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# Phylogeny and Biogeography of the Core Babblers (Aves: Timaliidae)

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*Abstract*.—The avian family Timaliidae is a species rich and morphologically diverse component of African and Asian tropical forests. The morphological diversity within the family has attracted interest from ecologists and evolutionary biologists, but systematists have long suspected that this diversity might also mislead taxonomy, and recent molecular phylogenetic work has supported this hypothesis. We produced and analyzed a data set of 6 genes and almost 300 individuals to assess the evolutionary history of the family. Although phylogenetic analysis required extensive adjustment of program settings, we ultimately produced a well-resolved phylogeny for the family. The resulting phylogeny provided strong support for major subclades within the family but extensive paraphyly of genera. Only 3 genera represented by more than 3 species were monophyletic. Biogeographic reconstruction indicated a mainland Asian origin for the family and most major clades. Colonization of Africa, Sundaland, and the Philippines occurred relatively late in the family's history and was mostly unidirectional. Several putative babbler genera, such as *Robsonius*, *Malia*, *Leonardina*, and *Micromacronus* are only distantly related to the Timaliidae. [Babbler; biogeography; convergence; parameter interaction; Timaliidae.]

The Timaliidae, generally known as the babblers, is a diverse family of oscine passerine birds that traditionally includes about 275 species in 50 genera (Dickinson 2003). These Old World insectivores are strikingly diverse, both in species richness and breadth of morphological and behavioral adaptations. Babblers are highly social forest birds that often are found in mixed-species flocks. Their diversity of forms and behaviors, which has led to comparisons with Neotropical antbirds (Thamnophilidae) and antthrushes (Formicariidae) in their ecological diversity (Collar 2003), is reflected in the English names of some babbler genera: wren-babblers, jungle-babblers, tit-babblers, thrush-babblers, parrotbills, scimitar-babblers, etc.

Babblers are a major component of the tropical Asian avifauna and a model system to study the biogeography of SE Asia. This species-rich family reaches its highest diversity in SE Asia and is almost entirely restricted to the Old World (one species occurs in North America). Babblers are a significant part of the forest community in Asia, with a dozen or more species co-occurring in most areas. This high level of sympatry suggests that they are ideal for assessing general diversification patterns and testing biogeographic congruence among multiple codistributed groups. Most species of babblers are restricted to the interior of tropical forests, have relatively limited distributions, and are not migratory. These attributes minimize the introduction of noise into biogeographic analyses. However, biogeographic inference has not been possible because relationships among babblers have mostly been unknown and even family membership is uncertain for many genera. The extent of taxonomic disarray was well characterized by Mayr and Amadon (1951), who stated that the Timaliidae had long been a "scrap basket" for genera that did not fit well into other families.

Recent molecular phylogenetic work has begun to shed light on the degree of disconnect between taxonomy and relationships in babblers (Cibois 2003; Gelang et al. 2009). Cibois (2003) sequenced mitochondrial DNA from 62 species of babblers and discovered that some putative ingroup taxa were not babblers (*Kakamega* and *Pteruthius*), whereas some outgroup genera (*Sylvia* [traditionally Sylviidae] and *Zosterops* [traditionally Zosteropidae]) were reconstructed within babblers. Furthermore, several genera were not recovered as monophyletic. Basal nodes in the phylogeny were not strongly supported, possibly because of the reliance on mitochondrial DNA alone. Gelang et al. (2009) shifted sampling strategies and included 4 nuclear markers in addition to one mitochondrial gene. This character sampling resulted in much better resolution of basal nodes in the family, allowing unambiguous subfamily delineation. However, the Gelang et al. (2009) study included only 41 species and so was unable to address the issue of paraphyletic genera identified by Cibois (2003).

Additional studies have focused on subsets of the Timaliidae, which made possible reinterpretations of some babbler relationships. For example, Philippine members of the genus *Stachyris* are closely related to the family Zosteropidae (Cibois et al. 2002; Zhang et al. 2007; Moyle et al. 2009), the genus *Pteruthius* (Reddy and Cracraft 2007), and *Erpornis zantholeuca* (Cibois et al. 2002; Barker et al. 2004) are closely related to New World vireos (Vireonidae), and the genus *Alcippe*, in fact, comprises 4 clades that are interspersed throughout the babbler phylogenetic tree (Pasquet et al. 2006). In general, modern systematic studies of babblers recover

paraphyly of genera, species, and even subspecies (e.g., Cibois et al. 2002; Cibois 2003; Reddy 2005; Pasquet et al. 2006; Zhang et al. 2007; Zou et al. 2007; Gelang et al. 2009; Luo et al. 2009; Dong et al. 2010; Reddy and Moyle 2011; Yeung et al. 2011). These molecular studies illustrate clearly what had been suspected by avian systematists (e.g., Newton et al. 1893; Mayr and Amadon 1951): extreme ecomorphological variation obscures every level of timaliid classification. Yet this same attribute that makes the taxonomy so vexing also makes the family intriguing for evolutionary study.

Our main objective was to produce a robust phylogenetic hypothesis for the babblers to evaluate current taxonomy and assess the evolution of the family. We assembled a large data set of nuclear and mitochondrial DNA sequences from almost 300 individuals, which included all but one genus and roughly 55% of babbler species, to reconstruct phylogenetic relationships and estimate divergence times within the Timaliidae. We used these to evaluate the geographic origin of major clades and assess the potential influence of major isolating features—such as the Isthmus of Kra, the oceanic islands of the Philippines, and the dry Middle East—on the structure and diversity of this family of tropical forest birds across these regions. The highest diversity of babblers is found in mainland Asia and we evaluated the biogeographic patterns to determine if this is the result of babblers originating in Asia or multiple colonization events from other regions. We also assessed whether there is support for multiple invasions of the same region being of the same time period, thereby providing support for a common mechanism or event leading to this expansion.

As we began preliminary analyses it became apparent that our data matrix exhibited many symptoms that might lead to unreliable phylogenetic results. The problems we encountered appear to be typical of large heterogeneous data sets (e.g., Miya et al. 2005; Soltis et al. 2007; Hackett et al. 2008; Parfrey et al. 2010; Thomson and Shaffer 2010). We used several methods to explore the behavior of the analysis and adjusted program settings in an attempt to ensure that we identified a reliable estimate of relationships among babblers. These methods included experimenting with many combinations of the number of heated chains and the amount of heating of those chains in Bayesian analysis, identification and removal of unstable taxa, and changing priors on branch lengths. Ultimately, we concluded that existing methods were amenable to analysis of our data, but careful consideration of the analytical process and the behavior of programs was required.

## Materials and Methods

### *Taxon and Character Sampling*

Taxon sampling included 296 individuals from approximately 50 genera and 151 species of babblers and an additional 10 sylvioid genera as outgroups (Appendix Table A1). The entire matrix was rooted with *E. zantholeuca*. This species had been included in the babblers until molecular data (Cibois et al. 2002; Barker et al. 2004) revealed that it was in fact a corvoid and only distantly related to babblers. The rest of the outgroup taxa were unconstrained in the analysis. We included 2 samples per species whenever possible for 2 reasons. First, we used the redundancy to guard against errors of misidentification, mislabeling, or sample contamination. Second, we used geographically disjunct sampling localities to obtain a preliminary idea of intraspecific genetic divergences. The source of this material breaks down as follows: 265 samples derived from vouchered fresh tissue samples, 28 samples of historical DNA derived from museum study skins, 2 samples derived from unvouchered blood samples, and sequences for one individual were downloaded from GenBank.

To provide phylogenetic signal at multiple levels in the phylogeny, we sequenced 3 mitochondrial genes and 3 nuclear introns. Sequences of the mitochondrial genes cytochrome b (Cytb), nicotinamide adenine dinucleotide dehydrogenase subunit 2 (ND2), and subunit 3 (ND3), the fifth intron of the transforming growth factor (TGF) β2, the fifth intron of the nuclear gene Beta-Fibrinogen (Fib5), and the third intron of the Z-linked muscle-specific kinase gene (MUSK) were amplified using the primers L14851 (Groth 1998), L428 and H494 (Reddy 2008), Hb745 (Reddy and Moyle 2011), L5215—H6313 (Sorenson et al. 1999), L10755—H11151 (Chesser 1999), TGF5 and TGF6 (Primmer et al. 2002), Fib5 and Fib6 (Marini and Hackett 2002), MUSK-I3F and MUSK-I3R (Kimball et al. 2009), respectively. Laboratory methods generally followed those described in Oliveros and Moyle (2010). For DNA samples extracted from museum study skins, conditions followed those described in Reddy (2008). Contigs were reconciled in Sequencher 4.9 (Genecodes) and fine-tuned manually following an initial alignment with MUSCLE v3.8 (Edgar 2004).

### *Data Exploration and Program Settings*

As is the case with most systematic studies, our primary concern in phylogenetic analysis was obtaining robust estimates of relationships among the ingroup taxa. Preliminary Bayesian and maximum likelihood (ML) analysis on our data indicated that several analytical hurdles would impede straight-forward phylogenetic analysis: failure to converge, parameter interaction, and unrealistic branch lengths in Bayesian runs, and taxon instability due to missing data in ML and Bayesian analyses. These issues were above and beyond the standard fine-tuning of program settings. Below we describe a general work flow of analytical approaches. In the Results section, we report additional fine-tuning to the analytical approach that we adopted in response to certain outcomes.

*Rogue taxa.*—Our data matrix contained several taxa represented by a small proportion of the total number of characters. DNA sequences for these taxa were derived from old museum study skins rather than fresh tissues, and some individuals had fewer than 700 bp

of sequence (~15% of the matrix). In the context of supermatrices, it has been shown that missing data can cause unstable placement of taxa in a phylogeny, so-called "rogue taxa," lowering support indices for clades that otherwise would receive strong support (Sanderson and Shaffer 2002; Thomson and Shaffer 2010). To test the stability of taxon placement, and its influence on phylogenetic reconstruction, we imported the trees from 1000 RAxML (Stamatakis 2006; Stamatakis et al. 2008) bootstrap replicates into Mesquite (Maddison and Maddison 2010) and measured taxon instability among trees. Taxa that had few data and highly variable phylogenetic placement among bootstrap replicates, which might obscure high support for clades, were removed from some analyses.

*Data partitions and evolutionary models.*—Preliminary runs of MrBayes using default settings did not converge after 20-million generations, as judged by the average standard deviation of split frequencies (ASDSF) reported by the program. Furthermore, plots of log-likelihoods from the posterior distribution shifted to new plateaus after several million generations of seeming stationarity. The lack of convergence precluded the use of Bayes Factors (Huelsenbeck and Imennov 2002; Nylander et al. 2004; Brandley et al. 2005) to determine optimal partitioning of the data. Because of this we used ML searches in GARLI-PART version 0.97 (Zwickl 2006) with the Akaike Information Criterion (AIC) (Akaike 1974) and Bayesian Information Criterion (Schwarz 1978) to test various partitioning strategies. Because of the large number of possible partitions in the data, we limited testing to a set of partitions that are biologically intuitive (i.e., genes and codon positions) and found to induce large increases in likelihood scores in other studies (e.g., Nylander et al. 2004; Brandley et al. 2005; McGuire et al. 2007). Appropriate evolutionary models for each partition were evaluated by the AIC in MrModeltest 2.3 (Nylander 2004) based on likelihood scores derived from PAUP* ver. 4b10 (Swofford 2003). Subsequent ML and Bayesian analysis utilized the chosen partitioning strategy and evolutionary models.

### *Phylogenetic Analysis*

We conducted tree searches under the ML criterion using Garli 0.97 (Zwickl 2006) and RAxML 7.2.6 (Stamatakis 2006; Stamatakis et al. 2008). RAxML searches consisted of 20 repetitions from random starting trees. Settings for Garli searches included 200 attachments per taxon, generation threshold for *topoterm* 10,000 and score threshold for termination 0.05. Likelihood scores from each program, and topologies from both programs, were compared with assess convergence on a common topology and likelihood. Support for nodes in the phylogeny was estimated with 1000 fast bootstrap repetitions in RAxML.

Bayesian analysis used the parallel version of MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; Altekar et al. 2004). All analysis used multiple concurrent runs and at least 3 heated chains for each cold chain. The substitution matrix, base frequencies, and gamma shape parameter were unlinked between data partitions, and the rate prior was set to variable (prset applyto = (all) ratepr=variable), allowing partitions to evolve at different rates. The number of attempted chain swaps was increased to 2 (nswaps = 2). Bayesian analysis was conducted on the entire matrix as well as each locus individually. The 3 mitochondrial genes were considered a single locus and analyzed together.

Examination of parameter estimates from preliminary Bayesian analysis revealed that default program settings would not be optimal for this data set and that extensive fine-tuning would be necessary to achieve reliable results. MCMC runs using default parameters resulted in a low proportion of accepted swaps between adjacent Markov chains, typically less than 5%, and independent runs had not converged after 40-million generations. To increase the efficiency of sampling, we incrementally lowered the *temp* value in MrBayes until the proportion of accepted swaps was in a range of ~0.2–0.7. Because of the incremental heating used in MrBayes, we also added more heated chains to some runs with lower *temp* values.

We used several methods to assess the results of our Bayesian analysis. We used the program splitsmb (Lakner and Ronquist 2008) to examine the ASDSF using a range of burn-in proportions. Tracer 1.5 (Rambaut and Drummond 2007) and Are We There Yet? (AWTY; Wilgenbusch et al. 2004) were used to visualize the convergence of parameter estimates and posterior probability of clades, respectively. Tree topologies and support values were compared with TreeGraph 2 (Stover and Muller 2010).

### *Timing of Diversification*

When estimating dates for nodes in a molecular phylogeny, the choice of calibration points and the way they are represented can have a large influence on node ages and confidence intervals (e.g., Inoue et al. 2010). The fossil record of passerine birds is sparse and does not provide useful calibration points for babblers. Instead, we used 2 secondary calibrations derived from other time-calibrated phylogenies. This is admittedly not an ideal strategy, and all age estimates must be evaluated with caution. One secondary calibration is derived from a study of *Zosterops* relationships (Moyle et al. 2009) that assessed the timing of diversification using island ages in the Solomon Islands as calibration points and estimated the crown *Yuhina* + Zosteropidae to be a maximum of 8.8 Ma. The second calibration is derived from the rifting of New Zealand from Australia, a putative vicariant event used to calibrate a higher level phylogeny of passerine birds (Barker et al. 2004). This calibration yielded a range of 27.1–37.3 Ma for the node separating megalurine warblers from all other sylvioids. Our taxon sampling incorporated these nodes and allowed us to use these age estimates to calibrate the timing of

diversification in babblers. The estimated ages of marine transgressions that inundated the Isthmus of Kra, which separates mainland Asia from Sundaland, have been used as calibration points in other studies (e.g., Fuchs et al. 2006, 2008), but we were interested in evaluating the influence of the Isthmus in generating or partitioning diversity so we avoided using it as a calibration in this study.

