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Near-complete phylogeny and taxonomic revision of the world's babblers (Aves: Passeriformes)

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ABSTRACT

The babblers are a diverse group of passerine birds comprising 452 species. The group was long regarded as a "scrap basket" in taxonomic classification schemes. Although several studies have assessed the phylogenetic relationships for subsets of babblers during the past two decades, a comprehensive phylogeny of this group has been lacking. In this study, we used five mitochondrial and seven nuclear loci to generate a dated phylogeny for babblers. This phylogeny includes 402 species (ca. 89% of the overall clade) from 75 genera (97%) and all five currently recognized families, providing a robust basis for taxonomic revision. Our phylogeny supports seven major clades and reveals several non-monophyletic genera. Divergence time estimates indicate that the seven major clades diverged around the same time (18–20 million years ago, Ma) in the early Miocene. We use the phylogeny in a consistent way to propose a new taxonomy, with seven families and 64 genera of babblers, and a new linear sequence of names.

1. Introduction

The babblers are a diverse group of oscine passerine birds, which includes more than 450 species in five families (Gill and Donsker, 2018). Species in the group are mainly distributed in Southeast Asia and the Afrotropics, with a few species occurring in the Palearctic, and only one species (Wrentit *Chamaea fasciata*) having colonized the New World (del Hoyo et al., 2007; Gill and Donsker, 2018). Most babblers are resident, but some of the northern breeders are long-distance migrants. The group inhabits a wide diversity of habitats, including tropical, subtropical and temperate forests, woodlands, thickets, marshlands and arid habitats, with species occurring from sea level to above the tree limit (del Hoyo et al., 2007). The species display great variation in body size (ca. 6–156 g), bill shape, plumage color, vocalizations, social behaviour and ecology (del Hoyo et al., 2007). Their great diversity in morphology and ecology, as well as high levels of sympatry, suggest that they are an ideal group for assessing biogeography, adaptive radiation theory and mechanisms of species coexistence (Moyle et al., 2012). The first step towards understanding these processes is to develop a robust phylogeny for the group. However, to date no comprehensive species-level phylogeny of babblers exists.

The babblers have a chequered taxonomic history, and the group was long regarded as a "scrap basket" for genera that did not fit well into other families (Mayr and Amadon, 1951). Delacour (1946, 1950) proposed the first pre-molecular classification of babblers based on plumage colour and bill shape. Delacour's lists placed most babblers in the family Timaliidae, which included six tribes: Pellorneini, Pomatorhinini, Timaliini, Chamaeini, Turdoidini and Picathartini, and was

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Table 1
Name, number of sequences, length of sequence and best substitution model for each locus included in the study.

Loci	Abbreviation	Taxa	Length (bp)	Model (Beast)
Cytochrome b	Cytb	329	1143	GTR + I + Γ
NADH dehydrogenase subunit 2	ND2	320	1041	GTR + I + Γ
NADH dehydrogenase subunit 3	ND3	267	351	GTR + I + Γ
Cytochrome c oxidase subunit I	COI	206	651	GTR + I + Γ
ATP synthase subunit 6	ATP6	71	684	GTR + I + Γ
Fibrinogen beta chain intron 5	FIB-5	176	571	GTR + Γ
Glyceraldehyde-3-phosphodehydrogenase intron 11	GAPDH-11	196	344	GTR + Γ
Muscle skeletal receptor tyrosine kinase intro 3	MUSK-3	155	575	GTR + Γ
Myoglobin intron 2	MB-2	205	647	GTR + Γ
Ornithine decarboxylase intron 6 and 7	ODC-6/7	198	612	GTR + I + Γ
Recombination activating protein 1	RAG1	139	961	GTR + I + Γ
Transforming growth factor beta 2 intron 5	TGFB2-5	279	601	GTR + Γ

considered to be most closely related to the Old World warblers (traditional Sylviidae). This classic taxonomy of babblers remained in use until Sibley and Ahlquist (1990) provided a new classification based on DNA-DNA hybridization data. These data and the taxonomy of Sibley and Monroe (1990) led to the removal of the genera *Garritornis*, *Pomatostomus* and *Picathartes* from babblers, and suggested that *Sylvia* was embedded within the babbler group. They suggested dividing the babblers into the subfamilies Sylviinae (with tribes Timaliini, Chamaeini and Sylviini) and Garrulacinae, both of which were placed in the family Sylviidae. The white-eyes (*Zosterops*) were placed in a seperate family Zosteropidae that was sister to the babblers (Sibley and Ahlquist, 1990).

Subsequent studies have attempted to clarify the phylogeny of babblers using DNA sequence data. Cibois (2003) published the first assessment of phylogenetic relationships among babblers using a broad representation of species with data for three mitochondrial genes. This phylogeny revealed that shrike babblers *Pteruthius* spp. and Grey-chested Kakamega *Kakamega poliothorax* were not members of the babblers, while suggesting that *Sylvia* and *Zosterops* belonged in this group. Several other studies also supported the close relationships of *Sylvia* and *Zosterops* to babblers (Alström et al., 2006; Barker et al., 2004). Subsequent studies showed that several taxa previously placed in this group should be removed from the babbler assemblage, whereas others have been shown to belong to this group (Alström et al., 2013; Gelang et al., 2009; Moyle et al., 2012). Gelang et al. (2009) considered Sylviidae as a separate family, and the white-eyes and "core babblers" as the family Timaliidae (including subfamilies Timaliinae, Pellorneinae, Leiothrichinae and Zosteropinae). With the first comprehensive sampling of babblers including 183 species (ca. 40% of the overall species), Moyle et al. (2012) proposed three families of babbler assemblages: Sylviidae, Zosteropidae and Timaliidae (with the subfamilies Timaliinae, Pellorneinae and Leiothrichinae). Using one mitochondrial and six nuclear genes with comprehensive sampling of the superfamily Sylvioidea, Fregin et al. (2012) and Alström et al. (2013) considered five primary clades at the rank of family for the babbler assemblage: Sylviidae, Zosteropidae, Timaliidae, Pellorneidae and Leiothrichidae. This taxonomy was gradually recognized by recent taxonomic lists (Dickinson and Christidis, 2014; Gill and Donsker, 2018). However, some phylogenetic relationships and generic names continue to differ.

In this study, we use a multi-locus dataset combining published and newly generated sequences to reconstruct a time-calibrated phylogeny for 89% of the world's babbler species. Our results reveal some novel relationships and non-monophyly for some genera. Based on this comprehensive tree, we propose a revised classification in which we strive to circumscribe families and genera in a consistent way based on divergence times.

