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Short Communication

Molecular phylogenetics and species limits in a cryptically coloured radiation of Australo-Papuan passerine birds (Pachycephalidae: *Colluricincla*)

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ABSTRACT

Detailed knowledge of species limits is an essential component of the study of biodiversity. Although accurate species delimitation usually requires detailed knowledge of both genetic and phenotypic variation, such variation may be limited or unavailable for some groups. In this study, we reconstruct a molecular phylogeny for all currently recognized species and subspecies of Australasian shrikethrushes (*Colluricincla*), including the first sequences of the poorly known *C. tenebrosa*. Using a novel method for species delimitation, the multi-rate Poisson Tree Process (mPTP), in concordance with the phylogenetic data, we estimate species limits in this genetically diverse, but phenotypically subtly differentiated complex of birds. In line with previous studies, we find that one species, the little shrikethrush (*C. megarhyncha*) is characterized by deep divergences among populations. Delimitation results suggest that these clades represent distinct species and we consequently propose a new classification. Furthermore, our findings suggest that *C. megarhyncha melanorhyncha* of Biak Island does not belong in this genus, but is nested within the whistlers (*Pachycephala*) as sister to *P. phaionota*. This study represents a useful example of species delimitation when phenotypic variation is limited or poorly defined.

1. Introduction

Species are the fundamental taxonomic units of biological classification and it is therefore natural that the delimitation of species is an essential component in studies of biodiversity and related disciplines. Examples of fields that are critically dependent on a rigorous and consistent species delimitation include ecological studies of community composition and assembly (Webb et al., 2002), the modelling of evolutionary diversification dynamics through time and space (Etienne and Rosindell, 2011) and conservation (Mace, 2004; Fujita et al., 2012). Although the definition of species is still contentious (de Queiroz, 2007), species delimitation remains an active field of research as is evident from the multitude of species delimitation methods that have become available in recent years (e.g. Pons et al., 2006; Tobias et al., 2010; Reid and Carstens, 2012; Zhang et al., 2013; Solís-Lemus et al., 2015). The majority of these methods take advantage of the dramatic recent increases in genetic data and associated molecular phylogenies. An underlying assumption of such approaches is that phylogenetic branching patterns can be divided into speciation and extinction processes that operate between species and the coalescent population processes that occur within species. As such, the delimitation methods aim to establish the threshold at which the shift from one process to another occurs. Here we use such delimitation approaches to resolve species limits in a genus of passerine birds with a long and convoluted taxonomic history.

Colluricincla shrikethrushes are confined to Australia, New Guinea and the nearest smaller islands and represent a clade of corvoid passerine birds in the family Pachyecphalidae (whistlers). One species in particular, the little shrikethrush (*C. megarhyncha*) has been suspected of harbouring significant unrecognized species diversity (Deiner et al., 2011; Beehler and Pratt, 2016). Historically, more than 30 subspecies were described for *C. megarhyncha*, reflecting the sometimes slight, but noticeable variation in morphology among local populations. Accordingly, its taxonomy has gained considerable interest by ornithologists, many of whom have suggested that *C. megarhyncha* represents multiple distinct species (e.g. Mayr, 1944; Ford, 1979; Deiner et al., 2011; Beehler and Pratt, 2016). This notion has been exacerbated by recent molecular studies, which have demonstrated significant genetic

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divergence among lineages comparable to other, highly divergent species or even genera (Deiner et al., 2011). Despite these findings, no attempts have been made to redefine species limits in this group, presumably due to the lack of concordance between genetic and morphological data, and limited morphological variation between populations.

