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# Improved systematics of lorikeets reflects their evolutionary history and frames conservation priorities

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**ABSTRACT**

A well-supported genus-level classification of any group of organisms underpins downstream understanding of its evolutionary biology and enhances the role of phylogenetic diversity in guiding its conservation and management. The lorikeets (Psittaciformes: Loriini) are parrots for which genus-level systematics (phylogenetic relationships and classification) has long been unstable and unsatisfactory. Instability has manifested through frequently changing compositions of some genera (e.g. *Trichoglossus* and *Psitteuteles*). Other genera (e.g. *Charmosyna, Vini*) have become so large that their phenotypic heterogeneity alone at least questions whether they are monophyletic assemblages that genera should comprise. Recent molecular phylogenetic and phenotypic studies have improved the framework with which to rationalise genus-level systematics in lorikeets but some trenchant uncertainty has remained. Here we utilise published genomic data and tetrahedral analysis of plumage colour to develop a full review of the genus-level classification of lorikeets. Using existing phylogenetic relationships and a newly estimated time-calibrated tree for lorikeets, we show where paraphyletic assemblages have misled the classification of genera. We assign six species to three new genera and six other species to four previously described generic names that have been in synonymy in recent literature. Our taxonomic revision brings a new perspective informing and guiding the conservation and management of the lorikeets and their evolutionary biology.

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Lorikeets; parrots; systematics; biogeography

## Introduction

Evolution, ecology and conservation of birds in the Indo-West Pacific are among ornithology's most intensely studied topics (Mayr and Diamond 2001; review in Joseph *et al.* 2019). A lesson repeatedly learned is that a robust understanding of the phylogeny, systematics and historical biogeography of the component taxa comprising any given radiation, in turn, underpins understanding of the ecological and morphological diversity of birds within and among islands or biogeographical patterns between islands and the Australian continent, and conservation and management needs. Examples abound and come from study of rails (Kirchman 2012), kingfishers (Andersen *et al.* 2015b, 2017, 2018), parrots (Joseph *et al.* 2011), pittas (Irestedt *et al.* 2013), honeyeaters (Andersen *et al.* 2019), whistlers (Andersen *et al.* 2014), monarchs (Filardi and Smith 2005; Andersen *et al.* 2015a), silktails (Andersen *et al.* 2017; Irestedt *et al.* 2008), cuckoo-shrikes (Jønsson *et al.* 2010; Pedersen *et al.* 2018), and white-eyes (Clegg *et al.* 2002; Moyle *et al.* 2009).

One group for which unresolved systematics and biogeography still hampers biological understanding and therefore a fully informed approach to their conservation and management is the lorikeets (Loriini *sensu* Joseph *et al.* 2012), nectarivorous parrots endemic to the Indo-West Pacific region (Mivart 1896; Forshaw 1973; Holyoak 1973; Smith 1975; Schodde 1997). In particular, resolving the limits of sometimes large, phenotypically heterogeneous genera and their apparent relatives (*Charmosyna, Trichoglossus, Psitteuteles*) and highly polytypic species complexes (Rainbow Lorikeet *Trichoglossus haematodus*) has proven particularly intransigent and all need a robust phylogenetic framework. The broad aim of this paper is to use a recently developed phylogenetic framework to clarify the genus-level systematics of lorikeets.

Lorikeets have been the subject of several recent phylogenetic and evolutionary analyses and one superficial taxonomic revision (del Hoyo and Collar 2014; Schweizer *et al.* 2014, 2015; Smith *et al.* 2020; Braun *et al.* 2017; Provost *et al.* 2018; Merwin *et al.* 2020). Yet final details concerning their systematics have remained impervious to resolution, evidently needing still more rigorous phylogenetic analyses. Schweizer *et al.* (2015) performed a multilocus phylogenetic analysis of most traditionally

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Supplementary data can be accessed here.

recognised genera. They identified some necessary generic changes (e.g. two species of *Glossopsitta* into *Parvipsitta; Chalcopsitta cardinalis* becoming *Pseudeos cardinalis*) and noted where further species-level sampling was needed before necessary generic restructuring could occur (break-up of *Trichoglossus* and *Psitteuteles*). At the species level, Braun *et al.* (2017) analysed cytochrome *b* sequences from a subset of taxa within the Rainbow Lorikeet *Trichoglossus haematodus* complex, which has long been considered one of the world's most polytypic species exemplifying allopatric divergence (Cain 1955). They suggested several phylogenetic units within the species complex, but without corroborating evidence from other genetic markers, their new species-level taxonomy for the group was premature. Similarly, del Hoyo and Collar's (2014) break-up of *T. haematodus* into several species based on the scoring of plumage traits is a working hypothesis for later phylogenetic analyses to test. Schweizer *et al.* (2014) examined the evolution of nectarivory in lorikeets in a phylogenetic context but needed only to sample a few representative species of some genera.

Two recent studies brought new perspectives to genomic and phenotypic study of the Loriini. First, Smith *et al.* (2020) introduced genome-wide markers to the group's phylogenetic analysis and expanded taxon sampling. They generated the most robust phylogenomic hypothesis to date and indicated where a taxonomic resolution was still required (e.g. *Trichoglossus haematodus* complex). Leveraging this recent phylogenetic work, Merwin *et al.* (2020) developed new approaches for studying the macroevolution of feather colour. They found that plumage regions likely under natural selection were constrained while regions known to be involved in sexual signalling underwent late-burst evolution. Overall, modelling individual regions of plumage independently showed that the extraordinary colour diversity in the lorikeets was likely generated by a mosaic of evolutionary processes acting on distinct portions of the plumage. This work on colour evolution highlighted the evolutionary biology underpinning how and why plumage can be such a misleading indicator of relationships among these birds. The same problem had become plain from the other studies just cited and others (Christidis *et al.* 2010).

In this paper, we have three specific aims: (1) to update and stabilise long unsettled systematics of the lorikeets, particularly for genera, to reflect an improved understanding of their phylogeny, (2) provide an improved foundation upon which to build an understanding of their biological diversity, history of colonisation and dispersal, (3) contribute to a phylogenetically informed approach to their conservation and management, and (4) to identify remaining areas for study. We focus on the composition of genera such as *Trichoglossus, Psitteuteles* and *Charmosyna*, the limits of which exemplify the long-term intractability described above. We acknowledge that subjectivity enters discussions of generic limits when deciding whether sister groups should be united or separated. Provost *et al.* (2018) reviewed this problem. They noted that genus-level systematic revisions of other parrots have generally recognised more rather than fewer genera to convey biological diversity and we adhere to their principles. Although recent phylogenomic work has sampled most currently recognised species (94% of described taxa) in the Loriini, our focus here is not primarily intraspecific. Yet, we take the opportunity to address the Papuan Lory *Charmosyna papou* group and the Rainbow Lorikeet *T. haematodus* complex. In discussing the latter, we follow the tentative classification of del Hoyo and Collar (2014) rather than that of Braun *et al.* (2017) because the former treated all taxa. We follow it as much for simplicity as to highlight the need for further work. To demonstrate how plumage colour in lorikeets may mislead definitions of taxonomic divisions, we also provide tetrahedral colour space plots of colour measurements taken from Merwin *et al.* (2020) for a subset of clades relevant to our proposed changes to genera. We make a case for recognition of three new genera and an Appendix lists all new combinations arising in consequence.

