, based on *Timalia*, to refer to clade C, by priority.

Within Timaliidae, we propose Zosteropinae Bonaparte 1853, based on *Zosterops*, to refer to clade D by priority over Yuhiniinae Wolters 1980 (1863) which replaced Ixulinae Jerdon 1863 after *Ixulus* was synonymized with *Yuhina*. We propose the members of clade E to be referred to as Timaliinae Vigors & Horsfield 1827. Several other names have been proposed later (Bock 1994 and references therein). Most of the members of clade F were included in Pellorneinae Delacour (1946). Cacopittinae Bonaparte (1854); based on *Cacopitta* Bonaparte (1850) is synonymized with *Napothera* Temminck 1828, (*Cacopitta* is used by Wolters 1975–82), but not Cacopittinae Bonaparte 1854). However, the Cacopittinae Bonaparte 1854 is not replaced and still available. We propose Pellorneinae Delacour (1946) to refer to clade F, based on *Pellorneum*, and not *Cacopitta* as this name is not in use. Regarding clade G, *Crateropus* was synonymized with *Turdoides* and Turdoidinae Richmond 1917 replaced Crateropodinae Swainson 1832. Turdoidinae Richmond 1917 (1832) and Leiothrichinae Swainson 1832 have the same priority, according to article 40.2 in the Code (ICZN, 1999). Therefore, the choice of name should be determined by the principle of first reviser (article 24.2 in the ICZN code). Cabanis (1850–1851) used both Liotrichinae and Crateropodinae, and included these in Liotrichidae, while no earlier classification has included both genera in one of the two potential family group names (i.e. Gray 1842; Bonaparte 1850). Later authors have not merged the two genera in one family group (e.g. Sharpe 1883, 1903; Oates 1889–90; Baker 1922; Deignan 1964) until Delacour (1946) included both *Leiothrix* and *Turdoides* in

Turdoidini. Sibley & Ahlquist (1990) and Sibley & Monroe (1990) used Garrulacinae Bonaparte (1850) for laughing-thrushes and liocichlas, but did not include *Turdoides* or *Leiothrix* in their study. We refer to clade G as Leiothrichinae, based on *Leiothrix*, by the principle of first reviser.

According to our results, the genus *Pnoepyga* falls well outside the babbler radiation. In our analysis, a long branch leads to *Pnoepyga*, and we find no reasons to believe it is nested within or closely related to any other family within Sylvioidea. However, resolution of the relationships between the families within Sylvioidea is beyond the scope of this paper. Compared to most members of the families of Sylvioidea, *Pnoepyga* shows a unique combination of morphological characters. The rounded and 'cup-shaped' wings and near absence of tail restrict the birds to an almost flightless behaviour. They typically inhabit dense undergrowth in mountain forest. Further, most taxa show an irregular pattern of the ventral feathers, with variable amounts of black and white centres to the contour feathers. Compared to most babblers, *Pnoepyga* is non-social, mostly living solitary or in pairs (Collar & Robson 2007). Based on the morphological, behavioural and phylogenetic uniqueness of these birds, we propose a new family name to refer to clade H:

Pnoepygidae fam. n.

Type genus. *Pnoepyga* Hodgson 1844.

**Diagnosis.** Separated from other families within Sylvioidea by the combination of short, rounded and 'cup-shaped' wings; very short or virtually absent tail; strong and long legs, with booted tarsus; cryptically patterned plumage with more or less irregular colour pattern of ventral feathers; and two colour morphs. Juveniles generally more uniformly coloured than adults. The members of this family inhabit dense undergrowth, and live in pairs or solitary. Typically, the birds hop among leaf litter on the ground or exceptionally climb or hop in low bushes, logs and branches. Song is constant within individuals and populations. Genetically, members of this family (included in this study) have synapomorphic deletions of 16 base pairs between positions 79–80 in GAPDH, two base pairs between positions 146–147 in ODC and two base pairs between positions 487–488 in ODC.