Here we assess species limits within *Colluricincla* by combining existing molecular data with newly generated DNA sequences. First, we infer a molecular phylogeny of all currently recognized species and subspecies within the genus *Colluricincla*, including for the first time the poorly known sooty shrikethrush (*C. tenebrosa*). Second, we investigate species limits in this particular group using a novel and improved method for species delimitation, the multi-rate Poisson Tree Process (mPTP, Kapli et al., 2017) as well as the more well-established Generalised Mixed Yule Coalescent (GMYC) method (Pons et al., 2006). Finally, finding that *C. megarhyncha* is comprised of seven highly divergent clades that are suggested to represent distinct species, we propose a new classification for the group.

2. Materials and methods

2.1. Taxon sampling

We included molecular data for all five species (264 individuals) of *Colluricincla* shrikethrushes (mainly sourced from Deiner et al., 2011; Nyari and Joseph, 2013; Jønsson et al., 2010) following the IOC World Bird List v7.2 (Gill and Donsker, 2017). As outgroups, we included *Pseudorectes ferrugineus* and *Melanorectes nigrescens*. We sequenced an additional 24 ND2, 5 GAPDH, 5 ODC and 5 Myo2 sequences using standard protocols. Our final dataset included the mitochondrial gene ND2 for all individuals and three nuclear introns (GAPDH, ODC and Myo-2) for 12 individuals representing all five currently recognized species and outgroups. All new sequences have been uploaded on GenBank under accession numbers MG288640-MG288673 (Appendix A).

2.2. Phylogenetic and dating analyses

DNA sequences were aligned for each gene individually using Seaview (Gouy et al., 2010). A large number of the ND2 sequences were identical and as this may bias some species delimitation approaches we removed these prior to further analyses, retaining ND2 sequences for 129 individuals of *Colluricincla* with dense geographical sampling (Fig. 1, Appendix A). We analysed both a concatenated dataset of all genes as well as a separate ND2 dataset using maximum likelihood (ML) as implemented in RAxML v8.2.4 (Stamatakis, 2014) and run on the CIPRES Science Gateway v3.3 (Miller et al., 2010) using default settings. For the concatenated analyses, we partitioned the data by codon position for the mitochondrial ND2 gene and by gene for the three nuclear introns. Using the rapid bootstrap technique we computed the most likely tree simultaneously with 100 bootstrap replicates, applying the default GTR + Γ substitution model to each partition.

We also analysed the ND2 and concatenated datasets using a Bayesian approach in BEAST v1.8.4 (Drummond et al., 2012). We used the same partitioning strategy as described for the ML analyses, but applied the most appropriate model of nucleotide substitutions to each partition as determined by jModelTest2 (Darriba et al., 2012), following the Bayesian Information Criterion (BIC). We thus used HKY + Γ for ND2 codons 1 and 3, HKY + I for ND2 codon 2, K80 for GAPDH and Myo2, and HKY + I for ODC. We unlinked clock models for all partitions except for ND2. Rates across the three ND2 codon partitions were linked and we applied a rate of 0.0145 substitutions per site per lineage (2.9%) per million years (Lerner et al., 2011). A relaxed uncorrelated lognormal distribution was used for the molecular clock model and we assumed a birth-death speciation process for the tree prior. We ran Markov Chain Monte Carlo (MCMC) chains for 100 million generations sampling every 10,000 generation for the analysis of the concatenated dataset, and for 50 million generations sampling every 5000 generation for the analysis of the ND2 alignment. Convergence diagnostics were assessed using Tracer v1.6 (Rambaut et al., 2014). Output trees were summarized as maximum clade credibility (MCC) trees using mean node heights after discarding 25% of generations as burnin using TreeAnnotator v1.8.4 (Drummond et al., 2012).

