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Multiple species within the Striated Prinia *Prinia crinigera*–Brown Prinia *P. polychroa* complex revealed through an integrative taxonomic approach

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We re-evaluated the taxonomy of the Striated Prinia *Prinia crinigera*–Brown Prinia *P. polychroa* complex using molecular, morphological and vocal analyses. The extensive seasonal, sexual, age-related, geographical and taxon-specific variation in this complex has never before been adequately studied. As no previous genetic or vocal analyses have focused on this group, misinterpretation of taxonomic signals from limited conventional morphological study alone was likely. Using mitochondrial and nuclear DNA, we found that *P. crinigera sensu lato* (*s.l.*) comprises two non-sister groups of taxa (Himalayan *crinigera* and Chinese *striata* groups) that differ substantially morphologically and vocally and that are broadly sympatric in Yunnan Province, China. *Prinia polychroa cooki* (Myanmar) and *P. p. rocki* (southern Vietnam) are each morphologically, vocally and genetically distinct. Thai, Cambodian and Laotian populations formerly ascribed to *P. p. cooki* are morphologically and vocally most similar to and most closely related to Javan *P. p. polychroa*, and require a new name, proposed here. *Prinia p. bangsi* of Yunnan is part of the *crinigera* group rather than of *P. polychroa*, and hence there is no evidence for sympatry between *P. polychroa s.l.* and *P. crinigera s.l.*, nor of the occurrence of *P. polychroa* in mainland China or Taiwan. We recommend the recognition of five species in the complex, with the following suggestions for new English names: Himalayan Prinia *P. crinigera sensu stricto* (*s.s.*; with subspecies *striatula*, *crinigera*, *yunnanensis* and *bangsi*); Chinese Prinia *P. striata* (subspecies *catharia*, *parumstriata* and *striata*); Burmese Prinia *P. cooki* (monotypic); Annam Prinia *P. rocki* (monotypic) and Deignan's Prinia *P. polychroa s.s.*

(subspecies Javan *polychroa* and the new Southeast Asian taxon). This study underlines the importance of using multiple datasets for the elucidation of diversity of cryptic bird species and their evolutionary history and biogeography.

Keywords: biodiversity, Cisticolidae, DNA, morphology, phylogeography, Sylvioidea, systematics, vocalizations.

INTRODUCTION

Recent studies of vocal and molecular variation have revealed many cryptic avian species (e.g. see Alström *et al.* 2013 for a review of findings in the Sylvioidea). The prinias (genus *Prinia*), which belong to the subfamily Priniinae of the Cisticolidae within the superfamily Sylvioidea (Alström *et al.* 2006, 2013, Johansson *et al.* 2008, Fregin *et al.* 2012, Olsson *et al.* 2013), have received very limited recent systematic study, as is generally true for other members of the Cisticolidae (Bowie *et al.* 2009, Mahood *et al.* 2013, Lim *et al.* 2014).

The Striated Prinia *Prinia crinigera*–Brown Prinia *P. polychroa* complex is currently treated as two marginally sympatric species, the former distributed in southern through eastern Asia, and the latter in Southeast Asia, including Java (Madge 2006; Fig. 1; distributions modified based on findings herein). Whereas *P. crinigera sensu lato* (*s.l.*) is mainly montane, distributed at 1200–3000 m (Inskipp & Inskipp 1991, Martens & Eck 1995, Rasmussen & Anderton 2005, Madge 2006), *P. polychroa* occurs mainly in lowlands up to 1500 m (MacKinnon & Phillipps 1993, Robson 2000, Madge 2006). All populations are sedentary, although *P. crinigera* may undertake seasonal altitudinal movements (Rasmussen & Anderton 2005, Madge 2006). Six or seven subspecies are currently accepted in *P. crinigera* and four in *P. polychroa* (Madge 2006, Dickinson & Christidis 2014, Gill & Donsker 2017; Table 1).

No comprehensive recent study has dealt with all taxa in this complex; the most recent review (Abdulali & Unnithan 1986) dealt only with *P. crinigera s.l.* Previously, Sharpe (1903) treated all mainland taxa as one species, *Suya crinigera*, while placing the Javan taxon in a different genus, *Prinia polychroa*. La Touche (1922) described two new subspecies, *P. c. bangsi* and *P. c. parvirostris*, both from southeastern Yunnan Province, China, and Bangs (1930) then raised the latter to species rank without comment, but this was not followed by others. Several authors recognized only one species, *P. polychroa* (Baker 1924a, Delacour & Jabouille 1931, Deignan 1942, Smythies 1953).

The most influential studies of this complex have been those by Deignan (1942, 1957), the first being a single-species treatment based on similarity of the southernmost mainland populations then known as *P. crinigera* to Javan *P. polychroa*. However, upon later re-examination of specimens, Deignan (1957) found that two morphologically distinct taxa, *parvirostris* and *bangsi*, occurred at Mengtz (= Mengzi, southeast Yunnan Province, China). He therefore proposed a northern species, *Prinia crinigera* (including *parvirostris*), and a southern species, *P. polychroa* (including *bangsi*), that were sympatric at Mengzi. Although some later authors recognized only a single species (e.g. Vaurie 1959, Ripley 1961, Morony *et al.* 1975, Fleming *et al.* 1976, Cheng 1987), Deignan's (1957) two-species taxonomy is still generally accepted (e.g. King *et al.* 1975, Madge 2006, Dickinson & Christidis 2014, del Hoyo & Collar 2016, Gill & Donsker 2017; Table 1). In contrast to most others, Meyer de Schauensee (1984) placed two taxa usually treated as subspecies of *P. crinigera* (*yunnanensis* and *parvirostris*) within *P. polychroa*.

Despite broad acceptance, Deignan's (1942, 1957) assignment of allopatric taxa to species based on plumage similarity risked the creation of non-monophyletic taxa. In addition, some subspecies (e.g. *P. crinigera catharia* and *P. c. parvirostris*) were described without reference to key taxa described previously. Specimens from central Southeast Asia were tentatively assigned to a named taxon (*P. p. cooki*) by Deignan (1957) without direct comparisons with topotypical *cooki*; this preliminary treatment then became entrenched in the literature without further study. Furthermore, the sole basis then known for recognizing two species, the sympatry of *P. crinigera*

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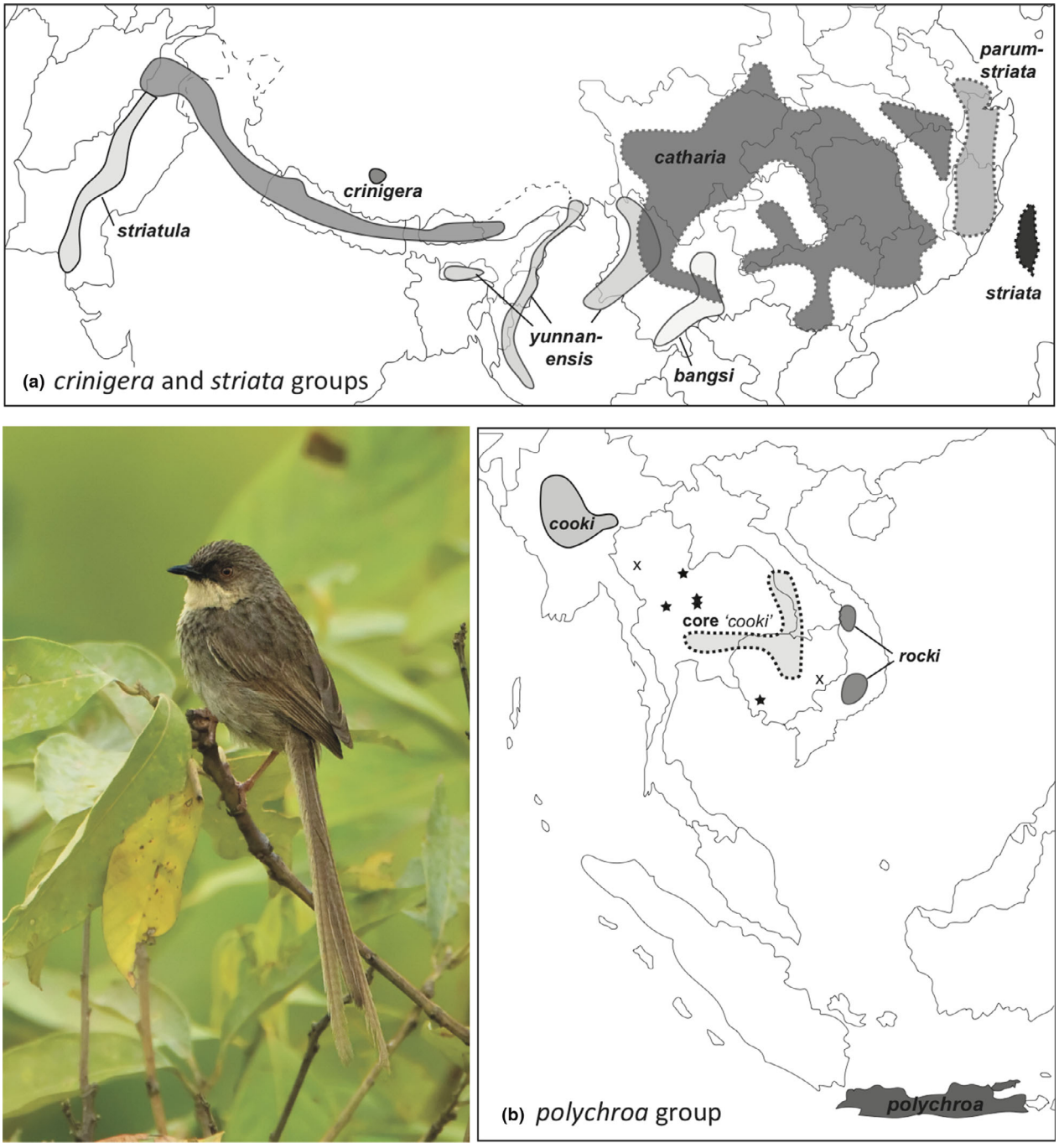

Figure 1. Distribution maps for taxa of the *Prinia crinigera*–*P. polychroa* complex: (a) the *crinigera* and *striata* groups, and (b) the *polychroa* group. These are based on verified specimens, photographs and sound recordings, and using the taxon names that we recommend (except for core '*cooki*', which we describe as a new taxon herein). In (a), taxa in the *crinigera* group have solid range borders, whereas these are dashed for taxa in the *striata* group. In (b), taxon ranges have solid borders except for core '*cooki*', which is dashed for the main range. Stars indicate other core '*cooki*' localities outside the main range. 'X' indicates records of uncertain taxon. Photo: *P. crinigera yunnanensis*, Pungro, Nagaland, May 2010 (Ramki Sreenivasan).

Table 1. Taxonomic recommendations, revised distributions and morphological characteristics for the *Prinia crinigera–P. polychroa* complex, compared with treatment in recent global lists (Dickinson & Christidis 2014, del Hoyo & Collar 2016, Gill & Donsker 2017).

Dickinson and Christidis (2014), del Hoyo and Collar (2016), Gill and Donsker (2017)	Revised taxonomy (type localities in parentheses)	Revised distribution	Morphological characteristics
Prinia crinigera	***Prinia crinigera***	Sympatric with *P. striata* in Yunnan Province, China	Strongly sexually size-dimorphic and dichromatic, and strongly seasonally variable, especially in males. Breeding males have blackish crown with variably paler edgings, and blackish face; dark-mottled breast-sides, indistinctly streaked mantle (mantle much less streaked than crown); wing panel dull. Breeding female darker and less streaked above than in non-breeding plumage. In non-breeding plumage, both sexes heavily streaked above, with paler supercilia, faint mottling on sides of face and breast. Tail long and rather broad, dark, cold-toned, and dark-barred above, with distinct dark subterminal crescents below. Bill all blackish in breeding male, pale pinkish with darker tip to lower mandible in female and non-breeding male. See Figure 5 and Table S6.
P. c. striatula	*P. c. striatula* (Hume, 1873) (Karachi, Sind, Pakistan)	W Pakistan south of Himalayas	Palest subspecies
P. c. crinigera	*P. c. crinigera* Hodgson, 1836 (Nepal)	E Afghanistan (?), Pakistan Himalayas through EC Himalayas	Medium-toned subspecies
P. c. assamica, *P. c. catharia* (part)	*P. c. yunnanensis* (Harington, 1913) (Momien = Tengchong, Yunnan, China) [Synonyms: *P. c. assamica* (Stuart Baker, 1922) (Shillong, Meghalaya, India) and *P. c. nebulosa* (Koelz, 1952), (Cherrapunji, Meghalaya, India)]	NE India from Assam through NE hill states, N Myanmar, W Yunnan, China	Darkest subspecies
P. p. bangsi	*P. c. bangsi* (La Touche, 1922) (Mengtsz = Mengzi, Yunnan, China)	SE Yunnan, China	Slightly paler than *yunnanensis*
	Prinia striata	Sympatric with *P. crinigera* in Yunnan Province, China	Moderate levels of sexual size-dimorphism, dichromatism and seasonal variation. Breeding birds of both sexes have pale face-sides, including pale supercilium; underparts whitish and hardly mottled; mantle usually clearly streaked (not much less prominently than crown); wing panel rufous unless worn. Bill as in *P. crinigera s.s.* Sexes similar in breeding plumage except for darker bill of male. Non-breeding adults much more heavily streaked above, with brighter rufous wing panel, than in breeding plumage. Tail rather long, thin, warm-toned above without strong dark barring on uppertail, lacking distinct dark subterminal crescents. See Figure 5 and Table S6.

(continued)

Table 1. (continued)

Dickinson and Christidis (2014), del Hoyo and Collar (2016), Gill and Donsker (2017)	Revised taxonomy (type localities in parentheses)	Revised distribution	Morphological characteristics
P. c. striata	*P. s. striata* Swinhoe, 1859 (Hongsan, Taiwan)	Taiwan	Less rufescent wing panel, bolder streaking above (darker black streaks and paler edges), more mottling on throat and breast sides even in breeding plumage, and paler rufescent flanks than *parumstriata*.
P. c. parumstriata (part), *P. c. catharia* (part), *P. p. bangsi*	*P. s. parumstriata* (David & Oustalet, 1877) (Fukien = Fujian, China) [Synonym: *P. s. parvirostris* (La Touche, 1922) (Shuitang, Yunnan, China)]	SE coastal China	See *striata* for differences; typically slightly darker and more rufescent above than *catharia*
P. c. catharia (part)	*P. s. catharia* Reichenow, 1908 (Ta-tsieng-lu-ting = Kangding, Sichuan)	Interior China	See *parumstriata* for differences
P. p. cooki	***Prinia cooki*** (Harington, 1913) (Thayetmyo, Myanmar)	C Myanmar	Strongly sexually size-dimorphic and dichromatic, and strongly seasonally variable in the same ways as *P. crinigera*. Much like *P. crinigera* but paler, browner, less streaked above, whiter and less mottled below, with more distinct pale supercilium in breeding male. Bill as in *P. crinigera s.s.* (which see). See Figure 5 and Table S6.
P. p. rocki	***Prinia rocki*** Deignan, 1957 (Fimnon = Fimnom, Vietnam)	C and S Vietnam	Less streaked above than *P. crinigera* or *P. striata*, without blackish face of breeding male *crinigera*. Strong seasonal changes in plumage saturation (more saturated buffy in fresh plumage), similar in both sexes. Moderately well-marked undertail markings with buffy tips. See Figure 5 and Table S9.
	Prinia polychroa		Very slight sexual or seasonal variation, except in bill colour in males in at least core Asian '*cooki*'. Very drab. No sympatry known with other species.
P. p. polychroa	*P. p. polychroa* (Temminck, 1828) (Java)	Java	Slightly to distinctly darker and greyer above; no rufescent wing panel or tertial edgings; prominent undertail markings when fresh.
P. p. cooki	Core '*cooki*', here described as a new taxon	Thailand, Laos, Cambodia	Slightly to distinctly paler and browner above; rufescent wing panel and tertial edgings in fresh plumage; weak or no undertail markings when fresh. See Figure 5 and Table S6

and *P. polychroa*, was rejected by Cheng (1987), who synonymized *P. p. bangsi* with *P. c. parvirostris*. Some checklist authors (Watson *et al.* 1986, Sibley & Monroe 1990, Clements 2007) listed both *P. polychroa* and *P. crinigera* for Taiwan, implying but not demonstrating sympatry there.