## Materials and methods

### *Phylogenomic hypothesis*

We used the phylogenomic hypothesis of Smith *et al.* (2020) reproduced as Figure 1, and an outline of the methodology used to produce it follows. The sampling included all 12 recently recognised genera, 58 of 59 species (only the presumed extinct New Caledonian Lorikeet *Charmosyna diadema* known from one extant specimen (Forshaw and Knight 2017) was not included), and 101 of 112 named species and subspecies of lories (*sensu* Clements *et al.* 2019) including three additional subspecies (*Glossopsitta concinna concinna, G. c. didimus,* and *Trichoglossus haematodus caeruleiceps*; see Forshaw 2010; Gill and Donsker 2019; Table S1). *Lorius lory viridicrissalis* was included in Smith *et al.* (2020) analysis but is excluded here because of high missing data at parsimony informative sites. Outgroup taxa were *M. undulatus* and two fig-parrots (*Psittaculirostris edwardsii* and *Cyclopsitta diophthalma*) because these groups are the sister group of the lorikeets

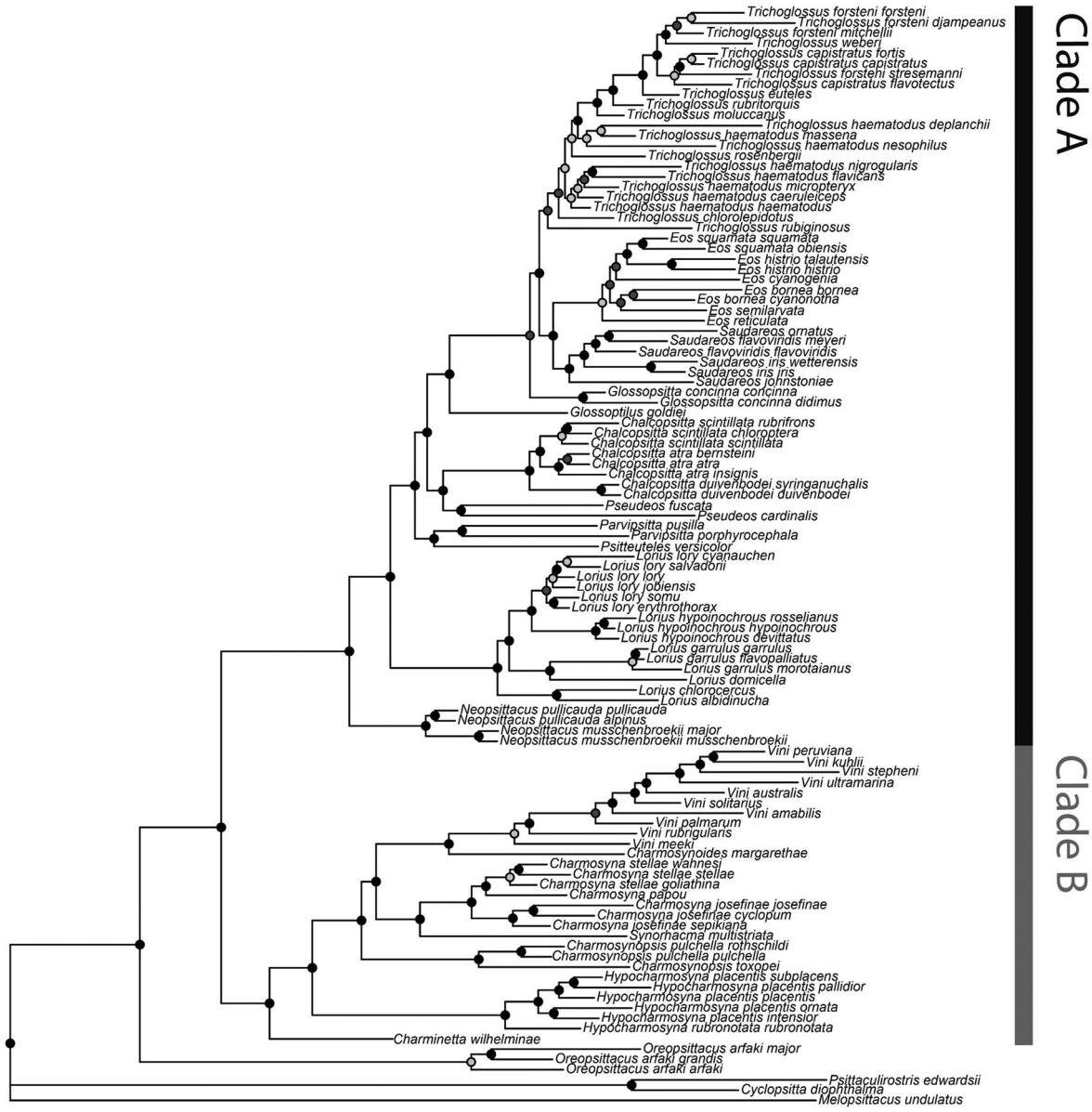


**Figure 1.** Maximum likelihood tree containing unique taxa in Loriini from Figure 6 in Smith *et al.* (2020) modified to illustrate Clades A and B discussed in the text and with our proposed taxonomic name changes. Bootstrap nodes are coloured on a gradient from 100% (black) to <70% (grey). See text for discussion of the *Charmosyna papou* and *Trichoglossus haematodus* complexes.

with which they form the Loriinae (Joseph *et al.* 2012; Provost *et al.* 2018). Specimen metadata is available in supplementary Table S1.

The molecular data were produced following standard wet lab techniques and a commercial service produced ultraconserved elements (UCE) from the Tetrapod UCE 5K probe set. Ultraconserved elements are highly conserved portions of the genome that contain variable sites in their flanking regions, which are phylogenetically informative (Faircloth *et al.* 2012). Demultiplexed and quality trimmed fastq files are available on the Sequence Read Archive (SRA BioProject ID: 498,485). To produce fasta files of UCE loci, the abbreviated steps were followed. Raw fastq files were processed using a modified pipeline of PHYLUCE and seqcap_pop (Faircloth 2015; Smith *et al.* 2014; Harvey *et al.* 2016). Contaminant DNA, low-quality bases, and adaptor sequences were filtered from reads using fastQ screen (Wingett and Andrews 2018) and illumiprocessor v1 (Faircloth 2013; Bolger *et al.* 2014). A single sample (*Lorius garrulus*), which had produced an assembly for the highest number of UCEs, was used as a reference sequence for subsequent mapping. The reference sequence was indexed and reads from each sample were independently mapped to the same reference using BWA v0.7.13-r1126 (Li and Durbin 2009),

SAM files were converted to BAM files then sorted with SAMtools (Li *et al.* 2009), and cleaned with Picard v1.106 (http://broadinstitute.github.io/picard). Variant sites were called and converted to fasta files in SAMtool, bcftools, vcfutils, and seqtk. Individuals within each locus alignment with >30% missing data per locus were removed. Locus fasta files were concatenated and aligned with MAFFT (Katoh and Standley 2013) and only loci with 75% of the taxa present in a locus were retained. We used the dataset in Smith *et al.* (2020), which removed outlier loci with Δ locus-wise log-likelihood scores >10 and included 3,730 UCE loci. Phylogenomic trees were estimated in IQ-TREE (Nguyen *et al.* 2014) using ModelFinder (Kalyaanamoorthy *et al.* 2017) to select the best-fit substitution model for each gene partition (Chernomor *et al.* 2016). To produce an image of the phylogeny, we used the R (R Core Team 2019) package phytools and ape (Paradis *et al.* 2004).

