

## 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 corvid 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)  $\beta$ 2, 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 Iennov 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 erythrogeus*) 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  $\sim 0.05$  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  $\sim 3$  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

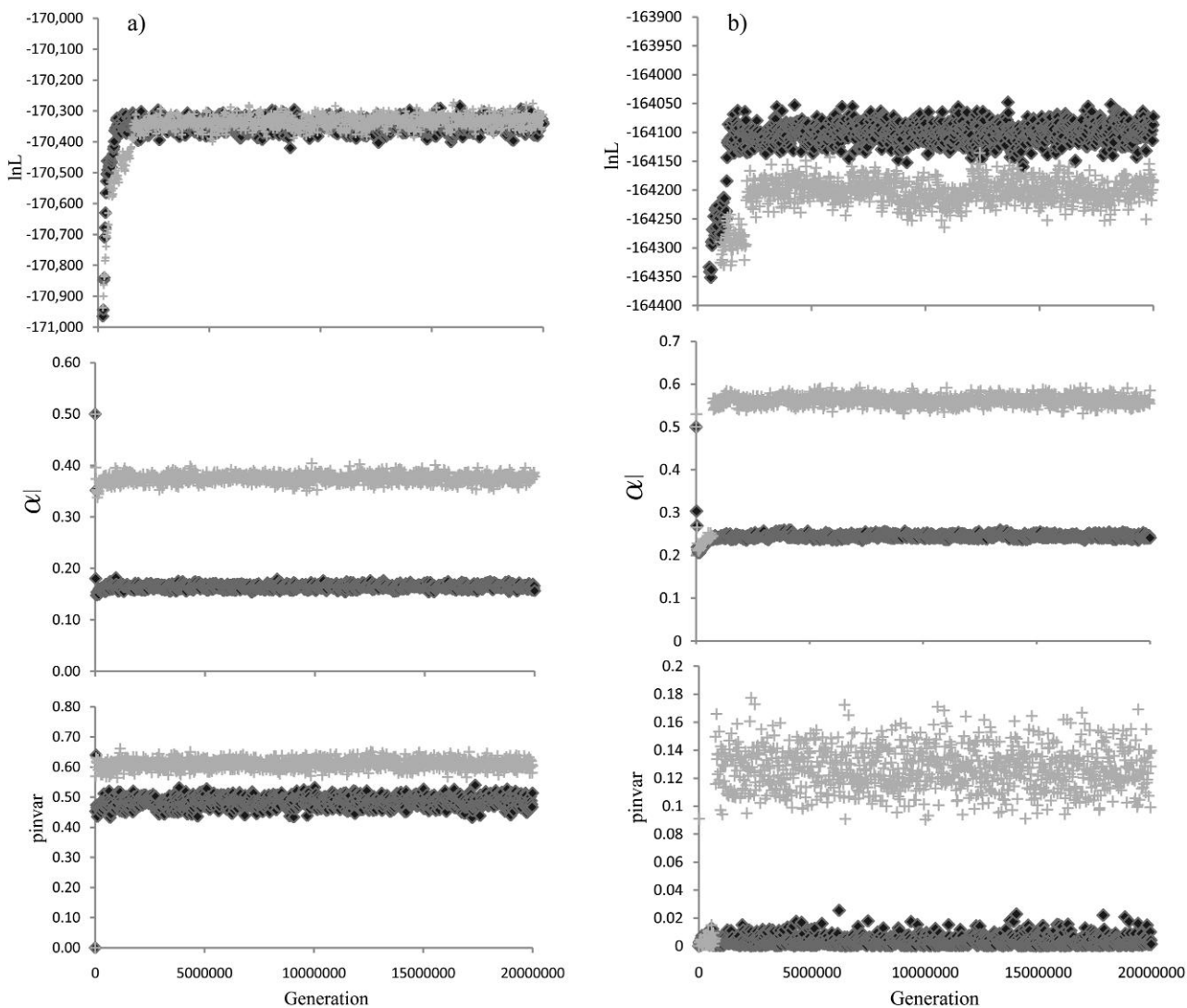


FIGURE 1. Likelihoods and parameter estimates for second codon positions (a) and the MUSK intron (b) from 20-million generation preliminary Bayesian runs. From top to bottom, log likelihood,  $\alpha$  parameter for gamma-distributed rates among sites, and proportion of invariant sites are plotted against 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

<i>N</i> <sup>a</sup>	Description	lnL	Free parameters	AIC <sup>b</sup>	BIC <sup>c</sup>
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	<b>327157.215</b>
12	3 codon positions × 3 mtgenes, 3 nuc	−163107.7703	119	<b>326453.5406</b>	327221.0906

<sup>a</sup>Number of partitions, each using GTR + G.  
<sup>b</sup>Calculated as 2\*(parameters - lnL).  
<sup>c</sup>Calculated as (-2lnL) + (parameters × ln base pairs).



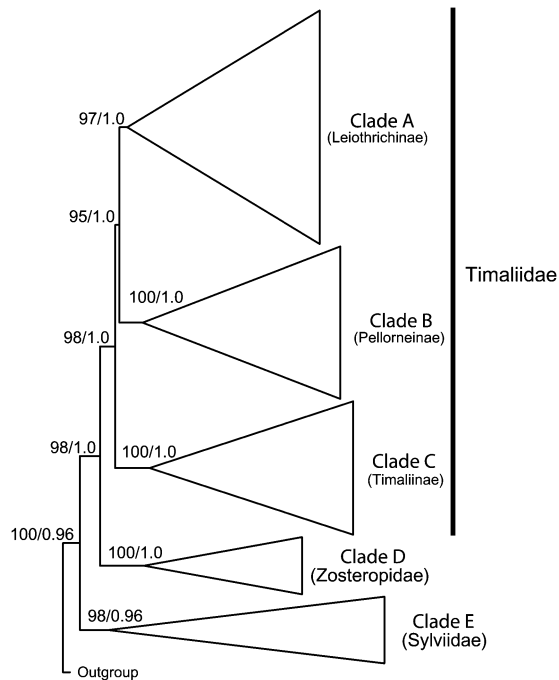


FIGURE 2. Summary of higher level relationships for babblers based on ML analysis of the combined data set with 12 partitions. Numbers by nodes refer to ML bootstrap support/Bayesian posterior probability.

