

## A review of the recent advances in the systematics of the avian superfamily Sylvioidea

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**Abstract** The systematics of the avian superfamily Sylvioidea are reviewed, focusing on studies of relationships among families and within genera, more superficially on taxonomic studies at the species level. For the families Bernieridae and Phylloscopidae, new analyses based on already published sequence data are presented. Our understanding of relationships has been vastly improved in recent years due to a large number of molecular studies. However, the relationships among the different families remain largely obscured, probably mainly as a result of rapid divergence of the different primary lineages (families). Also, species level taxonomy has been much improved in recent years due to a large number of studies applying molecular markers and/or vocalizations and other life-history data. It seems likely that the number of species will continue to increase, as new groups are being studied with modern integrative methods.

**Keywords** phylogenetic relationships, superfamily Sylvioidea, taxonomy

### Introduction

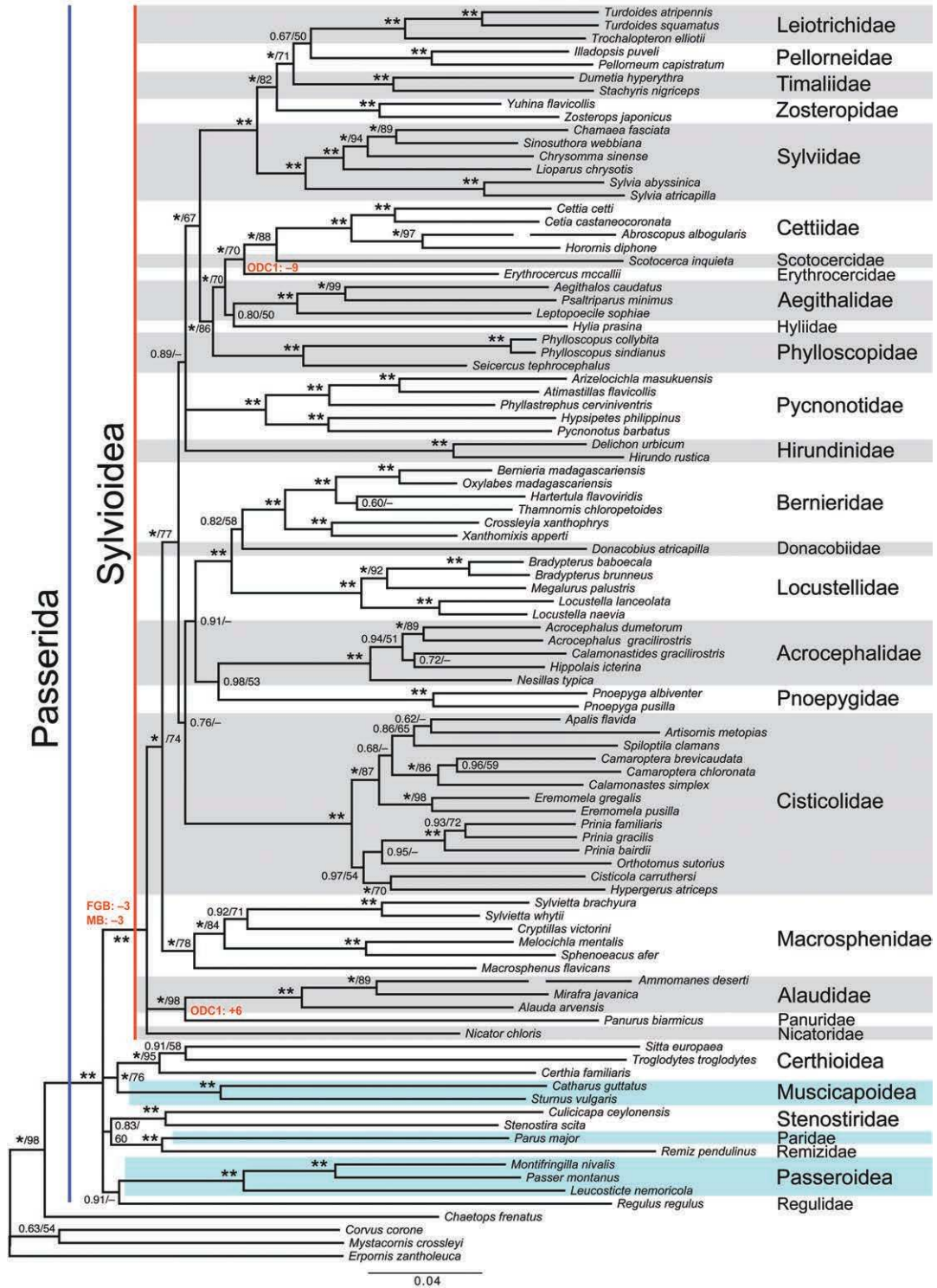
The Passerida was identified by Sibley and Ahlquist (1990) based on DNA-DNA hybridization studies as the largest radiation within oscine passerine birds (cf. Fig. 1). These authors recognized three superfamilies within Passerida: Muscicapoidea (e.g. waxwings, dippers, thrushes, Old World flycatchers, starlings and mockingbirds), Sylvioidea (e.g. nuthatches, treecreepers, tits, wrens, crests/kinglets, swallows, bulbuls, babblers and warblers), and Passeroidea (e.g. larks, pipits, wagtails, waxbills, weavers, finches, sparrows, cardinals,

tanagers, wood-warblers, and icterids). Subsequent studies of DNA sequence data have indicated that both Muscicapoidea and Passeroidea, after minor taxonomic adjustments, can be recovered as monophyletic (Barker et al., 2002, 2004; Ericson and Johansson, 2003; Voelker and Spellman, 2003; Cibois and Cracraft, 2004; Beresford et al., 2005; Jønsson and Fjeldså, 2006; Johansson et al., 2008a; Spellman et al., 2008; Treplin et al., 2008). However, Sylvioidea sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990) has not been corroborated by later studies (e.g. Chikuni et al., 1996; Sheldon and Gill, 1996; Barker et al., 2002, 2004; Ericson and Johansson, 2003; Spicer and Dunipace, 2004; Beresford et al., 2005; Alström et al., 2006; Fregin et al., 2012). In addition to Muscicapoidea, Passeroidea and Sylvioidea, the superfamily Certhioidea (containing treecreepers, nuthatches, gnatcatchers and wrens) has been proposed by Cracraft et al. (2004) (cf. Fig. 1).

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**Fig. 1** Phylogeny of superfamily Sylvioidea based on concatenated sequences of one mitochondrial (cytochrome *b*) and six nuclear loci (FGB, GAPDH, LDHB, MB, ODC1, RAG1; in total ~6.3 kbp), analyzed by Bayesian inference (partitioned by locus). Support values are given in the order posterior probability (PP) / maximum likelihood (ML) bootstrap; \*\* indicates posterior probability 1.00 or ML bootstrap 100%; – indicates no ML bootstrap support for this node, but clade recovered in ML search for best topology. Homoplasy-free insertions (+) and deletions (–) are indicated. From Fregin et al. (2012), two long branches have been shortened (broken). The family names are those recommended by Fregin et al. (2012); a few of the generic names have been changed to reflect more recent taxonomic recommendations (e.g. Alström et al., 2011b; Moyle et al., 2012).

The superfamily Sylvioidea has received much attention in recent years, with three major studies of inter-familial relationships (Alström et al., 2006; Johansson et al., 2008a; Fregin et al., 2012) and multiple studies focusing on different families within it (e.g. Cibois et al., 1999, 2001; Helbig and Seibold, 1999; Sheldon et al., 2005; Moyle and Marks, 2006; Nguembock et al., 2007; Fregin et al., 2009; Gelang et al., 2009; Alström et al., 2011a, b, 2013; Moyle et al., 2012; Olsson et al., 2013a). The first comprehensive study of the whole superfamily (Alström et al., 2006) was based on one nuclear and one mitochondrial sequence. That study identified 10 well-supported major clades, which were proposed to be recognized at family level (Acrocephalidae, Aegithalidae, Alaudidae, Cettiidae, Cisticolidae, Hirundinidae, Megaluridae, Phylloscopidae, Pycnonotidae and Timaliidae), as well as three lineages comprising one to two species each that were not recognized nomenclaturally (*Donacobius*, *Melocichla* + *Sylvietta* and *Panurus*). Johansson et al. (2008a) recognized also Bernieridae, of which Alström et al. (2006) had no representatives, and referred to the *Melocichla* + *Sylvietta* clade as the “*Sphenoeacus* group” (comprising *Macrosphenus*, *Sphenoeacus*, *Bradypterus victorini* and two species of *Sylvietta*). Both these groupings were previously identified by Beresford et al. (2005), the former as “Malagasy endemic ‘warblers’” and the latter as the “*Sphenoeacus* group” (containing also *Achaetops*, in addition to the previously mentioned genera).

The finding that the type genus of Sylviidae, *Sylvia*, was nested within the large Timaliidae group (as previously discovered by Fjeldså et al., 1999; Cibois, 2003a, b) caused a taxonomic problem, as the older name Sylviidae has priority over Timaliidae (ICZN, 1999), and it would be inconvenient both to discard the name Timaliidae and to use the name Sylviidae in a completely new context. To solve this difficulty, it was suggested that Sylviidae be suppressed, and Timaliidae used for the group including mostly traditional Timaliidae species (Cibois, 2003a, b; Alström et al., 2006). However, Gelang et al. (2009), again based on DNA sequence data, resurrected Sylviidae, but restricted it to a clade containing mostly traditional Timaliidae species, and this arrangement has been followed by subsequent authors (Fregin et al., 2012; Moyle et al., 2012; Gill and Donsker, 2013).

The latest and most comprehensive analysis of Sylvioidea (Fregin et al., 2012) proposed new family names for the genera *Scotocerca* and *Erythrocercus*, the Scoto-

cercidae (a monotypic family) and the Erythrocercidae (with three species), respectively, and formally proposed the name Macrosphenidae for the “*Sphenoeacus* group”. They also tentatively recommended the use of Hyliidae for *Hylia* and *Pholidornis*, and argued against inclusion of Paridae, Remizidae and Stenostiridae in Sylvioidea. In total, their classification comprised 23 families in Sylvioidea (Fig. 1), containing over 1200 species in more than 220 genera (Gill and Donsker, 2013).

Sylvioidea is essentially an Old World radiation. Most of the families are either absent or represented by just a few species in the New World. A striking exception concerns the family Hirundinidae, which is well represented on all continents (excluding Antarctica), likely the result of the extraordinary flight capability of its members.

The present review focuses on studies of relationships among the families within Sylvioidea, as well as on relationships within genera, but only cursorily deals with taxonomic studies at the species level. For the families Bernieridae and Phylloscopidae, new analyses based on previously published sequence data are presented. Recent advances in the species-level taxonomy of Indian subcontinent birds have been reviewed by Rasmussen (2012), which see for additional information.

## Relationships among families

In the study by Alström et al. (2006), based on two loci, one mitochondrial and one nuclear, most of the deep internal nodes were unresolved. However, three of the relationships among the 10 clades they proposed to be recognized at the family level had high posterior probability (0.95–1.00): the Megaluridae + *Donacobius* + Acrocephalidae clade, the Phylloscopidae + Aegithalidae + Cettiidae + Hirundinidae + Pycnonotidae clade, and the sister relationship between Alaudidae + *Panurus* and the other Sylvioidea. However, none of these clades obtained >50% parsimony bootstrap support, so they were not considered reliable. Johansson et al. (2008a), utilizing three nuclear introns (including the one used by Alström et al., 2006), found strong support for a Megaluridae + *Donacobius* + Bernieridae clade, as well as for the sister relationships between these and Acrocephalidae. They also found strong support for the position of the Alaudidae + *Panurus* clade and *Nicator* outside of the other Sylvioidea, but no other strongly supported relationships among families.

The analysis of six nuclear and one mitochondrial

loci by Fregin et al. (2012; Fig. 1) corroborated the Locustellidae (formerly Megaluridae; see below) + Donacobiidae (treated at family rank; see below) + Bernieridae clade, but found no statistical support for a close relationship between these and Acrocephalidae. They also found the Alaudidae + Panuridae clade and Nicatoridae (all treated at family level; see below) in a polytomy with the rest of Sylvioidea (the Sylvioidea clade excluding Alaudidae, Panuridae and Nicatoridae receiving 1.00 posterior probability and 74% maximum likelihood bootstrap support). Moreover, the Cettiidae + Scotocercidae clade and the Cettiidae + Scotocercidae + Erythroceridae + Aegithalidae + Phylloscopidae clade were strongly supported both in the Bayesian and maximum likelihood analyses. The Cettiidae + Scotocercidae grouping had previously been shown to be supported by morphological characters (Alström et al., 2011c). However, other relationships among families were generally unsupported, or strongly supported by Bayesian inference but with poor or moderate maximum likelihood bootstrap support. Most of the deep nodes with poor or conflicting support were very short, suggesting rapid divergence resulting in difficulties in reconstruction of relationships (e.g. Lewis et al., 2005; Rokas and Carroll, 2006).

With respect to the relationships among the five primary “babbler” clades, using partly different loci, Gelang et al. (2009), Fregin et al. (2012) and Moyle et al. (2012) recovered the same topology, i.e. (((Leiotrichidae/-inae, Pellorneidae/-inae), Timaliidae/-inae), Zosteropidae/-inae), Sylviidae/-inae) (cf. Fig. 1). The latter study was the only one that obtained unanimously strong support for these relationships, whereas the overall weakest support was found in the study with the largest number of unlinked loci (Fregin et al., 2012). The comparatively poor support (especially for the Leiotrichidae/-inae + Pellorneidae/-inae clade) in the Fregin et al. (2012) study might have been the result of the small number of species in each clade compared to the other studies.