Some of the constituent taxa vary greatly by season, age, sex and geography, and hence study of large series, in conjunction with genetic and vocal analyses, is required for accurate reconstruction of species limits. In this study, we assess patterns of morphological and song divergence, in combination with analyses of mitochondrial and nuclear DNA, to revise species limits in the *Prinia crinigera–P. polychroa* complex. During this analysis, we detected an undescribed taxon in Southeast Asia, which we describe herein.

METHODS

Operational taxonomic units and distributions

We follow David and Gosselin (2002) herein in using the name *P. crinigera* rather than the long-standing *P. criniger*. Based on our findings (detailed below and in Table 1) we consider *P. crinigera striatula*, *P. c. crinigera*, *P. c. yunnanensis*, *P. c. bangsi* and synonyms of these taxa as the *crinigera* group; *P. c. catharia*, *P. c. parumstriata*, and *P. c. striata* and a synonym as the *striata* group; and *P. polychroa polychroa*, *P. p. cooki* and *P. p. rocki* as the *polychroa* group. Because we found that *P. p. cooki s.l.* represents at least two distinct lineages, we distinguish between Myanmar *cooki* (all *Prinia polychroa s.l.* from Myanmar) and core '*cooki*' (*Prinia polychroa s.l.* from Thailand, Cambodia and Laos) throughout, and we describe the latter as a new subspecies.

Distributional maps (Fig. 1) were based on localities of: verified specimens; sound recordings (including our own) from publicly available archives AVoCet (avocet.zoology.msu.edu) and xeno-canto (xeno-canto.org), and our own sound recordings; and photos on eBird (ebird.org) and Oriental Bird Images (orientalbirdimages.org). Other sources, including literature records compiled for China by Richard Lewthwaite and eBird reports lacking photographic documentation, were consulted but not mapped due to the unverifiability of sight records therein, as unvouchered, undocumented sight reports of *Prinia crinigera s.l.* from Yunnan could refer either to members of the *crinigera* or *striata* groups. We have seen cases of confusion between *P. polychroa* and Plain Prinia *P. inornata* photos and specimens, and confusion between *P. polychroa* and a Rufescent Prinia *Prinia rufescens* photo.

Morphology

Specimens of all taxa of *Prinia polychroa s.l.* and *P. crinigera s.l.* were examined for qualitative plumage characters. Those studied were from the American Museum of Natural History, New York, NY, USA (AMNH); Academy of Natural Sciences, Philadelphia, PA, USA (ANSP); Field Museum of Natural History, Chicago, IL, USA (FMNH); Institute of Zoology, Chinese Academy of Sciences, Beijing, China (IOZ); Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China (KIZ); Museum of Comparative Zoology, Cambridge, MA, USA (MCZ); Museum National d'Histoire Naturelle, Paris, France (MNHN); Museum Zoologicum Bogoriense, Cibinong, West Java, Indonesia (MZB); Naturalis Biodiversity Center, Leiden, the Netherlands (NBC, specimen acronym RMNH); National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (NMNH, specimen acronym USNM); the Natural History Museum, Tring, UK (NHMUK, formerly BMNH); Royal Ontario Museum, Toronto, Canada (ROM); Thailand Natural History Museum (THNHM); University of Michigan Museum of Zoology, Ann Arbor, MI, USA (UMMZ); Yale Peabody Museum, New Haven, CT, USA (YPM); and Museum für Naturkunde, Berlin, Germany (ZMB). Specimens included in the final analysis of qualitative plumage scores were from AMNH, FMNH, NHMUK and USNM.

A total of 107 specimens were measured by P.C.R. for each of 18 characters, with 485 additional specimens measured for a subset of these characters: culmen length from skull base; culmen length from distal edge of feathers; bill width from distal edge of nares; bill depth from distal edge of nares; longest rictal bristle; unflattened wing (wing arc); flattened wing (wing chord); wingtip projection beyond longest secondary; primary shortfalls (distance from longest primary in folded wingtip of each primary 1–5, numbered ascendantly); tail length (with callipers inserted between middle two rectrices); tail graduation (distance from longest central rectrix to shortest, outermost rectrices in folded tail); maximum central rectrix width (only for feathers in good condition); tarsus length; and hindclaw length. Univariate statistics for mensural characters and Bonferroni-adjusted two-way *t*-tests using pooled variances, and principal component analyses (PCAs) using covariance matrices were conducted using MyStat (SYSTAT Software, Crane Software International). Mensural data showed some departures from normality, so preliminary analyses were conducted using either natural log-transformed data or a non-parametric test; in both cases, results and significance levels were much the same as for the untransformed data analysed using *t*-tests, although the Bonferroni-adjusted *t*-tests of untransformed data resulted in fewer statistically significant differences and thus we prefer its use. The full mensural dataset is provided (Supporting Information Table S1). Sexes were

separated for all analyses, and juveniles (identified by pointed fresh rectrices, reduced mantle-streaking and, in younger individuals, yellow-tinged underparts) were excluded. For analysis of tail characters, specimens were divided into breeding and non-breeding plumage; however, for taxa of *P. polychroa s.l.* other than Myanmar *cooki*, this could only be done on the basis of season, with October–February specimens considered non-breeding and March–September specimens breeding.

Based on preliminary results (below), specimens were grouped into the following taxa whose distributional limits differ from those widely accepted: (1) *yunnanensis* (including *assamica*), from Assam, India, through western Yunnan; (2) *bangsi*, eastern Yunnan; (3) *catharia*, inland China, from western Sichuan and western Yunnan Provinces east to Anhui and Guangdong Provinces; (4) *parumstriata*, Jiangsu to Fujian, coastal China; and (5) *cooki*, Myanmar; (6) core '*cooki*', described below as new, from Thailand, Laos and Cambodia.

For the new taxon description, Munsell Soil Color Charts (2000) were used as a colour standard. For 238 specimens, 13 external plumage and bill colour characters of specimens (as well as indications of age and sex, and whether in breeding or non-breeding plumage, often not determinable in *P. polychroa s.l.*) were scored by P.C.R. using a variable scale, as follows (see Supporting Information Fig. S1 for reference photos of specimens describing and showing each character state): lower mandible colour (1 = all pale; 6 = solid black); crown streak prominence (1 = unstreaked, 6 = crisply streaked); pale supercilium prominence (1 = none, 6 = very prominent pale supercilium); suborbital auriculars colour (1 = whitish, 6 = blackish); malar speckling (1 = none, 6 = heavy); mantle streak prominence (1 = none, 6 = crisply streaked); mantle edging colour (1 = greyish, 6 = strongly rufous); wing panel colour (1 = grey, 6 = bright rufous); tertial edge colour (1 = drab, 6 = rich rufous); breast feather base exposure through wear (1 = none, 6 = heavy); uppertail barring prominence (1 = none, 5 = prominent); uppertail rufescence (1 = grey, 6 = rich rufous); and undertail subterminal dark spots (1 = negligible, 10 = strongly contrasting, large). A few specimens of the *striata* group have blackish mantle streaks bordered by a narrow rufous strip and then edged greyish, in which case the outer edges were scored. When worn and fresh feathers were present in the same specimen, only fresh feathers were scored. Where sides differed, the side with the feature most pronounced was scored. Raw data are available in Table S1.

Univariate statistics for plumage scores, Kruskal–Wallis one-way analyses of variance, and PCAs using covariance matrices were conducted on plumage character scores using MyStat. Sexes were separated for all analyses and juveniles were excluded. Plumage scores of breeding and non-breeding plumaged specimens were analysed separately for all taxa of *P. crinigera s.l.* and for Myanmar *cooki* and *rocki*, but not for the other taxa of *P. polychroa s.l.*, in which seasonal plumage change is negligible. We also compared measurements and plumage scores statistically between *yunnanensis* and *assamica* (the latter often not recognized) using the above methods.

Songs

Sound recordings of territorial songs were obtained from 35 localities and for eight taxa (Supporting Information Table S2). For each individual, sonograms were generated in Raven Pro 1.5 (Cornell Laboratory of Ornithology, Ithaca, NY, USA). A 'note' was defined as an unbroken trace in a sonogram, and a 'phrase' was defined as the smallest stereotypic repetition of similar note sequences (Fig. 2). In some taxa, a phrase consisted of two 'subphrases', i.e. two different sets of notes separated by a brief interval (Fig. 2). The following variables were measured: (1) phrase duration; (2) interval between phrases; (3) phrase proportion (duration of phrase divided by phrase + interval between phrases); (4) number of notes; (5) note rate (number of notes per second); (6) number of rising notes; (7) number of falling notes; (8) number of rising and then falling (/\-shaped) notes; (9) number of falling and rising (\/-shaped) notes; (10) number of 'complex' notes (a note consisting of three or more elements which differ from each other in shape); and (11) number of trills (i.e. repetition of a single element) (Fig. 2). As the variation among different phrases from the same individual was negligible, we measured one to five phrases per individual and calculated their mean. The means of each individual were used as sample points for statistical analysis. We ran a discriminant function analysis (DFA) in SPSS v. 22 (IBM Corp.) to test whether the individuals could be correctly assigned to the groups defined by phylogeographical analysis

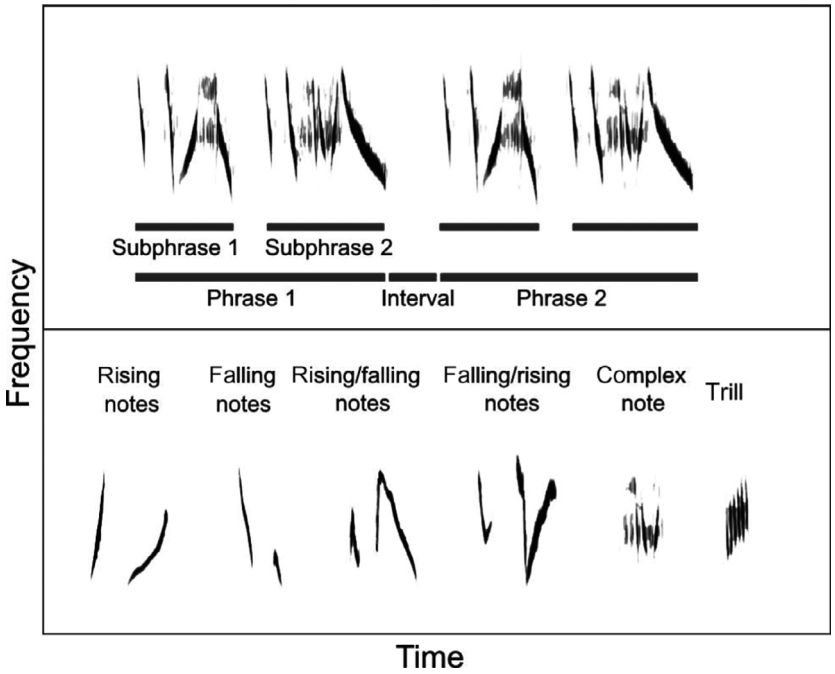

Figure 2. Terminology of song components (upper panel) and examples of note types found in songs of the *Prinia crinigera–polychroa* complex (lower panel).

(Supporting Information Materials S4 and S5). Bonferroni-adjusted two-sample *t*-tests were used to test differences between groups in univariate summary statistics using SPSS version 22. Most recordings analysed are freely available at AVoCet (http://www.avocet.zoology.msu.edu), and a few are available at xeno-canto (http://www.xeno-canto.org) (Table S2). One recording was from a commercial publication (Scharringa 2005). Published sonograms were sometimes 'cleaned' a little to remove background noise.

DNA collection, extraction and sequencing

In total, 29 blood, feather, muscle or toepad samples were obtained from birds from 21 localities, representing all recognized taxa except *P. c. parvirostris* (presently recognized from southeast Yunnan Province, China; Dickinson & Christidis 2014, del Hoyo & Collar 2016, Gill & Donsker 2017), including topotypical *bangsi* and the holotype of Myanmar *cooki* (Supporting Information Table S3 and Material S6). Sequences from two additional individuals were downloaded from GenBank (Table S3). DNA was extracted using QIA Quick DNEasy Kit (Qiagen, Inc.), according to the manufacturer's instructions, but with 30 μL dithiothreitol added to the initial incubation step for the extraction from feathers and toepads. We sequenced the mitochondrial cytochrome *b* (cyt*b*) gene for all samples. Amplification and sequencing of the fresh samples followed the protocols described in Olsson *et al.* (2005). The toepad samples were sequenced with specifically designed primers (Supporting Information Table S4). For a subset of samples, the nuclear myoglobin intron 2 (MB) and ornithine decarboxylase introns 6 and 7 (ODC) were also sequenced (Friesen *et al.* 1999, Allen & Omland 2003, Olsson *et al.* 2005, Irestedt *et al.* 2006). All sequences have been submitted to GenBank (Table S3). Several sequenced specimens were also included in the morphological analyses, as follows: NHMUK 1928.6.26.1198, core '*cooki*', Cambodia; NHMUK 1927.4.18.526, Javan *polychroa*; NHMUK 1886.10.1.1178, central Myanmar *cooki* (holotype); NHMUK 1913.12.24.107, east Myanmar *cooki*; MCZ 62929, *bangsi*, Mengzi, Yunnan; and NHMUK 1941.5.30.269, *striatula*, Sindh, Pakistan.

Phylogenetic analyses

Sequences were aligned using the MUSCLE algorithm in Geneious 7.1.9 (Biomatters Ltd). For the

nuclear loci, heterozygous sites were coded as ambiguous. Single-locus analyses were performed by Bayesian inference using BEAST 1.8.4 (Drummond *et al.* 2012). Model selection was based on the Bayesian information criterion calculated in jModeltest 2.1.7 (Darriba *et al.* 2012). For cyt*b*, the HKY + G model was selected, for ODC the HKY + I model, and for MB the JC model. Xml files were generated in the BEAST utility program BEAUti version 1.8.4 and are available as Supporting Information Material S1. All datasets were analysed using both a strict clock and an uncorrelated relaxed clock in alternative runs, but as the former had a higher likelihood in all comparisons (not shown), only the strict clock analyses are reported below. A 'Birth–death incomplete sampling' tree prior with a normal distribution with mean 2.0 and standard deviation 1.0 was applied. The cyt*b* gene was also analysed under the GTR + G model and a strict molecular clock with a normally distributed clock prior with a mean rate of 0.0105 and standard deviation 0.001, corresponding to a rate of 2.1%/million years (my) (Weir & Schluter 2008). Default settings were used for the other priors. In total, 100 million generations were run, sampled every 1000 generations. Convergence to the stationary distribution of the single chains was inspected in Tracer 1.6.0 (Rambaut & Drummond 2014) using a minimum threshold for the effective sample size. The joint likelihood and other parameter values reported large effective sample sizes (> 1000). Good mixing of the Markov chain Monte Carlo (MCMC) runs and reproducibility were established by multiple runs from independent starting points. Topological convergence was examined by eye. The first 25% of generations was discarded as 'burn-in', well after stationarity of chain likelihood values had been established, and posterior probabilities were calculated from the remaining samples. Trees were summarized using TreeAnnotator version 1.8.2 (included in the BEAST package), choosing 'Maximum clade credibility tree' and 'Mean heights', and displayed in FigTree version 1.4.0 (Rambaut 2002). Hill Prinia *Prinia superciliaris*, Bar-winged Prinia *P. familiaris* and Jungle Prinia *P. sylvatica* were used as outgroups.

