Molecular Phylogenetics and Evolution 90 (2015) 34–48

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes) ☆

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ARTICLE INFO

Article history:
Received 19 January 2015
Revised 1 April 2015
Accepted 12 April 2015
Available online 28 April 2015

Keywords:
Lories
Loriinae
Parrots
Phylogeny
Pacific
Biogeography
Systematics

ABSTRACT

The lories and lorikeets (Aves: Loriinae: Loriini) are a readily recognizable, discrete group of nectarivorous parrots confined to the Indo-Pacific region between Wallace's Line and the Pitcairn Island group in the central-east Pacific Ocean. We present the first phylogenetic analysis of all currently recognized genera in the group using two mitochondrial and five nuclear loci. Our analyses suggest a New Guinean origin for the group at about 10 million years ago (95% HPD 4.8–14.8) but this origin must be interpreted within the context of that island's complicated, recent geological history. That is, the origin and early diversification of the group may have taken place as New Guinea's Central Cordillera arose and the final constituent terranes that form present-day New Guinea were accreted. The latter activity may have promoted dispersal as a key element in the group's history. We have detected several instances of dispersal out of New Guinea that we argue constitute instances of founder-event speciation. Some phenotypically cohesive genera are affirmed as monophyletic but other genera are clearly in need of taxonomic dismantlement and reclassification. We recognize *Parvipsitta* Mathews, 1916 for two species usually placed in *Glossopsitta* and we advocate transfer of *Chalcopsitta cardinalis* into *Pseudeos* Peters, 1935. Other non-monophyletic genera such as *Charmosyna*, *Psitteuteles* and, probably, *Trichoglossus*, require improved taxon sampling and further phylogenetic analysis before their systematics can be resolved. Cursory examination of trait mapping across the group suggests that many traits are ancestral and of little use in determining genus-level systematics.

1. Introduction

Molecular phylogenetics continues to play a critical role in revealing the historical complexity underpinning present-day distribution patterns of biota. The Indo-Pacific, and in particular the Australia-New Guinea-Melanesia-Oceania region typifies this trend. Along with paleontological discoveries (Boyer et al., 2010; Iwaniuk et al., 2009; Steadman, 1995; Steadman, 2006a,b) that clarify the historical levels of biodiversity in this region, molecular phylogenetics has been vital in disentangling when and where processes of speciation and dispersal have operated and addressing consistency of rates of evolution (Cibois et al., 2011a,b; Fritz et al., 2012; Saitoh et al., 2012). One question of current interest is whether patterns of dispersal and colonization have been "downstream" (from continent to island) or "upstream" (from island to continent) (Filardi and Moyle, 2005; Jonsson et al., 2010; Jønsson et al., 2011). Several cases of "upstream" dispersal have called into question a long standing paradigm in island biogeography and revealed that an island may not always be the endpoint of the colonization process (*cf.* Bellemain and Ricklefs, 2008). Also of current interest is the role of the geological history of the present-day island of New Guinea in promoting dispersal of birds out of the region. Specifically, the question is whether the geological evolution from a proto-Papuan archipelago to the present-day configuration of land in the Indo-West Pacific fostered behavioral and morphological adaptations that facilitated dispersal of birds out

☆ This paper has been recommended for acceptance by Edward Louis Braun.

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http://dx.doi.org/10.1016/j.ympev.2015.04.021
1055-7903/

of the Australo-Papuan region (Jønsson et al., 2011). Among birds recent studies of platycercine parrots (Joseph et al., 2011; Schweizer et al., 2013), monarch flycatchers *Monarcha* and *Myiagra* (Filardi and Moyle, 2005; Fabre et al., 2014; Andersen et al. 2015) reed-warblers *Acrocephalus* spp (Cibois et al., 2011a,b; Saitoh et al., 2012), and whistlers (Jonsson et al., 2010; Andersen et al., 2014) have all improved our understanding of the region's historical biogeography. Another group that is especially attractive for exploring this complexity because of their Indo-West Pacific distribution is the group of parrots known as lories and lorikeets.

The lories (larger, stouter bodied species) and lorikeets (smaller, more streamlined species) (Loriinae: Loriini *sensu* Joseph et al., 2012) are a distinctive and readily recognizable group of mostly small, nectarivorous parrots consisting of 53 (Collar, 1997) to 61 species (del Hoyo and Collar, 2014). They comprise a clade that recently was found to be unexpectedly species-rich given its age in relation to all other parrots (Schweizer et al., 2011). Their range extends from Mindanao of the southern Philippines just west of Wallace's Line (Fig. 1), eastwards to remote Henderson Island in the Pitcairn Group, north to Pohnpei and south to the Australian island state of Tasmania (Fig. 1). Interestingly, none occur in New Zealand. Many lory and lorikeet species in the Indonesian and Pacific archipelagos are island endemics. They range in size from approximately 30–32 cm and 175–260 g (genera *Chalcopsitta*, *Lorius*, *Eos*, *Pseudeos*) to the two smallest species, the Pygmy and Little Lorikeets *Charmosyna wilhelminae* and *Glossopsitta pusilla*, at 13 and 15 cm, respectively (latter mostly 34–41 g; dimensions from Collar, 1997; Forshaw, 2002; specimens in Australian National Wildlife Collection, Canberra). Remaining species and genera (*Neopsittacus*, *Trichoglossus*, *Psitteuteles*, *Charmosyna*, *Glossopsitta*, *Vini*, *Phigys*, *Oreopsittacus*) are mostly around 18–19 cm and 42–45 g. The majority of genera and most species lack sexual dimorphism either in plumage or bare parts. All species have sleek, streamlined silhouettes and their tight, glossy plumage often has streaked or striated patterns arising from shaft-streaked feathers (Holyoak, 1973; Smith, 1975; Forshaw, 2002, 2011). The majority of smaller and mid-sized species are predominantly green with red, yellow or purple markings about their head. The genera with larger body-size species are more predominantly red or even brown and brown-orange (e.g., *Chalcopsitta duivenbodei*, *Pseudeos fuscata*). Two small species, the Tahitian Lorikeet *Vini peruviana* and Ultramarine Loikeet *V. ultramarina*, are exceptional among parrots generally in having blue and white plumage.

Lories and lorikeets are primarily birds of wetter temperate woodlands and forests or tropical rainforests. One species, the Purple-crowned Lorikeet *Glossopsitta porphyrocephala*, occurs primarily in southern Australian semi-arid woodlands. All are primarily nectarivorous and, unlike most other parrots, somewhat rarely feed on seed. As nectar is rich in carbohydrates and lacking in other essential nutrients, the better-studied Australian species at least are also known to harvest pollen as a complementary source of protein (Churchill and Christensen, 1970; Wooller et al., 1988; Gartrell and Jones, 2001). To efficiently harvest these resources, they have evolved distinctive papillate ("brush-tipped") tongues, which are longer and narrower than those found in all but one other parrot, the convergently similar platycercine Swift Parrot *Lathamus discolor* (Güntert and Ziswiler, 1972). Coupled with the unique structure of their digestive tracts (Richardson and Wooller, 1990), lories and lorikeets are well-adapted for the ingestion and extraction of pollen grains (Hopper and Burbidge, 1979; Schweizer et al., 2014). Indeed, Schweizer et al. (2014) considered the dietary shift to nectarivory (and presumably pollen) a key evolutionary innovation. They proposed that it promoted significant non-adaptive lineage diversification through allopatric speciation in which ancestors filled that same unexploited niche in different areas.