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 *Kupearis* 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 *Malacocincla* (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 (*Ptilochila 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

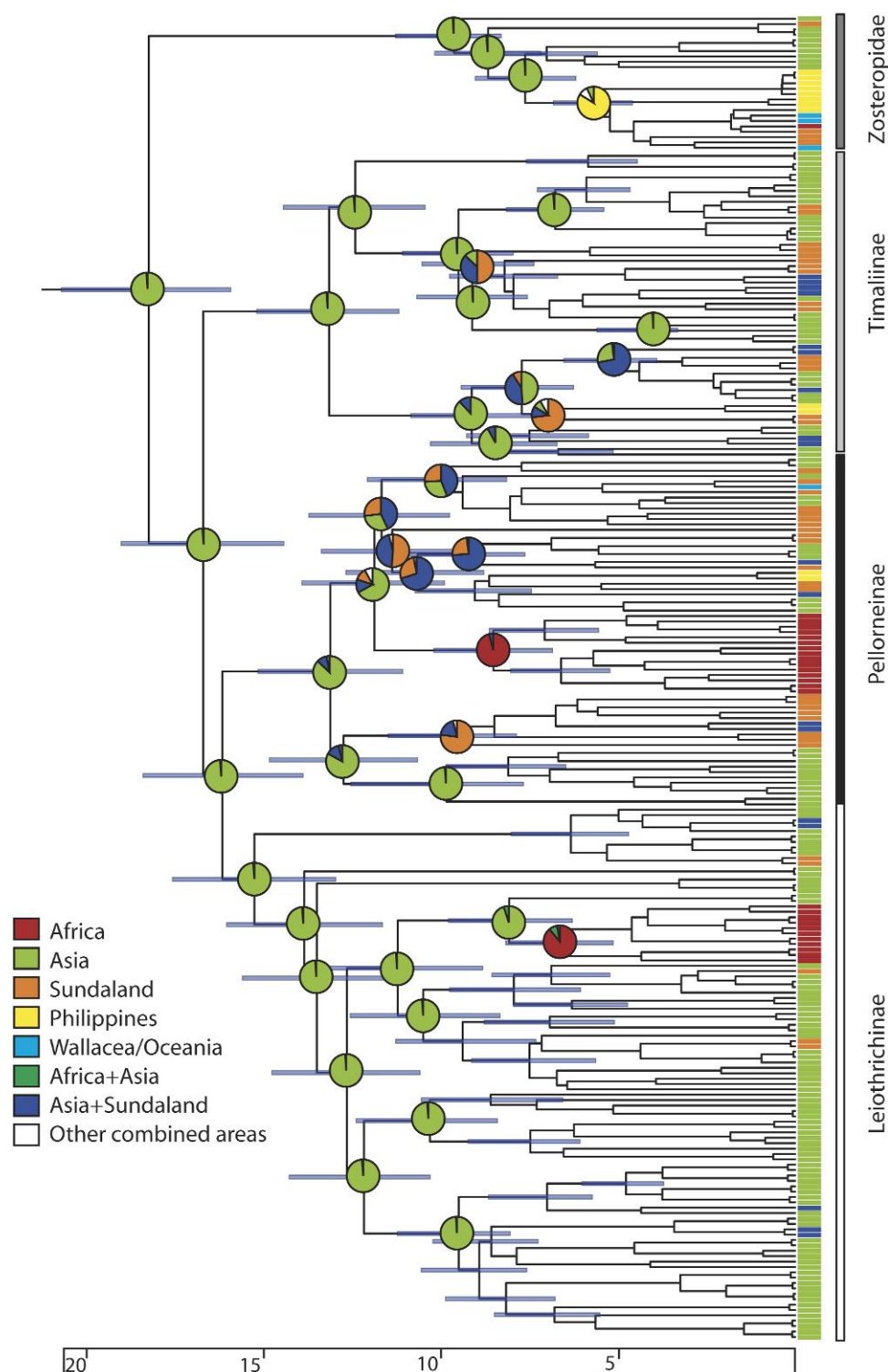


FIGURE 4. Temporal and geographic aspects of babbler diversification. The time scale was produced with a relaxed clock method and 2 calibrations (see text for details). Bars on nodes indicate 95% confidence interval for age estimates. The bar at the bottom gives the absolute time scale in millions of 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](http://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*] *albugulare*. *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*, *Dryonastes*, *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*, *erythropteron*, *melanothorax*, *pyrrhops*, *ruficeps*, *ambiguum*, *rufifrons*)

##### *Spelaeornis* (*caudatus*, *badeigularis*, *trogodytoides*, *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*, *castaneiceps*, *rufogularis*, *brunneus*, *dubius*)

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

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

*Kenopia* (*striata*)

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

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

*Turdinus* ([*Malacocincla*] *abbotti*, *sepiarius*, *perspicillatus*, [*Napothera*] *macrodactylus*, *rufipectus*, *atriangularis*, *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*, *palliatu*, *rufifrons*, *perspicillatus*, *leucolophus*, *monileger*, *lugubris*, *strepitans*, *milleti*, *maesi*, *merulinus*, *canorus*)

*Ianthocincla* ([*Garrulax*] *sukatschewi*, *cineracea*, *rufogularis*, *konkakinensis*, *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*, *elliottii*, *variegatum*, *henrici*, *affine*, *morrisonianum*, *erythrocephalum*, *ngoclinhensis*, *yersini*, *formosum*, *milnei*)

