

Comprehensive phylogeny of the laughingthrushes and allies (Aves, Leiothrichidae) and a proposal for a revised taxonomy

Alice Cibois¹  | Magnus Gelang² | Per Alström^{3,4,5} | Eric Pasquet⁶ | Jon Fjeldså⁷ | Per G. P. Ericson⁸ | Urban Olsson⁹

¹Natural History Museum of Geneva, Geneva, Switzerland

²Göteborgs Naturhistoriska Museum, Göteborg, Sweden

³Department of Ecology and Genetics, Animal Ecology, Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden

⁴Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

⁵Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing, China

⁶UMS MNHN/CNRS 2700 Outils et Méthodes de la Systématique Intégrative (OMSI) and UMR7205 Institut de Systématique, Evolution, Biodiversité CNRS MNHN UPMC EPHE, Sorbonne Universités, Muséum National d'Histoire Naturelle, Paris, France

⁷Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, Zoological Museum, Copenhagen, Denmark

⁸Department of Vertebrate Zoology, Molecular Systematics Laboratory, Swedish Museum of Natural History, Stockholm, Sweden

⁹Department of Zoology, University of Gothenburg, Göteborg, Sweden

Correspondence

Alice Cibois, Natural History Museum of Geneva, CP 6434, CH 1211 Geneva 6, Switzerland.

Email: alice.cibois@ville-ge.ch

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Abstract

DNA phylogenies have gradually shed light on the phylogenetic relationships of the large babbler group. We focus in this study on the family Leiothrichidae (laughingthrushes and “song babblers”), which represents the largest clade of babblers in terms of species diversity. Our phylogeny includes all genera and 82% of the recognized species, using mitochondrial and nuclear loci. The sister group to Leiothrichidae is composed of the Pellorneidae (“jungle babblers”) plus the genus *Alcippe*. Within Leiothrichidae, four strongly supported primary clades (A–D) are recovered. Clade A includes *Grammatoptila*, *Laniellus* and *Cutia*. Clade B includes a large group of laughingthrushes, all of them classified in *Trochalopteron*. In Clade C, the two laughingthrushes endemic to southern India, *T. fairbanki* and *T. cachinnans*, which have recently been proposed to be placed in the newly erected genus *Montecincla*, form a sister clade to the group comprising the “song babblers” (*Lioptila*, *Leiothrix*, *Heterophasia*, *Minla*, *Liocichla*, *Actinodura*, *Chrysominla*, *Siva*, and *Sibia*). Clade D includes the African babblers (*Turdoides*, *Phyllanthus*, *Kupearis*), Asian relatives (*Argya*, *Acanthoptila*, *Chatarrhaea*) and all remaining laughingthrushes (*Garrulax*). The time estimates suggest that the early diversification of the Leiothrichidae occurred in the mid-Miocene, a period that corresponds to the diversification of many passerine groups in Asia. A revised taxonomic classification of the family is proposed in the light of these results.

KEYWORDS

babblers, multilocus analysis, phylogeny, taxonomy

1 | INTRODUCTION

The babblers and allies, most of them previously included in the family Timaliidae, although now considered a group of five distinct families, comprise altogether >400 species (409 in Dickinson & Christidis, 2014; 473 in del Hoyo & Collar, 2016; 458 in the IOC 7.3, Gill & Donsker, 2017). These Old World insectivores inhabit Africa, Eurasia and Australasia, with most of their diversity found in temperate and subtropical habitats of the Sino-Himalayan montane region. The group has only one New World representative, the Wrenit *Chamaea fasciata* (Gill & Donsker, 2017). Because the babblers display great morphological and ecological diversity (del Hoyo & Collar, 2016; Delacour, 1946), they were for long considered as a “waste basket,” and the systematics of the group and related Old World insectivorous passerines have been particularly difficult (see, for instance, the detailed historical review in Sibley and Monroe (1990)).

DNA phylogenies have gradually shed light on the phylogenetic relationships of this group, showing a large disparity of morphotypes within clades and convergences between birds inhabiting similar habitats (see, e.g., Gelang et al., 2009; Moyle, Andersen, Oliveros, Steinheimer, & Reddy, 2012). These studies have led to substantial taxonomic changes, as reviewed in Cibois, Gelang, and Pasquet (2010) and Alström, Olsson, and Lei (2013). Following the results of these phylogenies, it is nowadays generally agreed to treat the five primary clades identified in the babbler group as families (del Hoyo & Collar, 2016; Dickinson & Christidis, 2014; Gill & Donsker, 2017). Three of these, Leiothrichidae, Pellorneidae and Timaliidae, are made up of traditional babblers, while Zosteropidae is a mixture of babblers (mainly *Yuhina*) and white eyes, and the Sylviidae comprises a group of “*Sylvia* warblers” along with several small babblers and parrotbills.

In this study, we focus on the family Leiothrichidae, which represents the largest clade of babblers in terms of species diversity, with c. 125 species. Distributed throughout Africa, most of southern Asia and the Great Sunda region, the Leiothrichidae are most diverse in the Sino-Himalayan and South-East Asian regions. The group includes all the “song babblers,” which were regrouped by previous ornithologists such as Delacour (1946), based on the melodious whistles of some species, sometimes dueting or including mimicry notes. The family contains also the species defined as “laughingthrushes” for their loud calls used when in large social groups, currently grouped in the genera *Grammatoptila*, *Garrulax* and *Trochalopteron*, and drab, chattering savanna species in the genera *Turdoides* and *Argya*. The Leiothrichidae are generally rather large birds of the understory of thickets of montane areas, with many species foraging mainly on the ground in a thrush-like manner. Some of the brightly coloured species among babblers also belong to this family, like the Silver-eared Mesia *Leiothrix argentauris*.

Although all molecular studies concurred globally on the genera that composed the Leiothrichidae, these works also highlighted the nonmonophyly of several genera as previously circumscribed (Cibois, 2003; Dong, Wu, Liu, & Yang, 2010; Gelang et al., 2009; Luo, Qu, Han, Li, & Lei, 2009; Moyle et al., 2012). Based on these results, Moyle et al. (2012) suggested a taxonomic revision of this clade. They proposed that *Garrulax* be divided into *Garrulax*, *Grammatoptila* (monotypic: *G. striata*), *Ianthocincla* and *Trochalopteron*, and *Babax* synonymized with *Ianthocincla*. Moreover, they proposed that *Kupeornis* and *Phyllanthus* be subsumed in *Turdoides*, *Heterophasia annectans* moved to *Minla*, and *Minla cyanouroptera* and *M. strigula* transferred to *Actinodura*. However, they did not include the type species of *Garrulax*, *G. rufifrons*, so the circumscription of that genus was considered preliminary. The reinstatement of *Trochalopteron* was proposed by Luo et al. (2009) based on molecular data as well as the observation that all species in that clade have speckled eggs, unlike any other traditional *Garrulax* species for which eggs have been described. Earlier, Rasmussen and Anderton (2005) and Collar and Robson (2007) proposed reclassifications based on morphological features, and some of these agree with the molecular results, whereas others do not, and some have not yet been tested by molecular markers. Dickinson and Christidis (2014) and del Hoyo and Collar (2016) followed most but not all recommendations of Moyle et al. (2012): In particular, some small genera such as *Kupeornis* and *Phyllanthus* were kept, pending more comprehensive analyses. They also resurrected two genera (*Chatarrhea* and *Argya*) to deal with the polyphyly of *Turdoides*, following the groups proposed by Wolters 1975–1982, where the sampling of molecular studies was incomplete. del Hoyo and Collar (2016) further divided *Turdoides* by resurrecting the monospecific genus *Acanthoptila*. Finally, Robin et al. (2017) recently described the new genus *Montecincla* for four taxa endemic to the Western Ghats Mountains, which differ from other laughingthrushes in morphology and represent a distinct lineage.