## Relationships within families

### Alaudidae

The Alaudidae (larks) are found on all continents, although by far the largest number of species are found in Africa, and only one species each is found in the New World and Australasia (de Juana et al., 2004). This is one of the least studied of the families within Sylvioi-

dea. The circumscription of this family has not been disputed, and it seems unlikely that its inclusiveness will change. However, the relationships within and among the different genera are uncertain, and the number of genera and their composition have fluctuated dramatically over the years (e.g. Roberts, 1940; Meinertzhagen, 1951; Vaurie, 1951; Macdonald, 1952a, b, 1953; Verheyen, 1958; Peters, 1960a; Clancey, 1966, 1980; Harrison, 1966; Maclean, 1969; Wolters, 1979; Dean et al., 1992; Dickinson, 2003; Pätzold, 2003; de Juana et al., 2004). Certain genera, notably *Mirafra*, have acted as “dumping grounds”, whereas several monotypic genera (e.g. *Pseudalaimon*, *Lullula*, *Ramphocoris*) with uncertain affinities have been erected.

Until recently, only one phylogeny of the Alaudidae, based on mitochondrial sequences from a small number of mostly African species, has been published (Tielemann et al., 2003). However, a phylogeny including 81 of the 97 species and representatives of all 21 recognized genera, based on two mitochondrial and three nuclear loci has just appeared (Alström et al., 2013). The latter has revealed many unpredicted relationships, including some non-monophyletic genera (*Calandrella*, *Mirafra*, *Melanocorypha*, *Spizocorys*), and proposed a revised generic classification. For example, the genus *Calandrella* is shown to be separated into two non-sister clades, with *C. brachydactyla*, *C. cinerea* and *C. acutirostris* being closely related to *Eremophila*, whereas the other *Calandrella* species (e.g. *C. rufescens* and *C. cheleensis*) are more closely related to a clade containing the two monotypic genera *Eremalauda* and *Chersophilus*; the close affinity between *Eremalauda* and *Chersophilus* was also totally unexpected. Alström et al. (2013) proposed that the name *Alaudala* be used for the second of these traditional *Calandrella* clades. Another surprising result from Alström et al.’s (2013) multilocus analysis was that *Melanocorypha leucoptera* and *M. mongolica* are not closely related, hence it was proposed that the former be moved to the genus *Alauda*.

Lark taxonomy based on morphology has received much attention in Africa (Meinertzhagen, 1951; Winterbottom, 1957; Lawson, 1961; Clancey, 1989; Ryan and Bloomer, 1997; García et al., 2008) and Eurasia (Meinertzhagen, 1951; Vaurie, 1951, 1954; Dickinson and Dekker, 2001). Recent studies have revealed considerable hidden diversity in some taxa, such as *Mirafra asamica*, which was proposed to be split into four species based mainly on vocal, behavioral and morphological data (Alström, 1998; corroborated by molecular study

by Alström et al., 2013); the *Calendulauda* (previously *Certhilauda*) *albescens* complex, which was suggested to consist of three instead of two species based on mitochondrial, morphological and vocal data (Ryan et al., 1998); the *Certhilauda curvirostris* complex, which was recommended to be treated as five instead of one species based on mitochondrial and morphological evidence (Ryan and Bloomer, 1999); and *Galerida cristata*, which was shown to consist of two partly sympatric and largely reproductively isolated species in Morocco, *G. cristata sensu stricto* and *G. macrorhyncha* (Guillaumet et al., 2005, 2006, 2008). In an analysis of mitochondrial data, Alström et al. (2013) found several unexpectedly deep divergences between taxa presently treated as conspecific (e.g. within *Ammomanes cinctura*, *Ammomanes deserti*, *Calandrella brachydactyla*, *Eremophila alpestris*), but also some shallow splits between currently recognized species (e.g. *Certhilauda brevirostris*–*C. semitorquata*–*C. curvirostris* [cf. Ryan and Bloomer, 1999]; *Calendulauda barlowi*–*C. erythrochlamys* [cf. Ryan et al., 1998]; *Mirafra cantillans*–*M. javanica*). Moreover, Zink et al. (2008) found a deep divergence in mitochondrial DNA between eastern and western populations of *Alauda arvensis*. It seems likely that the total number of recognized lark species is underestimated, and we predict that future studies based on molecular and/or vocal data will show that many of the currently recognized subspecies warrant recognition as separate species.

### Panuridae

The family Panuridae contains the single species *Panurus biarmicus*, which is widely distributed across the temperate parts of Eurasia. It was previously considered a babbler, closely related to parrotbills (e.g. Deignan, 1964a; Dickinson, 2003), but molecular studies have unanimously recovered it as sister to the Alaudidae (Ericson and Johansson, 2003; Alström et al., 2006; Johansson et al., 2008a; Fregin et al., 2012).

### Macrosphenidae

The realization that this exclusively African family exists as a distinct evolutionary lineage has gradually grown out of molecular evidence, which piece by piece brought together a morphologically diverse assemblage of species as a monophyletic group. Sefc et al. (2003) found that *Sylvietta*, which was placed in Acrocephalidae by Sibley and Monroe (1990), was not closely

related to any other warbler taxa in their analysis of mitochondrial markers. Beresford et al. (2005) included *Achaetops*, *Bradypterus victorini*, *Macrosphenus*, *Sphenoeacus* and *Sylvietta* in their analysis of nuclear RAG1 and RAG2 sequences and identified a clade consisting of these species as the “*Sphenoeacus* group”. The position of *Bradypterus victorini*, removed from other species in the genus, prompted a reversion to its older generic name *Cryptillas*. Fuchs et al. (2006) confirmed the close association of *Sylvietta*, *Macrosphenus* and *Sphenoeacus* based on one nuclear and one mitochondrial marker, and found that *Melocichla* was also a member of the “*Sphenoeacus* group”; Alström et al. (2006) also recovered a clade including *Sylvietta* and *Melocichla*. Johansson et al. (2008a) corroborated the existence of the “*Sphenoeacus* group” in their analysis of three nuclear loci by finding a clade consisting of *Cryptillas* (*Bradypterus*) *victorini*, *Macrosphenus*, *Sphenoeacus* and *Sylvietta*, but they did not consider *Achaetops* or *Melocichla*. Fregin et al. (2012) used one mitochondrial and six nuclear markers and again found support for a clade consisting of *Cryptillas victorini*, *Macrosphenus*, *Melocichla*, *Sphenoeacus* and *Sylvietta*, but did not include *Achaetops* in their analysis. Fregin et al. (2012) erected the family Macrosphenidae for this clade, although it lacks known diagnostic morphological features. In total, 18 species in 6 genera are presently placed in this family (Gill and Donsker, 2013).

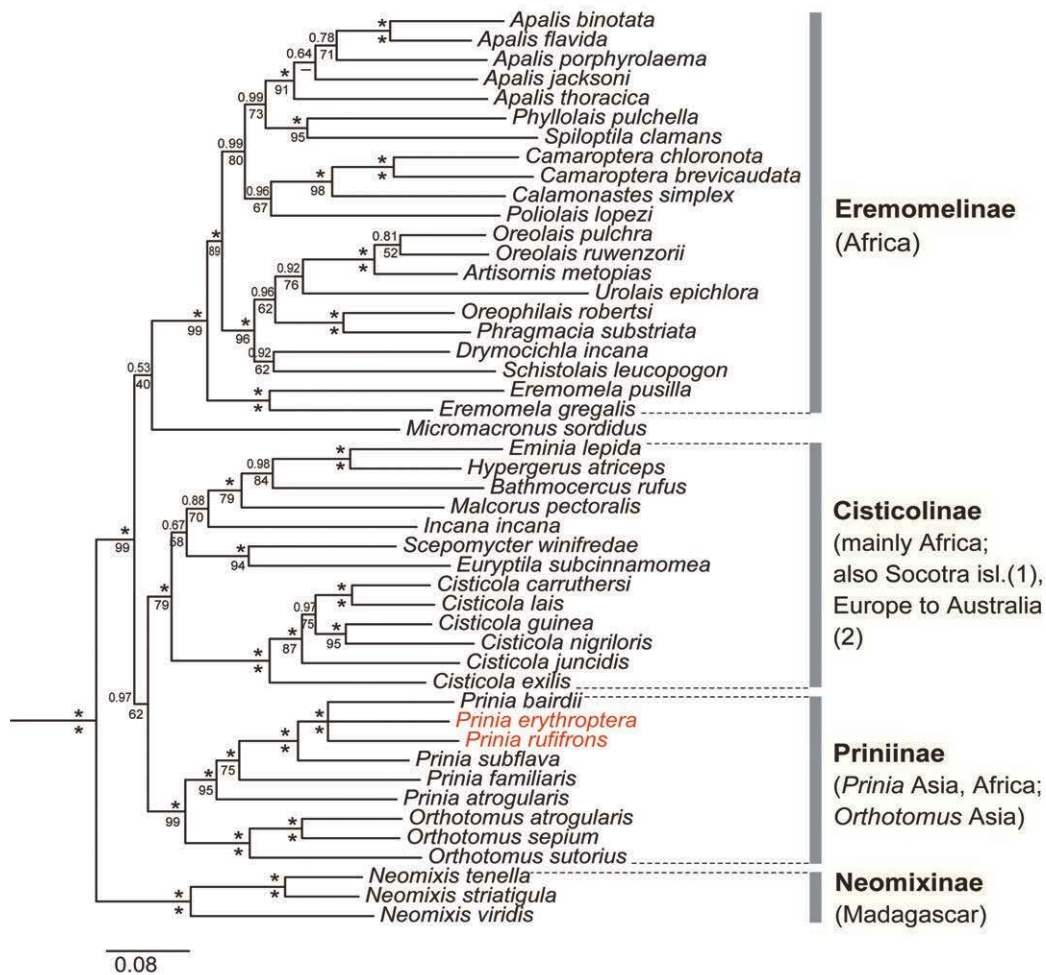
### Cisticolidae

The family Cisticolidae (cisticolas, prinias, apalises and allies) is the largest of the sylvioid families, with 160 species in 27 genera; 14 of the genera are monotypic, whereas the largest, *Cisticola*, contains more than 50 species (Gill and Donsker, 2013). All of the genera are found mainly or exclusively in Africa, except *Neomixis* (Madagascar), *Incana* (Socotra island) and *Orthotomus* (Asia), and the vast majority of the species occur in Africa (Ryan et al., 2006). The 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 (Sibley and Monroe, 1990). Several later studies have largely corroborated Sibley and Monroe’s (1990) circumscription of Cisticolidae (Cibois et al., 1999; Sefc et al., 2003; Beresford et al., 2005; Alström et al., 2006; Nguembock et al., 2007, 2008, 2012; Johansson et al.,

2008a; Alström et al., 2011c; Fregin et al., 2012). However, these later studies have also shown that the genera *Bathmocercus*, *Eremomela*, *Neomixis*, *Orthotomus*, *Poliolais* and *Scepomycter*, which were placed in Sylviidae by Sibley and Monroe (1990), belong to Cisticolidae. In contrast, the two monotypic genera *Rhopophilus* and *Scotocerca*, which were placed in Cisticolidae by Sibley and Monroe (1990) based on non-molecular data, have been shown by molecular analyses to have other affinities; the former is a “babbler” (Alström et al., 2006; Gelang et al., 2009; Olsson et al., 2013a), the latter sister to Cettiidae (Alström et al., 2011c; Fregin et al., 2012; placed in the monotypic family Scotocercidae by latter, see below).

Nguembock et al. (2007, 2012), who analyzed 15 and 17 cisticolid genera, respectively, using one to three

mitochondrial and one nuclear markers, and Olsson et al. (2013a; Fig. 2), who analyzed representatives of all genera believed to belong in Cisticolidae using two mitochondrial and two nuclear markers, are the most complete studies to date. These authors identified four main clades: (1) the speciose genus *Apalis* and several smaller (including monotypic) genera, all with exclusively African distributions; (2) the large genus *Cisticola* and several smaller (including monotypic) genera, of which all except two species of *Cisticola* are restricted to Africa; (3) the fairly large genera *Prinia* (Africa, Asia) and *Orthotomus* (Asia) and the two monotypic African genera *Heliolais* and *Urorhipis*; and (4) the genus *Neomixis* containing three species, all restricted to Madagascar. Olsson et al. (2013a) classified these clades as Eremomelinae, Cisticolinae, Priniinae and Neomixinae,



**Fig. 2** Family Cisticolidae based on concatenated nuclear MB and ODC and mitochondrial cytochrome *b* and ND2, based on Olsson et al. (2013). Posterior probabilities (above) and maximum likelihood bootstrap (below) values are indicated at the nodes; an asterisk represents posterior probability 1.00 or maximum likelihood bootstrap 100%. Changes of generic names are indicated in red (*Heliolais erythroptera* and *Urorhipis rufifrons* moved to genus *Prinia*).

respectively. A fifth lineage, containing the Philippine *Micromacronus sordidus*, which was shown by Oliveros et al. (2012) to be part of Cisticolidae, was in an *incertae sedis* position within Cisticolidae in the study by Olsson et al. (2013a).

Studies using molecular markers have found several of the cisticolid genera to be non-monophyletic, resulting in taxonomic revisions. The genus *Apalis* was shown by Nguembock et al. (2007) to be non-monophyletic, as *Apalis ruwenzorii* and *A. pulchra* were more closely related to *Artisornis metopias* than to other *Apalis* species, leading to erection of the genus *Oreolais* for the two former species (Nguembock et al., 2008). Moreover, the two African taxa currently placed in *Artisornis* have previously been placed in *Orthotomus* (e.g. Hall and Moreau, 1970; Watson et al., 1986), but this has been shown to be incorrect as *A. metopias* is not closely related to *Orthotomus* (Nguembock et al., 2007, 2008, 2012; Fregin et al., 2012; Olsson et al., 2013a). Recently, *Orthotomus cucullatus*<sup>1</sup> was moved from *Orthotomus* to *Phyllergates*, as it has been shown to be part of Cettiidae (Alström et al., 2006, 2011b; Fuchs et al., 2006; Nguembock et al., 2007, 2012). Olsson et al. (2013a) synonymized *Urorhipis* and *Heliolais* with *Prinia*. They also showed that *Prinia burnesii* is a babbler (Pellorneidae sensu Fregin et al., 2012), and reinstated the generic name *Laticilla* for this species.