To provide context for the degree of temporal divergence among higher-level taxa in the Loriini, we estimated a time-calibrated tree using BEAST v.2.6.1 (Bouckaert *et al.* 2019). The complete 3,730 loci dataset was too large for BEAST; therefore, we subsampled the dataset to the 200 loci that had the highest number of parsimony informative sites. The number of parsimony informative sites per locus was estimated using AMAS (Borowiec 2016). To reduce the number of samples we removed two outgroup taxa (*Psittaculirostris edwardsii* and *Cyclopsitta diophthalma*), and we removed three samples (*Trichoglossus haematodus deplanchii, T. h. flavicans*, and *T. h. nigrogularis*) that could not be accurately placed with only 200 loci. We linked site, clock, and tree models to reduce the number of parameters. We used a secondary calibration from Schweizer *et al.* (2015), the divergence of *Melopsittacus* from the Loriini and specified a normal prior distribution with a mean age of 14 million years and sigma of 1, and the ingroup (all of the lorikeet taxa) were specified to be monophyletic. We specified a generalised time reversible model of sequence evolution with gamma-distributed rates in four categories and an uncorrelated relaxed clock model (Drummond *et al.* 2006). For the ucld.mean parameter we specified a log normal distribution with a mean of 0.0005 with a standard deviation of 1 (with mean in real space checked, and a Yule model for the tree prior). For all other priors, we used default distributions and values. We independently ran BEAST four times for up to 13–15 million generations sampling every 5000 generations. We combined tree and log files from each of the runs using TreeAnnotator v2.6.0 and LogCombiner v.2.6.1., and specified a 50% burnin. We checked individual and combined log files for convergence of parameter values and age estimates by inspecting likelihood plots and effective sample sizes in Tracer v1.6 (Rambaut *et al.* 2007).

### Colour data

We used colour data from Merwin *et al.* (2020) to illustrate phenotypic and taxonomic relationships of particular interest. Briefly, colour data were collected from UV and visible light photographs taken with a Nikon D70 s affixed with two Baader spectral filters. Specimens representing 99 taxa were photographed. Colour data were collected from 35 regions across each bird and transformed into a tetrachromatic avian visual space and measured using the MSPEC plugin in ImageJ (Troscianko and Stevens 2015). Measurements were standardised based on five standards of known reflectance in each photo. Tetrahedral colour space plots were generated using the Pavo2 package in R, and points were coloured in using the RGB method (Maia *et al.* 2019). Illustrations of birds were generated directly from colour data using the RGB method to generate hand-drawn line-art of a stylised lorikeet; these are not to scale and do not reflect actual bill or tail lengths.

### Determination of generic limits

Aside from genera necessarily being monophyletic, we follow general guidelines reviewed in Provost *et al.* (2018) to delineate genera but use further key criteria pertinent to the Loriini based on Merwin *et al.* (2020) findings: (1) monophyly and phenotypic similarity strongly support recognition of a genus, but (2) conversely, phenotypic dissimilarity among species in a monophyletic group need neither prevent nor dictate their placement in one genus, or indeed their separation in more than one genus. Especially with monophyletic but phenotypically dissimilar groups, decisions on whether taxa should remain in one genus inevitably involve some subjectivity. Thus, we draw on other criteria such as depth of divergences (phenotypic, temporal, other aspects of biology) within the relevant clade in question and relative to other conventionally unquestioned genera, and biological information content of the alternatives. Concerning temporal depth of divergences within a clade, we examined our results to determine the range of shallowest divergences recognised at the generic level prior to this study and thereby build a criterion of a temporal threshold for generic separation within monophyletic groups. We hope that this approach lessens or eliminates concerns that phenotypically heterogeneous species should be placed in one genus.

## Results

Given Figure 1 as our phylogenetic hypothesis of relationships and that its branching pattern and support values have been discussed in detail elsewhere (Smith *et al*. 2020), Figure 2 is a time-calibrated tree of temporal divergences. For the combined log files that accompanied the time-calibrated tree, the effective sample sizes for parameters sampled from the MCMC were >200 except for the prior, rate mean and variance, and UCLD mean, which were around 100. Three central findings from these analyses are that the entire group comprises two reciprocally monophyletic clades (A and B for simplicity) that the species *Oreopsittacus arfaki* is sister to both of those clades, and that the temporal depth of divergence between Clade A and Clade B at 10.39 (7.62–12.83) million years ago (mya) far exceeds that at which genera are routinely and unquestioningly recognised in ornithology. Further, the shallowest temporal divergences in Figure 2 recognised at a generic level prior to this study are around 4 mya, e.g. 4.13 Mya (2.63–5.74) between *Parvipsitta* and *Psitteuteles*. In the Discussion, we, therefore, adopt divergence times as old or older than ~4 mya as a threshold at which to consider the merit of recognising particular divergences at generic rank.

Figure 3(a–d) compares tetrahedral colour spaces among various species that have emerged in Figures 1 and 2 as of particular interest to genus-level systematics within the Loriini. Similarly, Figure 4 and Supplemental Figures S1, S2, S3, S4 and S5 compare representative specimens of species that have emerged in Figures 1 and 2 as of similar interest to genus-level systematics within the Loriini. In the Discussion, we assess the systematics of these groups.