To place an approximate time scale on the babbler phylogeny, we used the 2 calibration points and the ML phylogram to produce an ultrametric tree with branch lengths proportional to time in Phylobayes (Lartillot and Philippe 2004, 2006). Phylobayes uses MCMC to sample a posterior distribution of node ages from a fixed topology under a variety of relaxed clock models. We used the lognormal model (Thorne et al. 1998) to describe the change of rates over time and applied a broad gamma-distributed prior to the root of the tree (mean 40, standard deviation 20). Soft bounds were used on the calibration points, which allowed 5% of the probability to be allocated outside of the calibration limits. A birth–death prior on divergence times was specified with p1 and p2 considered free parameters.

### *Biogeographic Analysis*

The broad geography inhabited by babblers and our incomplete species-level sampling induced us to perform biogeographic analysis at the broadest levels. We coded 6 geographic regions that are separated by substantial barriers: Africa, Eurasia, Sundaland, oceanic Philippines, east of Wallace's Line, and New World. The first 4 regions cover the vast majority of the species diversity in babblers. Our main goal was to infer the geographic origin of major clades of babblers. Our sampling of the Zosteropidae was especially sparse (20 of ca. 120 species) but we captured all the basal nodes in the family (Moyle et al. 2009), which are needed for biogeographic reconstruction of basal babbler nodes. We acknowledge that the regional coding lumps some biogeographical subregions, such as the Himalayas and Indochina. Future analysis with more complete species-level sampling will be required to assess the influence of these regions.

We used parsimony and Bayesian methods to reconstruct ancestral areas at nodes in the phylogeny. Both methods were implemented in the software program Reconstruct Ancestral States in Phylogenies v1.1 (RASP; Yu et al. 2011) and included summation of the results over trees from 50-million generations of the posterior distribution (10,000 trees) to account for topological uncertainty. First, we used the event-based method Statistical Dispersal–Vicariance Analysis (Yu et al. 2010), which allows multiple topology summation within DIVA (Ronquist 1997), thus accounting for phylogenetic uncertainty. DIVA is a parsimony-based method in which vicariance is assumed and inferred dispersal events are assigned a cost. Long-distance dispersal likely contributed to the current distribution of babblers; therefore, an a priori assumption of vicariance may not be appropriate. To account for this, DIVA contains a useful feature in which the maximum number of areas in the ancestral distribution can be limited. This option eliminates ancestral distributions that contain multiple far-removed regions and forces dispersal. No extant species of babbler spans more than 2 regions, and the few that span 2 regions only occur in Asia and Sundaland. Because of these geographic restrictions, we limited the maximum number of regions in ancestral areas to 2. Because DIVA only allows a maximum of 127 terminals, we excluded the second individual of all species, included only babblers and *Erpornis* and winnowed clades that included only a single geographic character state. For this reduced data set, we coded *Erpornis* as occurring in all regions to not bias reconstructions at the base of the tree.

Dispersal–Vicariance Analysis has been criticized because the assumption of vicariance might bias reconstructions and is unrealistic in oceanic island settings (e.g., Lamm and Redelings 2009; Kodandaramaiah 2010). Because the geographic regions we used contain oceanic islands, we also used a model-based Bayesian reconstruction of ancestral states. The Bayesian method in RASP (Yu et al. 2011) used the MrBayes 3.1.2 source code and implemented relatively simple models of character state evolution that assumed equal rates of change and fixed (JC) or estimated (F81) state frequencies. Character states (biogeographic regions) were analyzed as binary characters and gamma-distributed rate variation between sites (regions) could be enabled. Because some geographic regions contain few babbler species, and exchange between regions is expected to vary, we used the F81+gamma model. Two independent runs of 10 chains with a temperature of 0.1 were run for 1-million generations and sampled every 100 generations. A distance between runs (analogous to the ASDSF) of less than 0.01 was used as an indicator of convergence. We discarded 2500 samples (250,000 generations) before calculating the state frequencies. As in the DIVA analysis above, we limited to 2 the maximum number of areas included within ancestral distributions. The full taxon sampling was used in Bayesian reconstructions.

## RESULTS

The final DNA sequence matrix comprised 292 individuals and 4688 characters, of which 1760 were constant, 362 were variable but parsimony uninformative, and 2566 were parsimony informative. Informative sites were distributed across loci as follows: ND2 (669), ND3 (208), Cytb (546), TGF (390), Fib5 (363), and MUSK (395). Base composition varied among loci but was consistent with patterns recovered for the same markers in other bird groups. All mtDNA sequences appeared to be genuine mitochondrial sequence, rather than nuclear copies. Sequences contained no stop codons, overlapping fragments contained no conflicts, base composition was homogeneous across taxa, codon positions contained expected relative divergences ($3 > 1 > 2$), and there were no highly suspect relationships among taxa.

The data matrix and final trees are available at TreeBASE (http://www.treebase.org; S11986).

Based on nonmonophyly of conspecific samples, we determined several individuals that we suspected of being identified incorrectly. We checked with the loaning institution for each of the problematic samples and, because we used >99% vouchered material, we were able to obtain clarifications of all identifications. Some samples had already been reidentified by the host institution, whereas others were reidentified after our information requests. A few species (e.g., *Alcippe morrisonia*, *Pomatorhinus ruficollis*, and *Pomatorhinus erythrogenys*) remained paraphyletic, but corroborate results from other studies (e.g., Zou et al. 2007; Reddy and Moyle 2011).

### *Program Settings and Behavior of Analysis*

Preliminary Bayesian analysis that included only 6 data partitions revealed that simultaneously accounting for invariant sites and gamma-distributed rate variation among sites appeared to induce parameter interaction. In 2 subsets of the data, independent runs stabilized on different parameter estimate ranges. One run stabilized on a high proportion of invariant sites and a high value for $\alpha$ (describing the gamma distribution), whereas the other run stabilized on a lower proportion of invariant sites and a correspondingly lower $\alpha$ (Fig. 1). Apparently, using 2 methods to accommodate rate variation across sites allowed combinations of parameter estimates that produced multiple regions of high posterior probability. The effects of the interaction between rate heterogeneity parameters on our parameters of interest (topology and branch lengths) are unclear. Although one pair of runs stabilized on similar likelihood scores, both pairs of runs did not achieve topological convergence; the ASDSF after 20-million generations was ~0.05 for both pairs. MrModeltest 2.3 (Nylander 2004) indicated either GTR + G or GTR + I + G evolutionary models for all data partitions. Because of the potential for parameter interaction, we chose to omit the invariant sites parameter and used only gamma-distributed rate variation.

The AIC indicated that the most partitioned model best fit the data (Table 1). This model contained 12 partitions, dividing the data by each gene and codon position. The BIC indicated a more conservative scheme with 10 partitions, which included all 3 introns in a single partition. The 2 partitioning strategies produced almost identical results. Consensus-tree topologies were identical and posterior probabilities varied only slightly, especially for well-supported nodes.

Early Bayesian runs stabilized on tree lengths that were ~3 times larger than values obtained from ML analyses. This phenomenon has been noted in Bayesian analysis of partitioned data sets (Brown et al. 2010; Marshall 2010), and we used the workaround described by Marshall (2010) to overcome the unrealistic tree lengths by adjusting the branch-length prior in MrBayes to an exponential distribution with a smaller mean (0.01) via the command: prset applyto = (all) brlenspr = unconstrained:exponential(100). After this adjustment, all Bayesian runs converged on tree lengths similar to those recovered from ML analysis.

Taxon instability tests in Mesquite (Maddison and Maddison 2010) revealed that 2 species for which we had limited data varied in phylogenetic placement far more than all other taxa in the matrix. These 2 species, *Parophasma galinieri* and *Graminicola bengalensis*, were represented by 2 individuals each but all 4 samples contained less than a quarter, and as little as 7.5%, of the characters in the data matrix (351–958 bp). Removing these taxa from the analysis resulted in a marked increase in bootstrap support for many basal nodes in the tree. For example, when *P. galinieri* was included in the analysis, it was inferred to be the sister taxon of the Timaliinae (Fig. 2, clade C), albeit with only 55% bootstrap support but support for other basal nodes in the Timaliinae dropped dramatically. Support for the Timaliinae (exclusive of *P. galinieri*) fell from 100% to 66% and the 2 main subclades from 98% and 97% to 83% and 85%, respectively. Inclusion of the other unstable taxon, *G. bengalensis*, reduced support values across basal nodes within the Leiothrichinae (Fig. 2, clade A). All subsequent analysis omitted these taxa.

The *temp* setting in Bayesian analysis was lowered by increments until, at a setting of 0.06, the proportion of successful swaps for adjacent chains was between 0.2 and 0.5. This lower temperature did not, however, induce convergence between the posterior distribution of topologies of independent runs. Two runs of 4 chains with *temp* = 0.06 had failed to converge when the run was terminated after 50-million generations (Supplementary Fig. 1, http://datadryad.org, doi:10.5061/dryad.100jc764). Likewise, including additional heated chains to runs at higher *temp* settings did not seem to influence the rate of convergence either. However, the combination of a low *temp* value and extra heated chains changed the behavior of runs entirely. Two independent runs of 8 chains each (7 heated) and a *temp* = 0.06 converged rather quickly. The ASDSF using the default burn-in of 0.25 crossed below 0.01 by 10.5-million generations.

### *Phylogenetic Results*

Bayesian and ML analysis produced congruent phylogenetic trees, with differences not supported strongly by bootstrap resampling or posterior probability. Basal nodes subtending major clades of babblers all received strong support from both analysis methods (Fig. 2). Similar to recent molecular studies (e.g., Alström et al. 2006; Johansson et al. 2008; Gelang et al. 2009), several babbler genera (e.g., *Chamaea*, *Paradoxornis*, *Fulvetta*, *Conostoma*, and *Chrysomma*) were members of a clade (Fig. 3, clade E) separate from all other babblers and should more correctly be assigned to the Sylviidae. We also corroborated earlier results indicating that the white-eye family Zosteropidae is embedded within the babbler genus *Yuhina* (Fig. 3, clade D; Moyle et al. 2009). Within

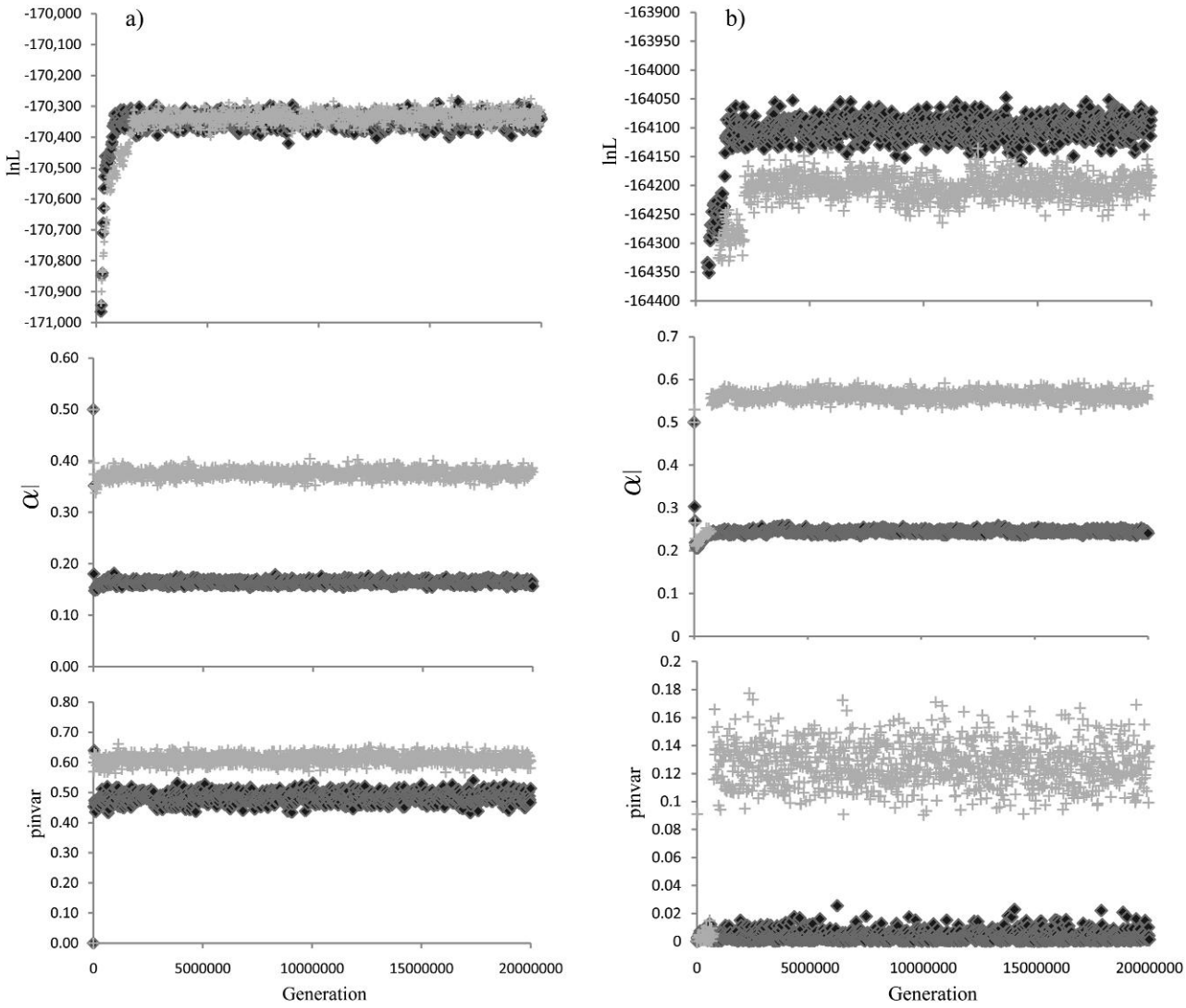


FIGURE 1. Likelihoods and parameter estimates for second codon positions (a) and the MUSK intron (b) from 2 different 20-million generation preliminary Bayesian runs. From top to bottom, log likelihood, $\alpha$ parameter for gamma-distributed rates among sites, and proportion of invariant sites are plotted against generation. Likelihood scores are not comparable because taxon sampling differed slightly between runs. The ASDSF at the end of each run was 0.049 (a) and 0.055 (b).

the core babblers, all analyses identified 3 subclades corresponding to the Leiothrichinae, Pellorneinae, and Timaliinae of Gelang et al. (2009). All 3 clades received high node support.

The first major subclade (Fig. 3, clade A), Leiothrichinae, included the species-rich genus *Garrulax* and several other smaller genera and was well supported, with bootstrap support/posterior probability of 97/1.0.