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

*Leiothrix* (*argentaurea*, *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 *Erythrogenys*. 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
<i>Actinodura</i>	<i>egertoni</i>	KUNHM	15098	Myanmar	JN826457	JN826715	JN826988	JN826213	JN825968	JN825741
<i>Actinodura</i>	<i>egertoni</i>	KUNHM	15186	Myanmar	JN826459	JN826716	JN826990	JN826215	JN825969	JN825742
<i>Actinodura</i>	<i>morrisoniana</i>	AMNH	DOT5203	Taiwan	JN826460	JN826717	JN826991	JN826216	JN825970	—
<i>Actinodura</i>	<i>morrisoniana</i>	AMNH	DOT5226	Taiwan	JN826461	JN826718	JN826992	JN826217	JN825971	—
<i>Actinodura</i>	<i>nipalensis</i>	AMNH	DOT15594	Nepal	JN826462	JN826719	JN826993	JN826218	—	—
<i>Actinodura</i>	<i>nipalensis</i>	AMNH	DOT15636	Nepal	JN826463	JN826720	JN826994	—	—	—
<i>Actinodura</i>	<i>ramsayi</i>	AMNH	DOT2629	Vietnam	JN826464	JN826721	JN826995	JN826219	JN825972	JN825743
<i>Actinodura</i>	<i>ramsayi</i>	AMNH	DOT2641	Vietnam	JN826465	JN826722	JN826996	JN826220	JN825973	JN825744
<i>Actinodura</i>	<i>waldeni</i>	CAS	95491	China	JN826466	JN826723	JN826997	JN826221	JN825974	JN825745
<i>Actinodura</i>	<i>waldeni</i>	CAS	95906	China	JN826467	JN826724	JN826998	JN826222	JN825975	JN825746
<i>Alcippe</i>	<i>brunneicauda</i>	KUNHM	12380	Borneo	JN826468	JN826725	JN826999	JN826223	JN825976	JN825747
<i>Alcippe</i>	<i>brunneicauda</i>	KUNHM	17766	Borneo	JN826469	JN826726	JN827000	JN826224	JN825977	JN825748
<i>Alcippe</i>	<i>grotei</i>	AMNH	DOT12309	Vietnam	JN826470	JN826728	JN827002	JN826226	JN825978	JN825749
<i>Alcippe</i>	<i>grotei</i>	AMNH	DOT10810	Vietnam	EF154809	JN826727	JN827001	JN826225	JN825979	JN825750
<i>Alcippe</i>	<i>morrisonia</i>	AMNH	DOT15142	Taiwan	JN826471	JN826729	JN827003	JN826227	JN825980	—
<i>Alcippe</i>	<i>morrisonia</i>	KUNHM	6662	China	JN826472	JN826730	JN827004	JN826228	JN825981	JN825751
<i>Alcippe</i>	<i>nipalensis</i>	KUNHM	15244	Myanmar	JN826473	JN826731	JN827005	JN826229	JN825982	JN825752
<i>Alcippe</i>	<i>peracensis</i>	AMNH	DOT12245	Vietnam	JN826474	JN826733	JN827007	JN826231	JN825984	JN825753
<i>Alcippe</i>	<i>peracensis</i>	AMNH	DOT10740	Vietnam	EF154811	JN826732	JN827006	JN826230	JN825983	JN825754
<i>Alcippe</i>	<i>poioicephala</i>	USNM	5606	Myanmar	JN826475	JN826734	JN827008	JN826232	JN825985	JN825755
<i>Alcippe</i>	<i>poioicephala</i>	USNM	6060	Myanmar	JN826476	JN826735	JN827009	JN826233	JN825986	JN825756
<i>Babax</i>	<i>lanceolata</i>	KUNHM	11238	China	JN826478	JN826737	JN827011	JN826234	JN825987	JN825758
<i>Chrysomma</i>	<i>pocilotis</i>	FMNH	68881*	China	JN826481	JN826740	—	JN826237	—	—
<i>Chrysomma</i>	<i>sinense</i>	USNM	6172	Myanmar	JN826482	JN826742	JN827013	JN826238	JN825990	JN825761
<i>Chrysomma</i>	<i>sinense</i>	USNM	6101	Myanmar	JN826483	JN826741	JN827012	JN826239	—	—
<i>Cutia</i>	<i>nipalensis</i>	FMNH	218230*	Nepal	JN826487	JN826746	—	JN826242	—	—
<i>Cutia</i>	<i>nipalensis</i>	FMNH	275829*	Nepal	JN826488	JN826747	—	JN826243	—	—
<i>Cutia</i>	<i>nipalensis</i>	USNM	475768*	Vietnam	JN826489	JN826748	—	JN826244	—	—
<i>Dumetia</i>	<i>hyperythra</i>	AMNH	388637*	India	JN826490	JN826749	JN827014	—	JN825993	JN825764
<i>Fulvetta</i>	<i>cinereiceps</i>	AMNH	DOT15181	Taiwan	JN826493	JN826752	JN827017	JN826247	JN825994	JN825765
<i>Fulvetta</i>	<i>cinereiceps</i>	AMNH	DOT15655	Nepal	JN826494	JN826753	JN827018	JN826248	JN825995	JN825766
<i>Fulvetta</i>	<i>vinipectus</i>	CAS	95904	China	JN826495	JN826754	JN827019	JN826249	—	—
<i>Gampsorhynchus</i>	<i>rufulus</i>	USNM	534967*	Thailand	JN826496	JN826755	—	JN826250	—	—
<i>Gampsorhynchus</i>	<i>rufulus</i>	USNM	584529*	India	JN826497	JN826756	—	JN826251	—	—
<i>Garrulax</i>	<i>affinis</i>	KUNHM	15099	Myanmar	JN826499	JN826758	JN827021	JN826256	JN825996	JN825767
<i>Garrulax</i>	<i>affinis</i>	AMNH	DOT15582	Nepal	JN826498	JN826757	JN827020	—	JN825997	JN825768
<i>Garrulax</i>	<i>albogularis</i>	AMNH	DOT15626	Nepal	JN826500	JN826759	JN827022	JN826252	JN825998	JN825769
<i>Garrulax</i>	<i>canorus</i>	KUNHM	10389	China	JN826501	JN826760	JN827023	JN826253	JN825999	JN825770
<i>Garrulax</i>	<i>chinensis</i>	KUNHM	10366	China	JN826502	JN826761	JN827024	JN826254	JN826001	JN825771
<i>Garrulax</i>	<i>cineraceus</i>	KUNHM	6725	China	JN826504	JN826763	JN827026	—	JN826000	—
<i>Garrulax</i>	<i>cineraceus</i>	KUNHM	11043	China	JN826503	JN826762	JN827025	JN826255	—	—
<i>Garrulax</i>	<i>erythrocephalus</i>	USNM	B5628	Myanmar	JN826506	JN826765	JN827028	JN826256	JN826002	JN825773
<i>Garrulax</i>	<i>erythrocephalus</i>	KUNHM	15193	Myanmar	JN826505	JN826766	JN827027	JN826257	JN826003	JN825774
<i>Garrulax</i>	<i>formosus</i>	AMNH	DOT19336	captive	JN826507	JN826767	JN827029	JN826258	JN826004	JN825775
<i>Garrulax</i>	<i>leucolophus</i>	KUNHM	15247	Myanmar	JN826508	JN826768	JN827030	JN826259	JN826005	JN825776
<i>Garrulax</i>	<i>lineatus</i>	FMNH	347872	Pakistan	JN826509	JN826769	JN827031	JN826260	JN826006	JN825777
<i>Garrulax</i>	<i>lineatus</i>	FMNH	347873	Pakistan	JN826510	JN826771	JN827032	—	—	—
<i>Garrulax</i>	<i>maesi</i>	AMNH	DOT10968	Vietnam	JN826512	JN826771	JN827034	—	—	—

(Continued)

TABLE A1. (continued)