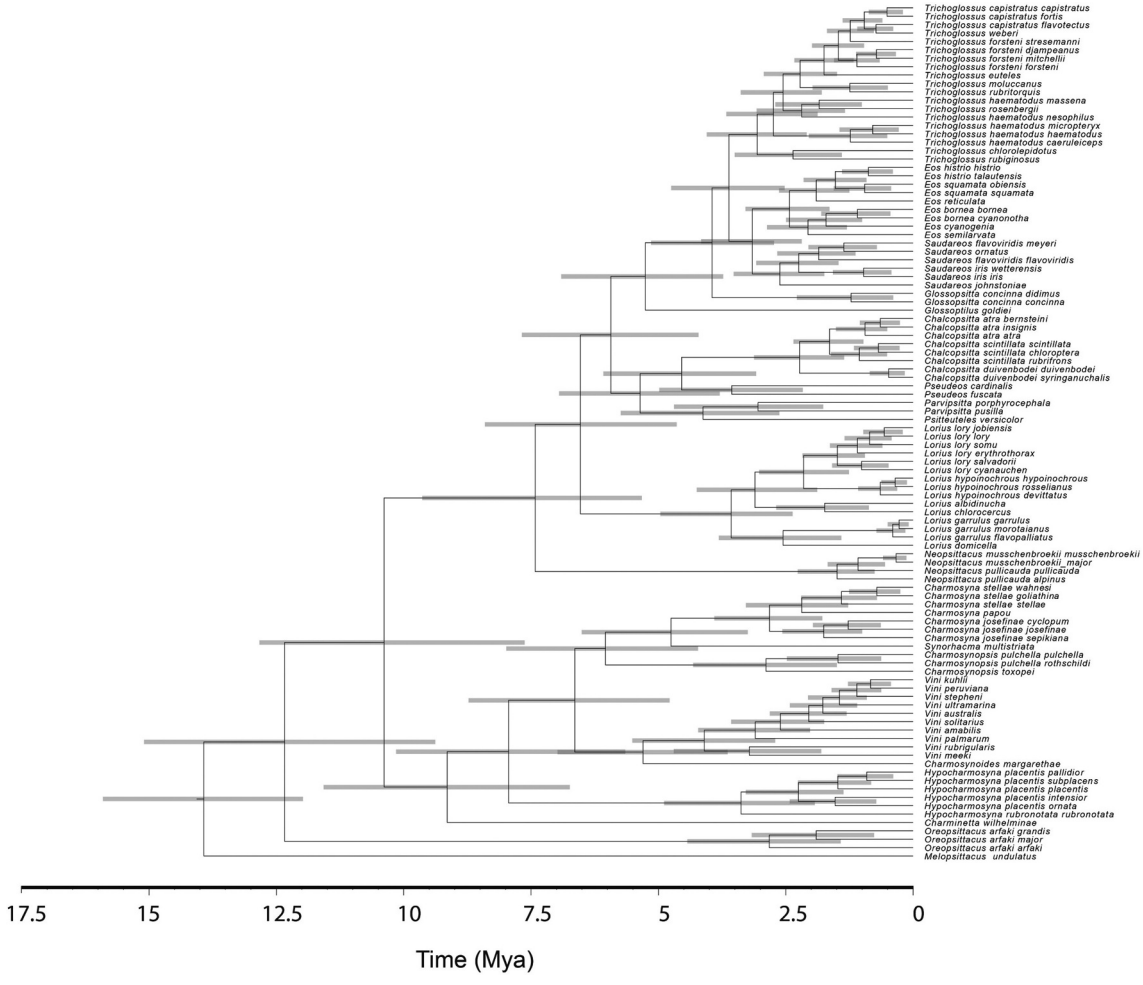


**Figure 2.** Time-calibrated tree for lories and lorikeets. The topology and branch lengths were estimated with a subset of 200 loci using an external calibration that dated the split between *Melopsittacus* and the Loriini. Shown are bars representing the 95% highest posterior density for mean node heights. Ages are in units of millions of years ago.

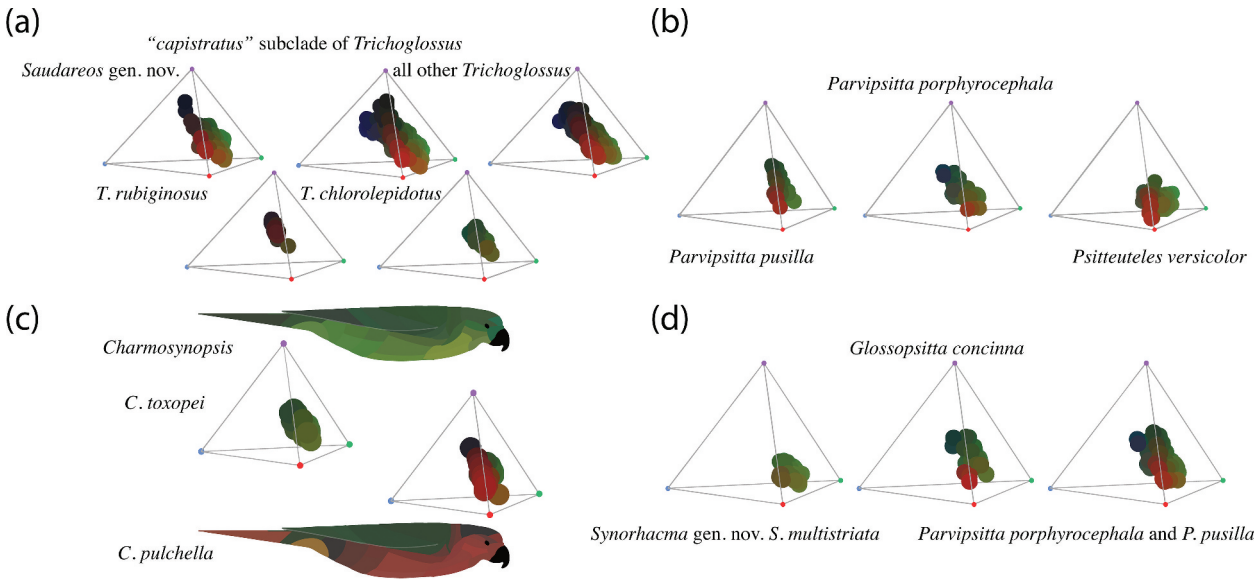


**Figure 3.** Tetrahedral colour space of various combinations of species of central interest to systematics of the Loriini as discussed in the text. (a) compares the newly recognised *Saudareos* clade with *Trichoglossus*. (b) compares the two *Parvipsitta* species with *Psitteuteles versicolor*. (c) compares the two taxa in the genus we place in *Charmosynopsis*, and (d) compares the colour space of the newly described genus *Synorhacma* to that of phenotypically similar *Glossopsitta* and *Parvipsitta*. Tetrahedral colour space plots contain four vertices for the four measured reflectance wavelengths: UV (purple, top), short (blue, left), medium (green/yellow, right), and long (orange/red, centre).

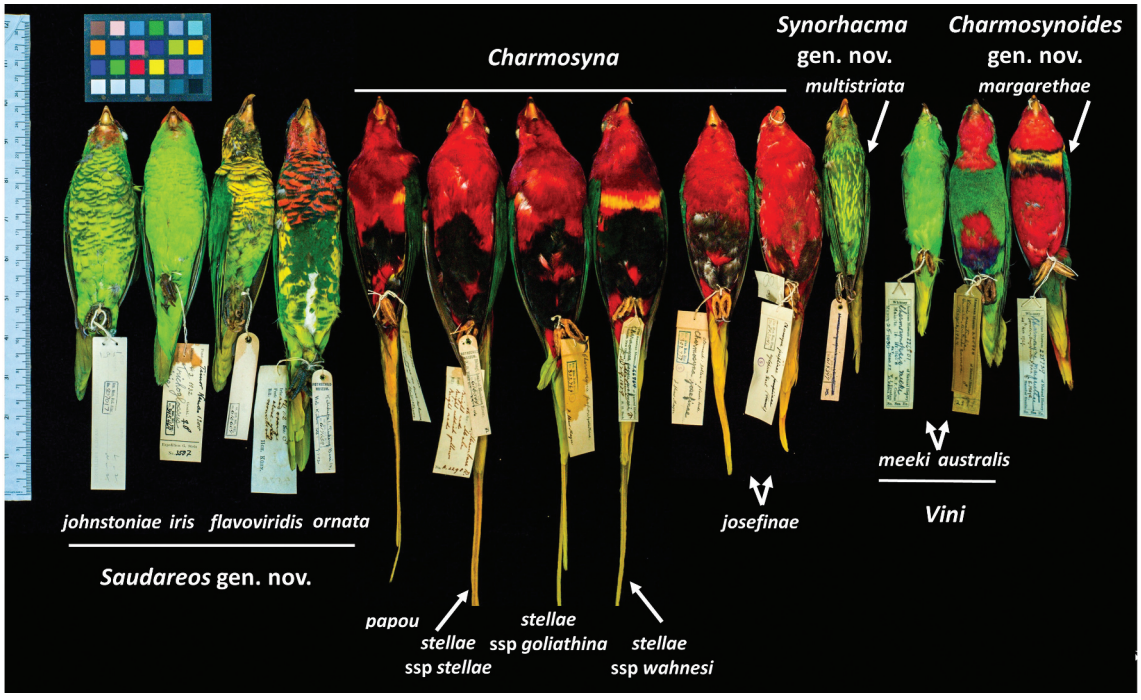


**Figure 4.** Ventral views of specimens held in the American Museum of Natural History (AMNH) to illustrate species emerging as special interest from Figures 1 and 2. See text for detail and discussion of relevant molecular data. Dorsal and lateral views are in Electronic Supplementary Material. AMNH specimens left to right are 807017; 345469; 618609; 617032; 618511; 618544; 302769; 266864; 301777; 293645; 618397; 226801; 205984; 228729. ssp - subspecies.