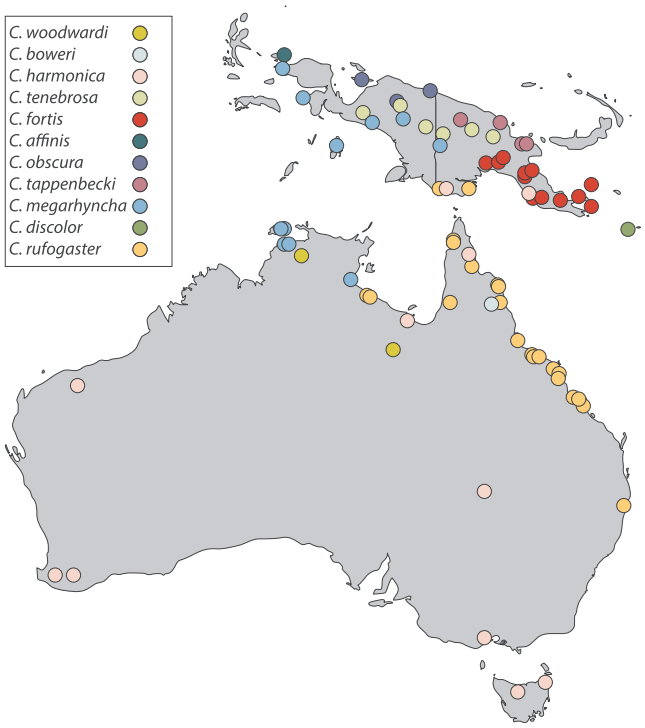

Fig. 1. Sampling localities for the 129 sequences included in this study. Colours and taxon names refer to the eleven species delimited in this study (this figure).

2.3. Single-locus species delimitation

To assess species limits in the little shrikethrush species complex, we applied the recently developed multi-rate Poisson Tree Process (mPTP) approach (Kapli et al., 2017). This method is an extension to the original PTP method introduced by Zhang et al. (2013), both of which attempt to delimit the transition from between- (speciation) to within-species (coalescence) processes. However, unlike PTP, which assumes that all species evolve with a single evolutionary rate, mPTP allows each species to have different rates. Using ML optimization, a separate parameter is estimated for the speciation and coalescence processes, respectively, and their fit to the data is evaluated. mPTP assumes that branching events within species will be more frequent than between species, with each substitution having a small probability of generating branching events. Unlike other species delimitation methods such as GMYC, mPTP does not require an ultrametric tree, thus eliminating potential errors and confounding effects associated with molecular dating.

We evaluated species limits with mPTP using the RAxML ND2 tree as input. As the presence of very similar sequences may confound the delimitation analyses leading to false positives (i.e. oversplitting), we calculated the minimum branch length to correct for this potential source of error. To assess the confidence of our ML species delimitation, we ran ten MCMC chains of 1 million steps each. Overall support for our ML estimate was then estimated by calculating average support values (ASV) across all ten MCMC runs following Kapli et al. (2017). Briefly, ASV values close to one indicate high support for the ML species delimitation. Convergence of each chain was assessed by calculating the

average standard deviation of delimitation support values (ASDDSV). The ASDDSV is computed by averaging the standard deviation of per-node delimitation support values across all our MCMC chains (Ronquist et al., 2012, Kapli et al., 2017), with values closer to zero indicating that the independent chains are converging on the same distribution.

In addition to the above approach, we also evaluated species limits using the single-threshold GMYC model of Pons et al. (2006) as implemented in the R package *splits* (Ezard et al., 2014) run on the MCC tree of the BEAST analysis of ND2. The significance of the delimitation is evaluated using a likelihood ratio test that compares the likelihood score of a null model in which all sequences belong to the same species, to the score of the model in which sequences are split into different species. As GMYC analyses applied to the whole *Colluricincla* tree seemed to result in unreasonably high numbers of delimited species, we ran GMYC on a tree pruned to only include the focal taxon *C. megarhyncha* as all newly delimited species identified by mPTP were found within this part of the tree.

