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Author for correspondence:

Per Alström

e-mail: per.alstrom@slu.se

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Phylogeny

Discovery of a relict lineage and monotypic family of passerine birds

Per Alström^{1,2}, Daniel M. Hooper³, Yang Liu⁴, Urban Olsson⁵, Dhananjai Mohan⁶, Magnus Gelong⁷, Hung Le Manh⁸, Jian Zhao⁴, Fumin Lei¹ and Trevor D. Price³

¹Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, 1 Beichen West Road, Chaoyang District, Beijing 100101, People's Republic of China

²Swedish Species Information Centre, Swedish University of Agricultural Sciences, PO Box 7007, Uppsala 750 07, Sweden

³Department of Ecology and Evolution, University of Chicago, Chicago, IL 60637, USA

⁴State Key Laboratory of Biocontrol and School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, People's Republic of China

⁵Systematics and Biodiversity, Department of Biology and Environmental Sciences, University of Gothenburg, Gothenburg 40530, Sweden

⁶Wildlife Institute of India, PO Box 18, Chandrabani, Dehradun 248001, India

⁷Department of Zoology, Swedish Museum of Natural History, Stockholm 10405, Sweden

⁸Zoology Museum Department, Institute of Ecology and Biological Resources, Hanoi, Vietnam

Analysis of one of the most comprehensive datasets to date of the largest passerine bird clade, Passerida, identified 10 primary well-supported lineages corresponding to Sylvioidea, Muscicapoidea, Certhioidea, Passeroidea, the 'bombycillids' (here proposed to be recognized as Bombycilloidea), Paridae/Remizidae (proposed to be recognized as Paroidea), Stenostiridae, Hyliotidae, Regulidae (proposed to be recognized as Reguloidea) and spotted wren-babbler *Spelaeornis formosus*. The latter was found on a single branch in a strongly supported clade with Muscicapoidea, Certhioidea and Bombycilloidea, although the relationships among these were unresolved. We conclude that the spotted wren-babbler represents a relict basal lineage within Passerida with no close extant relatives, and we support the already used name *Elachura formosa* and propose the new family name Elachuridae for this single species.

1. Introduction

Birds have been described and charted more completely than other taxa, and, thanks to molecular analyses, their relationships are beginning to be well understood [1,2]. These studies have revealed multiple examples, at both high and low levels, where the traditional classification has been contradicted. At lower taxonomic levels, rampant convergences in morphology or unequal rates of morphological divergence, often in combination with unusual biogeographic distributions, have confounded classifications based on phenotypic characters [2,3]. Some of the more notable examples of passerine species with previously misinterpreted relationships include the bearded reedling (*Panurus biarmicus*) [4–6], rail-babbler (*Eupetes macrocerus*) [7], white-bellied erpornis (*Erpornis zantholeuca*) [8,9], cinnamon ibon (*Hypocryptadius cinnamomeus*) [10], black-capped donacobius (*Donacobius atricapilla*) [5,6,11], yellow-bellied fantail (*Chelidorhynch hypoxantha*) [12], silktail (*Lamprolia victoriae*) [13], ground tit (*Pseudopodoces humilis*) [14,15] and malia (*Malia grata*) [16].

The past 10 years have witnessed a surge in taxonomic changes in Asian birds, partly as a result of molecular analyses [3,17]. A large fraction has been within the songbird group called 'bblers'. Based on several comprehensive molecular studies [5,6,18–20], five primary clades have been identified: Timaliidae,

Leiotrichidae, Pellorneidae, Zosteropidae and Sylviidae. Previously, the circumscription of Timaliidae included the majority of the ‘babblers’, whereas Sylviidae was traditionally applied to various groups of ‘warblers’ (review in [3]). Within Timaliidae, five species of *Spelaornis* ‘wren-babblers’ were recognized [21,22], until Collar & Robson [23] split *Spelaornis chocolatinus* into four species and moved the spotted wren-babbler, *Spelaornis formosus*, to the monotypic genus *Elachura* based on morphology and vocalizations.

Based on one of the most comprehensive datasets for the large Passerida clade, both regarding number of taxa and loci, we review the systematics of this taxon and show, for example, that *S. formosus* is not a babbler, but in fact represents a relict taxon with no close extant relatives.

