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Supermatrix phylogeny and biogeography of the Australasian Meliphagides radiation (Aves: Passeriformes)

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ABSTRACT

With nearly 300 species, the infraorder Meliphagides represents one of the largest and most conspicuous Australasian bird radiations. Although the group has been the focus of a number of recent phylogenetic studies, a comprehensive species-level phylogenetic hypothesis is still lacking. This has impeded the assessment of broad-scale evolutionary, biogeographic and ecological hypotheses. In the present study, we use a supermatrix approach including five mitochondrial and four nuclear markers to infer a time-calibrated phylogeny of the Meliphagides. Our phylogeny, which includes 286 of the 289 (99%) currently recognized species, is largely congruent with previous estimates. However, the addition of 60 newly sequenced species reveals some novel relationships. Our biogeographic analyses suggest an Australian origin for the group in the early Oligocene (31.3 Mya, 95% HPD 25.2–38.2 Mya). In addition, we find that dispersal events out of Australia have been numerous and frequent, particularly to New Guinea, which has also been the source of multiple back-colonizations to the Australian mainland. The phylogeny provides an important framework for studying a wide variety of macroecological and macroevolutionary themes, including character evolution, origin and timing of diversification, biogeographic patterns and species responses to climate change.

1. Introduction

Oscine passerines (Passeriformes: Passeri) form the largest and most diverse suborders of living birds, encompassing over 5000 species. The vast majority of these species belong to two major infraorders, the Passerides and the Corvides (Cracraft, 2014). In addition, there are a number of basal lineages that are almost confined to the Australasian region (Ericson et al., 2002; Barker et al., 2004). The most speciose of these basal lineages is the ecologically diverse infraorder Meliphagides (formerly known as Meliphagoidea) radiation, which is divided into five families: Maluridae (fairy-wrens and allies), Acanthizidae (thornbills and gerygones), Meliphagidae (honeyeaters), Pardalotidae (pardalotes) and Dasyornithidae (bristlebirds). The last two of these families are endemic to Australia, whereas the other three are centred in or confined to Australia and New Guinea. Despite having similar crown ages, the families vary significantly in species diversity, ranging from 187 species of honeyeaters to only three species of bristlebirds (Gill and Donsker, 2016). The Meliphagides is particularly diverse in Australia where it accounts for more than 45% of the passerine avifauna, but the group has also radiated extensively in New Guinea and to a lesser extent across the tropical Pacific, Wallacea and New Zealand archipelagos.

First recognized as a monophyletic assemblage by DNA-DNA hybridization data (Sibley and Ahlquist, 1990), the Meliphagides has since been the subject of numerous phylogenetic studies. However, the majority of these studies have primarily dealt with relationships within particular families and genera (e.g. Driskell and Christidis, 2004; Christidis et al., 2010; Driskell et al., 2011; Nyári and Joseph, 2012; Joseph et al., 2014; Jønsson et al., 2016). Nonetheless, these studies have revealed that many genera, as traditionally circumscribed, are not monophyletic and that there is little support for separate New Guinean and Australian radiations.

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The only detailed study of the entire radiation to date used a combination of mitochondrial and nuclear DNA to infer relationships among families and genera (Gardner et al., 2010). Although Gardner et al. (2010) provided strong support for monophyly for each of the five families, there was incomplete taxon sampling at the genus and species levels, particularly within the Meliphagidae. Consequently, the lack of a comprehensive species-level phylogenetic hypothesis for the Meliphagides has impeded the assessment of broad-scale ecological, evolutionary and biogeographical hypotheses.

Significant variation in ecology, morphology and life-history traits is evident in the Meliphagides, particularly within the species-rich Meliphagidae (honeyeaters) (Keast, 1976; Schodde and Mason, 1999; Higgins et al., 2008). Honeyeaters exhibit extreme variation in body size, ranging from the diminutive Mountain Myzomela (*Myzomela adolphinae,* 6–7 g) to the large MacGregor's Honeyeater (*Macgregoria pulchra*, >350 g) of New Guinea (Higgins et al., 2008). Meliphagids are widely distributed throughout all major habitat types in Australia and the Indo-Pacific. Most honeyeater species share adaptations towards a diet rich in nectar, including a long decurved bill and a brush-tipped tongue, but a few species appear to be exclusively insectivorous or frugivorous (Keast, 1985; Higgins et al., 2008). The four remaining families of Meliphagides all comprise very small- to medium-sized species that are largely or exclusively insectivorous, as well as the substantially granivorous Australian grasswrens (*Amytornis*) (Rowley and Russell, 1997; Schodde and Mason, 1999). With the exception of a single genus (*Gerygone*), members of Maluridae, Acanthizidae, Pardalotidae and Dasyornithidae are restricted to the continental landmasses of Australia and New Guinea. This biogeographic pattern in combination with their morphology (e.g., short rounded wings), is suggestive of poor dispersal abilities among species in these families.

Here we combine existing molecular data with novel sequence data to infer a near-complete species-level phylogeny for the Meliphagides. In order to accommodate sparse genetic sampling, limited overlap among species and strategic inclusion of novel sequence data, we use a supermatrix approach to reconstruct phylogenetic relationships (Sanderson et al., 1998; de Queiroz and Gatesy, 2007). We then use the resulting phylogeny to infer the biogeographical history of the Meliphagides radiation using a model-testing approach.

2. Materials and methods

2.1. Taxon and character sampling

We sampled 285 of the 288 species of the Meliphagides currently recognized by the IOC World Bird List version 6.2 (Gill and Donsker, 2016), including all recognized families (5) and genera (71). *Myzomela obscura rubrotincta* of the Moluccas was treated as a separate species because initial analyses suggested that this subspecies is more closely related to *M. cruentata* than to *M. obscura*, and it has been suggested to represent a distinct species based on morphology and vocalizations (Thibault et al., 2013). We lacked material for the following three species: *Gerygone hypoxantha, Melipotes carolae, Myzomela dammermani*. The following nine taxa representing major passerine lineages were included as outgroups for the analysis: *Acanthisitta, Bombycilla, Callaeas, Cormobates, Corvus, Menura, Picathartes, Pomatostomus,* and *Ptilonorhynchus.*

For the supermatrix assembly, we downloaded DNA sequences of meliphagoid species from GenBank. We focused on two nuclear introns (Fib-5 and GAPDH), two nuclear exons (RAG-1 and RAG-2) and five mitochondrial (12S, cyt-b, COI, ND2 and ND3) genes that have been used extensively in previous phylogenetic studies of meliphagoid species (e.g. Driskell and Christidis, 2004; Norman et al., 2007; Christidis et al., 2010; Gardner et al., 2010; Driskell et al., 2011; Andersen et al., 2014; Joseph et al., 2014). In addition, we generated 134 new sequences extracted from both fresh tissue and ancient DNA from footpad samples from study skins (Table 1 and S1). Extraction, amplification and sequencing of DNA followed standard protocols (Qiagen; Irestedt et al., 2006). In order to minimize risks of cross-contamination of samples, extractions of ancient DNA were performed in a specialized laboratory used solely for this purpose. For ancient DNA, we sequenced the NADH dehydrogenase subunit 2 (ND2, 1041 bp) for all taxa, as well as the nuclear non-coding beta-fibrinogen intron 5 (fib5, 567 bp) for a few select taxa. To this end, we designed a range of new primers (Table S2) that allowed us to amplify and sequence fragments of about 200 base pairs. For fresh tissue, in addition to the two genes mentioned above, we also obtained sequences of the nuclear intron glyceraldehyde-3-phosphodehydrogenase (GAPDH, 347 bp). Sequences were edited and checked for anomalous stop-codons and indels in Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). We then aligned the sequences using Muscle (Edgar, 2004) in SeaView v4.5.4 (Gouy et al., 2010).

2.2. Phylogenetic inference and dating

We used maximum likelihood (ML) and Bayesian inference to infer phylogenetic relationships within the Meliphagides, with many analyses run via the CIPRES Science Gateway v3.3 (Miller et al., 2010). Individual gene partitions were analysed using ML methods as implemented in RAxML v8.2.4 (Stamatakis, 2014). Using the rapid bootstrap technique (Stamatakis et al., 2008) we computed the most likely tree simultaneously with 100 bootstrap replicates, applying the default GTR+Γ substitution model to each gene partition. We also analysed the concatenated dataset of all nine genes (8021 bp) using the same settings. The concatenated dataset was also analysed using BEAST v1.8.3 (Drummond et al., 2012) in order to produce a time-calibrated tree. We applied the best fitting model of nucleotide evolution to each gene partition as determined by the Bayesian Information Criterion (BIC) in jModelTest2 (Darriba et al., 2012) (Table 2) and implemented a relaxed uncorrelated log-normal distribution for the molecular clock model that was unlinked across all gene partitions (Drummond et al., 2006). We used a Yule speciation process for the tree prior. Rate heterogeneity, base frequencies, and substitution rates were unlinked across the nine partitions.