Sheldon et al. (2012) reconstructed the phylogeny of all *Orthotomus* species based on mitochondrial and nuclear DNA. They revealed e.g. a deep split and non-monophyletic relationships within *O. castaneiceps*, and showed that several taxa previously considered subspecies of *O. atrogularis* were highly divergent.

*Prinia fluviatilis* was recognized as a species due to its distinctive song (Chappuis, 1974), and *P. superciliaris* was split from *P. atrogularis* on the basis of morphological and vocal evidence (Rasmussen and Anderton, 2005, 2012). Several studies underway suggest that the genus *Prinia* contains considerably more species than presently recognized, and this seems likely to be the case also in the speciose genus *Cisticola*.

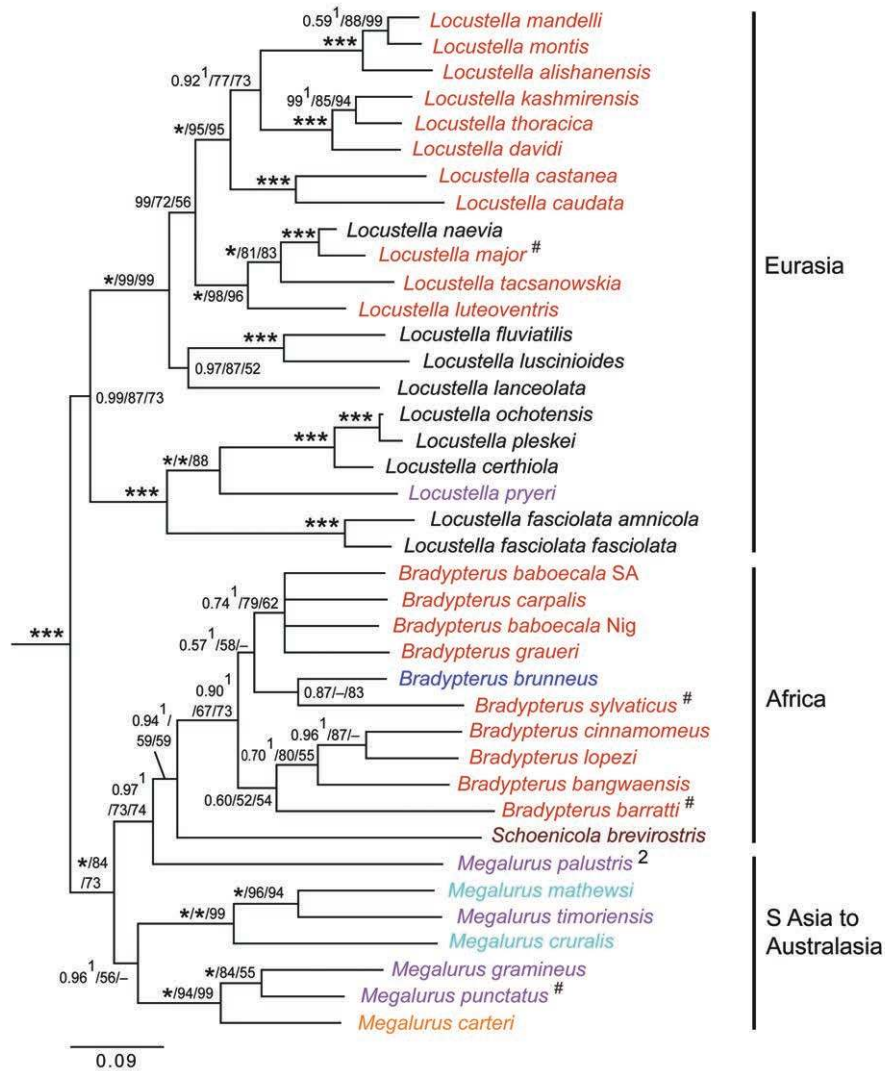
## Locustellidae

The family Locustellidae (grassbirds, bush warblers, grasshopper warblers and allies) is widely distributed across Africa, Eurasia and Australasia, with a total of

57 species in 9 genera (Gill and Donsker, 2013). It was first recognized by Sibley and Monroe (1990), partly based on DNA-DNA hybridization work by Sibley and Ahlquist (1990), as the subfamily Megalurinae, containing the genera *Megalurus*, *Cincloramphus*, *Eremiornis*, *Amphilais*, *Megalurulus*, *Buettikoferella*, *Chaetornis*, *Graminicola* and *Schoenicola*. Based on DNA sequence data from a broad selection of sylvioid genera, Alström et al. (2006) and Johansson et al. (2008a) recognized Megaluridae at the family level, comprising the genera *Megalurus*, *Bradypterus*, *Locustella* and *Dromaeocercus*. Hence, their circumscription included three of the genera placed in Acrocephalinae by Sibley and Monroe (1990). Moreover, molecular studies also revealed that the monotypic genus *Graminicola* is a babbler (Alström et al., 2006; Gelang et al., 2009; Olsson et al., 2013a), and that the aberrant *Bradypterus victorini* is not related to this clade (Beresford et al., 2005; now placed in *Cryptillas* – see under Macrosphenidae above). Alström et al. (2011a) noted that Locustellidae has priority over Megaluridae (as stated by Bock, 1994: 152).

The first comprehensive study of Locustellidae was published by Alström et al. (2011a; Fig. 3). It was based on a dataset comprising one mitochondrial and four nuclear loci for most of the species believed to belong in this family. The phylogeny strongly disagreed with earlier classifications at the generic level. All of the genera with more than one representative were found to be non-monophyletic: *Bradypterus* was separated into an Asian and an African clade, with *Locustella* and *Megalurus pryeri* nested within the former, and the monotypic Malagasy *Dromaeocercus* within the latter; only two of the five *Megalurus* species formed a clade that did not include other genera, and both *Cincloramphus* and *Eremiornis* were nested in one of the *Megalurus* clades. The non-monophyly of *Bradypterus* and *Locustella* had previously been found based on mitochondrial ND2 sequences of all *Locustella*, two Asian and three African *Bradypterus* and two *Megalurus* (*M. pryeri* and *M. gramineus*) (Drovetski et al., 2004). Moreover, the affinity of *M. pryeri* to *Locustella* had previously been suggested based on morphology (Morioka and Shigeta, 1993). Alström et al. (2011a) proposed a revised classification recognizing four instead of seven genera (Fig. 3). They acknowledged the non-monophyly of one of these genera (*Megalurus*), but stressed that the classification was tentative and took account of the phylogenetic uncertainty (i.e. conflict between their results and a study by Beresford et al., 2005 using another locus for five Lo-

<sup>1</sup> Note that the frequently used spelling *cucullatus* is apparently incorrect (Gill and Donsker, 2013).



**Fig. 3** Family Locustellidae based on concatenated nuclear ODC, MB, LDHB and GAPDH and mitochondrial cytochrome *b* sequences, based on Alström et al. (2011a). Species names follow revised taxonomy proposed by Alström et al. (2011c), but colors indicate genera according to Dickinson (2003) (red – *Bradypterus*; purple – *Megalurus*; dark blue – *Dromaeocercus*; pale blue – *Cincloramphus*; orange – *Eremiornis*). # indicates that only cytochrome *b* was available for analysis. Posterior probabilities and maximum likelihood and parsimony bootstrap values are indicated at the nodes, in this order; an asterisk represents posterior probability 1.00 or bootstrap 100%. *B. baboecala* SA and *B. baboecala* Nig refer to samples from South Africa (*transvaalensis/tongensis*) and Nigeria (*centralis*), respectively. <sup>1</sup>Node affected differently by different types of analyses. <sup>2</sup>Non-monophyletic *Megalurus* tentatively recognized due to conflicting results between present and another study based on different loci and DNA versus morphology.

Locustellidae species, as well as morphology and vocalizations).

A recent study by Oliveros et al. (2012) unexpectedly found that the monotypic Sulawesi genus *Malia* was nested in Locustellidae and that the Philippine *Robsonius* was sister to Locustellidae. Five putative Locustellidae genera remain to be studied genetically: *Amphilais* (monotypic, Madagascar), *Megalurulus* (four species, Melanesia), *Buettikoferella* (monotypic, Timor), *Chae-*

*tornis* (monotypic, Indian Subcontinent) and *Elaphrornis* (monotypic, Sri Lanka) (Gill and Donsker, 2013).

The species in the traditional genera *Locustella* and *Bradypterus* are renowned for being difficult to identify by morphological characters, and there has been much taxonomic confusion over the years (see Bairlein et al., 2006; Kennerley and Pearson, 2010). One new species, *Locustella* (*Bradypterus*) *alishanensis*, was described as recently as 2000 from Taiwan, where it had been known



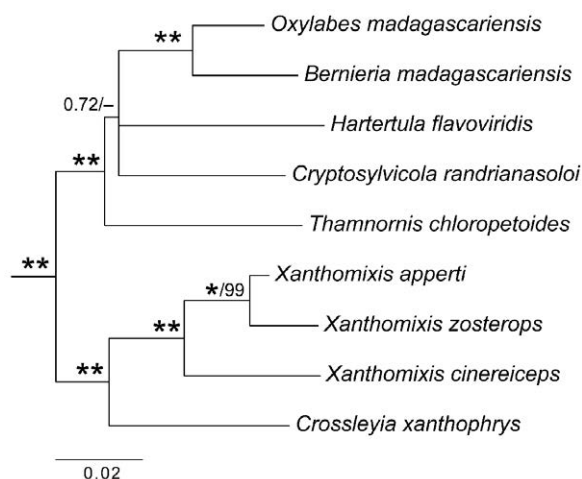
to exist for many years but with confused taxonomy (Rasmussen et al., 2000). Dickinson et al. (2000) revised the poorly known *Bradypterus seebohmi* complex based on morphology and vocalizations, and tentatively recommended recognition of four species: *B. seebohmi* sensu stricto (s.s.), *B. timorensis*, *B. montis* and *B. mandelli* (placed in *Locustella* by Alström et al., 2011). Alström et al. (2011a) analyzed mitochondrial cytochrome *b* from different populations of the latter two, and suggested that they were so similar that their status as separate species needs to be re-evaluated. *Locustella timorensis* (previously *Bradypterus timorensis*), until recently only known from two specimens collected in 1932 on Timor (Dickinson et al., 2000), was recently rediscovered, along with a putative undescribed taxon from nearby Alor (Trainor et al., 2012; Verbelen and Trainor, 2012). Another undescribed taxon in the same complex has recently been found on Taliabu island, Indonesia (Rheinhardt, 2010). The *L. thoracica* (previously *B. thoracicus*) complex was revised by Alström et al. (2008) based on multiple independent datasets, and they proposed that three instead of one species be recognized. *Locustella amnicola* has usually been treated as a subspecies of *L. fasciolata* (e.g. Dickinson, 2003; Kennerley and Pearson, 2010), but has also been given species status (Watson et al., 1986 [with a note by Ernst Mayr stating that “The status of this species is in doubt.”]; Stepanyan, 1990). Both Drovetski et al. (2004) and Alström et al. (2011a) showed that these two are markedly different genetically, supporting treatment as separate species. Alström et al. (2011a) also found deep cytochrome *b* divergences among some other taxa currently treated as conspecific, and suggested that species status might be warranted if corroborated by independent data: *B. baboecala tongensis* + *B. b. transvaalensis* vs. *B. b. centralis* + *B. b. elgonensis*; *B. lopezi mariae* + *B. l. usambarae* vs. *B. l. ufipae*; and *M. palustris toklao* vs. *M. p. forbesi*. Conversely, Alström et al. (2011a) and an earlier study by Drovetski et al. (2004), found slight divergences between *L. pleskei* and *L. ochotensis*, and noted that their status as separate species needs to be studied further.

## Bernieridae

The family name Bernieridae was proposed by Cibois et al. (2010) for a clade of Malagasy “warblers”. These were previously classified in the traditional families Timaliidae, Sylviidae and Pycnonotidae, but were shown by mitochondrial DNA to form an endemic Malagasy

radiation (Cibois et al., 1999, 2001; Fjeldså et al., 1999). Cibois et al. (2010) recognized 10 species in seven genera: *Bernieria madagascariensis*, *Xanthomixis zosterops*, *X. cinereiceps*, *X. apperti*, *X. tenebrosa*, *Oxylabes madagascariensis*, *Thamnornis chloropetoides*, *Crossleyia xanthophrys*, *Hartertula flavoviridis* and *Cryptosylvicola randrianasoloi*. Dickinson (2003) and Gill and Donsker (2013) included also *Randia pseudozosterops* in Bernieridae, although this species has not yet been included in any phylogenetic study. The first four species listed above have often been placed in the bulbul (greenbul) genus *Phyllastrephus*, and *H. flavoviridis* has been placed in the “warbler” genus *Neomixis* (e.g. Delacour, 1946).

The study by Fregin et al. (2012) is the most complete analysis of this family thus far with respect to number of loci, although the study by Alström et al. (2011), based on four nuclear and one mitochondrial loci, investigated one additional monotypic genus (*Cryptosylvicola*), and the mitochondrial study by Cibois et al. (2001) included two additional species in the genus *Xanthomixis*. The tree in Fig. 4, which is based on all previously published sequence data, is well resolved and well supported, except for some uncertain relationships within a clade containing *Oxylabes* + *Bernieria*, *Hartertula*, *Cryptosylvicola* and *Thamnornis*.



**Fig. 4** Family Bernieridae based on concatenated nuclear ODC, MB, LDHB, GAPDH and RAG1 and mitochondrial cytochrome *b* sequences (only cytochrome *b* for *X. cinereiceps*; no LDHB, GAPDH for *X. zosterops*; and no RAG1 for *C. randrianasoloi*), based on Cibois (1999, 2001), Alström et al. (2011c) and Fregin et al. (2012), reanalyzed by Bayesian inference in six partitions (by locus). See Supplementary Appendix for details of samples and analyses. Posterior probabilities and maximum likelihood bootstrap values are indicated at the nodes, in this order; an asterisk represents posterior probability 1.00 or bootstrap 100%.