<i>Garrulax</i>	<i>maesi</i>	KUNHM	10152	China	JN826511	JN826770	JN827033	JN826261	JN826007	JN825778
<i>Garrulax</i>	<i>merulinus</i>	AMNH	DOT10975	Vietnam	JN826514	JN826773	JN827036	JN826263	JN826009	—
<i>Garrulax</i>	<i>merulinus</i>	KUNHM	15190	Myanmar	JN826513	JN826772	JN827035	JN826262	JN826008	JN825779
<i>Garrulax</i>	<i>milloti</i>	AMNH	DOT10756	Vietnam	JN826515	JN826774	JN827037	JN826264	JN826010	—
<i>Garrulax</i>	<i>milnei</i>	KUNHM	11104	China	JN826516	JN826775	JN827038	JN826265	JN826011	JN825780
<i>Garrulax</i>	<i>milnei</i>	KUNHM	15101	Myanmar	JN826517	JN826776	JN827039	JN826266	JN826012	JN825781
<i>Garrulax</i>	<i>mitratus</i>	KUNHM	17728	Borneo	JN826518	JN826777	JN827040	JN826267	JN826013	JN825782
<i>Garrulax</i>	<i>mitratus</i>	LSUMNS	B36460	Borneo	F1460844	F1460844	JN827041	F1460912	JN826014	JN825783
<i>Garrulax</i>	<i>monileger</i>	USNM	5596	Myanmar	JN826519	JN826778	JN827042	JN826268	JN826015	—
<i>Garrulax</i>	<i>nuchalis</i>	USNM	15312	Myanmar	JN826520	JN826779	JN827043	JN826269	JN826016	JN825784
<i>Garrulax</i>	<i>nuchalis</i>	USNM	15315	Myanmar	JN826521	JN826780	JN827044	JN826270	JN826017	JN825785
<i>Garrulax</i>	<i>ocellatus</i>	AMNH	DOT5651	Nepal	JN826522	JN826781	JN827045	JN826271	JN826018	JN825786
<i>Garrulax</i>	<i>ocellatus</i>	KUNHM	11342	China	JN826523	JN826782	JN827046	JN826272	JN826019	JN825787
<i>Garrulax</i>	<i>palliatius</i>	KUNHM	17732	Borneo	JN826524	JN826783	JN827047	JN826273	JN826020	—
<i>Garrulax</i>	<i>pectoralis</i>	USNM	3537	Myanmar	JN826526	JN826785	JN827049	JN826275	JN826021	JN825789
<i>Garrulax</i>	<i>poecilorhynchus</i>	KUNHM	11125	China	JN826528	JN826784	JN827048	JN826274	JN826022	JN825788
<i>Garrulax</i>	<i>poecilorhynchus</i>	KUNHM	11128	China	JN826527	JN826786	JN827050	JN826276	JN826023	JN825790
<i>Garrulax</i>	<i>squameatus</i>	KUNHM	11172	China	JN826528	JN826787	JN827051	JN826277	JN826024	JN825791
<i>Garrulax</i>	<i>striatus</i>	KUNHM	15191	Myanmar	JN826529	JN826788	JN827052	JN826278	JN826025	JN825792
<i>Garrulax</i>	<i>striatus</i>	USNM	15221	Myanmar	JN826530	JN826789	JN827053	JN826279	JN826026	—
<i>Garrulax</i>	<i>striatus</i>	USNM	15255	Myanmar	JN826531	JN826790	JN827054	JN826280	JN826027	JN825793
<i>Garrulax</i>	<i>subunicolor</i>	USNM	15264	Myanmar	JN826532	JN826791	JN827055	JN826281	—	—
<i>Garrulax</i>	<i>variegatum</i>	AMNH	DOT5537	Nepal	JN826533	JN826792	JN827056	—	—	—
<i>Garrulax</i>	<i>virgatus</i>	USNM	5627	Myanmar	JN826534	JN826793	JN827057	JN826282	JN826028	—
<i>Heterophasia</i>	<i>annectens</i>	USNM	336017*	Thailand	JN826486	JN826745	—	—	—	—
<i>Heterophasia</i>	<i>auricularis</i>	AMNH	DOT15177	Taiwan	JN826535	JN826794	JN827058	JN826283	JN826029	JN825794
<i>Heterophasia</i>	<i>capistrata</i>	AMNH	DOT5553	Nepal	JN826536	JN826795	JN827059	—	—	—
<i>Heterophasia</i>	<i>capistrata</i>	AMNH	DOT5553	Nepal	JN826537	JN826796	JN827060	JN826284	JN826030	JN825795
<i>Heterophasia</i>	<i>gracilis</i>	USNM	5683	Myanmar	JN826538	JN826797	JN827061	JN826285	JN826031	JN825796
<i>Heterophasia</i>	<i>gracilis</i>	USNM	5685	Myanmar	JN826539	JN826798	JN827062	JN826286	JN826032	JN825797
<i>Heterophasia</i>	<i>melanoleuca</i>	AMNH	DOT10973	Vietnam	JN826540	JN826799	JN827063	JN826287	JN826033	JN825798
<i>Heterophasia</i>	<i>melanoleuca</i>	CAS	95600	China	JN826541	JN826800	JN827064	JN826288	JN826034	JN825799
<i>Heterophasia</i>	<i>picaoides</i>	USNM	15174	Myanmar	JN826542	JN826801	JN827065	JN826289	JN826035	JN825800
<i>Heterophasia</i>	<i>pulchella</i>	USNM	15254	Myanmar	JN826543	JN826802	JN827066	JN826290	JN826036	—
<i>Heterophasia</i>	<i>pulchella</i>	KUNHM	15166	Myanmar	JN826544	JN826803	JN827067	JN826291	JN826037	JN825801
<i>Horizorhinus</i>	<i>dohrni</i>	Genbank	—	—	F1976085	—	F1976085	—	—	—
<i>Illadopsis</i>	<i>albigpectus</i>	FMNH	357284	Congo	JN826805	JN826805	JN827069	JN826292	JN826039	JN825802
<i>Illadopsis</i>	<i>albigpectus</i>	FMNH	385068	Uganda	JN826546	JN826806	JN827070	JN826293	JN826040	—
<i>Illadopsis</i>	<i>cleaveri</i>	KUNHM	8483	Eq. Guinea	JN826549	JN826808	JN827072	JN826295	JN826042	JN825804
<i>Illadopsis</i>	<i>cleaveri</i>	KUNHM	15688	Ghana	JN826548	JN826807	JN827071	JN826294	JN826041	JN825803
<i>Illadopsis</i>	<i>fulvescens</i>	KUNHM	19886	Sierra Leone	JN826550	JN826809	JN827073	JN826296	JN826043	JN825805
<i>Illadopsis</i>	<i>fulvescens</i>	FMNH	391756	Uganda	JN826551	JN826810	JN827074	JN826297	JN826044	—
<i>Illadopsis</i>	<i>puzosi</i>	KUNHM	19887	Sierra Leone	JN826552	JN826811	JN827075	JN826298	JN826045	JN825806
<i>Illadopsis</i>	<i>pyrrhoptera</i>	FMNH	346417	Burundi	JN826553	JN826812	JN827076	JN826299	JN826046	—
<i>Illadopsis</i>	<i>pyrrhoptera</i>	FMNH	385058	Uganda	JN826554	JN826813	JN827077	JN826300	JN826047	JN825807
<i>Illadopsis</i>	<i>rufescens</i>	KUNHM	19729	Sierra Leone	JN826555	JN826814	JN827078	JN826301	JN826048	JN825808
<i>Illadopsis</i>	<i>rufescens</i>	KUNHM	19773	Sierra Leone	JN826556	JN826815	JN827079	JN826302	JN826049	JN825809
<i>Illadopsis</i>	<i>rufipennis</i>	KUNHM	8577	Eq. Guinea	JN826558	JN826817	JN827081	JN826303	JN826051	JN825811
<i>Illadopsis</i>	<i>rufipennis</i>	KUNHM	15583	Ghana	JN826557	JN826816	JN827080	JN826304	JN826050	JN825810
<i>Jabouilleia</i>	<i>daniou</i>	AMNH	DOT10947	Vietnam	HQ529039	JN826818	HQ529138	JN826305	JN826052	JN825812



TABLE A1. (continued)