Integrative species tree estimation was performed using *BEAST (Heled & Drummond 2010) in BEAST 1.8.4 for the 16 samples for which cyt*b* and the two nuclear loci were available (MB missing for one sample). Every taxon that was congruently identified based on morphology, songs and the other molecular analyses was defined *a priori* as a species. The best-fit substitution models as suggested by jModeltest above were used. Analyses were run under both a strict clock and an uncorrelated relaxed clock on all loci in alternative runs, with default priors. We applied a birth–death species tree prior with a mean growth rate with mean 2.0 and standard deviation 1.0, and a population size model with a piecewise linear and constant root. Default settings were used for the other priors. In all, 100 million generations were run, sampled every 1000 generations. Convergence to the stationary distribution of the single chains was inspected in Tracer 1.6.0 (Rambaut & Drummond 2014) as above. The xml file is available as Table S2.

RESULTS

Morphology

Characteristics of subspecies

Because interpretation of subsequent results depends on an understanding of subspecies characteristics (Table 1), we first present our findings for each subspecies, organized within currently recognized species approximately from east to west, then north to south, placing them in historical context.

Prinia crinigera striatula (Hume, 1873)

Type locality: Kurrachee = Karachi, Pakistan. Range: Sub-Himalayan and Baluchistan hills of western Pakistan. In univariate measurements with sample sizes sufficient for testing, male *striatula* are not significantly different from male nominate *crinigera* (Table S1); sample sizes of female *striatula* are too small to permit testing. In PCAs of measurements, all *striatula* for both sexes fall within the same morphospace as other subspecies of *P. crinigera sensu stricto* (*s.s.*) (Fig. 3). In direct comparisons at NHMUK, breeding plumage male *striatula* have a notably paler head and upperparts than a large series from the extreme northwest range of nominate *crinigera*. In breeding and non-breeding plumage, male *striatula* (too few females and non-breeding males were available for statistical analysis) are paler, greyer and less distinctly marked overall than other races of *P. crinigera s.s.* (Supporting Information Table S5); however, in a PCA of plumage scores, *striatula* cluster with other

crinigera (Fig. 4). See Table S3 for notes on the type of *striatula*.

Prinia crinigera crinigera (Hodgson, 1836)
Type locality: Nepal. Range: West and Central Himalayas. Based on direct comparisons of large series at NHMUK, the nominate subspecies varies little in overall depth of colour between western Pakistan and the Central Himalayas. The subspecific allocation of the population from Nuristan, northeastern Afghanistan, is uncertain. The only known Afghan specimen, not seen by us, was said to be intermediate but closer to *striatula* than to the nominate (Paludan 1959). It was assigned to *striatula* by Ali and Ripley (1973, 1997) but was not mentioned by Ripley (1982). However, as Nuristan is contiguous with the main Himalayan range rather than sub-Himalayan Pakistan, we tentatively place the Afghan population within the nominate.

Prinia crinigera assamica (Baker, 1924)
Type locality: Shillong, Meghalaya, India. Not recognized herein. We found no significant differences between the series of *assamica* (Baker, 1924) and *yunnanensis* in either measurements or plumage scores (results not presented). The former was considered by Baker (1924a) to occur in hills south of the Brahmaputra Hills, India, and Chin Hills, Myanmar. Baker's (1924b) original diagnosis of *assamica* as '[a]lmost as dark as *S. c. yunnanensis*, but differing...in having the head heavily streaked throughout the year' was based on a much smaller sample than that studied herein. Although direct comparison of the types of *assamica* (NHMUK 1895.7.14.1560) and *yunnanensis* (NHMUK 1876.4.7.77) show that the type of *assamica* has the crown slightly more streaked than that of the type of *yunnanensis*, Baker's (1924b) diagnosis does not hold within the expanded series. This suggests that *assamica* is synonymous with *yunnanensis*, so that east Himalayan birds from Assam east are *yunnanensis*, although variation appears to be clinal. However, see under *P. c. nebulosa* for the possible validity of *assamica* if restricted to the Meghalaya population. Importantly, *assamica* was erroneously synonymized with *catharia* by Ali and Ripley (1973).

Prinia crinigera nebulosa (Koelz, 1952)
Type locality: Cherrapunji (= Cherrapunjee), Khasi Hills, Meghalaya, India. Not recognized herein. *Prinia c. nebulosa* has long been synonymized with *yunnanensis* (e.g. Ripley 1961, Ali & Ripley 1973), but it is unclear whether these authors examined the holotype of *nebulosa* (UMMZ 147908). As *assamica* was earlier described from Meghalaya, it is doubtful that another valid form would occur in the same region; Koelz (1952) did not indicate the distribution of *nebulosa*, merely specifying the type locality. We examined the April-collected holotype of *nebulosa*, in early breeding plumage, and it is like *yunnanensis* but more streaked above than worn *yunnanensis* from later in the breeding season. However, as noted by Koelz (1952), a large UMMZ series of juveniles from Meghalaya is more richly coloured and darker above than the four UMMZ juveniles from Nagaland, and the same colour and darkness difference is true of small UMMZ samples of non-breeding adults (eight from Meghalaya vs. three from Manipur). Further study may thus show that *assamica*, if restricted to Meghalaya, is recognizable. In any case, *nebulosa* is a junior subjective synonym of *yunnanensis*, or of *assamica* if the latter is recognized.

Prinia crinigera yunnanensis (Harington, 1913)
Type locality: Momien (now Tengchong), Yunnan, China. Range: Eastern Himalayas to western Yunnan. Compared with nominate *crinigera*, *yunnanensis s.s.* (Fig. 5e) has a slightly larger bill and longer tarsus (Supporting Information Table S6). In series, male *yunnanensis* are usually notably darker above than nominate *crinigera*. Although *yunnanensis* was synonymized with *catharia* by Ali and Ripley (1973) and del Hoyo and Collar (2016), these taxa belong to different groups (see the following).

Prinia crinigera catharia (Reichenow, 1908)
Type locality: Ta-tsieng-lu-ting (now Kangding), Sichuan, China. Range: Mainland China east from western Yunnan. In the description of *catharia* (Fig. 5f), Reichenow (1908) compared his new taxon only to Javan *P. polychroa*, and then only in size. The type locality is distant from localities for the *crinigera* group, which is not known from Sichuan (see Fig. 1a). Reichenow's type (ZMB 2000/37893), examined by P.C.R. in May 2013 and May 2015, is clearly a member of the *striata* group (see below for differences between the *crinigera* and *striata* groups). Although labelled an adult female, it is immature, judging by the

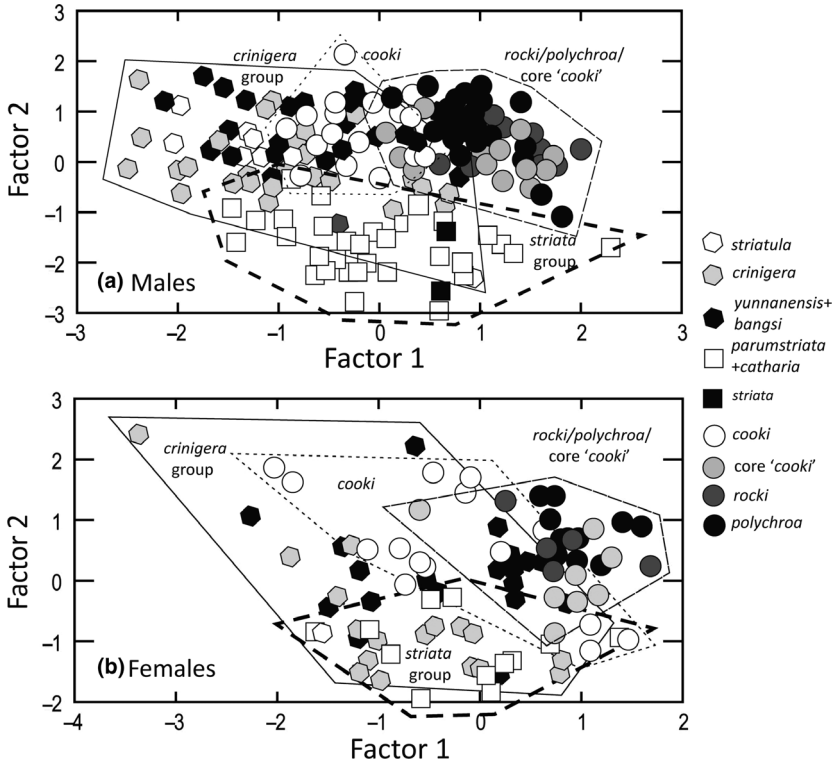

Figure 3. Principal components analysis (PCA) of external measurements of adult (a) males and (b) females of taxa in the *cinigera* group (*striatula*, *cinigera*, *yunnanensis*, *bangsi*); the *striata* group (*parumstriata*, *catharia*, *striata*); and the *polychroa* group (Myanmar *cooki*, core '*cooki*', *rocki*, Javan *polychroa*).

pointed tips to its fresh rectrices. Contrary to current treatments (Madge 2006, Dickinson & Christidis 2014, del Hoyo & Collar 2016, Gill & Donsker 2017), *catharia* is clearly not the form of northeast India or Myanmar, which we treat as *yunnanensis*.

Prinia cinigera parvirostris (La Touche, 1922)

Type locality: Shuitang, south-eastern Yunnan (which of several regional Shuitang places is uncertain), China. Not recognized herein. Preliminary analyses show no significant differences in measurements or plumage scores between our small sample (n = 5 adult males measured, n = 3 breeding plumage males) of *parvirostris* and a large sample of male *catharia* from eastern Sichuan and Yunnan through Anhui and Guangdong. La Touche (1922) explicitly compared *parvirostris* only with *yunnanensis*, a member of the *cinigera* group, and the characters he gave for *parvirostris* of darker, finer streaking above, greyer ground colour of crown, and smaller bill accord with the *striata* group and not the *cinigera* group. P.C.R. has examined the type of *parvirostris*, MCZ 129777, which is clearly a member of the *striata* group. We therefore treat *parvirostris* as a junior subjective synonym of *catharia*.

Prinia c. parumstriata (David & Oustalet, 1877)

Type locality: Fukien (now Fujian) Province, China. Range: Coastal eastern China from Jiangsu to Fujian provinces. With samples partitioned according to accepted range summaries (e.g. Madge 2006), we find no consistent differences between *P. c. parumstriata* and *P. c. catharia*. Measurements of adult males from the range of *catharia* in western Sichuan (following Madge 2006 for range delineation) do not differ significantly (as tested by Bonferroni-adjusted two-sample *t*-tests with sample sizes of at least 13 *parumstriata* and at least eight *catharia*; results not presented) in any mensural characters from individuals' samples from the range of *parumstriata*, nor do series of breeding plumage males partitioned in the same way appear to differ from one another in plumage. Some *catharia* have more rufous striations above

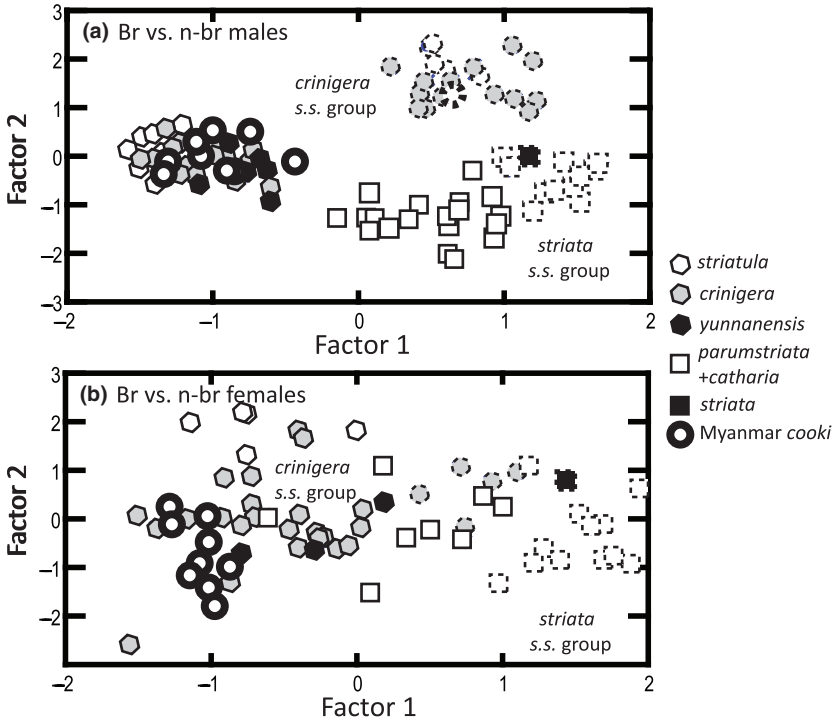

Figure 4. PCAs of plumage character scores for adult males (a) and females (b) of the *crinigera* and *striata* groups (all subspecies of each) and Myanmar *cooki*. Symbols have the same meanings as in Figure 3; dashed symbols and lines represent non-breeding individuals.

compared with *parumstriata*, and a few individuals of both taxa have much paler grey feather edgings above, but not in conformity with established subspecies.

However, comparisons between the NHMUK sample from southeastern coastal (nine non-breeders) vs. inland China (13 non-breeders) show that southeastern birds usually have darker, more rufescent feather edges on the crown and mantle, and slightly more prominent rufous wing patches (except for one central Sichuan bird, NHMUK 1946.49.1249, with very rufous wings) and are overall slightly more rufescent. These differences are less apparent in breeding birds (four adults from coastal provinces and 22 from central China in NHMUK), in which the pale crown feather edgings especially are worn, and the rufous wing panels typically weaker. The same trend exists among most other small series studied (ANSP, MCZ, USNM and UMMZ; but the three AMNH eastern China birds are not distinct). Thus, most interior birds have paler feather edgings above, whereas most coastal birds (*parumstriata s.s.*) examined have saturated plumage without much paler feather edgings. We therefore treat *parumstriata* as a weakly recognizable subspecies, limited to coastal southeastern China.

Prinia crinigera striata (Swinhoe, 1859)
Type locality: Hongsan, northwestern Taiwan. Range: Taiwan. Our seven adult male and four adult female *P. c. striata* from Taiwan showed no significant mensural differences from pooled *parumstriata* and *catharia*. Sample sizes of *striata* are too small to segregate by plumage, but compared with *parumstriata* and *catharia*, *striata* typically has blacker streaks above; a less rufous wing panel; more heavily speckled throat sides even in breeding plumage; and paler flanks. Compared with coastal *parumstriata s.s.*, *striata* also has more contrasting pale edges to the dark streaks, more like most *catharia*.