## Donacobiidae

The family Donacobiidae was proposed by Aleixo and Pacheco (2006). It contains the single species *Donacobius atricapilla*, which occurs in Central and South America. This taxon has a chequered history: it was placed in the family Mimidae by e.g. Mayr and Greenway (1960), and later in the subfamily Troglodytinae by Sibley and Ahlquist (1990) and Sibley and Monroe (1990). However, Barker et al. (2004) found evidence for an association with *Zosterops* and *Prinia* based on one mitochondrial and one nuclear marker, and Alström et al. (2006) confirmed that it was firmly nested within Sylvioidea also using one mitochondrial and one nuclear marker (different ones from those used in Barker et al., 2004). Johansson et al. (2008a) found strong support for the position of *Donacobius* in a clade with Locustellidae and Bernieridae based on three nuclear loci, and this was corroborated by Fregin et al. (2012) based on seven molecular markers. However, the relationships among these three families are uncertain, probably due to a short time between their separations, as indicated by the short internode between *Donacobius* and Bernieridae. From a biogeographical point of view, the distribution of *Donacobius* is remarkable, as all of its closest relatives, Locustellidae and Bernieridae, occur in the Old World.

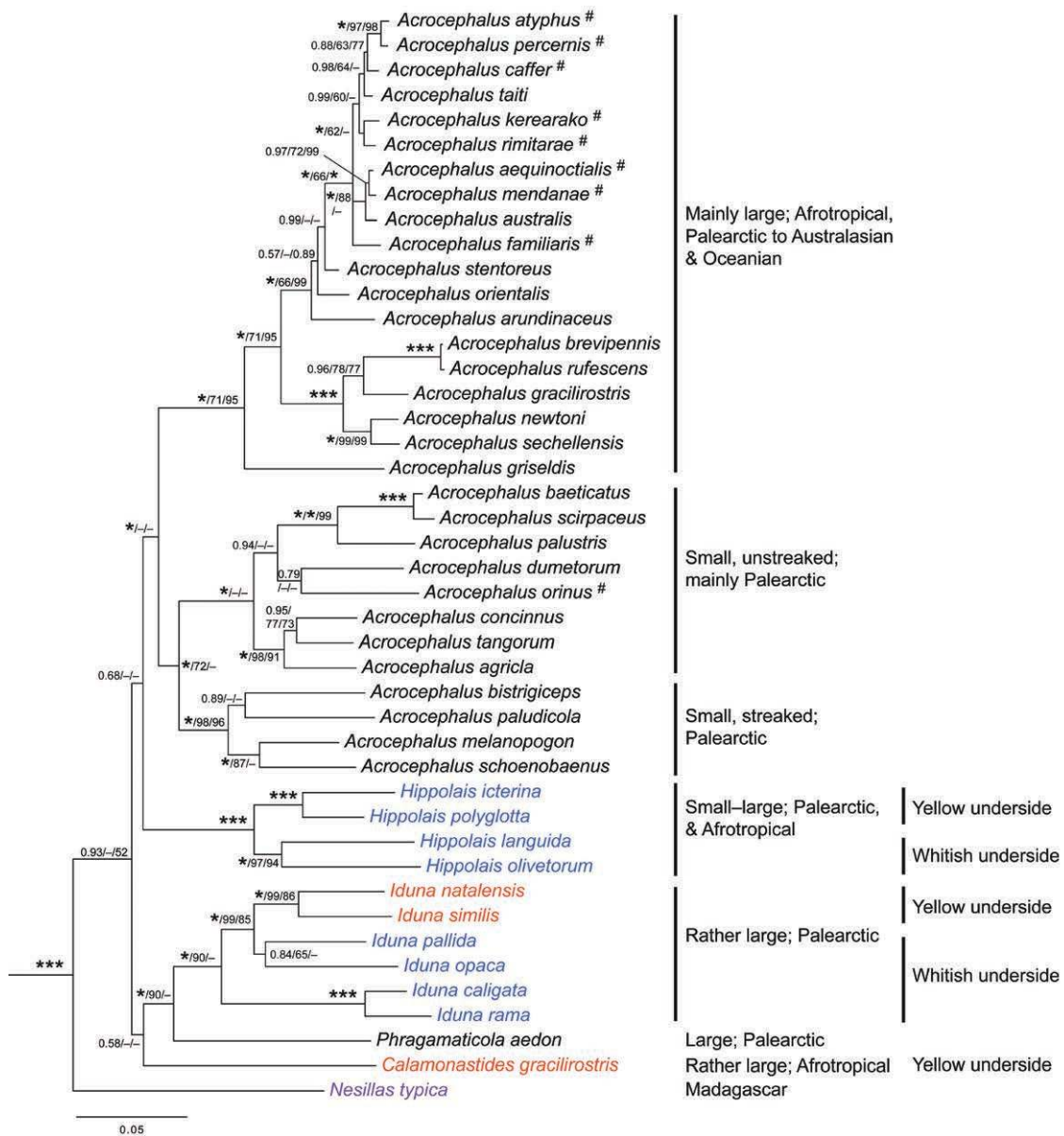
## Acrocephalidae

The relationships among the four genera in Acrocephalidae sensu Johansson et al. (2008a) and Fregin et al. (2009, 2012) [*Acrocephalus* (“reed warblers”), *Hippolais* (“tree warblers”), *Chloropeta* (“yellow warblers”) and *Nesillas* (“brush warblers”)] and their relationships to other taxa have long been debated based on morphology and oology (Hartert, 1909; Voous, 1977; Schönwetter, 1979; Wolters, 1982; Watson et al., 1986; Haffer, 1991; Cramp, 1992; Dickinson, 2003) as well as DNA (e.g. Sibley and Ahlquist, 1990; Leisler et al., 1997; Helbig and Seibold, 1999; Beresford et al., 2005; Alström et al., 2006; Johansson et al., 2008a; Fregin et al., 2009, 2012). The three genera *Acrocephalus*, *Hippolais* and *Chloropeta* have been split into several genera and/or subgenera, and there has been much disagreement regarding the classification of these taxa, especially *Acrocephalus* (Grant and Mackworth-Praed, 1941; Wolters, 1982; Watson et al., 1986; Sibley and Monroe, 1990; Dickinson, 2003; Haffer, 1991; Leisler et al., 1997; Helbig and

Seibold, 1999). Leisler et al. (1997) and Helbig and Seibold (1999) came to nearly identical conclusions based on analyses of cytochrome *b* sequence data. Neither of them found the genera *Acrocephalus* and *Hippolais* to be monophyletic. Leisler et al. (1997) discussed the option of dividing these into a number of genera, and Helbig and Seibold (1999) proposed a classification into a number of subgenera. Helbig and Seibold (1999) investigated only one species of *Chloropeta*, *C. gracilirostris*, which was shown to belong in the clade with *Acrocephalus* and *Hippolais*, albeit in an unresolved position; Leisler et al. 1997 did not study any *Chloropeta*.

Fregin et al. (2009) revised the family Acrocephalidae based on one mitochondrial and three nuclear loci for 32 out of the 38 species of *Acrocephalus* (mitochondrial data only for nine species), all eight *Hippolais*, all three *Chloropeta* and one *Nesillas* (Fig. 5). They recovered all *Acrocephalus* except *A. aedon* in one clade. The latter was sister to a clade with *C. natalensis* and *C. similis* as sisters to *H. pallida* and *H. opaca*, with *H. caligata* and *H. rama* as sisters to these four, and the generic name *Iduna* was erected for these seven species, with the suggested option of placing *I. aedon* in the monotypic genus *Phragamaticola*; the latter was adopted by Kennerley and Pearson (2010). The third species of *Chloropeta*, *C. gracilirostris*, was in an effectively unresolved position, and the monotypic genus *Calamonastides* was reinstated for it. The other four *Hippolais* (*H. icterina*, *H. polyglotta*, *H. olivetorum* and *H. languida*) formed a clade with two sister pairs, and the generic name *Hippolais* was suggested to be restricted to these four species.

At the species level, several taxa have been the subject of taxonomic debate. *Acrocephalus baeticatus* has been considered conspecific with *A. scirpaceus* (Dowsett-Lemaire and Dowsett, 1987) or regarded as a distinct species because of different migratory behavior and associated wing structure (Kennerley and Pearson, 2010). *Acrocephalus dumetorum* has been suggested to be a subspecies of *A. baeticatus* (Fry et al., 1974), although this suggestion has been refuted by molecular data (Leisler et al., 1997; Helbig and Seibold, 1999; Fregin et al., 2009). *Acrocephalus tangorum* has been treated as a subspecies of *A. bistrigiceps* (Williamson, 1968; Wolters, 1982; Watson et al., 1986; Sibley and Monroe, 1990) or *A. agricola* (Vaurie, 1959; Alström et al., 1991; Sibley and Monroe, 1993), but based on molecular data (Helbig and Seibold, 1999; Leisler et al., 1997; Fregin et al., 2009) is now generally recognized as a separate species (Dickinson, 2003; del Hoyo et al., 2006; Gill and



**Fig. 5** Family Acrocephalidae based on concatenated nuclear ODC, MB, LDHB and mitochondrial cytochrome *b* sequences, based on Fregin et al. (2009). # indicates that only cytochrome *b* was available for analysis. Posterior probabilities and maximum likelihood and parsimony bootstrap values are indicated at the nodes, in this order; an asterisk represents posterior probability 1.00 or bootstrap 100%. Colors represent taxonomy according to Dickinson (2003): black – *Acrocephalus*; blue – *Hippolais*; red – *Chloropeta*; purple – *Nesillas*.

Donsker, 2013). *Acrocephalus arundinaceus*, *A. orientalis*, *A. griseldis* and *A. stentoreus* have been considered conspecific at some stage (cf. Salomonsen, 1929; Mayr, 1948; Stresemann and Arnold, 1949; Vaurie, 1959; Williamson, 1968; Watson et al., 1986; Cramp, 1992; Eck, 1994). *Acrocephalus stentoreus* was first split off, as it was found to breed sympatrically with *A. arundinaceus* in central Asia and Israel (Stresemann and Arnold, 1949; Zahavi, 1957). *Acrocephalus griseldis* was shown

to be distinct morphologically (Pearson and Backhurst, 1988) and on the basis of molecular markers (Leisler et al., 1997; Helbig and Seibold, 1999; Fregin et al., 2009; cf. Fig. 5), and also *A. orientalis* was shown to be genetically distinct (Leisler et al., 1997; Helbig and Seibold, 1999; Fregin et al., 2009; cf. Fig. 5).

The *Acrocephalus* warblers occurring on different islands in eastern Polynesia were previously considered a single widespread species, *A.caffer* (Holyoak and

Thibault, 1984; Dickinson, 2003), whereas some authors suggested splitting this species into three, mainly because of wide geographical separation: *A. caffer* s.s. on the Society Islands, *A. atyphus* on Tuamotu, and *A. mendanae* in the Marquesas (Pratt et al., 1987; BirdLife International, 2000; Cibois et al., 2011a, b). Using mitochondrial sequence data, Cibois et al. (2007) showed that *A. mendanae* formed two independent lineages, which they proposed be treated as specifically distinct: *A. percernis* (closely related to *A. atyphus*) and *A. mendanae* s.s. (sister to *A. aequinoctialis*). In a later study, Cibois et al. (2008) analyzed mitochondrial DNA from extinct *Acrocephalus* taxa from different Society Islands, and concluded that *A. caffer* s.l. was more appropriately treated as one extant species, *A. caffer* s.s. (Tahiti), and two extinct ones, *A. longirostris* (Mo'orea) and *A. musae* (Raiatea, Huahine). A comprehensive study of Pacific *Acrocephalus* warblers (Cibois et al., 2011a) revealed complex colonization histories for several taxa, and revealed that *A. luscinius* is separated into three distantly related clades, calling for a taxonomic revision.

Until recently, *Acrocephalus orinus* was only known from a single specimen collected in winter in India in 1867, and its validity as a species was controversial. A series of studies, and the surprise finding of a live individual in Thailand in March 2006, gradually led to the discovery of a breeding population at high elevation in north-eastern Afghanistan and adjacent Tajikistan, and has been found during the breeding season, and almost certainly also breeds, in Kyrgyzstan, eastern Uzbekistan and south-eastern Kazakhstan (Bensch and Pearson, 2002; Round et al., 2007; Pearson et al., 2008; Svensson et al., 2008, 2010; Timmins et al., 2010; Ayé et al., 2010; Koblik et al., 2011).

The four Palearctic *Iduna* species (previously *Hippolais*) have long been treated as two species, *H. pallida* and *H. caligata* (e.g. Watson et al., 1986), although the former was suggested to be split into *H. pallida* s.s. and *H. opaca* based on morphological, vocal and behavioral characteristics (Svensson, 2001; Parkin et al., 2004), and the latter has often been split into *H. caligata* s.s. and *H. rama* on the same grounds, as well as sympatric breeding distributions (e.g. Stepanyan, 1990; Svensson, 2001; Parkin et al., 2004). Helbig and Seibold (1999) found deep divergences within both *H. pallida* s.l. and *H. caligata* s.l. in mitochondrial DNA, later confirmed by Ottosson et al. (2005) in an extensive study that also included morphological data, and by Fregin et al. (2009) using mitochondrial and nuclear loci (Fig. 5), further

supporting the splits based on non-molecular data.

## Hirundinidae

The globally distributed family Hirundinidae (swallows and martins) form a morphologically and ecologically rather homogeneous taxon, constrained by their aerial foraging behavior (Turner, 2004). In total, 88 species are recognized (Gill and Donsker, 2013). Mayr and Bond (1943) analyzed the swallows and martins based on morphology and nest-building characteristics, and judged that they could be divided into ten natural groups. *Phedina* was judged to be “possibly related to *Hirundo*”. White-backed Swallow (*Cheramoeca*), Grey-rumped Swallow (*Pseudhirundo*) and the African sawwings (*Psalidoprogne*) were judged to be “so clear-cut and isolated that they require no further comment”. The Barn and Cliff Swallow group consisted of *Delichon*, *Hirundo* and *Petrochelidon*. The genus *Riparia* was judged “a primitive genus without close relatives”, while the crag martins (*Ptyonoprogne*); the rough-wing swallow group (*Alopochelidon*, *Neochelidon* and *Stelgidopteryx*); the *Atticora* group (*Atticora*, *Notiochelidon*, *Orochelidon* and *Pygochelidon*); the tree swallows (*Tachycineta*, then split also into *Callichelidon*, *Lamprochelidon*, *Iridoprocne*) and the purple martin group (*Progne*) each qualified as a distinct group.