The definition of several genera within the Leiothrichidae has remained uncertain and in need of a comprehensive sampling. In this study, we present the densest phylogeny of the Leiothrichidae published so far, including all genera and 82% of the recognized species (Dickinson & Christidis, 2014), using mitochondrial and nuclear loci. We use calibrated molecular clock to infer divergence times, and we propose a revised taxonomic classification of the family in the light of these results.

2 | MATERIAL AND METHODS

2.1 | Study group and sampling

Taxonomy follows Dickinson and Christidis (2014), who recognized 21 genera and 125 species in the Leiothrichidae

(including seven species of *Alcippe*, see below). Our data set includes 102 species in 21 genera, with all the type species for the genera recognized by Dickinson and Christidis (2014), as well as those for the newly suggested classification. The species not sampled include *Argya altirostris*, *Kupeornis rufocinctus*, *Turdoides rufescens*, *T. melanops*, *T. hindei*, *Garrulax ferrarius*, *G. konkakinhensis*, *G. waddelli*, *G. koslowi*, *G. lugubris*, *G. calvus*, *Trochalopteron henrici*, *Heterophasia melanoleuca*, *Liocichla ripponi*, *L. bugunorum*, *L. omeiensis* and *Actinodura sodangorum*. We also sampled 22 species in 19 genera of nonleiothrichid babblers and sylvioids, as outgroups. These include one fulvetta of the genus *Alcippe*, a genus that was included in the Leiothrichidae by Moyle et al. (2012), whereas Gelang et al. (2009) provided support for placing it in the Pellorneidae, as sister to the other genera in that family, which also includes other fulvetta morphotypes (in *Schoeniparus*). DNA was obtained from tissue, blood or footpads, and some previously published sequences were retrieved from GenBank (Table S1).

2.2 | DNA extraction and sequencing

Amplification and sequencing followed the protocols described in Irestedt, Ohlson, Zuccon, Källersjö, and Ericson (2006), with specially designed primers (Table S2). We amplified and sequenced four nuclear introns, glyceraldehyde-3-phosphodehydrogenase intron 11 (GAPDH), myoglobin intron 2 (MYO), ornithine decarboxylase introns 6 to 7 (ODC) and transforming growth factor beta 2 (TGF-B2); and one protein coding mitochondrial gene, cytochrome oxidase subunit 1 (CO1).

2.3 | Phylogenetic analyses

To determine evolutionary models implemented in the model-based analyses of phylogeny and divergence times, we used PartitionFinder 2 (Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2016) with the Akaike's information criterion applied. The following models were proposed: GTR + I + Γ for CO1 first codon position, HKY + I + Γ for CO1 second codon position, GTR + I + Γ for CO1 third codon position, GTR + Γ for G3P, TVM + Γ for MYO, GTR + Γ for TGF-B2, and TVM + Γ for ODC. Phylogeny was estimated by Bayesian inference (BI) using MrBayes 3.2.6 (Ronquist et al., 2012) and by maximum-likelihood (ML) using RAxML (Stamatakis, 2014). In the BI, we estimated the posterior probability (PP) of trees and parameters by two simultaneous runs of four metropolis coupled Markov chain Monte Carlo (MCMC³) under the proposed substitution models, starting from random trees, with unlinked partitions. The MCMC³ was incrementally heated with temperature set to 0.1 and were run for 25 million generations, sampled every 1,000th generation. Phylogenies were inferred from the combined data set partitioned in the five loci (seven partitions with the

coding position of CO1), as well as for each locus separately. We used Tracer 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) to check the convergence of the posterior distributions with a 10% burn-in period. In the ML analysis, the data were partitioned by locus and by codon positions for CO1, and GTRGAMMAI was used both for the bootstrapping phase and for the final tree inference. We ran most phylogenetic analyses on the CIPRES Science Gateway V. 3.3 (Miller, Pfeiffer, & Schwartz, 2010).

2.4 | Molecular dating

We used BEAST 1.8.4 (Drummond, Suchard, Xie, & Rambaut, 2012) with a relaxed-clock and the divergence time between Leiothrichidae, Pellorneidae and Timaliidae obtained by Price et al. (2014), 20.92 million years ago (mya) with standard deviation 2.11, as a secondary calibration point. Price et al. (2014) proposed a well-supported phylogeny of Asian passerines using fossil and biogeographic calibrations. This secondary calibration was also used by Robin, Gupta, Thatte, and Ramakrishnan (2015) for a phylogeny of a subgroup of Leiothrichidae taxa. We used the models chosen for the MrBayes analysis for the partitions by genes. We selected a Yule speciation process for the tree prior and a normal distribution for the calibration point to reflect the nondirectional uncertainty on the estimate (Ho, 2007). The MCMC chain length was 200 million generations with a 10% burn-in period, and the same run was performed several times to ensure that convergence of the models had occurred. We used Tracer 1.6 to ensure stationarity of chains, with Effective Sample Size values above 200. We converted the ultrametric tree obtained using BEAST to a lineage-through-time (LTT) plot in order to visualize the temporal distribution of speciation events, using the package APE 4.1 (Paradis, Claude, & Strimmer, 2004) in R 3.4.1 (R Development Core Team, 2017). Lineage accumulation was tested for departure from a constant rate hypothesis (CR) by calculating the gamma statistic (Pybus & Harvey, 2000).