Prinia polychroa polychroa (Temminck, 1828)
Type locality: Java. Range: Java. Nominate *polychroa* of Java is generally larger and bigger-billed (Table S6), and greyer above, contrasting more with the buffy underparts, and with duller, less

Figure 5. *Prinia polychroa* 'core *cooki*' (here described as a new subspecies): (a) Sakaerat Environmental Research Station, Nakhon Ratchasima Province, Thailand, 4 Jan. 2014, presumed female (DZUG 3547) (Philip D. Round); (b) Thung Kamang, Phu Khieo, Chaiyaphum Prov., Thailand, 4 Feb. 2012 (Dave Sargeant); (c) *P. polychroa cooki* Bagan, Myanmar, 5 Apr. 2016 (James Eaton); (d) *P. polychroa rocki* Di Linh town, Da Lat Plateau, Lam Dong, Vietnam, 9 Jan. 2017 (Hung Le Manh); (e) *P. crinigera yunnanensis* Bhutan, Mar. 2017 (Shashank Dalvi); (f) *Prinia crinigera catharia* Wenzhou, Zhejiang Prov., China, 20 Jul. 2013 (Meijie Dai).

rufescent, whitish to dull buff wing edgings and uppertail, than other taxa of *P. polychroa s.l.* (Table S5). However, Javan *polychroa* does not have an especially long tail, so its overall larger size is not apparent in the mensural PCA (Fig. 3), in which Factor 1 is strongly influenced by tail length.

Prinia crinigera bangsi (La Touche, 1922)

Type locality: Mengtz (now Mengzi), Yunnan Province, China. Range: eastern Yunnan. Although considered by Deignan (1957) to be *P. polychroa bangsi*, examination by P.C.R. of the holotype (MCZ 129757) and other *bangsi* specimens showed that these are instead very like typical *P. crinigera yunnanensis* and do not belong with the *polychroa* group (as supported by analysis of cyt*b* of another Mengzi specimen, MCZ 62929, detailed below). However, adult male *bangsi* have significantly shorter wings than *yunnanensis* (mean = 53.5 ± 2.97 mm, n = 4 *bangsi* vs. 58.7 ± 2.45, n = 45 *yunnanensis*; P = 0.004 (Bonferroni-adjusted, pooled variances)), although no other measurements in the small sample of *bangsi* differed from *yunnanensis*. The two MCZ breeding plumage male *bangsi* have distinctly paler mantles than breeding male *yunnanensis*.

Prinia polychroa cooki (Harington, 1913)

Type locality: Thayetmyo, Rego District, Myanmar. Range of topotypical *cooki* (Fig. 5c): central Myanmar; range of new taxon (see below): central Thailand through western Cambodia and Laos. We found that two distinct forms have long been erroneously united under this taxon. Extensive series at NHMUK and a few at ZMB show that topotypical *cooki* from the Myanmar plains are similar in plumage, plumage changes and sexual dimorphism to nominate *crinigera* and *yunnanensis*. They differ significantly (Table S5) from taxa in the *crinigera* group in being paler and less heavily streaked above, usually retaining a pale supercilium and having the face browner and less dark in breeding plumage, in having the breast cleaner-looking with little or no dark mottling, and in typically having much weaker subterminal tail spots. In contrast, specimens long attributed to *P. p. cooki s.l.* from Thailand, Laos and Cambodia (referred to herein as core '*cooki*') are morphologically distinct from Myanmar *cooki* in several respects (Tables S5 and S6, Figs 3–5a,b), and we describe this population below as a new taxon. Furthermore, NHMUK specimens of eastern Myanmar *cooki* from the Southern Shan States hills are distinctly darker above and more brownish below with whiter central underparts than central plains Myanmar *cooki*, and might represent an undescribed subspecies, but are referred to herein as Myanmar *cooki* because a sequenced specimen (NHMUK 1913.12.24.107, Kalaw, Southern Shan States) is closest to central plains Myanmar *cooki* based on mitochondrial (mtDNA) (see below). See Supporting Information Material S3 for notes on the type of *cooki*.

Prinia polychroa rocki Deignan, 1957

Type locality: Fimnon (= Fimnom), 11°47′N, 108°24′E, southern Annam, Vietnam. Range: Central and southern Vietnam. This taxon (Fig. 5d) is obviously more saturated in overall colour than the others in fresh plumage, but in worn plumage is drab, often similar to that of core '*cooki*' (Table S5), to which it is also very similar in structure, with male *rocki* on average slightly deeper-billed and with a longer hindclaw (Table S6). Records of *P. polychroa s.l.* from eastern Cambodia might represent this taxon, but without confirmation they are not mapped as such in Figure 1(b).

Comparison between the crinigera and *striata* groups

As shown above, there are few morphological differences among *striatula*, nominate *crinigera*, *yunnanensis* and *bangsi* (the *crinigera* group), and likewise among *catharia*, *parumstriata* and *striata* (the *striata* group). However, there are numerous significant differences between the *crinigera* and *striata* groups (Tables S5 and S6), especially between breeding plumage males. On a PCA of external measurements, there is minimal overlap on Factor 2 between males of the *crinigera* and *striata* groups (primarily due to the much shorter wing of the *striata* group; Fig. 3a and Table S7), while females overlap extensively (Fig. 3b). The same is true in PCAs of plumage scores: both breeding and non-breeding *crinigera*-group males are completely separated on Factor 1 (which contrasts the degree of upperpart streaking and rufescence of wing and tail against bill colour, suborbital auriculars colour, and breast feather wear; Table S7) from *striata*-group males in comparable plumages (Fig. 4a), and much more overlap between females of the two groups (Fig. 4b). Basically, breeding *crinigera*-group males become more or less blackish-faced and completely lose

the supercilium, whereas breeding *striata*-group males remain pale-faced and retain the pale supercilium. The underparts of breeding *crinigera*-group males become buffier and the breast sides look mottled due to dark feather bases showing, whereas breeding *striata*-group males are whiter and hardly if at all mottled below. In non-breeding plumage, both sexes of the *crinigera* group have less clear-cut streaking on the mantle and lack or have a much weaker rufous wing panel than the *striata* group. In all post-juvenile plumages, the uppertail of the *crinigera* group is duller, often darker cold brown with obvious dark barring, and the central rectrices appear broader for most of their length, while the uppertail of the *striata* group is usually paler and at least slightly rufescent, with very weak or no barring, and the central rectrices appear narrower for their entire length. The undertail surface of the *crinigera* group shows prominent dark subterminal crescents, which are weak or scarcely discernible in the *striata* group. Thus, these complexes form two morphologically well-marked groups, and we have seen no evidence of intergradation; instead, specimens show broad sympatry in Yunnan (P.C. Rasmussen unpubl. data).

Comparisons among taxa in the polychroa *group*

Within the *P. polychroa s.l.* complex (excluding *bangsi*, shown herein to belong with *crinigera*), Javan *polychroa*, *rocki* and core '*cooki*' are similar to one another mensurally in both sexes (Table S6, Fig. 3) and in plumage (Table S5, Figs 5 and 6). However, Myanmar *cooki* is most similar to *P. crinigera* both mensurally and in plumage (Table S5), and is the only member of *P. polychroa s.l.* with sexual dichromatism and strong, *P. crinigera*-like, seasonal changes in males (Figs 3, 4 and S2, Table S6). In addition, *rocki* exhibits marked seasonal variation in overall plumage tone, from bright buffy in fresh non-breeding plumage to drab, much as in core '*cooki*', in worn breeding plumage.

Songs

At least six major territorial song types of two main groups were recorded. Type A songs (Fig. 6) consist of complex multi-note phrases repeated in long rattling series. Type B songs (Fig. 7) are simple, consisting of one or two pure notes repeated at longer intervals. Based on our sample, the *crinigera* and *striata* groups and Myanmar *cooki* produce only Type A songs. In contrast, for the *polychroa* group, core '*cooki*' produces only Type B songs, whereas Vietnam '*rocki*' and Javan *polychroa* usually produce Type B songs, but rarely and briefly give Type A song (both song types being sometimes given by the same individual).

Type A1

The song of *catharia/parumstriata* from Yunnan, Sichuan, Hunan and Fujian and *striata* from Taiwan consists of prolonged rattling 'reels' (Fig. 6a–c, Tables 2 and S2). In sonograms, these consist of monotonous quick repetitions of a single short (mean 0.208 ± 0.045 s) phrase of 6–8 rather simple, tightly spaced, mostly steeply deflected notes, of which the last one is frequently emphasized, but also commonly include /\-shaped notes. The intervals between the phrases are distinct and easily detectable by ear (mean 0.173 ± 0.036 s). The song contains no harsh buzzing rattles. In our sample, the song was produced for up to *c.* 30 s without pauses. We could not confirm variation among songs by the same male, but we found considerable variation in details in the phrases among males, although at least some males with neighbouring territories at Dali, Yunnan, sang very similar songs.

Type A2

Nominate *crinigera* in northern Pakistan, Uttarakhand (northwest India), Nepal and Bhutan, and *yunnanensis* in Nagaland (northeast India), western Myanmar and westernmost Yunnan, China (Liuku), also sing long rattling, grinding 'reels' (Fig. 6g–j, Tables 2 and S2). These are monotonous rapid repetitions of complex multi-note phrases 0.493 ± 0.119 s in duration separated by very short intervals (mean 0.089 ± 0.026 s). The song is normally arranged in two subphrases separated by very brief intervals; these intervals are usually slightly shorter than the ones between phrases, but sometimes of similar length. Each phrase consists of several closely spaced, rather simple, mostly steeply deflected, but sometimes also inflected, and sometimes rather drawn-out notes, the last generally emphasized. All individuals except three of the four birds from Bhutan included at least one series of very thin rattling, buzzing notes, which appear mainly as a dark smudge in sonograms. The song has a harsh, 'grating', somewhat 'squeaky' tone.

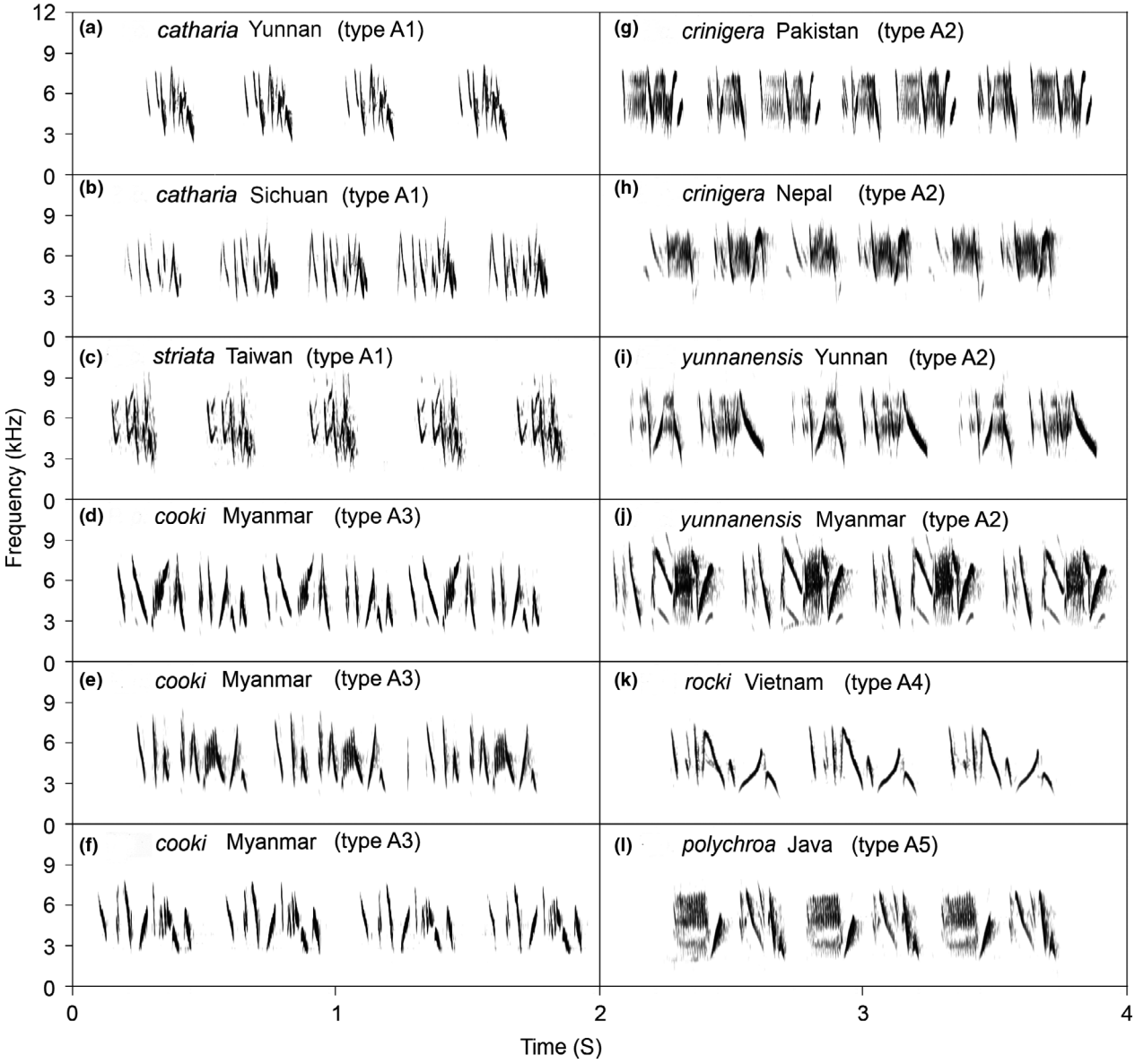

Figure 6. Sonograms of Type A songs of the *Prinia crinigera*–*P. polychroa* complex. This song type is rarely sung by taxa in the *polychroa* group (only noted in *rocki* and Javan *polychroa*). (a) *catharia*, Dali, Yunnan, 14 Jun. 2008 (AV19906); (b) *catharia*, Leibo, Sichuan, 30 May 2014 (AV19907); (c) nominate *striata*, Taiwan (AV19919; Cheng-te Yao); (d) Myanmar *cooki*, Bagan, Myanmar, 12 Apr. 2000 (AV19908); (e) Myanmar *cooki*, Bagan, Myanmar, 12 Apr. 2000 (AV19909); (f) Myanmar *cooki*, Mt Popa, Myanmar, 22 Apr. 2000 (AV19910); (g) nominate *crinigera*, Kaghan Valley, Pakistan, 7 Jun. 1998 (AV19902); (h) nominate *crinigera*, Pulchowki, Kathmandu Valley, Nepal (Raf Drijvers, from Scharringa 2005); (i) *yunnanensis*, Liuku, Yunnan, 28 May 2008 (AV19903); (j) *yunnanensis*, Mt Victoria, Myanmar, 16 Apr. 2000 (AV19904); (k) *rocki*, Dalat, Vietnam, 12 May 1999 (AV19911); (l) Javan *polychroa*, Type A2, G. Halimun, W Java, Indonesia, 29 Oct. 2011 (AV19916; Bas van Balen). Recordings are by Per Alström unless otherwise noted.