2. Methods

2.1. Taxon sampling and sequences

Taxonomic arrangements above the species level follow the Howard and Moore Complete Checklist of the Birds of the World (4th edition) (Dickinson and Christidis, 2014) with the exclusion of *Elachura formosa, Madanga ruficollis* and *Leonardina woodi* because the latest molecular evidence suggests they are not babblers (Alström et al., 2014, 2015; Oliveros et al., 2012). We include 47 taxa considered as subspecies in the Howard and Moore Checklist (Dickinson and Christidis, 2014) but recognized as species in the IOC world birds list 8.1 (Gill and Donsker, 2018). In total, we analyzed 402 species out of a total of 452 babbler species (Gill and Donsker, 2018). Additionally, we included 108 species representing closely related family groups (Aegithalidae, bushtits; Phylloscopidae, leaf warblers; Cettiidae, bush warblers) and Paroidea (tits and remizids) as outgroups (Alström et al., 2013; Fregin et al., 2012). We generated 179 new DNA sequences for babblers (MK068915–MK069083), and combined these with published sequences (Cibois, 2003; Cibois et al., 2018; Gelang et al., 2009; Liu et al., 2016; Luo et al., 2009; Moyle et al., 2012, 2009; Voelker and Light, 2011; Warren et al., 2006) to produce a supermatrix consisting of 12 loci (five mitochondrial; six nuclear introns; one nuclear coding gene; Tables 1 and Table S1).

We extracted DNA from ethanol-preserved tissue or blood samples using a DNEasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. DNA from toepads of museum specimens were extracted using a well-established ancient-DNA extraction protocol (Irestedt et al., 2016, 2006). The Polymerase Chain Reaction (PCR) amplification was performed for the fresh tissue samples using the published primers Table S2) (Friesen et al., 1999; Irestedt et al., 2001; Kimball et al., 2009; Sorenson et al., 1999). For toepad samples of *Zosterops*, a number of new primers were designed to amplify smaller fragments of mitochondrial genes (approximate 200–300 bp). The PCR conditions were set as follows: denaturation at 94 °C for 3 min, followed by 35–40 cycles (94 °C for 30 s, annealing temperature (Table S2) for 30 s, and 72 °C for 45 s), and a final 5 min at 72 °C. All PCR products were purified using a QIAquick PCR purification kit (Qiagen) and sequenced using the ABI 3730xl Analyzer.

In addition, we used *de novo* assembly to generate new sequences for 16 toepad samples. The preparation of paired-end genome libraries for Illumina high-throughput sequencing followed the protocol published by Meyer and Kircher (2010), except that no further fragmentation was needed of the DNA derived from museum skins as this is already fragmented through natural degradation. To reduce clonality each library was amplified with four different indexes. Four species with four indexes were each pooled, and each pool was then run on a single Illumina Hiseq X lane. The sequencing reads were processed using a custom designed workflow that is available at https://github.com/mozesblom. The workflow removes PCR duplicates, adapter contamination, low-

quality bases, low-complexity reads and merges overlapping read-pairs. Both adapter and quality trimming was done using TRIMMOMATIC (v.0.3221), PCR duplicates were removed with SuperDeduper (v.1.422), reads were merged with PEAR (v.0.9.623) and overall quality and length distribution of sequence reads were inspected prior and post the clean-up workflow using FASTQC (v.0.11.524).

Published DNA sequences were downloaded from GenBank and selected in the following way. First, we downloaded all available sequences of ingroup and outgroup taxa using family names as key words to search for each gene. After aligning sequences in MUSCLE 3.8.31 (Edgar, 2004) using default settings, we conducted 100 rapid bootstrap searches to obtain the Maximum Likelihood (ML) tree using RAxML 8.2.4 (Stamatakis, 2014). Next, we selected the best candidates (the longest sequences from the clade including most sequences of that species) based on the ML tree and geographical location of the sample. If available, we selected sequences from the same individual (searched until to June 2017).

2.2. Phylogenetic analyses

Before alignment, all protein-coding sequences were translated to amino acids to check for stop codons using the online tool EMBOSS Transeq (Li et al., 2015). Then, sequences were aligned for each locus individually using MUSCLE 3.8.31 (Edgar, 2004). Ambiguous regions in nucler introns were removed in Gblocks 0.9b (Talavera and Castresana, 2007), resulting in 4–18% of sequences being removed. A ML tree was reconstructed for each locus using 10,000 ultrafast bootstrap (Hoang et al., 2017) under the best model estimated by ModelFinder (-m MFP) (Kalyaanamoorthy et al., 2017) with Bayesian Information Criterion (BIC) option in IQ-TREE (Nguyen et al., 2014). These analyses allowed us to have an initial quality check of the sequences, enabling us to detect any spurious sequences.

Phylogenetic relationships were inferred using the concatenated alignment of 12 loci in the IQ-TREE 1.6.1 (Nguyen et al., 2014). We considered three partitioning schemes: (1) “unpartitioned”: all loci were combined as one partition; (2) “full”: each locus was regarded as a partition; and (3) “PF”: the optimal partitioning scheme suggested by Partitionfinder 2 (Lanfear et al., 2012) according to the BIC under the “greedy” search algorithm. The best substitution model for each partition was chosen by ModelFinder (-m MFP) (Kalyaanamoorthy et al., 2017) according to the BIC option in IQ-TREE. Nodal support was assessed using 10,000 ultrafast bootstrap replicates (Hoang et al., 2017).

Our DNA matrix contained some taxa represented by some missing or short sequences, which often proved difficult to place with any confidence in the phylogeny, and which we refer to as rogue taxa (Aberer et al., 2013; Moyle et al., 2012). To improve resolution of the phylogeny, we identified rogue taxa using 1000 RAxML (Stamatakis, 2014) fast bootstrap trees in RogueNaRok (Aberer et al., 2013). Some rogue taxa were removed from the complete data matrix (Data-1) to produce a pruned data matrix (Data-2). Then, using the reduced data matrix, we repeated ML tree searches following the same settings as for Data-1.

2.3. Divergence times

We used two calibration points to estimate divergence time of babblers. The first calibration was derived from the separation of Taiwan Island from mainland Asia in the early Pliocene. The mountains of Taiwan were progressively uplifted since the late Miocene–early Pliocene (~6–5 million years ago, Ma) (Huang et al., 2000; Sibuet and Hsu, 2004) due to the northward movement of the Luzon Shelf. Several phylogenetic analyses calibrated by fossil and substitution rate of mtDNA have suggested that the divergence between mainland and Taiwan Island pairs of birds occurred around 5–1.5 Ma (Cai et al., 2018; Qu et al., 2015; Wu et al., 2011). Thus, we used a normal prior with 5% and 95% quantiles age of 1.5–6 Ma to calibrate the node splitting between *Liocichla steerii* (endemic to Taiwan Island) and *L. ripponi* (mainland Asia). The second calibration was derived from the earliest appearance of a diversity of oscine passerine fossils on the Northern Hemisphere (Europe) from the late Oligocene (~26–25 Ma); these fossil remains have not been assigned to specific extant families (Manegold, 2008) but morphological details are shared with several deep lineages of the large Passerida radiation (*Elminia*, *Remiz*, *Regulus*, *Bombycilla* and *Hypocolius*; J.F., unpublished). Since phylogenetic studies with a broader sampling place the start of the radiation of sylvioid birds shortly after the basal Passerida radiation, we set the minimum age of the most recent common ancestor (MRCA) of Sylvoidea and Paroidea as 25 Ma with 5% and 95% quantiles of 25.5–37.6 Ma under the lognormal distribution.