3 | RESULTS

3.1 | Phylogenetic relationships—species level

No unexpected start or stop codons that could indicate the presence of nuclear copies were found in the CO1 sequences. The data set consisted of in total 3,078 characters, with 633 base pairs (bp) for COI, 381 bp for G3P, 750 bp for MYO, 657 bp for ODC and 657 bp for TGF-B2. The tree based on the concatenated sequences (Figure 1a,b) recovered a Leiothrichidae clade and four other “babbler” clades that represent the families Pellorneidae, Timaliidae and Zosteropidae, with good support for all relationships among these. The BI and ML trees were identical, with different support for only

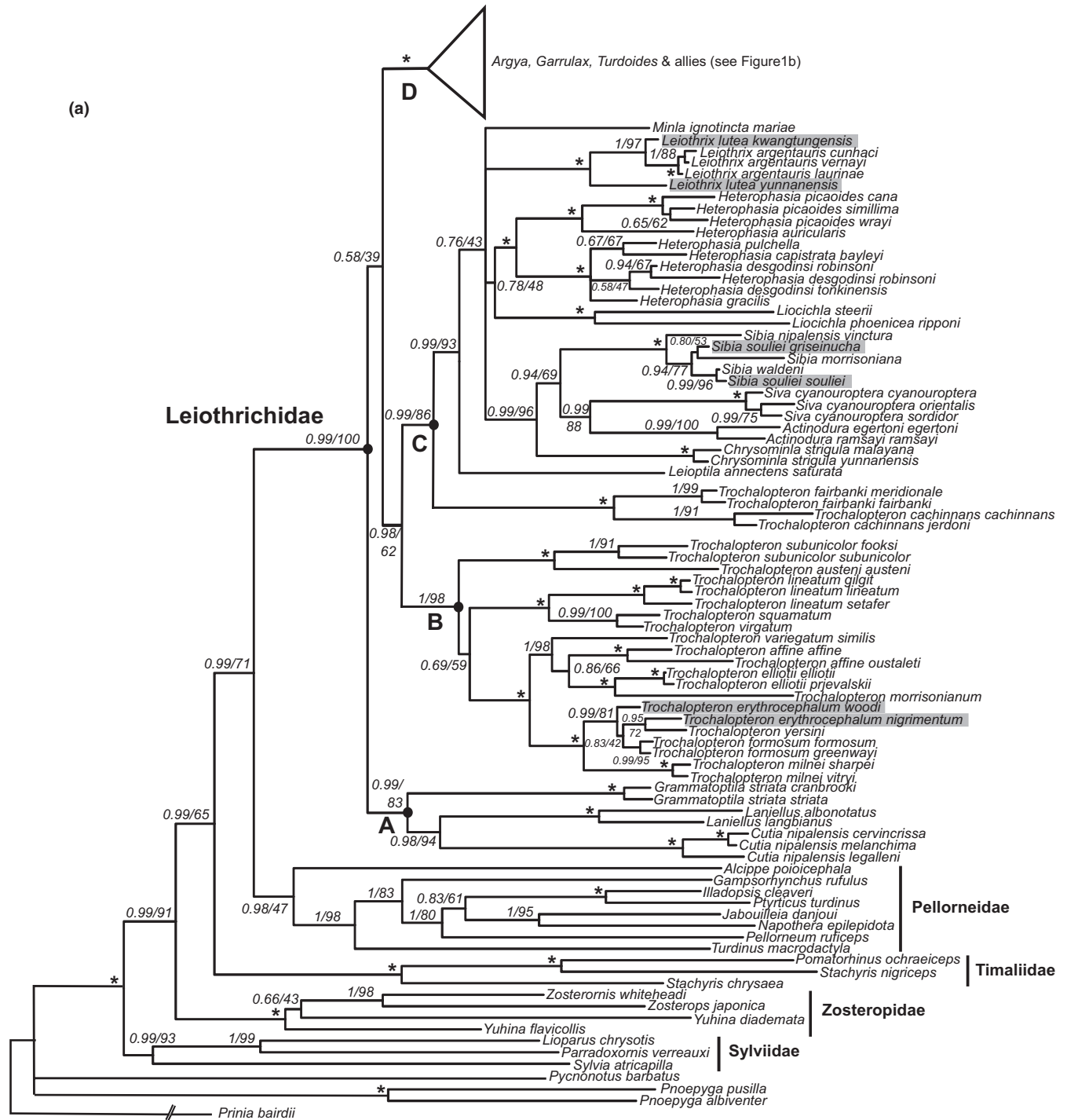


FIGURE 1 (a and b) Phylogenetic tree of the Leiothrichidae based on concatenated mitochondrial and nuclear sequence data, estimated using Bayesian and maximum-likelihood inferences. Node support is denoted as posterior probabilities and bootstrap values (in this order; * means both values 1.00/100%). Nonmonophyletic species are highlighted in grey

a few nodes. The sister group to Leiothrichidae was composed of the Pellorneidae including *Alcippe poioicephala*; the Pellorneidae plus *Alcippe* node, well-supported in the BI tree, was not supported in the ML analysis, but in all analyses, *Alcippe* was clearly outside the Leiothrichidae clade. Within Leiothrichidae, four strongly supported primary clades (A–D) were recovered, with uncertain relationships among them.

Clade A included *Grammatoptila striata*, *Cutia nipalensis* and the two species of *Laniellus*, with high support for the sister relationship between *Cutia* and *Laniellus*. Clade B included 13 species of *Trochalopteron*, including the type species, *T. subunicolor*. Two taxa classified into *Trochalopteron*, namely *T. cachinnans* and *T. fairbanki* (recently placed in a new genus *Montecincla*: Robin et al., 2015), did not belong