It was often delivered uninterrupted for long periods, once for almost 2.5 min. The pace of the song varies greatly. One recording from Uttarakhand (AV19918) is aberrant in that the phrases are separated by unusually long (*c.* 0.4 s) intervals, which contain a drawn-out 'squeaky' descending note with pronounced harmonics, producing a very unusual rhythm. We have no evidence that the same male had more than one song type, although there is considerable

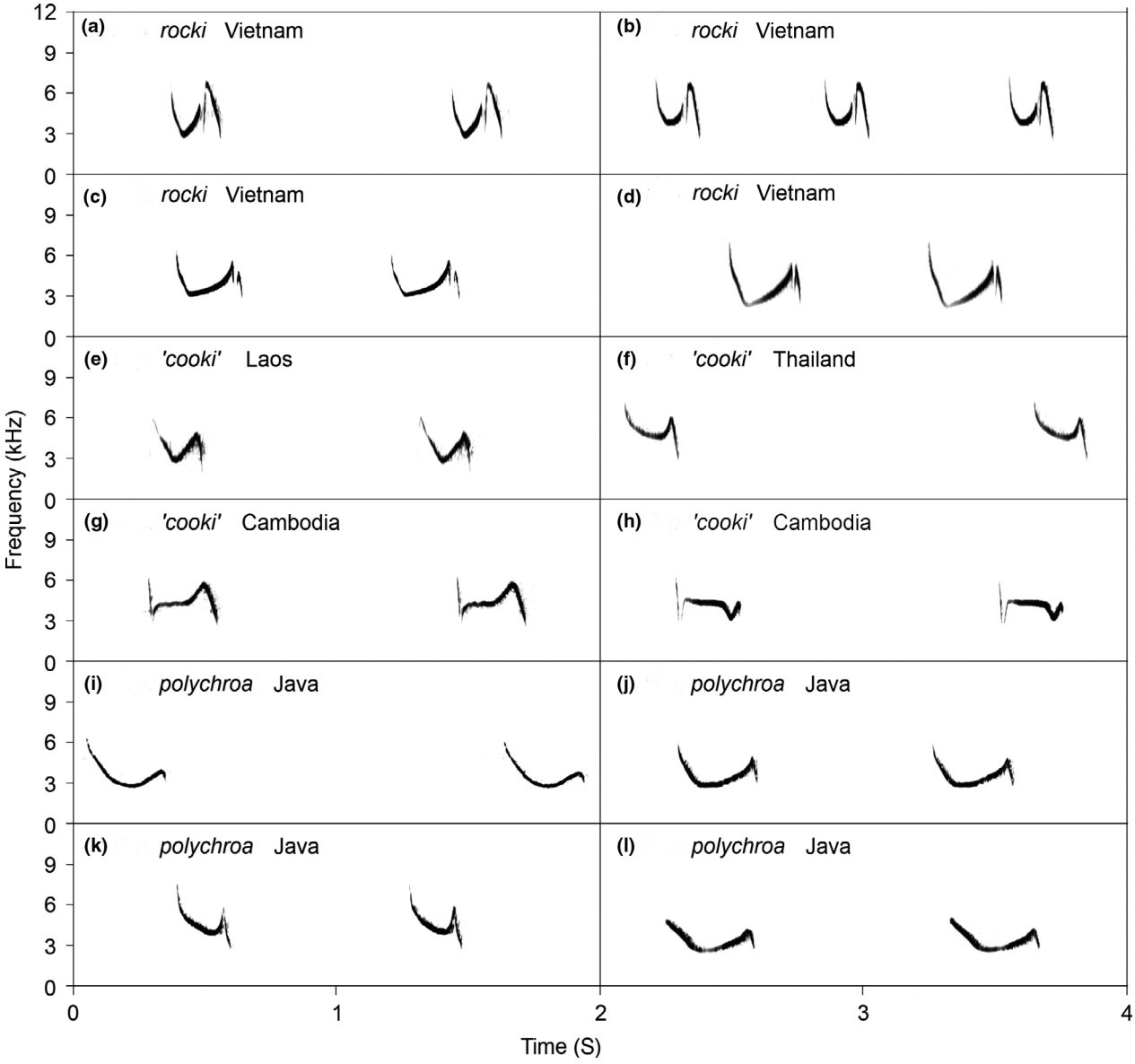

Figure 7. Sonograms of Type B songs of the *P. polychroa* complex. This is the usual song type of the *polychroa* group except Myanmar *cooki*, but it is not sung by any taxon of the *crinigera* or *striata* groups. (a) *rocki*, Dalat, Vietnam, 14 May 1999 (AV19912); (b) *rocki*, Dalat, Vietnam, 12 May 1999 (AV19914); (c) *rocki*, Dalat, Vietnam, 12 May 1999 (AV19913); (d) *rocki*, Dalat, Vietnam, 12 May 1999 (AV19915); (e) core '*cooki*', Dong Khan Thung, Champasak Prov., south Laos (AV19920; Philip D. Round); (f) core '*cooki*', Sabsadao Station, Thablan NP, Thailand, 3 Jul. 2014 (XC185665; Greg Irving); (g) core '*cooki*', Tmat Boey, Preah Vihear Prov., Cambodia, Feb. 2008 (XC27624; David Edwards); (h) core '*cooki*', Prey Veng, Preah Vihear Prov., Cambodia, 26 Dec. 2012 (XC124245; Patrik Åberg); (i) Javan *polychroa*, W Java, Indonesia, 14 Mar. 1986 (AV19905; Bas van Balen); (j) Javan *polychroa*, G. Halimun, W Java, 31 Oct. 2011 (AV19917; Bas van Balen); (k) Javan *polychroa*, G. Halimun, 29 Oct. 2011 (AV19916; Bas van Balen); (l) Javan *polychroa*, G. Halimun, 5 Nov. 2012 (XC142046; Frank Lambert). Note the two-note phrases in *rocki*. Recordings are by Per Alström unless otherwise noted.

variation in detail among males. The main differences from Type A1 are the longer, usually paired, phrases; shorter intervals between the phrases; presence of thin rattling, buzzing notes; a higher proportion of ascending notes, but lower frequency of /\-shaped notes; and distinctly harsher, more 'squeaky', 'nasal' tone. Type A1 and A2 are easily separable by ear.

Table 2. Characteristics of song types of the *Prinia crinigera–P. polychroa* complex (mean ± sd, range) (a), and statistical tests of differences (b). All comparisons are based on Mann–Whitney *U*-tests, except those marked with an asterisk which are based on ANOVA with Bonferroni correction. All significant Mann–Whitney *U*-test results remained so after sequential Holm–Bonferroni correction. Type A songs of *P. p. rocki* (A4) and *P. p. polychroa* (A5) were not included in statistical analyses due to their small sample size (two each).

(a) Variable	Song type A1 *striata* group (n = 25)	Song type A2 *crinigera* group (n = 21)	Song type A3 *P. p. cooki* Myanmar (n = 7)	Song type A4 *P. p. rocki* (n = 2)	Song type A4 *P. p. polychroa* (n = 2)	Song type BCore SE Asian *P. p.* '*cooki*' (n = 11)	Song type B *P. p. rocki* (n = 6)	Song type B *P. p. polychroa* (n = 12)
Phrase duration[a]	0.208 ± 0.045 (0.143–0.296)	0.493 ± 0.119 (0.275–0.721)	0.419 ± 0.050 (0.354–0.496)	0.414 ± 0.008 (0.409–0.420)	0.344 ± 0.116 (0.262–0.426)	0.225 ± 0.047 (0.149–0.300)	0.224 ± 0.046 (0.172–0.273)	0.281 ± 0.068 (0.159–0.394)
Interval between phrases[a]	0.173 ± 0.036 (0.117–0.252)	0.089 ± 0.026 (0.053–0.177)	0.109 ± 0.029 (0.058–0.139)	0.123 ± 0.007 (0.118–0.128)	0.116 ± 0.054 (0.078–0.154)	1.121 ± 0.401 (0.641–2.060)	0.704 ± 0.181 (0.553–1.043)	0.990 ± 0.233 (0.619–1.344)
Phrase proportion	0.549 ± 0.076 (0.403–0.696)	0.842 ± 0.046 (0.743–0.911)	0.793 ± 0.054 (0.724–0.896)	0.771 ± 0.006 (0.767–0.776)	0.738 ± 0.152 (0.630–0.845)	0.179 ± 0.049 (0.092–0.243)	0.248 ± 0.047 (0.200–0.311)	0.226 ± 0.058 (0.140–0.354)
Number of notes	6.7 ± 0.6 (6.0–8.0)	11.6 ± 2.5 (8.0–17.0)	9.9 ± 0.7 (9.0–11.0)	6.5 ± 0.7 (6.0–7.0)	6.0 ± 0.0 (6.0–6.0)	1.0 ± 0.0 (1.0–1.0)	2.0 ± 0.0 (2.0–2.0)	1.0 ± 0.0 (1.0–1.0)
Note rate	34.02 ± 8.42 (20.28–48.98)	24.22 ± 5.23 (14.59–34.18)	23.87 ± 3.53 (20.18–28.28)	15.71 ± 2.01 (14.29–17.13)	18.52 ± 6.25 (14.10–22.94)	4.65 ± 1.09 (3.34–6.70)	9.25 ± 1.92 (7.34–11.66)	3.94 ± 1.00 (2.94–6.28)
Number of rising notes	0.4 ± 0.8 (0.0–3.0)	2.0 ± 1.5 (0.0–6.0)	1.7 ± 0.8 (1.0–3.0)	1.0 ± 0.0 (1.0–1.0)	1.0 ± 0.0 (1.0–1.0)	0.0 ± 0.0 (0.0–0.0)	0	0
Number of falling notes	2.6 ± 1.0 (0.4–5.0)	5.1 ± 1.8 (2.2–8.0)	4.9 ± 1.5 (2.0–6.0)	3.0 ± 0.0 (3.0–3.0)	3.5 ± 0.7 (3.0–4.0)	0.0 ± 0.0 (0.0–0.0)	0	0
Number of rising and falling notes	3.3 ± 0.4 (2.8–4.0)	2.2 ± 1.4 (0.0–5.0)	2.6 ± 1.3 (0.0–4.0)	2.5 ± 0.7 (2.0–3.0)	1.0 ± 0.0 (1.0–1.0)	0.2 ± 0.4 (0.0–1.0)	1.0 ± 0.0 (1.0–1.0)	0
Number of falling and rising notes	0.5 ± 0.8 (0.0–3.0)	0.4 ± 0.7 (0.0–3.0)	0	0	0	0.8 ± 0.4 (0.0–1.0)	1.0 ± 0.0 (1.0–1.0)	1.0 ± 0.0 (1.0–1.0)
Number of 'complex' notes	0	1.8 ± 1.1 (0.0–4.0)	0	0	0.5 ± 0.7 (0.0–1.0)	0	0	0
Number of trills	0	0	0.7 ± 0.5 (0.0–1.0)	0	0	0	0	0

	Type A			Type B		
(b) Variable	Type A1 vs. A2	Type A1 vs. A3	Type A2 vs. A3	Core SE Asian *P. p.* '*cooki*' vs. *P. p. rocki*	Core SE Asian *P. p.* '*cooki*' vs. *P. p. polychroa*	*P. p. rocki* vs. *P. p. polychroa*
Phrase duration[a]	< 0.001	< 0.001	n.s.	n.s.	< 0.05	n.s.
Interval between phrases[a]	< 0.001*	< 0.001*	n.s.	< 0.05*	n.s.	< 0.05

(continued)

Table 2. (*continued*)

(b) Variable	Type A: Type A1 vs. A2	Type A: Type A1 vs. A3	Type A: Type A2 vs. A3	Type B: Core SE Asian *P. p.* '*cooki*' vs. *P. p. rocki*	Type B: Core SE Asian *P. p.* '*cooki*' vs. *P. p. polychroa*	Type B: *P. p. rocki* vs. *P. p. polychroa*
Phrase proportion	< 0.001	< 0.001	< 0.05	< 0.05*	n.s.	n.s.
Number of notes	< 0.001	< 0.001	n.s.	< 0.001	n.s.	< 0.001
Note rate	< 0.001	< 0.005	n.s.	< 0.001	n.s.	< 0.001
Number of rising notes	< 0.001*	< 0.005	n.s.	n.s.	n.s.	n.s.
Number of falling notes	< 0.001	< 0.005	n.s.	n.s.	n.s.	n.s.
Number of rising and falling notes	< 0.005	n.s.	n.s.	< 0.005	n.s.	< 0.001
Number of falling and rising notes	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Number of 'complex' notes	< 0.001	n.s.	< 0.001	n.s.	n.s.	n.s.
Number of trills	n.s.	< 0.005	< 0.005	n.s.	n.s.	n.s.

[a]Single phrases or pairs of phrases, when phrases were paired.

Type A3

Songs of Myanmar *cooki* (Fig. 6d–f, Tables 2 and S2) are built up of quickly repeated phrases, longer than those of Type A1 (mean duration 0.419 ± 0.050 s), and consist of 9–11 well-spaced, steeply descending or, less commonly, ascending or /\-shaped notes. All songs also include a brief trill, often on an ascending scale, in various positions within or ending a phrase. The phrases are separated by short intervals (mean duration 0.109 ± 0.029 s). One individual sang an unusual dry, rasping song of two subphrases separated by only 0.06-s intervals and equally brief between-phrase intervals (Fig. 6d). One male gave three different phrase types. Type A3 differs from type A1 in, for example, having considerably longer phrases and shorter intervals between these, and the presence of a trill. It differs from Type A2 in having 'cleaner-looking', less 'messy' and varied sonograms, and usually having just a single phrase-type; it sounds 'drier' and clearly less 'squeaky' than Type A2.

Type A4

We have only two recordings of this song type by Vietnam *rocki* (Fig. 6k, Tables 2 and S2). The phrases consist of six or seven notes, including steeply descending as well as rather drawn-out descending and ascending notes.

Type A5

We have only two recordings of Type A songs of Javan *polychroa*. The phrases have six notes, including four or five steeply descending or ascending notes. Songs in one recording also include a buzz consisting of very thin notes (Fig. 6l).

Type B

This song type is typical of the *polychroa* group, and has been recorded in Thailand, Cambodia, Laos, Vietnam and Java.

In Vietnamese *rocki*, Type B song (Fig. 7a–d, Tables 2 and S2) consists of soft whistled, usually clearly disyllabic notes, which in sonograms show up as a pure-sounding, drawn-out U-shaped note, followed by a shorter, /\-shaped one. One bird lacks a distinct /\-shaped note, and instead has a thin downstroke with a tiny hook at the top that is almost connected to the first note, whereas another individual produced a more complex note consisting of one thick downslurred note and three

thin notes; the latter male also sang with a typical Type B song, and was the only one that certainly had a repertoire of more than one Type B song. The notes were repeated at intervals of *c.* 0.5–1 s. In the field, we have noted presumed female *rocki* duetting with males, producing thinner, higher-pitched notes.

In core '*cooki*', Type B song consists of a single note (Fig. 7e–h, Tables 2 and S2) that varies considerably in our sample of recordings (n = 11). The note may be drawn-out U-shaped; it may have a rather short deflected element with a thin up-and-downstroke at the end; it may be V-shaped with a downstroke at the end; it may begin with a thin downstroke followed by a slightly descending element that ended in a V-shaped hook; and one male gave two different variants of the previous one, one with a deflected hook at the end and the other with an /\-shaped element at the end. One recording (XC27624) includes a note in the background that we suspect to be a female duetting with the male.

Type B songs of Javan *polychroa* (Fig. 7i–l, Tables 2 and S2) consist of a single drawn-out, somewhat variably shaped, but basically U-shaped note with a more or less pronounced downstroke or downward-pointing hook at the end; a few recordings have a drawn-out, rather straight descending element with a V at the end; occasionally, the U-shaped note appeared broken centrally; and one song consists of a disconnected downstroke and upstroke. The U-shaped notes are distinctive, whereas the descending note with the terminal 'V' was similar to a note given by some core '*cooki*'.