Divergence time was estimated in BEAST 1.8.4 (Drummond and Rambaut, 2007) using the relaxed molecular clock model based on the full partition strategy and the best substitution model for each locus chosen by Partitionfinder 2 under BIC option (Table 1) (Lanfear et al., 2012). We implemented the best ML tree as a starting tree, and applied the Yule speciation tree prior. In addition, we also employed the substitution rate of mitochondrial genes (2.1%/Ma) (Weir and Schluter, 2008) with a relaxed-clock to estimate the divergence time. These analyses were run for 200 million generations in total and was sampled every 1000 generations. TRACER v1.6 (Rambaut et al., 2014) was used to examine the effective sample size (ESS) to evaluate the convergence of MCMC chains. Finally, we discarded the first 80,000 trees as ‘burnin’ and used the remaining 120,000 trees to produce a maximum clade credibility (MCC) tree.

2.4. Temporal banding for consistent families and genera

Temporal banding is an approach to assess the consistency of taxonomic ranks and provides a practical solution to temporal inconsistencies (Avise and Johns, 1999; Holt and Jønsson, 2014). This approach identifies temporally consistent taxonomic ranks by splitting a dated phylogeny at specified points in time, such that the descendent taxa of the independent lineages form taxonomic units of comparable age (Holt and Jønsson, 2014; Jønsson et al., 2016). To do this, Jønsson et al. (2016) provided a “least disruption” approach to revise taxonomic ranks, which tested all possible splitting points for the MCC tree and then compared these to current taxonomic families and genera. The best cut-off points would result in the fewest changes of the original taxonomy (with highest percentage consistency). In this study, we used the R script provided by Jønsson et al. (2016) to delimit consistent families and genera of babblers, providing a basis for taxonomic revisions. We used this approach pragmatically rather than strictly, and we explicitly tried to be conservative and to propose a minimal number of changes.

3. Results

Our DNA supermatrix consisted of 2538 sequences from 402 babbler species (89%) in 75 out of 77 recognized genera (missing genera: *Rukia* and *Megazosterops*), including five mitochondrial and seven nuclear loci (mean = 6.3 loci/taxon) (Table 1). The final complete data matrix (Data-1) included a total of 8181 bp including five mitochondrial genes and seven nuclear genes, of which 4000 sites were parsimony informative. Based on the analysis of rogue taxa, we removed 42 rogue taxa (81% represented by *Zosterops*) from Data-1 to produce a pruned data matrix (Data-2). Different partition strategies produced congruent phylogenetic trees with differences in support values at some nodes. Generally, tree inference using the “full partition” data produced on average higher support values than other partition schemes. Thus, in the following we present only the results from the analyses under “full partition”.

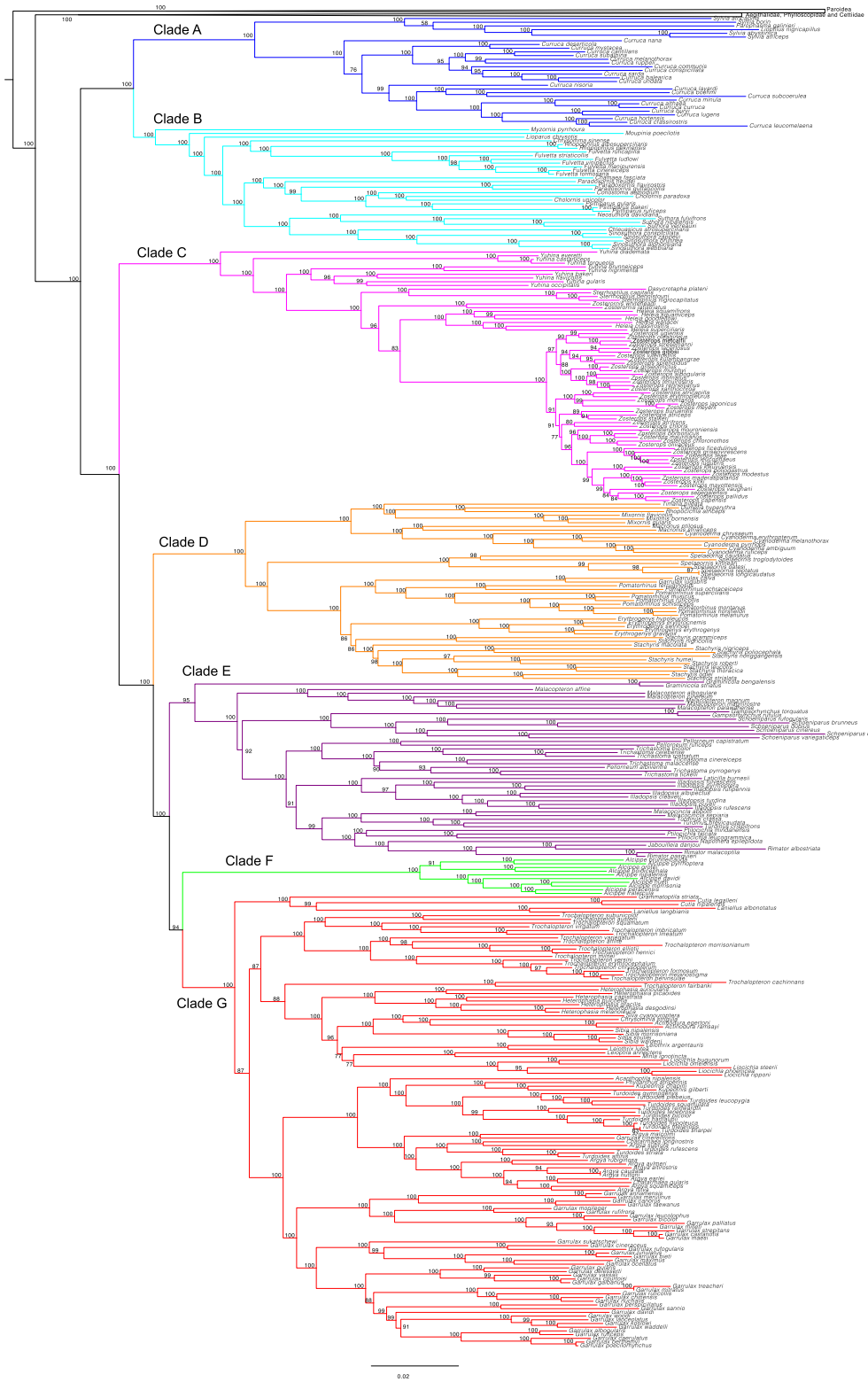

Fig. 1. Maximum likelihood phylogeny derived from 12 loci with rogue taxa removed from the matrix (Data-2). Bootstrap values are indicated at the nodes.

3.1. Phylogenetic analysis

Phylogenetic analyses of the two different DNA matrices (Data-1 and Data-2) reconstructed very similar topologies (Figs. 1 and S1). As expected, trees with rogue taxa removed (Data-2) produced on average higher bootstrap support (BS) values than the complete DNA matrix (Data-1). Seven well supported primary clades (A–G) were identified in our phylogeny. Clades A and B were strongly supported as sisters (together forming the Sylviidae), and formed the sister clade to the others. Clades C (Zosteropidae), D (Timaliidae), E (Pellorneidae), F (*Alcippe*; part of Leiothrichidae) and G (Leiothrichidae *sensu stricto*) were sequential sisters. The position of the *Alcippe* clade (F) as sister to Leiothrichidae (G) received higher BS value in the analysis of Data-2 than in the analysis of Data-1 (BS: 94% and 56%, respectively).