Genus- and species-level systematics of the lorikeets have been essentially stable since Peters (1937). This stability mainly reflects the fact that molecular and morphological characters examined to date have given little resolution on relationships within the group (Christidis et al., 1991; Schodde, 1997; see also Jetz et al., 2012; Burleigh et al., 2015). Two recent reassessments proposed some species- and subspecies-level changes (Dickinson and Remsen, 2013; del Hoyo and Collar, 2014) but these works analyzed no new data sets. Currently, 12 genera are recognized as follows

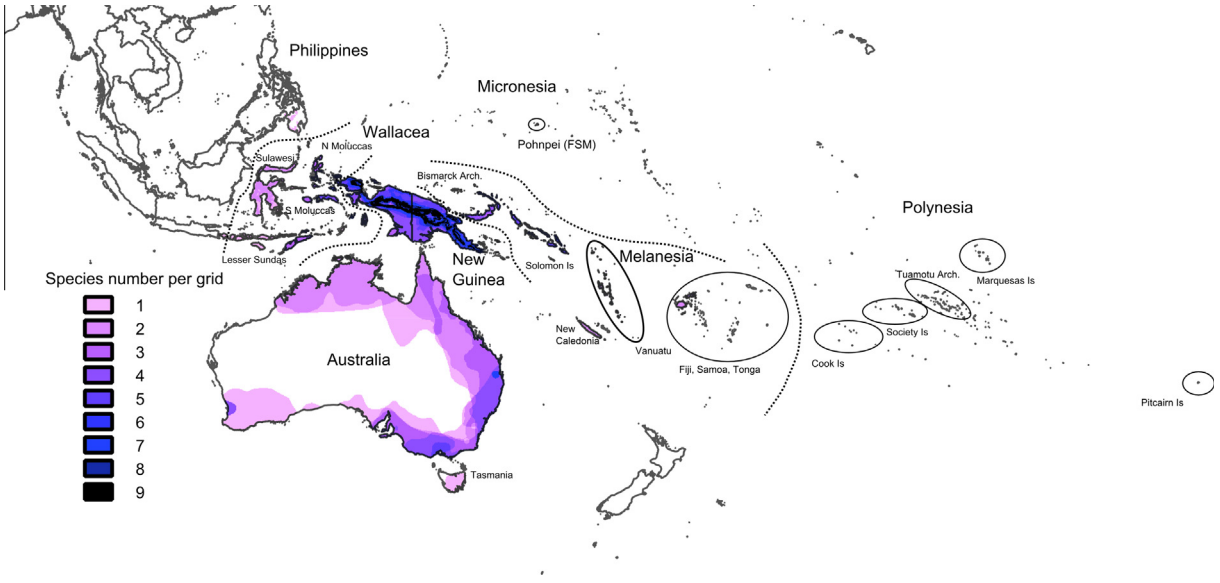

Fig. 1. Heat map showing the numbers of lory and lorikeet species throughout their Indo-Pacific range and highlighting the prevalence of species in New Guinea. Map prepared using base range maps from BirdLife International and NatureServe (2014). Island groups where lories and lorikeets occur are encircled. Delimitation used for biogeographic analyses are shown by dotted lines. The westernmost dotted line indicates Wallace's Line, the western limit of Wallacea. Relevant geographic regions are also indicated.

(* indicates residual species-level taxonomic debate within a genus): *Eos* (6 species), *Chalcopsitta* (4), *Lorius* (6*), *Trichoglossus* (7*), *Psitteuteles* (3), *Charmosyna* (14), *Vini* (5), *Glossopsitta* (3), *Neopsittacus* (2), and *Pseudeos, Phigys*, *Oreopsittacus* (each monotypic). Most genera are phenotypically homogeneous and can reasonably be predicted to be monophyletic. Several, however, are extraordinarily heterogeneous in size and plumage pattern and their monophyly and limits have rightly been questioned (Forshaw, 2006). Most notable in this category are *Charmosyna*, *Glossopsitta*, *Trichoglossus*, *Psitteuteles* and *Vini*. The smaller, predominantly green species of *Charmosyna* are superficially similar to *Glossopsitta* in plumage patterns but very different from their mostly larger, predominantly red congeners. This pattern raises the question of whether *Charmosyna* is paraphyletic and whether some species are more closely related to *Glossopsitta*.

Biogeographically, lorikeets are of considerable interest for several reasons. First, their current centre of diversity is the island of New Guinea where up to 9 species occur sympatrically (22 species, 9 genera – Pratt and Beehler, 2015; Fig. 1), smaller numbers of species occurring in Australia (4–5) and throughout Oceania. Second, they are highly vagile birds, capable of roaming landscapes in search of flowering trees. Their strong flight capabilities suggest a capacity for relatively frequent cross-water dispersal. On the other hand, the high frequency of island endemics would seem surprising if dispersal has been a relatively continuous phenomenon in the group's history.

This paper has two primary aims. The first is to perform a complete genus-level phylogenetic analysis of lories and lorikeets. This will test the monophyly and relationships of the genera within the constraints of our species-level taxon sampling. The second is to use the molecular phylogenetic analysis as the basis for a biogeographical overview of the group. Earlier broad analyses of parrots that have included lories and lorikeets but not focussed solely on them (Wright et al., 2008; Joseph et al., 2011; Schweizer et al., 2011, 2014; Schirtzinger et al., 2012). These studies placed the group as a whole in phylogenetic context but it was beyond their scope to review genus-level systematics and biogeography. We are particularly interested in where the group's origin lies, the relative roles of downstream and upstream colonization and the role, if any, of a proto-Papuan archipelago in shaping the group's history. Finally, we ask whether a biogeographical analysis, particularly an understanding of diversification times, can shed light on why there are so many narrowly distributed island endemics.

2. Materials and methods

2.1. Taxon sampling and specimens

Our sampling of the lories and lorikeets from blood or cryo-frozen tissue samples is summarized in Table 1 and details of individuals and samples and associated GenBank accession numbers of the DNA sequences are given in Appendix A. All currently recognized genera within the Loriini were sampled. As outgroups, two other representatives of Loriinae, the Budgerigar (*Melopsittacus undulatus*) and Edward's Fig Parrot (*Psittaculirostris edwardii*), and two more distantly-related parrot species the Yellow-tailed Black-Cockatoo (*Calyptorhynchus funereus*) and the Rosy-faced Lovebird (*Agapornis roseicollis*), were included. Only samples associated with vouchered specimens or from individuals held in zoos were used and species available only as dried museum skins were excluded. Hybridization in the ancestry of one specimen originally supplied as *T. ornatus* emerged only after results were analyzed and was subsequently confirmed (S. Cardiff, pers. comm.); the specimen's parentage is not known but *T. flavoviridis* is likely involved (see Section 3, Appendix A). Extensive sampling of subspecies and variants included in the Rainbow Lorikeet *T. haematodus* complex was not attempted as a full phylogenetic analysis of this large complex was beyond the scope of this study.

2.2. DNA extraction and sequencing

Following laboratory protocols of Wright et al. (2008) and Schweizer et al. (2010), two mitochondrial genes (cytochrome oxidase I gene – COI; NADH dehydrogenase 2 – ND2), two nuclear exons c-mos and Rag-1, as well as the three nuclear introns (tropomyosin alpha-subunit intron 5 – TROP; transforming growth factor ß-2 – TGFB2, intron 5 rhodopsin intron 1 – RDPSN) were sequenced.

Geneious Pro 5.6. (Drummond et al., 2011) was used for sequence preparation and editing and sequences for every marker were aligned separately using the MAFFT algorithm (Katoh et al., 2002) implemented as a plug-into Geneious Pro using default settings. Individual sequences of coding markers were checked by searching for apparent stop codons after the translation of sequences into amino acids.

Final alignments comprised 570 base pairs (bp; COI), 1041 bp (ND2), 603 bp (c-mos), 1458 bp (Rag-1), 754 bp (RDPSN), 634 bp

Table 1
Summary of distribution and numbers of lory and lorikeet species following Forshaw (2006). Numbers of species in each genus sampled in the present study are in parentheses. Abbreviations used: E – east; NG – island of New Guinea; FSM – Federated States of Micronesia (Pohnpei).

Genus	Species in genus (sampled)	Philippines	Wallacea/ Islands west of NG	NG	Australia	Bismarcks	FSM	Solomons	New Caledonia, Vanuatu	Fiji, Samoa, Tonga	E of Fiji (Cook, Society, Tuamotu)
Charmosyna	14(6)		1(0)	7(4)		1(1)		2(1)	2(0)	1(0)	
Vini/Phigys	6(3)									2(2)	4(1)
Neopsittacus	2(2)			2(2)							
Oreopsittacus	1(1)			1(1)							
Glossopsittacus	3(3)				3(3)						
Lorius	6(6)		2(2)	2(2)[a]		2(2)[a]		1(1)			
Psitteuteles	3(3)		1(1)	1(1)	1(1)						
Trichoglossus n.b. *T. haematodus s.l. = 1*	7(6)[c]	1(1)	4(4)[b]	1(1)[b]	2(2)[b]	1(1)[b]	1(0)	1(1)[b]	1(1)[b]		
Eos	6(6)		5(5)	1(1)							
Chalcopsitta	4(4)		1(1)[d]	3(3)[d]		1(1)[e]		1(1)[e]			
Pseudeos	1(1)			1(1)							

[a] 1 *L. hypoinochrous* shared by NG and Bismarcks.
[b] *T. haematodus* is shared across 6 locations.
[c] Sample obtained as *T. ornatus* later established to be of hybrid origin and of uncertain parentage possibly involving *T. flavovoridis*.
[d] *C. atra* is shared by islands west of NG and NG.
[e] *C. cardinalis* is shared by Bismarcks and Solomons.

(TGFB 2), and 534 bp (TROP). A concatenated alignment of 5594 bp from all markers was used for further analyses.