Sheldon and Winkler (1993) performed the first molecular study of the family, using the DNA-DNA hybridization to estimate the phylogeny of a limited number of species, and later used the phylogeny to superimpose nest construction data. Their results largely corroborated the groups defined by Mayr and Bond (1943). Winkler and Sheldon (1993) reconstructed the nest-excavating *Psalidoprogne* as sister to all other swallows, which were divided into two monophyletic groups, the mud-nesting *Hirundo* group, and a clade containing both nest excavating and cavity-nesting species. The ancestral mode of nest-building in this clade appeared to be nest-excavating, as cavity nesting is reconstructed as a recent apomorphy, which is only found in two lineages out of three in a polytomy containing the nest-excavating *Riparia riparia*, the cavity-nesting New World endemics (*Atticora*, *Haplochelidon*, *Neochelidon*, *Progne*, *Pygochelidon* and *Stelgidopteryx*) and the cavity-nesting New World tree swallows (*Tachycineta*). The nest-excavating *Cheramoeca*, *Phedina*, *Pseudhirundo* and *Riparia cincta* all trace their ancestry to nodes basal to the cavity-nesting species.

The most comprehensive molecular study of swallow phylogeny (Sheldon et al., 2005) identified the two river martins *Pseudochelidon* as sisters to all other swallows, albeit based on mitochondrial sequence data only. The combined mitochondrial and nuclear data available for a wide range of other swallows reconstructed two large clades comprising the remaining species, which Sheldon et al. (2005) termed “core martins, mud nesters and basal relicts”. The core martin clade was dominated by *Progne*, *Riparia* and *Tachycineta*, and also included the less speciose *Alopocheilidon*, *Atticora*, *Haplocheilidon*, *Neochelidon*, *Notiocheilidon*, *Phedina*, *Pygocheilidon* and *Stelgidopteryx*. The mud-nesters contained *Cecropis*, *Delichon*, *Hirundo*, *Petrocheilidon* and *Ptyonoprogne*. The basal relicts were placed as sisters to the mud-nesters and consisted of the groups judged by Mayr and Bond (1943) to be highly distinct and isolated from the others: White-backed Swallow (*Cheramoeca*), Grey-rumped Swallow (*Pseudhirundo*) and the African saw-wings (*Psalidoprogne*). Although Sheldon et al. (2005) were unable to determine the exact branching sequence of the “core martins, mud nesters and basal relicts”, they concluded that excavation of nests is the ancestral condition in swallows, and that the mud-nesters constitute a monophyletic radiation. Similarly, the core martins constituted a monophyletic group, within which two clades are cavity-nesters. The position of these two clades was unresolved in relation to the nest-excavating sand martins, so it was not possible to determine whether cavity-nesting arose once or twice.

Beside these major analyses, several studies focusing on particular genera have further clarified the phylogeny of swallows. Babin (2005) analyzed the geographic variation and speciation in the rough-winged swallows (*Stelgidopteryx*), shedding light on a complex picture of ancestral polymorphism not yet sorted among lineages. Dor et al. (2010) analyzed the *Hirundo* clade, arriving at results that are entirely congruent with Sheldon et al. (2005) but with the addition of *H. megaensis* and *H. nigrorufa*, which were not investigated in the latter analysis. Dor et al. (2010) and Zink et al. (2006) also undertook phylogeographical studies of *H. rustica*. Moyle et al. (2008) estimated a phylogeny of the New World martins (*Progne*), and discovered remarkably intricate and close relationships, polyphyly and possible hybrid introgression, and came to the conclusion that a population genetic perspective would probably be required to clarify the taxonomy, particularly among Amazonian populations.

Whittingham et al. (2002), Cerasale et al. (2012) and Dor et al. (2012) studied the phylogeny of *Tachycineta* using different approaches. Whittingham et al. (2002) used concatenated mitochondrial loci, Cerasale et al. (2012) used complete mitochondrial genomes, while Dor et al. (2012) used 16 nuclear introns to compare concatenation to a coalescent-based species tree inference method. All these approaches yielded different topologies, particularly concerning the positions of the North American *T. bicolor*, Peruvian *T. stolzmanni*, Hispaniolan *T. euchrysea* and Bahamian endemic *T. cyaneoviridis*. Dor et al. (2012) argued that the method of extracting information from the variability in coalescence times between independent gene genealogies outperforms other methods of analysis, thus advocating their species tree as the currently most reliable hypothesis. Similarly, Kirchman et al. (2000) analyzed relationships among different populations of the *Petrocheilidon fulva* complex, and confirmed previous suggestions that the South American populations are distinct (*P. rufocolaris*).

A phylogeographical study of *Riparia riparia* and *R. diluta*, which were previously considered a single species (e.g. Peters, 1960b), was undertaken by Pavlova et al. (2008). It corroborated fieldwork suggesting that these are specifically distinct (Gavrilov and Savchenko, 1991; Goroshko, 1993), and suggested that they diverged sometime between the late Pliocene and middle Pleistocene. It also suggested a Pleistocene split between samples from central Siberia and Mongolia. However, no molecular studies have been carried out yet on the southern, mainly Chinese, populations, which have usually been treated as conspecific with *R. diluta*.

## Pycnonotidae

The Pycnonotidae comprises approximately 150 species (Gill and Donsker, 2013) distributed across Africa and southern Asia. The first major molecular study of bulbuls (27 species; Pasquet et al., 2001), using mitochondrial sequence data, focused on the genus *Crimiger*, but their taxon sampling allowed general inferences about the family as a whole. Their results found a basal division into an African and a mainly Asian clade, and revealed that African and Asian clades of *Crimiger* were not closely related. Warren et al. (2005) showed that the bulbuls on Madagascar and on the islands of the Indian Ocean (*Hypsipetes*) originated from Asian ancestors. Moyle and Marks (2006) followed up by using also

nuclear genes and additional taxa (in total 57 species). Their phylogeny provided further detail and corroborated the two major clades, of which only the Asian clade included taxa also occurring in Africa, namely representatives of the genus *Pycnonotus*. In addition to the two main clades, Moyle and Marks (2006) found the monotypic African genus *Calyptocichla* to be sister to the Asian clade, but with weak support. A study by Johansson et al. (2007a) further clarified the phylogeny of the Afrotropical clade, among other things placing *Calyptocichla* in this clade, and proposing a revised taxonomy in which the genus *Atimastillas* was split from *Chlorocichla*, and the polyphyletic *Andropadus* was divided into four genera, *Andropadus*, *Arizelocichla*, *Eurillas* and *Stelgidillas*. Oliveros and Moyle (2010) studied the origin of the Philippine bulbuls, adding substantial resolution to the Asian clade. They found a number of instances of high genetic divergence within species, e.g. three deeply divergent lineages within *Ixos philippinus* (confirmed for two of these by Silva-Iturriza et al., 2010), and non-monophyly of the genus *Ixos*. Their preferred taxonomic solution was to include the genus *Microscelis* and Philippine members of *Ixos* in *Hypsipetes*, a genus to which they have previously been allocated (e.g. Rand and Deignan, 1960).

The phylogenetic position of *Neolestes torquatus*, which was originally described as an aberrant malacotid by Cabanis (1875), has been studied genetically and morphologically, and has been shown to be a bulbul, belonging in the Afrotropical clade (Dowsett et al., 1999; Moyle and Marks, 2006; Johansson et al., 2007a; Oliveros and Moyle, 2010; Zuccon and Ericson, 2010). Johansson et al. (2007a) and Zuccon and Ericson (2010) found good support for *Calyptocichla* in a sister group to the Afrotropical clade, in a clade that also contained *Andropadus importunus* and *A. gracilirostris*. Today, all generally recognized genera in Pycnonotidae have been included in molecular phylogenies, but much work remains to be done at the intra- and interspecific levels, as illustrated by Fuchs et al. (2011), who found significant biometric differences between lowland and montane populations of *Phyllastrepus debilis* in Tanzania.

### **Timaliidae sensu lato**

The “babblers” and allies, as presently circumscribed, comprise in total more than 450 species in five families, spread across Africa, Eurasia and Australasia, with par-

ticularly high diversity in temperate and sub-tropical parts of the Sino-Himalayan region; only one species (*Chamaea fasciata*) is found in the New World (Gill and Donsker, 2013). They are ecologically highly diverse, and exhibit a multitude of morphological and behavioral adaptations that have confounded morphology-based taxonomic judgment in the past. Reflecting the fact that the babblers were used as a “scrap basket” (Mayr and Amadon, 1951) for taxa that were difficult to classify with confidence, several taxa previously placed in this group have been removed as a result of molecular evidence. Recent molecular work on Passerida (Johansson et al., 2008a) and Sylvioidea (Alström et al., 2006; Fregin et al., 2012) in general, on the large scale phylogeny of babblers (Cibois, 2003a; Gelang et al., 2009; Moyle et al., 2012), and on several specific groups of babblers (e.g. Cibois et al., 2002; Pasquet et al., 2006; Reddy and Cracraft, 2007; Zhang et al., 2007; Zou et al., 2007; Luo et al., 2009; Dong et al., 2010a, b; Reddy and Moyle, 2011) have gradually clarified the phylogeny of this complex group. These studies have revealed that the traditional babblers (e.g. Deignan, 1964b; Dickinson, 2003) do not constitute a monophyletic group, and some taxa have been removed from the babbler assemblage (e.g. the Australasian “babblers” *Garritornis* and *Pomatostomus* [Sibley and Ahlquist, 1990]; Malagasy “babblers” *Mystacornis*, *Oxylabes*, *Hartertula* and *Neomixis* [Cibois et al., 1999; Johansson et al., 2008a, b; Fregin et al., 2012]; *Chaetops frenatus* [Ericson and Johansson, 2003; Barker et al., 2004; Beresford et al., 2005]; *Panurus biarmicus* [Ericson and Johansson, 2003; Alström et al., 2006; Fregin et al., 2012]; *Erpornis* [previously *Yuhina*] *zantholeuca* [Cibois et al., 2002; Barker et al., 2004]; *Eupetes macrocerus* [Jönsson et al., 2007]; *Robsonius*, *Micromacronus*, *Leonardina* and *Mallia* [Moyle et al., 2012; Oliveros et al., 2012]; *Kakamega* [Johansson et al., 2008a]; *Pnoepyga* [Gelang et al., 2009; Fregin et al., 2012]; and *Pteruthius* [Cibois, 2003; Reddy and Moyle, 2011]), whereas some additional taxa have been shown to belong there (e.g. *Sylvia* and *Zosterops* [Cibois, 2003; Alström et al., 2003; Gelang et al., 2009; Fregin et al., 2012; Moyle et al., 2012]; *Chamaea fasciata* [Sibley and Ahlquist, 1990; Cibois, 2003; Gelang et al., 2009; Fregin et al., 2012; Moyle et al., 2012]; *Lioptilus nigricapillus* [Johansson et al., 2008a; Moyle et al., 2012]; *Parophasma galinieri* [Gelang et al., 2009; Moyle et al., 2012]; *Rhopophilus pekinensis* [Alström et al., 2006; Gelang et al., 2009], *Graminicola bengalensis* [Alström et al., 2006; Gelang et al., 2009]; *Laticilla* [previ-

ously *Prinia burnesii* [Olsson et al., 2013a]).

Five primary clades have been identified in the babbler group, three of which are made up of traditional babblers, one of a mixture of babblers (mainly *Yuhina*) and white-eyes (latter traditionally Zosteropidae), and one containing babblers and *Sylvia* warblers (Cibois, 2003a; Alström et al., 2006; Gelang et al., 2009; Fregin et al., 2012; Moyle et al., 2012). The three most recent of these papers all recovered the same five primary clades, but differed in their taxonomic recommendations. Gelang et al. (2009) separated Sylviidae and Timaliidae at the family level, and treated Leiothrichinae, Pelloroneinae, Timaliinae and Zosteropinae as subfamilies within Timaliidae. Fregin et al. (2012) recognized all five clades at the family level: Leiothrichidae, Pelloroneidae, Timaliidae, Sylviidae and Zosteropidae. Moyle et al. (2012) took a third position in recognizing Sylviidae, Timaliidae and Zosteropidae at the family level, with Leiothrichinae, Pelloroneinae and Timaliinae as subfamilies in Timaliidae. We here follow Fregin et al. (2012) and Gill and Donsker (2013) and treat the five primary babbler clades at the rank of family, as we consider that to be in better agreement with the treatment of the other primary clades in Sylvioidea than the treatments of Gelang et al. (2009) and Moyle et al. (2012).

### Timaliidae

The Timaliidae clade is restricted to (southern) Asia, and comprises the genera *Dumetia*, *Macronus* (see below), *Pomatorhinus* (see below), *Rhopocichla*, *Spelaornis*, *Sphenocichla* (see below), *Stachyris* (see below), *Timalia* and *Xiphirhynchus* (see below) (Cibois, 2003; Gelang et al., 2009; Moyle et al., 2012), in total c. 55 species (Gill and Donsker, 2013). *Macronus*, *Pomatorhinus* and *Stachyris*, as traditionally circumscribed (e.g. Deignan, 1964b; Dickinson, 2003), have all been found to be non-monophyletic, and Moyle et al. (2012) suggested a number of rearrangements: resurrection of *Mixornis* (for *M. gularis*, *M. flavicollis* and *M. kellei*); two latter unstudied by molecular methods); restricting *Macronus* to *M. striaticeps* and *M. ptilosus*; reinstatement of *Cyanoderma* for several species placed in *Stachyris* or *Stachyridopsis* (e.g. *C. chrysaemum*, *C. erythropterum*, *C. ruficeps* and *C. rufifrons*); restricting *Stachyris* to a group containing e.g. *S. nigriceps*, *S. striolata*, the recently described *S. nonggangensis* (Zhou and Jiang, 2008; not studied by molecular methods) and *Sphenocichla*; and splitting *Pomatorhinus* into *Pomato-*

*rhinus* s.s. (comprising most species, including *P.* [previously *Xiphirhynchus*] *superciliaris*) and *Megapomatorhinus* (new genus name, containing *M. hypoleucos*, *M. erythrocnemis*, *M. erythrognis* and *M. swinhoei*).