To obtain a time-calibrated tree, we used two Meliphagides fossils and a secondary calibration point. The fossils were used to provide minimum ages for their respective clades, using uniform prior distributions. The first fossil represents a recently discovered crown acanthizid from an early Miocene deposit from the Riversleigh World Heritage Area, Australia (Nguyen in prep.). Using radiometric U-Pb dating, the minimum age of this deposit has recently been estimated to be 16.24 Mya (Woodhead et al., 2016). This calibration point was used to provide a minimum age for the Acanthizidae. The second fossil is a crown meliphagid from a middle Miocene deposit at Riversleigh (Boles, 2005) with an estimated minimum age of 14.17 Mya based on radiometric U-Pb dating (Woodhead et al., 2016). This calibration point was used to provide a minimum age for the Meliphagidae. Finally, we used a secondary calibration point from a recent study by Prum et al. (2015) to date the divergence of *Acanthisitta* from all other passerines, using a normally distributed prior (mean = 51.33, st. d. = 5).

For the final analysis, we ran BEAST for 250 million generations across four independent runs, sampling every 5000 generations. We assessed convergence in Tracer v1.6 (Rambaut et al., 2014), by assessing the Effective Sample Size (ESS) and mean distribution

Table 1
List of new sequences generated for this study, including information of sample type, voucher identity and sampling location. Taxonomy follows that of the IOC World Bird List v6.2 (Gill and Donsker, 2016). Institutional abbreviations are as follows: AMNH = American Museum of Natural History, New York; ANWC = Australian National Wildlife Collection, Canberra; BMNH = British Museum of Natural History, Tring; NRM = Swedish Museum of Natural History, Stockholm; RMNH = Naturalis Biodiversity Center, Leiden; ZMUC = Natural History Museum of Denmark, Copenhagen.

Taxon	Type	Voucher	Location	GenBank accession number		
				ND2	Fib5	GAPDH
Myzomela blasii	Toepad	RMNH 133750	Seram, Indonesia	KY230273		
Myzomela albigula	Toepad	BMNH 1899.5.17.21	Rossel Island, Papua New Guinea	KY230274		
Myzomela eques	Tissue	ZMUC 145266	Kausi, Bismarck Range, Papua New Guinea	KY230275	KY230211	KY230241
Myzomela obscura rubrotincta	Tissue	ZMUC 149490	Obi, Indonesia	KY230276	KY230212	KY230242
Myzomela cruentata	Toepad	ZMUC 142275	Lemkamin, New Ireland, Papua New Guinea	KY230277		
Myzomela nigrita	Toepad	ZMUC 145122	Mafulu, C.D., Papua New Guinea	KY230278		
Myzomela pulchella	Toepad	ZMUC 142243	Lemkamin, New Ireland, Papua New Guinea	KY230279		
Myzomela kuehni	Toepad	BMNH 1904.6.10.21	Wetar, Indonesia	KY230280		
Myzomela adolphinae	Toepad	ZMUC 145121	Mafulu, C.D., Papua New Guinea	KY230281		
Myzomela boiei	Toepad	RMNH 133841	Banda Neira, Indonesia	KY230282		
Myzomela chloroptera	Toepad	NRM 572022	Toemaratas, North Sulawesi, Indonesia	KY230283		
Myzomela wakoloensis	Toepad	RMNH 133833	Seram, Indonesia	KY230284		
Myzomela caledonica	Toepad	RMNH 133849	New Caledonia	KY230285		
Myzomela chermesina	Toepad	NRM 572023	Rotuma, Fiji	KY230286		
Myzomela rubratra	Toepad	NRM 572024	Truk, Caroline Islands	KY230287		
Myzomela sclateri	Toepad	ZMUC 143653	Credner Island, Papua New Guinea	KY230288		
Myzomela pammelaena	Toepad	ZMUC 143159	Nago Island, Papua New Guinea	KY230289		
Myzomela eichhorni	Toepad	NRM 572025	Kulambangra, Solomon Islands	KY230290		
Myzomela malaitae	Toepad	NRM 572021	Malaita, Solomon Islands	KY230291	KY230213	
Myzomela melanocephala	Toepad	NRM 572026	Guadalcanal, Solomon Islands	KY230292		
Myzomela tristrami	Tissue	ZMUC 139433	Makira, Solomon Islands	KY230293	KY230214	KY230243
Myzomela erythromelas	Toepad	ZMUC 143979	Yalom, New Britain, Papua New Guinea	KY230294	KY230215	
Myzomela vulnerata	Toepad	ANWC B30138	Near Baukau, Timor-Leste	KY230295		
Glycichaera fallax	Tissue	ZMUC 145472	Kausi, Bismarck Range, Papua New Guinea			KY230244
Ptiloprora meekiana	Toepad	ANWC B04466	Wengomanga, Morobe, Papua New Guinea	KY230296		
Ptiloprora erythropleura	Toepad	NRM 572029	Tombrok, Vogelkop, West Papua, Indonesia	KY230297		
Ptiloprora mayri	Toepad	AMNH 294315	Cyclops Mts., West Papua, Indonesia	KY230298		
Ptiloprora perstriata	Tissue	ZMUC 145268	Lake Piunde, Mt. Wilhelm, Papua New Guinea	KY230299	KY230216	KY230245
Anthornis melanocephala	Toepad	NRM 568480	Chatham Islands, New Zealand	KY230300		
Pycnopygius ixoides	Toepad	NRM 572030	Klamono, Vogelkop, West Papua, Indonesia	KY230301		
Pycnopygius stictocephalus	Toepad	ANWC B27106	Kuriva River, Papua New Guinea	KY230302	KY230217	
Lichmera lombokia	Toepad	AMNH 694925	Lombok, Indonesia	KY230303	KY230218	
Lichmera argentauris	Toepad	AMNH 694333	Gebe Island, Indonesia	KY230304		
Lichmera limbata	Toepad	NRM 554302	Nassiko, Timor, Indonesia	KY230305		
Lichmera squamata	Toepad	AMNH 694265	Larat Island, Tanimbar Islands, Indonesia	KY230306		
Lichmera deningeri	Tissue	ZMUC 147353	Buru, Indonesia	KY230307	KY230219	KY230246
Lichmera monticola	Tissue	ZMUC 148333	Seram, Indonesia	KY230308	KY230220	KY230247
Lichmera flavicans	Toepad	AMNH 346312	Mt. Ramelan, Timor, Indonesia	KY230309		
Lichmera notabilis	Toepad	AMNH 694338	Wetar, Indonesia	KY230310		
Xanthotis polygramma	Tissue	ZMUC 145303	Memeku, Bismarck Range, Papua New Guinea			KY230248
Melitograis gilolensis	Toepad	RMNH 84782	Bacan, Indonesia		KY230221	
Melilestes megarhynchus	Tissue	ZMUC 145212	Kausi, Bismarck Range, Papua New Guinea			KY230249
Melipotes gymnops	Toepad	NRM 572027	Bivak October, Vogelkop, West Papua, Indonesia	KY230311		
Melipotes fumigatus	Tissue	ZMUC 145252	Bruno Sawmill, Bismarck Range, Papua New Guinea			KY230250
Melipotes ater	Toepad	ANWC B25649	Mindik Area, Huon Peninsula, Papua New Guinea	KY230312		
Timeliopsis fulvigula	Tissue	ZMUC 145263	Denge Numbu, Bismarck Range, Papua New Guinea			KY230251
Conopophila whitei	Toepad	ANWC B19637	Wiluna, Western Australia	KY230313	KY230222	
Caligavis subfrenata	Tissue	ZMUC 145215	Lake Piunde, Mt. Wilhelm, Papua New Guinea	KY230314	KY230223	KY230252
Manorina melanotis	Toepad	AMNH 694536	Lingerandye, Victoria	KY230315		
Meliarchus sclateri	Tissue	ZMUC 139470	Makira, Solomon Islands	KY230316	KY230224	KY230253
Melidectes fuscus	Tissue	ZMUC 145209	Lake Piunde, Mt. Wilhelm, Papua New Guinea	KY230317	KY230225	KY230254
Melidectes nouhuysi	Toepad	AMNH 342684	Lake Habbema, West Papua, Indonesia	KY230318		
Melidectes princeps	Tissue	ZMUC 145211	Kombuno Mambuno, Mt. Wilhelm, Papua New Guinea	KY230319	KY230226	KY230255
Melidectes leucostephes	Toepad	NRM 572028	Tombrok, Vogelkop, West Papua, Indonesia	KY230320		
Melidectes rufocrissalis	Tissue	ZMUC 145259	Denge Numbu, Bismarck Range, Papua New Guinea	KY230321	KY230227	KY230256
Melidectes foersteri	Toepad	AMNH 268048	Sevia, Huon Peninsula, Papua New Guinea	KY230322		
Melidectes belfordi	Tissue	ZMUC 145214	Lake Piunde, Mt. Wilhelm, Papua New Guinea			KY230257
Meliphaga montana	Tissue	ZMUC 145300	Memeku, Bismarck Range, Papua New Guinea			KY230258
Meliphaga vicina	Toepad	AMNH 695929	Tagula, Papua New Guinea	KY230323		
Meliphaga aruensis	Tissue	ZMUC 145301	Kausi, Bismarck Range, Papua New Guinea			KY230259
Oreornis chrysogenys	Toepad	AMNH 342814	Mt. Wilhelmina, West Papua, Indonesia	KY230324		
Oreornis chrysogenys	Toepad	AMNH 342813	Mt. Wilhelmina, West Papua, Indonesia		KY230228	
Gymnomyza aubryana	Toepad	ZMUC 145119	Mt. Paompai, New Caledonia	KY230325	KY230229	
Dasyornis brachypterus	Tissue	ANWC B34386	Hymes Beach, Shoalhaven, New South Wales	KY230326	KY230230	KY230260
Dasyornis longirostris	Toepad	RMNH 34837	Lake Gardines, Two Peoples Bay, WA, Australia	KY230327		
Dasyornis broadbenti	Tissue	ANWC B40391	Robe, South Australia			KY230261
Pardalotus quadragintus	Toepad	NRM 572031	Tasmania	KY230328		
Pardalotus rubricatus	Tissue	ANWC B33106	Shaw River, Western Australia		KY230231	KY230262
Calamanthus montanellus	Tissue	ANWC B31752	Gnowangerup, Western Australia	KY230329	KY230232	KY230263
Crateroscelis murina	Tissue	ZMUC 145271	Memeku, Bismarck Range, Papua New Guinea	KY230330	KY230233	KY230264