2.3. Phylogenetic analysis

We acknowledge debate over the merit of concatenation *versus* species tree (multispecies coalescent) methods in phylogenetic analysis. Given substantial evidence that concatenation can under many conditions estimate phylogeny as robustly as species tree methods (Patel et al., 2013; Gatesy and Springer, 2014; Tonini et al., 2015; see also Mirarab et al., 2015), we here present a concatenated analysis. Individual gene trees are presented in the Supplementary material.

PartitionFinder 1.0.1 (Lanfear et al., 2012) was used to select the best-fitting partitioning schemes and models of nuclear evolution using the greedy algorithm and unlinked branch lengths corresponding to separate models with varying base frequencies, rate matrix, shape parameters and proportion of invariable sites for the different markers and/or their codon positions if a coding sequence was involved.

MrBayes v 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003; Ronquist et al., 2012) was used to perform Bayesian inference (BI) based on the best-fitting partitioning scheme. Two independent runs of Metropolis-coupled Markov chain Monte Carlo analyses were performed, each run comprising one cold chain and three heated chains at a default temperature of 0.2. The chains were run for 25 million generations and sampled every 100 generations. The average standard deviation of split frequencies was checked for convergence toward zero and the length of the burn-in was assessed by visually inspecting trace files with TRACER v 1.5 (Rambaut and Drummond, 2007). The first 25% of samples were then discarded as burn-in well after the chains had reached stationarity. Likelihoods, posterior distributions and effective samples sizes of all parameters and splits were compared to assess convergence between the two independent runs with TRACER. A maximum likelihood (ML) search was employed with RAxML v 7.0.4 (Stamatakis, 2006) on a web server with 100 rapid bootstrap inferences (Stamatakis et al., 2008). All free model parameters were estimated by the software (substitution rates, gamma shape parameter, base frequencies) based on the best-fitting partitioning scheme.

BEAST v. 1.8.0 (Drummond and Rambaut, 2007) was used to estimate divergence times and simultaneously establish a phylogenetic hypothesis. A relaxed molecular clock with uncorrelated log-normal distribution of branch lengths and a Yule tree prior was used. A calibration point in our dating analyses of 14 Ma (million years ago) and a normal distribution having a standard deviation of 3.0 for the split between Loriini (lories and lorikeets) and its sister, the Budgerigar *Melopsittacus undulatus* were incorporated. This calibration point was derived from the results of Schweizer et al. (2011), which used fossils outside parrots to calibrate parrot phylogeny; the 95% interval of this normal distribution included the 95% highest posterior density (HPD) for the same split as estimated in Schweizer et al. (2011). The best-fitting partitioning scheme as evaluated with PartitionFinder (see above) was used, but clock models were linked. For the ucld.mean parameter, a gamma distribution with offset 0, shape and scale parameters of 0.05 and 10.0, respectively, were used. The upper value was set to 5 to exclude extreme values. Additionally, a more conservative prior using a gamma distribution with offset 0, shape and scale parameters of 0.5 and 1, respectively, and again an upper value of 5 was tested, but this led to congruent parameter estimates. Default prior distributions were implemented for all other parameters. Furthermore, to test the validity of our calibration point, we wanted to compare estimated substitution rates with published rates. Therefore, we did additional BEAST analyses using separate clock and substitution models for each marker (i.e., unlinked clock and substitution models) to derive an estimate of the substitution rate for each marker separately. The HKY + I + G substitution model and the same prior for the ucld.mean parameter as above were implemented for all markers. Three independent chains of MCMC with 25 million generations sampled every 1000 generations were run and TRACER was used to confirm appropriate burn-in, adequate effective sample sizes of the posterior distribution for all parameters and to assess convergence among runs by comparing likelihoods and posterior distributions of all parameters. The three independent runs were combined with LogCombiner v. 1.8.0 (Drummond and Rambaut, 2007). The resulting maximum clade credibility tree and the 95% highest posterior density (HPD) distributions of each estimated node were calculated with TreeAnnotator v. 1.8.0 (Drummond and Rambaut, 2007) and visualized in FigTree v. 1.2.1 (Rambaut, 2008). Based on the results of the BEAST analyses, semi-logarithmic lineage through time plots were computed using the R Packages Ape (Paradis et al., 2004) and Phytools (Revell, 2012).

2.4. Data analyses: biogeography

Biogeographic reconstruction was performed using the R package BioGeoBears (Matzke, 2013a) following the analytical approach of Voelker et al. (2014) based on the maximum clade credibility tree of the BEAST analyses with all ingroup and outgroup taxa. Species were assigned to one or more of the following biogeographic realms according to their current distributions (Forshaw, 2011; BirdLife International and NatureServe, 2014): Australia, Melanesia, New Guinea, Philippines, Polynesia, Wallacea (see Fig. 1). The maximum range size was set to 4 as no extant species occurs in more than four of the biogeographic realms and dispersal was restricted to adjacent areas. The following models of geographic range evolution were compared in a likelihood framework. First, a Dispersal-Extinction Cladogenesis Model (DEC) as originally implemented in the software Lagrange (Ree and Smith, 2008) was used. It has two free parameters specifying the rate of "dispersal" (i.e., range expansion) and "extinction" (i.e., range contraction), but the cladogenesis model remains fixed. This means that the geographical range of the ancestral lineage is inherited with equal probability by the two daughter lineages through a variety of plausible cladogenenetic scenarios (e.g., sympatry, parapatry, vicariance). Next, the DEC + j model (Matzke, 2013b; Matzke, 2014), which adds a third free parameter to the Dispersal-Extinction Cladogenesis (DEC) framework, that of long-distance dispersal (parameter j – DEC + j model), was used. This effectively mimics the process of founder-event speciation as one daughter lineage can disperse to an area beyond the ancestral range. The classic DEC model is nested within the DEC + j. Dispersal Vicariance Analysis (DIVA) (Ronquist, 1997), Dispersal Vicariance Analysis with founder parameter (DIVA + j) (Matzke, 2013b), Bayesian inference of historical biogeography for discrete areas (BayArea) (Landis et al., 2013), and Bayesian inference of historical biogeography for discrete areas with founder parameter (BayAreaj) (Matzke, 2013b) were also used. Model fit was assessed using the Akaike information criterion (AIC).

3. Results

3.1. Phylogeny

PartitionFinder identified a GTR + I + G for the third codon position of the two mtDNA markers and a HKY + I + G for the remaining data as the best-fitting substitution models and partitioning scheme. The maximum clade credibility tree of BI from MrBayes

was highly congruent with the best tree of the ML inference, though node support was generally higher in the former approach (Fig. 2). The first divergence in the group was robustly and consistently supported as being between monotypic *Oreopsittacus* and all other genera. The next divergence was similarly well-supported and was between a clade comprising five species of *Charmosyna* (*papou*, *pulchella*, *multistriata*, *meeki*, *placentis*), the only two sampled species of *Vini* (*australis*, *peruviana*) and monotypic *Phigys versus* all remaining species. Support values within this clade were high and all between 0.99 and 1. The five species of *Charmosyna*, however, were not closest relatives and fell on four main sub-branches within the clade, each of which was paraphyletic with respect to any of the other three. Thus *C. placentis* was recovered as sister to all other species in this clade. *C. papou* and *C. multistriata* were sister species. *C. meeki* was recovered as sister to the two *Vini* and monotypic *Phigys*, and *C. pulchella* was in turn sister to this clade.

The next divergence was between the two species of *Neopsittacus* and a clade consisting of all remaining genera. Relationships within the latter clade were characterized by strong support values for some currently recognized genera, a polytomy comprising four main branches, and relatively poorly supported patterns of relationships among the remaining genera. The main elements of the polytomy comprised (i) *G. concinna*, (ii) *Trichoglossus johnstoniae*, (iii) a clade containing the remaining sampled species of *Trichoglossus* and *Psitteuteles iris*, and (iv) a clade containing all six of the sampled species in the genus *Eos*. In addition to *Eos*, the two other currently recognized genera within this larger clade that were recovered as monophyletic were *Neopsittacus* and *Lorius*. In contrast, the three representatives of the genus *Psitteuteles* were recovered on three separate branches, and the three members of *Glossopsitta* were recovered in two separate clades. The species of the genus *Chalcopsitta* were recovered in two well-supported clades that also included the monotypic species *Pseudeos fuscata*. The latter species was sister to *Chalcopsitta cardinalis* in a well-supported clade that was sister to the other sampled species of *Chalcopsitta*. Likewise, within *Trichoglossus*, *T. ornatus* and *T. flavoviridis* were a strongly supported sister pair aligned with *Psitteuteles iris* and therefore paraphyletic with respect to the other sampled taxa *Trichoglossus*. The latter, excepting *T. johnstoniae*, were a strongly supported clade within which relationships could not, however, be discerned. The grouping