The relationships within *Pomatorhinus* s.l. have recently been examined by Dong et al. (2010a) using two mitochondrial and four nuclear markers for a relatively small number of taxa and by Reddy and Moyle (2011) based on the same two mitochondrial markers for a larger number of taxa. Both studies, as well as Moyle et al. (2012), inferred *Stachyris* s.s. nested within *Pomatorhinus* s.l., although there was conflict between the studies regarding the position of the *Stachyris* s.s. clade in relation to the primary *Pomatorhinus* s.l. clades. Moreover, all these, as well as Cibois (2003a) and Gelang et al. (2009), recovered *Xiphirhynchus* (see above) deep inside the *Pomatorhinus* s.l. clade. Reddy and Moyle (2011) found multiple deep divergences within traditional species of *Pomatorhinus* s.l. as well as non-monophyletic species, and also identified 27 lineages with diagnosable plumage differences (i.e. phylogenetic species sensu Cracraft, 1989). Previously, Collar (2006) and Collar and Robson (2007) suggested elevation of several taxa treated as subspecies to the rank of species based on morphology and vocalizations.

Also other Timaliidae, e.g. the genus *Spelaornis*, were revised recently, by Rasmussen and Anderton (2005, 2012), Collar (2006) and Collar and Robson (2007) based mainly on morphological and vocal characters.

### Leiothrichidae

The genera *Actinodura*, *Babax* (see below), *Cutia*, *Garrulax* (see below), *Heterophasia*, *Leiothrix*, *Liocichla*, *Minla*, *Turdoides*, *Kupeornis* (see below) and *Phyllanthus* (see below) have been recovered as members of the Leiothrichidae clade (Cibois, 2003; Gelang et al., 2009; Moyle et al., 2012), in total c. 130 species (Gill and Donsker, 2013). They are widely distributed across (southern) Asia, although the *Turdoides* clade (including *Kupeornis* and *Phyllanthus*; see below) has radiated extensively in Africa.

The genera *Garrulax*, *Actinodura*, *Minla*, *Heterophasia* and *Turdoides*, as generally circumscribed (e.g. Deignan, 1964b; Dickinson, 2003), have been found to be non-monophyletic (Cibois, 2003; Gelang et al., 2009; Luo et al., 2009; Dong et al., 2010b; Moyle et al., 2012), and based on these results Moyle et al. (2012) suggested a taxonomic revision of this clade. They proposed that

*Garrulax* be divided into *Garrulax*, *Grammatoptila* (monotypic: *G. striata*), *Ianthocincla* and *Trochalopteron*, and *Babax* synonymized with *Ianthocincla*. Moreover, they proposed that *Kuipoornis* and *Phyllanthus* be subsumed in *Turdoides*, *Heterophasia annectans* moved to *Minla*, and *Minla cyanouroptera* and *M. strigula* transferred to *Actinodura*. However, it should be noted that no molecular study has included the type species of *Garrulax*, *G. rufifrons*, so the circumscription of this genus should be considered preliminary. The reinstatement of *Trochalopteron* was earlier proposed by Luo et al. (2009) based on molecular data as well as the observation that all species in that clade have speckled eggs, unlike any other traditional *Garrulax* (though eggs have not been studied for all species). Earlier, Rasmussen and Anderton (2005) and Collar and Robson (2007) proposed reclassifications based on morphological features, and some of these agree with the molecular results, whereas others do not, and some have not yet been tested by molecular markers; Rasmussen and Anderton (2012) followed various genetic analyses in further revising *Garrulax* and other laughingthrush genera.

The taxonomy of *Garrulax canorus* has been assessed by molecular markers by Li et al. (2006, 2009), who proposed that the Taiwanese taxon should be treated as specifically distinct, *G. taewanus* (placed in genus *Leucodiotron* in latter study). The same conclusion was previously reached by Collar (2006) based on morphology. Several other taxa were also elevated from the rank of subspecies to species by Rasmussen and Anderton (2005, 2012), Collar (2006) and Collar and Robson (2007), mainly based on morphology and vocalizations. A new species, *Liocichla bugunorum*, was described as recently as 2006 (Athreya, 2006).

### Pellorneidae

The Pellorneidae clade comprises species in the genera *Gampsorhynchus*, *Gramminicola*, *Illadopsis*, *Jabouilleia* (see below), *Kenopia*, *Malacocincla*, *Malacopteron*, *Napothera*, *Pellorneum*, *Ptilocichla*, *Ptyrticus* (see below), *Rimator* (see below), *Schoeniparus* (formerly *Alcippe*; see below), *Trichastoma* (see below) and *Turdinus* (Cibois, 2003; Gelang et al., 2009; Moyle et al., 2012), in total c. 70 species (Gill and Donsker, 2013). In addition, *Laticilla* (previously *Prinia*) *burnesii* was found by Olsson et al. (2013a) to belong in this clade. With the exception of the African *Illadopsis*, this family occurs only in Asia.

The genera *Illadopsis*, *Napothera*, *Malacocincla* and *Pellorneum*, as traditionally defined (e.g. Deignan, 1964b; Dickinson, 2003), have been inferred to be non-monophyletic (Cibois, 2003; Moyle et al., 2012), and in the taxonomic revision suggested by Moyle et al. (2012) several taxa were synonymized: *Ptyrticus* with *Illadopsis*; *Trichastoma* with *Pellorneum*; and *Jabouilleia* and *Rimator* with *Napothera*. These authors also moved some *Napothera* and some *Malacocincla* to *Turdinus*, while the remaining *Malacocincla* were placed in *Pellorneum*. However, the name *Turdinus* seems to be misapplied. The type species of this genus, *T. macrodactylus*, was not included in the analysis by Moyle et al. (2012), but in the study by Gelang et al. (2009), it was sister to *Gramminicola*, with strong support, while *Malacocincla abbotti*, which was also placed in *Turdinus* by Moyle et al. (2012), was in a different clade (with high posterior probability but low maximum likelihood bootstrap support). The revised classification by Collar and Robson (2007), which was based mainly on morphological traits, agrees in some respects but differs in others from the treatment by Moyle et al. (2012).

A new species, *Jabouilleia naungmungensis*, was recently described from Myanmar (Rappole et al., 2005), although this was considered a subspecies of *J. (=Rimator) danjouei* by Collar and Robson (2007) and Collar (2011). *Gramminicola bengalensis* was recently suggested to be split into two species, *G. bengalensis* s.s. (Indian subcontinent) and *G. striatus* (southern China, northern South-East Asia) (Leader et al., 2010).

### Sylviidae sensu stricto

The circumscription of Sylviidae today is radically different from the traditional usage of this name (e.g. Watson et al., 1986; Sibley and Monroe, 1990; Dickinson, 2003; Bairlein et al., 2006; see introduction). The Sylviidae s.s. clade includes the genera *Chamaea*, *Chrysomma*, *Conostoma* (see below), *Fulvetta* (see below), *Horizorhinus* (see below), *Lioparus* (see below), *Lioptilus*, *Moupinia* (sometimes synonymized with *Chrysomma*), *Myzornis*, *Paradoxornis* (see below), *Parisoma* (see below), *Parophasma*, *Pseudoalcippe* (see below), *Rhopophilus* and *Sylvia* (Barhoum and Burns, 2002; Cibois, 2003; Gelang et al., 2009; Moyle et al., 2012), in total c. 70 species (Gill and Donsker, 2013). This family is geographically more widespread than the previous babbler clades. Although the majority occurs in southern Asia, *Sylvia* (including *Horizorhinus*, *Parisoma* and



*Pseudoalcippe*; see below) is also distributed in northern Asia, Europe and Africa, *Parophasma* and *Lioptilus* are restricted to Africa, and *Chamaea* is restricted to western North America, as the only babbler representative in the New World.

The genus *Paradoxornis* has been shown to be non-monophyletic, with at least *Conostoma* nested within *Paradoxornis* (Yeung et al., 2011). In a comprehensive analysis of the parrotbills, Yeung et al. (2011) identified three major clades in both mitochondrial and nuclear gene trees, further supported by body size and plumage coloration. The monotypic genus *Conostoma* was confirmed to belong in one of these clades. However, while trees inferred by combined nuclear sequences supported monophyly of the parrotbills, mitochondrial DNA suggested that one of the parrotbill clades was more closely related to *Chamaea*, *Fulvetta* and *Lioparus* (two latter treated in genus *Alcippe*) than to the other parrotbills; however, the latter topology received no maximum likelihood bootstrap support (but high posterior probability). Penhallurick and Robson (2009) proposed a reclassification of the parrotbills into eight genera (including a new genus name, *Sinosuthora*, containing *S. alphonsiana*, *S. brunnea*, *S. conspicillata*, *S. przewalskii*, *S. webbiana* and *S. zappayi*), based on size, plumage and vocalizations, backed up by a published study of mitochondrial DNA (Yeung et al., 2006; see correction of one of these generic names in Penhallurick, 2010). Previously, King and Robson (2008) had suggested splitting *Paradoxornis ruficeps* into two species, *P. ruficeps* s.s. and *P. bakeri*.

Shirihai et al. (2001) and Voelker and Light (2011) inferred the relationships of the genus *Sylvia* based on mitochondrial DNA, and found that the African species previously placed in the genus *Parisoma* were nested within the essentially Palearctic *Sylvia*. The latter authors, and previously Voelker et al. (2009), also found that *Horizorhinus dohrni* and *Pseudoalcippe abyssinica* formed a sister clade to *Sylvia borin*, and placed both in the genus *Sylvia*; *P. abyssinica* had previously been found to be closely related to *Sylvia* (*S. melanocephala*) by Cibois (2003a). This was later corroborated by Moyle et al. (2012; using *P. atriceps*), who also found *Lioptilus nigricapillus* to be part of this clade. Several groups of *Sylvia* warblers have been the subject of taxonomic studies based on multiple character sets, usually including DNA, which have resulted in the recognition of a larger number of species, e.g. the splitting of *S. crassirostris* from *S. hortensis* (Shirihai et al., 2001), *S. balearica*

from *S. sarda* (Shirihai et al., 2001), and *S. subalpina* (synonym *S. moltonii*) from *S. cantillans* (Brambilla et al., 2008a, b, c). The long-standing uncertainty over species limits in the *S. curruca* complex (e.g. Watson et al., 1986; Cramp, 1992; Martens and Steil, 1997; Shirihai et al., 2001; Loskot, 2001, 2005; Bairlein et al., 2006) was recently investigated using mitochondrial DNA (Olsson et al., 2013b), but although six long-separated clades representing the taxa *althaea*, *blythi*, *curruca*, *halimodendri*, *margelanica* and *minula* were recovered, the gene tree partly disagreed with morphological evidence, and it was concluded that independent data were required to resolve the issue.

### Zosteropidae

The following genera have been found to belong in the Zosteropidae clade: *Chlorocharis*, *Cleptornis*, *Heleia*, *Lophozosterops*, *Oculocincta*, *Rukia*, *Speirops*, *Sterrhoptilus*, *Yuhina*, *Woodfordia*, *Zosterops* and *Zosterornis* (latter placed in *Stachyris* in earlier studies) (Cibois et al., 2002; Cibois, 2003a; Zhang et al., 2007; Gelang et al., 2009; Moyle et al., 2009, 2012). Most of these have been represented by single species in these analyses, but those that have been represented by two or more species (*Lophozosterops*, *Yuhina*, *Zosterops* and *Zosterornis*) have been found to be non-monophyletic. For example, *Yuhina* is separated into at least three (Moyle et al., 2012) or four (Zhang et al., 2007; Moyle et al., 2009) monophyletic groups, with *Y. diademata* being sister to all Zosteropidae, and one of these *Yuhina* clades is sister to the rest of the Zosteropidae. The main *Zosterops* clade, which also includes at least *Chlorocharis*, *Rukia*, *Speirops* and *Woodfordia*, has been termed a “great speciator” by Moyle et al. (2009), as it shows evidence of an exceptionally rapid speciation rate and expansion over a vast area covering subsaharan Africa, much of southern Asia and Australasia. The monotypic genus *Hypocryptadius* was previously considered related to *Zosterops*, but was recently shown to be a forest-adapted sparrow (Fjeldså et al., 2010). A thorough taxonomic revision of the Zosteropidae is obviously greatly needed.

Detailed studies in *Zosterops* have been carried out on both Australian (Degnan and Moritz, 1992), Philippine (Jones and Kennedy, 2008), Indian Ocean (Warren et al., 2006; Milá et al., 2010) and South African (Oatley et al., 2011, 2012) species complexes, often revealing complex patterns of genetic and morphological divergence.

### *Alcippe sensu lato*

The genus *Alcippe* provides one of the most extreme examples of the difference between past taxonomic judgments based on morphology (e.g. Deignan, 1964b; Dickinson, 2003) and recent molecular phylogenies. In a study based on mitochondrial DNA by Pasquet et al. (2006) the genus was found to consist of four different unrelated clades, the positions of which have gradually been clarified in multilocus analyses by Gelang et al. (2009) and Moyle et al. (2012). One clade, *Schoeniparus* (containing *S. cinereus*, *S. castaneiceps*, *S. rufogularis*, *S. brunneus* and *S. dubius*), was found to be nested in Pellorneidae; two clades, *Fulvetta* (including e.g. *F. cinereiceps*, *F. ruficapilla* and *F. vinipectus*) and *Lioparus* (monotypic: *L. chrysotis*), were nested in Sylviidae; whereas the position of the *Alcippe* s.s. clade (comprising e.g. *A. poioicephala* and *A. morrisonia*) is somewhat uncertain. The latter clade was recovered by Gelang et al. (2009) as sister to Pellorneidae with good support, whereas Moyle et al. (2012) recovered it as sister to Leiothrichidae, also with good support. The latter authors remarked that the position of this clade is mainly weakly supported or even contradicted by single loci. More research is needed to establish where the *Alcippe* s.s. clade belongs in the babbler phylogeny.