### Acknowledgements

Authors thank Dario Zuccon, Sven Kullander, Walter Bock and Richard Schodde for help with the nomenclatural issues. Authors thank Jon Fjeldså and Jan Bolding Kristensen (Zoological Museum, Copenhagen, Denmark), Silke Fregin (Vogelwarte Hiddensee/Ernst-Moritz-Arndt-Universität Greifswald, Germany), Mikhail V. Kalyakin (Zoological Museum of Moscow, Russian-Vietnamese Tropical Research Center) and David E. Willard (Field Museum of Natural History, Chicago, USA) for providing samples. Dewi Prawiradilaga

and Irfham Mohammad (Zoological Museum, Bogor, Indonesia), Obhas Khobkhet (Kasetsart University, Bangkok) and Han Lian-xian (South-west Forestry University, Kunming, China) are thanked for valuable help during field work. The field work done in Asia by EP and AC was supported by the Programme Pluri-formations Asie du Sud-Est (MNHN). Authors are grateful to Mari Källersjö, Pia Eldenäs, Martin Irestedt, Dario Zuccon and the staff at the Molecular Systematics Laboratory, Swedish Museum of Natural History, Stockholm for hospitality and help with various matters. Jan Ohlson and Ulf Johansson (Swedish Museum of Natural History), and two anonymous referees are thanked for valuable comments. The molecular work was partly conducted at, and supported by, the Service de Systématique Moléculaire, CNRS-IFR101, MNHN and by the Natural History Museum of the city of Geneva. Funding for this project was provided by the Swedish Research Council (grant no. 621-2004-2913 to PE).

### References

- Akaike, H. (1973). Information theory as an extension of the maximum likelihood principle. In B. N. Petrov & F. Csaki (Eds) *Second International Symposium on Information Theory*. Budapest: Akademiai Kiado.
- Alström, P., Ericson, P. G. P., Olsson, U. & Sundberg, P. (2006). Phylogeny and classification of the avian superfamily Sylvioidea. *Molecular Phylogenetics and Evolution*, 38, 381–397.
- Baker, E. C. S. (1922). *The Fauna of British India, Including Ceylon and Burma*, 2nd edn. London: Taylor & Francis.
- Barker, F. K., Barrowclough, G. F. & Groth, J. G. (2002). A phylogenetic hypothesis for passerine birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proceedings of the Royal Society of London B*, 269, 295–308.
- Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. (2004). Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences, USA*, 101, 11040–11045.
- Beecher, W. J. (1953). A phylogeny of the Oscines. *Auk*, 70, 270–333.
- Beresford, P., Barker, F. K., Ryan, P. G. & Crowe, T. M. (2005). African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary 'enigmas'. *Proceedings of the Royal Society of London B*, 272, 849–858.
- Bock, W. J. (1994). History and nomenclature of avian family-group names. *Bulletin of the American Museum of Natural History*, No. 222.
- Bonaparte, C. L. (1850). *Conspectus Generum Avium*. Lugduni Batavorum.
- Cabanis, J. (1850–51). *Verzeichniss der ornithologischen sammlung des oberamtmann Ferdinand Heine, auf Gut St. Buchard vor Halberstadt. Mit kritischen anmerkungen und beschreibung der neuen arten, systematisch bearbeitet*. Erstem Kustos der Königlichen zoologischen sammlung zu Berlin.
- Cibois, A. (2003a). Mitochondrial DNA phylogeny of babblers (Timaliidae). *Auk*, 120, 35–54.
- Cibois, A. (2003b). Sylvia is a babbler: taxonomic implications for the families Sylviidae and Timaliidae. *Bulletin of the British Ornithologists Club*, 123, 257–261.