Genus	Species	Institution	Sample #	Locality	ND2	ND3	Cyt b	TGF	Fib	Musk
<i>Kenopia</i>	<i>striata</i>	LSUMNS	B36395	Borneo	FJ460775	FJ460843	JN827082	FJ460911	JN826053	JN825813
<i>Kupeornis</i>	<i>chapini</i>	AMNH	348502*	Congo	JN826559	JN826819	—	—	—	—
<i>Leiothrix</i>	<i>argentea</i>	AMNH	DOT2623	Vietnam	JN826561	JN826820	JN827084	JN826307	JN826055	JN825815
<i>Leiothrix</i>	<i>argentea</i>	KUNHM	15203	Myanmar	JN826560	JN826821	JN827083	JN826306	JN826054	JN825814
<i>Leiothrix</i>	<i>lutea</i>	AMNH	DOT6507	Vietnam	JN826562	JN826822	JN827085	JN826308	JN826056	JN825816
<i>Leiothrix</i>	<i>lutea</i>	KUNHM	6724	China	JN826563	JN826823	JN827086	JN826309	JN826057	JN825817
<i>Leonardina</i>	<i>woodi</i>	KUNHM	19115	Philippines	JN826564	JN826824	JN827087	JN826310	JN826058	JN825818
<i>Liocichla</i>	<i>phoenicea</i>	KUNHM	10078	China	—	JN826825	JN827088	JN826311	JN826059	JN825819
<i>Liocichla</i>	<i>phoenicea</i>	KUNHM	15195	Taiwan	JN826565	JN826826	—	JN826312	JN826060	JN825820
<i>Liocichla</i>	<i>sterii</i>	AMNH	DOT15178	Taiwan	JN826566	JN826827	JN827089	JN826313	JN826061	JN825821
<i>Lioparus</i>	<i>sterii</i>	AMNH	DOT15198	Taiwan	JN826567	JN826828	JN827090	JN826314	JN826062	—
<i>Lioparus</i>	<i>chrysotis</i>	KUNHM	11078	China	JN826568	JN826829	JN827091	JN826315	JN826063	JN825822
<i>Liopitilus</i>	<i>nigrocapillus</i>	UWBM	53158	South Africa	JN826569	JN826830	JN827092	JN826316	JN826064	—
<i>Macronus</i>	<i>nigrocapillus</i>	UWBM	71300	South Africa	JN826570	JN826831	JN827093	JN826317	JN826065	JN825823
<i>Macronus</i>	<i>gularis</i>	KUNHM	17726	Borneo	JN826571	JN826832	JN827095	JN826318	JN826067	JN825825
<i>Macronus</i>	<i>gularis</i>	AMNH	DOT10805	Vietnam	JN826572	JN826833	JN827096	JN826319	JN826068	JN825826
<i>Macronus</i>	<i>ptilosus</i>	KUNHM	12325	Borneo	JN826573	JN826834	JN827097	JN826320	JN826069	JN825827
<i>Macronus</i>	<i>ptilosus</i>	LSUMNS	B36391	Borneo	FJ460774	FJ460842	JN827098	FJ460910	JN826070	JN825828
<i>Macronus</i>	<i>striaticeps</i>	KUNHM	14130	Philippines	JN826574	JN826835	JN827099	JN826321	JN826071	JN825829
<i>Macronus</i>	<i>striaticeps</i>	FMNH	357464	Philippines	HQ529041	JN826836	HQ529140	JN826322	JN826072	JN825830
<i>Macronus</i>	<i>abboti</i>	USNM	2131	Myanmar	JN826575	JN826837	JN827100	JN826323	JN826073	—
<i>Malacocincla</i>	<i>cinericeps</i>	KUNHM	12693	Palawan	JN826576	JN826838	JN827101	JN826324	JN826074	JN825831
<i>Malacocincla</i>	<i>malaccensis</i>	KUNHM	12341	Borneo	JN826577	JN826839	JN827102	JN826325	JN826075	JN825832
<i>Malacocincla</i>	<i>malaccensis</i>	KUNHM	17776	Borneo	JN826578	JN826840	JN827103	JN826326	JN826076	JN825833
<i>Malacocincla</i>	<i>sepiaria</i>	LSUMNS	B47108	Borneo	JN826579	JN826841	JN827104	JN826327	JN826077	JN825834
<i>Malacopteron</i>	<i>affine</i>	KUNHM	12383	Borneo	JN826580	JN826842	JN827105	JN826328	JN826078	JN825835
<i>Malacopteron</i>	<i>albobugulare</i>	LSUMNS	B47244	Borneo	JN826581	JN826843	JN827106	JN826329	JN826079	JN825836
<i>Malacopteron</i>	<i>albobugulare</i>	LSUMNS	B50348	Borneo	JN826582	JN826844	JN827107	JN826330	JN826080	JN825837
<i>Malacopteron</i>	<i>cinereum</i>	KUNHM	12320	Borneo	JN826583	JN826845	JN827108	JN826331	JN826081	JN825838
<i>Malacopteron</i>	<i>cinereum</i>	AMNH	DOT10778	Vietnam	JN826584	JN826846	JN827109	JN826332	JN826082	JN825839
<i>Malacopteron</i>	<i>magnirostre</i>	KUNHM	12358	Borneo	JN826585	JN826847	JN827110	JN826333	JN826083	JN825840
<i>Malacopteron</i>	<i>magnirostre</i>	LSUMNS	B36421	Borneo	FJ460778	FJ460846	JN827111	FJ460914	JN826084	JN825841
<i>Malacopteron</i>	<i>magnum</i>	KUNHM	17770	Borneo	JN826586	JN826848	JN827112	JN826334	JN826085	JN825842
<i>Malacopteron</i>	<i>magnum</i>	LSUMNS	B38590	Borneo	JN826587	JN826849	JN827113	JN826335	—	—
<i>Malacopteron</i>	<i>palawanense</i>	KUNHM	12600	Palawan	JN826588	JN826850	JN827114	JN826336	JN826086	JN825843
<i>Malia</i>	<i>grata</i>	AMNH	299482*	Sulawesi	JN826589	JN826851	—	—	—	—
<i>Micromacronus</i>	<i>sordidus</i>	USNM	579793*	Philippines	JN826592	JN826854	—	JN826339	—	—
<i>Minla</i>	<i>cyanouroptera</i>	KUNHM	11087	China	JN826593	JN826855	JN827117	JN826340	JN826089	JN825846
<i>Minla</i>	<i>cyanouroptera</i>	KUNHM	11281	China	JN826594	JN826856	JN827118	JN826341	JN826090	JN825847
<i>Minla</i>	<i>ignotincta</i>	KUNHM	11346	China	JN826595	JN826857	JN827119	JN826342	JN826091	JN825848
<i>Minla</i>	<i>strigula</i>	KUNHM	15184	Myanmar	JN826596	JN826858	JN827120	JN826343	JN826092	JN825849
<i>Napothera</i>	<i>brevicaudata</i>	AMNH	DOT2639	Vietnam	HQ529042	JN826860	HQ529141	JN826345	JN826093	JN825851
<i>Napothera</i>	<i>brevicaudata</i>	KUNHM	10351	China	JN826598	JN826861	JN827122	JN826344	JN826094	JN825850
<i>Napothera</i>	<i>crassa</i>	KUNHM	17805	Borneo	JN826599	JN826862	JN827123	JN826346	JN826096	JN825852
<i>Napothera</i>	<i>crassa</i>	LSUMNS	B36469	Borneo	FJ460773	FJ460841	JN827124	FJ460909	JN826097	—
<i>Napothera</i>	<i>crispifrons</i>	FMNH	75755*	Vietnam	JN826600	JN826863	—	—	—	—
<i>Napothera</i>	<i>epilepidota</i>	LSUMNS	B52626	Borneo	JN826601	JN826864	JN827125	JN826347	JN826098	JN825853

(Continued)

TABLE A1. (continued)