## Discussion

### *Two genera for Clades A and B?*

We first address whether there is merit in placing each of Clades A and B in two genera, one for each clade. The biological utility of two genera for these two major clades is so low as to be unhelpful and far from serving a classification's purpose of being biologically informative. We proceed to the recognition of genera within Clades A and B (summary in Table 1).

*Clade A: Trichoglossus* and *Psitteuteles*

Limits and composition of these two genera have long been contentious and unsettled (Mathews 1927; Deignan 1964; Forshaw 1969; Dickinson and Remsen 2013; Beehler and Pratt 2016). The three species usually assigned to *Psitteuteles* (*versicolor, iris, goldiei*; species-group epithets hereafter used for brevity where possible) are sometimes included in *Trichoglossus* (Dickinson and Remsen 2013) and two species most often placed in *Trichoglossus* (*flavoviridis* (including *meyeri), johnstoniae*) have been placed in *Psitteuteles* (Peters 1937). Achieving satisfactory generic assignment for all of these species is not simply a taxonomic reshuffling of these few species because both genera are deeply paraphyletic assemblages interspersed among other genera (see also Schweizer *et al*. 2015; Smith *et al*. 2020). We suggest resolution of generic limits, however, as follows.

An entirely novel clade, which emerged as one of the most strongly supported phylogenetic findings, comprises three species usually placed in *Trichoglossus* (*ornatus, flavoviridis, johnstoniae*) and a fourth usually assigned to *Psitteuteles* (*iris*) (Figures 3(a) and 4; supplemental Figure S1). None of the species is the type-species of any genus-group name applied to lorikeets. The clade is sister to *Eos*, one of the most phenotypically cohesive and readily diagnosable clades of lorikeets and to which none of these species bear any close phenotypic resemblance. It is also like *Eos* biogeographically, in that none of its four species occur on the main island of New Guinea, being found to its west in the Philippines, Sulawesi, and the Lesser Sundas (*iris*). As *Eos* is so uniquely and clearly diagnosable, and given the robust support for this novel clade, we do not advocate expanding *Eos* to include the clade. We recommend a new genus-group name, which we introduce at the rank of genus for this clade within the family Psittaculidae (*sensu* nomenclature of Joseph *et al*. 2012) as follows:

## Family Psittaculidae
## Subfamily Loriinae
## Tribe Loriini

### ***Saudareos* Joseph, Merwin and Smith gen. nov.**

*Zoobank: urn:lsid:zoobank.org:act:DD601654-F69 F -43F7-B31A-97DF275EDCEC*

### *Diagnosis*

The need for recognition of *Saudareos* has primarily arisen from molecular data reported herein and in Merwin *et al*. (2020) and Smith *et al*. (2020). Phenotypic traits diagnosing each of the four

**Table 1.** Summary of changes proposed here to generic classification of species within the Loriini.

| Species | Genus/genera in recent literature | Recommended generic assignment here |
|---|---|---|
| *arfaki* | *Oreopsittacus* | *Oreopsittacus* |
| *wilhelminae* | *Charmosyna* | ***Charminetta*** |
| *rubronotata, placentis* | *Charmosyna* | ***Hypocharmosyna*** |
| *toxopei, pulchella* | *Charmosyna* | ***Charmosynopsis*** |
| *papou, stellae, josefinae* | *Charmosyna* | *Charmosyna* |
| *multistriata* | *Charmosyna* | ***Synorhacma* gen. nov.** |
| *margarethae* | *Charmosyna* | ***Charmosynoides* gen. nov.** |
| *australis, kuhlii, stepheni, peruviana, ultramarina, palmarum, rubrigularis, meeki, diadema, amabilis* | *Vini* | *Vini* |
| *solitarius* | *Phigys* | *Vini* |
| *versicolor* | *Psitteuteles* | *Psitteuteles* |
| *pusilla, porphyrocephala* | *Glossopsitta* | ***Parvipsitta**** |
| *atra, duivenbodei, scintillata* | *Chalcopsitta* | *Chalcopsitta* |
| *fuscata* | *Pseudeos* | *Pseudeos* |
| *cardinalis* | *Chalcopsitta* | *Pseudeos** |
| *goldiei* | *Psitteuteles* | ***Glossoptilus*** |
| *ornata, flavoviridis, johnstoniae,* | *Trichoglossus* | ***Saudareos* gen. nov.** |
| *iris* | *Trichoglossus* or *Psitteuteles* | ***Saudareos* gen. nov.** |
| *haematodus, forsteni, weberi, capistratus, rosenbergii, moluccanus, rubritorquis, euteles, rubiginosus, chlorolepidotus* | *Trichoglossus* | *Trichoglossus* |
| *concinna* | *Glossopsitta* | *Glossopsitta* |

Changes proposed in the most recent study prior to this (Schweizer *et al*. 2015) are indicated with an asterisk (*). Genera with no changes proposed and omitted for brevity are *Lorius, Eos, Neopsittacus*. ***Bold italics*** indicate new genera and reinstatement of older names proposed here. See text for discussion of the *Charmosyna papou* and *Trichoglossus haematodus* complexes.

component species apart from species usually placed in *Trichoglossus* and from which we here advocate their separation (*haematodus sensu lato, chlorolepidotus, rubiginsosus, euteles*) are difficult to discern. Superficially similar to the broad *T. haematodus* complex, but is distinguished by a relatively smaller UV peak, generally more pronounced transverse ventral barring, and the mostly green colouration (e.g. *johnstoniae* and *flavoviridis* in Figures 3(a) and 4; supplemental Figure S1). Yellow is present in every species to some extent whether restricted to a band running almost anteriocaudally between the auriculars and the side of the neck or upper chest (*ornata, iris, flavoviridis*), or to the chest (*flavoviridis*) or abdominal feathering (*johnstoniae*). The phenotypic diversity, which we hypothesise shows complex patterns of derived traits and retention and loss of ancestral traits especially in the pattern of marking about the heads of these five species, has been reviewed by Merwin *et al.* (2020) and Smith *et al.* (2020). Endemic to the Philippines and Sulawesi (*ornata, johnstoniae, flavoviridis*) or Timor and Wetar (*iris*).

### Type-species

*Psittacus ornatus* Linnaeus, 1758, *Syst. Nat.*, tenth edition, 1: 98.