2.4. Phylogenetic position of Colluricincla megarhyncha melanorhyncha

Initial data exploration and analysis revealed that the subspecies *C. m. melanorhyncha* of Biak Island was not closely related to other species of shrikethrush but instead is nested within whistlers (*Pachycephala*). We therefore performed additional analyses to assess its position within the whistlers more precisely. To do this, we obtained ND2 sequences of 45 species of Pachycephalidae from GenBank including *Coracornis raveni*, *Pseudorectes ferrugineus*, *Colluricincla boweri* and 42 species of *Pachycephala*. We used both ML and Bayesian methods in RAxML and BEAST, respectively, to estimate the phylogenetic placement of *C. m. melanorhyncha* within the *Pachycephala* radiation, using *Oriolus oriolus* to root the tree. For the BEAST analysis, we applied the HKY + I + Γ substitution model allowing separate rates for each codon position, and using a Yule speciation tree prior. Other settings were the same as described above for our analysis of the *Colluricincla* dataset.

3. Results

3.1. Molecular phylogeny and divergence dating

In this study, we present the first complete estimate of phylogenetic relationships among subspecies of *Colluricincla* shrikethrushes (Figs. 2 and S1). Whereas the monophyly of many clades were strongly supported, relationships among them were largely unresolved. We found that *Colluricincla* consists of two clades, one comprised of *C. harmonica*, *C. woodwardi* and *C. boweri* (PP = 1.00, 94% bootstrap), and the other of *C. tenebrosa* and *C. megarhyncha* (PP = 0.92, 69% bootstrap). Whereas *C. harmonica* and *C. megarhyncha* were found to exhibit high levels of within-species divergences this was not the case for *C. tenebrosa,* which showed limited genetic variation despite a broad geographic sampling. Despite limited sampling (two individuals per subspecies) within *C. harmonica*, we recovered high levels of divergence among populations. In particular, we demonstrate a deep divergence between populations in eastern and western Australia. Similarly, we recovered seven strongly supported (PP = 1.00) clades in *C. megarhyncha*, but relationships among them were unresolved. Our divergence dating analyses in BEAST suggested an origin of *Colluricincla* in the late Miocene (11.5 Mya, 95% HPD 9.7–13.5 Mya). Finally, our phylogenetic analysis of the position of *C. m. melanorhyncha* within the *Pachycephala* whistlers provided support for its placement as sister to *P. phaionota* (PP = 0.97, 97% bootstrap, Figs. S2–S4).

3.2. Species delimitation and revised taxonomy

Our mPTP species-delimitation analyses of shrikethrushes suggested that *C. megarhyncha* should be split in seven species and that the genus is composed of eleven distinct species (Figs. 2 and S5, Table 1). The ML delimitation results using mPTP were strongly supported (ASV = > 0.94) with all ten MCMC chain converging on the same delimitation distributions (ASDDSV = < 0.001). Species delimitation performed using the single-threshold GMYC model within *C. megarhyncha* also suggested that this species should be split in seven with an identical grouping of sequences (Fig. S6). The likelihood ratio test also provided strong support for the GMYC model over the null model ($P < 0.001$) and the threshold separating the speciation and coalescent processes was identified as having occurred ca. 2.02 Mya. Thus, for both analyses, five of the delimited species are restricted to New Guinea and surrounding islands and two species are distributed in both Australia and parts of southern and western New Guinea.