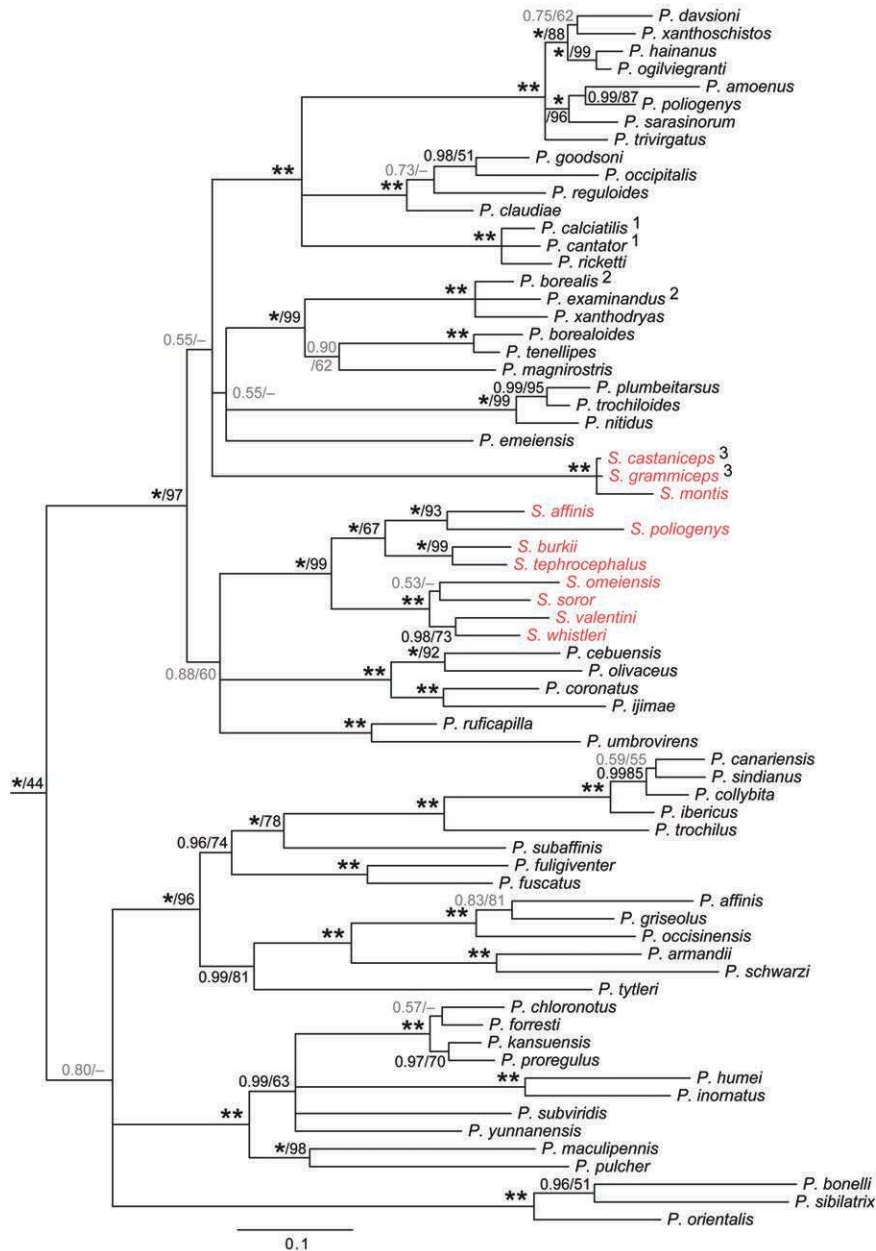
Phylogeographical studies of the *Alcippe morrisonia* complex by Zou et al. (2007) and Song et al. (2009) revealed unexpectedly deep divergences between different geographical areas (oldest split dated to 11.6 million years ago by Song et al., 2009). Moreover, Zou et al. (2007) found that one of these clades (*A. m. fratercula* from Yunnan, China) is more closely related to *A. peracensis annamensis* (Vietnam) than to other taxa treated as *A. morrisonia*. Based on these results, Gill and Donsker (2013) split *A. morrisonia* into four species: *A. morrisonia* s.s. (Taiwan), *A. davidi* (Shaanxi, Gansu, Sichuan, Hunan, Guangxi Provinces in China, northern Vietnam), *A. fratercula* (Yunnan Province in China to central Myanmar and northern Thailand) and *A. hueti* (Fujian, Guangdong and Hainan Provinces, China). Collar (2006) and Collar and Robson (2007) revised the taxonomy of several species of *Fulvetta* and *Alcippe* s.s. based mainly on morphological characters; several of these have a contorted taxonomic history.

### Phylloscopidae

The family Phylloscopidae, as presently circumscribed,

comprising the genera *Phylloscopus* and *Seicercus*, was proposed by Alström et al. (2006). Sibley and Ahlquist (1990) and Sibley and Monroe (1990) placed these genera in the subfamily Acrocephalinae together with many other genera, while Dickinson (2003) put them in the subfamily Phylloscopinae, together with *Tickellia*, *Abroscopus*, *Eremomela*, *Sylvietta* and *Graueria*. Neither of the classifications by Sibley and Ahlquist (1990), Sibley and Monroe (1990) or Dickinson (2003) are consistent with phylogenetic studies (Beresford et al., 2005; Alström et al., 2006; Johansson et al., 2007b; Fregin et al., 2012; Olsson et al., 2013a), although *Graueria* has not yet been studied phylogenetically. The most comprehensive phylogeny of Phylloscopidae to date (Johansson et al., 2007b) was based on two mitochondrial and one nuclear loci for 55 of the 68 species recognized at that time (Dickinson, 2003). Other studies based on smaller, but partly different datasets have been published (Richman and Price, 1992; Martens et al., 2004, 2008; Olsson et al., 2004, 2005; Päckert et al., 2004, 2009). Figure 6 shows a tree for all of the species in these studies based on the same sequences, but reanalyzed here. As has already been remarked in some of the previous studies, the tree shows that *Seicercus* is nested within *Phylloscopus*, rendering the latter genus non-monophyletic. The tree also suggests that *Seicercus* is non-monophyletic, although this has poor statistical support. As has also been suggested by previous authors, the taxonomic implications are that either *Seicercus* be synonymized with *Phylloscopus* or the complex be split into more than two genera. We await a more complete taxonomic study that is in preparation.

The genera *Phylloscopus* and *Seicercus* have undergone dramatic taxonomic changes in the past 20 years, due to studies of especially vocalizations and DNA. No fewer than six species new to science have been described in that period: *P. hainanus* (Olsson et al., 1993), *P. emeiensis* (Alström and Olsson, 1995), *S. omeiensis* (Martens et al., 1999), *S. soror* (Alström and Olsson, 1999), *P. occisinensis* (Martens et al., 2008) and *P. calciatilis* (Alström et al., 2010). Moreover, taxonomic revisions have led to the recognition of several new species: *P. canariensis* and *P. ibericus* (previously treated as subspecies of *P. collybita*; *P. ibericus* formerly incorrectly called *P. brehmii*) (Helbig et al., 1996; Salomon et al., 1997; Helbig et al., 2001; Bensch et al., 2002; Salomon et al., 2003); *P. orientalis* (previously subspecies of *P. bonelli*; Helbig et al., 1995); *P. borealoides* (previously synonym of *P. tenellipes*; Martens, 1988); *P. chloronotus*



**Fig. 6** Family Phylloscopidae based on concatenated nuclear MB and mitochondrial cytochrome *b* and 12S sequence data, based on Olsson et al. (2004, 2005), Alström et al. (2006, 2010, 2011d), Saitoh et al. (2010) and Johansson et al. (2007), reanalyzed by Bayesian inference in three partitions (by locus). See Supplementary Appendix for details of samples and analyses. Posterior probabilities and maximum likelihood bootstrap (MLBS) values are indicated at the nodes, in this order; an asterisk represents posterior probability 1.00 or bootstrap 100%. <sup>1</sup> *P. calciatilis* + *P. cantator* 85% MLBS; <sup>2</sup> *P. borealis* + *P. examinandus* 60% MLBS; <sup>3</sup> *S. castaniceps* + *S. grammiceps* MLB 87%.

(previously subspecies of *P. proregulus*; Alström and Olsson, 1990; Martens et al., 2004); *P. forresti* (previously synonym of *P. proregulus chloronotus*; Martens et al., 2004); *P. kansuensis* (previously synonym of *P. p. proregulus*; Alström et al., 1997; Martens et al., 2004); *P. yunnanensis* (previously synonym of *P. proregulus chloronotus*; Alström et al., 1990, 1992 [described as *P. sichua-*

*nensis* in latter study]; Martens et al., 2004); *P. claudiae*, *P. goodsoni* and *P. ogilviegranti* (two former previously subspecies of *P. reguloides*, third previously subspecies of *P. davisoni*; Olsson et al., 2005; Päckert et al., 2009); *P. examinandus* and *P. xanthodryas* (previously subspecies of *P. borealis*; Saitoh et al., 2006, 2008, 2010; Reeves et al., 2008; Martens, 2010; Alström et al., 2011d); *S.*

*valentini*, *S. whistleri* and *S. tephrocephalus* (previously subspecies of *S. burkii*; Alström and Olsson 1999, 2000; Martens et al., 1999; Olsson et al., 2004; Päckert et al., 2004). The taxonomic rank of some currently recognized species, e.g. *P. subaffinis* and *P. humei*, has been debated over the years, but has been settled due to recent studies of vocalizations and/or DNA (Alström and Olsson, 1992; Irwin et al., 2001b). In the case of the *P. trochiloides*–*P. plumbeitarsus*–*P. nitidus* complex, the debate is still ongoing due to different interpretations of the available data (Irwin, 2000; Irwin et al., 2001b, 2005, 2008; Knox et al., 2002; Dickinson, 2003; Gill and Donsker, 2013). One species, *P. xanthoschistos*, has been transferred from *Seicercus* to *Phylloscopus* (Olsson et al., 2005; Päckert et al., 2009), and one subspecies from one species to another, *P. fuscatus weigoldi* to *P. fuligiventer weigoldi* (Martens et al., 2008). See reviews by Irwin et al., (2001a), Rheindt (2006) and Martens (2010).

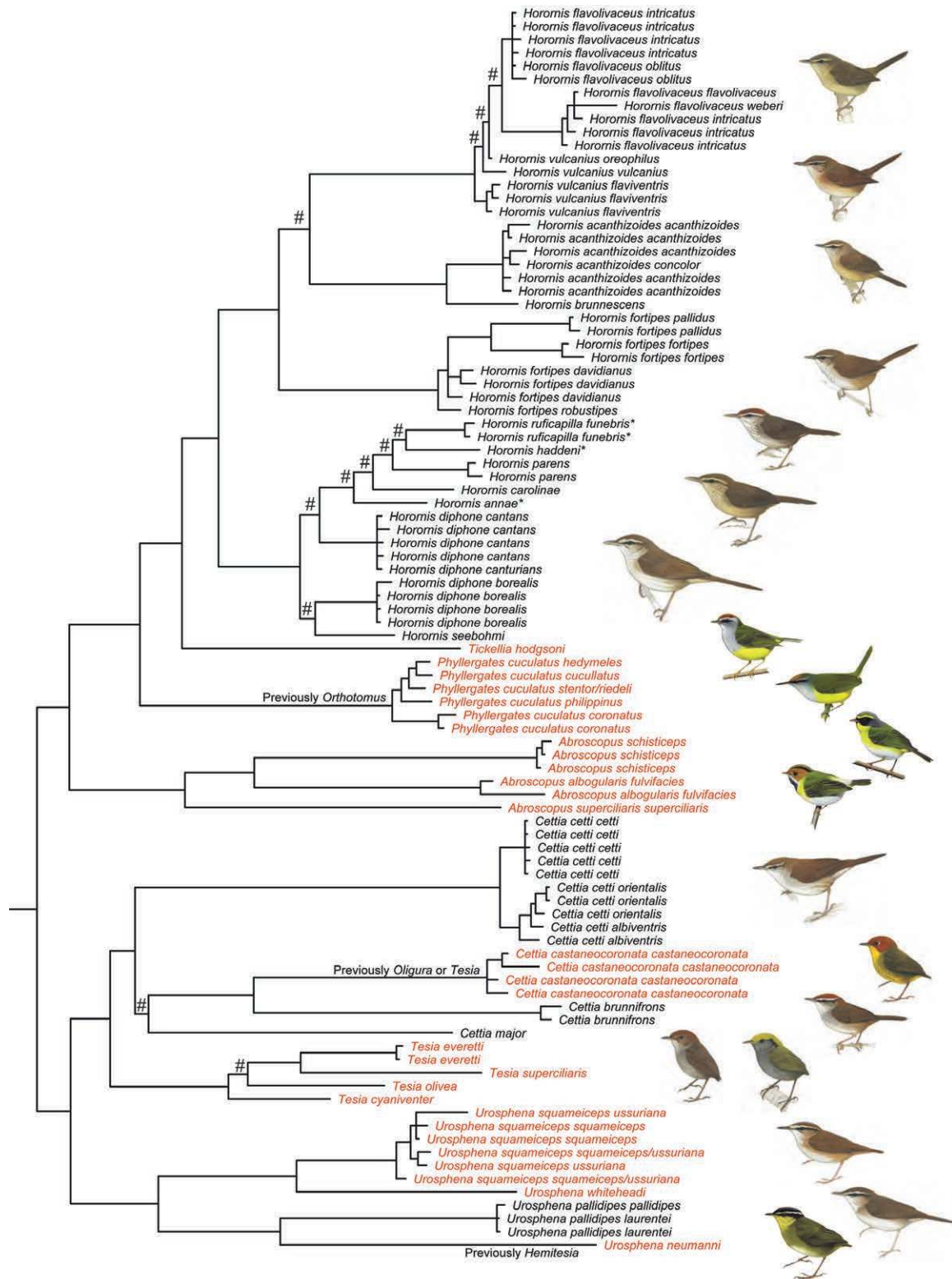
## Cettiidae

Alström et al. (2006) found that, based on sequence data from two loci, one mitochondrial and one nuclear, that two species of *Cettia*, one species each of *Urosphena*, *Tesia*, *Abroscopus* and *Tickellia*, and *Orthotomus cuculatus* formed a clade, well separated from a diverse number of other passerines. They proposed the family name Cettiidae for this group. This clade (limited to one species each of *Cettia*, *Abroscopus* and *Tickellia*) was corroborated by Johansson et al. (2008a) based on three nuclear loci. Irestedt et al. (2011) concluded, based on four loci, that *Hemitesia* is also part of this clade. Two of these studies (Alström et al., 2006; Irestedt et al., 2011) indicated that the genus *Cettia* is non-monophyletic. Alström et al. (2011a) revised the family based on one mitochondrial and three nuclear loci (Fig. 7). They confirmed the previous findings, including the strong non-monophyly of the genus *Cettia*, as this genus is scattered across the entire family tree. Based on these results, they proposed a revised classification in which *Cettia* is divided into *Cettia* s.s. and *Horornis* and one species (*C. pallidipes*) transferred to *Urosphena* (where it was sometimes placed previously); *Oligura* (*Tesia*) *castaneocoronata* moved to *Cettia*; *Hemitesia* synonymized with *Urosphena*; and *Phyllergates* reinstated as the generic name for *O. cuculatus* (Fig. 7). Previously, King (1989) proposed a new classification of some *Tesia* and *Urosphena* based on morphology, vocalizations and behavior, which is partly in agreement with the