### Etymology

Derived from saudara the Bahasa for 'sister' in combination with the name of its sister genus *Eos*. Its gender is feminine and so comprises four new combinations *S. ornata, S. iris, S. flavoviridis* and *S. johnstoniae*.

Another robustly supported, novel phylogenetic result albeit foreshadowed by Forshaw (1973) places *goldiei* as sister to a large assemblage comprising *Glossopsitta concinna, Eos* and all other taxa traditionally assigned to *Psitteuteles* and *Trichoglossus* including *Saudareos* just described. The species *goldiei* has most often been placed in *Psitteuteles* but, notably, Mathews (1927) placed it in *Glossopsitta*. The case for it to be placed in a monotypic genus, however, is another of Smith *et al.*'s (2020) clearest phylogenomic results. Rothschild and Hartert (1896) used the name *Glossoptilus* for *goldiei*. We agree with Peters (1937) that this appears to have been a *lapsus*, i.e. a misspelling for *Glossopsitta* but that it is consistent with Articles 11, 12 and 13 of the International Code of Zoological Nomenclature (ICZN 1999). Therefore, *Glossoptilus* Rothschild and Hartert (1896) having type-species *goldiei* is valid and available and we advocate its recognition as a monotypic genus.

The remaining species traditionally assigned to *Trichoglossus* are essentially the Rainbow Lorikeet *T. haematodus* complex and form a moderately supported clade. Within this clade, there is one well-resolved and well-supported subclade (Figure 1), relationships among remaining taxa being unresolved. This '*capistratus*' subclade comprises the taxa *capistratus, forsteni, euteles, rubritorquis, moluccanus, massena, deplanchii* and *nesophilus*. The sister to that subclade is *rosenbergii* but with limited support so its position is unclear. The remaining taxa are *rubiginosus, chlorolepidotus*, and all other members of the *haematodus* group (*haematodus, nigrogularis, flavicans, micropteryx*, and *caeruleiceps*). With more complete DNA sequence data additional taxa could move into the '*capistratus*' subclade. We stress again that our findings for this complex are but a first tentative step to clarifying relationships and taxonomy within it. We have found, for example, that some species recognised by del Hoyo and Collar (2014) such as *T. forsteni* appear paraphyletic in our analyses. This must be tempered, however, with recognition of variable support values in our tree and indeed the possibility of close relatives being paraphyletic (e.g. Haffer 1992).

In addition to the strong and taxonomically confounding phenotypic similarities across most members of *capistratus* subclade and the rest of *Trichoglossus* (Figure 3(a)), new issues to confound resolution of generic limits now arise. First, the crown age of the clade has a mean age of ~ three million years ago and the ages among splits of its taxa are short (Figure 2), indicating rapid diversification and challenging for resolution of relationships. Second, the sampling underpinning Figure 1, itself from Smith *et al.* (2020), heavily relied on historical DNA from museum specimens. These often contained high rates of missing data at phylogenetically informative sites and tended to cluster together potentially misleading reconstruction of relationships. Although Figure 1 is based on an alignment where loci biased by missing data were excluded, the accurate placement of taxa within the *T. haematodus* complex clearly still requires larger genomic and population-level sampling.

Generic assignment of two species, *rubiginosus* and *chlorolepidotus*, warrants comment. The species *rubiginosus* is isolated on the remote Micronesian island of Pohnpei. It is phenotypically unique being almost completely dark reddish-purple in plumage, its underparts being barred blackish, and only its tail and bill being contrastingly yellow (Figure 3(a)). The genetic basis to this distinctive phenotype may, of course, be simple, and the patterning of its underparts closely resembles other *Trichoglossus* taxa. The species *chlorolepidotus* of eastern Australia is similarly patterned

but is primarily green with yellow barring, red being confined to its underwing and shoulder (Figure 3(a)). Although a genus comprising these two species with little phenotypic or biogeographic cohesion may be acceptable, no analysis has robustly placed either of these two species in a monophyletic group outside what is essentially the *T. haematodus* complex. Therefore, the valid, available genus-group names for which these two species are the type-species, *Eutelipsitta* Mathews, 1911 (type-species *chlorolepidotus*) and *Oenopsittacus* Reichenow 1913 (type-species *rubiginosus*) should only be applied at the rank of subgenus within *Trichoglossus*. Only if any later analyses confidently place these two species outside the *T. haematodus* complex should either be elevated to the rank of genus.

Turning to species-level systematics of the *T. haematodus* complex, which is arguably the most trenchant remaining problem in the entire Loriini, we note that dissatisfaction with *T. haematodus* as traditionally construed led to proposals for its break-up into multiple species (Dickinson and Remsen 2013; del Hoyo and Collar 2014; Braun *et al.* 2017). Given our sampling, we affirm the paraphyly of taxa traditionally assigned to this complex. Braun *et al.* (2017) assumed but did not test the monophyly of this group because their outgroup taxa, *Charmosyna papou* and *Glossoptilus goldiei* are too far removed from the ingroup, which we argue must include *T. rubiginosus* and *T. chlorolepidotus*.

Recognition of *Saudareos* and *Glossoptilus* as argued above leaves only *versicolor*, the type-species of *Psitteuteles*, among species traditionally assigned to either *Trichoglossus* or *Psitteuteles* to be generically assigned. With *versicolor* now robustly supported as distant to those species and sister to the two species of *Parvipsitta* (*porphyrocephala, pusilla*), which was reinstated by Schweizer *et al.* (2015), the question of uniting all three arises. All three are endemic to Australia; they have essentially non-overlapping ranges, largely in semiarid southern and mesic southwestern (*porphyrocephala*), mesic eastern (*pusilla*) and northern monsoonal (*versicolor*) parts of the continent. The three have similar overall colours (Figure 3(b)), but the distribution of colour across their plumage varies greatly between species. Their vocalisations all differ markedly from each other (described in Forshaw 1969, 1973). Temporal divergence between the two *Parvipsitta* species is substantial (3.04 Mya (1.77–4.70); Figure 2). Adding a third species, *versicolor*, that shared a common ancestor with *Parvipsitta* at 4.13 Mya (2.63–5.74; Figure 2) is similarly divergent from them and expedient. Yet it would unite three phenotypically disparate species more divergent *from each other* than those in almost any other genus we advocate across the entire Loriini. *Psitteuteles* Bonaparte, 1854 is the oldest of all relevant genus-group names (*Ptilosclera* Bonaparte, 1857 and *Parvipsitta* Mathews, 1916 being the others) so the two alternatives become: (1) unite all three in *Psitteuteles* or (2) retain *Parvipsitta* and *Psitteuteles*, the latter being monotypic for *versicolor*. Following Provost *et al.* (2018) and using the estimated times of divergence above, we advocate recognition of monotypic *Psitteuteles* and ditypic *Parvipsitta*.

*Remaining genera in Clade A: Eos, Lorius, Neopsittacus, Chalcopsitta and Pseudeos*

*Eos, Lorius* and *Neopsittacus* are each monophyletic and phenotypically cohesive. We advocate their continued usage. While *Lorius* exhibits similar plumage colour motifs to *Charmosyna* (Merwin *et al.* 2020), the large body and tail size differences between these taxa are highly informative. Our results affirm the findings of Schweizer *et al.* (2015) in recognising the Cardinal Lory as *Pseudeos cardinalis* (i.e. transferring it from *Chalcopsitta*), the genera *Chalcopsitta* and *Pseudeos* otherwise being unchanged.