- Cibois, A., Pasquet, E. & Schulenberg, T. (1999). Molecular systematics of the Malagasy babblers (Passeriformes: Timaliidae) and warblers (Passeriformes: Sylviidae), based on cytochrome b and 16S rna sequences. *Molecular Phylogenetics and Evolution*, 13, 581–595.
- Cibois, A., Slikas, B., Schulenberg, T. S. & Pasquet, E. (2001). An endemic radiation of Malagasy songbirds is revealed by mitochondrial DNA sequence data. *Evolution*, 55, 1198–1206.
- Cibois, A., Kalyakin, M. V., Han, L.-X. & Pasquet, E. (2002). Molecular phylogenetics of babblers (Timaliidae): revaluation of the genera *Yubina* and *Stachyris*. *Journal of Avian Biology*, 33, 380–390.
- Collar, N. J. (2006). A partial revision of the Asian babblers (Timaliidae). *Forktail*, 22, 85–112.
- Collar, N. J. & Robson, C. (2007). Family Timaliidae (Babblers). In J. del Hoyo, A. Elliott & D. A. Christie (Eds) *Handbook of the Birds of the World Vol. 12. Picathartes to tits and Chikadees*. (pp. 70–291). Barcelona: Lynx Edicions.
- Deignan, H. G. (1964). Timaliinae, Panurinae, Picathartinae. In: E. Mayr & R. A. Paynter Jr. (Eds) *A check-list of Birds of the World: A Continuation of the Works of James L. Peters*. (pp. 240–442). Massachusetts: Museum of Comparative Zoology, Cambridge.
- Delacour, J. (1946). Les timaliïnés. *L'Oiseau*, 16, 7–36.
- Delacour, J. (1950). Les timaliïnés: Additions et modifications. *L'Oiseau*, 20, 186–191.
- Dickinson, E. C. (Ed.) (2003). *The Howard and Moore Complete Check-list of the Birds of the World*. London: Christopher Helm.
- Ericson, P. G. P. & Johansson, U. S. (2003). Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution*, 29, 126–138.
- Ericson, P. G. P., Christidis, L., Irestedt, M. & Norman, J. A. (2002). Systematic affinity of the lyrebirds (Passeriformes: Menura), with a novel classification of the major groups of passerine birds. *Molecular Phylogenetics and Evolution*, 25 (1), 53–62.
- Fuchs, J., Fjeldså, J., Bowie, R. C. K., Voelker, G. & Pasquet, E. (2006). The African warbler genus *Hylia* as a lost lineage in the oscine songbird tree: molecular support for an African origin of the Passerida. *Molecular Phylogenetics and Evolution*, 39 (1), 186–197.
- Gray, G. R. (1842). *A List of the Genera of Birds*. London: Richard and John E. Taylor.
- Grimmet, R., Inskipp, C. & Inskipp, T. (1998). *Birds of the Indian Subcontinent*. London: A. & C. Black/Christopher Helm.
- Gu, X., Fu, Y.-X. & Li, W.-H. (1995). Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. *Molecular Biology and Evolution*, 12, 546–557.
- Hartert, E. (1910). *Die Vögel der Paläarktischen Fauna*. Berlin, Germany: R. Friedlander.
- Hasegawa, M., Kishino, H. & Yano, T. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, 22, 160–174.
- Hellmar, L. E. (1903). Paridae, Sittidae, and Certhiidae. *Das Tierreich*, no. 18. Berlin, Germany: Friedlander und Sohn.
- Higgins, D. G., Bleasby, A. J. & Fuchs, R. (1992). Clustal V: Improved software for multiple sequence alignment. *CABOIS*, 8, 189–191.
- Huelsenbeck, J. P. & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17, 754–755.
- Irestedt, M., Ohlson, J. I., Zuccon, D., Kjällersjö, M. & Ericson, P. G. P. (2006). Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). *Zoologica Scripta*, 35 (6), 567–580.
- Jobb, G. (1997–2008) Treefinder, version of (January 2008). Available via <http://www.treefinder.de>.
- Johansson, U. S., Fjeldså, J., Lokugallappatti, S. & Bowie, R. C. K. (2007). A nuclear DNA phylogeny and proposed taxonomic revision of African greenbuls (Aves, Passeriformes, Pycnonotidae). *Zoologica Scripta*, 36 (5), 417–427.
- Johansson, U. S., Fjeldså, J. & Bowie, R. C. K. (2008). Phylogenetic relationships within Passerida (Aves: Passeriformes): a review and a new molecular phylogeny based on three nuclear intron markers. *Molecular Phylogenetics and Evolution*, 48, 858–876.
- Jönsson, K. A., Fjeldså, J., Ericson, P. G. P. & Irestedt, M. (2007). Systematic placement of an enigmatic Southeast Asian taxon *Eupetes macrocerus* and implications for the biogeography of a main songbird radiation, the Passerida. *Biology Letters*, 3, 323–326.
- Lanave, C., Preparata, C., Saccone, C. & Serio, G. (1984). A new method for calculating evolutionary substitution rates. *Journal of Molecular Evolution*, 20, 86–93.
- MacKinnon, J. & Phillipps, K. (1999). *A Field Guide to the Birds of Borneo, Sumatra, Java, and Bali*. UK: Oxford University Press.
- Mayr, E. (1946). History of the North American bird fauna. *Wilson Bulletin*, 58, 3–41.
- Mayr, E. & Amadon, D. (1951). A classification of recent birds. *American Museum Novitates*, no. 1496.
- Mayr, E. & Greenway, J. C. Jr. (1956). Sequence of passerine families (Aves). *Breviora*, 58, 1–11.
- Mayr, E. & Short, L. L. (1970). Species taxa of North American birds. *Publications of the Nuttall Ornithological Club*, 9, 1–127.
- Moyle, R. G. & Marks, B. D. (2006). Phylogenetic relationships of bulbuls (Aves: Pycnonotidae) based on mitochondrial and nuclear DNA sequence data. *Molecular Phylogenetics and Evolution*, 40 (3), 687–695.
- Nylander, J. (2005). *Mrmmodeltest V2.2*. [Program distributed by the author]. Uppsala University. Department of Systematic Zoology.
- Oates, E. W. (1889–90) *Fauna of British India, Birds*, Vols 2, London: Taylor & Francis.
- Pasquet, E., Bourdon, E., Kalyakin, M. V. & Cibois, A. (2006). The fulvettas (*Alcippe*, Timaliidae, Aves): a polyphyletic group. *Zoologica Scripta*, 35 (6), 559–566.
- Rand, A. L. (1967). The flower-adapted tongue of a Timaliinae bird, and its implications. *Fieldiana Zoology*, 51 (3), 53–61.
- Ridgway, R. (1904). Birds of North and Middle America, family Chamaeidae. *Bulletin of the Smithsonian Institution, U.S. National Museum*, 50, 683–691.
- Robson, C. (2000). *A Field Guide to the Birds of South-East Asia*. UK: New Holland Publishers Ltd.
- Rodríguez, J., Oliver, L., Marín, A. & Medina, R. (1990). The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology*, 142, 485–501.
- Sefc, K. M., Payne, R. B. & Sorenson, M. D. (2003). Phylogenetic relationships of African sunbird-like warblers: *Moho Hypergerus atriceps*, *Green Hylia Hylia prasina* and *Tit-Hylia Pholidornis rufibae*. *Ostrich*, 74, 8–17.
- Sharpe, R. B. (1883). *Catalogue of the Passeriformes or Perching Birds in the Collections of the British Museum*, Vol. 7. London.
- Sharpe, R. B. (1903). *Catalogue of the Genera and Species of Birds*, Vol IV. London.
- Sibley, C. G. (1970). A comparative study of the egg-white proteins of the passerine birds. *Peabody Museum of Natural History, Yale University*, 32, 1–131.