Table 1 (*continued*)

Taxon	Type	Voucher	Location	GenBank accession number		
				ND2	Fib5	GAPDH
Crateroscelis nigrorufa	Tissue	ZMUC 145279	Denge Numbu, Bismarck Range, Papua New Guinea	KY230331	KY230234	KY230265
Crateroscelis robusta	Tissue	ZMUC 145275	Denge Numbu, Bismarck Range, Papua New Guinea	KY230332	KY230235	KY230266
Sericornis spilodera	Tissue	ZMUC 145437	Memeku, Bismarck Range, Papua New Guinea	KY230333	KY230236	KY230267
Sericornis papuensis	Tissue	ZMUC 145281	Bruno Sawmill, Bismarck Range, Papua New Guinea	KY230334	KY230237	KY230268
Sericornis beccarii	Tissue	ANWC B56102	Bensbach Lodge, Papua New Guinea	KY230335	KY230238	KY230269
Sericornis virgatus	Toepad	AMNH 829372	Mt. Menawa, Bewani Mts., Papua New Guinea	KY230336		
Sericornis nouhuysi	Tissue	ZMUC 145297	Bruno Sawmill, Bismarck Range, Papua New Guinea	KY230337	KY230239	KY230270
Sericornis perspicillatus	Tissue	ZMUC 145288	Denge Numbu, Bismarck Range, Papua New Guinea			KY230271
Sericornis rufescens	Toepad	NRM 572033	Bivak October, Vogelkop, West Papua, Indonesia	KY230338		
Sericornis arfakianus	Toepad	NRM 572032	Bivak October, Vogelkop, West Papua, Indonesia	KY230339		
Gerygone insularis	Toepad	AMNH 606805	The Pines, Lord Howe Island	KY230340		
Gerygone albofrontata	Toepad	AMNH 212556	Rangatira Island, Chatham Islands, New Zealand	KY230341		
Gerygone dorsalis	Toepad	AMNH 607066	Larat Island, Tanimbar Islands, Indonesia	KY230342		
Acanthiza murina	Tissue	ZMUC 145299	Lake Piunde, Mt. Wilhelm, Papua New Guinea	KY230343	KY230240	KY230272
Aphelocephala pectoralis	Toepad	AMNH 683496	Watna Pilla Swamp, South Australia	KY230344		

Table 2
Alignment details. Best models of nucleotide substitution were determined using jModelTest2 following the Bayesian Information Criterion and subsequently applied in BEAST.

Locus	Length (n base pairs)	N taxa (ingroup)	Substitution model (BIC)
Mitochrondrial genes			
Cytochrome *b* (*cyt-b*)	1044	110	GTR+I+Γ
12S ribosomal DNA (*12S*)	840	105	GTR+I+Γ
Cytochrome oxidase subunit 1 (*COI*)	1430	75	GTR+I+Γ
NADH dehydrogenase 2 (*ND2*)	1041	282	GTR+I+Γ
NADH dehydrogenase 3 (*ND3*)	351	52	TrN+I+Γ
Nuclear non-coding (introns)			
Beta-fibrinogen intron-5 (*fib5*)	567	196	GTR+Γ
Glyceraldehyde-3-phosphodehydrogenase intron-11 (*GAPDH*)	347	108	TrN+Γ
Nuclear coding (exons)			
Recombination activating protein 1 (*RAG1*)	1389	70	TrN+Γ
Recombination activating protein 2 (*RAG2*)	1012	45	K80+I+Γ
Concatenated	8021	286	

values across runs. Fifty million trees were discarded as burn-in from each run. Log and tree files from the different runs were combined using LogCombiner v1.8.3 (Drummond et al., 2012). Finally, we summarized the resulting posterior distribution as a maximum clade credibility (MCC) tree with mean node heights using TreeAnnotator v1.8.3 (Drummond et al., 2012).

2.3. Biogeographical analyses

To investigate the biogeographical history of the Meliphagides, we applied a model-testing approach using the R package BioGeoBEARS v0.2.1 (Matzke, 2013a, 2013b) based on the MCC tree from the BEAST analyses of the concatenated data matrix. We assigned species to one or more of the following five biogeographical regions according to their current distributions: Australia, New Guinea, New Zealand, the Tropical Pacific and Wallacea. Maximum range size was set to 2 as no extant species occupy more than two regions. Given the uncertainty in area connectivity through time (e.g. Hall et al., 2011), we did not apply any dispersal constraints to the analyses. Using this framework, we compared the following biogeographical inference models of range evolution: a Dispersal-Extinction Cladogenesis model (DEC) (Ree and Smith, 2008); a maximum-likelihood version of the dispersal-vicariance model (DIVALIKE) (Ronquist, 1997) and a Bayesian biogeographical inference model (BAYAREALIKE) (Landis et al., 2013). In addition, we repeated the analyses of the three above models, but included an additional free parameter that allows for founder-effect speciation (+j), which models the process of a daughter lineage dispersing to an area outside the distribution of its parental lineage (Matzke, 2014). Model fit was assessed using the Akaike Information Criterion (AIC) and Akaike weights.

3. Results

3.1. Sequence data

We included both mitochondrial and nuclear loci for a total of 286 meliphagoid taxa representing all currently recognized families and genera (Table 1 and S1). Our initial analyses of individual gene trees revealed some spurious sequences derived from GenBank. Cross-checking of specimen voucher numbers revealed that these sequences derived from misidentified specimens and/or mislabelled samples. Such sequences were excluded from subsequent analyses and we have notified GenBank. We sourced sequences for 222 species from GenBank and generated sequence data for 64 species. Of these 64 species, 60 species had not been previously sequenced. We also sequenced additional genetic markers for 23 species. The final data matrix included a total of 1041 Meliphagides sequences, with 60% missing data and with a mean of 3.6 (SD = 2.12) loci per taxon. This included 419 sequences of nuclear loci, with 64% missing data and a mean of 1.4 (SD = 1.17) loci per taxon, and 622 sequences of mitochondrial loci, with 57% missing data and a mean of 2.2 (SD = 1.24) loci per taxon. The full concatenated data matrix, including GenBank accession numbers for all sequences used in this study, is available in the online appendix (Table S1). Sequences generated for this study have GenBank accession numbers KY230211–KY230344.

3.2. Phylogeny and divergence dating

Analyses of the concatenated dataset in BEAST produced a well-resolved dated phylogeny of the Meliphagides, with most nodes and most major clades having high posterior probabilities (Figs. 1–4). However, although the independent BEAST chains all achieved sufficient effective sample sizes for the vast majority of parameters (ESS values > 1000), the likelihoods for the ND2, ND3, fib5 and RAG1 partitions did not for some chains. Increases in likelihood values for one partition were often associated with a decrease in the other and vice versa. Similarly, although independent chains achieved large effective sample sizes for parameters the mean likelihood estimates often differed between chains. These were visible

as multimodal posterior densities for some of the partition likelihoods. This behaviour in the analysis may stem from discordance between gene trees. For instance, the fib5 intron has been shown to sometimes produce a strong phylogenetic signal that is in conflict with a large number of other loci among the Meliphagides (Andersen et al., 2014) and among birds as a whole (Hackett et al., 2008; Kimball et al., 2013). However, although removing fib5 from the dataset resulted in better convergence it did not result in strongly supported alternative tree topologies.