TABLE 1. Results of ML-based partition testing of the combined matrix

| $N^a$ | Description | lnL | Free parameters | AIC[b] | BIC[c] |
|---|---|---|---|---|---|
| 1 | All together | −169226.0831 | 9 | 338470.1662 | 338528.2162 |
| 2 | mt, nuc | −166517.8794 | 19 | 333073.7588 | 333196.3088 |
| 4 | mt, 3 nuc | −166472.0646 | 39 | 333022.1292 | 333273.6792 |
| 4 | 3 mtgenes, nuc | −166299.429 | 39 | 332676.858 | 332928.408 |
| 4 | 3 codon positions, nuc | −163539.1057 | 39 | 327156.2114 | 327407.7614 |
| 6 | 3 codon positions, 3 nuc | −163494.4529 | 59 | 327106.9058 | 327487.4558 |
| 10 | 3 codon positions × 3 mtgenes, nuc | −163160.3325 | 99 | 326518.665 | **327157.215** |
| 12 | 3 codon positions × 3 mtgenes, 3 nuc | −163107.7703 | 119 | **326453.5406** | 327221.0906 |

[a]Number of partitions, each using GTR + G.
[b]Calculated as 2*(parameters - lnL).
[c]Calculated as (-2lnL) + (parameters × ln base pairs).

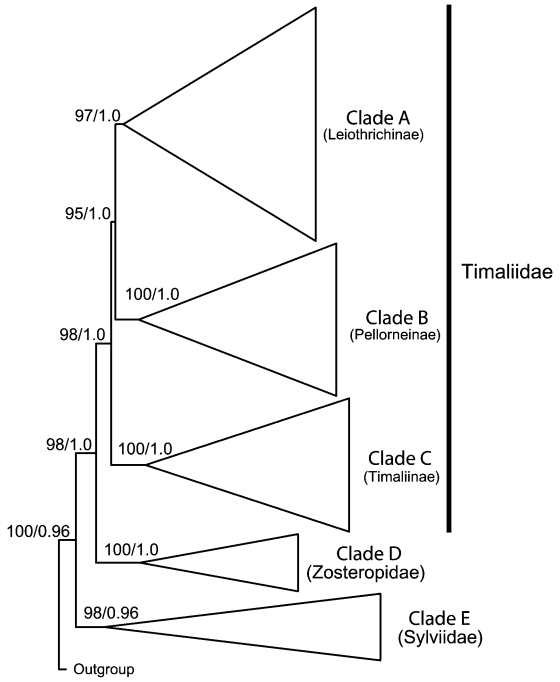


FIGURE 2. Summary of higher level relationships for babblers based on ML analysis of the combined data set with 12 partitions. Numbers by nodes refer to ML bootstrap support/Bayesian posterior probability.

The basal node in the clade divided the genus *Alcippe* (sensu Pasquet et al. 2006) from the rest of the taxa and was also well supported (96/1.0). Uncertainty exists about relationships just above this basal node. Bayesian results (not shown) placed *Garrulax striatus* sister to *Cutia nipalensis*, whereas ML results placed each species branching sequentially from the base of their clade. Neither relationship was well supported, with a posterior probability of 0.88 separating the 2 taxa and bootstrap support of 43% uniting them as sisters. Moving up from the base of the tree, the next clade (77/0.99) subdivided into 2 large subclades. One of the subclades included a clade with a large number of *Garrulax* species sister to a clade including *Phyllanthus* and *Kupeornis* imbedded inside of *Turdoides*. The second subclade included the remainder of the *Garrulax* species sister to a clade including *Heterophasia*, *Actinodura*, *Minla*, *Crocias*, *Liocichla*, and *Leiothrix*. Well-supported nodes in clade A rendered *Garrulax*, *Turdoides*, *Actinodura*, and *Minla*, nonmonophyletic.

The second major subclade of babblers (Fig. 3, clade B), Pellorneinae, was sister to clade A with strong support (95/1.0). Support for the clade was unequivocal (100/1.0) but some basal relationships within the clade were not well resolved. The clade was divided into 2 large subclades. One subclade (97/0.95) included a monophyletic *Malacopteron* (100/1.0) sister to a clade that united *Gampsorhynchus* sister to *Schoeniparus*. The other major subclade within clade B comprised 4 well-supported clades, but relationships among the 4 were equivocal. The first clade (100/1.0) included *Ptyrticus* embedded inside of *Illadopsis*. The second clade (100/1.0) included *Trichastoma*, a nonmonophyletic *Pellorneum*, and 2 of the 4 *Malacocincla* species included in the study. The third clade included the remaining 2 *Malacocincla* species, *Napothera*, *Ptilocichla*, *Jabouillea*, and *Rimator*. The final clade comprised only a single species, *Kenopia striata*. Well-supported nodes in clade B rendered *Illadopsis*, *Pellorneum*, *Malacocincla*, and *Napothera* nonmonophyletic.

The third major subclade of babblers (Fig. 3, clade C), Timaliinae, was sister to the clade formed by clades A and B. This group included the large genera *Stachyris* and *Pomatorhinus* as well as several smaller genera. *Pomatorhinus*, *Xiphirhynchus*, *Sphenocichla*, *Spelaeornis*, and the larger-bodied *Stachyris* species formed a clade with strong support (97/1.0). Within that clade *Spelaeornis* was sister to all other species. *Sphenocichla* was reconstructed among the larger bodied *Stachyris*, which formed a clade with low support and, in turn, was embedded within *Pomatorhinus*, as was *Xiphirhynchus*. The other half of clade C included *Dumetia*, *Rhopocichla*, *Timalia*, *Macronus*, and the smaller bodied *Stachyris* species. *Macronus* was not monophyletic, with *Macronus gularis* reconstructed in a weakly supported clade (61/0.98) with *Dumetia*, *Timalia*, and *Rhopocichla*, whereas *Macronus striaticeps* and *Macronus ptilosus* formed a clade (95/1.0) sister to the small-bodied *Stachyris* clade (100/1.0). Of genera represented by more than one species in clade C, only *Spelaeornis* was monophyletic.

All analyses placed 4 traditional genera of babblers outside of the clades described above. Because of the sparse outgroup sampling in families more distantly related to the babblers, these genera could not be placed with any certainty. Three of the aberrant babbler genera—*Leonardina*, *Robsonius*, and *Micromacronus*—are endemic to the Philippines, whereas *Malia* is endemic to Sulawesi.

Individual gene trees (Supplementary material) were largely congruent with the combined results, but with lower support for most relationships. Two notable, well-supported differences occurred in single gene trees. First, analysis of TGF alone produced strong support for a sister relationship between the Zosteropidae (Fig. 2, clade D) and Leiothrichinae (Fig. 2, clade A). This relationship is not supported by any of the other markers, which placed the Zosteropidae sister to the babblers with significant support (mtDNA and MUSK) or unresolved (Fib). The second discrepancy concerned the placement of *Alcippe* with respect to the Leiothrichinae (Fig. 3, clade A). Analysis of 2 introns alone placed the genus sister to the Pellorneinae with posterior probabilities of 0.99 (MUSK) and 0.31 (Fib5), whereas the other 2 markers placed it as the basal lineage in the Leiothrichinae with posterior probability of 0.66 (mtDNA) and 1.0 (TGF). The lack of topological convergence in independent Bayesian runs under default program settings did not appear to be caused by this conflict in phylogenetic signal. Analysis of the combined matrix without *Alcippe*

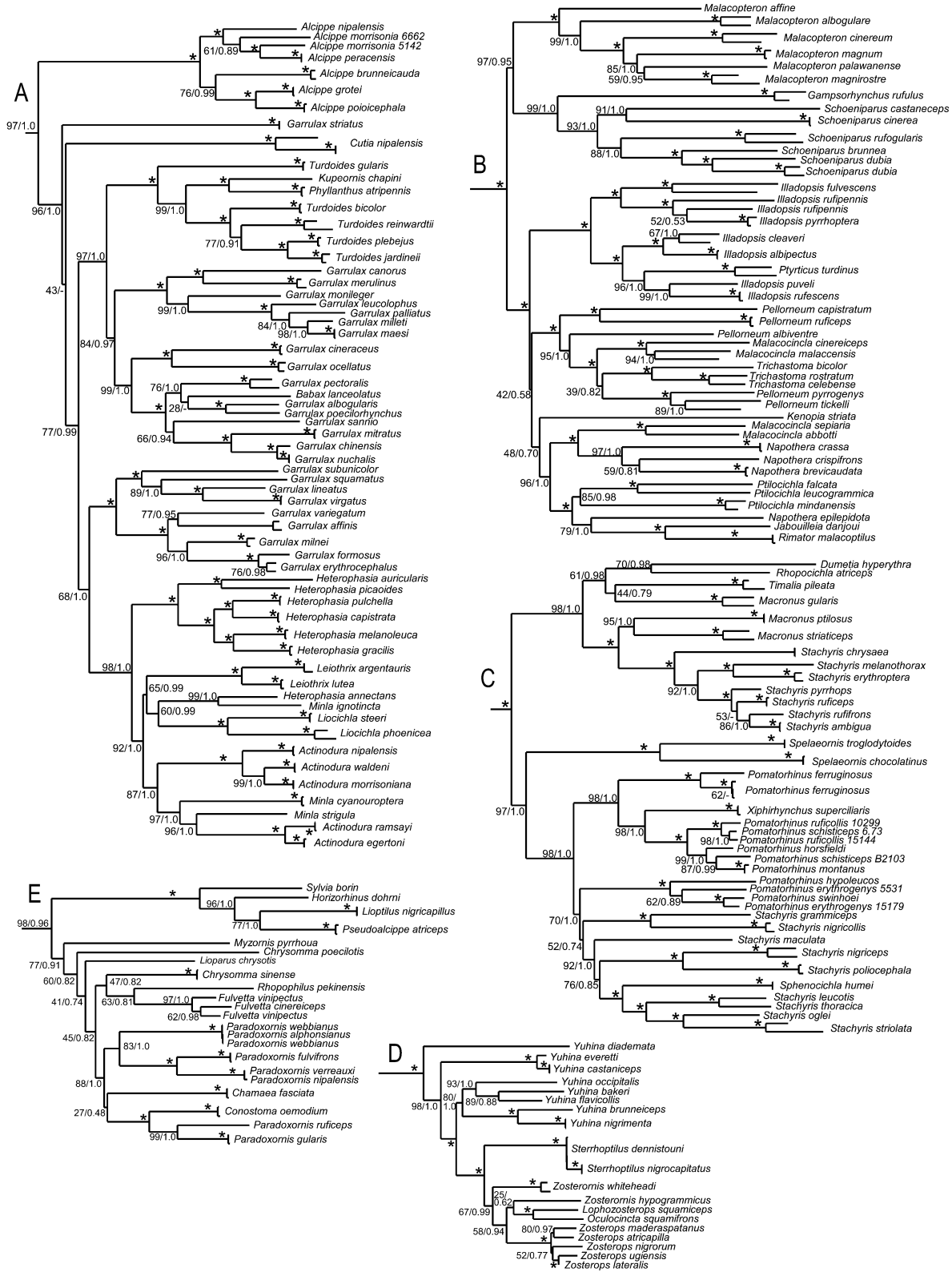


FIGURE 3. Detailed phylogeny of clades based on ML analysis of the combined data set with 12 partitions. Numbers by nodes refer to ML bootstrap support/Bayesian posterior probability. Clade letters correspond to Figure 2. Asterisks indicate 1.0 posterior probability and 100% bootstrap support.

did not converge after 40-million generations under default program settings.

### *Biogeographic Results*

Bayesian and parsimony reconstruction of ancestral areas produced congruent results for most basal nodes (Fig. 4). Two of the 3 core babbler clades (Leiothrichinae and Timaliinae), as well as the Zosteropidae, were reconstructed unambiguously as originating in mainland Asia. The 2 methods differed regarding the ancestral area of the Pellorneinae, with the Bayesian results strongly supporting a mainland Asia origin possibly shared with Sundaland, whereas DIVA was more equivocal, indicating plausible support for 4 ancestral areas: Asia, Sundaland, Asia + Sundaland, and Africa + Asia.

As expected from the preponderance of Asian taxa in the Leiothrichinae, the subfamily appears to have evolved mostly within mainland Asia, with a single colonization of Africa (*Turdoides*, *Phyllanthus*, and *Kupeornis*) and a few colonizations of Sundaland (e.g., *Garrulax mitratus*, *Garrulax palliatus*, and *Alcippe brunneicauda*). Although the origin of the Timaliinae was unambiguous, both biogeographic methods produced many equivocal reconstructions within the subfamily, indicating multiple colonizations of Sundaland and one of the Philippines, as well as the possibility of infrequent back colonizations to Asia. This pattern of ambiguity was expanded in the Pellorneinae, with multiple disjunctions between Asian and Sundaland along with a single colonization event of the Philippines (*Ptilocichla mindanensis*, from Sundaland), and a single colonization of Africa (*Illadopsis*, from an uncertain ancestral distribution).

DIVA and Bayesian methods reconstructed some biogeographic events in different ways. For example, the colonization of Africa by *Turdoides* appears to be an uncomplicated pattern but is reconstructed differently by the 2 methods. The genus is embedded within an unambiguously Asian clade, and a single colonization of Africa is evident. However, Bayesian analysis produces an unequivocal Asian distribution for the ancestor of the African clade and its Asian sister taxon (*Turdoides gularis*), whereas DIVA (not shown) reconstructs a larger ancestral distribution of Asian + Africa.

### *Time Scale of Evolution*

Relaxed clock analysis using the 2 secondary calibrations produced a time scale for babbler evolution (Fig. 4) that placed early diversification events in the Miocene. The node uniting the Zosteropidae with the core babblers was estimated at 16.1–21.0 Ma, and the 3 babbler clades (A, B, C) began diversifying from 11.2 to 17.8 Ma. Inferred continental dispersal/vicariance events were not contemporaneous in most cases. For example, 2 large African radiations split from Asian sister clades at 10.0–14.1 Ma (origin of *Illadopsis*/*Ptyrticus*) and 6.4–9.9 Ma. (within *Turdoides*). We lacked samples for several Asian species of *Turdoides*. Including those samples might have altered this age estimate but would probably have induced a more recent estimate, further from the estimate for *Illadopsis*. We included all species of *Illadopsis* and dense sampling of related genera.