- Sibley, C. G. & Ahlquist, J. E. (1982). The relationships of the wren-tit as indicated by DNA-DNA hybridization. *Condor*, 84, 40–44.
- Sibley, C. G. & Ahlquist, J. E. (1990). *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. New Haven, CT: Yale University Press.
- Sibley, C. G. & Monroe, B. L. Jr. (1990). *Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.
- Swofford, D. L. (2001). PAUP\*: *Phylogenetic Analysis Using Parsimony (\*and other methods)*, Ver. 4.08b. Sunderland, MA: Sinauer Associates.
- Tavaré, S. (1986). Some probabilistic and statistical problems on the analysis of DNA sequences. *Lectures on Mathematics in the Life Sciences*, 17, 57–86.
- Voous, K. H. (1977). List of Holarctic bird species. Passerines. *Ibis*, 119 (223–250), 376–406.
- Wetmore, A. (1960). *A Classification for the Birds of the World*. Smithsonian Miscellaneous Collections, No. 139.
- Wittingham, L. A., Slikas, B., Sheldon, F. H. & Winkler, D. W. (2002). Phylogeny of the tree swallow genus, *Tachycineta* (Aves: Hirundinidae), by Bayesian analyses of mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 22 (3), 430–441.
- Wolters, H. E. (1975–82). *Die Vogelarten der Erde*. Berlin: Parey.
- Zhang, S., Yang, L., Yang, X. & Yang, J. (2007). Molecular phylogeny of the yuhinas (Sylviidae: *Yuhina*): a paraphyletic group of babblers including *Zosterops* and Philippine *Stachyris*. *Journal of Ornithology*, 148, 417–426.
- Zuccon, D. (2005). A molecular phylogeny of starlings (Aves: Sturnini): evolution, biogeography and classification in a passerine family. Doctoral Thesis, Italy: University of Turin.
- Zuccon, A. & Zuccon, D. (2005–08). *MrEnt 2.0*. Program distributed by the authors (July 2008). Available at: <http://www.nrm.se>

### Supporting Information

Additional supporting information may be found in the online version of this article.

**Table S1.** Primers used in this study, with annealing temperatures for amplification. Samples marked with asterisk are only used for old study skins, and with asterisk inside parenthesis used mainly for old study skins. Previously published primers can be found in: 1: Irestedt *et al.* (2002); 2: Slade *et al.* (1993); 3: Heslewood *et al.* (1998); 4: Irestedt *et al.* (2006); 5: Jönsson *et al.* 2008; 6: Zuccon (2005); 7: Allen & Omland (2003); 8: Barker *et al.* (2002); 9: Groth & Barrowclough (1999); 10: Irestedt *et al.* (2001). The primers G3P13b is only used for amplification, and G3PintL1 only for sequencing.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.