Tree inferences using newly generated sequences revealed the phylogenetic positions of some taxa previously not studied (Fig. S1). Most taxa with new sequences were placed in the corresponding genera defined by Dickinson and Christidis (2014). For example, a total of 11 newly sequenced *Zosterops* were placed in the *Zosterops* clade. *Stachyris nonggangensis* was strongly supported as sister to *S. humei* and *S. roberti*. *Schoeniparus variegaticeps* was sister to *S. castaneceps*, and *Alcippe pyrrhoptera* was sister to *A. brunneicauda*. *Mixornis flavicollis* was close to *M. gularis* and *M. bornensis*. *Spelaeornis kinneari* and *S. oatesi* were closely related to *S. reptatus* and *S. longicaudatus*. *Pomatorhinus melanurus* was sister to *P. horsfieldii*. *Garrulax bieti* was sister to *G. lunulatus*, and *G. woodi*, *koslowi* and *waddelli* were close to *G. lanceolatus*. *Trochalopteron melanostigma* and *T. peninsulae* were sisters, both of which were close to *T. formosum*. *Turdoides rufescens* was sister to *T. affinis* and *T. striata*. *Argya altirostris* was closely related to *A. caudata* and *A. huttoni*. We found *Tephrozosterops stalkeri* to be strongly supported as sister to *Zosterops*. *Garrulax calva* and *G. lugubris* formed a well-supported sister clade to the *Pomatorhinus* clade.

3.2. Divergence times

ESSs of all parameters were higher than 200 after 5 million generations. The two calibration methods obtained very similar divergence times. However, the tree based on the mitochondrial clock rate reported higher 95% highest posterior densities (HPD) than the tree based on fossil and biogeographic event calibrations (Figs. 2 and 3, S2). Thus, the latter is presented as our main result (Figs. 2 and 3). According to this analysis, babblers split from their close extant relatives in the late Oligocene–early Miocene (23.5 Ma, 95% HPD 28–20 Ma). The MRCA of babblers was estimated to have occurred at 21.9 Ma (95% HPD 26.4–18.6). Soon thereafter, the seven primary lineages diverged from each other within a relatively short period (up to 18 Ma, 95% HPD 21.5–15 Ma).

3.3. Temporal banding to delimit consistent families and genera

The temporal banding analyses (Fig. S3, Table S3) suggested classifying the babblers into 6 families (with the most recent split at 18.1 Ma) and 50 genera (most recent split at 10.8 Ma), of which 94% of the families and 60% of the genera were unchanged from the current taxonomic list (Dickinson and Christidis, 2014). The revised genera of babblers were well matched with the taxonomy of Dickinson and Christidis (2014). In addition, temporal banding also suggested that Sylviidae should be considered as two families represented by clade A and clade B, respectively.

4. Discussion

4.1. Effects of rogue taxa in phylogenic inference

In this study, we used newly generated and previously published DNA sequences from 12 loci to construct a phylogeny comprising 89% of the world's babbler species. In the analyses of the complete dataset (Data-1), 80% of the nodes received BS ≥ 95%. However, some deep nodes were poorly supported. This lack of resolution could be due to some rogue taxa with incomplete sequence data. Some previous studies have confirmed this assumption, because the support values for many nodes increase after removing rogue taxa (Aberer et al., 2013; Moyle et al., 2012; Shakya and Sheldon, 2017). This also seems true for this study, because after removal of the 42 rogue taxa (Data-2), 90% of the nodes received BS ≥ 95%.

Support for the relationship of the genus *Alcippe* (Clade F) appears to be dependent on the sampling scheme. Gelang et al. (2009) included only one species of *Alcippe*, and found strong support for placing it as sister to Pellorneidae. In contrast, Moyle et al. (2012) recovered a clade with seven *Alcippe* in a strongly supported sister position to Leiothrichidae. However, individual gene trees showed various relationships of *Alcippe*, and the support for a sister position to Leiothrichidae derives from the transforming growth factor beta 2 (TGFB2) gene (Moyle et al., 2012). Our phylogeny with all 10 species of *Alcippe* included placed *Alcippe* as sister to Leiothrichidae, but the support values were not unanimously high (BS = 56%, posterior probability (PP) = 0.99). In the analyses without the rogue taxa, the support values for this position were significantly improved (BS = 94%, PP = 1.00). Thus, the phylogenetic position of *Alcippe* seems to be largely affected by the rogue taxa. This may be assessed in the future using more comprehensive data for these rogue taxa.

4.2. Divergence times

Our phylogeny using a fossil and a biogeographic event as a calibration implies that babblers originated in the late Oligocene to early Miocene, at approximately 23.5 Ma (28–20 Ma). The dates are slightly younger than the time from a previous study estimated by a large DNA matrix and multiple fossil calibrations of modern birds at 30.5 Ma (36–25 Ma) (Claramunt and Cracraft, 2015). The earlier study did not use calibrations within the Sylvioidea, thus it is not surprising that their calibrations produced a broader range of divergence times than our phylogeny. Our estimated divergence times for babblers are well matched with the divergence times in previous studies of the same group (Moyle et al., 2012; Price et al., 2014). Using two secondary calibrations, Moyle et al. (2012) estimated that the split of Zosteropidae and "core babblers" occurred at approximately 18 Ma (21–16.1 Ma), consistent with our estimate of that split at 20.4 Ma (24.6–17.4 Ma). Price et al. (2014) used fossil and biogeographic data to calibrate the phylogeny for the Himalayan passerines. They concluded that the MRCA of the core babblers (Timaliidae, Pellorneidae and Leiothrichidae) occurred at 20.9 Ma, which is closely similar to our results (19.2 Ma). However, our calibrations suggested a much older divergence time between *Sylvia* and *Timalia* (21.9 Ma; 18.6–26.4 Ma) than found by Moyle et al. (2016), which derived calibrations from Prum et al. (2015) and Jarvis et al. (2014) and indicated the split time between *Sylvia* and *Timalia* at 13.5 Ma (12–15.5 Ma). In addition, our estimated times are consistent with calibrations using the evolutionary rate of mitochondrial genes, i.e., the Old World warblers (Voelker and Light, 2011) and *Alcippe morrisonia* complex (Qu et al., 2015).