<i>Pellorneum albiventre</i>	KUNHM	10145	China	JN826613	JN826876	JN827138	JN826358	JN826111	JN825864
<i>Pellorneum capistratum</i>	LSUMNS	B36430	Borneo	FJ460840	FJ460840	JN827139	FJ460908	JN826112	JN825865
<i>Pellorneum erythrognys</i>	KUNHM	17798	Borneo	JN826614	JN826877	JN827140	JN826359	—	JN825866
<i>Pellorneum ruficeps</i>	USNM	2155	Myanmar	JN826615	JN826878	JN827141	JN826360	JN826113	JN825867
<i>Pellorneum ruficeps</i>	USNM	6133	Myanmar	JN826616	JN826879	JN827142	JN826361	JN826114	JN825868
<i>Pellorneum tickelli</i>	KUNHM	10186	China	JN826617	JN826880	JN827143	JN826362	JN826115	JN825869
<i>Pellorneum tickelli</i>	KUNHM	15242	Myanmar	JN826618	JN826881	JN827144	JN826363	JN826116	—
<i>Phyllanthus atripennis</i>	AMNH	DOT2033	Liberia	JN826620	JN826883	JN827146	JN826365	JN826118	—
<i>Phyllanthus atripennis</i>	KUNHM	19806	Sierra Leone	JN826619	JN826882	JN827145	JN826364	JN826117	JN825870
<i>Pomatiorhinus erythrognys</i>	AMNH	DOT5531	Nepal	HQ529044	JN826889	HQ529143	JN826371	JN826123	JN825876
<i>Pomatiorhinus erythrognys</i>	AMNH	DOT5179	Taiwan	HQ529043	JN826888	HQ529142	JN826370	JN826122	JN825875
<i>Pomatiorhinus ferruginosus</i>	KUNHM	15146	Myanmar	JN826625	JN826890	JN827151	JN826372	JN826124	JN825877
<i>Pomatiorhinus ferruginosus</i>	AMNH	DOT10777	Vietnam	HQ529057	JN826891	HQ529156	JN826373	JN826125	JN825878
<i>Pomatiorhinus ferruginosus</i>	KUNHM	15090	Myanmar	JN826627	JN826895	JN827153	JN826376	JN826127	JN825882
<i>Pomatiorhinus ferruginosus</i>	KUNHM	15241	Myanmar	JN826628	JN826896	JN827154	JN826377	JN826128	—
<i>Pomatiorhinus horsfieldi</i>	AMNH	344452*	India	HQ529073	—	HQ529172	—	—	—
<i>Pomatiorhinus hypoleucos</i>	BMNH	2000.5.22	Cambodia	HQ529069	JN826892	HQ529168	—	—	JN825879
<i>Pomatiorhinus montanus</i>	KUNHM	17781	Borneo	JN826626	JN826893	JN827152	JN826374	JN826126	JN825880
<i>Pomatiorhinus montanus</i>	LSUMNS	B47063	Borneo	HQ529075	JN826894	HQ529174	JN826375	—	JN825881
<i>Pomatiorhinus ruficollis</i>	KUNHM	10299	China	JN826629	JN826897	JN827155	JN826378	JN826129	JN825883
<i>Pomatiorhinus ruficollis</i>	KUNHM	15144	Myanmar	JN826630	JN826898	JN827156	JN826379	—	JN825884
<i>Pomatiorhinus schisticeps</i>	MNH	6.73#	Thailand	HQ529126	JN826900	HQ529225	—	JN826130	JN825886
<i>Pomatiorhinus schisticeps</i>	USNM	B2103	Myanmar	HQ529127	JN826899	HQ529226	—	—	JN825885
<i>Pomatiorhinus scotinotus</i>	KUNHM	6715	China	JN826631	JN826901	JN827157	JN826380	JN826131	JN825887
<i>Pilatichla falcata</i>	KUNHM	12816	Palawan	JN826634	JN826904	JN827160	JN826383	JN826134	JN825890
<i>Pilatichla leucogrammica</i>	LSUMNS	B50350	Borneo	JN826635	JN826905	JN827161	JN826384	JN826135	JN825891
<i>Pilatichla mindanensis</i>	KUNHM	18187	Philippines	JN826636	JN826906	JN827162	JN826385	JN826136	JN825892
<i>Pilatichla mindanensis</i>	KUNHM	19070	Philippines	JN826637	JN826907	JN827163	JN826386	JN826137	JN825893
<i>Pyrticus turdinus</i>	FMNH	298643*	Sudan	JN826638	JN826908	—	—	—	—
<i>Pyrticus turdinus</i>	USNM	583567*	Angola	JN826639	JN826909	—	—	—	—
<i>Rhopocichla atriceps</i>	AMNH	344476*	India	JN826641	JN826911	JN827165	—	—	—
<i>Rhopocichla malacoptilus</i>	USNM	15203	Myanmar	JN826643	JN826913	JN827166	JN826388	JN826139	—
<i>Rhopocichla malacoptilus</i>	USNM	15204	Myanmar	JN826644	JN826914	JN827167	JN826389	JN826140	—
<i>Robsonius rabori</i>	FMNH	433008	Luzon	JN826645	JN826915	JN827168	JN826390	JN826141	JN825895
<i>Schoeniparus brunnea</i>	KUNHM	6655	China	JN826647	JN826917	—	JN826392	JN826143	JN825897
<i>Schoeniparus castaneiceps</i>	KUNHM	15156	Myanmar	JN826648	JN826918	JN827170	JN826393	JN826144	JN825898
<i>Schoeniparus cinerea</i>	KUNHM	15152	Myanmar	JN826649	JN826919	JN827171	JN826394	JN826145	JN825899
<i>Schoeniparus cinerea</i>	USNM	15213	Myanmar	JN826650	JN826920	JN827172	JN826395	JN826146	JN825900
<i>Schoeniparus dubia</i>	KUNHM	11340	China	JN826651	JN826921	JN827173	JN826396	JN826147	JN825901
<i>Schoeniparus dubia</i>	KUNHM	15160	Myanmar	JN826652	JN826922	JN827174	JN826397	JN826148	JN825902
<i>Schoeniparus dubia</i>	USNM	5623	Myanmar	JN826646	JN826916	JN827176	JN826391	JN826149	JN825896
<i>Schoeniparus rufogularis</i>	AMNH	DOT10750	Vietnam	JN826654	JN826924	JN827177	JN826398	JN826150	JN825904
<i>Schoeniparus rufogularis</i>	USNM	15184	Myanmar	JN826653	JN826923	JN827175	JN826398	JN826151	JN825903
<i>Spelaornis chocolatinus</i>	KUNHM	15105	Myanmar	JN826655	JN826925	JN827177	JN826400	JN826152	JN825905
<i>Spelaornis chocolatinus</i>	KUNHM	15199	Myanmar	JN826656	JN826926	JN827178	JN826401	JN826153	JN825906
<i>Spelaornis troglodytoide</i>	KUNHM	15107	Myanmar	JN826657	JN826927	JN827179	JN826402	JN826154	JN825907
<i>Spelaornis troglodytoide</i>	KUNHM	15108	Myanmar	JN826658	JN826928	JN827180	JN826403	JN826155	JN825908
<i>Sphenocichla humei</i>	KUNHM	15201	Myanmar	JN826659	JN826929	JN827181	JN826404	JN826156	JN825909
<i>Sphenocichla humei</i>	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
<i>Stachyris</i>	<i>ambigua</i>	USNM	6152	Myanmar	JN826661	JN826931	JN827183	JN826406	JN826157	JN825911