Univariate comparisons of songs of Type A1 vs. Type A2, Type A2 vs. Type A3 and Type A2 vs. Type A3 show significant differences in three to nine characters (Table 2). The sample size for Type A4 songs is too small (n = 2) for meaningful comparisons. Type B songs of *rocki*, core '*cooki*' and Javan *polychroa* also differ statistically, with significant differences between all three pairs compared (Table 2). The number of significant differences among these three populations range from one (between core '*cooki*' and Javan *polychroa*) to five (between *rocki* and core '*cooki*').

In the DFA of the Type A songs (Figs 8a and S4), all variables passed the tolerance test, except 'number of trills', which was excluded from the analysis. The DFA was highly significant (Wilks' lambda = 0.011; Chi-square$_{40}$ = 2216.9; $P < 0.0001$), and resulted in 96.5% correct classification of the five taxa, 87.7% after cross-validation. The first two discriminant functions account for 94.5% of the variance. The variables most important in the discrimination are 'interval between phrases', 'phrase proportion' and 'note rate' on Function 1 and 'number of notes', 'number of rising notes' and 'number of falling notes' on Function 2. A plot of Function 1 vs. Function 2 (Fig. 8a) separates the *striata* group from the others (except one Javan *polychroa*) by Function 1 and five of seven Myanmar *cooki* from the others by Function 2. Two of the Myanmar *cooki* (our only sound recordings from Mt Popa, Myanmar) cluster closer to the *crinigera* group than to the other Myanmar *cooki* recordings, and closest to one recording of *crinigera* from Bhutan, which is slightly outside the main cluster of *crinigera* group samples. Songs of *crinigera* and *yunnanensis* are not separable, and the same is true for *catharia* and *striata*. The two songs of *rocki* were correctly assigned in both the original analysis and after cross-validation.

In the DFA of Type B songs (Fig. 8b and Table S5), all variables passed the tolerance test, except 'number of notes' and 'number of falling and then rising notes', which were excluded from the analysis. The DFA was highly significant (Wilks' lambda = 0.04; Chi-square$_{10}$ = 75.9; $P < 0.0001$), and resulted in 75.9% correct classification of the five taxa, 69.0% after cross-validation. Only discriminant Function 1 has an Eigenvalue > 1, and it accounts for 96.1% of the variance. The variables most important in the discrimination are 'interval between notes', 'phrase proportion' and 'note rate'. A plot of Function 1 vs. Function 2 (Fig. 8b) separates *rocki* from the others on Function 1, and all recordings of this taxon are correctly assigned according to the analysis. There is some separation of Javan *polychroa* from core '*cooki*' by Factor 2, with much overlap.

Analyses of molecular data

The cyt*b* tree (Fig. 9) recovered six strongly supported primary clades within the *P. crinigera–P. polychroa* complex, corresponding to: (1) *striata* (Taiwan) plus *catharia* and *parumstriata* (mainland China); (2) *striatula* (southern Pakistan), *crinigera* (northern Pakistan), *yunnanensis* (Meghalaya, India, and western Myanmar) and *bangsi* (south-east Yunnan); (3) *rocki* (south Vietnam); (4)

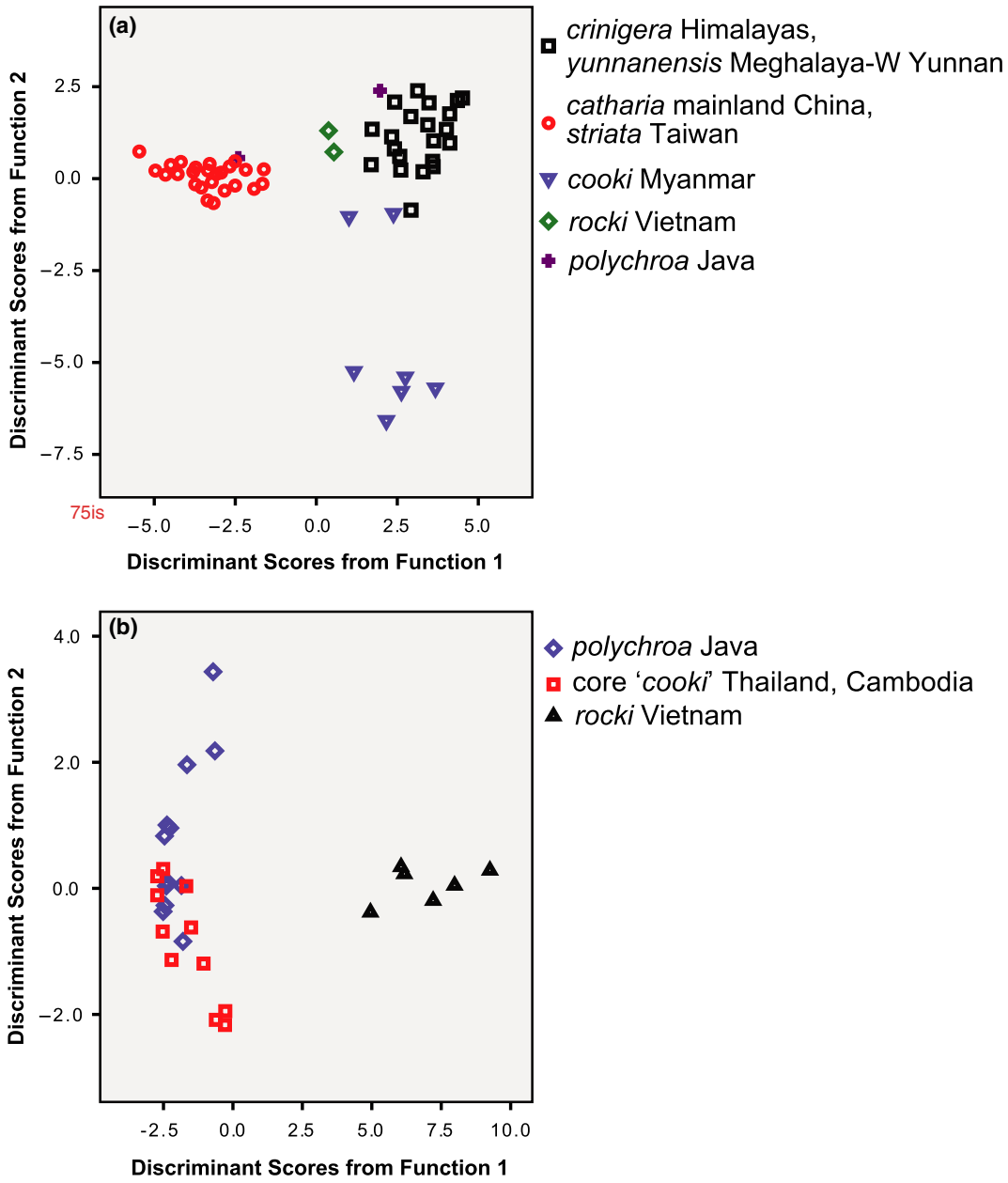

Figure 8. Discriminant function scatterplot of the first two discriminant functions based on measurements of 11 acoustic variables of Type A (a) and Type B songs (b) of the *Prinia cinigera*–*P. polychroa* complex.

Myanmar *cooki*; (5) core '*cooki*' (Thailand and Cambodia); and (6) *polychroa* (Java). Within these clades, there is very slight differentiation, although within the *crinigera* group the samples segregate into western and eastern clades (although we lack samples from intervening parts of the Himalayas). All relationships among the six primary clades received strong support, except the sister relationship between Javan *polychroa* and core '*cooki*' from Thailand and Cambodia. *Prinia crinigera s.l.* is evidently non-monophyletic, as the *crinigera* group is more closely related to *P. polychroa* than to the *striata* group.

Separate analyses of ODC and MB (Supporting Information Fig. S2) as well as the *BEAST phylogeny (Fig. 9) support a clade with the *striata*

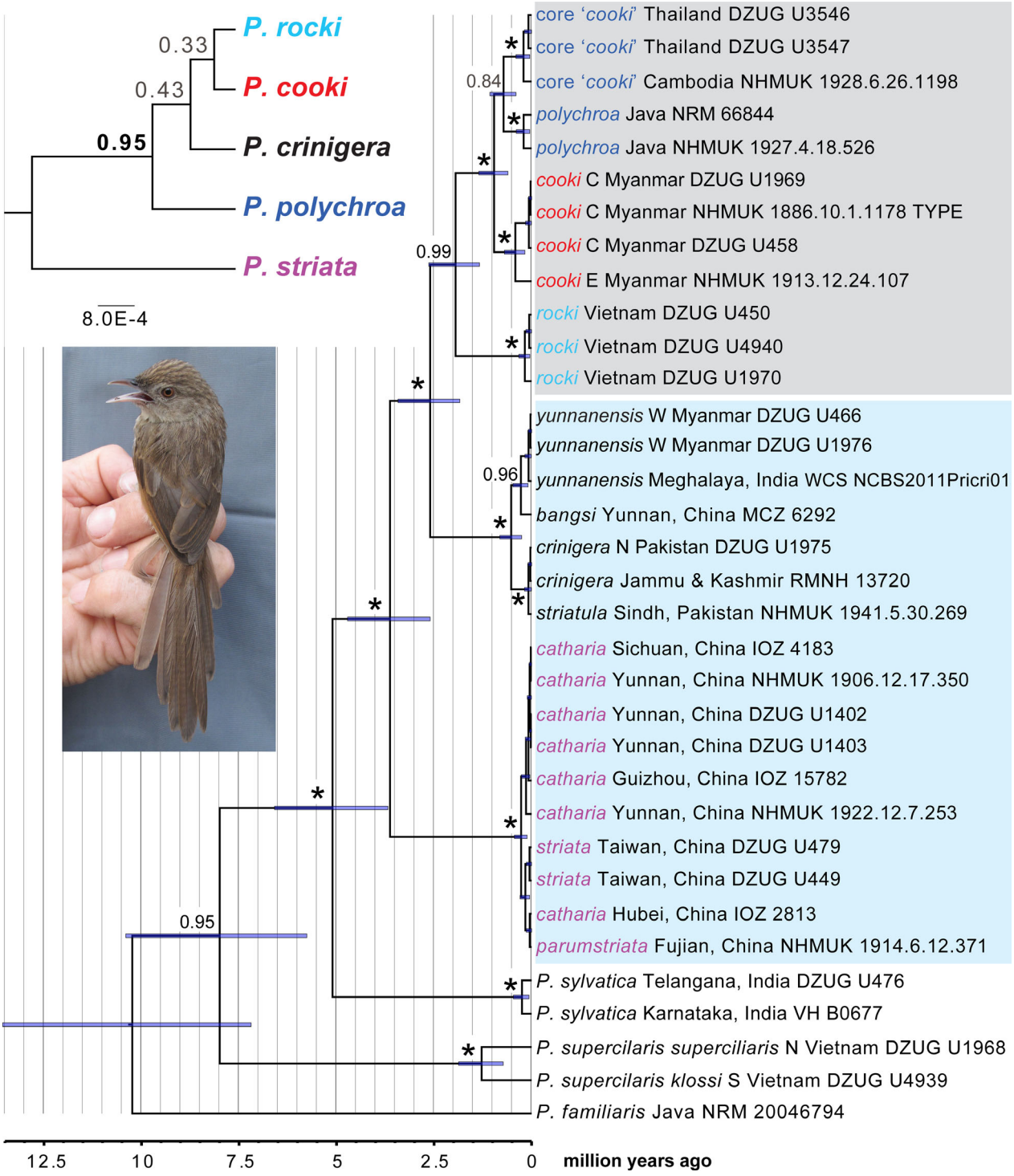

Figure 9. Mitochondrial cytochrome *b* (cyt*b*) chronogram of the *Prinia crinigera*–*P. polychroa* complex, based on a molecular clock rate of 2.1%/million years, with 95% highest posterior density bars. The numbers at the nodes represent posterior probability (PP); *, PP = 1.00. Taxa traditionally treated as *P. polychroa s.l.* are shaded grey, and taxa traditionally treated as *P. crinigera* are shaded pale blue. Inset: *BEAST phylogeny based on cyt*b* and nuclear ODC and myoglobin introns. The taxonomy in the inset phylogeny is the one we recommend based on the present study. *Inset photo*: *Prinia polychroa* core '*cooki*' (described as a new taxon herein), presumed male, Sakaerat, Nakhon Ratchasima Prov., Thailand, 4 Jan. 2014 (DZUG U3546) (Philip D. Round).

group as sister to the others, the latter in effect forming an unresolved polytomy. The topological incongruence between the cyt*b* and *BEAST trees are unsupported because of the low statistical support in the *BEAST tree.

The chronogram (Fig. 9) suggests that the oldest split within the *P. crinigera–P. polychroa* complex, between the *striata* group and the rest, took place 3.6 million years ago (mya) (95% highest posterior density (HPD), 2.6–4.7 mya), whereas the youngest separation among the six primary clades, between core '*cooki*' and Javan *polychroa*, was 0.7 mya (95% HPD 0.4–1.1 mya). According to the same analysis, *rocki* diverged from the other taxa in the *polychroa* group 1.95 mya (95% HPD 1.3–2.6 mya), and Myanmar *cooki* from core '*cooki*' and Javan *polychroa* 0.96 mya (95% HPD 0.6–1.4 mya). The tree inferred under the HKY + G model is identical in topology and virtually identical in dating (not shown).

Distribution and habitat

Our field observations of habitat preferences and elevational distributions agree well with the literature. We have found all of the taxa in the *crinigera* group on open hill and mountain sides with scrub and tall grass and scattered trees. In the Himalayas, *crinigera* and *yunnanensis* breed at 1200–2300 m, exceptionally up to 3100 m, and possibly as low as 600 m in the west (Ali & Ripley 1973, Inskipp & Inskipp 1991, Martens & Eck 1995, Rasmussen & Anderton 2005). The sub-Himalayan *striatula* breeds mostly at lower elevations (Whistler 1963) and has been reported at 300 m in March (Roberts 1992). On Mt Victoria, western Myanmar, we have observed *yunnanensis* at *c.* 1100–2400 m (but there was little suitable habitat lower down). For the *striata* group in mainland China, we have found *catharia* in similar habitat and at generally similar elevations to *crinigera*, although it has been observed commonly during the breeding season in Hunan province as low as 30 m asl (Jonathan Martínez *in litt.*). In Taiwan, *striata* has been observed at 300–2500 m asl.

For the *polychroa* group, we have found Myanmar *cooki* in the dry barren central plains in areas with scrub, grass and scattered trees, and one individual in similar, although lusher, habitat near the top of Mt Popa at 1400 m asl. In Thailand, Laos and Cambodia, core '*cooki*' occurs mainly in better quality dry dipterocarp woodland of the plains and lower hills (Lekagul & Round 1991, Duckworth *et al.* 1999, Goes 2013, P.D. Round pers. obs.). While it ascends locally to 800–1000 m in Thailand, it is very scarce and patchily distributed there, and is absent from most areas with seemingly suitable habitat within the expected elevational range. In only one or two Thai sites is it found in areas of degraded dry dipterocarp, scrub or grassland. On the Da Lat plateau in south Vietnam, we have observed *rocki* in bushes and grass on open hillsides and in forest clearings at around 1000–1500 m asl, although we lack detailed information from this area. Simon Mahood (*in litt.*) stated that it is common there 'in degraded dry woodland and areas of introduced pine with a grassy understory, where this forms a human-induced fire climax habitat'. We have found Javan *polychroa* in scrubby open hillsides and open fields with a mixture of low exotic and native vegetation and scattered small trees, and our sound recordings are from 250 to 1000 m asl (Bas van Balen *in litt.*).