Some of the molecular dating results indicated that the 2 calibration points may have been providing age information at odds with one another. Although the age ranges applied to the 2 calibration nodes were broad, the analysis produced narrow confidence intervals around each of the calibration nodes, and the confidence intervals extended beyond the calibration range, which was permitted by using soft bounds on the calibration ranges. For example, age estimates for the crown Zosteropidae (8.4–11.4 Ma) were mostly older than the calibration range, which was a maximum of 8.8 Ma. Likewise, the estimated split between *Megalurus* and other sylvioids (25.7–28.8 Ma) is narrow but extends beyond the broad calibration interval (27–37 Ma). With our data, model, and program settings, the analysis seemed to favor a smaller time interval between the calibration nodes than was allowed by the calibration intervals; in essence the calibration nodes were pulled toward each other. We interpret this to mean that one or both of the calibration intervals may be invalid, the model or program settings biased the analysis or that substantial shifts in the rate of molecular evolution occurred across portions of the tree.

## Discussion

Considering their ecological, morphological, and taxonomic diversity, babblers are a promising group for exploring many facets of evolution. However, evolutionary inference requires a robust hypothesis of relationships among taxa, and our results show clearly that current taxonomy is rife with unnatural groups. Producing a reliable estimate of phylogeny was not a straightforward task because the data matrix was not amenable to stock analysis and instead required extensive data exploration and testing of program settings. A combination of low temperature and an increased number of heated chains markedly increased the rate of convergence of independent Bayesian runs. This strategy has been identified previously (Beiko et al. 2006), and studies of large data sets that struggle to obtain convergence (e.g., Miya et al. 2005; Soltis et al. 2007; Hackett et al. 2008; Parfrey et al. 2010; Thomson and Shaffer 2010) may benefit from similar strategies.

Two partitions in our data—second codon positions of the mtDNA and the nuclear intron MUSK—exhibited signs of parameter interaction between invariant sites and gamma-distributed rates (Fig. 1). A set of invariant (or slowly evolving) sites can be accounted for in 2 ways: a low proportion of invariant sites and a low $\alpha$ (indicating a high proportion of slowly evolving sites) or a high proportion of invariant sites and a corresponding high $\alpha$. For the second codon-position partition, the 2 runs appeared to converge because likelihoods stabilized in the same range, but the runs did not sample similar posterior distributions of topologies. Issues of parameter identifiability when simultaneously

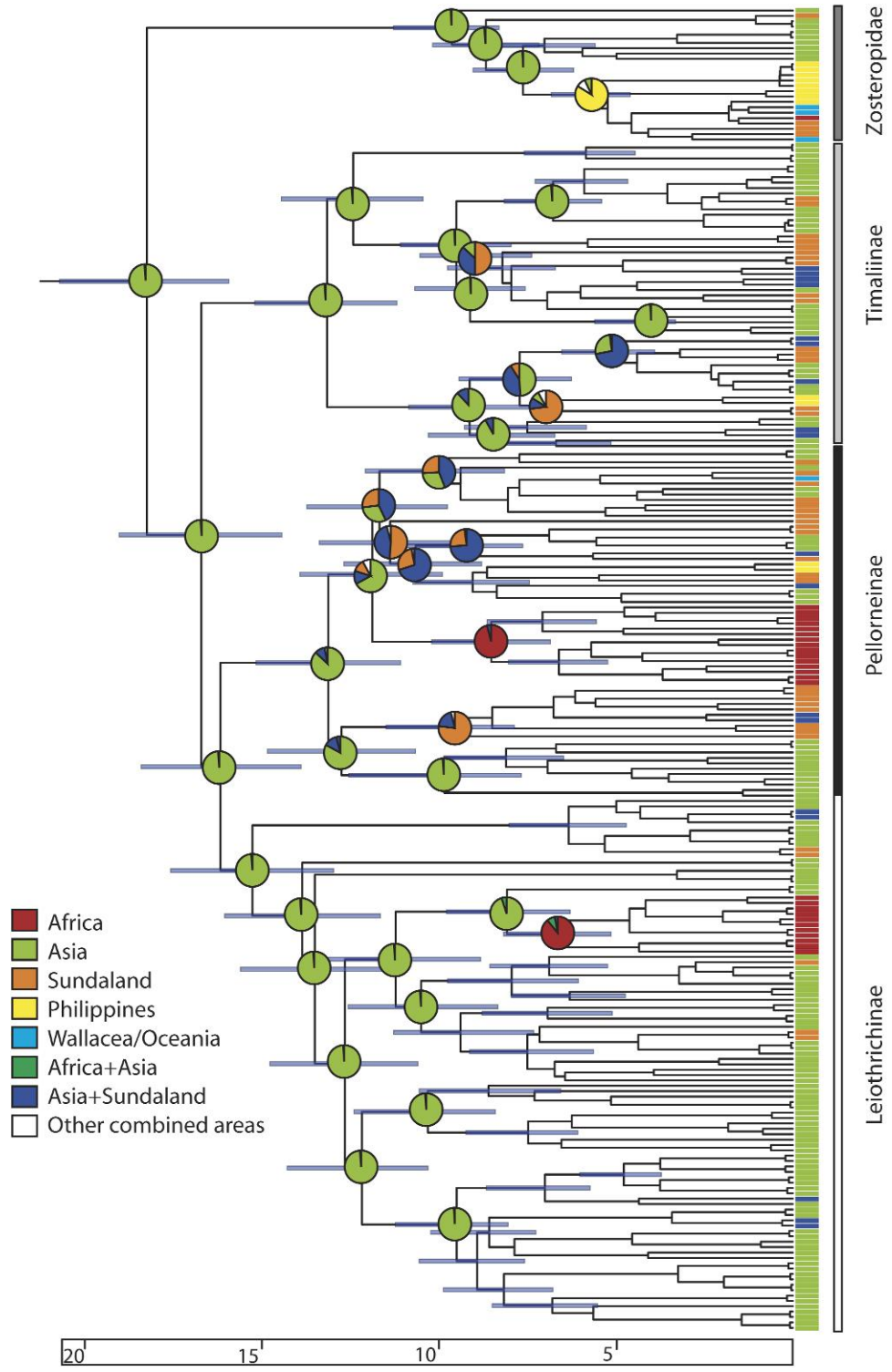


FIGURE 4. Temporal and geographic aspects of babbler diversification. The time scale was produced with a relaxed clock method and 2 calibrations (see text for details). Bars on nodes indicate 95% confidence interval for age estimates. The bar at the bottom gives the absolute time scale in millions of years before present. Pie diagrams at nodes indicate probability of various ancestral area combinations from the Bayesian analysis. Only ancestral areas for basal nodes are shown.

accounting for invariant sites and gamma-distributed rates have been demonstrated with simulated data (Sullivan et al. 1999) and discussed in informal settings (e.g., http://treethinkers.blogspot.com/2009/04/when-we-fail-mrbayes.html), but to our knowledge have not been demonstrated in published empirical studies. Our results suggest that omitting the invariant sites model may be preferable in some situations.

Ultimately, we were able to produce a robust phylogenetic hypothesis, as judged by congruence of results between ML and Bayesian analysis and across multiple independent trials for each method starting from random topologies. These results allowed us to assess timaliid relationships and biogeographic history, discuss analytical issues, and make taxonomic recommendations for the family.

### *Phylogenetic Relationships*

Allowing for substantial differences in taxon sampling, our phylogenetic results broadly corroborate the higher level relationships and taxonomy outlined by Gelang et al. (2009). After removal of the 2 rogue taxa, each of the 3 clades of core babblers received strong support but with one notable difference compared with Gelang et al. (2009). In our phylogeny, the 6 species of *Alcippe* formed a clade strongly supported as a basal lineage in clade A (Fig. 3). Gelang et al. (2009) included a single species of *Alcippe* (*A. poioicephala*) that was strongly supported as a basal lineage of the Pellorneinae (Fig. 3, clade B). Our denser taxon sampling may have influenced this difference, but gene tree–species tree discordance may have played a role as well. Individual gene trees from each study reveal a variety of relationships for *Alcippe*, most with weak support. The support in our phylogeny derives largely from the TGF data, whereas RAG-1 and ODC provide significant support for the relationship in Gelang et al. (2009). Additional markers and species-tree methods (e.g., Maddison and Knowles 2006; Liu 2008) may be required to assess this relationship further.

Babbler family limits are a matter of conjecture. Alström et al. (2006) and Johansson et al. 2008 subsumed all 5 of our clades (A–E) into an expanded Timaliidae, but this recommendation was based on sampling only 10 and 8 species in the family, respectively. Because of the focus on higher level relationships, subfamilies were not identified. Gelang et al. (2009) recommended that the Sylviidae (clade E) be retained as a family and that the Timaliidae be split into 4 subfamilies (our clades A–D). We mostly agree with this decision but would retain the family Zosteropidae for clade D, rather than subsume it as a subfamily of the Timaliidae. Species of the traditional Zosteropidae still constitute the vast majority of the species diversity in the clade. Furthermore, although *Yuhina* is distributed mostly in the Asian mainland, zosteropids are quite unlike the core babblers; most of their diversity lies outside of Asia and is instead centered on oceanic islands of Wallacea and the tropical Pacific.

Of 19 core babbler genera represented in this study by more than one species, 12 were not monophyletic and some, such as *Garrulax* and *Stachyris*, comprised multiple clades. Only 3 genera represented by more than 3 species (*Malacopteron*, *Alcippe*, and *Schoeniparus*) were monophyletic. If not for the recent taxonomic revision of *Alcippe* by Pasquet et al. (2006), *Malacopteron* would have been the only well-sampled, monophyletic genus. These results underscore both the dire state of systematics in even the most well known of groups but also the tremendous ecomorphological diversity and convergence within the babblers.

Four genera previously included in the Timaliidae were strongly supported as belonging to other passerine families. Three of the genera—*Robsonius*, *Micromacronus*, and *Leonardina*—are endemic to the oceanic islands of the Philippines, whereas *Malia* is endemic to Sulawesi. Another Philippine endemic, *Hypocryptadius cinnamomeus*, which had been included in the Zosteropidae, and thus within or close to the babblers, was recently shown to be distantly related to any of these taxa (Moyle et al. 2009; Fjeldsa et al. 2010). Denser outgroup sampling will be required to identify more specifically their relationships.

Several recent taxonomic revisions of babblers have been proposed in the absence of phylogenetic evidence. These revisions can now be compared with a phylogenetic hypothesis for the family, and it is apparent that they do not remedy the poor state of babbler taxonomy. Attempts to break up the large heterogeneous genera often result in multiple paraphyletic groups. For example, the monophyly of *Malacopteron* is sundered by Collar and Robson's (2007) resurrection of a monotypic genus for *Malacopteron* [*Ophrydornis*] *albogulare*. *Malacopteron* is among the few examples in our phylogeny of monophyletic genera, and we recommend that it retains its traditional membership. Collar and Robson (2007) were correct to split the nonmonophyletic *Stachyris* and *Garrulax*, yet their proposed taxonomy yields multiple genera that are still paraphyletic (e.g., *Garrulax*, *Dryonnastes*, *Trochalopteron*, *Stachyris*, and *Stachyridopsis*). Likewise, *Napothera* is not monophyletic but revision based on body size (Collar 2006) produces additional paraphyly.

### *Biogeographic History and Timing of Diversification*

The time estimates and biogeographic reconstruction imply an origin and early diversification of the core babblers in mainland Asia in the mid-Miocene. Because they are derived from 2 secondary calibrations, our date estimates must be considered with caution. Nguembock et al. (2009) estimated the timing of diversification within the babbler genus *Illadopsis* and produced dates broadly younger than our estimates, with confidence intervals that barely overlapped ours. We did not use the date estimates from Nguembock et al. (2009) as secondary calibrations in our study because their estimates are based on secondary calibrations from Barker et al. (2004), one of the sources we also used. It is worrisome, but not surprising, that 2 studies based on the same secondary calibrations would produce disparate divergence times. Nonetheless, most divergence dates within passerine birds have been calibrated with the vicariance date used by Barker et al. (2004) or secondary calibrations therein.

The overall biogeographic pattern is of an origin in mainland Asia with repeated colonization of other regions. Unambiguous recolonization of mainland Asia

from other regions was rare, although the direction of colonization is ambiguous at some nodes. Asia and Sundaland, the 2 regions that currently (or at the Last Glacial Maximum for the islands) have land connections, had the most frequent interchange of lineages. This supports the hypothesis that babblers are most diverse in mainland Asia because the family, and most subclades, originated in Asia.

In birds, much biogeographic analysis in SE Asia has focused at the level of genera or species complexes (e.g., Moyle et al. 2005; Outlaw and Voelker 2008; Reddy 2008; Reddy and Moyle 2011). Other studies included higher level taxa that were not very species rich (Hosner et al. 2010) or focused on subsets of the region, such as the Philippines (Oliveros and Moyle 2010) or the Himalayas (Johansson et al. 2007). Thus, hypotheses about diversification have necessarily been limited to regional aspects and have been unable to address broader patterns of diversification in the Asian tropics, let alone interaction with other regions. Interestingly, a vicariant hypothesis for the generation of diversity and geographic structure that has received increased attention involves the Isthmus of Kra, which separates Sundaland from Southern Asia, the regions of highest babbler diversity, and 2 of the regions in our biogeographic analysis. Marine transgressions are hypothesized to have separated mainland Asia from Sundaland in the Miocene and Pliocene, providing a potential vicariance event and isolation of taxa in the 2 regions (Hughes et al. 2003; Woodruff 2003).

The hypothesis that marine transgressions across the Isthmus of Kra during the Miocene and Pliocene were the vicariance event that differentiated much of the Sunda and Indochinese biotas is not supported by our data. Ambiguous area reconstructions at some internal nodes preclude identification of all Asia/Sunda splits, but we can identify several unambiguous relationships and compare them with ages of marine transgressions. Several Sunda species are clearly derived from mainland Asian relatives (e.g., *G. mitratus*, *G. palliatus*, *A. brunneicauda*, *Pomatorhinus montanus*, and *Stachyris rufifrons*), yet their estimated divergence times span 1.2–7.0 Ma, and several are nonoverlapping. The origin of the genus *Malacopteron* (10.8–15.0 Ma) and the split between the clades containing *Stachyris nigriceps* and *Pomatorhinus hypoleucos* (7.6–10.8 Ma) also represent fairly clear disjunctions between Asia and Sundaland. Thus, biogeographic patterns potentially caused by vicariance at the Isthmus of Kra span 1.2–15.0 Ma, and we can conclude that little, if any, of the geographic structure was caused by a single vicariant event at the Isthmus of Kra.

The isthmus is now a narrow corridor of land approximately 70 km across in places, but at the last glacial maximum the connection between Indochina and Sundaland was greater than 1000 km across. Furthermore, climate and forest cover changes in the Pleistocene altered the distribution of suitable habitat for forest dwelling species. Refined interpretation of sea level change in the Neogene indicates that the isthmus was never breached in the past 10 million years, and faunal turnover in the region is best explained by the cycle of habitat expansion and contraction in the Plio-Pleistocene (Woodruff and Turner 2009). Marine transgressions at the isthmus have been used to calibrate the timing of diversification (Fuchs et al. 2006, 2008) and the rate of molecular evolution (Weir and Schluter 2008) in birds, but the accuracy and precisions of such calibrations seems questionable.