4. Discussion

Our molecular phylogenetic analyses reveal that the genus *Colluricincla* represents a genetically diverse assemblage with deep divergences within hitherto recognized species. However, the levels of genetic divergence within species varies greatly. At one extreme, the sooty shrikethrush (*C. tenebrosa*) is characterized by low levels of variation, perhaps associated with past population bottlenecks and/or recent range expansions. This finding is in strong contrast to those of the little shrikethrush, which is found to exhibit high levels of divergence among clades indicative of unrecognized species diversity within this group (Deiner et al., 2011; Beehler and Pratt, 2016). Utilizing a recently developed species-delimitation method using single-locus data (mPTP), we find that this complex can reasonably be divided into seven species. An alternative method for species delimitation, GMYC, corroborates these findings. Although there is a noticeable lack of topological resolution among the delimited lineages, the monophyly of each species is strongly supported. Coupled with the substantial age of the divergences between clades, our delimitations should thus be robust to topological uncertainty. As with the little shrikethrush, we also recover deep genetic divergences within the widespread grey shrikethrush (*C. harmonica*) and, although there is some indication that even this taxon may be composed of several species, our results are not significant. A more robust assessment of population structuring and species limits in this group requires a denser sampling from across its entire distributional range. Another novel finding of our study is the placement of *C. m. melanorhyncha* within the *Pachycephala* whistlers as sister to *P. phaionota*. This taxon has been recorded as having a surprisingly whistler-like song, so this finding is not entirely unexpected (Beehler and Pratt, 2016). However, as our results pertaining to this taxon are based on an incomplete sequence amplified from a single museum skin, our findings should be corroborated by additional data. Finally, although our results are largely based on analyses of mitochondrial DNA, we believe our main conclusions with regard to species delimitations should be robust to inclusion of nuclear DNA. Nonetheless, future studies should aim to include nuclear loci preferably targeted using next-generation sequencing approaches, which would potentially improve topological resolution and reaffirm the species limits we propose here.

All of the newly delimited species within *C. megarhyncha* are geographically separated (Table 1). Five species are restricted to New Guinea, whereas two species occur in both New Guinea and Australia. Although the lack of topological resolution among the different clades precludes a robust assessment of their evolutionary and biogeographical history, some general patterns emerge. First, in line with a growing number of studies (e.g. Gardner et al., 2010; Jønsson et al., 2016; Marki et al., 2017), we find no support for separate Australian and New Guinean radiations. On the contrary, several recent exchanges between the two regions are evident, possibly as a result of dispersal via Pleistocene land-bridges. Second, in concordance with the findings of Deiner et al. (2011), our results suggest that well-known barriers to dispersal and gene flow, such as the Aure Trough and New Guinea's Central Range, separate several of the delimited species. The divergence between *C. megarhyncha* and *rufogaster,* does not match with the well-