4.3. Phylogenetic conclusions and taxonomic revisions

Based on our results, we propose a revised classification of the babbler radiation where we aim to break up in monophyletic units all currently defined taxa (del Hoyo et al., 2007; Dickinson and Christidis, 2014; Gill and Donsker, 2018) that were found to be poly- or paraphyletic based on the molecular data. We also used divergence times from the time-calibrated tree to circumscribe genera. Our temporal banding analysis suggests recognition of 50 genera using a cut-off limit of 10.8 Ma, of which 60% of the genera were consistent with current taxonomy (Dickinson and Christidis, 2014). Analyzing a supermatrix tree for corvoid birds, Jønsson and Fjeldså (2006) also found that a cut-off limit of 10 Ma for recognizing genera was generally in good agreement with traditional classification, and ongoing analysis of other passerine groups (J.F. et al., in progress) suggests that this cut-off level also causes little conflict with traditional classification of most other passerines, except for the most rapidly diversifying groups of New World nine-primaried oscines (Barker et al., 2015). We therefore strive to apply this cut-off level (ca. 10 Ma) for the babbler genera, and only a few currently recognised genera older than this threshold were identified. The main avian taxonomic references (Bock, 1994; Deignan, 1964; Richmond, 1992; Sharpe, 1881, 1883; Wolters, 1975–1982) were used when resurrection of names previously treated as junior synonyms was necessary. The taxonomic names that we recommend can be found in Table S4, and for families and genera in Figs. 2 and 3.

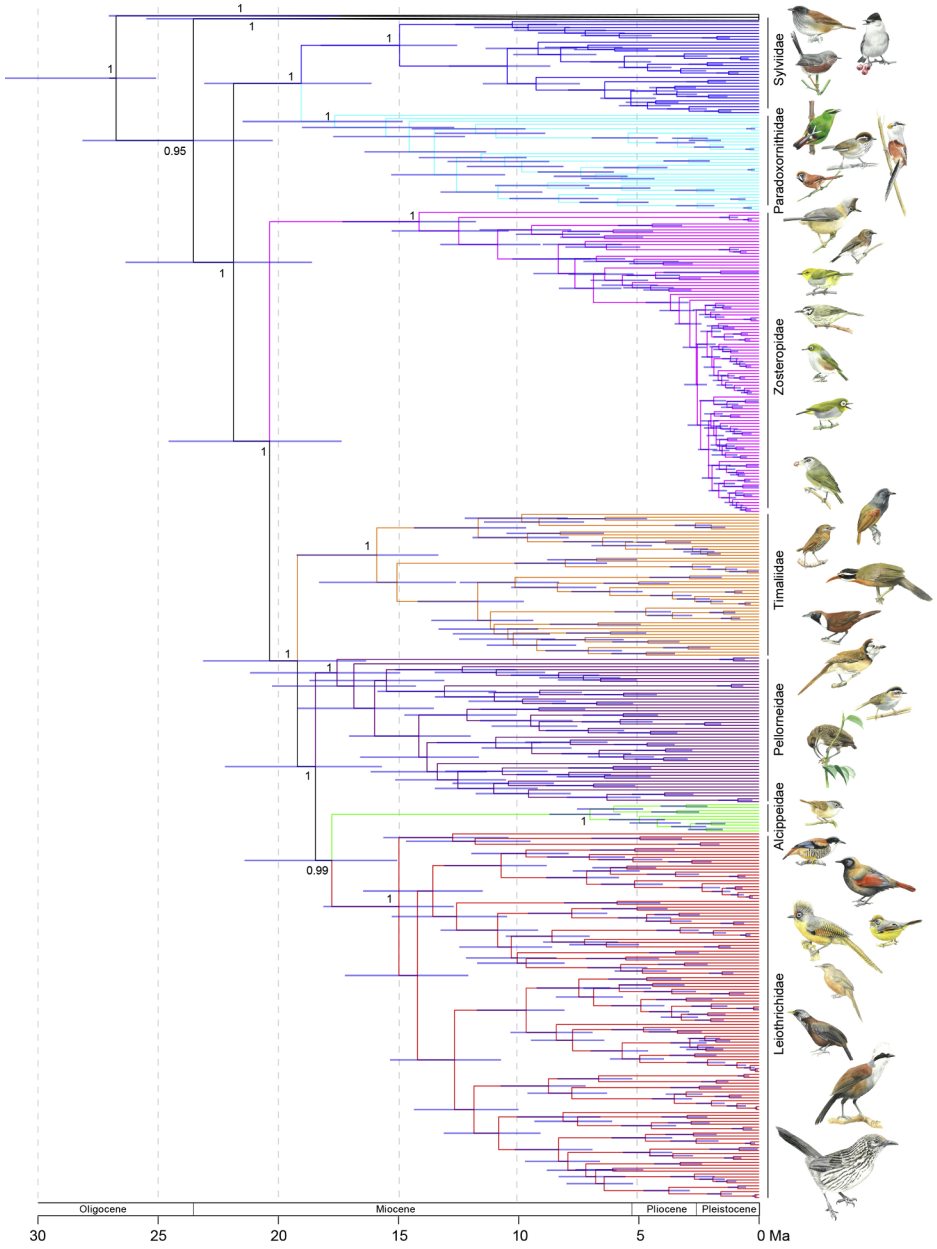

Fig. 2. Divergence time estimates of the babbler radiation based on the complete supermatrix (Data-1) estimated in BEAST using two calibrations. Bars on nodes indicate 95% highest posterior density of age estimates. Posterior probabilities are only shown at the deeper nodes. Family names are those recommend based on the present study. Illustrations of birds by J.F.

4.3.1. Family Sylviidae

The Sylviidae includes the type genus *Sylvia*, with representatives in the western part of the Palearctic and in the Afrotropics, the two Afrotropical genera *Parophasma* and *Lioptilus*, and the Palearctic genus *Curruca*, as well as an assemblage of Oriental taxa, such as fulvettas (e.g. *Fulvetta*, *Lioparus*), parrotbills (e.g. *Paradoxornis*) and allies, and the only babbler found in the New World, the Wrentit *Chamaea fasciata* (del Hoyo et al., 2007; Dickinson and Christidis, 2014). According to our results, the Sylviidae as currently circumscribed are divided into two large clades (A and B) that diverged in the early Miocene (19.5 Ma; 95% HPD 23–16.1 Ma), similar in time to the other families of babblers. We therefore suggest the name Sylviidae be restricted to the western clade (A) that includes the genera *Sylvia*, *Curruca*, *Parophasma* and *Lioptilus*, whereas we propose to reinstall the family group name Paradoxornithidae for the eastern clade B. Within the Sylviidae, we propose the recognition of only two genera corresponding to the two main clades that diverged around the 10 Ma limit: the genus *Sylvia* Scopoli, 1769 (type species *S. atricapilla*), and the genus *Curruca* Bechstein, 1802 (type species *C. curruca*). This change necessitates that *Parophasma* Reichenow, 1905 and *Lioptilus* Bonaparte, 1850 be treated as junior synomyns of *Sylvia*.