*Clade B: Charmosyna, Phigys, Vini*

*Charmosyna wilhelminae* is the sole sister taxon to all other Clade B genera, i.e., the rest of paraphyletic *Charmosyna sensu lato, Vini* and its sister *Phigys*. The type-species of *Charmosyna* is *papou* so a monotypic genus for *wilhelminae* becomes appropriate, especially considering the traits setting it apart from other *Charmosyna* species: dark green wings, bright UV-blue nape feathers, and small size, and its divergence from those genera being estimated at 9.15 (6.74–11.57) million years. The type-species of *Charminetta* Iredale, 1956 is *wilhelminae* so we here follow Iredale (1956) and recommend recognition of monotypic *Charminetta*.

The sister species pair *rubronotata* and *placentis* are in turn sister to the remaining taxa of Clade B. The two resemble each other phenotypically and both occur on mainland New Guinea so there is also biogeographical cohesion in uniting them generically. We estimate their divergence from their closest relative at 7.94 (5.65–10.15) million years. *Hypocharmosyna* Salvadori, 1891 has type-species *placentis* and we advocate its use for *rubronotata* and *placentis*. Rothschild (1911) rejected the use of *Hypocharmosyna* on the grounds that it was based only on colour differences, a perspicacious view given Merwin *et al.* (2020) findings. Nonetheless, the blue cheek patches and red under-wing and lateral patches on the underparts are unique in the

Loriini and suggest shared history. We argue that phylogenetic evidence now justifies recognition of *Hypocharmosyna* for these two species.

*Charmosyna toxopei* and *pulchella* form a phenotypically heterogeneous clade. Notably, *toxopei* is the only species in all of Clade B west of New Guinea and *pulchella* is across most of New Guinea including its westernmost parts closest to *toxopei*. This again suggests biogeographical cohesion when uniting these taxa generically despite their marked colour differences (Figure 3c). We note the possibility that plumage mimicry of other species may be involved in the case of *pulchella* (see Diamond 1982). *Charmosynopsis* Salvadori, 1877 has type-species *pulchella* and we advocate its use for the *toxopei* and *pulchella* clade.

Among remaining taxa traditionally assigned to *Charmosyna*, we first note that the divergence date of 2.2 Mya (1.3–3.3) between *papou* and *stellae* strongly supports the recognition of species status for these taxa, as already advocated in detail on morphological grounds by Beehler and Pratt (2016). *Charmosyna papou*, which is the type-species of *Charmosyna*, is restricted to the Bird's Head (Vogelkop) Peninsula of western New Guinea and is thus monotypic. *Charmosyna stellae*, which occurs in the rest of New Guinea, would comprise three currently recognised subspecies *stellae, goliathina* and *wahnesi*.

*Charmosyna multistriata* is sister to three other *Charmosyna* species (*papou, stellae* and *josefinae*) and the four form a mainland New Guinean clade (Figure 1; supplemental Figure S2). These taxa could comprise *Charmosyna sensu stricto* (type-species *papou*), but the temporal depth of the phylogenetic divergence between *multistriata* and those species is similar to that between *Psitteuteles* and *Parvipsitta* (Figure 2). Further, *multistriata* has two phenotypic traits unique or almost so in the Loriini and in birds generally. Both are shown in supplemental Figure S3: red in the undertail-coverts as noted by Rothschild (1911) and apparently never illustrated in any major reference work, and bicoloured blue and orange maxilla (Pratt and Beehler 2016). It shares few plumage traits with the other three species, which are ventrally red not green, for example (Figure 4). Similarities in patterning and colour between *multistriata* and other species involve species progressively more distantly related to it (Figure 4; supplemental Figure S2) in Clades A and B. Examples are the brown nape and nuchal patch present in Clade A (*Glossopsitta, Parvipsitta*; supplemental Figure S3), or the overall green plumage of the smaller predominantly green *Charmosyna* species to be discussed below, and strong ventral striations seen also to varying but always lesser extents in *Charmosynopsis pulchella, Glossoptilus goldiei* and *Chalcopsitta scintillata*. We argue that, given our phylogenetic hypothesis, these similarities have no significance to genus-level systematics. The temporal divergence of *multistriata* from *papou/stellae* and *josefinae* (4.75 Mya (3.24–6.51); Figure 2) and its unique traits (admittedly autapomorphic) warrant its placement in a monotypic genus. No available genus-group name has *multistriata* as its type-species so we propose a new genus-group name, which we introduce at the rank of genus within the family Psittaculidae (*sensu* nomenclature of Joseph *et al.* 2012) as follows:

## Family Psittaculidae
## Subfamily Loriinae
## Tribe Loriini

### *Synorhacma* Joseph, Merwin and Smith gen. nov.

*Zoobank: urn:lsid:zoobank.org:act:2AFE9FBF-956B-401E-9BA1-5522742F48C0*

#### Diagnosis

As for the type-species *Charmosynopsis multistriata* Rothschild, 1911, a dark green lorikeet with yellow streaking or 'striated' appearance formed by the barbs closest to the rachis through *entire* underparts from throat to undertail-coverts, except at their most proximal parts, being yellow, this colour being brightest yellow on the breast and abdomen, and greener in the gular and crissal feathering and the sides of the head and nape. Red variably present in proximal parts of undertail-coverts feathers but most consistently present in feathers closest to cloaca. Hind-crown and nape brown variably tinged violet but with orange-tinged or yellow streaking on the nape closest to the mantle. Thin black post-ocular stripe variably extending as partial or complete lunar ring between eyes and passing between brown hind-crown and yellow to orange streaked portion of the nape. Bicoloured maxilla is blueish to blue-grey proximally but fading to black in older museum specimens and orange towards tomium. Mandible orange. Endemic to southern slopes of ranges in western New Guinea from foothills to 1800 m above sea level (Beehler and Pratt 2016).

#### Type-species

*Charmosynopsis multistriata* Rothschild, 1911. *Bull. Brit. Orn. Club* 27: 45

#### Etymology

*Synorhacma* is an anagram of *Charmosyna* the genus in which this species has mostly been placed since it was described. Its gender is feminine. It is chosen to symbolise the reshuffling of plumage traits through the natural and sexual selection that appears to have confounded

the genus-level systematics of the Loriini and resulted in genera that frequently have little phenotypic cohesion.

Last to consider are *Phigys solitarius* Gray, 1870, and all species routinely assigned either to *Vini* Lesson, 1831 (*peruviana, kuhlii, stepheni, ultramarina, australis*) or the rest of *Charmosyna* that have been sampled for molecular data (*margarethae, rubrigularis, meeki, palmarum, amabilis*). One could restrict *Vini* to the five species currently assigned to *Vini* and its sister *Phigys solitarius* given (1) their monophyly, (2) that *Phigys solitarius* is sister to *Vini* as traditionally construed, and (3) *Phigys solitarius* in its plumage pattern (with green wings, red faces, variable crowns and abdominal patches) closely resembles three species of *Vini* (*australis, kuhlii, stepheni*). The latter three are not monophyletic within this subclade so the plumage similarities among them and *Phigys solitarius* are likely ancestral. The two notably blue-plumaged species of *Vini, V. peruviana* and *V. ultramarina*, are also not sister to each other. Uniting traditional *Vini* and *Phigys* in one genus would leave the five remaining species that we have sampled and that are traditionally assigned to *Charmosyna* as a paraphyletic group among which we find no clear structure. None of the latter five species have been the type-species of a genus-group name so this clade could become an expanded *Vini* Lesson 1831. This would have biogeographical cohesion: all species are Pacific island taxa and none of them are on mainland New Guinea or Australia. Additionally, all current *Vini* except for *V. stepheni* exhibit blue streaked crown or nuchal collars and similarly small body sizes. Uniting them in a genus would parallel the radiation of other Pacific Island parrots of the genus *Cyanoramphus* (Joseph *et al.* 2011) except that their sister is in New Guinea not Australia.