DISCUSSION

Species taxonomy

Based on an analysis integrating morphology, song, cyt*b* sequence data and geographical distributions, six groups were identified: (1) the *crinigera* group comprising *striatula*, *crinigera*, *yunnanensis* and *bangsi*; (2) the *striata* group comprising *catharia*, *parumstriata* and *striata*; (3) Myanmar *cooki*; (4) core '*cooki*'; (5) *rocki*; and (6) Javan *polychroa*.

Morphological differences are pronounced between the *crinigera* group, Myanmar *cooki* and *striata* group (especially with respect to the two former vs. the third), and between these groups and the *polychroa* group. Differences are subtle among *rocki*, core '*cooki*' and Javan *polychroa*, especially the latter two. The *crinigera* and *striata* groups and Myanmar *cooki* show strong seasonal changes and sexual size dimorphism and dichromatism: breeding males attain black bills, and females are much smaller and do not become black-billed, and breeding males of the *crinigera* group and, to a lesser extent, Myanmar *cooki* become dark-faced. The other members of the *polychroa s.l.* group have weaker, inconsistent seasonal and sexual differences, although breeding males of core '*cooki*', and probably also *rocki*, usually also attain a blackish bill and gape.

The songs of the *crinigera* and *striata* groups and Myanmar *cooki* (Type A) are very different from the typical songs of core '*cooki*', *rocki* and Javan *polychroa* (Type B), although the three latter taxa occasionally sing a Type A song which, therefore, is probably plesiomorphic. The differences in song among the *crinigera* and *striata* groups and Myanmar *cooki* are easily audible with practice, and DFA permitted discrimination of songs of all except two Myanmar *cooki* and one nominate *crinigera*. The simple Type B songs of core '*cooki*', *rocki* and Javan *polychroa* are less well-differentiated, and although 100% of *rocki* songs were correctly discriminated by DFA, larger samples from more localities are required to evaluate whether these three groups differ consistently.

The molecular markers, combined and independently, support a sister relationship between the *striata* group and the others, suggesting that *P. crinigera s.l.* (e.g. Madge 2006, Dickinson & Christidis 2014, del Hoyo & Collar 2016, Gill & Donsker 2017) is paraphyletic. All six groups form reciprocally monophyletic groups in the cyt*b* gene tree, with separations dating back to *c.* 2–3.6 mya, except between Myanmar *cooki*, core '*cooki*' and Javan *polychroa*, which separated more recently (*c.* 0.70–0.96 mya).

Most taxa are allopatric, except the sympatry first noted by Deignan (1957) as two taxa (which he considered to be *P. c. parvirostris* and *P. p. bangsi*) at Mengzi, Yunnan Province, China, which led to the two-species treatment. However, we found that the two taxa in apparent sympatry (*catharia* and *bangsi*) at Mengzi belong in the *striata* and *crinigera* groups, respectively. We also found several specimens of both species from other localities that overlap in Yunnan (P.C. Rasmussen unpubl. data), so *catharia* is evidently sympatric with both *bangsi* and *yunnanensis*. Field research in the breeding season is needed to understand their distributions and interactions in these areas.

In summary, the mainly Himalayan *crinigera* group and the Chinese mainland–Taiwanese *striata* group are best treated as separate species, as they differ consistently and congruently in morphology, song and cyt*b*; they are strongly suggested to be non-sisters; and they are sympatric in Yunnan. The taxa *crinigera/striatula* and *yunnanensis/bangsi* are reciprocally monophyletic in our cyt*b* tree, and differ marginally in plumage, but they seem vocally inseparable, so we treat them as subspecies. The newly circumscribed *P. crinigera* Hodgson, 1836 *s.s.* comprises the subspecies *striatula*, *crinigera*, *yunnanensis* and *bangsi*, whereas *P. striata* Swinhoe, 1859 comprises the subspecies *catharia*, *parumstriata* and *striata* (Table 1).

Myanmar *cooki* resembles *P. crinigera s.s.* in having distinct seasonal plumage variation of the same type in males and strong sexual size dimorphism, and breeding males are more similar to *P. crinigera s.s.* than to core '*cooki*', *rocki* and Javan *polychroa* in plumage. Also, the song of Myanmar *cooki* (Type A), while being clearly separable, resembles those of *P. crinigera s.s.* and *P. striata* much more than the usual song type of core '*cooki*', *rocki* and Javan *polychroa* (Type B). In contrast, cyt*b* shows Myanmar *cooki* to be more closely related to core '*cooki*' and Javan *polychroa*, with a comparatively recent separation (*c.* 0.96 mya), than to *P. crinigera s.s.* or *P. striata* (nuclear markers unresolved in this respect). Based on its distinctness in morphology, song and cyt*b* we recommend recognition of *P. cooki* (Harington, 1913) as a monotypic species restricted to Myanmar (Table 1). However, at Shan States, southeast Myanmar, specimens are darker and more richly coloured, and the only sample sequenced from there is marginally divergent from the three samples from the plains of central Myanmar, so further study is needed to determine whether yet another undescribed taxon exists there.

With respect to *rocki*, core '*cooki*' and Javan *polychroa*, the taxonomy is not straightforward. The first of these is the most divergent in its warmer-toned breeding plumage. Although the Type B song of *rocki* sounds rather similar to those of *polychroa* and core '*cooki*', it was consistently different from the latter two in details in sonograms, and had 100% discrimination in the DFA. Based on cyt*b*, *rocki* is the most divergent, and is sister to Javan *polychroa*, core '*cooki*' and Myanmar *cooki*, with an estimated separation *c.* 2 mya. However, as this is only based on one locus, corroboration from additional loci is needed to ascertain that the topology represents the species tree and is not due to hemiplasy (Avise & Robinson 2008) or ancient introgression. In addition, the habitat differences between *rocki* and core '*cooki*' are notable, with *rocki* occurring in a wide variety of open areas, including grassy undergrowth of pine plantations, while core '*cooki*' is essentially limited to dry dipterocarp forest. Based on the combined evidence, we propose recognition of *rocki* as a monotypic species, *P. rocki* Deignan, 1957 (Table 1). More data are needed on its distribution and potential interactions with core '*cooki*' (see below).

Based on the suggested sister relationship between Javan *polychroa* and core '*cooki*' and the rather slight morphological, vocal and molecular divergence between them, we treat the latter as a subspecies of *P. polychroa* (Temminck, 1828). However, treatment as separate species may be equally appropriate, as core '*cooki*' is much more distinct than any other subspecies we recognize in the *P. crinigera s.l.–P. polychroa s.l.* complex, and unlike Javan nominate, which occurs in highly disturbed habitats, core '*cooki*' is restricted to dry dipterocarp woodland. Treatment of *deignani* as a distinct species would be further supported by the widely allopatric distributions of core '*cooki*' and Javan *polychroa*, which render them effectively genetically completely isolated from each other. Moreover, although only three *deignani* and two Javan *polychroa* have been sequenced, they are reciprocally monophyletic in cyt*b*.

Prinia polychroa s.s. is one of a suite of open-country species with a relict distribution in Southeast Asia and Java, and was probably much more widespread when the Greater Sundas were connected by lowered sea levels and savannahs were regionally extensive (Heaney 1991, Cannon 2012, Sheldon *et al.* 2015). Other taxa with similar distributions that have differentiated only at the subspecies level include Green Peafowl *Pavo muticus*, Lineated Barbet *Psilopogon lineatus*, Small Minivet *Pericrocotus cinnamomeus*, Black Drongo *Dicrurus macrocercus*, Common Tailorbird *Orthotomus sutorius*, Chestnut-capped Babbler *Timalia pileata* and Streaked Weaver *Ploceus manyar*.

Intraspecific taxonomy and distributions

Vaurie (1959) listed *P. polychroa* for Assam, India, but as no specimens or other evidence is known from there, it is considered regionally hypothetical (Rasmussen & Anderton 2005). Also, because *catharia* is a subspecies of *P. striata* rather than of *P. crinigera s.s.*, there is no evidence that *striata* occurs in India either. Furthermore, because sympatry in Yunnan involves *P. striata* and *P. crinigera s.s.* instead of *P. crinigera s.l.* and *P. polychroa s.l.* (*contra* Deignan 1957), the occurrence of *P. polychroa s.l.* in China is unsupported. We have found no evidence of the occurrence of more than one taxon (*P. striata*) in Taiwan, and consider this highly unlikely, in agreement with Severinghaus *et al.* (2012).

We conclude that *yunnanensis* (Harington, 1913) is a moderately well-marked subspecies, both in colour and in structure, especially given that the size differences between *yunnanensis* and nominate *crinigera* are the reverse of the usual size cline (cf. Rasmussen & Anderton 2005). We find little support for the taxon *assamica* Baker, 1924, unless restricted to Meghalaya (as may be warranted, see above), and so consider it a junior synonym of *yunnanensis*. Rasmussen and Anderton (2005) considered on the basis of plumage that three subspecies occur in South Asia; however, they used the name *assamica* instead of *yunnanensis*, as did Dickinson and Christidis (2014) and Gill and Donsker (2017). del Hoyo and Collar (2016) synonymized both *assamica* and *yunnanensis* with *catharia*. In future, *yunnanensis* should be the subspecies listed for northeastern India.

Given the apparent range discontinuity between *yunnanensis* (west Yunnan) and *bangsi* (southeast Yunnan), and the shorter wing and paler mantles in the small sample of *bangsi* compared with *yunnanensis*, we tentatively treat *bangsi* as a valid subspecies of *P. crinigera s.s.*

Because specimens of nominate *striata* are generally darker and more richly coloured than *parumstriata*, we continue to recognize both.

Description of a new subspecies of *Prinia polychroa* s.s

Morphology, song and cyt*b* congruently demonstrates that core '*cooki*' from Thailand, Cambodia and Laos represents a distinct taxon that we consider a subspecies, but for which no available name is known. We propose to name it:

***Prinia polychroa deignani,* subsp. nov.**

Holotype

USNM 450982, male, t.n.e. [testes not enlarged], Siam: Kamphaeng Phet; Ban Khlong Khlung (*c.* 16.18°N, 99.72°E); H. G. Deignan #1683, 24 April 1953. Adult. See Figure S4.

Measurements of holotype: culmen (mm) from skull base 14.3; culmen from distalmost feathers 10.7; wing (flattened) 57; tail 80.4; tarsus 23.6. See Tables S1 and S6 for more measurements.

Paratypes

USNM 451940, male, Thailand: Loei; Amphoe Wang Saphung; Phu Krading (16.87°N, 101.75°E); R. E. Elbel #RE3250, 1 Jan. 1954. Adult.

USNM 450984, male, t.n.e. [testes not enlarged], Siam: Kamphaeng Phet; Ban Khlong Khlung; H. G. Deignan #1713, 26 April 1953. Adult.

USNM 278580, female, E. Siam: Lat Bua Kao (14.86°N, 101.60°E); 14 Oct. 1916; C. Boden Kloss; total length 144; iris ochreous; bill horn, lr man [lower mandible] fleshy; feet fleshy. Probably a subadult.

All paratypes (see Fig. S3) were available for direct comparison with the holotype during preparation of the description.

Diagnosis

In fresh adult plumage, differs from Javan *polychroa* in comparable plumage in its more rufescent and distinct pale edgings to tertials and more prominently barred uppertail.

Typically also differs from *polychroa* in having slightly warmer, browner, paler upperparts; less contrasting face pattern, with supercilium contrasting less with dark lores, and auriculars more spotted and thus appearing browner; more rufescent edgings to secondaries; paler, distinctly to slightly less buffy underparts; and smaller and less prominent dark subterminal spots and pale terminal spots to undertail. Sex-for-sex, it is also significantly smaller overall than Javan *polychroa*.

Based on a single juvenile specimen of each taxon, the juvenile of *deignani* appears to be much warmer brown above than that of Javan *polychroa*.

Differs from Vietnamese *rocki* in comparable plumage in its supercilium (when evident), being whitish or greyish, not buffy (though may be whitish also in *rocki*); in typically being slightly paler brown above, and never as warm brown as in fresh or immature *rocki*; in its much drabber, paler underparts coloration, lacking stronger rufescence on thighs, flanks and undertail-coverts; and in its rather less rufescent wing panel and less strongly rufescent tertial edgings, the rufescent tertials and wing panel contrasting less with the pale-edged greater secondary coverts than in *rocki*. The two taxa are more similar in the above characters when fresh *deignani* are compared with worn *rocki*, but *rocki* almost always has at least the lower flanks and especially the thighs and undertail-coverts strongly rufescent, unlike *deignani*. In addition, unless the tail is excessively worn, *deignani* shows smaller, weaker dark subterminal spots and duller, less obvious, less buffy terminal spots to the undertail compared with *rocki*.

Differs from Myanmar *cooki* in lacking marked seasonal changes in head and mantle colour and pattern. Compared with adult male breeding *cooki*, *deignani* has much paler, browner crown and upper auriculars, and a whiter supercilium; shorter tail, with smaller and less prominent dark subterminal spots and pale terminal spots to undertail; and less marked sexual size dimorphism. Very similar to breeding adult female *cooki*, but with slightly weaker and less uniform yellow-buff wash below. From non-breeding adult *cooki*, *deignani* differs in lacking the diffuse whitish area around the eye; being colder brown above; having a much shorter tail; and having smaller, weaker subterminal and terminal tail marks.

Description of holotype. (Colour names and notations in parentheses from Munsell Color 2000.)

Crown feathers fairly distinctly streaked, the feathers mainly very dark brown (very dark grey, 10YR 3/1) with narrow very pale grey-brown (light grey, 10YR 7/1) edgings, the streaking changing to weak, narrow pale scalloped edgings on nape; fairly prominent pale greyish-white (white, 10YR 8/1) supercilium before eye, ending less than halfway above eye, but a dull mid-grey line extends to behind eye; lores broadly dark brownish-grey (dark grey, 10YR 4/1); sides of face just below eye and upper auriculars dull grey-brown (greyish brown, 10YR 5/2), grading to paler and with tiny dark speckles on lower auriculars; sides of neck and breast grey-brown (grey, 10YR 5/1) with narrow, weak dark brown shaft streaks; mantle including scapulars weakly and broadly streaked dark brown (dark greyish brown, 10YR 4/2) grading to weakly paler edgings (grey, 10YR 6/1); lower back grades to browner and less streaked (brown, 10YR 5/3) and uppertail-coverts slightly more rufescent (brown, 7.5YR 5/4); lesser and median upperwing coverts dark grey-brown (dark grey, 10YR 4/1) edged (as scalloping) with pale grey-buff (light grey, 10YR 7/1); greater upperwing coverts paler and browner (dark greyish brown, 10YR 4/2) with narrowly paler and slightly more rufescent (very pale brown, 10YR 8/2) edgings; tertials grey-brown (greyish brown, 10YR 5/2) with narrow pale rufous-buff edgings (very pale brown, 10YR 8/3) encircling the tip and along the outer web; narrow dull rufescent outer edgings (pale red, 7.5YR 6/4) to inner secondaries and primaries create a weak rufescent wing panel; uppertail surface medium dull brown (yellowish brown, 10YR 5/4)

Table 3. Localities (listed from west to east, then north to south) from which the new taxon has been recorded, based on examined specimens (museum acronym followed by number of examined specimens; full museum names in Acknowledgments and further specimen data in Table S1); documented, identifiable photographs examined; sound recordings studied; and tissue samples. Country codes (ISO-3166): TH = Thailand; KH = Cambodia; LA = Laos. NHA = Non-Hunting Area; NP = National Park; WS = Wildlife Sanctuary; OBI = orientalbirdimages.org, photos only; XC = xeno-canto.org, recordings only; AV = avocet.zoology.msu.edu; ML = macaulaylibrary.org; IBC = Internet Bird Collection, hbw.com.