Babblers colonized Africa twice, leading to moderately diverse radiations. Both colonization events are inferred to have originated from mainland Asia but at different times. The wet-forest adapted *Illadopsis* are inferred to have colonized Africa from 10.0 to 14.1 Ma, whereas the more dry-adapted and open country genus *Turdoides* is inferred to have colonized Africa from 6.4 to 9.9 Ma. Although the specific dates are open to interpretation, it is notable that the confidence intervals do not overlap and thus it is unlikely that the 2 events were linked to the same climate/earth history events. The sequence of colonization events makes intuitive sense considering that southern Asia, the putative colonization route, experienced increased seasonal aridity in the Late Miocene (Molnar 2005; Lu et al. 2010; Molnar et al. 2010) accompanied by expansion of more open habitats (Barry et al. 1985). Indeed, *Turdoides* species currently inhabit drier parts of southern Asia and the Middle East, whereas most of the closest relatives of *Illadopsis* are currently restricted to the wet forests of Southeast Asia and Sundaland.

A surprising finding of this study is that most Philippine babblers are not babblers at all. These results add to previous findings (Cibois et al. 2002; Moyle et al. 2009) that removed Philippine members of *Stachyris* from the family. The result is that the oceanic islands of the Philippines only host 2 species of babblers (*P. mindanensis* and *M. striaticeps*) and can be considered a peripheral region in terms of biogeographic history of the family. Further work is required to identify the affinities of several of these Philippine taxa (in preparation).

### *Taxonomic Recommendations*

We recommend the following taxonomic arrangement for the Timaliidae based on the results from this study, Gelang et al. (2009), Cibois (2003), and Pasquet et al. (2006). Species level taxonomy follows Clements (2007). Species following a genus name in square brackets have been moved from that genus.

FAMILY Timaliidae
SUBFAMILY Timaliinae
*Timalia* (*pileata*)
*Mixornis* ([*Macronus*] *gularis*, *flavicollis*, *kelleyi*)
*Dumetia* (*hyperythra*)
*Rhopocichla* (*atriceps*)
*Macronus* (*striaticeps*, *ptilosus*)
*Cyanoderma* ([*Stachyris*] *chrysaeum*, *erythropterum*, *melanothorax*, *pyrrhops*, *ruficeps*, *ambiguum*, *rufifrons*)
*Spelaeornis* (*caudatus*, *badeigularis*, *troglodytoides*, *formosus*, *chocolatinus*, *longicaudatus*)
*Pomatorhinus* (*ferruginosus*, *ochraceiceps*, *ruficollis*, *horsfieldii*, *schisticeps*, *montanus*, [*Xiphirhynchus*] *superciliaris*)

*Megapomatorhinus* ([*Pomatorhinus*] *hypoleucos*, *erythrocnemis*, *erythrogenys*, *swinhoei*)

*Stachyris* (*grammiceps*, *nigricollis*, *maculata*, *nigriceps*, *poliocephala*, *leucotis*, *thoracica*, *oglei*, *striolata*, *rodolphei*, *herberti*, *nonggangensis*, [*Sphenocichla*] *humei*)

SUBFAMILY Pellorneinae

*Malacopteron* (*palawanense*, *magnirostre*, *affine*, *cinereum*, *magnum*, *albogulare*)

*Gampsorhynchus* (*rufulus*)

*Schoeniparus* ([*Alcippe*] *cinereus*, *castaneceps*, *rufogularis*, *brunneus*, *dubius*)

*Illadopsis* (*fulvescens*, *rufipennis*, *pyrrhoptera*, *cleaveri*, *albipectus*, *rufescens*, *puveli*, [*Ptyrticus*] *turdina*)

*Pellorneum* (*ruficeps*, *capistratum*, *fuscocapillus*, *palustre*, *albiventre*, *tickelli*, *pyrrogenys*, [*Malacocincla*] *malaccense*, *cinereiceps*, [*Trichastoma*] *rostratum*, *celebense*, *bicolor*)

*Kenopia* (*striata*)

*Napothera* (*epilepidota*, [*Jabouilleia*] *danjoui*, *naungmungensis*, [*Rimator*] *malacoptila*)

*Ptilocichla* (*leucogrammica*, *mindanensis*, *falcata*)

*Turdinus* ([*Malacocincla*] *abbotti*, *sepiarius*, *perspicillatus*, [*Napothera*] *macrodactylus*, *rufipectus*, *atrigularis*, *marmoratus*, *crispifrons*, *brevicaudatus*, *crassus*)

*Graminicola* (*bengalensis*)

SUBFAMILY Leiothrichinae

*Alcippe* (*variegaticeps*, *ludlowi*, *brunneicauda*, *poioicephala*, *morrisonia*, *pyrrhoptera*, *peracensis*, *nipalensis*, *grotei*)

*Grammatoptila* ([*Garrulax*] *striata*)

*Cutia* (*nipalensis*)

*Turdoides* (*nipalensis*, *altirostris*, *caudata*, *earlei*, *gularis*, *longirostris*, *malcolmi*, *squamiceps*, *fulva*, *aylmeri*, *rubiginosa*, *subrufa*, *striata*, *rufescens*, *affinis*, *reinwardtii*, *tenebrosa*, *sharpie*, *hartlaubii*, *melanops*, *squamulata*, *leucopygia*, *bicolor*, *hypoleuca*, *hindei*, *leucocephala*, *plebejus*, *jardineii*, *gymnogenys*, [*Kupeornis*] *gilberti*, *rufocincta*, *chapini*, [*Phyllanthus*] *atripennis*)

*Garrulax* (*cinereifrons*, *palliatus*, *rufifrons*, *perspicillatus*, *leucolophus*, *monileger*, *lugubris*, *strepitans*, *milleti*, *maesi*, *merulinus*, *canorus*)

*Ianthocincla* ([*Garrulax*] *sukatschewi*, *cineracea*, *rufogularis*, *konkakinhensis*, *ocellata*, *lunulata*, *bieti*, *maxima*, *pectoralis*, *albogularis*, *ruficollis*, *nuchalis*, *chinensis*, *vassali*, *galbana*, *delesserti*, *gularis*, *davidi*, *caerulata*, *poecilorhyncha*, *mitrata*, *sannio*, [*Babax*] *lanceolata*, *waddelli*, *koslowi*)

*Trochalopteron* ([*Garrulax*] *cachinnans*, *jerdoni*, *lineatum*, *virgatum*, *subunicolor*, *austeni*, *squamatum*, *elliotii*, *variegatum*, *henrici*, *affine*, *morrisonianum*, *erythrocephalum*, *ngoclinhensis*, *yersini*, *formosum*, *milnei*)

*Heterophasia* (*capistrata*, *gracilis*, *melanoleuca*, *desgodinsi*, *auricularis*, *pulchella*, *picaoides*)

*Leiothrix* (*argentauris*, *lutea*)

*Minla* (*ignotincta*, [*Heterophasia*] *annectans*)

*Crocias* (*langbianis*, *albonotatus*)

*Liocichla* (*omeiensis*, *bugunorum*, *steerii*, *phoenicea*)

*Actinodura* (*sodangorum*, *nipalensis*, *waldeni*, *souliei*, *morrisoniana*, *egertoni*, *ramsayi*, [*Minla*] *cyanouroptera*, *strigula*)

*Megapomatorhinus*.—Among the genus names used in the past for the group/members of the group now newly separated from *Pomatorhinus* based on molecular-genetic markers, none is available according to the Code (ICZN 1999): *Orthorhinus* Blyth 1844: 124 is preoccupied by *Orthorhinus* Schönherr 1825, Coleoptera; *Erythrogenys* E. C. S. Baker 1930, is preoccupied by *Erythrogenys* Brandt 1841, itself a *nomen emendatum* of Gould's *Erythrogonys*. Hodgson's (1836, Asiatic Researches vol. 20: p. 180) use of the name *Erythrogenys* is without a proper genus description and the original description in the paper refers to a new species only; thus also this name is not available. We therefore formally establish here *Megapomatorhinus* gen. nov., diagnosed by its general appearance and proportions like *Pomatorhinus* babblers but generally larger, and in adult birds a curved bill roughly as long as the head, upperparts olive brown to brown, white underparts gradually becoming rusty or brown toward the vent, on breast and/or on flanks striped/dotted light to dark brown/umber, white supercilium lacking or, if present, thin and not reaching distally in front of the eyes, sexes alike; the type species is *Orthorhinus hypoleucos* Blyth 1844; molecular-genetically studied material: AMNH DOT5531, AMNH DOT5179, BMNH 2000.5.22, KUNHM 6715. The name acknowledges the similarity to species of *Pomatorhinus*, but also the large, heavy-bodied, and large-billed nature of species in the named genus.

## Supplementary Material

Supplementary material, including data files and/or online-only appendices, can be found in the Dryad data repository (doi:10.5061/dryad.100jc764).

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## APPENDIX

TABLE A1. List of samples used in the study

| Genus | Species | Institution | Sample # | Locality | ND2 | ND3 | Cyt b | TGF | Fib | Musk |
|---|---|---|---|---|---|---|---|---|---|---|
| *Actinodura* | *egertoni* | KUNHM | 15098 | Myanmar | JN826457 | JN826715 | JN826988 | JN826213 | JN825968 | JN825741 |
| *Actinodura* | *egertoni* | KUNHM | 15186 | Myanmar | JN826459 | JN826716 | JN826990 | JN826215 | JN825969 | JN825742 |
| *Actinodura* | *morrisoniana* | AMNH | DOT5203 | Taiwan | JN826460 | JN826717 | JN826991 | JN826216 | JN825970 | — |
| *Actinodura* | *morrisoniana* | AMNH | DOT5226 | Taiwan | JN826461 | JN826718 | JN826992 | JN826217 | JN825971 | — |
| *Actinodura* | *nipalensis* | AMNH | DOT5594 | Nepal | JN826462 | JN826719 | JN826993 | JN826218 | — | — |
| *Actinodura* | *nipalensis* | AMNH | DOT5636 | Nepal | JN826463 | JN826720 | JN826994 | — | — | — |
| *Actinodura* | *ramsayi* | AMNH | DOT2629 | Vietnam | JN826464 | JN826721 | JN826995 | JN826219 | JN825972 | JN825743 |
| *Actinodura* | *ramsayi* | AMNH | DOT2641 | Vietnam | JN826465 | JN826722 | JN826996 | JN826220 | JN825973 | JN825744 |
| *Actinodura* | *waldeni* | CAS | 95491 | China | JN826466 | JN826723 | JN826997 | JN826221 | JN825974 | JN825745 |
| *Actinodura* | *waldeni* | CAS | 95906 | China | JN826467 | JN826724 | JN826998 | JN826222 | JN825975 | JN825746 |
| *Alcippe* | *brunneicauda* | KUNHM | 12380 | Borneo | JN826468 | JN826725 | JN826999 | JN826223 | JN825976 | JN825747 |
| *Alcippe* | *brunneicauda* | KUNHM | 17766 | Borneo | JN826469 | JN826726 | JN827000 | JN826224 | JN825977 | JN825748 |
| *Alcippe* | *grotei* | AMNH | DOT12309 | Vietnam | JN826470 | JN826728 | JN827002 | JN826226 | JN825978 | JN825749 |
| *Alcippe* | *grotei* | AMNH | DOT10810 | Vietnam | EF154809 | JN826727 | JN827001 | JN826225 | JN825979 | JN825750 |
| *Alcippe* | *morrisonia* | AMNH | DOT5142 | Taiwan | JN826471 | JN826729 | JN827003 | JN826227 | JN825980 | — |
| *Alcippe* | *morrisonia* | KUNHM | 6662 | China | JN826472 | JN826730 | JN827004 | JN826228 | JN825981 | JN825751 |
| *Alcippe* | *nipalensis* | KUNHM | 15244 | Myanmar | JN826473 | JN826731 | JN827005 | JN826229 | JN825982 | JN825752 |
| *Alcippe* | *peracensis* | AMNH | DOT12245 | Vietnam | JN826474 | JN826733 | JN827007 | JN826231 | JN825984 | JN825753 |
| *Alcippe* | *peracensis* | AMNH | DOT10740 | Vietnam | EF154811 | JN826732 | JN827006 | JN826230 | JN825983 | JN825754 |
| *Alcippe* | *poioicephala* | USNM | 5606 | Myanmar | JN826475 | JN826734 | JN827008 | JN826232 | JN825985 | JN825755 |
| *Alcippe* | *poioicephala* | USNM | 6060 | Myanmar | JN826476 | JN826735 | JN827009 | JN826233 | JN825986 | JN825756 |
| *Babax* | *lanceolata* | KUNHM | 11238 | China | JN826478 | JN826737 | JN827011 | JN826234 | JN825987 | JN825758 |
| *Chrysomma* | *poecilotis* | FMNH | 68881* | China | JN826481 | JN826740 | — | JN826237 | — | — |
| *Chrysomma* | *sinense* | USNM | 6172 | Myanmar | JN826483 | JN826742 | JN827013 | JN826239 | JN825990 | — |
| *Chrysomma* | *sinense* | USNM | 6101 | Myanmar | JN826482 | JN826741 | JN827012 | JN826238 | — | JN825761 |
| *Cutia* | *nipalensis* | FMNH | 218230* | Nepal | JN826487 | JN826746 | — | JN826242 | — | — |
| *Cutia* | *nipalensis* | FMNH | 275829* | Nepal | JN826488 | JN826747 | — | JN826243 | — | — |
| *Cutia* | *nipalensis* | USNM | 475768* | Vietnam | JN826489 | JN826748 | — | JN826244 | — | — |
| *Dumetia* | *hyperythra* | AMNH | 388637* | India | JN826490 | JN826749 | JN827014 | — | — | — |
| *Fulvetta* | *cinereiceps* | AMNH | DOT5181 | Taiwan | JN826493 | JN826752 | JN827017 | JN826247 | JN825993 | JN825764 |
| *Fulvetta* | *vinipectus* | AMNH | DOT5655 | Nepal | JN826494 | JN826753 | JN827018 | JN826248 | JN825994 | JN825765 |
| *Fulvetta* | *vinipectus* | CAS | 95904 | China | JN826495 | JN826754 | JN827019 | JN826249 | JN825995 | JN825766 |
| *Gampsorhynchus* | *rufulus* | USNM | 534967* | Thailand | JN826496 | JN826755 | — | JN826250 | — | — |
| *Gampsorhynchus* | *rufulus* | USNM | 584529* | India | JN826497 | JN826756 | — | JN826251 | — | — |
| *Garrulax* | *affinis* | KUNHM | 15099 | Myanmar | JN826499 | JN826758 | JN827021 | — | JN825996 | JN825767 |
| *Garrulax* | *affinis* | AMNH | DOT5582 | Nepal | JN826498 | JN826757 | JN827020 | — | — | — |
| *Garrulax* | *albogularis* | AMNH | DOT5626 | Nepal | JN826500 | JN826759 | JN827022 | JN826252 | JN825997 | JN825768 |
| *Garrulax* | *canorus* | KUNHM | 10389 | China | JN826501 | JN826760 | JN827023 | JN826253 | JN825998 | JN825769 |
| *Garrulax* | *chinensis* | KUNHM | 10366 | China | JN826502 | JN826761 | JN827024 | JN826254 | JN825999 | JN825770 |
| *Garrulax* | *cineraceus* | KUNHM | 6725 | China | JN826504 | JN826763 | JN827026 | — | JN826001 | JN825772 |
| *Garrulax* | *cineraceus* | KUNHM | 11043 | China | JN826503 | JN826762 | JN827025 | JN826255 | JN826000 | JN825771 |
| *Garrulax* | *erythrocephalus* | USNM | B5628 | Myanmar | JN826506 | JN826765 | JN827028 | — | — | — |
| *Garrulax* | *erythrocephalus* | KUNHM | 15193 | Myanmar | JN826505 | JN826764 | JN827027 | JN826256 | JN826002 | JN825773 |
| *Garrulax* | *formosus* | AMNH | DOT9336 | captive | JN826507 | JN826766 | JN827029 | JN826257 | JN826003 | JN825774 |
| *Garrulax* | *leucolophus* | KUNHM | 15247 | Myanmar | JN826508 | JN826767 | JN827030 | JN826258 | JN826004 | JN825775 |
| *Garrulax* | *lineatus* | FMNH | 347872 | Pakistan | JN826509 | JN826768 | JN827031 | JN826259 | JN826005 | JN825776 |
| *Garrulax* | *lineatus* | FMNH | 347873 | Pakistan | JN826510 | JN826769 | JN827032 | JN826260 | JN826006 | JN825777 |
| *Garrulax* | *maesi* | AMNH | DOT10968 | Vietnam | JN826512 | JN826771 | JN827034 | — | — | — |