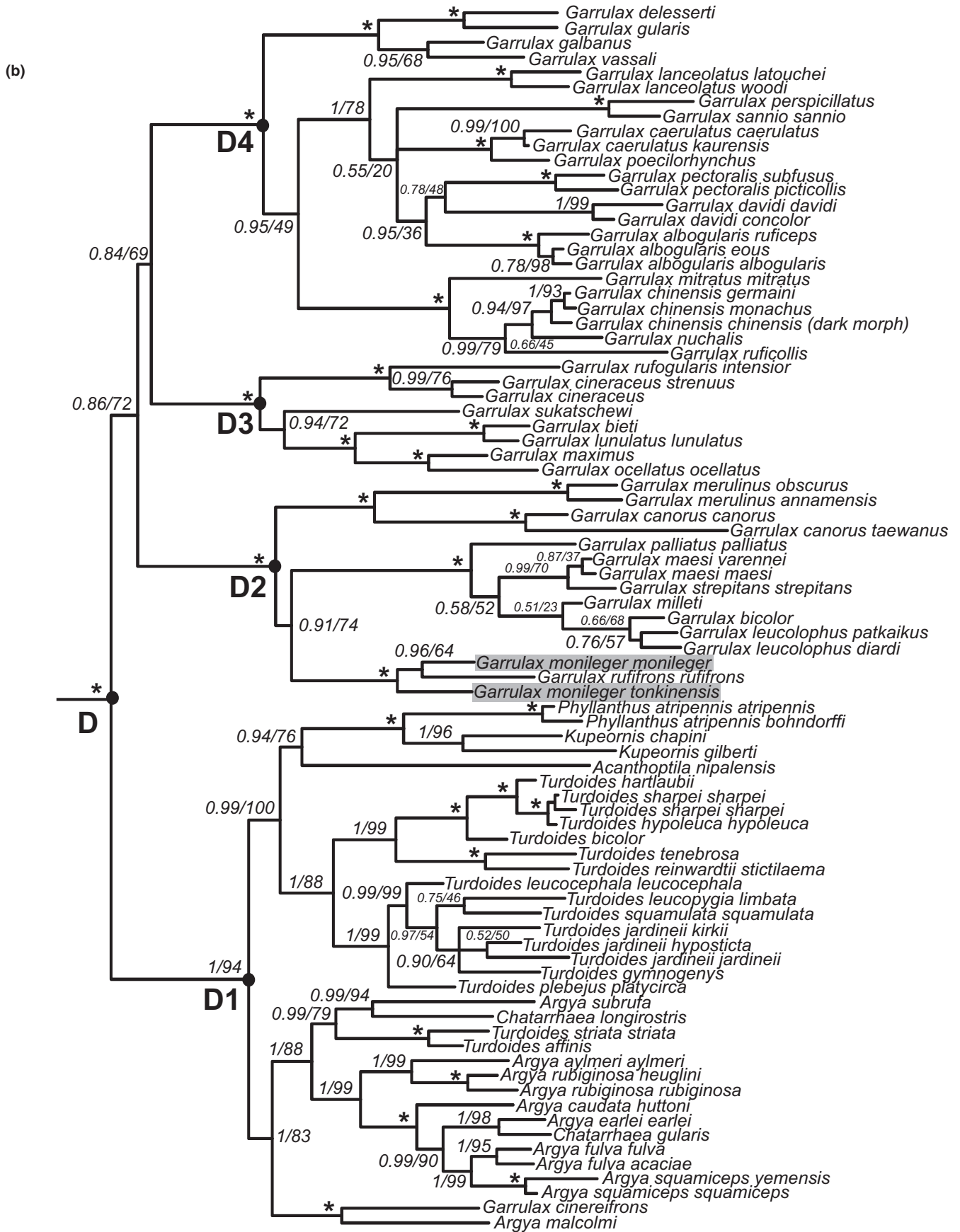


FIGURE 1 (Continued)

to this clade but were included with good support in Clade C. In addition to species already analysed by others, *T. austeni* and *T. yersini* were included, the former recovered in a strongly supported sister position to *T. subunicolor*, the latter in a strongly supported clade composed of *T. erythrocephalum*, and *T. formosum*. *T. morrisonianus* was sister species to *T. elliotii*, together in a clade with *T. affine* and *T. variegatum*.

In Clade C, the above-mentioned *T. cachinnans* and *T. fairbanki* of India's Western Ghats Mountains formed a well-supported sister clade to an equally strongly supported clade comprising *Leioptila annectens*, *Leiothrix* (two species), *Heterophasia* (six species), *Minla ignotincta*, *Liocichla* (two species), *Actinodura* (two species), *Chrysominla strigula*, *Siva cyanouroptera* and *Sibia* (four species). The four latter genera formed a well-supported clade, with *Actinodura* sister to *Siva*, grouped with *Sibia*, and *Chrysominla* as sister to the rest of the clade. The relationships among the other genera were poorly supported.

All remaining members of the Leiothrichidae were grouped in Clade D, which was subdivided into four well-supported subclades. Clade D1 included all African babblers, with a few Asian taxa, divided into two subclades. The first contained the Asian and North African species classified within *Argya* [eight species of the nine proposed by Dickinson and Christidis (2014)], two *Chatarrahaea* (*C. longirostris* and *C. gularis*, not sister taxa) and two Indian *Turdoidea* (*T. affinis* and *T. striata*, sister taxa with good support). *Garrulax cinereifrons*, an endemic to Sri Lanka, also belonged to this clade, as sister to *Argya malcolmi* from India. The second subclade comprised all the remaining Sub-Saharan African *Turdoidea* species. A subclade included the Himalayan *Acanthoptila nipalensis*, sister to the two species of *Kupeornis* (out of three recognized species in this genus) and the monotypic genus *Phyllanthus* (in a strongly supported sister relationship with *Kupeornis*). Clade D2 contained 10 species placed in the genus *Garrulax*, including the type species, *G. rufifrons*. Clade D3 included a group of seven *Garrulax* species with similar brown plumage, often with scaly patterns, for example *G. ocellatus*. Clade D4 comprised all 16 remaining *Garrulax* species, including *G. lanceolatus*. In all, clades D2, D3 and D4, which formed a monophyletic group in both BI and ML trees but with low support, comprised 33 of the 40 species recognized in this genus by Dickinson and Christidis (2014).

3.2 | Phylogenetic relationships—single-locus analyses

The single-locus trees (Figures S1–S5) were less well resolved and supported than the tree based on the concatenated analysis. There were only two incongruences on supported nodes among these single-locus trees. First, *Leiothrix lutea* was recovered as (a) paraphyletic by CO1 (Figure S1) and

G3P (Figure S2), with the same topology as in the concatenation analysis (*L. lutea yunnanensis*, (*L. argentauris*, *L. lutea kwangtungensis*)) and ML bootstrap > 90%; (b) paraphyletic but with the alternative topology (*L. lutea kwangtungensis* (*L. lutea yunnanensis*, *L. argentauris*)) by TGF-B2 (Figure S5, ML bootstrap 76%); (c) monophyletic by MYO (Figure S3; ML bootstrap 92%); and (d) polytomous but with low support by ODC (Figure S4; ML bootstrap < 50%). Second, *Alcippe poioicephala* was placed within the Leiothrichidae by TGF-B2 (Figure S5; ML bootstrap 70%), although all other loci recovered it outside the Leiothrichidae clade, with low support except for ODC (Figure S4; ML bootstrap 97% for inclusion of *Alcippe* in Pellorneidae).

3.3 | Phylogenetic relationships—infraspecific level

Four Leiothrichidae species were inferred to be nonmonophyletic. In Clade B, the two subspecies of *Trochalopteron erythrocephalum*, namely *T. e. woodi* and *T. e. nigrimentum*, were not sister taxa, the latter being closely related to *T. yersini*. In Clade C, *Leiothrix lutea kwangtungensis* was sister to *L. argentauris*, with *L. l. yunnanensis* sister to these, with strong support. However, the topology varied among loci (see above) and might be influenced by incomplete lineage sorting. The two allopatric subspecies of *Sibia souliei* were not sister taxa: the nominate was sister with good support to *Sibia waldeni*, whereas *Sibia souliei griseinucha* was sister to *Sibia morrisoniana*, although with low support. In Clade D, the two sampled subspecies of *Garrulax monileger* were not sisters, as *G. m. tonkinensis* was sister to *G. rufifrons*.