Parrotbills have been the subject of several recent phylogenetic studies (Liu et al., 2016; Yeung et al., 2006, 2011) suggesting that the genus *Paradoxornis* Gould, 1836 was paraphyletic, notably by the inclusion of *Conostoma*. Penhallurick (2010) proposed a complete revision of the group, in which the parrotbills were divided into eight genera, based on morphological, call and song characters that were also consistent with the clades obtained in phylogenetic studies. The genus *Paradoxornis* as defined by Penhallurick and Robson (2009) contained three species: the type species *P. flavirostris*, and *P. guttaticollis* and *P. heudei*. The characters used to group these three species were their large size, a strongly graduated tail, and a short and strong bill, with a deep,

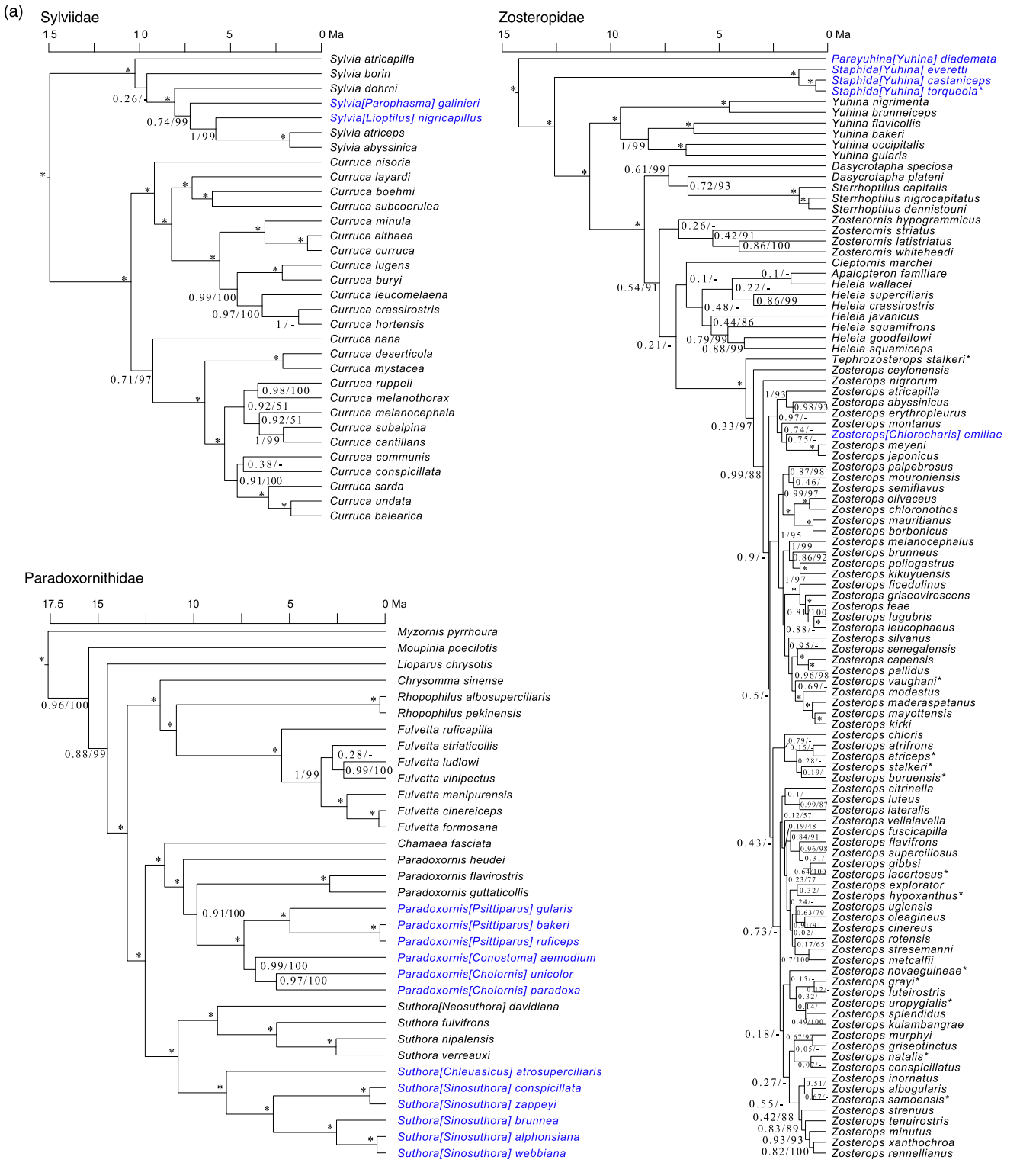

Fig. 3. Detailed phylogeny of babblers based on BEAST analysis using the complete supermatrix (Data-1). Numbers at nodes refer to Bayesian posterior probability/ML bootstrap support. Family names correspond to Fig. 2. Asterisks indicate 100% bootstrap support and 1.0 posterior probability. Species names with an asterisk (*) indicate newly sequenced species. Species names in blue color are the generic names that we recommend.

S-shaped curve of the cutting edge of the upper mandible (del Hoyo et al., 2007). The three species formed a clade in Liu et al. (2016) and Yeung et al. (2011), but they are paraphyletic in our larger phylogeny. In all studies, P. *flavirostris* and *P. guttaticollis* were sisters, but *P. heudei* was sister to a clade including P. *flavirostris*/*P. guttaticollis* and the group formed by *Conostoma aemodium* and the newly resurrected genera *Psittiparus* and *Cholornis* [see Penhallurick (2010) for a correction on the use of *Hemirhynchus* Hodgson, 1843 in Penhallurick and Robson (2009)]. The estimated divergence between *P. heudei* and the rest of the clade is close to the 10 Ma threshold, so two taxonomic approaches are possible. The first option corresponds to the finer split at the genus level, following the propositions of Penhallurick and Robson (2009) based on morphological and vocal characters. In this case, the species *heudei* should be removed from *Paradoxornis* and the genus *Calamornis*,

