Discovery of a relict lineage and monotypic family of passerine birds

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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 macrocercus) [7], white-bellied erpornis (Erpornis zantholeuca) [8,9], cinnamon ibon (Hypocryptadius cinnamomeus) [10], black-capped donacobius (Donacobius atricapilla) [5,6,11], yellow-bellied fantail (Chelidorhynx 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 ‘babblers’. 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 Spelaeornis ‘wren-babblers’ were recognized [21,22], until Collar & Robson [23] split Spelaeornis choklatinus into four species and moved the spotted wren-babbler, Spelaeornis 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 Spelaeornis 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 Sylvoidea, Muscicapoidea, Certhioidea and Passeroidea were recovered with strong support. At the ‘same level’ in the tree, five well-supported smaller clades representing Remizidae þ Paridae, Stenostiridae, the ‘bombycillids’ (Bombycillidae, Hyllocitreidae, Ptilogonatidae and Dulidae), Regulidae and Hyliotidae were recovered. Spelaeornis formosus sat on a ‘bare’ branch among these basal lineages. Sylvoidea, Remizidae þ Paridae, Stenostiridae and Hyliotidae formed a clade, and Muscicapoidea, 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 Sylvoidea, Remizidae þ Paridae, Stenostiridae and Hyliotidae, and another one containing Muscicapoidea, 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.

Spelaeornis 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 with Muscicapoidea, 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 Spelaeornis led Collar & Robson [23] to place it in the monotypic genus Elachura. The phenotypic similarities between S. formosus and some Spelaeornis 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 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.)
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, Reguluoidea and Bombycoidea, respectively.

Species on long terminal branches (‘old’ species) are disproportionately distributed among the non-passerines, e.g. the palaeognaths (ostriches, kiwis, etc.), kagu (Rhinoceros 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 (Chaetopodidae). 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.

Acknowledgements. Normand David, Edward Dickinson, Steven Gregory and Johan Liljeblad are acknowledged for advice on nomenclature; Nigel Collar, Jon Fjeldså, Lars Larsson, Pamela Rasmussen and Craig Robson for various forms of assistance; Guoqin Chen for laboratory assistance; the Government of India and Chief Wildlife Warden of Arunachal Pradesh and Jiangxi Wuyi Shan National Nature Reserve for permits.


Funding statement. We thank the Jornvall Foundation and the Chinese Academy of Sciences for a Visiting Professorship for Senior International Scientists (no. 2011T2504) awarded to P.A., the One Hundred Talents project of Sun Yat-sen University (Y.L.) and the National Science Foundation (U.S.A.) (T.D.P.).

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