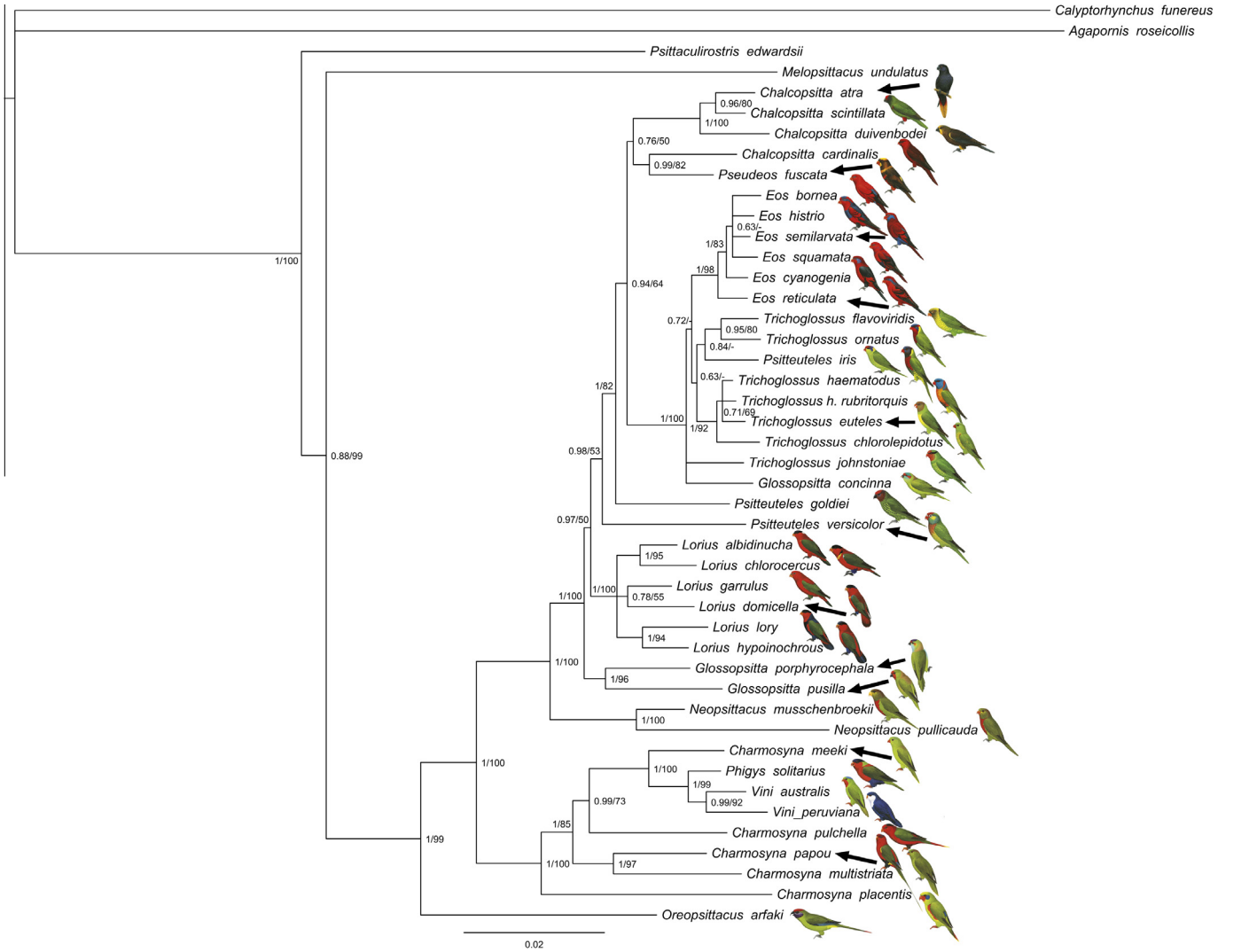

Fig. 2. Results of the MrBayes phylogenetic analysis of the lories and lorikeets. 50% majority-rule consensus tree of the Bayesian inference using MrBayes. Posterior probabilities (left) and bootstrap values above 50 of the maximum-likelihood inference with RAxML (right) are indicated at each node. Figures of birds reproduced with permission from del Hoyo and Collar (2014).

together of a *Trichoglossus* specimen of presumed hybrid origin (see Appendix A) and *T. flavoviridis* was notable and is considered further in Section 4.

3.2. Divergence time estimates

One of the rate parameters of the GTR + I + G substitution model for the third codon position of the two mtDNA partitions did not converge in the BEAST analyses. Consequently, we also applied an HKY + I + G model for this partition. Subsequently, the three independently run chains of the BEAST analysis showed high convergence among all parameters. The runs were then combined with 10% burn-in each resulting in ESS values > 1770 for all parameters. The topology of the resulting maximum clade credibility tree was generally congruent with the BI from MrBayes and the ML inference. However, the genus *Trichoglossus* was monophyletic but with very low support. The diversification of Loriini occurred within the last 10 million years (my) and the majority of cladogenetic events were after about five Ma (Figs. 3 and 4). Most of the sampled speciation events were found to have occurred earlier than 1 Ma with the exception of some events in *Eos* and *Trichoglossus*. When substitution and clock models were unlinked, resulting node ages were highly congruent. The following mean values of the posterior for the ucld.mean parameters were reported (substitution/site/Ma): COI: 0.0118; ND2: 0.0136; c-mos: 0.000876; Rag 1: 0.000613; RDPSN: 0.00164; TGFB: 2 0.00176; TROP: 0.000509. These substitutions rates were found to be comparable to published rates (Ellegren, 2007; Lerner et al., 2011, Weir and Schluter, 2008) indicating that our node calibration might be valid.

3.3. Biogeography

A DEC + j model was found to be the overall best-fitting model of geographic range evolution (Table 2). The inclusion of founder-event speciation increased model fit for all basic models tested. The island of New Guinea was the most strongly supported place of origin (Fig. 4). All *Eos* species appear to have evolved via dispersal to Wallacea west of New Guinea, and one species, Black-winged Lory *E. cyanogenia*, has evolved through secondary recolonization of Biak Island in Geelvink Bay in westernmost New Guinea. The evolution of *Trichoglossus* appears to have involved several dispersals to the west of New Guinea, to the Philippines and to Australia. All other Australian species of lories and lorikeets also appear to have been derived through multiple dispersal events to Australia although arguably some may have involved vicariance associated with repeated joining and isolation of the Australian and New Guinean land masses. *Vini*, *Phigys* and *Lorius* appear to have dispersed east across the Pacific Ocean. *Charmosyna*, for which we had only limited sampling, appears to have had only one dispersal event, into Melanesia.

4. Discussion

We aimed to provide a first DNA sequence-based estimation of the phylogenetic relationships and systematics among the genera of the nectarivorous lories and lorikeets of the Indo-Pacifc region and reconstruct the historical biogeography of this group. Central findings were that the group's evolution appears to have taken place within the last 10 my, that the island of New Guinea was a likely centre of origin (noting the geological recency of that island in its present form) and that while several phenotypically homogeneous genera were affirmed as monophyletic, several genera that are more phenotypically diverse were not. Below we discuss these phylogenetic patterns and resulting implications for taxonomy, biogeography, and phenotypic evolution.

4.1. Plumage patterns and systematics

The Plum-faced Lorikeet *Oreopsittacus arfaki* consistently emerged as the sister to all other lories and lorikeets. Christidis et al. (1991) could not resolve its position in their allozyme analysis although some of their analyses hinted at its position as sister to all other lories and lorikeets. The phenotypic distinctiveness of this species has long been recognized by its placement as either the first or last in sequences of Lorinii genera (Dickinson and Remsen, 2013; del Hoyo and Collar, 2014). Mivart (1896), noted it as unique among all parrots, not just lories and lorikeets, in having 14 not 12 tail feathers. He further remarked on its unique facial pattern and other characteristics that are at least unusual among lorikeets, such as the all red undersides of tail feathers and its relatively long, thin and pointed black maxilla. It is a species of montane New Guinean rainforests and rainforest edges (Parr and Juniper, 1998; Forshaw, 2006).

Our analyses affirm that *Eos, Lorius* and *Neopsittacus* are each monophyletic and should remain as genera. Non-monophyly of several other genera is clear and we advocate the following changes to genus-level systematics.

First, the three species of *Glossopsitta* need reclassification into two genera. The type-species of *Glossopsitta* Bonaparte, 1854 is *G. concinna* (Shaw, 1791) so it is the other two smaller species, *porphyrocephala* and *pusilla*, that require a different generic name. *Parvipsitta* Mathews, 1916 (type species *Parvipsitta pusilla* (White, 1790)) is available for them. Accordingly, we recognize the Little Lorikeet *Parvipsitta pusilla* and the Purple-crowned Lorikeet *P. porphyrocephala*. They form a sister pair comprising one mesic and one semi-arid species, respectively, but share little in common phenotypically other than being smaller relative to *G. concinna*.