RAxML analyses of the concatenated data recovered a tree that was largely concordant with the BEAST tree (Fig. S1). The individual gene trees varied in their extent of resolution, with some conflicts among trees but primarily for poorly supported nodes (Fig. S2–S10). In the analyses of the concatenated data, the Maluridae was found to be the sister lineage to the remainder of the radiation, with strong support (PP = 1.00, 100% bootstrap). In the BEAST analysis Dasyornithidae was strongly supported as the sister group to Acanthizidae + Pardalotidae + Meliphagidae (PP = 1.00). This contrasts with the RAxML analysis which found Dasyornithidae to be the sister group to Pardalotidae + Acanthizidae, although this relationship was poorly supported (31% bootstrap). Meliphagidae was recovered as the sister lineage to Acanthizidae + Pardalotidae with high support in the RAxML analysis (99% bootstrap), but with only moderate support in the BEAST analysis (PP = 0.83), which may stem from the conflicting placement of Dasyornithidae in the two analyses. The phylogenetic placements and interrelationships of several lineages (e.g. *Gymnomyza aubryana, Conopophila whitei*) were difficult to resolve. A significant number of genera were found to be para- and polyphyletic, particularly within the Meliphagidae, suggesting the need for extensive taxonomic revision. Divergence date estimates suggested an origin of the Meliphagides in the early Oligocene (31.3 Mya, 95% HPD 25.2–38.2 Mya), which is only slightly older than the time of origin found in the analyses of Joseph et al. (2014, Fig. S1), but significantly younger than the date estimated by Ericson et al. (2014) (mean = 42.88, 95% HPD 31.75–53.98 Mya).

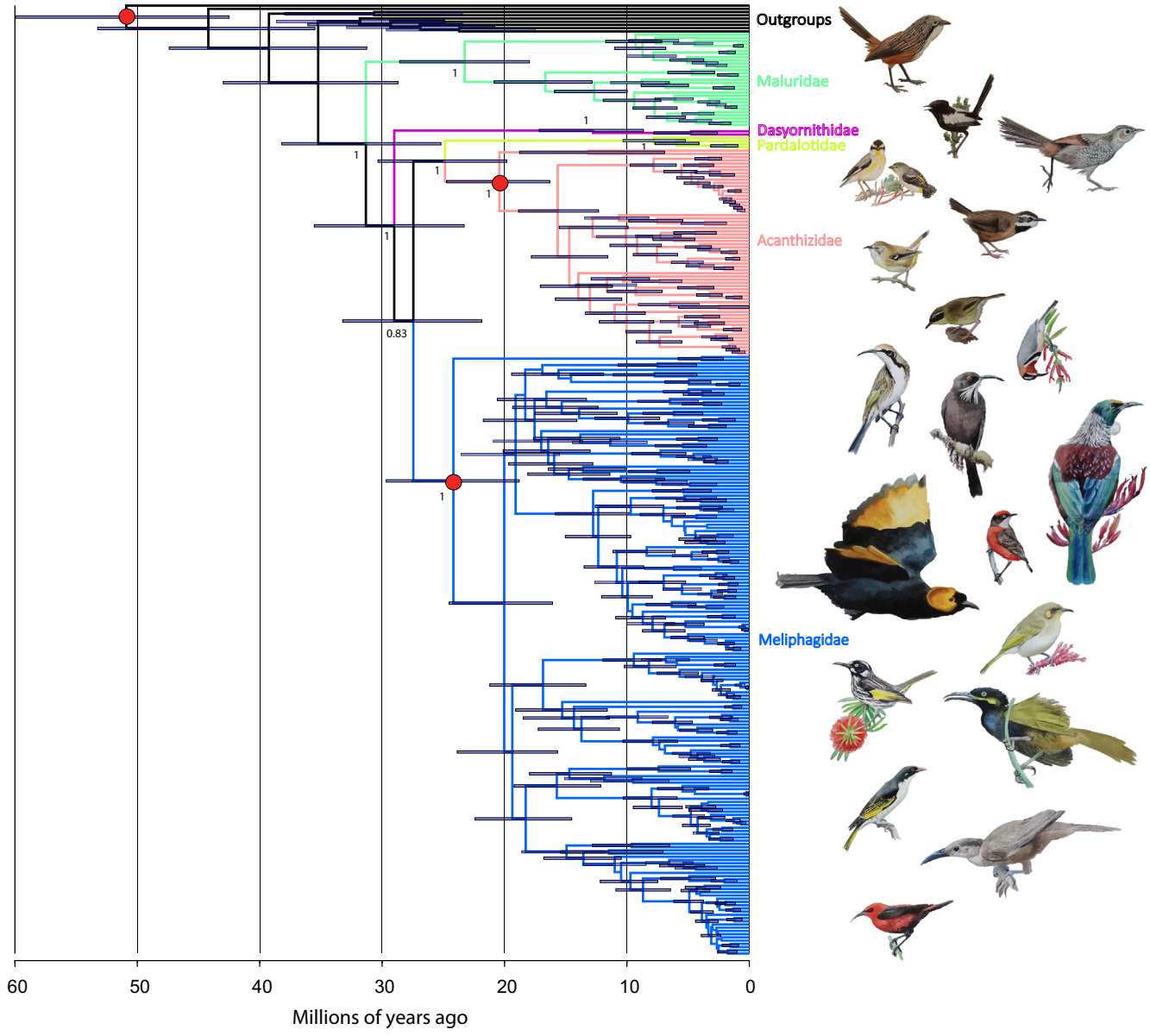

Fig. 1. The time-calibrated maximum clade credibility tree of the Meliphagides derived from the divergence estimation of the concatenated alignment of all nine loci in BEAST. Clades are colored according to currently recognized families. Posterior probabilities are given at major nodes. Horizontal bars represent 95% Highest Posterior Density (HPD) intervals. Red dots indicate the three calibration points used for this study. Inserted watercolor paintings by Jon Fjeldså.

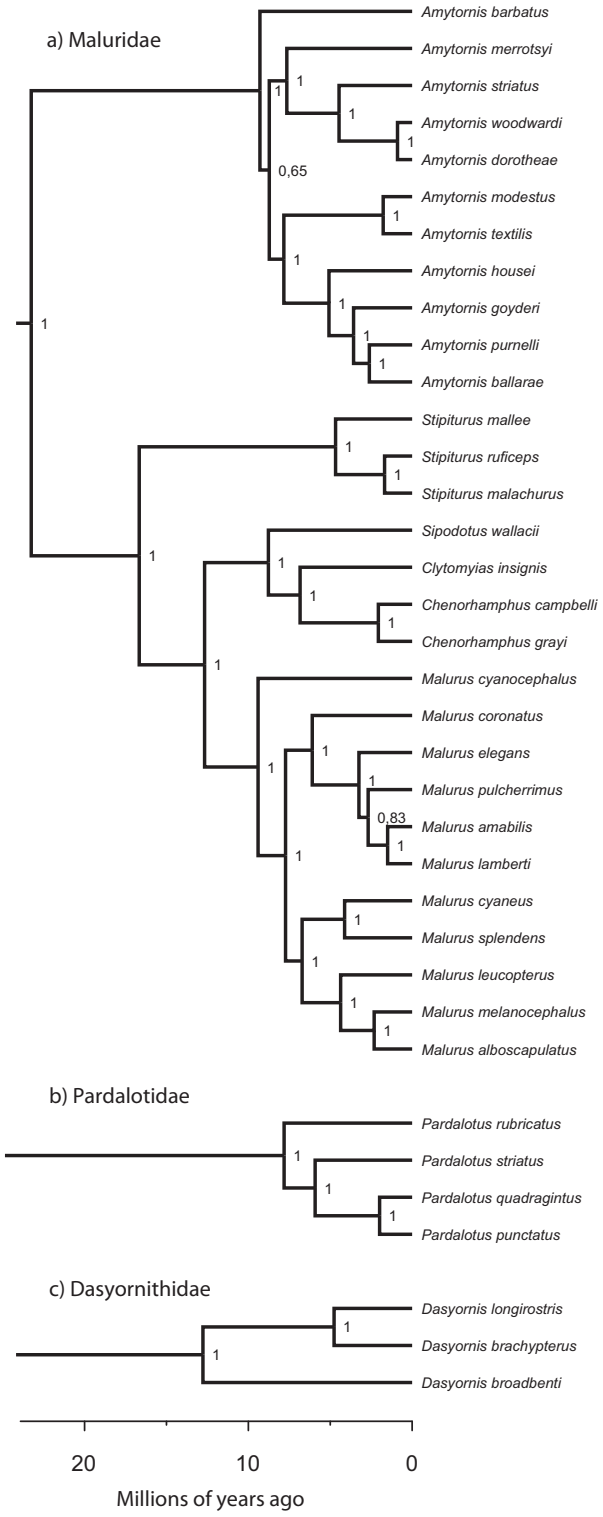

Fig. 2. Results of the BEAST analyses of the concatenated dataset of nine genes for the following families: (a) Maluridae, (b) Pardalotidae, (c) Dasyornithidae. Topology and divergence dates are derived from the maximum clade credibility tree presented in Fig. 1. Posterior probabilities are indicated at each node.

3.3. Biogeography

Our biogeographical analyses found that the best model of geographical range evolution in the Meliphagides was a dispersal-extinction cladogenesis model that also includes founder-event speciation (DEC+j, AIC weight = 0.995, Table 3). In general, the inclusion of founder-event speciation (+j) improved model fit for all models that were compared. The DEC+j model identified Australia as the most likely center of origin for the group (Fig. 5), a finding that was consistent across all of the models compared. In addition, we found that the origin of all five families appears to have been in Australia. There have been multiple independent colonizations of other regions, particularly New Guinea. With the exception of a single dispersal event to Sulawesi in the late Oligocene (*Myza*), the majority of these events appear to have taken place more recently (<15 Mya). New Guinea in particular, but also Wallacea, have subsequently been the source of numerous independent back-colonizations to Australia. *Myzomela, Philemon* and *Lichmera* stand out as genera that have very wide distributions, with numerous island species in Wallacea and the Pacific.