*(Continued)*

TABLE A1. *(continued)*

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Garrulax* | *maesi* | KUNHM | 10152 | China | JN826511 | JN826770 | JN827033 | JN826261 | JN826007 | JN825778 |
| *Garrulax* | *merulinus* | AMNH | DOT10975 | Vietnam | JN826514 | JN826773 | JN827036 | JN826263 | JN826009 | — |
| *Garrulax* | *merulinus* | KUNHM | 15190 | Myanmar | JN826513 | JN826772 | JN827035 | JN826262 | JN826008 | JN825779 |
| *Garrulax* | *milleti* | AMNH | DOT10756 | Vietnam | JN826515 | JN826774 | JN827037 | JN826264 | JN826010 | — |
| *Garrulax* | *milnei* | KUNHM | 11104 | China | JN826516 | JN826775 | JN827038 | JN826265 | JN826011 | JN825780 |
| *Garrulax* | *milnei* | KUNHM | 15101 | Myanmar | JN826517 | JN826776 | JN827039 | JN826266 | JN826012 | JN825781 |
| *Garrulax* | *mitratus* | KUNHM | 17728 | Borneo | JN826518 | JN826777 | JN827040 | JN826267 | JN826013 | JN825782 |
| *Garrulax* | *mitratus* | LSUMNS | B36460 | Borneo | FJ460776 | FJ460844 | JN827041 | FJ460912 | JN826014 | JN825783 |
| *Garrulax* | *monileger* | USNM | 5596 | Myanmar | JN826519 | JN826778 | JN827042 | JN826268 | JN826015 | — |
| *Garrulax* | *nuchalis* | USNM | 15312 | Myanmar | JN826520 | JN826779 | JN827043 | JN826269 | JN826016 | JN825784 |
| *Garrulax* | *nuchalis* | USNM | 15315 | Myanmar | JN826521 | JN826780 | JN827044 | JN826270 | JN826017 | JN825785 |
| *Garrulax* | *ocellatus* | AMNH | DOT5651 | Nepal | JN826522 | JN826781 | JN827045 | JN826271 | JN826018 | JN825786 |
| *Garrulax* | *ocellatus* | KUNHM | 11342 | China | JN826523 | JN826782 | JN827046 | JN826272 | JN826019 | JN825787 |
| *Garrulax* | *palliatus* | KUNHM | 17732 | Borneo | JN826524 | JN826783 | JN827047 | JN826273 | JN826020 | — |
| *Garrulax* | *pectoralis* | USNM | 3537 | Myanmar | JN826526 | JN826785 | JN827049 | JN826275 | JN826022 | JN825789 |
| *Garrulax* | *pectoralis* | KUNHM | 11125 | China | JN826525 | JN826784 | JN827048 | JN826274 | JN826021 | JN825788 |
| *Garrulax* | *poecilorhynchus sannio* | KUNHM | 11128 | China | JN826527 | JN826786 | JN827050 | JN826276 | JN826023 | JN825790 |
| *Garrulax* | *sannio* | KUNHM | 11172 | China | JN826528 | JN826787 | JN827051 | JN826277 | JN826024 | JN825791 |
| *Garrulax* | *squamatus* | KUNHM | 15191 | Myanmar | JN826529 | JN826788 | JN827052 | JN826278 | JN826025 | JN825792 |
| *Garrulax* | *striatus* | USNM | 15221 | Myanmar | JN826530 | JN826789 | JN827053 | JN826279 | JN826026 | — |
| *Garrulax* | *striatus* | USNM | 15255 | Myanmar | JN826531 | JN826790 | JN827054 | JN826280 | JN826027 | JN825793 |
| *Garrulax* | *subunicolor* | USNM | 15264 | Myanmar | JN826532 | JN826791 | JN827055 | JN826281 | — | — |
| *Garrulax* | *variegatum* | AMNH | DOT5537 | Nepal | JN826533 | JN826792 | JN827056 | — | — | — |
| *Garrulax* | *virgatus* | USNM | 5627 | Myanmar | JN826534 | JN826793 | JN827057 | JN826282 | JN826028 | — |
| *Heterophasia* | *annectens* | USNM | 336017* | Thailand | JN826486 | JN826745 | | — | — | — |
| *Heterophasia* | *auricularis* | AMNH | DOT5177 | Taiwan | JN826535 | JN826794 | JN827058 | JN826283 | JN826029 | JN825794 |
| *Heterophasia* | *capistrata* | AMNH | DOT5553 | Nepal | JN826536 | JN826795 | JN827059 | — | — | — |
| *Heterophasia* | *capistrata* | AMNH | DOT5573 | Nepal | JN826537 | JN826796 | JN827060 | JN826284 | JN826030 | JN825795 |
| *Heterophasia* | *gracilis* | USNM | 5683 | Myanmar | JN826538 | JN826797 | JN827061 | JN826285 | JN826031 | JN825796 |
| *Heterophasia* | *gracilis* | USNM | 5685 | Myanmar | JN826539 | JN826798 | JN827062 | JN826286 | JN826032 | JN825797 |
| *Heterophasia* | *melanoleuca* | AMNH | DOT10973 | Vietnam | JN826540 | JN826799 | JN827063 | JN826287 | JN826033 | JN825798 |
| *Heterophasia* | *melanoleuca* | CAS | 95600 | China | JN826541 | JN826800 | JN827064 | JN826288 | JN826034 | JN825799 |
| *Heterophasia* | *picaoides* | USNM | 15174 | Myanmar | JN826542 | JN826801 | JN827065 | JN826289 | JN826035 | JN825800 |
| *Heterophasia* | *pulchella* | USNM | 15254 | Myanmar | JN826543 | JN826802 | JN827066 | JN826290 | JN826036 | — |
| *Heterophasia* | *pulchella* | KUNHM | 15166 | Myanmar | JN826544 | JN826803 | JN827067 | JN826291 | JN826037 | JN825801 |
| *Horizorhinus* | *dohrni* | Genbank | | | FJ976085 | — | FJ976085 | — | — | — |
| *Illadopsis* | *albipectus* | FMNH | 357284 | Congo | JN826546 | JN826805 | JN827069 | JN826292 | JN826039 | JN825802 |
| *Illadopsis* | *albipectus* | FMNH | 385068 | Uganda | JN826547 | JN826806 | JN827070 | JN826293 | JN826040 | — |
| *Illadopsis* | *cleaveri* | KUNHM | 8483 | Eq. Guinea | JN826549 | JN826808 | JN827072 | JN826295 | JN826042 | JN825804 |
| *Illadopsis* | *cleaveri* | KUNHM | 15688 | Ghana | JN826548 | JN826807 | JN827071 | JN826294 | JN826041 | JN825803 |
| *Illadopsis* | *fulvescens* | KUNHM | 19886 | Sierra Leone | JN826550 | JN826809 | JN827073 | JN826296 | JN826043 | JN825805 |
| *Illadopsis* | *fulvescens* | FMNH | 391756 | Uganda | JN826551 | JN826810 | JN827074 | JN826297 | JN826044 | — |
| *Illadopsis* | *puveli* | KUNHM | 19887 | Sierra Leone | JN826552 | JN826811 | JN827075 | JN826298 | JN826045 | JN825806 |
| *Illadopsis* | *pyrrhoptera* | FMNH | 346417 | Burundi | JN826553 | JN826812 | JN827076 | JN826299 | JN826046 | — |
| *Illadopsis* | *pyrrhoptera* | FMNH | 385058 | Uganda | JN826554 | JN826813 | JN827077 | JN826300 | JN826047 | JN825807 |
| *Illadopsis* | *rufescens* | KUNHM | 19729 | Sierra Leone | JN826555 | JN826814 | JN827078 | JN826301 | JN826048 | JN825808 |
| *Illadopsis* | *rufescens* | KUNHM | 19773 | Sierra Leone | JN826556 | JN826815 | JN827079 | JN826302 | JN826049 | JN825809 |
| *Illadopsis* | *rufipennis* | KUNHM | 8577 | Eq. Guinea | JN826558 | JN826817 | JN827081 | JN826304 | JN826051 | JN825811 |
| *Illadopsis* | *rufipennis* | KUNHM | 15583 | Ghana | JN826557 | JN826816 | JN827080 | JN826303 | JN826050 | JN825810 |
| *Jabouilleia* | *danjou* | AMNH | DOT10947 | Vietnam | HQ529039 | JN826818 | HQ529138 | JN826305 | JN826052 | JN825812 |

TABLE A1. *(continued)*

| Genus | Species | Institution | Sample # | Locality | ND2 | ND3 | Cyt b | TGF | Fib | Musk |
|---|---|---|---|---|---|---|---|---|---|---|
| *Kenopia* | *striata* | LSUMNS | B36395 | Borneo | FJ460775 | FJ460843 | JN827082 | FJ460911 | JN826053 | JN825813 |
| *Kupeornis* | *chapini* | AMNH | 348502* | Congo | JN826559 | JN826819 | — | — | — | — |
| *Leiothrix* | *argentauris* | AMNH | DOT2623 | Vietnam | JN826561 | JN826821 | JN827084 | JN826307 | JN826055 | JN825815 |
| *Leiothrix* | *argentauris* | KUNHM | 15203 | Myanmar | JN826560 | JN826820 | JN827083 | JN826306 | JN826054 | JN825814 |
| *Leiothrix* | *lutea* | AMNH | DOT6507 | Vietnam | JN826562 | JN826822 | JN827085 | JN826308 | JN826056 | JN825816 |
| *Leiothrix* | *lutea* | KUNHM | 6724 | China | JN826563 | JN826823 | JN827086 | JN826309 | JN826057 | JN825817 |
| *Leonardina* | *woodi* | KUNHM | 19115 | Philippines | JN826564 | JN826824 | JN827087 | JN826310 | JN826058 | JN825818 |
| *Liocichla* | *phoenicea* | KUNHM | 10078 | China | — | JN826825 | JN827088 | JN826311 | JN826059 | JN825819 |
| *Liocichla* | *phoenicea* | KUNHM | 15195 | Myanmar | JN826565 | JN826826 | — | JN826312 | JN826060 | JN825820 |
| *Liocichla* | *steerii* | AMNH | DOT5178 | Taiwan | JN826566 | JN826827 | JN827089 | JN826313 | JN826061 | JN825821 |
| *Liocichla* | *steerii* | AMNH | DOT5198 | Taiwan | JN826567 | JN826828 | JN827090 | JN826314 | JN826062 | — |
| *Lioparus* | *chrysotis* | KUNHM | 11078 | China | JN826568 | JN826829 | JN827091 | JN826315 | JN826063 | JN825822 |
| *Lioptilus* | *nigrocapillus* | UWBM | 53158 | South Africa | JN826569 | JN826830 | JN827092 | JN826316 | JN826064 | — |
| *Lioptilus* | *nigrocapillus* | UWBM | 71300 | South Africa | JN826570 | JN826831 | JN827093 | JN826317 | JN826065 | JN825823 |
| *Macronus* | *gularis* | KUNHM | 17726 | Borneo | JN826571 | JN826832 | JN827095 | JN826318 | JN826067 | JN825825 |
| *Macronus* | *gularis* | AMNH | DOT10805 | Vietnam | JN826572 | JN826833 | JN827096 | JN826319 | JN826068 | JN825826 |
| *Macronus* | *ptilosus* | KUNHM | 12325 | Borneo | JN826573 | JN826834 | JN827097 | JN826320 | JN826069 | JN825827 |
| *Macronus* | *ptilosus* | LSUMNS | B36391 | Borneo | FJ460774 | FJ460842 | JN827098 | FJ460910 | JN826070 | JN825828 |
| *Macronus* | *striaticeps* | KUNHM | 14130 | Philippines | JN826574 | JN826835 | JN827099 | JN826321 | JN826071 | JN825829 |
| *Macronus* | *striaticeps* | FMNH | 357464 | Philippines | HQ529041 | JN826836 | HQ529140 | JN826322 | JN826072 | JN825830 |
| *Malacocincla* | *abbotti* | USNM | 2131 | Myanmar | JN826575 | JN826837 | JN827100 | JN826323 | JN826073 | — |
| *Malacocincla* | *cinereiceps* | KUNHM | 12693 | Palawan | JN826576 | JN826838 | JN827101 | JN826324 | JN826074 | JN825831 |
| *Malacocincla* | *malaccensis* | KUNHM | 12341 | Borneo | JN826577 | JN826839 | JN827102 | JN826325 | JN826075 | JN825832 |
| *Malacocincla* | *malaccensis* | KUNHM | 17776 | Borneo | JN826578 | JN826840 | JN827103 | JN826326 | JN826076 | JN825833 |
| *Malacocincla* | *sepiaria* | LSUMNS | B47108 | Borneo | JN826579 | JN826841 | JN827104 | JN826327 | JN826077 | JN825834 |
| *Malacopteron* | *affine* | KUNHM | 12383 | Borneo | JN826580 | JN826842 | JN827105 | JN826328 | JN826078 | JN825835 |
| *Malacopteron* | *albogulare* | LSUMNS | B47244 | Borneo | JN826581 | JN826843 | JN827106 | JN826329 | JN826079 | JN825836 |
| *Malacopteron* | *albogulare* | LSUMNS | B50348 | Borneo | JN826582 | JN826844 | JN827107 | JN826330 | JN826080 | JN825837 |
| *Malacopteron* | *cinereum* | KUNHM | 12320 | Borneo | JN826583 | JN826845 | JN827108 | JN826331 | JN826081 | JN825838 |
| *Malacopteron* | *cinereum* | AMNH | DOT10778 | Vietnam | JN826584 | JN826846 | JN827109 | JN826332 | JN826082 | JN825839 |
| *Malacopteron* | *magnirostre* | KUNHM | 12358 | Borneo | JN826585 | JN826847 | JN827110 | JN826333 | JN826083 | JN825840 |
| *Malacopteron* | *magnirostre* | LSUMNS | B36421 | Borneo | FJ460778 | FJ460846 | JN827111 | FJ460914 | JN826084 | JN825841 |
| *Malacopteron* | *magnum* | KUNHM | 17770 | Borneo | JN826586 | JN826848 | JN827112 | JN826334 | JN826085 | JN825842 |
| *Malacopteron* | *magnum* | LSUMNS | B38590 | Borneo | JN826587 | JN826849 | JN827113 | JN826335 | — | — |
| *Malacopteron* | *palawanense* | KUNHM | 12600 | Palawan | JN826588 | JN826850 | JN827114 | JN826336 | JN826086 | JN825843 |
| *Malia* | *grata* | AMNH | 299482* | Sulawesi | JN826589 | JN826851 | — | — | — | — |
| *Micromacronus* | *sordidus* | USNM | 579793* | Philippines | JN826592 | JN826854 | — | JN826339 | — | — |
| *Minla* | *cyanouroptera* | KUNHM | 11087 | China | JN826593 | JN826855 | JN827117 | JN826340 | JN826089 | JN825846 |
| *Minla* | *cyanouroptera* | KUNHM | 11281 | China | JN826594 | JN826856 | JN827118 | JN826341 | JN826090 | JN825847 |
| *Minla* | *ignotincta* | KUNHM | 11346 | China | JN826595 | JN826857 | JN827119 | JN826342 | JN826091 | JN825848 |
| *Minla* | *strigula* | KUNHM | 15184 | Myanmar | JN826596 | JN826858 | JN827120 | JN826343 | JN826092 | JN825849 |
| *Napothera* | *brevicaudata* | AMNH | DOT2639 | Vietnam | HQ529042 | JN826861 | HQ529141 | JN826345 | JN826095 | JN825851 |
| *Napothera* | *brevicaudata* | KUNHM | 10351 | China | JN826598 | JN826860 | JN827122 | JN826344 | JN826094 | JN825850 |
| *Napothera* | *crassa* | KUNHM | 17805 | Borneo | JN826599 | JN826862 | JN827123 | JN826346 | JN826096 | JN825852 |
| *Napothera* | *crassa* | LSUMNS | B36469 | Borneo | FJ460773 | FJ460841 | JN827124 | FJ460909 | JN826097 | — |
| *Napothera* | *crispifrons* | FMNH | 75755* | Vietnam | JN826600 | JN826863 | — | — | — | — |
| *Napothera* | *epilepidota* | LSUMNS | B52626 | Borneo | JN826601 | JN826864 | JN827125 | JN826347 | JN826098 | JN825853 |