Second, the Cardinal Lory, long recognized as *Chalcopsitta cardinalis*, and the Dusky Lory *Pseudeos fuscata*, which are sister species in our analyses, should become congeneric. The type-species of *Chalcopsitta* Bonaparte, 1850 is *C. ater* (Scopoli, 1786) so *C. cardinalis* needs to be transferred *Pseudeos* Peters, 1935 and not *Pseudeos* synonymized with *Chalcopsitta* if two genera are to be maintained. Accordingly, we recognize *Pseudeos cardinalis* and *Ps. fuscata*. We note that these two species both lack the distinctive, striation-like markings of *Chalcopsitta* as now circumscribed and that they share a presumably derived pattern of plumage showing more transverse barring and prominent red and orange. Given that *Chalcopsitta* and *Pseudeos* as so circumscribed are reasonably well-supported clades, we suggest that it is justifiable to maintain *Pseudeos* as a separate genus rather than merging all into *Chalcopsitta*.

Next, we address generic changes that will likely be necessary but require either improved taxon sampling or improved phylogenetic resolution, or both. First, monophyly of *Trichoglossus* is certainly questionable for two reasons: (1) in the BI and ML analyses all species are part of a polytomy in which *T. johnstoniae* is on its own branch and so not necessarily sister to the others and monophyly is not supported in the BEAST analyses, and (2) in the BI and ML analyses all other species form a poorly supported clade that includes *Psitteueteles iris* on another branch of the polytomy. *Ps. iris* is sister to the pair of *T. flavoviridis* and a *Trichoglossus* specimen of hybrid origin. The relationships of *T. flavoviridis* therefore remain uncertain.

Second, *Charmosyna* Wagler, 1832 (type-species *C. papou*) is clearly not monophyletic. Which of the two additional available generic names for current *Charmosyna* species (*Hypocharmosyna* Salvadori, 1891, type-species *C. placentis*; *Charmosynopsis* Salvadori, 1877, type-species *C. pulchella*) should be used, however,

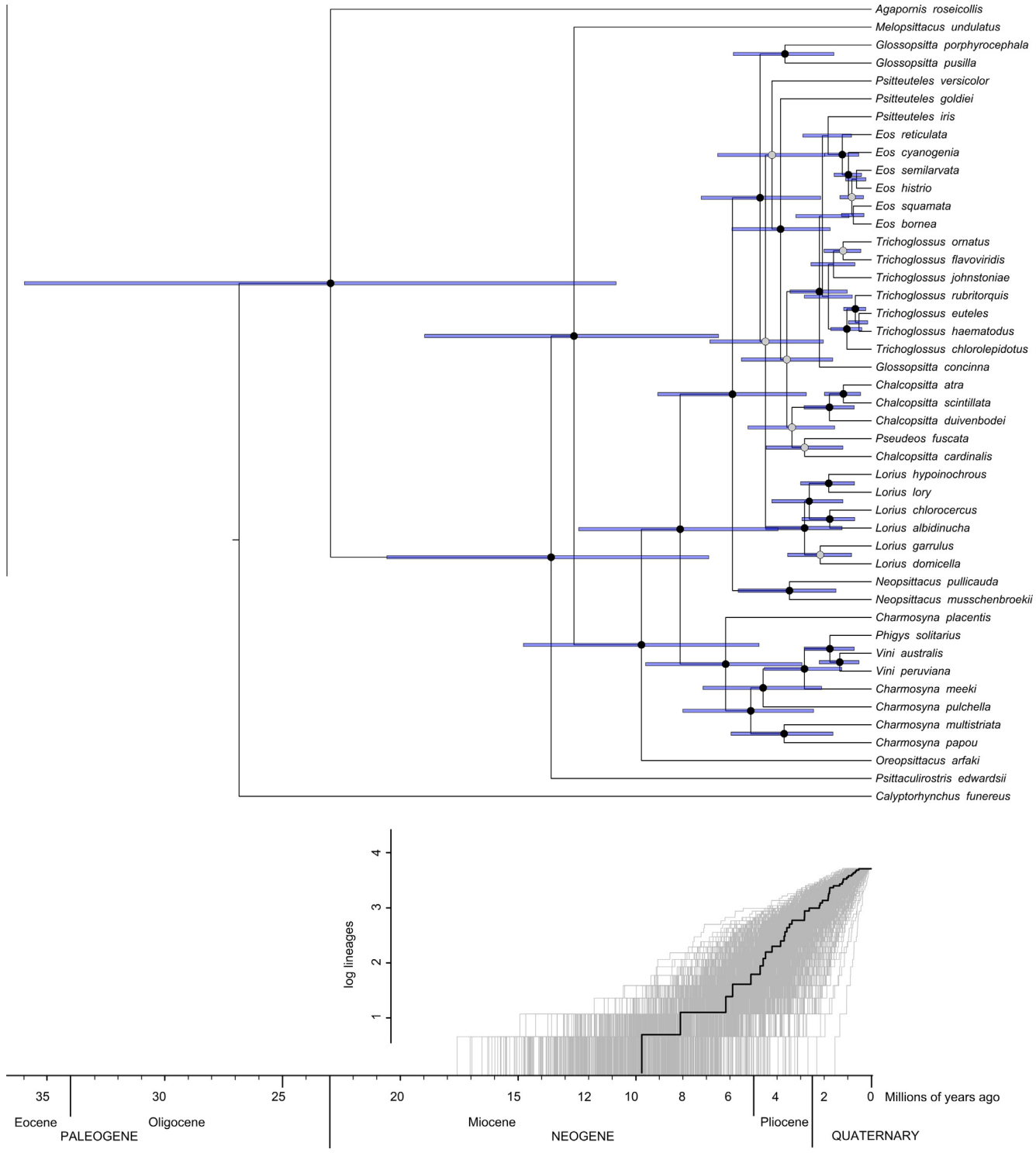

Fig. 3. Maximum clade credibility tree of the dating analysis using BEAST. The 95% highest posterior density (HPD) distributions are shown at the nodes. Well-supported nodes (Bayesian posterior probabilities, BPP, $\geqslant 0.95$) are marked with a black circle, while moderately supported nodes ($0.5 \leqslant$ BPP < 0.95) are marked with a gray circle. The lower part of the figure displays semi-logarithmic lineage through time plots for 1000 random trees from the posterior distribution in gray and for the maximum clade credibility tree in black.

or indeed whether new generic names are needed, requires a more complete phylogenetic analysis.

Third, our analyses confidently point to the non-monophyly of *Psitteuteles* Bonaparte, 1854: the type-species, *Ps. versicolor*, is not closely related to the other two species, the placement of which relative to each other and to *Trichoglossus* is uncertain. We predict that *Psitteuteles* will be retained as a monotypic genus for *Ps. versicolor*, but that the generic assignment of the other two species requires further phylogenetic analysis.

The final generic level issue we can address concerns *Vini* and *Phigys*. Our taxon sampling is too preliminary to affirm monophyly of all species of *Vini* and indeed whether monotypic *Phigys* is its