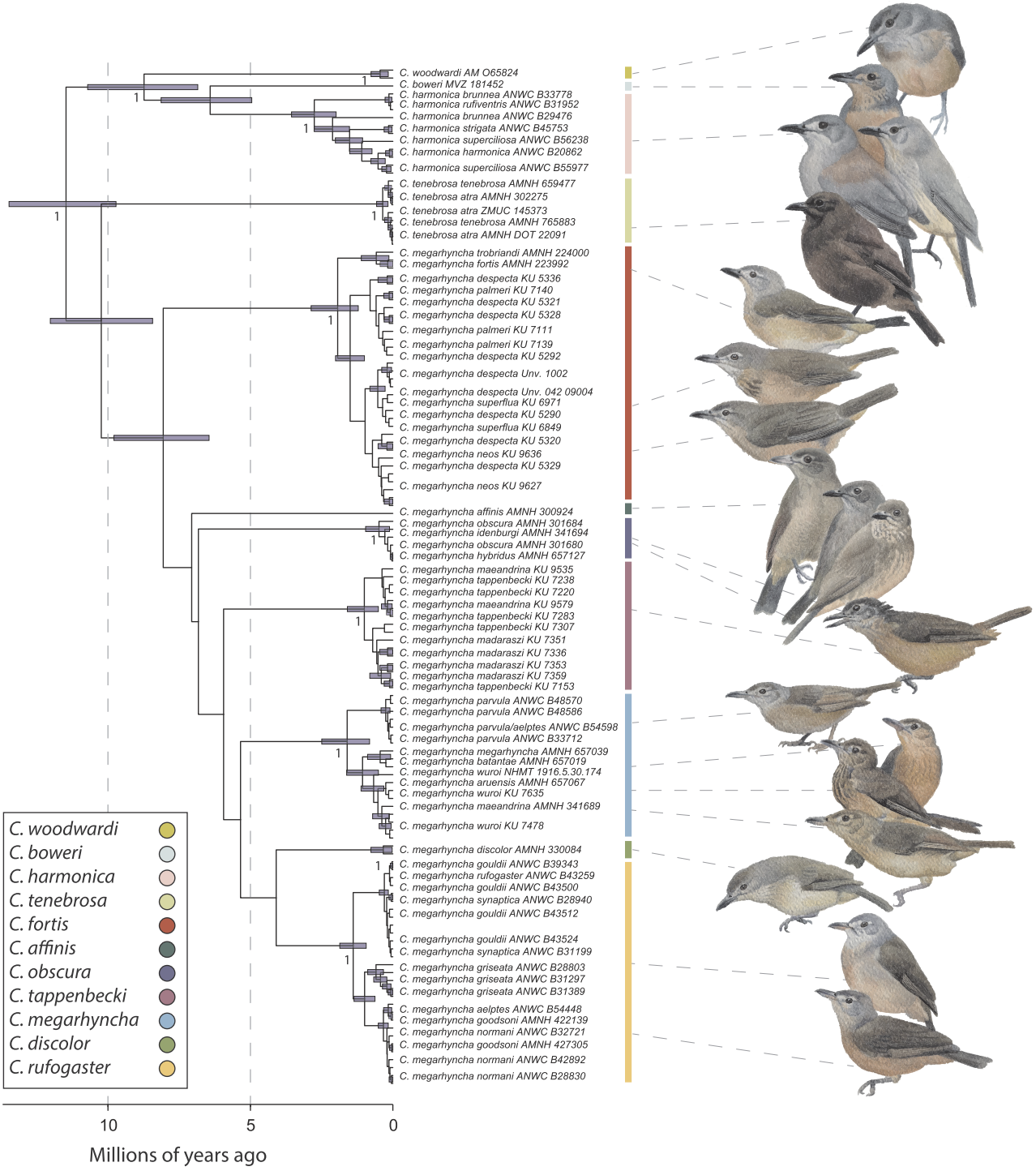

Fig. 2. A time-calibrated maximum clade credibility tree of *Colluricincla* shrikethrushes derived from the divergence estimation of the one mitochondrial gene and three nuclear introns in BEAST. Posterior probabilities are shown for major nodes. Error bars show the 95% highest posterior density intervals for the divergence time estimates. Vertical bars indicate the species identified by the mPTP-approach. Species names reflect the new taxonomy proposed in this study. Illustrations are watercolours by Jon Fjeldså and show all eleven delimited species. For species that exhibit significant within-species morphological variation, multiple illustrations are shown.

known Carpentarian Barrier, with the point of contact between these two species located hundreds of kilometres further to the west. Thus, it is unclear what (if any) the role of the Carpentarian Barrier has played in the divergence between these two clades, and the present distribution of the two taxa may instead represent recent westward expansion of *C. rufogaster* across the barrier. Surprisingly, water barriers such as the Arafura Sea and Torres Strait appear to have been comparatively weak barriers in shaping the diversity of this group with no across-barrier speciation. Third, we find that taxa on more distant satellite islands around New Guinea are more differentiated than those occurring on islands that are in closer proximity to the mainland. Thus, whereas populations on islands such as Yapen, Batanta, Salawati, D'Entrecasteaux and the Trobriands are only weakly differentiated from populations on mainland New Guinea, those on more distant islands separated by deeper water channels such as Waigeo and Tagula, are highly divergent, suggesting that these populations have been isolated for extended periods of time. Finally, we find a general lack of concordance between the species delimited in this study and their known

Table 1
Proposed species-level taxonomy of *C. megarhyncha* based on the results of the mPTP and GMYC species-delimitation analyses. Pending further study, we follow the IOC v7.2 World Bird List (Gill and Donsker, 2017) in recognizing 20 subspecies. In addition, we recognize both *C. m. neos* and *C. m. madaraszi* here, as these forms were found to belong to distinct genetic clades, despite their morphological similarity (Beehler and Pratt, 2016).