4. Discussion

In this study, we present a supermatrix phylogenetic hypothesis of the infraorder Meliphagides that combines data from five mitochondrial and four nuclear markers. The phylogeny samples 99% of species, and thus represents one of the most complete avian phylogenies at the infraorder level to date. Our findings provide support for many previously suggested relationships but also reveal surprising placements of newly sequenced species. Our biogeographic analysis suggests that Australia was the area of origin but that independent colonization of other regions, notably New Guinea, has been frequent throughout the history of the radiation. This is particularly evident among the Meliphagidae, whose biogeographic history is likely to have been highly dynamic and complex. Below, we discuss our findings in more detail, including the implications for our understanding of meliphagoid relationships, biogeography and diversification.

4.1. Phylogenetic findings

Higher-level relationships among the Meliphagides have been studied and reviewed by others (e.g. Gardner et al., 2010; Joseph et al., 2014) and, given that most of our results are in agreement with these, we focus our discussion on the placement of newly sequenced taxa. Although the Bayesian analysis of the concatenated dataset recovered a strongly supported topology, the high level of discordance between gene trees with respect to interfamiliar relationships (e.g. placement of Dasyornithidae) warrants further study. We recovered a number of strongly supported clades within the Meliphagidae, however their interrelationships remain largely unsolved. These relationships are characterized by short internodes which is suggestive of rapid early rates of cladogenesis in the Meliphagidae. Missing data in our matrix may have contributed to this lack of resolution, although previous simulation studies have shown that the benefit of including genes with missing data greatly outweigh potential negative consequences and should indeed improve resolution power (e.g. Wiens and Moen, 2008; Jiang et al., 2014). Hence, resolving the Meliphagides tree, particularly the relationships among the honeyeaters, will most likely require genomic-scale data (Jarvis, 2016). Finally, as has been noted for other major passerine radiations, including the Corvides (Jønsson et al., 2015) and Thraupidae (Burns et al., 2014), we find that the delimitation of genera appears to be inconsistent with respect to phylogeny and time. This suggests that a thorough revision of generic limits within the Meliphagides may be required in addition to what has already been suggested in other molecular studies. However, such a revision was beyond the scope of this study and will be dealt with elsewhere.

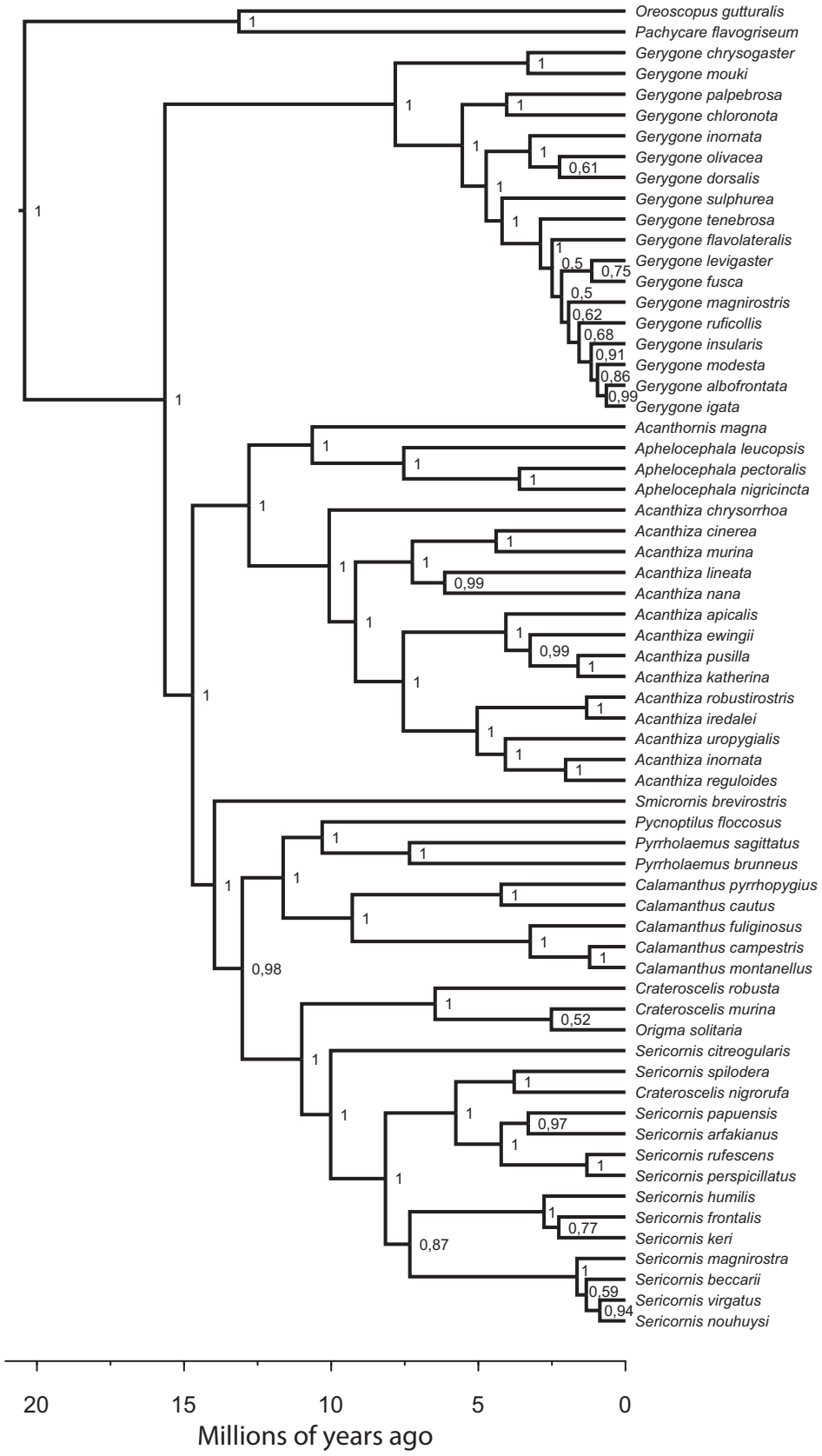

Fig. 3. Results of the BEAST analyses of the concatenated dataset of nine genes for the family Acanthizidae. Topology and divergence dates are derived from the maximum clade credibility tree presented in Fig. 1. Posterior probabilities are indicated at each node.

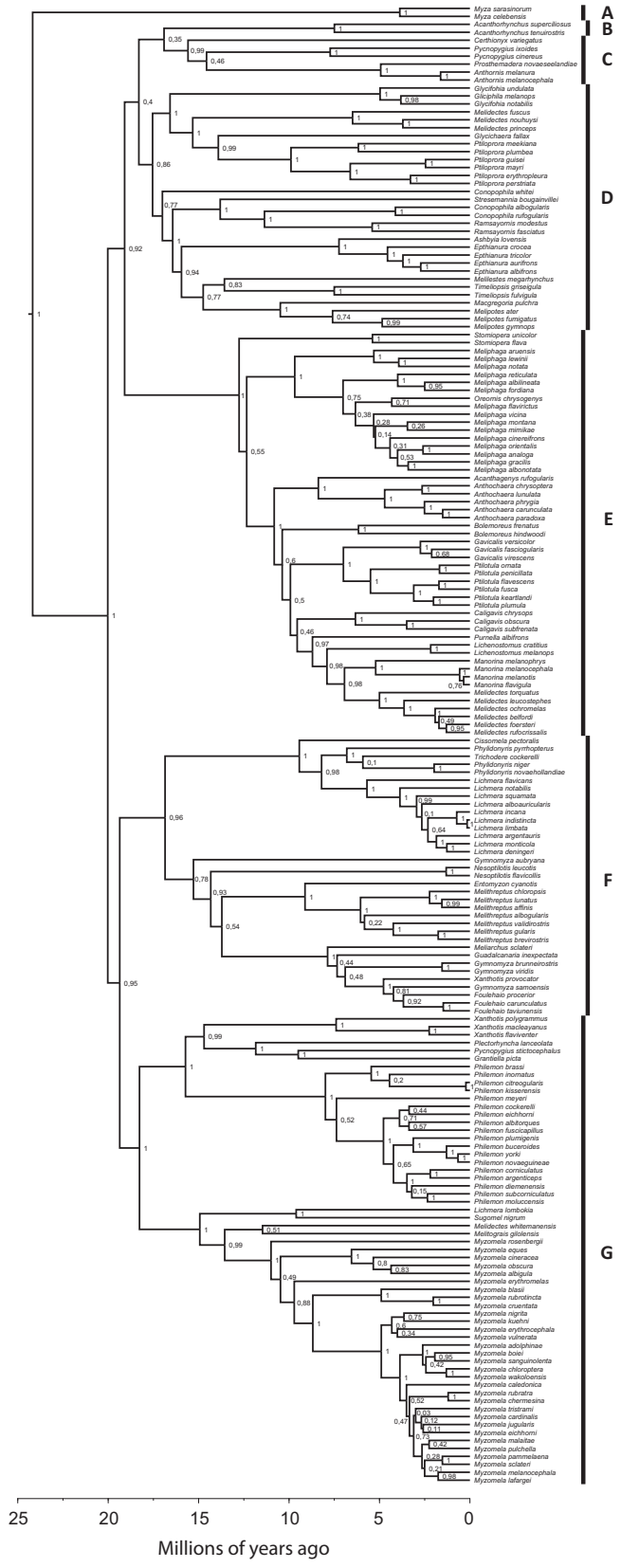

Fig. 4. Results of the BEAST analyses of the concatenated dataset of nine genes for the family Meliphagidae. Clade lettering refers to seven strongly supported clades as discussed in the text. Topology and divergence dates are derived from the maximum clade credibility tree presented in Fig. 1. Posterior probabilities are indicated at each node.