Complicating this expansion of *Vini* are two points concerning the species *margarethae*: (1) it is sister to the rest of the clade under discussion, its divergence from the rest of the clade here estimated at 5.30 million years (3.64–6.98), and (2) phenotypically it is by far the most divergent within the clade resembling the predominantly red species of *Charmosyna* but notably different from them in three plumage traits (complete yellow collar bordered purplish black, and rump and undertail coverts colours; Figure 4; supplemental Figure S4). Further, with *meeki,* it is one of the two species in this group endemic to the Greater Bukida archipelago, i.e., Bougainville-Solomon Islands region, which is well known for highly divergent species and genera such as the monotypic pigeon, owl and frogmouth genera *Microgoura, Nesasio*, and *Rigidipenna*, respectively (Mayr and Diamond 2001; Cleere *et al.* 2007; Smith and Filardi 2007; Gregory 2017).

We recommend the generic separation of *margarethae*. The clade of species to which it is sister (*solitarius, peruviana, kuhlii, stepheni, ultramarina, australis, rubrigularis, meeki, palmarum, amabilis*) then comprise *Vini* Lesson 1831. Separation of the two Greater Bukida endemic species (*margarethae, meeki*) in different genera highlights biogeographical complexity of that archipelago. No available genus-group name has *margarethae* as its type-species so we propose a new genus-group name, which we introduce at the rank of genus within the family Psittaculidae (*sensu* nomenclature of Joseph *et al.* 2012) as follows:

## Family Psittaculidae
## Subfamily Loriinae
## Tribe Loriini

### *Charmosynoides* Joseph, Merwin and Smith gen. nov.

*Zoobank: urn:lsid:zoobank.org:act:9716A1F5-72EC-4297-A2CB-517D4B633B65*

#### *Diagnosis*

As for the type-species *Charmosyna margarethae* Tristram, 1879. Adults superficially similar to species of *Charmosyna sensu stricto* in having a predominantly red head, chest, abdomen and green upper back and wings, but distinguished from them by having a complete yellow collar encircling the body around the upper chest and mantle, broader on the former, narrowest on the latter. The yellow collar is itself bordered by a dark purplish-black margin, which is narrow on the anterior edge of the yellow collar on both upperparts and underparts but broad and diffuse on its distal edge ventrally. Yellow feathers in the central part of the chest band are proximally blackish and distally yellow leading to a barred appearance. Olive green rump and green undertail coverts. Colour of feathering at sides of rump also is sexually dimorphic as in *C. pulchella* (red in males, yellow in females). Purplish-black central coronal band extends laterally to the eyes and is not fringed with blue. Central tail feathers are almost completely red having only a barely discernible slight yellow distal tip unlike the more pronounced yellow tipping in red and green *Charmosyna*. Endemic to the archipelago of the Solomon Islands and Bougainville.

#### *Type-species*

*Charmosyna margarethae* Tristram, 1879. *Ibis* 21: 437–444

### Etymology

*Charmosynoides*, meaning like or resembling *Charmosyna*, has been chosen to reflect the similarity of the species to the predominantly red and green species of *Charmosyna*. Its gender is feminine.

Finally, we address the one species we have been unable to sample, the probably extinct New Caledonian Lorikeet *Charmosyna diadema*. Given its phenotypic similarity to species such as *rubrigularis, palmarum* and *amabilis*, and its occurrence on New Caledonia in the south-west Pacific, we assign it here to *Vini* as just defined.

### Concluding remarks

Although introducing three new genus-group names into the systematics of the Loriini (summary in Table 1) may be seen as promoting instability, we counter that it is far more advantageous to remove paraphyletic genera that have confounded understanding the group's biogeography, ecology and conservation priorities. We hope that taxonomic stability, biological understanding, and conservation and management will all be enhanced with this new framework. Coupled with the earlier studies of Merwin *et al.* (2020) and Smith *et al.* (2020), we hope that dissatisfaction with how genus-level systematics of the Loriini has for so long framed its puzzling phenotypic diversity can now be eliminated.

Specifically concerning conservation and management, we note several points. One of the new monotypic genera, *Charmosynoides*, reinforces the already high biodiversity value of the Solomon Islands-Bougainville archipelago and we hope this will contribute to conservation and management in that region. Similarly, recognition of *Synorhacma* as a monotypic genus for the species *multistriata* and of *Saudareos* for four Indonesian species highlights new awareness of their evolutionary and biogeographical uniqueness and significance. We consider it crucial that conservation and management accommodate these kinds of evolutionary distinctiveness. Though it has not been our prime focus, we acknowledge that the few areas where species-group systematics needs closer study are often where conservation and management issues come into clearest focus. For example, the still intransigent *T. haematodus* complex, which appears to be one of the most challenging areas for an adequate determination of species limits in all of ornithology, clearly has more species-level diversity than the long-standing single species taxonomy has acknowledged. Clarifying where species limits lie, however, will provide an essential road map with which to guide conservation and management across the geographical range of the group. These are among the most difficult challenges remaining for the conservation of the lorikeets.

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No potential conflict of interest was reported by the authors.

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## Appendix: New Combinations introduced in this paper

This section lists new nomenclatural combinations arising from the description of three new genera in this paper. Each new combination is shown in **bold text** and the corresponding usage prevalent in recent literature is shown below it in plain text.

***Saudareos* new genus**

Type-species *Psittacus ornatus* Linnaeus, 1758, *Syst. Nat*., tenth edition, 1: 98.

***Saudareos ornata* (Linnaeus, 1758) new combination**

*Trichoglossus ornatus* (Linnaeus, 1758)

***Saudareos johnstoniae* (E. Hartert, 1903) new combination**

*Trichoglossus johnstoniae* E. Hartert, 1903

***Saudareos flavoviridis* (Wallace, 1863) new combination**

*Trichoglossus flaviviridis* Wallace, 1863

***Saudareos iris* (Temminck, 1835) new combination**

*Psitteuteles iris* (Temminck, 1835)

***Synorhacma* new genus**

Type-species *Charmosynopsis multistriata* Rothschild, 1911. *Bull. Brit. Orn. Club* 27: 45

***Synorhacma multistriata* (Rothschild, 1911) new combination**

*Charmosyna multistriata* (Rothschild, 1911)

***Charmosynoides* new genus**

Type-species *Charmosyna margarethae* Tristram, 1879. *Ibis* 21: 437–444

***Charmosynoides margarethae* (Tristram, 1879) new combination**

*Charmosyna margarethae* Tristram, 1879