molecular study of Alström et al. (2011a).

Two of the species, *Horornis carolinae* and *H. haddeni*, were recently described (Rozendaal, 1987; LeCroy and Barker, 2006; respectively). Moreover, the taxonomy of several taxa has been much debated. *Horornis diphone* has variously been treated as a single species, or split into *H. diphone* s.s. and *H. canturians*, generally without explanation (cf. Delacour, 1942–1943; King and Dickinson, 1975; Morony et al., 1975; Watson et al., 1986; Sibley and Monroe, 1990; Inskipp et al., 1996; Baker, 1997; Dickinson, 2003; Bairlein et al., 2006; Kennerley and Pearson, 2010). According to mitochondrial DNA, the Japanese *H. diphone cantans* and central Chinese *H. d. canturians* were recently found to form a clade separate from the northern *H. d. borealis* (cf. Fig. 7). This is inconsistent with morphology, as the two latter are similar in plumage and structure, while the first one is more divergent. The authors concluded that a more comprehensive study was needed before any conclusions could be drawn. Furthermore, *Horornis seebohmi* has often been treated as a subspecies of *H. diphone* s.l. (e.g. Delacour, 1943; Watson et al., 1986; Baker, 1997), although some authors considered *H. seebohmi* to be a distinct species, based on unpublished differences in song and lack of the pronounced sexual size dimorphism of *H. diphone*/*H. canturians* (King and Dickinson, 1975; Inskipp et al., 1996; Dickinson, 2003). The specific status of *H. seebohmi* has recently been supported based on vocalizations and mitochondrial DNA (Hamao et al., 2008) as well as multilocus data (Alström et al., 2011a).

*Horornis acanthizoides* has recently been split into *H. acanthizoides* s.s. and *H. brunnescens* based on a study of morphology, vocalizations and mitochondrial DNA (Alström et al., 2007). Olsson et al. (2006) concluded, based on congruence of gene trees from one mitochondrial and one nuclear loci, that *H. vulcanius* is nested within *H. flavolivaceus*, and that some of the subspecies of *H. flavolivaceus* be moved to *H. vulcanius*. This was, however, contradicted in the study by Alström et al. (2011a; Fig. 7), which comprised a larger number of loci and samples (including all of the samples from Olsson et al., 2006). The latter study inferred deep divergences between two main *H. flavolivaceus* clades, with the taxon *intricatus* represented in both (Fig. 7). The authors concluded that more data, including unsampled subspecies, would be needed to resolve this issue. Deep divergences have also been found between different populations of *Horornis fortipes* (Alström et al., 2011a; cf. Fig. 7), although contradictory results from different



**Fig. 7** Family Cettiidae based on concatenated nuclear ODC, MB and GAPDH and mitochondrial cytochrome *b* sequence data (only cytochrome *b* for the three species indicated with \*, and for most of the samples of different subspecies), based on Alström et al. (2011b). Species names follow revised taxonomy proposed by Alström et al. (2011b). Names in black were previously placed in *Cettia*. # indicates node with poor support. Illustrations by Ren Hathway (*Phyllergates*), Brian Small (*U. neumanni*) and Jan Wilczur (*Abroscopus*, *Tickellia*) from Bairlein et al. (2006), and by Brian Small (others) from Kennerley and Pearson (2010).

analyses prevented taxonomic conclusions from being drawn. The same study also found that western and eastern populations of *Cettia cetti* were separated into rather divergent clades (cf. Fig. 7), calling for additional studies.

### Scotocercidae

The family Scotocercidae was recently proposed, comprising the single species *Scotocerca inquieta* (Fregin et al., 2012). This was based on molecular (Alström et al., 2011c; Fregin et al., 2012) and morphological data (Alström et al., 2011c). The earlier of these studies also suggested that western and eastern populations might be different at the species level, and called for further studies.

### Erythroceridae

The Afrotropical genus *Erythrocerus* has been reconstructed in an unresolved position in relation to Cettidae and Aegithalidae (Alström et al., 2011c; Fregin et al., 2012). The three species in the genus (Dickinson, 2003; Gill and Donsker, 2013) are morphologically and ecologically divergent from both Cettidae and Aegithalidae, and Fregin et al. (2012) proposed the family name Erythroceridae based on molecular, morphological and ecological evidence.

### Aegithalidae

The family Aegithalidae, bushtits (or long-tailed tits), is one of the smallest families within Sylvioidea, comprising only 13 species (Gill and Donsker, 2013). Nine of these are Eurasian *Aegithalos*, two are Asian *Leptopoe-cile*, one is the Javan endemic *Psaltria*, and one is the North and Central American *Psaltriparus*. *Psaltria* does not appear to have been investigated in any molecular phylogeny, but three multilocus studies have shown *Aegithalos* and *Psaltriparus* to be sisters, with *Leptopoe-cile* sister to these (Johansson et al., 2008a; Päckert et al., 2010; Fregin et al., 2012). Dai et al. (2010) analyzed mitochondrial DNA for four Chinese *Aegithalos* species, while the relationships among all Aegithalidae species except *Psaltria* were studied by a combination of mitochondrial and nuclear markers by Päckert et al. (2010). The latter study obtained a well-resolved and strongly supported tree, except for a surprising lack of differentiation among four of the species recognized by Gill and Donsker (2013): *A. fuliginosus*, *A. iouschistos*, *A.*

*bonvaloti* and *A. sharpei*. Additionally, they found deep splits among different populations of especially *A. concinnus*. Dai et al. (2011, 2013) confirmed the existence of deep splits within *A. concinnus*, and evaluated their causes. In a study of mitochondrial DNA of *A. caudatus* sampled across Russia, Zink et al. (2008) found no strong geographical structure.

### Hylidae

Few taxa can show a record of taxonomic volatility as extreme as that of the Afrotropical *Pholidornis*, which has been placed in Dicaeidae, Estrildidae, Hylidae, Meliphagidae, Nectariniidae, Remizidae and Sylviidae (Sefc et al., 2003 and references therein). The uncertainty regarding the Afrotropical *Hylia* has been less extreme, but opinion has been divided. The most favored positions have been to treat it as a sunbird (Sclater, 1930; Bannerman, 1948; Brosset and Erard, 1986) or a warbler (Chapin, 1953; Sibley and Monroe, 1990; Dowsett and Dowsett-Lemaire, 1993; Keith, 1997), but e.g. Meliphagidae (Beecher, 1953) and Paridae (Keith, 1997) have also been suggested. There is morphological evidence for a relationship between the two genera in the form of a brush-tipped tongue and a long hyoid with flattened epibranchial horns, characters that also suggest a relationship with Nectarinidae (Bannerman and Bates, 1924). These similarities prompted Bates (1930) to erect the family Hylidae, but this was not widely accepted by subsequent authors, most of whom did not consider *Pholidornis* and *Hylia* as members of the same family. The phylogenetic position of both *Hylia* and *Pholidornis* continued to be contentious up to the first molecular analysis by Sefc et al. (2003), who showed that they were closely related and belong in Sylvioidea, later corroborated for *Hylia* by Beresford et al. (2005), Fuchs et al. (2006), Irestedt et al. (2011) and Fregin et al. (2012). Fregin et al. (2012) tentatively proposed that the family Hylidae should be resurrected for *Hylia* and *Pholidornis*.

Marks (2010) revealed the existence of four (five) markedly divergent haplotype groups within *Hylia prasina*, indicating that further taxonomic studies are warranted.

### Pnoepyidae

The Asian *Pnoepyga* wren babblers were classified as babblers (Timaliidae s.l.) until Gelang et al. (2009)

found that they were not closely related to any of the babbler clades, and erected the monotypic family Pnoepygidae. The family contains only four species (Gill and Donsker, 2013). The taxonomy of the Taiwanese endemic *P. formosana* has been debated, and it has variously been treated as conspecific with *P. pusilla* (Deignan, 1964b; Cheng, 1987) or with *P. albiventer* (Dickinson, 2003; Liu et al., 2010). Collar (2006) suggested, based on morphological evidence, that the Taiwanese taxon should be considered a distinct species, and the same conclusion was reached by Päckert et al. (2012) based on DNA sequence data and analyses of songs. Päckert et al. (2012) also found both molecular and acoustic evidence of a divergence within *P. albiventer*. They proposed that the Chinese taxon should be treated as a species, *P. mutica*, but refrained from suggesting any taxonomic action for a genetically equally divergent Myanmar population within the *P. albiventer* complex, for which they lacked acoustic data.

### Nicatoridae

The Afrotropical genus *Nicator*, with just three species, has variously been placed in the shrike family Laniidae (Reichenow, 1902–1903; Sclater, 1930; Wolters, 1979) or with the Pycnonotidae (Chapin, 1953; Hall and Moreau, 1970; Rand and Deignan, 1960), based on morphological criteria. DNA-DNA hybridization studies (Sibley and Ahlquist, 1985) and feather protein electrophoresis (Hanotte et al., 1987) placed *Nicator* with Pycnonotidae. However, based on sequence data, Beresford et al. (2005), Johansson et al. (2008a) and Fregin et al. (2012) found *Nicator chloris* and the Alaudidae + Panuridae clade in unresolved sister positions to the rest of the Sylvioidea (cf. Fig. 1). Gill and Donsker (2013), based on the above-mentioned recent studies, placed *Nicator* in a monotypic family.

### Conclusions

The relationships within the superfamily Sylvioidea have been enormously clarified in recent years thanks to a large number of molecular studies. These analyses have confirmed numerous conclusions drawn from earlier morphological studies, but they have also suggested multiple cases of previously unexpected relationships. Some of the surprising findings revealed by molecular methods have been supported by more careful re-evaluation of morphological data (earlier morphology-

based classifications have generally been based on superficial morphological similarity rather than thorough analyses). However, many of the results from molecular studies need to be corroborated by independent data. Most molecular phylogenies are based on a small number of loci (sometimes only mitochondrial), and even in multilocus analyses, strongly supported relationships frequently receive their support from a small fraction of the analyzed loci, with the majority of the loci neither supporting nor contradicting these relationships. As genomic data are becoming cheaper and more easily obtainable, many of the recent discoveries will be re-evaluated by considerably larger datasets in the not too distant future. One of the challenges will be to resolve the relationships among the different families within Sylvioidea, which are still largely unresolved. However, if, as seems likely to be the case based on the presently available data, the lack of resolution results mainly from rapid divergence of the primary lineages (families), these relationships might remain obscure.

The total number of species within Sylvioidea has increased much in recent years, mainly due to studies applying molecular markers and/or vocalizations and other life-history data, and in many groups multiple cryptic species have been detected. It seems likely that the number of species is going to continue to increase, as new groups are being studied with modern integrative methods (using a combination of morphological, vocal, genetic, behavioural and other data). In particular, some polytypic species of larks, “warblers”, bulbuls, and “babblers” are likely to comprise considerably more species than presently recognized. As good taxonomic assessments are a fundamental basis for many evolutionary studies, as well as for conservation purposes, continued efforts to revise the species-level taxonomy within Sylvioidea are much needed.

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### Supplementary material

Available on Chinese Birds website, links at <http://www.chinese-birds.net>, including Appendix 1. Sequences and phylogenetic methods



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## 莺总科鸟类的系统分类进展评述

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**摘要:** 本文评述了莺总科鸟类的系统分类, 并重点探讨科间、属内系统发育关系以及种级分类地位。基于已发表的 DNA 序列数据, 对马岛莺科 (Bernieridae) 和柳莺科 (Phylloscopidae) 重新进行了分析。大量的分子水平的研究让我们对鸟类系统发育的认识有了很大提高。但是, 由于一些主要进化分支 (科) 的快速分化, 使得这些科之间的相互关系依然不明确。同样, 分子标记和 (或) 鸣声及其他生活史资料在大量研究中的应用, 大大提高了种级水平的分类可靠性。我们推测, 随着人们运用现代的整合方法对新类群的不断研究, 物种数量会不断增加。

**关键词:** 系统发育关系, 莺总科, 系统分类