2. Material and methods

Sequence data were obtained from representatives of all families within Passerida except three monotypic families, including three *S. formosus* from different parts of its range (figure 1) and four other *Spelaornis* species (deposited in Dryad). Seven loci were analysed: the mitochondrial cytochrome *b* (*cytb*) and *ND2*, nuclear *GAPDH*, *ODC*, myoglobin (*myo*) and *LDH* introns and coding *RAG1*, although not all loci were obtained for all species (deposited in Dryad). The data were analysed by Bayesian inference in MrBAYES [25] and by maximum-likelihood bootstrapping with RAxML [26]. See the electronic supplementary material for the laboratory procedures and phylogenetic analyses. Details of samples, including GenBank numbers, uploaded to Dryad.

3. Results

A ‘condensed’ multilocus tree is shown in figure 2; the same tree with all branches visible and single-locus trees appear in the electronic supplementary material, figures S1 and S2. Within Passerida, the superfamilies Sylvioidea, Muscipoidea, Certhioidea and Passeroidea were recovered with strong support. At the ‘same level’ in the tree, five well-supported smaller clades representing Remizidae + Paridae, Stenostiridae, the ‘bombycillids’ (Bombycillidae, Hylocitridae, Ptilonotidae and Dulidae), Regulidae and Hyliotidae were recovered. *Spelaornis formosus* sat on a ‘bare’ branch among these basal lineages. Sylvioidea, Remizidae + Paridae, Stenostiridae and Hyliotidae formed a clade, and Muscipoidea, Certhioidea, the ‘bombycillids’ and *S. formosus* another one, both well supported. Other relationships among the primary lineages were uncertain, and the base of Passerida was characterized by extremely short internodes.

4. Discussion

This study is the first to our knowledge to provide strong support for a clade comprising Sylvioidea, Remizidae + Paridae, Stenostiridae and Hyliotidae, and another one containing Muscipoidea, Certhioidea and the ‘bombycillids’ (and *S. formosus*; cf. [27,28]). However, the relationships among these and the other basal lineages within Passerida remain uncertain, probably due to an explosive divergence of these primary lineages, as suggested by the phylogeny.

Spelaornis formosus is clearly not a ‘babbler’, but instead on its own forms one of the 10 primary lineages within the Passerida radiation. Although the data support a relationship