4.1.1. Maluridae, Dasyornithidae, and Pardalotidae

Our findings regarding relationships within the Maluridae show that the family comprises two well-supported major clades: the grasswrens (Amytornithinae) and the fairywrens and emu-wrens (Malurinae) (Fig. 2a) (PP = 1.00, 100% bootstrap), which is consistent with previous studies (Christidis and Schodde, 1997; Gardner et al., 2010; Driskell et al., 2011; Lee et al., 2012). The divergence time between Amytornithinae and Malurinae is estimated to be in the late Oligocene/early Miocene (23.4 Mya, 95% HPD 18.3–29.2 Mya). Although our taxon-sampling for this family does not extend that of previous studies, our analyses do offer some additional insights. For example, our concatenated analyses strongly support a sister relationship between *Malurus coronatus* and a clade consisting of *M. pulcherrimus*, *M. elegans*, *M. amabilis*, and *M. lamberti* (PP = 1.00, 99% bootstrap). Thus, our results regarding the relationships of *M. coronatus* agree with those of Driskell et al. (2011), but contrasts with those of Lee et al. (2012) and Gardner et al. (2010), which suggest two alternative placements of *M. coronatus* as sister to all other *Malurus* (excluding *M. cyanocephalus*) or to *M. splendens* and *M. cyaneus*, respectively. *Malurus coronatus* is notable for having very low rates of extra-pair paternity compared to other species in the genus (Kingma et al., 2009; Rowe and Pruett-Jones, 2013). Thus, in order to increase the understanding of the evolution of such life-history strategies, resolving the placement of this species is of great interest. Lee et al. (2012) strongly supported *Stipiturus malachurus* as sister to *S. mallee* and *S. ruficeps*, whereas our results were more ambiguous. Our Cyt-b results were congruent with those by Lee et al. (2012), however our analysis of ND2 as well as that of the concatenated dataset strongly supported an alternative topology, in which *S. mallee* is sister to the two remaining species.

The BEAST analyses of the concatenated dataset support the sister relationship of the bristlebirds (Dasyornithidae) and the non-malurid Meliphagides (Meliphagidae + Pardalotidae + Acanthizidae) (PP = 1.00), a result which was also strongly supported in the analyses of Gardner et al. (2010). However, our ML analyses did not confidently resolve the position of the Dasyornithidae. Our study is the first to sample and sequence molecular data for *Dasyornis longirostris* and thus analyse all three species of bristlebirds. Consistent with external morphological aspects, we find strong support for *D. broadbenti* as the sister lineage to *D. brachypterus* + *D. longirostris* (Fig. 2c) (PP = 1.00, 100% bootstrap). Our divergence date estimates suggest that *D. broadbenti* diverged from its relatives in the mid-Miocene ca. 13 Mya (95% HPD 8.7–17.2 Mya), and that *D. brachypterus* and *D. longirostris* diverged in the early Pliocene, ca. 5 Mya (95% HPD 2.6–7.8 Mya). This suggests that genetic divergences in this family may be much greater than morphology alone would suggest. Given the highly threatened status of several populations of bristlebirds (Gregory, 2007a), we urge that denser sampling at the population level be undertaken for this group to evaluate the possibilities of overlooked cryptic species.

Our analysis of the Pardalotidae suggests that the Tasmanian endemic and newly sequenced *Pardalotus quadragintus* is the sister species to *P. punctatus* (Fig. 2b) (PP = 1.00, 99% bootstrap). This is consistent with previous suggestions based on the resemblance of the former species to immature plumages of the latter (Higgins and Peter, 2002; Christidis et al., 2011). Finally, we recover a novel sister relationship between *P. rubricatus* and the three remaining species in the genus (PP = 1.00, 100% bootstrap).

4.1.2. Acanthizidae

In general, our results concerning the relationships of this group agree with those of previous studies, particularly that of Gardner et al. (2010), which previously contained the most complete

Table 3
Comparison of model fit and parameters from biogeographical analyses in BioGeoBEARS. The best fitting model is highlighted in bold.

Model	LnL	n parameters	Dispersal	Extinction	Jump dispersal	AICc	AIC weight
DEC	−439.7920	2	0.010	0.002	0.000	883.6	0.000
DEC+J	**−371.8165**	**3**	**0.004**	**0.000**	**0.031**	**749.6**	**0.995**
DIVALIKE	−436.8974	2	0.012	0.000	0.000	877.8	0.000
DIVALIKE+J	−377.2015	3	0.004	0.000	0.031	760.4	0.004
BAYAREALIKE	−538.7539	2	0.011	0.057	0.000	1082	0.000
BAYAREALIKE+J	−378.8685	3	0.003	0.000	0.036	763.7	0.000

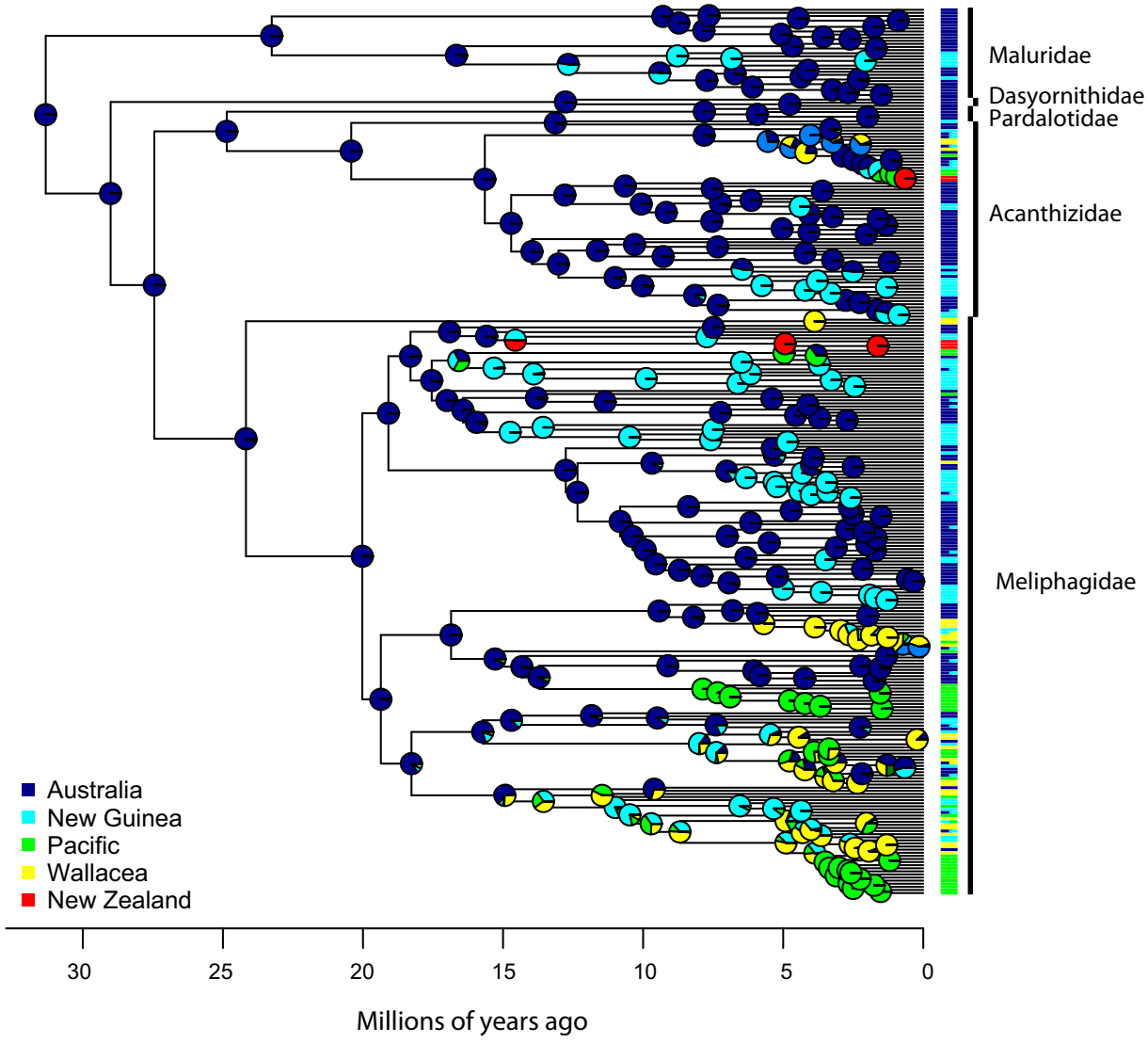

Fig. 5. Biogeographical area estimation of the Meliphagides based on the best-fitting model (DEC+j) inferred using BioGeoBEARS. Pie charts represent the relative probabilities of each region being the ancestral area of the node.