*(Continued)*

TABLE A1. *(continued)*

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Pellorneum* | *albiventre* | KUNHM | 10145 | China | JN826613 | JN826876 | JN827138 | JN826358 | JN826111 | JN825864 |
| *Pellorneum* | *capristratum* | LSUMNS | B36430 | Borneo | FJ460772 | FJ460840 | JN827139 | FJ460908 | JN826112 | JN825865 |
| *Pellorneum* | *pyrrogenys* | KUNHM | 17798 | Borneo | JN826614 | JN826877 | JN827140 | JN826359 | — | JN825866 |
| *Pellorneum* | *ruficeps* | USNM | 2155 | Myanmar | JN826615 | JN826878 | JN827141 | JN826360 | JN826113 | JN825867 |
| *Pellorneum* | *ruficeps* | USNM | 6133 | Myanmar | JN826616 | JN826879 | JN827142 | JN826361 | JN826114 | JN825868 |
| *Pellorneum* | *tickelli* | KUNHM | 10186 | China | JN826617 | JN826880 | JN827143 | JN826362 | JN826115 | JN825869 |
| *Pellorneum* | *tickelli* | KUNHM | 15242 | Myanmar | JN826618 | JN826881 | JN827144 | JN826363 | JN826116 | — |
| *Phyllanthus* | *atripennis* | AMNH | DOT2033 | Liberia | JN826620 | JN826883 | JN827146 | JN826365 | JN826118 | — |
| *Phyllanthus* | *atripennis* | KUNHM | 19806 | Sierra Leone | JN826619 | JN826882 | JN827145 | JN826364 | JN826117 | JN825870 |
| *Pomatorhinus* | *erythrogenys* | AMNH | DOT5531 | Nepal | HQ529044 | JN826889 | HQ529143 | JN826371 | JN826123 | JN825876 |
| *Pomatorhinus* | *erythrogenys* | AMNH | DOT5179 | Taiwan | HQ529043 | JN826888 | HQ529142 | JN826370 | JN826122 | JN825875 |
| *Pomatorhinus* | *ferruginosus* | KUNHM | 15146 | Myanmar | JN826625 | JN826890 | JN827151 | JN826372 | JN826124 | JN825877 |
| *Pomatorhinus* | *ferruginosus* | AMNH | DOT10777 | Vietnam | HQ529057 | JN826891 | HQ529156 | JN826373 | JN826125 | JN825878 |
| *Pomatorhinus* | *ferruginosus* | KUNHM | 15090 | Myanmar | JN826627 | JN826895 | JN827153 | JN826376 | JN826127 | JN825882 |
| *Pomatorhinus* | *ferruginosus* | KUNHM | 15241 | Myanmar | JN826628 | JN826896 | JN827154 | JN826377 | JN826128 | — |
| *Pomatorhinus* | *horsfieldi* | AMNH | 344452* | India | HQ529073 | — | HQ529172 | — | — | — |
| *Pomatorhinus* | *hypoleucos* | BMNH | 2000.5.22 | Cambodia | HQ529069 | JN826892 | HQ529168 | — | — | JN825879 |
| *Pomatorhinus* | *montanus* | KUNHM | 17781 | Borneo | JN826626 | JN826893 | JN827152 | JN826374 | JN826126 | JN825880 |
| *Pomatorhinus* | *montanus* | LSUMNS | B47063 | Borneo | HQ529075 | JN826894 | HQ529174 | JN826375 | — | JN825881 |
| *Pomatorhinus* | *ruficollis* | KUNHM | 10299 | China | JN826629 | JN826897 | JN827155 | JN826378 | JN826129 | JN825883 |
| *Pomatorhinus* | *ruficollis* | KUNHM | 15144 | Myanmar | JN826630 | JN826898 | JN827156 | JN826379 | — | JN825884 |
| *Pomatorhinus* | *schisticeps* | MNHN | 6.73# | Thailand | HQ529126 | JN826900 | HQ529225 | — | JN826130 | JN825886 |
| *Pomatorhinus* | *schisticeps* | USNM | B2103 | Myanmar | HQ529127 | JN826899 | HQ529226 | — | — | JN825885 |
| *Pomatorhinus* | *swinhoei* | KUNHM | 6715 | China | JN826631 | JN826901 | JN827157 | JN826380 | JN826131 | JN825887 |
| *Ptilocichla* | *falcata* | KUNHM | 12816 | Palawan | JN826634 | JN826904 | JN827160 | JN826383 | JN826134 | JN825890 |
| *Ptilocichla* | *leucogrammica* | LSUMNS | B50350 | Borneo | JN826635 | JN826905 | JN827161 | JN826384 | JN826135 | JN825891 |
| *Ptilocichla* | *mindanensis* | KUNHM | 18187 | Philippines | JN826636 | JN826906 | JN827162 | JN826385 | JN826136 | JN825892 |
| *Ptilocichla* | *mindanensis* | KUNHM | 19070 | Philippines | JN826637 | JN826907 | JN827163 | JN826386 | JN826137 | JN825893 |
| *Ptyrticus* | *turdinus* | FMNH | 298643* | Sudan | JN826638 | JN826908 | — | — | — | — |
| *Ptyrticus* | *turdinus* | USNM | 583567* | Angola | JN826639 | JN826909 | — | — | — | — |
| *Rhopocichla* | *atriceps* | AMNH | 344476* | India | JN826641 | JN826911 | JN827165 | — | — | — |
| *Rimator* | *malacoptilus* | USNM | 15203 | Myanmar | JN826643 | JN826913 | JN827166 | JN826388 | JN826139 | — |
| *Rimator* | *malacoptilus* | USNM | 15204 | Myanmar | JN826644 | JN826914 | JN827167 | JN826389 | JN826140 | — |
| *Robsonius* | *rabori* | FMNH | 433008 | Luzon | JN826645 | JN826915 | JN827168 | JN826390 | JN826141 | JN825895 |
| *Schoeniparus* | *brunnea* | KUNHM | 6655 | China | JN826647 | JN826917 | — | JN826392 | JN826143 | JN825897 |
| *Schoeniparus* | *castaneceps* | KUNHM | 15156 | Myanmar | JN826648 | JN826918 | JN827170 | JN826393 | JN826144 | JN825898 |
| *Schoeniparus* | *cinerea* | KUNHM | 15152 | Myanmar | JN826649 | JN826919 | JN827171 | JN826394 | JN826145 | JN825899 |
| *Schoeniparus* | *cinerea* | USNM | 15213 | Myanmar | JN826650 | JN826920 | JN827172 | JN826395 | JN826146 | JN825900 |
| *Schoeniparus* | *dubia* | KUNHM | 11340 | China | JN826651 | JN826921 | JN827173 | JN826396 | JN826147 | JN825901 |
| *Schoeniparus* | *dubia* | KUNHM | 15160 | Myanmar | JN826652 | JN826922 | JN827174 | JN826397 | JN826148 | JN825902 |
| *Schoeniparus* | *dubia* | USNM | 5623 | Myanmar | JN826646 | JN826916 | JN827169 | JN826391 | JN826142 | JN825896 |
| *Schoeniparus* | *rufogularis* | AMNH | DOT10750 | Vietnam | JN826654 | JN826924 | JN827176 | JN826399 | JN826150 | JN825904 |
| *Schoeniparus* | *rufogularis* | USNM | 15184 | Myanmar | JN826653 | JN826923 | JN827175 | JN826398 | JN826149 | JN825903 |
| *Spelaeornis* | *chocolatinus* | KUNHM | 15105 | Myanmar | JN826655 | JN826925 | JN827177 | JN826400 | JN826151 | JN825905 |
| *Spelaeornis* | *chocolatinus* | KUNHM | 15199 | Myanmar | JN826656 | JN826926 | JN827178 | JN826401 | JN826152 | JN825906 |
| *Spelaeornis* | *troglodytoide* | KUNHM | 15107 | Myanmar | JN826657 | JN826927 | JN827179 | JN826402 | JN826153 | JN825907 |
| *Spelaeornis* | *troglodytoides* | KUNHM | 15108 | Myanmar | JN826658 | JN826928 | JN827180 | JN826403 | JN826154 | JN825908 |
| *Sphenocichla* | *humei* | KUNHM | 15201 | Myanmar | JN826659 | JN826929 | JN827181 | JN826404 | JN826155 | JN825909 |
| *Sphenocichla* | *humei* | KUNHM | 15202 | Myanmar | JN826660 | JN826930 | JN827182 | JN826405 | JN826156 | JN825910 |