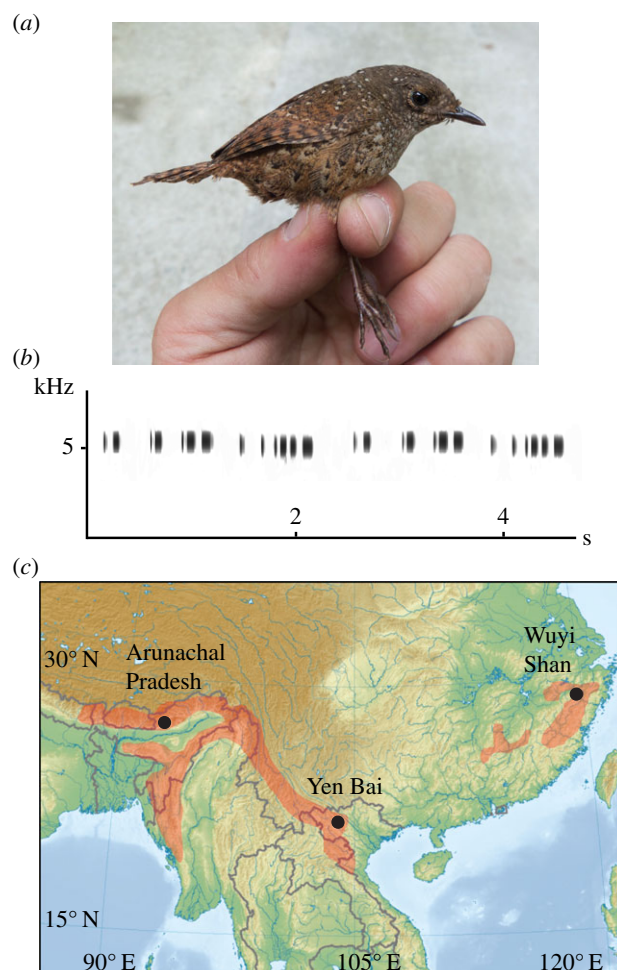


Figure 1. (a) Spotted wren-babbler *Elachura formosa* (previously *S. formosus*); Wuyi Shan, Jiangxi, China, April 2013 (IOZ 18251) (P.A.). (b) The song of *E. formosa* is a continuous repetition of units of high-pitched, short notes (two such units, each ca 2 s long, shown); Wuyi Shan, Fujian, April 1993 (P.A.). (c) Distribution based on [23,24]. Sampling localities are indicated by dots. (Online version in colour.)

with Muscipoidea, Certhioidea and the ‘bombycillids’, the precise position of *S. formosus* within this clade is uncertain. The distinctness of *S. formosus* is most unexpected. Morphologically and ecologically, it closely resembles several ‘wren-babblers’ [23]. In many respects, it is also very similar to some *Troglodytes* wrens. However, its song bears little resemblance to other continental Asian passerines ([23]; personal observation; figure 1), and this in combination with its ‘decidedly longer bill’ compared with other *Spelaornis* led Collar & Robson [23] to place it in the monotypic genus *Elachura*. The phenotypic similarities between *S. formosus* and some *Spelaornis* and *Troglodytes* have apparently evolved in parallel. This has previously been shown to be the case for the *Pnoepyga* ‘wren-babblers’, which were recently placed in a monotypic family, Pnoepygidae [19].

Our results support the placement of the spotted wren-babbler in a separate genus, *Elachura*. Moreover, based on its phylogenetic distinctness, we recommend that it be placed in a monotypic family, for which we propose a new family name: Elachuridae. Type genus *Elachura* Oates, 1889. Diagnosis: The monotypic genus *Elachura* includes *Elachura formosa*, which is a small (ca 10 cm), short-tailed (ca 3 cm) oscine with grey–brown crown, nape, ear-coverts and upperparts with whitish or pale buffish terminal spots and blackish