Scientific name	Included subspecies	Proposed English name	Distribution
C. megarhyncha (Quoy & Gaimard, 1832)	*megarhyncha* *batantae* *parvula*	Arafura Shrikethrush	NE Western Australia, NW and N Northern Territory (AUS), South Papuan Basin, Vogelkop/Bintuni Basin, Aru, Misool, Salawati, Batanta (NG)
C. tappenbecki Reichenow, 1898	*tappenbecki* *madaraszi* *maeandrina*	Sepik-Ramu Shrikethrush	Sepik-Ramu, Huon Peninsula, North Coastal Ranges, northern Central Range (NG)
C. rufogaster Gould, 1845	*rufogaster* *aelptes* *gouldii* *griseata* *normani* *rufogaster* *synaptica*	Rufous Shrikethrush	NE Northern Territory, coastal Queensland, NE New South Wales (AUS), Trans-Fly (NG)
C. discolor De Vis, 1890	monotypic	Tagula Shrikethrush	Tagula (NG)
C. obscura (Meyer, 1874)	*obscura* *idenburgi*	Mamberamo Shrikethrush	Yapen, Mamberamo Basin (NG)
C. affinis (Gray, 1862)	monotypic	Waigeo Shrikethrush	Waigeo (NG)
C. fortis (Gadow, 1883)	*fortis* *despecta* *neos* *superflua*	Variable Shrikethrush	SE Peninsula, D'Entrecasteaux and Trobriand Islands (NG)

morphology. The difficulty in reconciling evolutionary history with morphology likely explains the reluctance of previous researchers to attempt taxonomic revisions of this group (Beehler and Pratt, 2016). Whereas some of the newly delimited species exhibit distinctive and readily identifiable morphologies (e.g. *C. affinis*), others are non-descript and/or highly variable (e.g. *C. fortis, obscura and megarhyncha*, see illustrated variation in Fig. 2). These latter species comprise subpopulations that differ in colour hues and amount of streaking that is even greater or equal to that shown among other species. These findings suggest that morphology is a poor indicator of phylogenetic affinities in this group and should be interpreted with caution in respect to species delimitation. That genetically divergent species share similar morphotypes may thus represent the outcome of convergent evolution to similar ecological environments and/or weak selection on plumage colouration, rather than homology. These patterns mirror those found in the related variable pitohui (*Pitoui kirhocephalus* sensu lato), a species that is also characterized by significant genetic divergence among three major clades, but with confusing and conflicting phenotypic variation within and among clades (Dumbacher et al., 2004, 2008). Unlike for the little shrikethrush however, recent taxonomic work has made specific recommendations to split the variable pitohui into three species (e.g. Beehler and Pratt, 2016).

Our revised and phylogenetically-informed classification of *C. megarhyncha* contrasts with a recent, alternative classification of passerine birds (del Hoyo and Collar, 2016) that utilized a phenotype-based, quantitative scoring system (Tobias et al., 2010), to delineate species. Thus, presumably due to the lack of, and/or confusing nature of phenotypic variation in *C. megarhyncha*, del Hoyo and Collar (2016) did not attempt to apply their scoring system to the *megarhyncha* complex (N.J. Collar pers. comm.). Together, our findings thus illustrate the importance of including genetic data in the delimitation of species, particularly if phenotypic variation is subtle and/or clinal.

5. Conclusion

In this study, we present a densely sampled molecular phylogeny for the Australasian shrikethrushes. Our results suggest that species diversity within this complex is underestimated, and we consequently propose a revised classification. Nonetheless, we view our proposed taxonomy as preliminary and hope that this study may stimulate further study of species limits in this group. In particular, we believe that increased study of behaviour, contact zone dynamics and vocalizations coupled with the analysis of genome-wide data are likely to be promising in this respect.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ympev.2018.02.029.

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