3.4 | Divergence time

The divergence time analysis, summarized in Figure 2a,b, suggested that the basal divergences of the Leiothrichidae occurred during the mid-Miocene (15 mya). The main clades (A to D4) dated from 13 to 9 mya, except Clade D3, which occurred more recently at ca. 7 mya. Lineage-through-time (LTT) plots (Figure 3) showed the temporal accumulation of lineages for the Leiothrichidae. The hypothesis of a constant rate model was not rejected ($g = -0.94$, $p = 0.052$), suggesting consistency of the rate of speciation through time, under the assumption that speciation and extinction are both time-homogeneous (Ricklefs, 2007).

4 | DISCUSSION

4.1 | Phylogeny—comparisons with previous studies

We recovered *Alcippe* in Pellorneidae, as sister to the rest of this family, as opposed to sister to Leiothrichidae in the

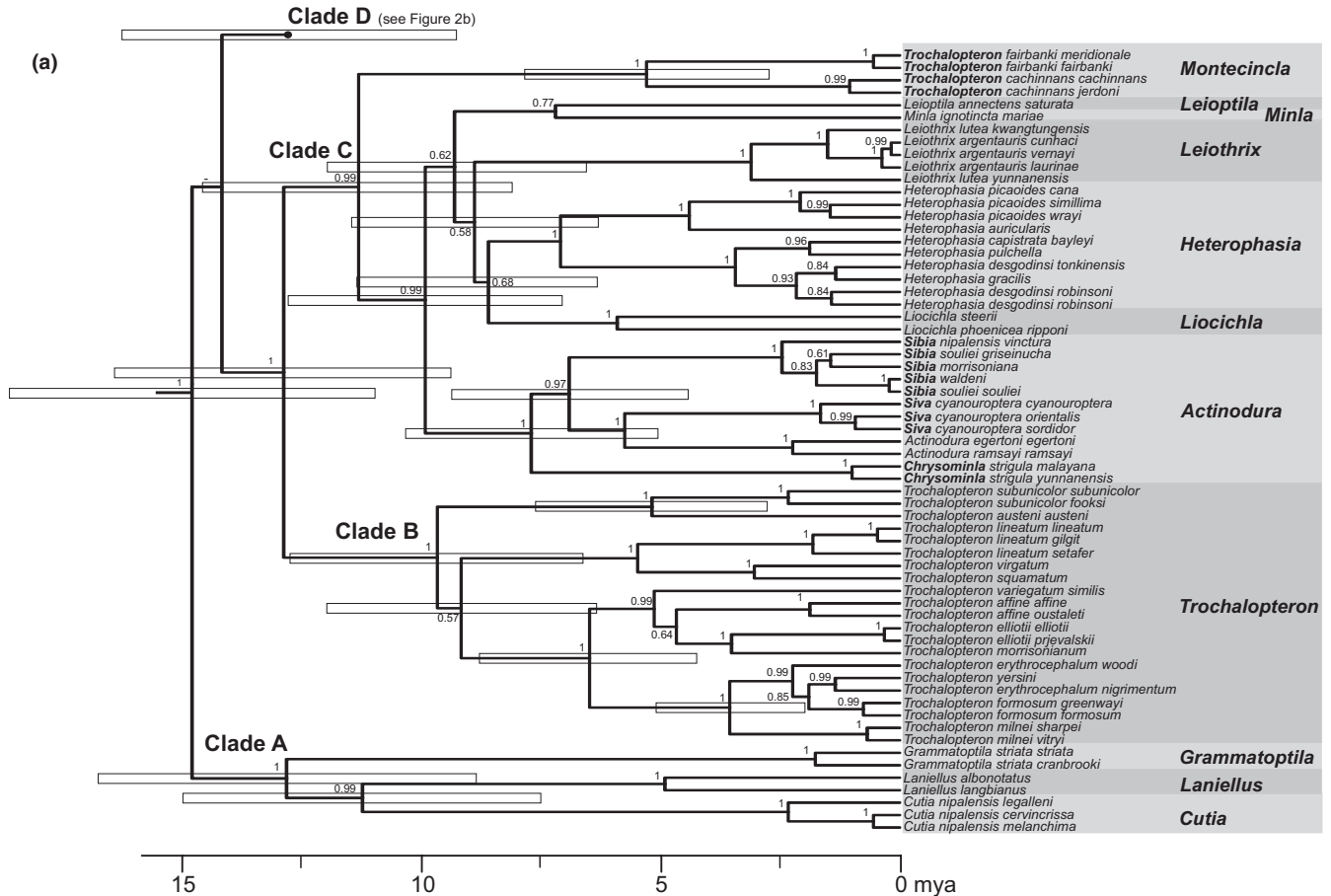


FIGURE 2 (a and b) Bayesian chronogram for the Leiothrichidae inferred using BEAST. Timescale is in million years ago. Node support is denoted as posterior probabilities. Taxonomic changes are highlighted using boldface

phylogeny by Moyle et al. (2012). The sister relationship to Pellorneidae was also recovered by Gelang et al. (2009) but was well-supported only in our BI analysis. However, the monophyly of the clade Leiothrichidae, excluding *Alcippe*, is strongly supported in all analyses. It is possible that the position of *Alcippe* could only be resolved with a denser sampling of all the babbler families or a considerably larger number of loci.

In all, the present study included 47 ingroup species that were not covered by Moyle et al. (2012), including the type species of *Garrulax*. Clade A was not recovered in Moyle et al. (2012) (*Laniellus* was not sampled), but *Grammatoptila* and *Cutia* were similarly in sister positions to the rest of the Leiothrichidae. Clades B, C and D were recovered in both studies, with similar relationships among species. In Clade C, the position of *Chrysominla*, as sister to the clade (*Sibia*, (*Siva*, *Actinodura*)), had PP 0.94 and ML bootstrap support 69% in the present study, so it does not strongly contradict the relationship found by Moyle et al. (2012), that is (*Sibia*, (*Siva*, (*Chrysominla*, *Actinodura*))). In Clade D4, we did not recover exactly the same relationships as Moyle et al. (2012) for several *Garrulax*, but the support values within this group were low in both studies. Similarly, in Clade D2

the respective positions of *G. palliatus*, *G. maesi*, *G. milleti* and *G. leucolophus* differed from the tree found in Moyle et al. (2012), but in our data set, the support values were low. Robin et al. (2017) recovered, with a more restricted taxon sampling, the same clades as the present study. One should, however, note that *Laniellus albonotatus* in their Figure 1a was mislabelled: According to the Supporting Information, it should be *Leioptila (Heterophasia) annectens*.