taxon-sampling of this group. However, our extended taxon sampling of the Acanthizidae, including 12 newly sequenced species, revealed several novel relationships (Fig. 3). The scrubwrens (*Sericornis*) are rendered paraphyletic as the newly sequenced *Crateroscelis nigrorufa* and *Sericornis spilodera* are found to be sister taxa with strong support (PP = 1.00, 100% bootstrap). *Crateroscelis nigrorufa* has previously been noted to be more arboreal compared with congeners *C. robusta* and *C. murina* (Gregory, 2007b) and thus more similar to many scrubwrens in this respect. The hypothesis that the narrow elevational range of this species may be due to competitive exclusion by *C. robusta* and *C. murina* inhabiting higher and lower elevations respectively (Diamond, 1972), may thus need re-evaluation. The species *C. robusta* and newly sampled *C. murina* on the other hand, form a strongly supported clade with *Origma solitaria* (PP = 1.00, 94% bootstrap). Although the Bayesian analyses were unable to solve their interrelationships, the ML analyses of the concatenated dataset strongly support a sister relationship between the two former species (96% bootstrap).

Our increased sampling confirms the monophyly of the *Sericornis magnirostra* superspecies complex (*S. beccarii, magnirostra, nouhuysi, virgatus*) (PP = 1.00, 100% bootstrap), although we are unable to resolve the relationships among the four species. Species limits

in this complex are contentious, further complicated by potential widespread introgression among the many populations (Christidis et al., 1988; Gregory, 2007b). However, our lack of taxon sampling at the subspecies level precludes any taxonomic recommendations at this stage.

Our findings pertaining to the gerygones (*Gerygone*) are largely consistent with the comprehensive study of Nyári and Joseph (2012), although some differences are apparent, possibly stemming from their more extensive sampling of nuclear loci. We recovered *G. chloronota* and *G. palpebrosa* as sister species with strong support (PP = 1.00, 97% bootstrap), but this finding was only supported by the Fib5 gene tree and mtDNA (ND2 and ND3) tree of Nyári and Joseph (2012), and not in their combined analyses of 13 loci. Our study is the first to include sequences of three species of *Gerygone* that are restricted to islands in the South Pacific, including *G. modesta* of Norfolk Island, *G. albofrontata* of the Chatham Islands and the recently extinct *G. insularis* of Lord Howe Island. These three species are suggested to represent a monophyletic group together with *G. igata* of New Zealand, although support is low (PP = 0.91, 69% bootstrap). Furthermore, our sequencing of additional loci for *Acanthiza murina* strongly supports its sister relationship to the only other New Guinean species in the genus, *A. cinerea* (PP = 1.00, 99% bootstrap). Although both species have been included in previous studies (e.g. Nicholls et al., 2000; Gardner et al., 2010; Nyári and Joseph, 2012), none have included both species in a single framework as different loci had been sequenced for each of them. Finally, we find that the range-restricted *Aphelocephala pectoralis* is most closely related to *A. nigricincta* (PP = 1.00, 100% bootstrap), and that *Aphelocephala* is sister to *Acanthornis* (PP = 1.00, 96% bootstrap), an unexpected relationship first noted by Gardner et al. (2010).

4.1.3. Meliphagidae

The major clades that we recover in this family are consistent, in general, with those identified in previous studies, particularly those of Gardner et al. (2010) and Joseph et al. (2014), although there are some conflicts with regard to their inter-relationships. However, given the large number of new sequences included in the present study, with 46 Meliphagidae species sequenced for the first time, several novel relationships emerge (Fig. 4). For ease of presentation, we discuss the relationships within seven major honeyeater clades (Fig. 4) that received moderate to strong support in the Bayesian analyses (PP > 0.85, Fig. 1).

Clade A is represented by two species in the genus *Myza*, a deeply divergent lineage confined to Sulawesi that forms the sister group to all other honeyeaters (Joseph et al., 2014). Our date estimates suggest that this clade diverged from the remaining honeyeaters in the late Oligocene (ca. 24 Mya). Although species of *Myza* appear similar to other honeyeaters in overall appearance and ecology, such a long history of independent evolution suggests that their recognition as a distinct subfamily or family may be warranted.

Clade B is represented by the two Australian species in the genus *Acanthorhynchus*. Driskell and Christidis (2004) and Gardner et al. (2010) proposed that this clade was sister group to all remaining honeyeaters, whereas Joseph et al. (2014) suggested a sister relationship between *Acanthorhynchus* and a clade comprising *Certhionyx variegatus*, *Prosthemadera*, *Anthornis* and *Pycnopygius*. We recovered the same result as Joseph et al. (2014) in both our Bayesian and ML results but without support (PP = 0.35, 21% bootstrap).

Clade C is comprised of six species in four genera. First identified as a monophyletic assemblage by Driskell and Christidis (2004), this clade is notable for the high level of morphological and distributional disparity. Within this group, the New Guinean genus *Pycnopygius* is found to be polyphyletic. Our analyses identified *P. cinereus* and the newly sequenced *P. ixoides* as sister taxa, but the Streak-headed Honeyeater *P. stictocephalus* as a member of a distantly related clade (Clade G). The recently extinct *Anthornis melanocephala* of the Chatham Islands, also newly sampled, is recovered as sister taxon to *A. melanura* of mainland New Zealand.

Clade D consists of 31 species in 14 genera primarily distributed in the arid-zone of Australia and the montane regions of New Guinea. However, this clade was only moderately supported in the Bayesian analyses (PP = 0.86) and only received low support in the ML analyses (39% bootstrap). In this group, the Australian arid-zone endemic *Conopophila whitei* is suggested to represent a deep lineage, although this placement is unsupported. *Ptiloprora* is found to be monophyletic with strong support (PP = 1.00, 99% bootstrap), where the smaller *P. plumbea* and *P. meekiana* form the sister group to a clade comprising the remaining, larger species. Among these, *P. guisei* and *P. perstriata* are found to be sister species of *P. mayri* and *P. erythropleura,* respectively. The two former species were previously hypothesized to be closely related, representing an example of altitudinal segregation by competitive exclusion (Diamond, 1972, 1973), although recent field observations suggest that they co-occur at some sites (Sam and Koane, 2014; Marki et al., 2016). Three New Guinean high montane species of the genus *Melidectes* (*fuscus, nouhuysi* and *princeps*) form a subclade which is sister group to *Ptiloprora* + *Glycichaera* (PP = 1.00, 92% bootstrap), to the exclusion of other species of *Melidectes*.

Clade E includes 51 species in 13 genera. Our estimates of the relationships within this group are largely consistent with those of previous studies. However, some novel relationships emerge. For example, our study is the first to include genetic data for the monotypic genus *Oreornis* of highland New Guinea. Notably, we find that *O. chrysogenys* is nested within *Meliphaga*, with the ND2 and the concatenated BEAST trees suggesting a sister relationship with *M. flavirictus* (Fig. S5, 77% bootstrap and PP 0.71 respectively). We were unable to resolve the position of *M. vicina*. The remaining species of *Melidectes* (except for *fuscus, princeps, nouhuysi and whitemanensis*) form a group within Clade E. In this group, *M. torquatus* represents the most basal branching species followed by *M. leucostephes*. Relationships among the four remaining species of *Melidectes* (*belfordi, ochromelas, foersteri* and *rufocrissalis*) are unresolved, which may reflect a long history of interspecific hybridization in this complex (Mayr and Gilliard, 1952). Finally, we find that the endangered *Manorina melanotis* forms a young and strongly supported clade with *M. melanocephala* and *M. flavigula* (PP = 1.00, 100% bootstrap), but relationships among these three species are unresolved.

Clade F is comprised of 35 species in 12 genera. Although most species are confined to Australia, this clade is notable for the large number of species in the Pacific. In agreement with Andersen et al.'s (2014) study of Pacific honeyeaters, we find that *Gymnomyza* is polyphyletic, with *G. samoensis* embedded in a clade that includes *Foulehaio* and *Xanthotis provocator* (PP = 1.00, 99% bootstrap). *Gymnomyza viridis* + *G. brunneirostris* are found to be sister species (PP = 1.00, 100% bootstrap) but their placement is unresolved. Furthermore, our data suggest that the critically endangered *G. aubryana* of New Caledonia represents a separate and ancient lineage, although we were unable to resolve its exact position. Clearly, extensive taxonomic revision of Pacific honeyeaters is needed. Other novel findings include the polyphyly of the genus *Lichmera*, as *L. lombokia* is found to be the sister species to *Sugomel nigrum* of clade G. However, the remaining *Lichmera* species are found to be monophyletic, with strong support (PP = 1.00, 98% bootstrap). Interestingly, the deepest lineages within this genus are presently confined to small Wallacean islands (e.g. *L. flavicans*, *notabilis* and *squamata*).