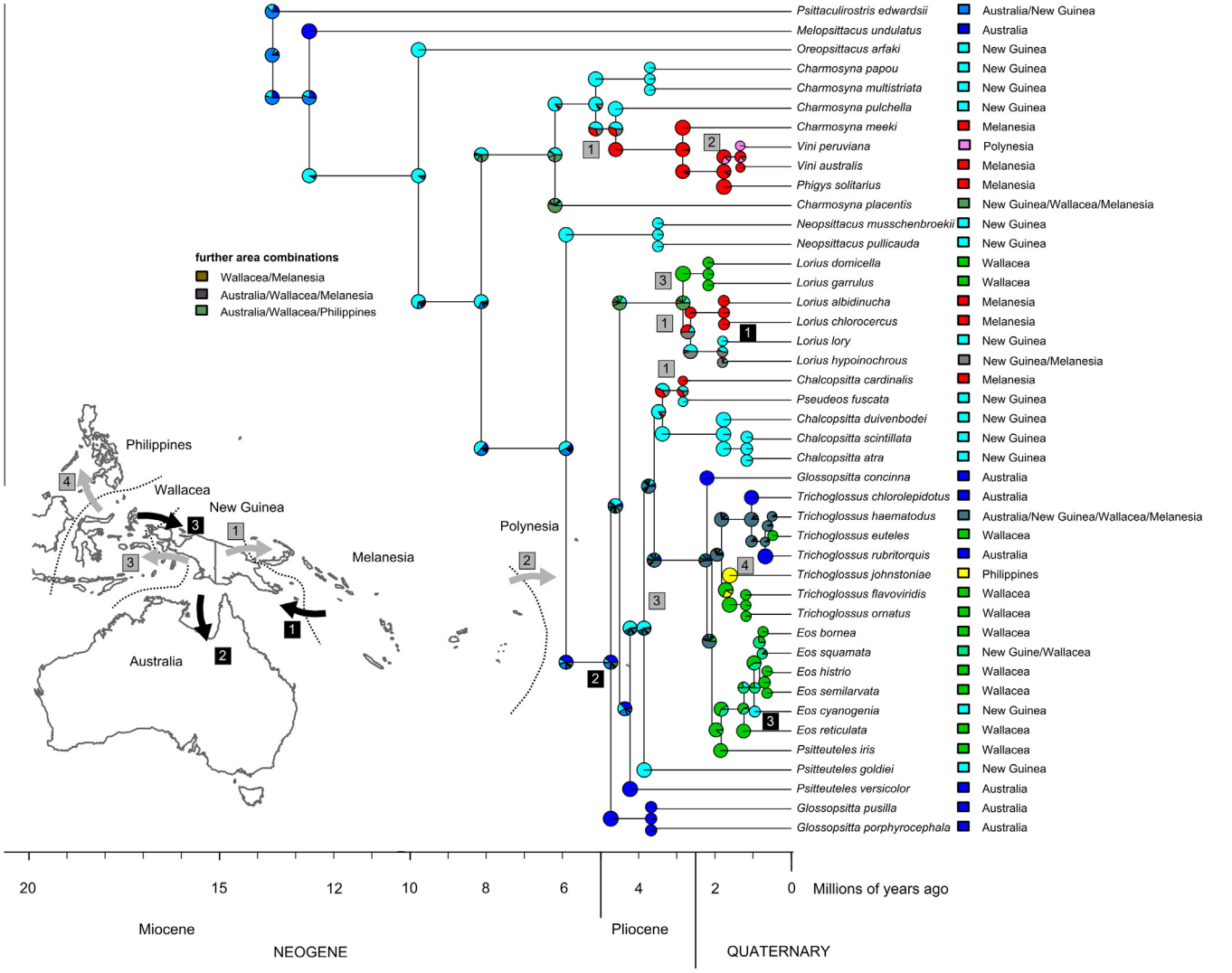

Fig. 4. Ancestral area reconstructions based on the DEC + j model implemented in BioGeoBears. Pie charts reflect relative probabilities of each area being ancestral at nodes. Numbers in gray and black boxes are putative dispersal events and correspond to their locations as shown on the map at the top of the figure with downstream dispersal events marked in black and upstream dispersal events in gray. Range delimitations used for biogeographic analyses are also indicated in the map.

Table 2
Comparison of the fit of different models of geographic range evolution and model specific estimates for the different parameters. *d* = dispersal, *e* = extinction, *j* = weight of jump dispersal (founder speciation).

Model	LnL	nb of parameters	*d*	*e*	*j*	AIC
DEC	−93.845	2	0.036	1.88E−02	0.000	191.7
DEC + J	−78.243	3	0.018	1.00E−12	0.086	162.5
DIVALIKE	−98.078	2	0.050	2.44E−02	0.000	200.2
DIVALIKE + J	−80.319	3	0.020	1.00E−12	0.090	166.6
BAYAREALIKE	−110.910	2	0.051	1.89E−01	0.000	225.8
BAYAREALIKE + J	−81.891	3	0.017	1.00E−07	0.094	169.8

sister or should be merged with *Vini*. If the latter, then *Vini* Lesson, 1831, which has priority over *Phigys* G.R. Gray 1870, would be the generic name in use.

Concerning species-level systematics, we again stress that our taxon sampling has not been designed to address species limits within the highly polytypic Rainbow Lorikeet *Trichoglossus haematodus* complex. del Hoyo and Collar (2014) divided the complex into seven species based on the scoring system of Tobias et al. (2010). We laud their pioneering effort to address what has clearly been a questionable and unsatisfactory classification. We consider their conclusions entirely premature, however, until phylogenetic relationships have been robustly determined within the group so that patterns of plumage evolution can be addressed in a phylogenetic framework. We look forward to the application of next-generation sequencing methods to full species- and subspecies level sampling of the whole group.

4.2. Biogeography

Founder-event speciation has long been considered important in the evolution of island biota. Its prevalence has become more readily testable, however, with the advent of current probabilistic models of geographic range evolution (Matzke, 2014). In our case, the implementation of founder-event speciation increased model

fit for different biogeographic models. Accordingly, the overall best-fitting model included founder-event speciation. From this we conclude that dispersal and subsequent founder-event speciation have likely been important in the diversification of the lories and lorikeets.

Our analyses provide strong arguments for a New Guinean origin of the lories and lorikeets and for multiple independent dispersals out of that island and its geological antecedents over the last 8 my. Having evolved within the last 10 my, the group's dispersal and evolution as a whole appears too young to have followed the same scenario proposed for corvoid passerine birds by Jønsson et al. (2011). They argued that corvoid passerines underwent an initial diversification within the proto-Papuan Archipelago and then began dispersing some 20 Ma, or earlier, at the Eocene/Oligocene boundary. There may nonetheless be some similarities between the lorikeets and lories and with Jønsson et al.'s (2011) model for the corvoids. The Central Range of present-day New Guinea likely did not begin to appear as land until the early-middle Miocene 14–16 Ma (van Ufford and Cloos, 2005) and the entire island is thought to have existed in its present form only for the last 4 to 5 my (Heinsohn and Hope, 2006). Given that the earliest divergence in lories and lorikeets occurred around 10 Ma, it is possible that such founder events may have involved island-hopping across the final remnants of a proto-Papuan archipelago.

It is noteworthy that the timing of the evolution of lories and lorikeets that we have recovered here is strikingly similar to that documented for similarly dispersive invertebrate groups by Toussaint et al. (2013, 2014). The dysticid diving beetles they studied (*Rhantus, Excelina*) may have evolved from ancestral forms of lowlands by passive uplift accompanying the Central Range Orogeny of the last 5 my (van Ufford and Cloos, 2005). In the case of these highly vagile lories and lorikeets, an evolutionary role of passive uplift may more likely have been one of opening up new ecological opportunities such as new habitats that formerly lowland ancestral forms could colonize. This model is consistent with the fact that the sister species of all lories and lorikeets is a lowland Australian species, the Budgerigar *Melopsittacus undulatus*. It is also consistent with the earliest divergence in lories and lorikeets involving present-day montane *Oreopsittacus* on one branch and, of course, some lowland species (e.g., *Charmosyna placentis*, *C. pulchella*) on the other.

Some genera such as *Charmosyna, Vini*, and *Trichoglossus,* are particularly notable for their inferred dispersal abilities. The genus *Vini* has reached some of the most remote islands in the Pacific, including Fiji, the Cook Islands, and the Tuamotu Islands. Likewise, *Charmosyna* occurs on islands in the Moluccas and the Solomons, Vanuatu, New Caledonia and Fiji. Species currently classified in *Trichoglossus* occur in western New Guinea-Wallacea and the Phillipines, and the *T. haematodus* complex alone occurs from Bali and the islands in the Flores Sea in the west to New Caledonia in the east. The most far-flung, and phenotypically divergent, species of the genus as it is currently construed is the Pohnpei Lorikeet *T. rubiginosus*. We were unable to sample this species but presume that it too evolved following dispersal to Pohnpei. *Charmosyna placentis* is also of interest in this regard. Essentially a lowland bird recorded up to 1400 m above sea level, it occurs from Sulawesi across most of New Guinea and its satellite islands to the Bismarck Archipelago. It is polytypic so presumably has evolved differentiated forms recognized as subspecies essentially through founder-event dispersals.

4.3. Downstream and upstream dispersal

Trichoglossus may exemplify both downstream and upstream colonization as defined in the Introduction. Improved phylogenetic resolution, particularly within the *T. haematodus* complex, will clarify that but we predict that downstream dispersal from New Guinea to the Philippines and Wallacea has been involved. Conversely, upstream dispersal into Australia may have occurred but is complicated by the past connections between Australia and New Guinea to form the larger land mass of Sahul, the extent of which has fluctuated during the Pleistocene (Hantoro et al., 1995; Voris, 2000).

Downstream dispersal east from New Guinea is apparent in *Charmosyna*, and *Vini*/*Phigys* but its full details await more complete taxon sampling. In *Lorius*, one scenario would depict downstream dispersal east and west out of New Guinea as well as a possible example of upstream in *L. lory*. Support for this scenario is weak relative to the alternative that this species has always been in New Guinea. *Pseudeos cardinalis* has dispersed east from New Guinea, and *Chalcopsitta atra* appears to have reached one island to the west of the main New Guinea landmass.