Locality	Latitude (°N)	Longitude (°E)	Documentation	Dates
TH: Mae Hongson Prov.; Mae Sarieng, Huai Mae Sanam	18.15	98.30	THNHM (2)	15–20 Mar. 1960
TH: Kamphaengphet Prov.; Ban Khlong Khlung	16.18	99.72	USNM (3)	23–26 Apr. 1953
TH: Phitsanulok Prov.; Khao Noi-Khao Pradu NHA	17.08	100.47	photo, M. Taengtum[b]	8 Mar. 2014
TH: Nakhon Ratchasima Prov.; Khao Yai NP, Nong Phak Chi	14.45	101.37	ML 49490501, photo	24 Feb. 2017
TH: Nakhon Ratchasima Prov.; Pak Chong, Nong Nam Daeng	14.61	101.38	photo, I. Sa-ar	20 Mar. 2017
TH: Nakhon Ratchasima Prov.; Pak Jong (= Pak Chong)	14.67	101.44	NHMUK (1)	19 Feb. 1924
TH: Nakhon Ratchasima Prov.; Chan Tuk (= Chan Thuek)	14.82	101.46	USNM (1)	12 Jun. 1934
TH: Phetchabun Prov.; Nam Nao NP, Pa Paek (Dong Paek)	16.74	101.55	photo, M. Taengtum[a]	4 Aug. 2012, juvenile
			XC350874	10 Jan. 2017
Phetchabun Prov.;	16.74	101.57	XC329486, XC329487	7 May 2015
Nam Nao NP			XC384875, XC384876	29 Aug. 2017
TH: Chaiyaphum Prov.; Phu Khieo WS, Thung Kamang	16.39	101.57	photo, D. Sargeant	4 Feb. 2012
TH: Nakhon Ratchasima Prov.; Lat Bua Khao	14.86	101.60	USNM (2), NHMUK (3)	9–18 Oct. 1916
TH: Nakhon Ratchasima Prov.; Khorat (= Korat)	14.84	101.62	USNM (1)	18 Sep. 1969
TH: Loei Prov.; Phu Krading;	16.87	101.75	USNM (1)	1 Jan. 1954
TH: Nakhon Ratchasima Prov.; Sakaerat Environmental Research Station	14.51	101.94	THNHM (2)	26 Jun. 196718 Aug. 1971
			DZUG 3546, DZUG 3547	4 Jan. 2014[c]
TH: Nakhon Ratchasima Prov.; Thap Lan NP, Sap Sadao (= Thablan NP, Sabsadao)	14.40	102.17	AV 19921, AV 19922, XC185665, ML 46307681, photo	Dec. 19994 Jan. 20143 Jul. 201428 May 2016
KH: Odder Meanchey Prov.; Andong Bor	14.02	103.21	XC88100, 88120–1	5–7 Nov. 2010
KH: Plateau Kiri Rom	*c.* 11.3	*c.* 104.1	USNM (1)	3 Apr. 1961
KH: Siem Reap Prov.; Bengal Florican Reserve	13.02	104.44	ML 51742341, photo	14 Feb. 2017
KH: Prey Veng Prov.; Preah Vihear	13.91	104.55	XC124245	26 Dec. 2012
LA: Savannakhet	*c.* 16.55	*c.* 104.75	YPM (14)	19 Jul. 1943–24 Dec. 1944
KH: Prey Veng Prov.; Preah Vihear; Tmat Boey	13.97	104.88	OBI (2 photos) IBC (videos, photo)	Feb. 2008 2011–2017
			ML 26935341, photo	4 Mar. 2016
			XC27624	Feb. 2008
			XC295728	4 Mar. 2015
TH: Amnat Charoen Prov.; Chanuman District	16.13	104.92	ANSP (1)	13 Feb. 1936
KH: Prey Veng Prov.; Preah Vihear; T'beng Meachey	13.81	104.99	ML 52635191, photo	11 Dec. 2014
KH: Kampong Thom (= Kompong Thom)	*c.* 12.90	*c.* 105.23	NHMUK (1)	3 Jan. 1928
LA: Champasak Prov., Don Khanthung, Ban Kadan	14.37	105.51	AV 19920, sightings, recordings	Jul. 1998

[a]http://www.lowernorthernbird.com/checklist.php?cat_xml:id=34&c_xml:id=461&b_xml:id=1451. [b]http://www.lowernorthernbird.com/checklist.php?cat_xml:id=34&c_xml:id=461&b_xml:id=712. [c]Additional specimen(s) unverified by us collected 27 Feb.–6 Mar. 1967 and/or 13–24 Jan. 1968; also a sound recording unverified by us, UF:Audio:2566. [d]Tail feathers collected from two birds, P.D. Round.

with weak, narrowly spaced, narrow darker bars (only visible on close inspection); underparts from chin to undertail-coverts very pale brownish-white (mostly very pale brown, 10YR 8/2), the breast, sides, thighs and undertail-coverts slightly more yellow-buff (similar to but paler than very pale brown, 10YR 8/4), the outer thighs narrowly darker brown; central belly almost white. No soft part colour information on labels, but on dried specimen upper mandible is all dark brown, lower is dark brown on distal half and pale fleshy horn on proximal half and lower edge; narrow unfeathered orbital ring appears to be dull red; tarsi are dull orange-horn, the toes and claws slightly darker orange-horn.

Distribution

Examined specimens of *P. p. deignani* are listed in Tables 3 and S1, along with documented photographs and sound recordings. Based on these data, the new subspecies is confirmed to occur in scattered localities in northwest, central and eastern Thailand, southwestern Laos, and northwestern Cambodia. A sequenced specimen from Cambodia (NHMUK 1928.6.26.1198) is very similar in cyt*b* to the two sequenced Thai specimens.

Etymology

We wish to honour Herbert Girton Deignan (1906–1968) for his contributions to the understanding of this complex specifically, and to Thai birds in general, by naming this new subspecies after him.

Variation

The paratypes are all very similar to the holotype, with the following notable departures: USNM 278580, the lone female in the type series, has a much paler bill, especially the lower mandible, has slightly paler and warmer brown upperparts, especially the tail and tertial edgings, and is washed brighter buffy below.

One dark-billed June male specimen from Savannakhet, Laos (YPM 18329; not a member of the type series), shows a dark grey face, very weak supercilium, and dark breast sides, in a plumage reminiscent of breeding *Prinia cooki* from the Burmese plains.

Photographs of living adults (e.g. Fig. 5 and Table S6) show a fleshy-grey to brownish-pink orbital ring and orange-brown iris; bill and gape varying from all-blackish in breeding season males to grey on the upper mandible and pale pink or pale orange on the lower mandible and along the cutting edges of the upper mandible, with or without a diffuse darker tip to the lower mandible in the non-breeding season; and pale pink legs and claws (or claws slightly darker and greyer or paler than legs).

We have examined a single juvenile specimen (YPM 18373) in fresh plumage. It differs strongly from adults in being unstreaked warm brown above, with bright rufous primary and secondary edgings and uppertail surface; the tertials and greater secondary coverts are indistinctly edged rufous; below it is tinged yellow on a white background, the breast sides dull medium olive-brown, flanks and undertail-coverts tinged warm rufescent; virtually no undertail markings are present on the fresh rectrices.

Conservation

Most taxa of this complex have extensive ranges in open scrubby or grassy habitats, including wooded savanna, often in understorey of pine forests or exotic tree plantations. Some of the habitats they favour are created by habitat disturbance and succession. While no taxa are at present considered at risk, some conservation issues nevertheless pertain to Javan *P. polychroa*, which is subject to considerable (though not yet intensive) trapping (Chng *et al.* 2015) and now seems common only in a few areas such as Gunung Merapi, central Java (P.C. Rasmussen pers. obs. 2014). With the effective disappearance from the wild of other Javan species more valued as cage birds, it seems likely that pressure on this taxon will increase.

Additionally, the new taxon *P. p. deignani* is also likely to be of conservation concern, as its core lowland deciduous dipterocarp habitat has already been cleared from virtually its entire Thai range (including at the type locality) while upland metapopulations are small and few. In Laos, the only records are from lowlands. Although not presently considered at risk in Laos, it has declined there due to habitat loss, and could become threatened if present trends continue (Duckworth *et al.* 1999, SUFORD 2010; J.W. Duckworth *in litt.*). More extensive dry dipterocarp habitat remains in the northern plains of Cambodia, where *deignani* is still relatively widespread and common (Goes 2013), but it is similarly intolerant of habitat disturbance (S. Mahood *in litt.*). While

remaining *deignani* populations in Thailand are already fragmented and patchily distributed, those in Laos and Cambodia are likely to become more so.

CONCLUSIONS

Based on our integrative taxonomic approach, analysing morphology, songs, DNA and geographical distributions, we recommend recognition of five species in the *P. crinigera s.l.–P. polychroa s.l.* complex, and suggest the following English names: Himalayan Prinia *P. crinigera s.s.* (with four subspecies); Chinese Prinia *P. striata* (with three subspecies); Burmese Prinia *P. cooki* (monotypic); Annam Prinia *P. rocki* (monotypic); and Deignan's Prinia *P. polychroa s.s.* (with two subspecies), as summarized in Table 1. We found no evidence that *P. polychroa s.l.* or *s.s.* occurs in mainland China, Taiwan or India, or that *P. striata* occurs in India. Acceptance of this revision implies the existence of three new single-country endemics: *P. cooki* from Myanmar, *P. rocki* from Vietnam and *P. striata* from China (mainland China and Taiwan). We describe a new subspecies of *P. polychroa s.s.* from Thailand, Laos and Cambodia.

This study highlights the importance of taxonomic revisions of poorly studied polytypic birds using a modern integrative taxonomic approach to better estimate the true diversity of bird species.

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DATA AVAILABILITY

The song data that support the findings of this study are available in AVoCet at https://avocet.integrativebiology.natsci.msu.edu and in xeno-canto at https://www.xeno-canto.org/collection/area/asia; see Table S2 for reference numbers. The genetic data are available in NCBI GenBank at https://www.ncbi.nlm.nih.gov/genbank; see Table S3 for reference numbers.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Specimens used as standards for plumage scores for each character (all left to right). In each case, 1 is the leftmost specimen, numbered through 5 or 6 on the right. All specimens from NHMUK. Lower mandible colour: 1 = all pale; 2 = hint of dusky; 3 = moderate dusky; 4 = very dusky; 5 = nearly solid black; 6 = solid black. Crown streak prominence: 1 = unstreaked; 2 = very slight streaking; 4 = slight streaking; 4 = moderately prominent streaking; 5 = fairly prominent streaking; 6 = crisply streaked. Supercilium prominence: 1 = none; 2 = barely indicated; 3 = slight supercilium; 4 = moderate supercilium; 5 = fairly prominent; 6 = very prominent. Suborbital auricular colour: 1 = whitish; 2 = very pale brownish; 3 = pale brownish; 4 = mid-brownish/greyish; 5 = dark greyish; 6 = blackish. Malar speckling: 1 = none; 2 = tiny, few; 3 = small, few; 4 = moderate; 5 = prominent; 6 = heavy. Mantle streak prominence: 1 = none; 2 = vague streaking; 3 = slight streaking; 4 = moderate streaking; 5 = fairly strong streaking; 6 = crisply streaked. Mantle edging colour: 1 = grey; 2 = sandy; 3 = neutral pale brown; 4 = slightly warm brown; 5 = warm brown; 6 = rufous. Wing panel colour: 1 = grey; 2 = neutral; 3 = slightly rufescent; 4 = pale rufous; 5 = warm rufous; 6 = bright rufous. Tertial edge colour: 1 = drab; 2 = neutral; 3 = slightly rufescent; 4 = pale rufous; 5 = warm rufous; 6 = rich rufous. Breast feather wear: 1 = none; 2 = very slight; 3 = light; 4 = moderate; 5 = fairly heavy; 6 = heavy. Uppertail barring prominence: 1 = none; 2 = very slight; 3 = slight but readily apparent; 4 = moderate; 5 = prominent. Uppertail rufescence (darkness not

scored): 1 = grey; 2 = sandy; 3 = neutral; 4 = slightly rufous; 5 = warm rufous; 6 = rich rufous. Undertail subterminal dark spots: 1= negligible; 2 = slight; 3 = weak but apparent spots; 4 = moderate; 5 = fairly prominent; 6 = strongly contrasting, large.

Figure S2. PCAs of plumage character scores for breeding (a) and non-breeding (b) adult males of the crinigera and striata groups (all subspecies of each) and Myanmar *cooki*.

Figure S3. Myoglobin and ODC gene trees reconstructed using BEAST.

Figure S4. Type series of *Prinia polychroa deignani*, new subspecies, left to right, all views: USNM 450982, holotype; USNM 451940, paratype; USNM 450984, paratype; USNM 278580, paratype. From left to right: dorsal view lateral view and ventral view.

Table S1. Original data for specimens measured and plumage-scored.

Table S2. Raw measurement data and localities for sound recordings.

Table S3. Samples used in phylogenetic analyses, with GenBank accession numbers. Sequences with GenBank numbers in italics were not generated for this study.

Table S4. Cytochrome *b* primers designed for toepad samples.

Table S5. Univariate statistics for plumage scoring of the *Prinia crinigera–P. polychroa* complex. Breeding and non-breeding specimens are separate for taxa of *P. crinigera s.l.* and Myanmar *P. p. cooki*, but not for *P. p. rocki*, *P. p. polychroa* or core *P. p.* '*cooki*'. Significance levels from Kruskal–Wallis one-way analyses of variance used for samples of 7 or larger: ns, $P > 0.05$; * $P \leq 0.05$; $P \leq 0.01$; $P \leq 0.001$.

Table S6. Univariate statistics for measurements of the *Prinia crinigera–P. polychroa* complex. L = length, w = width, d = depth, s = shortfall. Significance levels for measurements using Bonferroni-adjusted two-sample *t*-tests (samples smaller than 7 not tested): ns, $P > 0.05$; * $P \leq 0.05$; $P \leq 0.01$; $P \leq 0.001$.

Table S7. Summary statistics for results of principal component analyses of morphological characters of taxa of the *Prinia crinigera–P. polychroa* complex. Important variables on each factor are in bold, especially important ones in bold italic.

Material S1. Xml files for BEAST analysis of cytochrome *b* (a), myoglobin (b) and ODC (c) for all samples.

Material S2. Xml file for *BEAST analysis of cytochrome *b*, myoglobin and ODC for subset of samples.

Material S3. Notes on types of *P. c. striatula* and *P. cooki*.

Material S4. DFA of Type A songs of the *Prinia crinigera–P. polychroa* complex.

Material S5. DFA of Type B songs of the *P. polychroa* complex.

Material S6. Photos (a) or video (b,c,d) of individuals for which blood samples were taken for the genetic analyses. (b) *Prinia polychroa rocki* female Tuyen Lam, Dalat, Vietnam 12 May 1999 (DZUG U450).m4v; (c) *Prinia polychroa rocki* female Dalat, Vietnam 14 May 1999 (DZUG U1970).m4v; (d) *Prinia polychroa cooki* Bagan, Myanmar, 12 Apr. 2000 (DZUG U458).