4.2 | Diversification time and biogeographic elements

The biogeographic analysis of this family will be developed, along with that of the other babbler families, in another study (Cai et al. in prep.). Thus, only a few generalities are discussed in this study. Moyle et al. (2012) suggested that the Leiothrichidae, and in fact all babbler families, originated in Asia. Our phylogeny is consistent with at least two subsequent dispersals to Africa, both in Clade D1 (most *Turdoides* species and two *Argya* species). The time estimates suggest that the early diversification of the Leiothrichidae occurred in the mid-Miocene, similar to the previous estimates for this group (Moyle et al., 2012; Robin et al., 2017). Martens, Tietze,

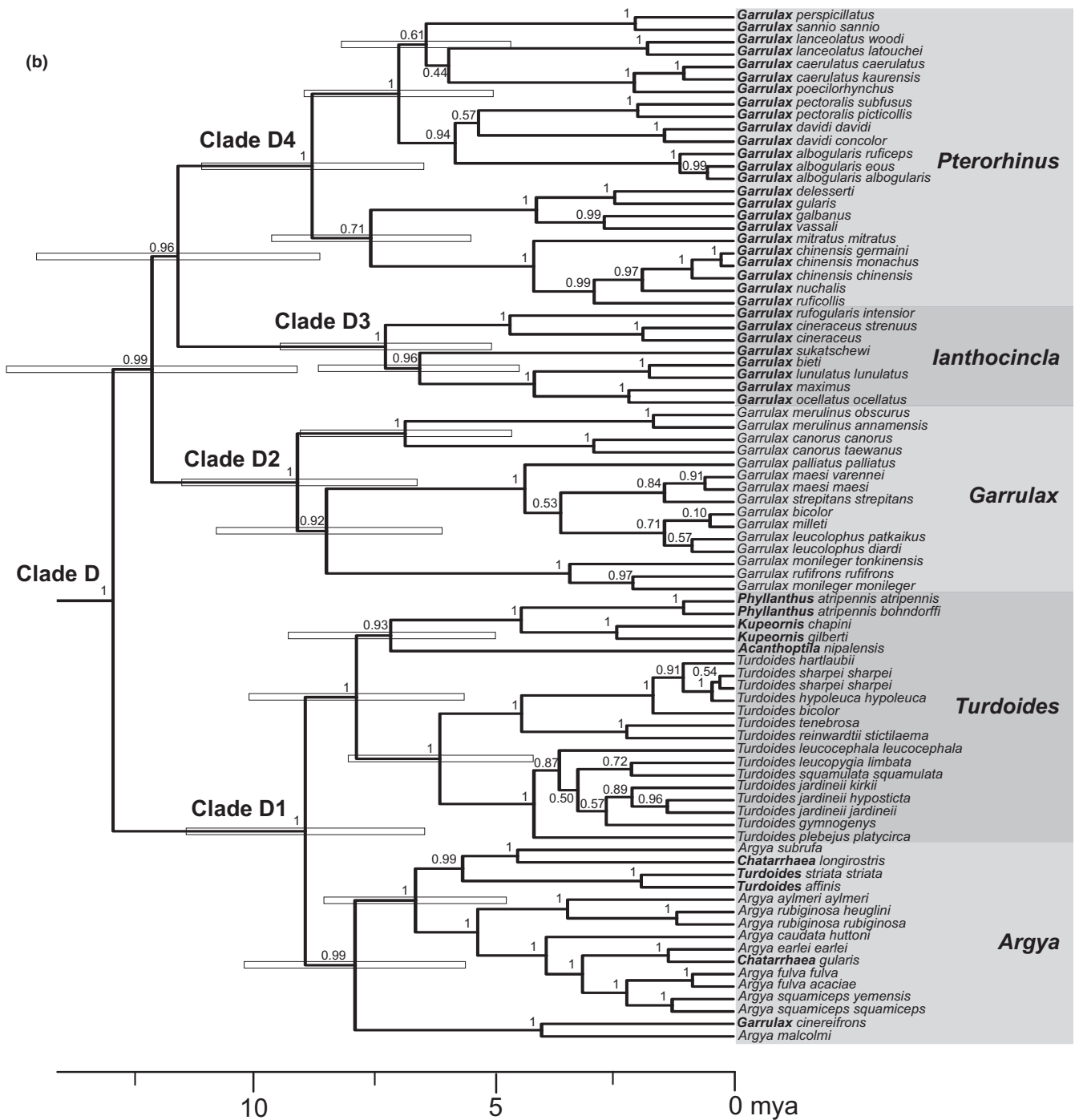


FIGURE 2 (Continued)

and Päckert (2011) found an older basal divergence for the Leiothrichidae, in the early Miocene, using a molecular clock based solely on the mitochondrial cytochrome b gene, an approach that might explain this difference. Mays et al. (2015) obtained mid-Miocene estimates for the divergence between *Leiothrix* and *Liocichla* (and ca. 9 mya for the basal split within *Liocichla*), thus suggesting an older origin for the whole Leiothrichidae family, but their results were probably biased by their limited taxon sampling. The mid-Miocene period corresponds to the diversification of many passerine groups in Asia

(Johansson, Nylinder, Ohlson, & Tietze, 2018; Moyle et al., 2016; Päckert et al., 2012; Shakya & Sheldon, 2017; Sheldon, Lim, & Moyle, 2015; Tietze, Päckert, Martens, Lehmann, & Sun, 2013), probably linked to severe climatic changes in South-East Asia (see Päckert et al., 2012 for a review). During this period, deciduous forest and savanna expanded, and the evergreen forests of the Sino-Himalayan montane region were separated from the rainforests of Sundaland (Guo et al., 2008; Reddy, 2008). However, whether these climatic changes were linked to the uplift of the Himalayas and the development of

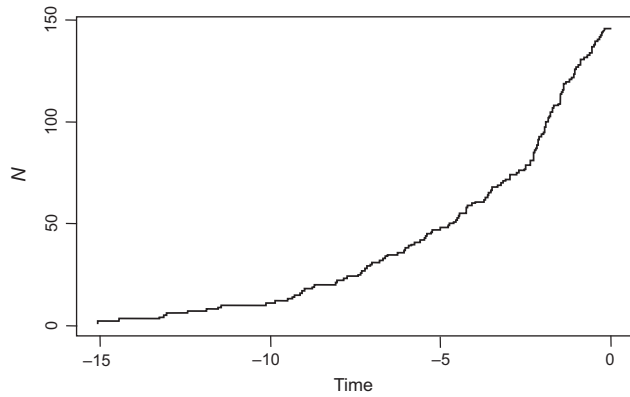


FIGURE 3 Lineage-through-time (LTT) plots, showing the number of extant lineages (n) for the Leiothrichidae. Timescale is in million years

the monsoon system during the Miocene is debated (Renner, 2016). In the early Pliocene, the emergence of many Taiwan endemics is noticeable. In agreement with Päckert et al. (2012), but contrary to Mays et al. (2015), we found that the divergence time between the Taiwan endemics and their continental sister species never predated the time estimate for the major uplift phase of the central mountain ridge of Taiwan (ca. 4–5 mya; Liu, Chen, Chen, & Jiang, 2000). Finally, our phylogeny adds to the body of evidence that during the Pleistocene, intraspecific splits occurred between populations from the Sino-Himalayas/Indochina and southern populations from the Thai-Malay Peninsula and Sundaland (for instance, in *Pteruthius* shrike-babblers, Reddy, 2008; in Pycnonotidae, Dejtaradol et al., 2016).