Similarly, one scenario for *Eos* places it as originating in New Guinea and dispersing west out of it, *E. cyanogenia* representing a secondary recolonization of western New Guinea. Alternatively, we cannot reject that the genus originated to the west of New Guinea and diversified there.

Although upstream dispersal may not be as prevalent as in other groups such as monarch flycatchers or whistlers (Filardi and Moyle, 2005; Jonsson et al., 2010; Andersen et al., 2014, 2015), it seems nonetheless to be an important part of the colonization history of lories and lorikeets. This adds to the growing body of evidence that island systems should not be considered solely as evolutionary sinks.

It might reasonably be asked whether human introductions have played a role in the spread of lories and lorikeets, particularly to the remote island in Polynesia and Micronesia. Notwithstanding our incomplete species-level taxon sampling, we suggest not. Our analyses suggest that the diversification of the group, even at the more recent stages of species-level divergences, was complete long before humans arrived. For example, the dispersal of the ancestor of *Vini peruviana* to Polynesia probably occurred in the early Pleistocene, and recent estimates of human arrival to in region are around just 3,000 years ago (Burley et al., 2012).

4.4. Integration of phenotypic and phylogenetic data

A striking result in our analyses is the diverse patterns of concordance and discordance among phenotypic and phylogenetic patterns. For example, genera such as *Eos* and *Lorius*, which by any measure are phenotypically distinctive and the member species of which are easily identifiable to their respective genera, have been unsurprisingly affirmed as monophyletic. Conversely, other genera and indeed the newly suggested generic alignments, show much less phenotypic cohesion. The two species of *Parvipsitta* (until recently synonymised with *Glossopsitta*) are an example. One species, the Little Lorikeet *P. pusilla*, is a small almost uniformly green bird with red about the face and a brownish nape patch. The other, the Purple-crowned Lorikeet *P. porphyrocephala*, has a purple coronal patch, orange auriculars, unique pale blue underparts and a red underwing patch. This disparity where present-day closest relatives are phenotypically dissimilar is seen in other Australo-Papuan groups such as the Meliphagoidea (Gardner et al., 2010; Joseph et al., 2014) and may well reflect extinction of other, intermediate taxa. Consistent with this is that Byrne et al. (2011) noted the prevalence of inferred extinction events in the history of the eastern Australian mesic biota. Similarly, certain phenotypic traits such as shaft-streaked feathering in the plumage, coronal, throat and chest patches, a brownish nape, predominantly plain green coloration, and UV reflectant plumage, are scattered across the whole group. Clearly, these may be ancestral traits that have been retained in various lineages during evolution. Indeed, the facial pattern of the

Budgerigar *Melopsittacus undulatus*, the sister species to all lories and lorikeets, shares blue shaft-streaked feathering with many of the latter. Full character reconstruction would be best attempted after phylogenetic analyses achieve more complete taxon sampling.

4.5. Conclusion

We provide a first DNA-based estimate of the phylogenetic relationships among lories and lorikeets. We estimate that the clade arose in New Guinea at about 10 Ma and that ongoing geological evolution of that island, which took its present-day shape only about 4–5 Ma, may well have selected for dispersal as a significant process in the group's speciation. Within the limitations imposed by our taxon sampling we have suggested some generic reclassifications and noted others that require improved phylogenetic analysis. Lastly, a conundrum posed at the outset of this paper arguably remains. Why has the speciation that has resulted in these highly dispersive birds not been diluted or obliterated by repeated instances of dispersal? Is it simply that once an island is colonized and speciation begins, that there is no ecological space for later immigrants to diversify? Or are remote island archipelagos so rarely reached by the birds that speciation has also been rare? Although the model of diversification of corvoid passerines out of a proto-Papuan archipelago posits that that process began at least 10 my earlier than what we find for the lories and lorikeets, we note some potential similarities between the two groups. In contrast to the corvoid passerines however, lories and lorikeets except for one species have not crossed Wallace's Line and reached South-East Asia. Further work could address whether this is explained by factors such as competition with other similarly nectarivorous birds already occupying relevant ecological niche space west of Wallace's Line (e.g., *Aethopyga* sunbirds (Passeriformes: Nectariniidae, see Hosner et al., 2013).

Acknowledgments

We thank the following institutions and people for the generous loan of tissue specimens that have supported our collective work on this group: American Museum of Natural History (P. Sweet), Academy of Natural Sciences of Philadelphia (N. Rice), Australian National Wildlife Collection (R. Palmer), Federal Veterinary Office Bern, Field Museum of Natural History (D. Willard), Kansas University Natural History Museum, Lawrence, (A. Nyári, A.T. Peterson, M. Robbins), Fundación Loro Parque (D. Waugh), Museum of Natural Science (S. Cardiff, D. Dittmann), Smithsonian Museum of Natural History (G. Graves), University of Washington, Burke Museum (S. Birks), Vertebrate Museum of New Mexico State University (P. Houde), Zoological Museum, University of Copenhagen (J. Fjeldså, J.-B. Kristensen), R. Burkhard, A. Fergenbauer-Kimmel, H. Gygax, R. Low, H. Rosenberger, D. Ruess, P. Sandmeier, T. and P. Walser, and G.Weis. We particularly acknowledge the support of Gary Graves (Smithsonian Institution) in this work. A CSIRO Newton-Turner Fellowship supported LJ in this work. We are indebted to BirdLife International (M. Balman) and NatureServe for their generous permission to use their range maps in compiling Fig. 1. We also are grateful to Lynx Edicions (E. Badia, J.L. Copete) for permission to reproduce images of birds used in Fig. 2 from del Hoyo and Collar (2014). MS thanks M. Güntert, S.T. Hertwig and C. Sherry for valuable support and TW thanks K. Brown for assistance in the laboratory.

Appendix A. List of specimens studied and their provenance, type of tissue and loci sequenced and Genbank accession numbers

Taxa	Source	Number	Locality data, other notes	Type	COI	ND2	TROP	TGFB2	RDPSN	c-mos	RAG-1
Chalcopsitta atra	LSUMNS	B-26966 = LSUMZ 166395	San Antonio Zoo, unsexed bird, died 15 July 1998	T	EU621593	EU327596	EU665562	EU660234	EU665501	KP644719	KP644670
Chalcopsitta duivenbodei	NMNH	B6396	Presumably either USNM 263748 or USNM 542231	T	EU621604	EU327607	EU665573	EU660245	EU665511	KP644706	KP644643
Chalcopsitta scintillata	AMNH	DOT 7778	Captive bred; prepared as a skeleton AMNH SKEL-27315	T	KP644566	KP644673	KP644636	KP644593		KP644695	KP644658
Charmosyna meeki	AMNH	DOT 208	Kolombangara Island, Solomon Islands; prepared as skeleton AMNH-28101 and a spread wing AMNH SKIN 836237	T	KP644580	KP644686	KP644634	KP644592	KP644739	KP644709	KP644666
Charmosyna multistriata	LSUMNS	B-19411 = LSUMZ 159751	Female, skeleton. Donated by D.	T	KP644581	KP644687	KP644638	KP644590	KP644738	KP644711	KP644661