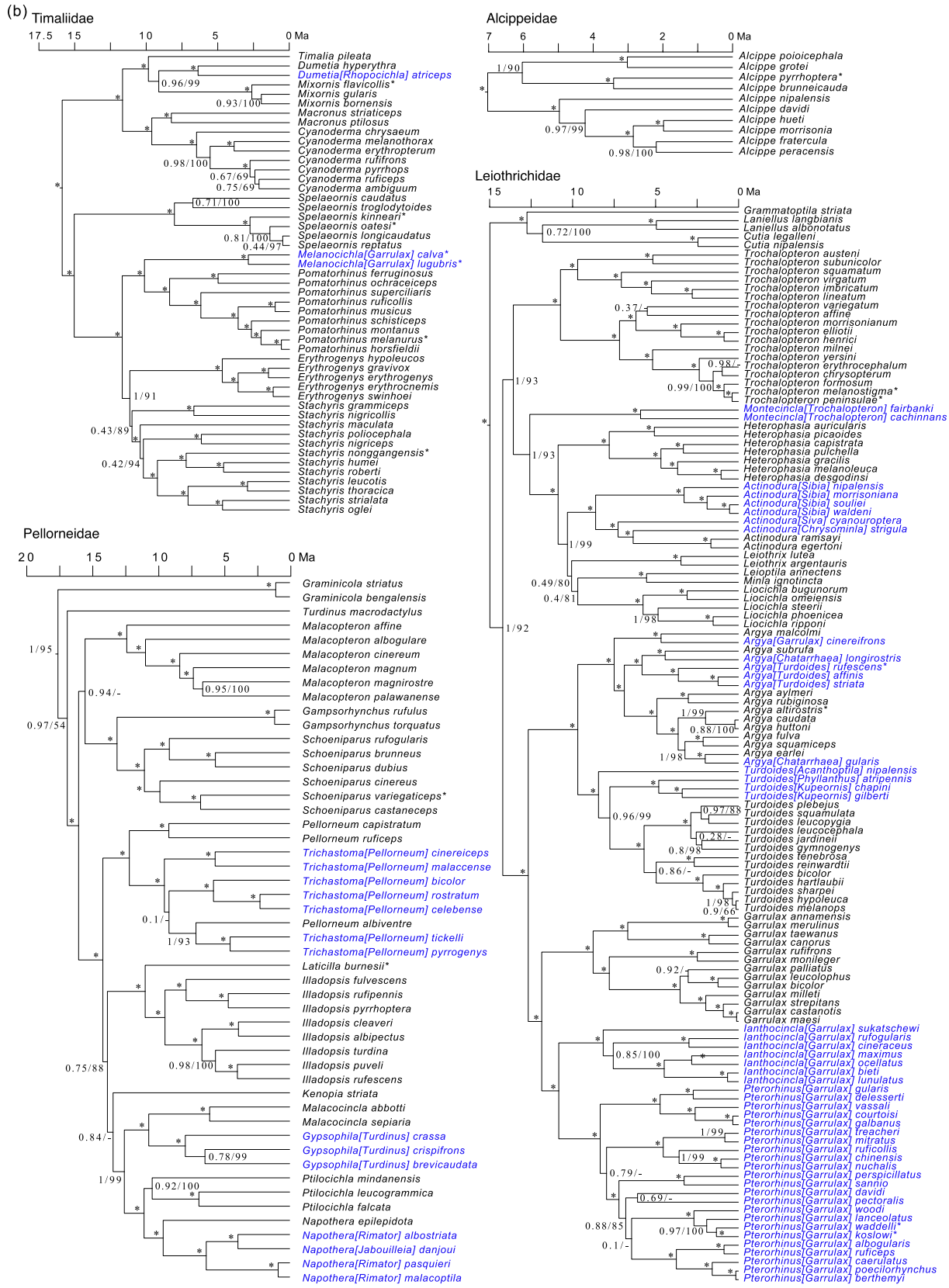

Fig. 3. (*continued*)

Gould 1874 resurrected for this taxon. The alternative option favours a broader genus definition for *Paradoxornis* Gould, 1836, that includes all of the species in this clade (*heudei, flavirostris, guttaticollis, gularis, bakeri, ruficeps, aemodium, paradoxa, unicolor)*, in which case the generic names *Psittiparus* Hellmayr, 1903, *Cholornis* J. Verreaux, 1870, and *Conostoma* Hodgson, 1842 would become junior synonyms. We favour this second option in which the taxonomy of the group is not inflated compared with other babbler families. Similarly, the second primary

clade of parrotbills should be treated as a single genus, *Suthora* Hodgson, 1837 and the names *Chleuasicus* Blyth, 1845, *Neosuthora* Hellmayr, 1911, and *Sinosuthora* Penhallurick and Robson, 2009 be treated as junior synonyms. *Chleuasicus* Blyth, 1845 was resurrected by Penhallurick and Robson (2009) for the species *atrosuperciliaris*, *Neosuthora* Hellmayr, 1911 for the species *davidiana*, and *Sinosuthora* Penhallurick and Robson (2009) was created to provide a name for the five-species clade of small parrotbills with greyish to rufous brown fringes to the flight feathers and no lateral crown-stripes (*conspicillata, zappeyi, brunnea, alphonsiana, webbiana*); *przewalskii,* although not sequenced by Yeung et al. (2011), was also included into *Sinosuthora*.

We do not propose additional changes for the remaining genera within Paradoxornithidae, although the case of *Chamaea fasciata* is worth mentioning. *Chamaea fasciata* is sister to the (now redefined) genus *Paradoxornis*, with a divergence close to the 10 Ma threshold. However, the ecology and morphology of this New World endemic differ from the typical parrotbills and it has been isolated for a long time from its Asian sister-group. We therefore retain this monotypic genus.

4.3.2. Family Zosteropidae

Several studies already suggested that *Yuhina* was paraphyletic (Cibois et al., 2002; Moyle et al., 2012; Zhang et al., 2007), and our comprehensive analysis, which is the first one to include almost all of the species, confirms this result and identifies three sequential sister lineages. The type species of *Yuhina* Hodgson, 1836 (*Y. gularis*) belongs to the largest clade, with six species. The genus *Staphida* Gould, 1871 can be resurrected for the clade formed by its type species *torqueola* and the two species *castaniceps* and *everetti*. Finally, the species *diademata* is sister to all other Zosteropidae and requires its own genus. As far as can be determined, there is no available generic or subgeneric name associated with this species. Therefore, we propose a new generic name:

***Parayuhina* gen. nov.**

Type species: *Parayuhina diademata* (Verreaux, 1869) **comb. nov**.

Diagnosis: 14–18 cm in length, 15–29 g; mostly greyish-brown plumage with a darker brown erectable crest, prominent white supercilium/nuchal collar from above the eye across the nape, contrastingly blackish basal parts of primaries and secondaries, and white underwing-coverts; shallowly forked tail; and pale yellowish/orange legs. Differs from *Staphida* in lacking broad white tips to the outer tail feathers, and from *Yuhina* by its larger size, slightly forked tail and absence of streaks on head or flanks. Sexes similar.

Etymology: This feminine name is based on the name previously used for a group of crested babblers, *Yuhina*, that proved to be paraphyletic based on phylogenetic results. This name was itself based on the Nepalese word for these birds, “Yuhin” (Richmond, 1992). We add the prefix *Para*, from Ancient Greek παρά “near”, to remind the fact that this taxon does not form a monophyletic group with the other yuhinas.

Remarks: A monospecific genus. Occurs in forested mountainous areas of central and south China, north-east Myanmar and north Vietnam.

The white-eyes form a large clade, with a long internode leading to an exceptionally rapid island diversification, comprising more than 100 species. We refrain from merging all species into a single genus because of the morphological diversity within this group, although diversification within the clade was rapid and occurred within less than 10 Ma. Several genera might not be monophyletic (*Dasycrotapha*, *Heleia*, *Zosterornis*), but the nodes are not well supported and further decisions on this group must await a more comprehensive analysis. In particular, the position of *Apalopteron familiare*, embedded within *Heleia,* is delicate, because if this result is confirmed the name of the entire clade should be changed to the senior name *Apalopteron* Bonaparte, 1854 (vs. *Heleia* Hartlaub, 1865). However, this topology was not supported by our ML trees. We confirmed the inclusion of *Chlorocharis* Sharpe, 1888 (one species: *emiliae*) within *Zosterops* Vigors & Horsfield, 1827 (Lim et al., 2018; Moyle et al., 2009). *Tephrozosterops stalkeri* is sister to the large *Zosterops* clade, and this monotypic genus could be retained to reflect the unique morphology of this taxon. Lastly, phylogenetic relationships are still uncertain for two small genera not yet sampled (*Rukia* and *Megazosterops*).