4.3 | Taxonomic implications at the generic level

In general, we agree with the classifications proposed based on previous phylogenetic studies, with some modifications, principally at the genus level. Our aim is to obtain a consistent treatment at the genus level with groups that have a similar age. Therefore, we use a general guideline that a genus within the Leiothrichidae represents a lineage that radiated from approximately 7–8 mya, a limit overall in agreement with the subdivision practiced in other oscine passerines (Johansson et al., 2018; Price et al., 2014). Our taxonomic changes are summarized in Figure 2. Clade A (Figure 2a) is composed of three genera with one (*Grammatoptila* and *Cutia*) or two species (*Laniellus*) each, for which no changes are proposed. Clade B corresponds to the genus *Trochalopteron*, which includes *T. lineatum* and *T. virgatum*, contra Collar and Robson (2007), but in agreement with Dickinson and Christidis (2014), del Hoyo and Collar (2016) and Gill and Donsker (2017). This genus is characterized by a distinctive colour pattern on the wings, as blackish primary coverts contrast with brighter, often colourful, remiges. The colourful wings appear

to be used in display (Collar & Robson, 2007). Within Clade C, our results support the proposal by Robin et al. (2017) to place *Trochalopteron fairbanki* and *T. cachinnans* in the new genus *Montecincla* (a genus already recognized in Gill & Donsker, 2017). *Sibia*, *Siva*, *Actinodura* and *Chrysominla* form a well-supported clade, and we suggest to include them all in a single genus, *Actinodura* Gould, 1836 (by priority). The species in this broader genus are characterized by having short, loose crests, long tails and barred wings and tail, with the exception of *strigula*, which lacks barring, and *cynouoptera* which is more aberrant in especially plumage pattern; all except *strigula* and *cynouoptera* were placed in *Actinodura* until molecular analyses suggested that *strigula* and *cynouoptera* were nested within that genus (Dong et al., 2010; Moyle et al., 2012). Gill and Donsker (2017) maintained these two species plus *ignoticta* in the genus *Minla*, but placed all other taxa in *Actinodura*. We propose no further taxonomic recommendations for the rest of clade C.

Within Clade D1 (Figure 2b), we suggest to expand the genus *Argya* (type species *A. squamiceps*) sensu Dickinson and Christidis (2014), to include five additional species presently placed in other genera: *Chatarrhaea gularis* and *C. longirostris*, *Turdoides striata* and *T. affinis*, and *Garrulax cinereifrons*. The genus *Chatarrhaea* was resurrected by Dickinson and Christidis (2014) and by del Hoyo and Collar (2016), following Wolters 1975–1982, on the basis of the polyphyly of *Turdoides* found in Moyle et al. (2012). However, only four species were studied by Moyle and collaborators, and our larger data set shows that *gularis* and *longirostris* are not sister species and are embedded with other *Argya* babblers. We preliminarily suggest that *Argya altirotis*, although not included in our sampling, should remain in this genus, which includes predominantly species from Asia and the Middle East (except African *aylmeri* and *rubiginosa*), whereas *Turdoides* includes all the remaining African taxa of Clade D1. We suggest also to include *Kupeornis*, *Phyllanthus* and *Acanthoptila* in *Turdoides*, as proposed already by Moyle et al. (2012). The two first ones share morphological and ecological characters, and diverged <5 mya. They are closely related to *Acanthoptila* from Nepal, which presents *Turdoides*-like characters, with shiny black rigid feather shafts. By uniting these small genera into *Turdoides*, the genus corresponds to a clade relatively equivalent in term of size and age to *Argya*, both diverging around 8 mya.

The genus *Garrulax* sensu Dickinson and Christidis (2014) includes species found in three large clades (D2, D3 and D4), all with deep Miocene origins (7–9 mya), and we suggest to treat them as three distinct genera. Thus, *Garrulax* Lesson, 1831 (type species *G. rufifrons*) would be restricted to Clade D2, *Ianthocinchla* Gould, 1835 (type species *Garrulax ocellatus*) would correspond to Clade D3, and *Pterorhinus* Swinhoe, 1868 (type species *Garrulax davidi*) to Clade D4. This more restricted definition of

Garrulax corresponds to a heterogeneous group of laughingthrushes found mostly in South-East Asia, with a large diversity of plumage types. A few species of *Garrulax* sensu stricto (*G. palliatus*, *G. merulinus* and *G. canorus*) show a blue eyering, but this character is found also in Clade D4 (genus *Pterorhinus*).

Based on their molecular phylogeny, Luo et al. (2009) proposed to resurrect *Ianthocincla* for a subclade of laughingthrushes (four species studied). With a larger sampling, our results support a broader definition of this genus, as originally defined by Wolters 1975–1982, with eight species in total (preliminarily including *konkakhinhensis* that was not studied here). All except *I. sukatschewi* and *I. cineraceus* have plumages with black scales or spots, and all have strongly patterned tertials and tails. Clade D3 thus corresponds to the circumscription of *Ianthocincla* by Collar and Robson (2007) based on morphological characters. Baker 1922–1930, and Rasmussen and Anderton (2005) included the species *austeni* in *Ianthocincla*, but despite its scaled underparts it belongs to the *Trochalopteron* clade. Most *Ianthocincla* species are endemic to China and/or the Himalaya region.

Pterorhinus was resurrected by Collar and Robson (2007) for only two species: *davidi* (the type species) and *sannio*. Clade D4 includes these two species and also 14 other species previously classified in *Garrulax*. They are mostly found in South-East Asia, a few also in the Indian region. Several species present a black pattern on the face and chest, but this is the most diverse group of laughingthrushes in terms of plumage patterns. This group includes the large species previously classified in the genus *Babax* (three closely related high-elevation species; only *lanceolatus* sampled here).

Several other resurrected names have been proposed recently for the laughingthrushes, mostly based on morphological differences (Collar & Robson, 2007; Rasmussen & Anderton, 2005), resulting in a much finer splitting of the group: *Dryonastes* Sharpe, 1883 (type species *Garrulax ruficollis*), *Melanocichla* Sharpe, 1883 (type species *Garrulax lugubris*), *Rhinocichla* Sharpe, 1883 (type species *Garrulax mitrata*), *Stactocichla* Sharpe, 1883 (type species *Garrulax merulinus*), *Leucodioptron* Bonaparte, 1854 (type species *Garrulax canorus*), and *Strophocincla* Wolters, 1980 (type species *Trochalopteron lineatum*). Some of these names could be matched to monophyletic groups within Clade D, and future analyses including the few species not sampled here might support the resurrection of some of these genera.