*(Continued)*

TABLE A1. *(continued)*

| Genus | Species | Institution | Sample # | Locality | ND2 | ND3 | Cyt b | TGF | Fib | Musk |
|---|---|---|---|---|---|---|---|---|---|---|
| *Stachyris* | *ambigua* | USNM | 6152 | Myanmar | JN826661 | JN826931 | JN827183 | JN826406 | JN826157 | JN825911 |
| *Stachyris* | *ambigua* | USNM | 6183 | Myanmar | JN826662 | JN826932 | JN827184 | JN826407 | — | JN825912 |
| *Stachyris* | *chrysaea* | KUNHM | 15096 | Myanmar | JN826664 | JN826934 | JN827186 | JN826408 | JN826159 | JN825914 |
| *Stachyris* | *chrysaea* | KUNHM | 15240 | Myanmar | JN826665 | JN826935 | JN827187 | JN826409 | JN826160 | JN825915 |
| *Stachyris* | *erythroptera* | KUNHM | 12327 | Borneo | JN826668 | JN826938 | JN827190 | JN826412 | JN826163 | JN825918 |
| *Stachyris* | *erythroptera* | LSUMNS | B36417 | Borneo | FJ460771 | FJ460839 | JN827191 | FJ460907 | JN826164 | JN825919 |
| *Stachyris* | *grammiceps* | LSUMNS | B45463# | Java | JN826669 | JN826939 | JN827192 | JN826413 | JN826165 | JN825920 |
| *Stachyris* | *leucotis* | LSUMNS | B36340 | Borneo | JN826671 | JN826941 | JN827194 | JN826415 | JN826167 | JN825921 |
| *Stachyris* | *maculata* | LSUMNS | B36423 | Borneo | JN826672 | JN826942 | JN827195 | JN826416 | JN826168 | JN825922 |
| *Stachyris* | *melanothorax* | AMNH | 448000* | Java | HQ529129 | JN826943 | HQ529228 | — | — | — |
| *Stachyris* | *nigriceps* | KUNHM | 10167 | China | JN826673 | JN826944 | JN827196 | JN826417 | JN826169 | JN825923 |
| *Stachyris* | *nigriceps* | LSUMNS | B36288 | Borneo | JN826674 | JN826945 | JN827197 | JN826418 | JN826170 | JN825924 |
| *Stachyris* | *nigricollis* | KUNHM | 12330 | Borneo | JN826675 | JN826946 | JN827198 | JN826419 | JN826171 | JN825925 |
| *Stachyris* | *nigricollis* | LSUMNS | B38564 | Borneo | JN826676 | JN826947 | JN827199 | JN826420 | JN826172 | JN825926 |
| *Stachyris* | *oglei* | KUNHM | 15189 | Myanmar | JN826679 | JN826950 | JN827202 | JN826423 | JN826175 | JN825929 |
| *Stachyris* | *poliocephala* | LSUMNS | B36426 | Borneo | JN826680 | JN826951 | JN827203 | JN826424 | JN826176 | JN825930 |
| *Stachyris* | *poliocephala* | LSUMNS | B47008 | Borneo | JN826681 | JN826952 | JN827204 | JN826425 | JN826177 | — |
| *Stachyris* | *pyrrhops* | AMNH | 778719* | India | HQ529130 | JN826953 | HQ529229 | — | — | — |
| *Stachyris* | *ruficeps* | KUNHM | 6645 | China | JN826683 | JN826955 | JN827206 | JN826427 | JN826179 | JN825932 |
| *Stachyris* | *ruficeps* | KUNHM | 11083 | China | JN826682 | JN826954 | JN827205 | JN826426 | JN826178 | JN825931 |
| *Stachyris* | *rufifrons* | LSUMNS | B36462 | Borneo | JN826684 | JN826956 | JN827207 | JN826428 | JN826180 | JN825933 |
| *Stachyris* | *striolata* | KUNHM | 10003 | China | JN826686 | JN826958 | JN827209 | JN826430 | JN826182 | JN825935 |
| *Stachyris* | *striolata* | KUNHM | 10136 | China | JN826685 | JN826957 | JN827208 | JN826429 | JN826181 | JN825934 |
| *Stachyris* | *thoracica* | AMNH | 589844* | Java | HQ529133 | JN826959 | HQ529232 | — | — | — |
| *Timalia* | *pileata* | FMNH | 236339* | Nepal | — | JN826964 | JN827214 | — | — | — |
| *Timalia* | *pileata* | FMNH | 218211* | Nepal | — | JN826963 | JN827213 | — | — | — |
| *Trichastoma* | *bicolor* | LSUMNS | B36396 | Borneo | JN826690 | JN826965 | JN827215 | JN826434 | JN826186 | JN825939 |
| *Trichastoma* | *celebense* | AMNH | DOT12612 | Sulawesi | JN826691 | JN826966 | JN827216 | JN826435 | JN826187 | JN825940 |
| *Trichastoma* | *rostratum* | KUNHM | 17713 | Borneo | JN826692 | JN826967 | JN827217 | JN826436 | JN826188 | JN825941 |
| *Turdoides* | *bicolor* | UWBM | 53074 | South Africa | JN826693 | JN826968 | JN827218 | JN826437 | JN826189 | JN825942 |
| *Turdoides* | *bicolor* | UWBM | 70438 | South Africa | JN826694 | JN826969 | JN827219 | JN826438 | JN826190 | JN825943 |
| *Turdoides* | *gularis* | USNM | 5705 | Myanmar | JN826695 | JN826970 | JN827220 | JN826439 | JN826191 | JN825944 |
| *Turdoides* | *gularis* | USNM | 5712 | Myanmar | JN826696 | JN826971 | JN827221 | JN826440 | JN826192 | JN825945 |
| *Turdoides* | *jardineii* | UWBM | 52803 | South Africa | JN826698 | JN826973 | JN827223 | JN826442 | JN826194 | JN825947 |
| *Turdoides* | *jardineii* | FMNH | 455533 | Malawi | JN826697 | JN826972 | JN827222 | JN826441 | JN826193 | JN825946 |
| *Turdoides* | *plebejus* | KUNHM | 20025 | Sierra Leone | JN826699 | JN826974 | JN827224 | JN826443 | JN826195 | JN825948 |
| *Turdoides* | *plebejus* | LSUMNS | B39249 | Ghana | JN826700 | — | JN827225 | JN826444 | JN826196 | JN825949 |
| *Turdoides* | *reinwardtii* | KUNHM | 20055 | Sierra Leone | JN826701 | JN826975 | JN827226 | JN826445 | JN826197 | JN825950 |
| *Turdoides* | *reinwardtii* | FMNH | 396646 | Ghana | JN826702 | JN826976 | JN827227 | JN826446 | — | JN825951 |
| *Xiphirhynchus* | *superciliaris* | KUNHM | 15092 | Myanmar | JN826703 | JN826977 | JN827228 | JN826447 | JN826198 | JN825952 |
| *Xiphirhynchus* | *superciliaris* | CAS | 95887 | China | JN826704 | JN826978 | JN827229 | JN826448 | JN826199 | JN825953 |
| Zosteropidae | | | | | | | | | | |
| *Lophozosterops* | *squamiceps* | AMNH | DOT12549 | Sulawesi | FJ460793 | FJ460861 | JN827094 | FJ460930 | JN826066 | JN825824 |
| *Oculocincta* | *squamifrons* | LSUMNS | B51197 | Borneo | FJ460795 | FJ460863 | JN827126 | FJ460932 | JN826099 | JN825854 |
| *Sterrhoptilus* | *dennistouni* | USNM | 3621 | Philippines | JN826663 | JN826933 | JN827185 | — | JN826158 | JN825913 |
| *Sterrhoptilus* | *dennistouni* | KUNHM | 20186 | Philippines | JN826666 | JN826936 | JN827188 | JN826410 | JN826161 | JN825916 |
| *Sterrhoptilus* | *dennistouni* | KUNHM | 20225 | Philippines | JN826667 | JN826937 | JN827189 | JN826411 | JN826162 | JN825917 |
| *Sterrhoptilus* | *nigrocapitatus* | KUNHM | 18040 | Philippines | JN826677 | JN826948 | JN827200 | JN826421 | JN826173 | JN825927 |
| *Sterrhoptilus* | *nigrocapitatus* | FMNH | 449755 | Philippines | JN826678 | JN826949 | JN827201 | JN826422 | JN826174 | JN825928 |

*(Continued)*

TABLE A1. *(continued)*

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|---|---|---|---|---|---|---|---|---|---|---|
| *Yuhina* | *bakeri* | USNM | 631884* | Myanmar | JN826705 | JN826979 | — | JN826449 | — | — |
| *Yuhina* | *brunneiceps* | AMNH | DOT5153 | Taiwan | JN826706 | JN826980 | JN827230 | JN826450 | JN826200 | JN825954 |
| *Yuhina* | *castaniceps* | KUNHM | 10367 | China | JN826707 | JN826981 | JN827231 | — | JN826201 | JN825955 |
| *Yuhina* | *castaniceps* | KUNHM | 13784 | China | JN826708 | JN826982 | JN827232 | JN826451 | JN826202 | JN825956 |
| *Yuhina* | *diademata* | KUNHM | 11118 | China | FJ460781 | FJ460849 | JN827233 | FJ460917 | JN826203 | — |
| *Yuhina* | *everetii* | KUNHM | 17756 | Borneo | JN826709 | JN826983 | JN827234 | JN826452 | JN826204 | JN825957 |
| *Yuhina* | *flavicollis* | KUNHM | 15170 | Myanmar | JN826710 | JN826984 | JN827235 | JN826453 | JN826205 | JN825958 |
| *Yuhina* | *nigrimenta* | KUNHM | 9997 | China | JN826712 | JN826986 | JN827237 | JN826455 | JN826207 | JN825960 |
| *Yuhina* | *nigrimenta* | KUNHM | 11150 | China | JN826711 | JN826985 | JN827236 | JN826454 | JN826206 | JN825959 |
| *Yuhina* | *occipitalis* | KUNHM | 15177 | Myanmar | JN826713 | JN826987 | JN827238 | JN826456 | JN826208 | JN825961 |
| *Zosterops* | *atricapilla* | LSUMNS | B36444 | Borneo | FJ460802 | FJ460870 | JN827239 | FJ460939 | JN826209 | JN825962 |
| *Zosterops* | *lateralis* | KUNHM | 6094 | Australia | FJ460814 | FJ460882 | JN827240 | FJ460951 | — | JN825963 |
| *Zosterops* | *maderaspatanus* | FMNH | 345980 | Madagascar | FJ460813 | FJ460881 | JN827241 | FJ460950 | JN826210 | JN825964 |
| *Zosterops* | *nigrorum* | FMNH | 432997 | Philippines | FJ46080 | FJ460876 | JN827242 | FJ460945 | JN826211 | JN825965 |
| *Zosterops* | *ugiensis* | KUNHM | 12803 | Solomon Is. | FJ460836 | FJ460903 | JN827243 | FJ460972 | JN826212 | JN825966 |
| *Zosterornis* | *whiteheadi* | FMNH | 429219 | Philippines | JN826688 | JN826961 | JN827211 | JN826432 | JN826184 | JN825937 |
| *Zosterornis* | *whiteheadi* | KUNHM | 18001 | Philippines | JN826687 | JN826960 | JN827210 | JN826431 | JN826183 | JN825936 |
| *Zosterornis* | *hypogrammicus* | FMNH | 455063 | Philippines | JN826670 | JN826940 | JN827193 | JN826414 | JN826166 | — |
| Outgroups | | | | | | | | | | |
| *Acrocephalus* | *australis* | KUNHM | 19430 | Solomon Islands | JN826458 | JN826714 | JN826989 | JN826214 | JN825967 | JN825740 |
| *Alophoixus* | *bres* | KUNHM | 17701 | Borneo | GU112681 | GU112727 | JN827010 | GU112589 | — | JN825757 |
| *Chamaea* | *fasciata* | SDSU | 2188 | USA | JN826479 | JN826738 | DQ109822 | JN826235 | JN825988 | JN825759 |
| *Chamaea* | *fasciata* | SDSU | 2220 | USA | JN826480 | JN826739 | DQ109846 | JN826236 | JN825989 | JN825760 |
| *Conostoma* | *oemodium* | FMNH | 297082* | Nepal | JN826484 | JN826743 | — | JN826240 | — | — |
| *Conostoma* | *oemodium* | FMNH | 297083* | Nepal | JN826485 | JN826744 | — | JN826241 | — | — |
| *Erpornis* | *zantholeuca* | KUNHM | 10015 | China | JN826491 | JN826750 | JN827015 | JN826245 | JN825991 | JN825762 |
| *Erpornis* | *zantholeuca* | KUNHM | 13848 | China | JN826492 | JN826751 | JN827016 | JN826246 | JN825992 | JN825763 |
| *Hypocryptadius* | *cinnamomeus* | KUNHM | 19117 | Philiippines | JN826545 | JN826804 | JN827068 | — | JN826038 | — |
| *Megalurus* | *timoriensis* | KUNHM | 16461 | New Guinea | JN826590 | JN826852 | JN827115 | JN826337 | JN826087 | JN825844 |
| *Melocichla* | *mentalis* | KUNHM | 15406 | Ghana | JN826591 | JN826853 | JN827116 | JN826338 | JN826088 | JN825845 |
| *Myzornis* | *pyrrhoura* | KUNHM | 15109 | Myanmar | JN826597 | JN826859 | JN827121 | — | JN826093 | — |
| *Orthotomus* | *sericeus* | KUNHM | 17792 | Borneo | JN826602 | JN826865 | JN827127 | JN826348 | JN826100 | JN825855 |
| *Paradoxornis* | *alphonsianus* | KUNHM | 11096 | China | JN826603 | JN826866 | JN827128 | JN826349 | JN826101 | JN825856 |
| *Paradoxornis* | *fulvifrons* | CAS | 95908 | China | JN826605 | JN826868 | JN827130 | JN826351 | JN826103 | JN825858 |
| *Paradoxornis* | *fulvifrons* | CAS | 95884 | China | JN826604 | JN826867 | JN827129 | JN826350 | JN826102 | JN825857 |
| *Paradoxornis* | *gularis* | KUNHM | 6706 | China | JN826607 | JN826870 | JN827132 | — | JN826105 | JN825860 |
| *Paradoxornis* | *gularis* | KUNHM | 11037 | China | JN826606 | JN826869 | JN827131 | JN826352 | JN826104 | JN825859 |
| *Paradoxornis* | *nipalensis* | AMNH | DOT5190 | Taiwan | JN826608 | JN826871 | JN827133 | JN826353 | JN826106 | JN825861 |
| *Paradoxornis* | *ruficeps* | KUNHM | 15116 | Myanmar | JN826609 | JN826872 | JN827134 | JN826354 | JN826107 | — |
| *Paradoxornis* | *verreauxi* | KUNHM | 11041 | China | JN826610 | JN826873 | JN827135 | JN826355 | JN826108 | JN825862 |
| *Paradoxornis* | *webbianus* | KUNHM | 6740 | China | JN826612 | JN826875 | JN827137 | JN826357 | JN826110 | — |
| *Paradoxornis* | *webbianus* | KUNHM | 13794 | China | JN826611 | JN826874 | JN827136 | JN826356 | JN826109 | JN825863 |
| *Phylloscopus* | *cebuensis* | KUNHM | 20262 | Philippines | JN826621 | JN826884 | JN827147 | JN826366 | JN826119 | JN825871 |
| *Pnoepyga* | *albiventer* | KUNHM | 15196 | Myanmar | JN826623 | JN826886 | JN827149 | JN826368 | JN826120 | JN825873 |
| *Pnoepyga* | *albiventer* | AMNH | DOT5558 | Nepal | JN826622 | JN826885 | JN827148 | JN826367 | — | JN825872 |
| *Pnoepyga* | *pusilla* | KUNHM | 15250 | Myanmar | JN826624 | JN826887 | JN827150 | JN826369 | JN826121 | JN825874 |
| *Pseudoalcippe* | *atriceps* | FMNH | 355697 | Uganda | JN826632 | JN826902 | JN827158 | JN826381 | JN826132 | JN825888 |
| *Pseudoalcippe* | *atriceps* | FMNH | 358056 | Burundi | JN826633 | JN826903 | JN827159 | JN826382 | JN826133 | JN825889 |
| *Pycnonotus* | *plumosus* | KUNHM | 12667 | Philippines | JN826640 | JN826910 | JN827164 | JN826387 | JN826138 | JN825894 |
| *Rhopophilus* | *pekinensis* | USNM | 526697* | | JN826642 | JN826912 | — | — | — | — |
| *Sylvia* | *borin* | KUNHM | 15471 | Ghana | JN826689 | JN826962 | JN827212 | JN826433 | JN826185 | JN825938 |

Notes: Ancient DNA samples denoted by "*" and unvouchered blood samples denoted by "#." Institutional abbreviations: AMNH, American Museum of Natural History; BMNH, Natural History Museum (Tring, UK); CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; KUNHM, University of Kansas Natural History Museum; LSUMNS, Louisiana State University Museum of Natural Science; MNHN, Muséum National d'Histoire Naturelle; SDSU, San Diego State University; USNM, United States National Museum; UWBM, University of Washington Burke Museum.