4.3.3. Family Timaliidae

The Timaliidae, as presently circumscribed, represents a group of Asian birds with diverse morphology and ecology, distributed across the entire Oriental region east to Wallace’s line (del Hoyo et al., 2007). We first propose to merge the two monospecific genera *Dumetia* Blyth, 1849 and *Rhopocichla* Oates, 1889 into the senior *Dumetia*. The divergence between the two taxa is below the 10 Ma threshold and their morphological differences are within the range of differences found within other babbler genera. Second, we propose a revision for two species previously classified as laughingthrushes in the Leiothrichidae: *Garrulax lugubris* and *G. calva*. The first has a small range restricted to south Thailand, Peninsular Malaysia and Sumatra, and the second is endemic to north Borneo. Both are medium-sized blackish birds, similar by size and shape to laughingthrushes, but with a unique head pattern: a wattle and patch of blue orbital and postocular skin in *G. lugubris*, and a featherless yellowish crown with a blue submoustachial area in *G. calva* (as seen also in some other Timaliidae species), and red bill (as in two species of *Pomatorhinus*). These two rare birds have never been the subject of molecular analyses until our data showed that they are unrelated to the true laughingthrushes and instead belong to the family Timaliidae. They were sister taxa with strong support, and diverged from the clade that comprises all *Pomatorhinus* species earlier than 10 Ma. The striking morphology of these two species and their phylogenetic divergence from other babblers support their placement in their own genus: we suggest to resurrect *Melanocichla* Sharpe, 1883, named with *lugubris* as type species, for these two closely related species.

Moyle et al. (2012) showed that the genus *Sphenocichla* Godwin-Austen & Walden, 1875 was embedded within *Stachyris* Hodgson, 1844, a result followed by Dickinson and Christidis (2014). We confirmed this result with sampling the two taxa that composed this genus (*S. humei* and *S. roberti*, the latter being a recent split). With the inclusion of these two species, the genus *Stachyris* is monophyletic, although with low support. Because of the absence of robust support for the nodes within the *Stachyris* clade, we favour a conservative approach and suggest no further divisions within the genus. Finally, we do not propose additional modifications for the remaining genera within this family.

4.3.4. Family Pellorneidae

Gelang et al. (2009) found *Turdinus macrodactylus* sister to *Graminicola*, whereas our analyses supported *Graminicola* as sister to the rest of Pellorneidae, and our MCC and ML trees using Data-1 recovered *Turdinus* as sister to the others (except *Graminicola*), but with low support in the ML tree. Despite the uncertainty of the position of *Turdinus macrodactylus*, both studies confirmed with good support the polyphyly of *Turdinus* as defined by Dickinson and Christidis (2014) (as well as the genus *Napothera* as defined by Gill and Donsker (2018)). We suggest to restrict the genus *Turdinus* to its type species *macrodactylus* (*T. atrigularis*, not sampled yet, might also stay in this genus), and to resurrect the name *Gypsophila* Oates, 1883 (type *Turdinus crispifrons*, Blyth) for the clade composed of *T. crassa*, *T. brevicaudata* and *T. crispifrons* (*T. calcicola* and *T. rufipectus*, not sampled yet but morphologically similar, are likely also part of this group). Richmond (1992) and Zimmer (1926) gave “March” as publication date for Oates’ *Handbook to Birds of British Burma*, whereas Sharpe’s Catalogue of the Birds in the British Museum was published in July 1883 (Sherborn, 1934). This suggests that *Gypsophila* Oates, 1883 has priority over *Corythocichla* Sharpe, 1883 (indeed *Gypsophila* Oates was used by Sharpe (1903) in his hand-list rather than his own name).

We confirmed the position of *Napothera epilepidota* as sister to the four species placed in *Rimator*, with a divergence close to 10 Ma. We suggest to place all five species found in this clade (*N. epilepidota, R.*

malacoptila, R. albostriata, R. pasquieri and Jabouilleia danjoui), as well as *J. naungmungensis* (not sampled here but confirmed in this clade by Renner et al. (2018)) in *Napothera* Gray, 1842 (type species *epilepidota*), with *Rimator* Blyth, 1847, and *Jabouilleia* Delacour, 1927, as junior synonyms. The last species classified in *Turdinus* (*marmoratus*), with a unique scaled pattern and a large size, might be left as it is until it has been analysed phylogenetically.

Pellorneum Swainson, 1832, as currently defined, is also polyphyletic. Because the type species (*ruficeps*) forms a clade with *P. capistratum*, one option could be to move the species *albiventre* to the genus *Trichastoma* Blyth, 1842. However, the limits between these two closely related genera have often been debated (Deignan, 1964; Delacour, 1946), and several species have not been sampled yet in genetic studies (*Pellorneum nigrocapitatum*, *P. fuscocapillus*, *P. palustre* and *Trichastoma buettikoferi*). Although the divergence between the two genera is older than 10 Ma, we suggest to merge all species within the senior name *Pellorneum*, in agreement with Eaton et al. (2016). This group would then unite all species with similar ground-foraging ecology and adaptations. We propose no modifications for *Schoeniparus*, *Malacopteron, Malacocincla, Gampsorhynchus, Laticilla, Illadopsis, Kenopia* or *Ptilocichla*.

4.3.5. Family Leiothrichidae and the genus Alcippe

The taxonomic revision within Leiothrichidae has been treated in another paper (Cibois et al., 2018). However, the comprehensive phylogeny presented here highlighted the particularity of the genus *Alcippe*, whose position relative to Leiothrichidae and Pellorneidae is not unanimously strongly supported in our analyses (see Section 4.1), and also varies among other studies (Gelang et al., 2009; Moyle et al., 2012). Because the divergence between these three clades occurred early during the Miocene, we suggest the genus *Alcippe* Blyth, 1844 be placed in a separate family. The family name Alcippidae is however preoccupied by Alcippidae Hancock, 1849, which refers to a family of marine invertebrates, now a synonym of Trypetesidae Stebbing, 1910 (Truesdale, 1993). To avoid homonymy in family-group names, as stated in Art. 29.6 of the International Code of Zoological Nomenclature 4th edition (International Commission on Zoological Nomenclature, 1999), we propose a new family name based on the entire name of the type genus:

Alcippeidae fam. nov.

Type genus: *Alcippe* Blyth, 1844

Diagnosis: A group of small birds, 12.5–16.5 cm in length, 13.2–18.3 g, with brown or olive-grey upperparts, wings and tail, buffy-white underparts, brown or grey crown, nape and ear-coverts, and often white eye-ring and blackish lateral crownstripes. Sexes similar. The species in Alcippeidae are smaller than those in the Leiothrichidae (laughingthrushes and allies), with duller plumage. They are more arboreal in habits than the Pellorneidae, which have stronger legs.

Etymology: In the Greek mythology, Alcippe is the daughter of Ares and Aglauros.

Remarks: Occur in forests and scrub of the Oriental region (mainly Southeast Asia).

5. Conclusions

In this study, we presented a time-calibrated phylogeny including 89% of the described species of babblers based on a supermatrix analysis of five mitochondrial and seven nuclear loci. This well supported phylogeny provides a robust basis for taxonomic revision and further biogeographic and macroevolutionary analyses. Our phylogeny supports seven primary clades, and we suggest that babblers could be recognized as seven families and 64 genera. One new family and one new genus are proposed.

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Declaration of interest

None.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ympev.2018.10.010.

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