4.4 | Taxonomic considerations at species level

Although our taxon sampling was not designed to study the Leiothrichidae at the species level, we included multiple

subspecies, and the taxonomy can be discussed for a few taxa. In Clade A, *Cutia nipalensis* was split into *C. nipalensis* sensu stricto (*s.s.*) and *C. legalleni* by Collar (2006) followed by del Hoyo and Collar (2016) and Gill and Donsker (2017) on the basis of distinct plumages and sizes. The distinctness of these two taxa is supported by our data with an relatively old separation (2.3 mya; 95% HPD 1.1–4.1 mya). In Clade B, the situation of *Trochalopteron erythrocephalum* is difficult to resolve. The taxonomy of this taxon is complex, with 15 subspecies in Dickinson and Christidis (2014), whereas Collar and Robson (2007), del Hoyo and Collar (2016) and Gill and Donsker (2017) split the group into five species. Our results showed that the taxa *woodi* (Yunnan Province, China and Myanmar) and *nigri-mentum* (Himalayas) are not closely related, because the latter is sister to *T. yersini* (Vietnam) and these two are sister to *T. formosum*. A similar paraphyly between *T. e. kali* from the Himalayas and *T. e. woodi*, which was sister to *T. formosum*, was found by Päckert et al. (2012). Further decisions on this group must await a denser sampling.

In Clade C, the two allopatric subspecies of *Actinodura* (previously *Sibia*) *souliei souliei* (south-central China) and *A. s. griseinucha* (South China and North Vietnam) differ in several plumage characters and are not sister taxa, suggesting that species recognition might be warranted, as already suggested by Collar and Robson (2007). In the time-calibrated tree (Figure 2a), *Heterophasia desgodinsi* is paraphyletic with respect to *H. gracilis* but with weak node support, whereas in Figure 1a, *H. desgodinsi* was monophyletic (also not with strong support). Further study of this species will require a denser sampling, including, in particular, the nominal subspecies. We sampled two of the five subspecies currently recognized for *Leiothrix lutea*: *L. l. yunnanensis* (Yunnan and Myanmar) and *L. l. kwangtungensis* (south-central to south-east China and North Vietnam). They are not sister taxa, as *kwangtungensis* is more closely related to *Leiothrix argenta-auris*. The divergence between these two *Leiothrix lutea* taxa is ancient, ca. 3 mya (95% HPD 1.8–5.0 mya), and they differ in several plumage patterns. Thus, recognition of *kwangtungensis* as a distinct species might be justified, but because we found conflicts between loci (see Results), and because not all subspecies of *L. lutea* were sampled, more comprehensive studies will be needed to confirm this proposal.

In Clade D1, *Phyllanthus atripennis* has been split into three species by del Hoyo and Collar (2016) based on plumage differences. We only sequenced two of the three taxa (*P. atripennis atripennis* and *P. atripennis bohndorffi*), which diverged ca. 1 mya (95% HPD 0.4–2.0 mya). Further decisions on this group must await a denser sampling, particularly in the contact zones between taxa.

In Clade D2, *Garrulax canorus* has been assessed by molecular markers by Li et al. (2006, 2009), who proposed that the Taiwanese taxon should be treated as specifically distinct,

G. taewanus. The same conclusion was previously reached by Collar (2006) based on morphology and was accepted by del Hoyo and Collar (2016) and Gill and Donsker (2017). The divergence of the two taxa is ancient, ca. 3 mya (95% HPD 1.4–4.6 mya), similar to that between most Taiwan endemics and their sister species from the mainland, and supports species rank for *taewanus* [e.g. *T. ellioti*/*T. morrisonianum* (3.6 mya, 95% HPD 2.2–5.1 mya) and *G. poecilorhynchus*/*G. caeruleatus* (2.1 mya, 95% HPD 1.0–3.5 mya), but see below for *Garrulax albogularis ruficeps*. Päckert et al. (2012) showed that *G. berthemyi*, previously included within *G. poecilorhynchus* sensu Dickinson and Christidis (2014), is sister to *G. caeruleatus*]. del Hoyo and Collar (2016) and Gill and Donsker (2017) also followed Collar (2006) in elevating *G. annamensis* (formerly a subspecies of *G. merulinus*) to species level. Our genetic data only moderately support their distinctness, with a time of divergence between the two taxa (1.7 mya; 95% HPD 0.6–3.0 mya) that is similar to that found in other polytypic laughingthrushes (i.e. *pectoralis*, *cineraceus*). *Garrulax maesi varennei* is treated as a subspecies of *G. castanotis* and hence specifically different from *G. m. maesi*, by del Hoyo and Collar (2016) and Gill and Donsker (2017). The divergence (0.6 mya; 95% HPD 0.1–1.2 mya) is not markedly deep, although it is deeper than some other taxa that are recognized as different species (e.g. *G. bicolor*–*G. milleti*; 0.5 mya; 95% HPD 0.0013–1.3 mya). *Garrulax monileger* is a polytypic species with ten subspecies distributed over South-East Asia, whereas *G. rufifrons*, which is embedded with the two *monileger* subspecies sampled in this study, is restricted to Java. Although the divergence between the three taxa is deeper than that of most *Garrulax* (3.5 mya; 95% HPD 2.0–5.4 mya), further decisions on this group must await a denser sampling.

In Clade D4, *Pterorhinus lanceolatus woodi* (previously in *Garrulax*) was treated as a separate species from *G. lanceolatus* by del Hoyo and Collar (2016) and Gill and Donsker (2017) based on morphological and preliminary vocal data. The time of divergence between the two taxa is similar to that found in other polytypic laughingthrushes (1.8 mya; 95% HPD 0.7–3.1 mya), and analyses of the other taxa in this complex would be desirable before a taxonomic change. Similarly, *Garrulax albogularis ruficeps* was given species status by del Hoyo and Collar (2016) and Gill and Donsker (2017) following the plumage differences outlined by Collar (2006). The divergence between the Taiwanese *G. a. ruficeps* and the two mainland taxa (*G. a. albogularis*, *G. a. eous*) (1.1 mya; 95% HPD 0.5–2.0 mya) is not as deep as between *G. canorus* and *G. taewanus*, and it seems preferable to continue to treat *ruficeps* as a subspecies of *G. albogularis*. del Hoyo and Collar (2016) also treated *Garrulax chinensis monachus* (endemic to Hainan Island, China) as a separate species from continental *G. chinensis* based on morphology, supported by

a molecular study (Wu et al., 2012). However, that split would only be valid if *G. chinensis germaini* (not studied by Wu and collaborators) is treated as conspecific with *G. monachus*; moreover, the divergence between *G. c. chinensis* and *G. c. monachus*/*G. c. germaini* is not particularly deep (0.8 mya; 95% HPD 0.3–1.6 mya).

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ORCID

Alice Cibois  <http://orcid.org/0000-0002-3668-071X>

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