Clade G is the final and most speciose clade, comprising 60 species in 10 genera. Overall, our estimates of the relationships within this group are largely concordant with those of previous studies, but with some exceptions. For example, the present study is the first to include genetic data for *Pycnopygius stictocephalus,* as previously available sequences generated by Driskell and Christidis (2004) were found to represent mislabelled samples from *P. cinereus*. Our results indicate that *P. stictocephalus,* which is restricted to the lowland rainforest of New Guinea, is the sister species of *Grantiella picta*, a nomadic mistletoe-specialist restricted to eastern Australia (PP = 1.00, 81% bootstrap). This is another highly surprising and novel result. Together with *Plectorhyncha lanceolata*, these species represent an old and remarkably heterogenous assemblage, both in terms of geographical distributions, ecologies and external morphologies.

Our study is also the first to include a broad sampling of the genus *Myzomela,* the most speciose genus in the family. Consistent with previous studies we corroborate the monophyly of *Myzomela*, but the relationships within the genus are complex and many are unsupported. Whereas *M. rosenbergii* and *M. erythromelas* are suggested to represent old lineages with unresolved placements, the remaining species form two strongly supported clades. One clade comprises the sexually monomorphic and large-sized *M. cineracea*, *M. obscura, M. albigula* and *M. eques,* whereas the second clade comprises the remaining species of this genus, the majority of which are comparatively small and predominantly sexually dimorphic. Furthermore, we find that *M. obscura* as currently construed is not monophyletic because *M. o. rubrotincta* is found to be more closely related to *M. cruentata* (PP = 1.00, 97% bootstrap). Finally, as suggested by Diamond (1976), the all-black taxa *M. nigrita*, *M. tristrami* and *M. pammelaena* are not closely related to each other despite their superficial resemblance and previous taxonomic treatments (e.g. Koopman, 1957). The rapid and repeated evolution of melanistic plumages has been previously demonstrated in a wide range of passerine birds (e.g. Theron et al., 2001; Uy et al., 2009; Driskell et al., 2010; Fabre et al., 2012; Uy and Vargas-Castro, 2015). The remaining species of *Myzomela* do not appear to form monophyletic assemblages with regards to their regional distributions, but the poor resolution of this group hinders a robust assessment of their phylogenetic relationships and biogeographic history.

A recent study by Jønsson et al. (2016) showed that *Melitograis gilolensis* is not closely related to other friarbirds (*Philemon*), but the lack of dense sampling of other meliphagid taxa precluded a robust assessment of its relationships. Our Bayesian analysis of the concatenated dataset show weak support for a sister relationship between *M. gilolensis* and *Melidectes whitemanensis,* but this relationship was not supported in any of the ML analyses. Together with *Myzomela*, these two species, nonetheless, form a strongly supported clade together with *Sugomel nigrum* and *Lichmera lombokia* (PP = 1.00, 97% bootstrap). The latter two species are found to be sister species with strong support (PP = 1.00, 97% bootstrap), another novel finding.

4.2. Biogeography

Our analyses of the biogeographical history among the Meliphagides suggests that Australia was the area of origin for the entire group and for each of the five constituent families (Fig. 5), which is consistent with previous suggestions (Jønsson et al., 2011). This finding is unsurprising given the overall high diversity of meliphagoid taxa and near endemicity of other basal oscine lineages (e.g. Menuridae, Atrichornithidae, Ptilonorhynchidae, Climacteridae) on the continent (Ericson et al., 2002; Barker et al., 2004; Claramunt and Cracraft, 2015). There have also been several independent colonizations of other regions, particularly to New Guinea. Interestingly, the majority of New Guinean lineages appear to be comparatively young given the overall age of the group, which is in stark contrast to the Corvides radiation (Jønsson et al., 2011, 2015). Whereas the Corvides is suggested to have originated in the proto-Papuan archipelago in the late Eocene/early Oligocene, the oldest New Guinean meliphagid clades, such as those represented by *Ptiloprora + Glycichaera + Melidectes* (*fuscus, nouhuysi* and *princeps*) and *Melipotes + Macgregoria + Melilestes + Timeliopsis,* appear to have crown ages of around 15 My (95% HPD 12.4–19.3 Mya and 11.4–18.1 Mya respectively). This is suggestive of rapid colonization following the estimated first emergence (14–16 Mya) of what is today the Central Range of the island (van Ufford and Cloos, 2005). Although many of these taxa are currently restricted to nutrient-poor montane forest and alpine moorland, they may have evolved from ancestral lowland forms in parallel with the rapid uplift of the island, as has been suggested for other New Guinean highland lineages (Toussaint et al., 2014; Schweizer et al., 2015). It is unclear why the Meliphagides have such a comparatively short history in the New Guinea region, compared to the Corvides radiation. Such questions may prove hard to resolve, but will likely require significant advances in our understanding of geological and extinction dynamics and history of the region.

Given the relatively young age of New Guinea in its present form, it is notable that several of the most ancient non-Australian meliphagoid lineages are found on other islands that are estimated to be considerably older. Sulawesi, Halmahera, New Britain, Bougainville and New Caledonia are examples of old islands that all harbour ancient honeyeater lineages, having diverged more than 10 Mya from their continental relatives. Most notably among these is *Myza*, which is estimated to have colonized Sulawesi in the late Oligocene. Many of these isolated and mountainous islands surrounding the Australian continent may have allowed the persistence of ancient linages, thereby acting as museums of honeyeater diversity (Gaston and Blackburn, 1996). Such patterns are also consistent with the idea of taxon cycles (Wilson, 1959, 1961), whereby old relictual lineages that represent the later stages of formerly more diverse radiations are currently confined to the largest and most mountainous islands (Ricklefs and Cox, 1972, 1978).

Our results suggest that models that specifically incorporate founder-event speciation consistently perform better than those that do not (Table 3). This finding was also reported for another Indo-Pacific bird radiation, the lories and lorikeets (Schweizer et al., 2015). Thus, our study further corroborates the importance of dispersal for many radiations (Matzke, 2014). Meliphagoid taxa in regions other than Australia are not the result of single independent radiations, but rather a mixture of a large number of independent colonizations, some of which have spurred further radiation. Many of these colonizations have been followed by further dispersal, including apparent back-colonization to Australia. The connection between Australia and New Guinea appears to have been particularly strong and complex. Exchanges between these two regions have been frequent and multi-directional, many of which undoubtedly have been aided by the frequent formation of land-bridges during glacial maxima. Our findings thus corroborate those reported previously for other vertebrate groups, such as mammals (Aplin et al., 1993; Malekian et al., 2010), snakes (Wüster et al., 2005), and turtles (Le et al., 2013; Todd et al., 2014). Although founder-event speciation is likely to have been important in meliphagoid diversification, vicariance, for example within and between Australia and New Guinea, has undoubtedly also played a significant role, particularly among lineages with poor dispersal abilities. For instance, there are a number of species occurring in both New Guinea and Australia that appear incapable of long-distance overwater dispersal (e.g. *Sericornis*, *Malurus*). The importance of barrier formation is especially likely to apply to taxa with

poor dispersal abilities, which is particularly prominent among many non-meliphagid taxa. For example, well-known barriers such as the Carpentarian Barrier and the Nullarbor Plain and its fringing arid habitats have been important for the generation of species diversity in several meliphagoid taxa, including fairywrens (Lee and Edwards, 2008; Kearns et al., 2009; Dolman and Joseph, 2012), grasswrens (Austin et al., 2013) and honeyeaters (Toon et al., 2010; Dolman and Joseph, 2012). Notably, many of these taxa are characterized by high levels of sociality and/or cooperative breeding, a trait that has been suggested to inhibit long-distance dispersal and thus reduce opportunities for allopatric speciation (Cockburn, 2003; Marki et al., 2015). Differences in social organization and/or general dispersal ability may thus have influenced the extent of species range fragmentation following the gradual aridification of the Australian continent that commenced in the mid-Miocene (Byrne et al., 2008), and may also explain differences in species richness among meliphagoid clades. Overall, our results are consistent with theoretical predictions of the relative importance of vicariance and dispersal in speciation of lineages with different dispersal abilities (e.g. Diamond et al., 1976; Mayr and Diamond, 2001; Claramunt et al., 2012; Smith et al., 2014).

5. Conclusions

In this paper we present a near-complete species-level phylogenetic hypothesis of the Meliphagides. The major relationships within the Meliphagides are largely consistent with previous studies, but our significantly expanded taxon sampling provides greater insight into meliphagoid relationships and biogeography, including some novel findings. Although the supermatrix approach provides valuable data for macroevolutionary and macroecological studies, genomic-scale data will most likely be required in future studies to resolve a number of short internodes and to confidently resolve relationships of certain lineages (e.g. *Gymnomyza aubryana*, *Conopophila whitei*), particularly among the honeyeaters. However, the supermatrix approach will, when combined with data on morphology, ecology, life-history traits and distributions, continue to offer great potential for exploring patterns and processes underlying the diversification of large radiations.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.12.021.

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