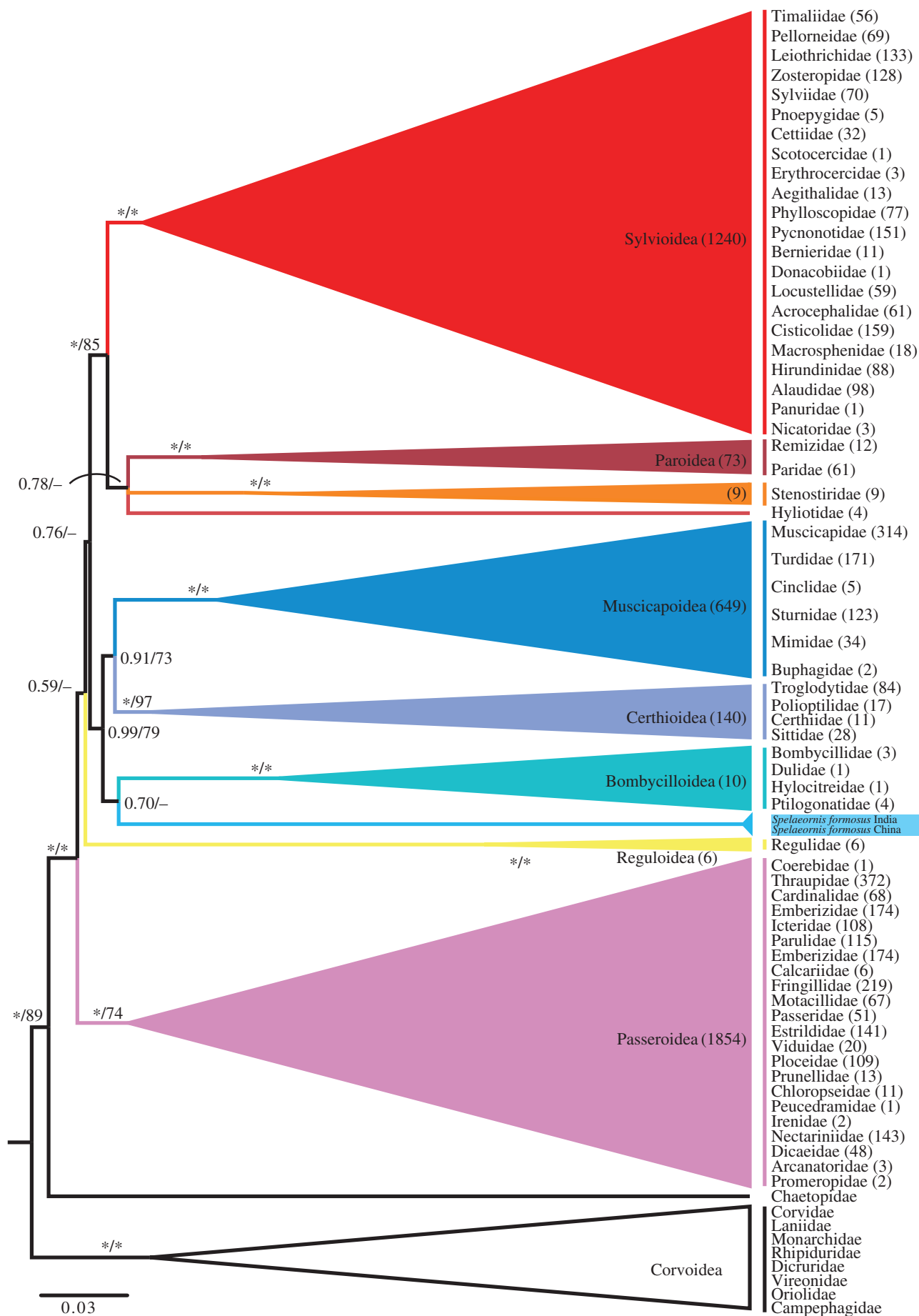


Figure 2. Relationships of the primary lineages within Passerida based on mitochondrial *cytb* and *ND2* and nuclear myoglobin, *ODC*, *GAPDH*, *LDH* and *RAG1*, analysed by Bayesian inference in 10 partitions under a relaxed clock model. Posterior probabilities (PP) and maximum-likelihood bootstrap (MLBS) values are shown at the nodes, in this order; asterisk (*) indicates PP 1.00 or MLBS 100%. Numbers in parentheses indicate the number of species in the different groups. (Online version in colour.)

subterminal markings to many of the feathers; throat and breast mottled with grey–brown and whitish and some blackish subterminal markings; rest of underparts pale rufous with blackish subterminal markings and whitish tips to many of the feathers, especially on the flanks; remiges (outer webs) and rectrices rufous with broad, widely spaced blackish bars. See figure 1 and [23, p. 176 and Plate 7]. The name Elachuridae has been registered in ZooBank under LSID zoobank.org: act: E95131EF-4849-46A4-915B-1789ABC08143. We suggest that the English name be changed to Elachura to highlight its uniqueness.

It could be argued that the phylogenetic distinctness of Elachuridae warrants recognition also at the rank of superfamily, as could be claimed for all of the well-supported primary lineages within Passerida. The case is strongest for Paridae + Remizidae, Regulidae and the ‘bombycillids’, which have consistently proved highly distinctive in previous studies [5,6,9,15,29]. We propose that these be recognized at the level of superfamily, Paroidea, Reguloidea and Bombycilloidea, respectively.

Species on long terminal branches (‘old’ species) are disproportionately distributed among the non-passerines, e.g. the

palaeognaths (ostriches, kiwis, etc.), kagu (*Rhynchoceros jubatus*), hoatzin (*Opisthocomus hoazin*), oilbird (*Steatornis caripensis*) and cuckoo roller (*Leptosomus discolor*) [30]. Owing to their overall younger age, relatively few passerines display the same pattern, e.g. the four New Zealand wrens (Acanthisittidae), the two lyrebirds (Menuridae) and the two rockjumpers (Chaetopidae). Within Passerida, which contains ca 36% of all birds and 60% of all passerines, the spotted wren-babbler is unique, as it is the only extant species that on its own represents one of the most basal lineages.

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Data accessibility. Data deposited in Dryad: doi:10.5061/dryad.hd765.

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