<i>Stachyris</i>	<i>ambigua</i>	USNM	6183	Myanmar	JN826662	JN826932	JN827184	JN826407	—	JN825912
<i>Stachyris</i>	<i>chrysaea</i>	KUNHM	15096	Myanmar	JN826663	JN826933	JN827186	JN826408	JN826159	JN825914
<i>Stachyris</i>	<i>chrysaea</i>	KUNHM	15240	Myanmar	JN826665	JN826935	JN827187	JN826409	JN826160	JN825915
<i>Stachyris</i>	<i>erythroptera</i>	KUNHM	12327	Borneo	JN826668	JN826938	JN827190	JN826412	JN826163	JN825918
<i>Stachyris</i>	<i>erythroptera</i>	LSUMNS	B36417	Borneo	FJ460839	FJ460839	JN827191	FJ460907	JN826164	JN825919
<i>Stachyris</i>	<i>grammiceps</i>	LSUMNS	B45463#	Java	JN826669	JN826939	JN827192	JN826413	JN826165	JN825920
<i>Stachyris</i>	<i>leucotis</i>	LSUMNS	B36340	Borneo	JN826671	JN826941	JN827194	JN826415	JN826167	JN825921
<i>Stachyris</i>	<i>maculata</i>	LSUMNS	B36423	Borneo	JN826672	JN826942	JN827195	JN826416	JN826168	JN825922
<i>Stachyris</i>	<i>melanothorax</i>	AMNH	448000*	Java	HQ529129	JN826943	HQ529228	—	—	—
<i>Stachyris</i>	<i>nigriceps</i>	KUNHM	10167	China	JN826673	JN826944	JN827196	JN826417	JN826169	JN825923
<i>Stachyris</i>	<i>nigriceps</i>	LSUMNS	B36288	Borneo	JN826674	JN826945	JN827197	JN826418	JN826170	JN825924
<i>Stachyris</i>	<i>nigricollis</i>	KUNHM	12330	Borneo	JN826675	JN826946	JN827198	JN826419	JN826171	JN825925
<i>Stachyris</i>	<i>nigricollis</i>	LSUMNS	B38564	Borneo	JN826676	JN826947	JN827199	JN826420	JN826172	JN825926
<i>Stachyris</i>	<i>ogilei</i>	KUNHM	15189	Myanmar	JN826679	JN826950	JN827202	JN826423	JN826175	JN825929
<i>Stachyris</i>	<i>poliocephala</i>	LSUMNS	B36426	Borneo	JN826680	JN826951	JN827203	JN826424	JN826176	JN825930
<i>Stachyris</i>	<i>poliocephala</i>	LSUMNS	B47008	Borneo	JN826681	JN826952	JN827204	JN826425	JN826177	—
<i>Stachyris</i>	<i>pyrrhops</i>	AMNH	778719*	India	HQ529130	JN826953	HQ529229	—	—	—
<i>Stachyris</i>	<i>ruficeps</i>	KUNHM	6645	China	JN826683	JN826955	JN827206	JN826427	JN826179	JN825932
<i>Stachyris</i>	<i>ruficeps</i>	KUNHM	11083	China	JN826682	JN826954	JN827205	JN826426	JN826178	JN825931
<i>Stachyris</i>	<i>rufifrons</i>	LSUMNS	B36462	Borneo	JN826684	JN826956	JN827207	JN826428	JN826180	JN825933
<i>Stachyris</i>	<i>striolata</i>	KUNHM	10003	China	JN826686	JN826958	JN827209	JN826430	JN826182	JN825935
<i>Stachyris</i>	<i>striolata</i>	KUNHM	10136	China	JN826685	JN826957	JN827208	JN826429	JN826181	JN825934
<i>Stachyris</i>	<i>thoracica</i>	AMNH	589844*	Java	HQ529133	JN826959	HQ529232	—	—	—
<i>Timalia</i>	<i>pileata</i>	FMNH	236339*	Nepal	—	JN826964	JN827214	—	—	—
<i>Timalia</i>	<i>pileata</i>	FMNH	218211*	Nepal	—	JN826963	JN827213	—	—	—
<i>Trichastoma</i>	<i>bicolor</i>	LSUMNS	B36396	Borneo	JN826690	JN826965	JN827215	JN826434	JN826186	JN825939
<i>Trichastoma</i>	<i>celebense</i>	AMNH	DOT12612	Sulawesi	JN826691	JN826966	JN827216	JN826435	JN826187	JN825940
<i>Trichastoma</i>	<i>rostratum</i>	KUNHM	17713	Borneo	JN826692	JN826967	JN827217	JN826436	JN826188	JN825941
<i>Turdoides</i>	<i>bicolor</i>	UWBM	53074	South Africa	JN826693	JN826968	JN827218	JN826437	JN826189	JN825942
<i>Turdoides</i>	<i>bicolor</i>	USNM	70438	South Africa	JN826694	JN826969	JN827219	JN826438	JN826190	JN825943
<i>Turdoides</i>	<i>gularis</i>	USNM	5705	Myanmar	JN826695	JN826970	JN827220	JN826439	JN826191	JN825944
<i>Turdoides</i>	<i>gularis</i>	USNM	5712	Myanmar	JN826696	JN826971	JN827221	JN826440	JN826192	JN825945
<i>Turdoides</i>	<i>jardineii</i>	FMNH	52803	South Africa	JN826698	JN826972	JN827223	JN826442	JN826194	JN825947
<i>Turdoides</i>	<i>jardineii</i>	FMNH	455533	Sierra Leone	JN826697	JN826973	JN827222	JN826441	JN826193	JN825946
<i>Turdoides</i>	<i>plebejus</i>	KUNHM	20025	Ghana	JN826699	JN826974	JN827224	JN826443	JN826195	JN825948
<i>Turdoides</i>	<i>plebejus</i>	LSUMNS	B39249	Sierra Leone	JN826700	—	JN827225	JN826444	JN826196	JN825949
<i>Turdoides</i>	<i>reinwardtii</i>	KUNHM	20055	Sierra Leone	JN826701	JN826975	JN827226	JN826445	JN826197	JN825950
<i>Turdoides</i>	<i>reinwardtii</i>	FMNH	396646	Ghana	JN826702	JN826976	JN827227	JN826446	—	JN825951
<i>Xiphirhynchus</i>	<i>superciliaris</i>	KUNHM	15092	Myanmar	JN826703	JN826977	JN827228	JN826447	JN826198	JN825952
<i>Xiphirhynchus</i>	<i>superciliaris</i>	CAS	95887	China	JN826704	JN826978	JN827229	JN826448	JN826199	JN825953
Zosteropidae										
<i>Lophozosterops</i>	<i>squamiceps</i>	AMNH	DOT12549	Sulawesi	FJ460793	FJ460861	JN827094	FJ460930	JN826066	JN825824
<i>Oculocincta</i>	<i>squamifrons</i>	LSUMNS	B51197	Borneo	FJ460795	FJ460863	JN827126	FJ460932	JN826069	JN825854
<i>Sterrhoptilus</i>	<i>dennistouni</i>	USNM	3621	Philippines	JN826663	JN826933	JN827185	—	JN826158	JN825913
<i>Sterrhoptilus</i>	<i>dennistouni</i>	KUNHM	20186	Philippines	JN826666	JN826936	JN827188	JN826410	JN826161	JN825916
<i>Sterrhoptilus</i>	<i>dennistouni</i>	KUNHM	20225	Philippines	JN826667	JN826937	JN827189	JN826411	JN826162	JN825917
<i>Sterrhoptilus</i>	<i>nigrocapitatus</i>	KUNHM	18040	Philippines	JN826677	JN826948	JN827200	JN826421	JN826173	JN825927
<i>Sterrhoptilus</i>	<i>nigrocapitatus</i>	FMNH	449755	Philippines	JN826678	JN826949	JN827201	JN826422	JN826174	JN825928