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Taxa	Source	Number	Locality data, other notes	Type	COI	ND2	TROP	TGFB2	RDPSN	c-mos	RAG-1
			Schroeder Aviary, Inglewood, California								
Charmosyna papou	NMNH	B6379	Presumably in ORNIS2 with a different USNM number for the voucher	T	EU621605	EU327608	EU665574	EU660246	EU665512	KP644697	KP644662
Charmosyna placentis	SDZ	399141	Unvouchered specimen held in zoo	B					KP644742	KP644712	KP644668
Charmosyna placentis	AMNH	DOT 7797	Captive bred, donated by San Diego Zoo, bird #34817	T	HQ629761	HQ629726	HQ629685	HQ629640			
Charmosyna pulchella	NMBE	1056241	Captive; prepared as a skeleton	T	KP644582	KP644688		KP644591	KP644736	GQ505126	GQ505237
Eos bornea	AMNH	DOT 7803	Captive; prepared as a skeleton AMNH SKEL-27260	T	KP644567	KP644673	KP644624	KP644602	KP644723	KP644710	KP644650
Eos cyanogenia	NMBE	1056237	Captive; prepared as a skeleton	T	KP644568	KP644674	KP644626	KP644604	KP644725	GQ505122	GQ505233
Eos histrio	SDZ	406013	Unvouchered specimen held in zoo	B					KP644726	KP644696	KP644639
Eos histrio	AMNH	DOT 7703	Captive bred, donated by San Diego Zoo, bird #43679	T	HQ629762	HQ629727	HQ629686	HQ629642			
Eos reticulata	NMNH	B6397	USNM 542232	T	EU621618	EU327622	EU665588	EU660259	EU665523	KP644704	KP644651
Eos semilarvata	LP	Unvouchered	Specimen held in zoo	B	KP644584		KP644621	KP644598			
Eos squamata	LP	Unvouchered	Specimen held in zoo	B	KP644585	KP644690	KP644622	KP644599			
Glossopsitta concinna	AMNH	DOT 7825	Captive; no date; prepared as a skeleton AMNH SKEL-27258	T	KP644575	KP644679	KP644616	KP644595	KP644735	KP644694	KP644659
Lorius albidinucha	NMNH	B4029	Hans Meyer Range, New Ireland, Papua New Guinea	T	EU621628	EU327632	EU665597	EU660268	EU665528	KP644700	KP644654
Lorius chlorocercus	LP	Unvouchered	Specimen held in zoo	B	KP644586	KP644691	KP644628	KP644608			
Lorius domicella	AMNH	DOT 7695	Captive bred; prepared as a skeleton AMNH SKEL-27038	T	KP644577	KP644682	KP644635	KP644610	KP644732	KP644701	KP644645
Lorius garrulus	NMNH	B6387	Captive, locality unknown	T	KP644576	KP644683	KP644615	KP644607	KP644733	KP644702	KP644644
Lorius hypoinochrous	LP	Unvouchered	Specimen held in zoo	B	KP644587	KP644692	KP644623	KP644609			
Lorius lory	NMNH	B6576	Captive, locality unknown	T	HQ629767	HQ629732	HQ629693	HQ629648			
Neopsittacus musschenbroekii	NMNH	B6398	Captive, donated by Miami Zoo	T	EU621636	EU327640	EU665605	EU660275	EU665535	KP644713	KP644655

(*continued*)

Taxa	Source	Number	Locality data, other notes	Type	COI	ND2	TROP	TGFB2	RDPSN	c-mos	RAG-1
Neopsittacus pullicauda	LP	Unvouchered	Specimen held in zoo	B	KP644588	KP644693	KP644629	KP644614			
Oreopsittacus arfaki	KUMNH	4789	Abalgamut Camp, 16.3 km from Teptep Airstrip, Morobe Province, PNG	T	KP644583	KP644689	KP644632	KP644613	KP644741	KP644714	KP644667
Parvipsitta porphyrocephala	ANSP	10645 old = 22727 new	Yardea, South Australia, Australia 32deg25'S, 135deg26'E	T	EU621623	EU327627	EU665592	EU660264	EU665526	KP644707	KP644652
Parvipsitta pusilla	ANWC	44246	Shoalwater Bay Army Training Reserve, Queensland, Australia, -22.4417, 150.2972	T	KP644578	KP644684	KP644633	KP644611	KP644737	KP644708	KP644656
Phigys solitarius	AMNH	DOT 7693	Captive bred; prepared as a skeleton AMNH SKEL-27039	T	EU621642	EU327646	EU665611	EU660281	EU665540		KP644663
Pseudeos cardinalis	AMNH	DOT 6626	Solomon Islands; Isabel Island, Tunuche; prepared as a skeleton AMNH SKEL-23404	T	HQ629760	HQ629725	HQ629684	HQ629639	KP644722	KP644703	KP644640
Pseudeos fuscata	AMNH	DOT 7858	Captive bred; prepared as a skeleton AMNH SKEL-27284	T	EU621654	EU327658	EU665622	EU660292	EU665549	KP644705	KP644642
Psitteuteles goldiei	AMNH	DOT 7897	Aroa River, Papua New Guinea; prepared as a spirit specimen AMNH FLUID-11111	T	HQ629777	HQ629741	HQ629706	HQ629661	KP644734		KP644646
Psitteuteles iris	AMNH	DOT 7722	Captive bred; prepared as a skeleton AMNH SKEL-27036	T	KP644572	KP644680	KP644631	KP644605	KP644724	KP644717	KP644648
Psitteuteles versicolor	ANWC	34002	Ban Ban Springs Station, NE of Pine Creek, Northern Territory, Australia	T	KP644579	KP644685	KP644625	KP644612	KP644740	KP644699	KP644660
Trichglossus euteles	LP	Unvouchered	Unvouchered specimen held in zoo	B	KP644589		KP644627	KP644600			
Trichoglossus chlorolepidotus	NMNH	B6422	Townsville, Queensland, Australia	T	KP644574	KP644676	KP644620	KP644601	KP644731		KP644647
Trichoglossus flavoviridis	AMNH	DOT 13122	Captive bred; prepared as a skeleton AMNH SKEL-27700	T	KP644569		KP644617	KP644606	KP644730		GQ505234
Trichoglossus h. rubritorquis	SDZ	395448	Unvouchered specimen held in zoo	B	KP644571	KP644677	KP644619	KP644597	KP644728		
Trichoglossus	SDZ	402131	Unvouchered specimen	B						KP644698	KP644649

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Taxa	Source	Number	Locality data, other notes	Type	COI	ND2	TROP	TGFB2	RDPSN	c-mos	RAG-1
haematodus (subspecies ID unknown)			held in zoo								
Trichoglossus hybrid origin (?)	LSUMNS	B-19422 = LSUMZ 159759	Male, skeleton, prepared 19993. Sample initially thought to be *T. ornatus* but queries arising from results of this work suggest possible history of hybridization but unknown parentage.	T	KP644570	KP644681	KP644618	KP644596	KP644727	KP644718	KP644653
Trichoglossusj ohnstoniae	NMBE	1056238	Captive, private, prepared as skeleton	T	KP644573	KP644678	KP644637	KP644603	KP644729	GQ505123	GQ505234
Vini australis	AMNH	DOT 7705	Captive bred; prepared as a skeleton AMNH SKEL-27042	T	EU621668	EU327672	EU665636	EU660306	EU665561		KP644665
Vini peruviana	AMNH	DOT 7694	Captive bred; prepared as a skeleton AMNH SKEL-27044	T	HQ629784	HQ629748	HQ629713	HQ629669	KP644743		KP644664
Outgroups											
Melopsittacus undulatus	NMNH	610565 (B06360)	20 km NW Griffith, New South Wales, Australia	T	EU621629	EU327633	EU665598	EU660269	EU665529		
Melopsittacus undulatus	UWBM	60748/1998-068	Kulkinbah Creek, Roy Hill Station, Newman, Western Australia, Australia	T						GQ505222	GQ505166
Psittaculirostris edwardsii	NMNH	B6383	Captive, locality unknown	T	EU621656	EU327660	EU665624	EU660294	EU665551	GQ505132	GQ505243
Psittaculirostris edwardsii	NMBE	1056245	Captive; prepared as a skeleton	T						GQ505132	GQ505243
Agapornis roseicollis	NMNH	601838 (B08798)	Captive, locality unknown	T	EU621593	EU327596	EU665562	EU660234	EU665501	GQ505086	GQ505194
Calyptorhynchus funereus	NMNH	542615 (B06460)	Captive, Moggill, Brisbane, Queensland, Australia	T	EU621603	EU327606	EU665572	EU660244	EU665510	GQ505118	GQ505229

Abbreviations used: NMNH: United States National Museum of Natural History, Washington DC, USA; AMNH: American Museum of Natural History, New York, USA; ANSP: Academy of Natural Sciences at Drexel University, Philadelphia, USA; ANWC: Australian National Wildlife Collection, Canberra, Australia; KUMNH: University of Kansas Museum of Natural History, Kansas, USA; LP: Loro Parque, Tenerife, Canary Islands, Spain; LSUMNS: Louisiana State University Museum of Natural Science, Baton Rouge, USA; NMBE: Naturhistorisches Museum der Burgergemeinde Bern, Bern, Switzerland; SDZ: San Diego Zoological Park, San Diego, USA; UWBM: University of Washington, Burke Museum, Seattle, USA. Type – T: cryofrozen tissue (liver, or heart or breast muscle); B: Blood.

Appendix B. Supplementary material

Figs. S1–S7. Best-scoring Maximum Likelihood (ML) trees for COI, ND2, cmos, RAG, RDPSN, TGFB2, TROPO, respectively, estimated with RAxML v 7.0.4 (Stamatakis, 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690) on a web server with 100 rapid bootstrap inferences (Stamatakis et al., 2008. A rapid bootstrap algorithm for the RAxML web servers. Syst. Biol. 57, 758–771). All free model parameters were estimated by the software (substitution rates, gamma shape parameter, base frequencies). Bootstrap values above or equal to 50 are given. Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2015.04.021.

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