(Continued)

TABLE A1. (continued)

<i>Yuhina bakeri</i>	USNM	631884*	Myanmar	JN826705	JN826979	JN826449	JN825954
<i>Yuhina brunneiceps</i>	AMNH	DOT5153	Taiwan	JN826706	JN826980	JN826450	JN825955
<i>Yuhina castaneiceps</i>	KUNHM	10367	China	JN826707	JN826981	—	JN825956
<i>Yuhina diademata</i>	KUNHM	13784	China	JN826708	JN826982	JN826451	—
<i>Yuhina everetti</i>	KUNHM	11118	China	FJ460781	FJ460849	FJ460917	JN825957
<i>Yuhina flavicollis</i>	KUNHM	17756	Borneo	JN826709	JN826983	JN826452	JN825958
<i>Yuhina nigritenta</i>	KUNHM	15170	Myanmar	JN826710	JN826984	JN826453	JN825959
<i>Yuhina nigritenta</i>	KUNHM	9997	China	JN826712	JN826986	JN826455	JN825960
<i>Yuhina occipitalis</i>	KUNHM	11150	China	JN826711	JN826985	JN826454	JN825959
<i>Yuhina atricapilla</i>	LSUMNS	15177	Myanmar	JN826713	JN826987	JN826456	JN825961
<i>Zosterops lateralis</i>	KUNHM	B36444	Borneo	FJ460802	FJ460870	JN826208	JN825962
<i>Zosterops lateralis</i>	KUNHM	6094	Australia	FJ460814	FJ460882	FJ460951	JN825963
<i>Zosterops madagascariensis</i>	FMNH	345980	Madagascar	FJ460813	FJ460881	FJ460951	JN825964
<i>Zosterops nigrorum</i>	FMNH	432997	Philippines	FJ46080	FJ460876	FJ460945	JN825965
<i>Zosterops ugensis</i>	KUNHM	12803	Solomon Is.	FJ460836	FJ460903	FJ460972	JN825966
<i>Zosterornis whiteheadi</i>	FMNH	429219	Philippines	JN826688	JN826961	JN826432	JN825937
<i>Zosterornis whiteheadi</i>	KUNHM	18001	Philippines	JN826687	JN826960	JN826431	JN825936
<i>Zosterornis hypogrammicus</i>	FMNH	455063	Philippines	JN826670	JN826940	JN826414	—
<b>Outgroups</b>							
<i>Acrocephalus australis</i>	KUNHM	19430	Solomon Islands	JN826458	JN826714	JN826214	JN825740
<i>Allophoxus bres</i>	KUNHM	17701	Borneo	GU112681	GU112727	GU112589	JN825757
<i>Chamaea fasciata</i>	SDSU	2188	USA	JN826479	JN826738	JN826235	JN825759
<i>Chamaea fasciata</i>	SDSU	2220	USA	JN826480	JN826739	JN826236	JN825760
<i>Conostoma oenodum</i>	FMNH	297082*	Nepal	JN826484	JN826743	JN826240	—
<i>Conostoma oenodum</i>	FMNH	297083*	Nepal	JN826485	JN826744	JN826241	—
<i>Erpornis zantholeuca</i>	KUNHM	10015	China	JN826492	JN826751	JN826245	JN825762
<i>Erpornis zantholeuca</i>	KUNHM	13848	China	JN826491	JN826750	JN826246	JN825763
<i>Hypocryptadius cinnamomeus</i>	KUNHM	19117	Philippines	JN826545	JN826804	—	—
<i>Megalurulus timoriensis</i>	KUNHM	16461	New Guinea	JN826590	JN826852	JN826337	JN825844
<i>Melocichla mentalis</i>	KUNHM	15406	Ghana	JN826591	JN826853	JN826338	JN825845
<i>Myzornis pyrrhura</i>	KUNHM	15109	Myanmar	JN826597	JN826859	JN826093	—
<i>Myzornis sericeus</i>	KUNHM	17792	Borneo	JN826602	JN826865	JN826348	JN825855
<i>Paradoxornis alphonisianus</i>	KUNHM	11096	China	JN826603	JN826866	JN826349	JN825856
<i>Paradoxornis fulvifrons</i>	CAS	95908	China	JN826605	JN826868	JN826351	JN825858
<i>Paradoxornis fulvifrons</i>	CAS	95884	China	JN826604	JN826867	JN826350	JN825857
<i>Paradoxornis gularis</i>	KUNHM	6706	China	JN826607	JN826870	—	JN825860
<i>Paradoxornis gularis</i>	KUNHM	11037	China	JN826606	JN826869	JN826105	JN825859
<i>Paradoxornis nipalensis</i>	AMNH	DOT5190	Taiwan	JN826608	JN826871	JN826106	JN825861
<i>Paradoxornis ruficeps</i>	KUNHM	15116	Myanmar	JN826609	JN826872	JN826107	—
<i>Paradoxornis verreauxi</i>	KUNHM	11041	China	JN826610	JN826873	JN826108	JN825862
<i>Paradoxornis webbianus</i>	KUNHM	6740	China	JN826612	JN826875	JN826110	—
<i>Paradoxornis webbianus</i>	KUNHM	13794	China	JN826611	JN826874	JN826356	JN825871
<i>Phylloscopus cebuensis</i>	KUNHM	20262	Philippines	JN826621	JN826884	JN826366	JN825872
<i>Phylloscopus alberti</i>	KUNHM	15196	Myanmar	JN826623	JN826886	JN826368	JN825873
<i>Phoenicogon alberti</i>	AMNH	DOT5558	Nepal	JN826622	JN826885	JN826367	JN825872
<i>Phoenicogon pusilla</i>	KUNHM	15250	Myanmar	JN826624	JN826887	JN826369	JN825874
<i>Pseudalcippe atriceps</i>	FMNH	355697	Uganda	JN826632	JN826902	JN826121	JN825871
<i>Pseudalcippe atriceps</i>	FMNH	358056	Burundi	JN826633	JN826903	JN826133	JN825888
<i>Pycnonotus plumosus</i>	KUNHM	12667	Philippines	JN826640	JN826910	JN826382	JN825889
<i>Rhopophilus pectinatus</i>	USNM	526697*	Philippines	JN826642	JN826912	JN826387	JN825894
<i>Sylvia borin</i>	KUNHM	15471	Ghana	JN826689	JN826962	JN826433	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.