Zoologica Scripta

A new synthesis of the molecular systematics and biogeography of honeyeaters (Passeriformes: Meliphagidae) highlights biogeographical and ecological complexity of a spectacular avian radiation

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Submitted: 31 October 2013
Accepted: 23 January 2014
doi:10.1111/zsc.12049

Joseph, L., Toon, A., Nyári, Á.S., Longmore, N.W., Rowe, K.M.C., Haryoko, T., Trueman, J., Gardner, J.L. (2014). A new synthesis of the molecular systematics and biogeography of honeyeaters (Passeriformes: Meliphagidae) highlights biogeographical and ecological complexity of a spectacular avian radiation. — *Zoologica Scripta*, *00*, 000–000.

The passerine family Meliphagidae (the honeyeaters) comprises 175–180 species in 40–50 genera. It is an iconic element of the Australo-Papuan avifauna and also occurs in Indonesia and on remote Pacific Ocean islands. Building on previous molecular studies that have pioneered a renewed understanding of the family's circumscription and systematics, we present an updated phylogenetic and systematics synthesis of honeyeaters derived from 112 mostly Australian, New Guinean and Wallacean species- and subspecies-rank taxa aligned across 9246 positions spanning four mitochondrial and four nuclear genes. We affirm many of the recent changes advocated to the group's genus-level systematics and offer some further refinements. The group's radiation appears to coincide broadly with the aridification of Australia in the Miocene, consistent with the time of origin of diversification of extant lineages in several other groups of Australian organisms. Most importantly, the complexity of the biogeography underlying the group's spectacular radiation, especially within Australia, is now apparent. Foremost among such examples is the robust evidence indicating that multiple, independent lineages of honeyeaters, including several monotypic genera, are endemic to the Australian arid zone, presumably having diverged and evolved within it. Also apparent and warranting further study are the phenotypic diversity among close relatives and the remarkably disjunct distributions within some clades, perhaps implying extinction of geographically intermediate lineages. Given such complexity, understanding the evolution of this radiation, which has thus far been intractable, relies on integration of molecular data with morphology, ecology and behaviour.

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Introduction

The resurgence of interest in higher-level systematics of birds in the last 20 years has seen a focus on relationships of the largest avian order, the Passeriformes – passerine birds (Barker *et al.* 2002, 2004; Ericson *et al.* 2002; Hackett *et al.* 2008). Among the numerically larger families of passerines is the Meliphagidae (honeyeaters), an iconic and largely Australo-Papuan group comprising some 175–180 species in 40–50 genera (see Salomonsen 1967; Longmore 1991; Higgins *et al.* 2001, 2008). Higgins *et al.* (2008) thoroughly reviewed the ecology of honeyeaters, most notable here being their diverse feeding ecology (nectarivory, insectivory, frugivory; diet specialists and generalists), habitats (montane tropics to extremely arid habitats), movements (sedentary to migratory), morphology (9–50 cm in size, 7–150 g) and social organization (solitary to group living). Many species are aggressive and this has been hypothesized as driving the evolution of plumage mimicry by other passerines and even a meliphagid (Diamond 1982). Honeyeaters increasingly are a model system for addressing a range of ecological and evolutionary questions (Keast 1968; Diamond 1982; McFarland & Ford 1991; Chan 2001; Griffioen & Clarke 2002; Symonds & Johnson 2006; Symonds *et al.* 2006; Toon *et al.* 2010; Matysioková *et al.* 2011; Remeš *et al.* 2012; Andersen *et al.* 2014; Norman & Christidis 2013), which in turn, requires robust phylogenetic hypotheses for adequate interpretation of biological data.

Increasing recognition of the great diversity and ecological significance of honeyeaters and long-standing questions about their relationships have generated recent research on phylogenetic relationships within the family (Driskell & Christidis 2004; Fleischer *et al.* 2008; Nyári & Joseph 2011) and to its closest relatives (Gardner *et al.* 2010). This work has principally focused on Australian and, to a lesser extent, some New Guinean and the few New Zealand taxa (Christidis & Schodde 1993; Christidis *et al.* 1993; Schodde & Mason 1999; Cracraft & Feinstein 2000; Driskell & Christidis 2004; Driskell *et al.* 2007; Norman *et al.* 2007; Gardner *et al.* 2010; Nyári & Joseph 2011). Christidis & Boles (2008) and Schodde & Mason (1999) produced a much-improved understanding of the phylogenetic relationships and systematics within the Meliphagidae. Their syntheses were informed by morphological, allozyme, DNA hybridization and DNA sequence data (see studies cited above), and revealed that the Meliphagidae and two other iconic Australo-Papuan families, the Acanthizidae and Maluridae, dominate the superfamily Meliphagoidea. Furthermore, circumscription of the Meliphagidae itself has become better understood. *Toxoramphus* and *Oedistoma* are now placed in the berrypeckers, Melanocharitidae (Christidis *et al.* 1993). Monotypic *Notiomystis* of New Zealand is now placed in its own family Notiomystidae (Driskell *et al.* 2007), and *Macgregoria pulchra*, formerly thought to be a bird-of-paradise (Paradisaeidae), is recognized as the largest honeyeater species (Cracraft & Feinstein 2000). Also, paraphyletic genera such as *Phylidonyris*, *Certhionyx* and *Lichenostomus* have been dismantled and generic limits clarified (e.g., Driskell & Christidis 2004; Nyári & Joseph 2011).

Four key studies addressing relationships within the Meliphagidae have been based on DNA sequences (Driskell & Christidis 2004; Driskell *et al.* 2007; Norman *et al.* 2007; Nyári & Joseph (2011). Those studies used data matrices of up to 3843 base pairs (bp) comprising sequences from up to three mitochondrial genes (cytochrome *b*, ND 2 and 12S RNA) and one nuclear intron (Fib5), and, at most 116 meliphagid taxa. As those key papers appeared, sequence data have become available from a total of four mitochondrial and four nuclear loci for nearly 100 nominal species of honeyeaters, the majority of which are Australian. Some species have had multiple individuals sampled, but not all species have been sequenced for all eight loci. Given this increased sequence availability and the importance of honeyeaters in ecological studies, the specific aims of this paper are to report phylogenetic analyses of all available DNA sequence data for the well-sampled Australian Meliphagidae, estimate divergence times and re-assess the family's genus-level systematics. Sampling of honeyeater species beyond Australia is still patchy, so our scope here is necessarily cautious. We wish to understand the phylogenetic basis to the radiation of the whole family but especially its Australian species (about half of the species in the family, 73 species in 23 genera, are Australian); here, we include sequences for all but two Australian species, the Grey Honeyeater *Conopophila whitei*, and the Black-eared Miner *Manorina melanotis*. Also, we present an updated synthesis of their relationships and include non-Australian species where possible. We estimate divergence times and suggest fruitful areas for further biogeographical study. We also lay a foundation for subsequent analyses needed when taxa from New Guinea, Indonesia and the Pacific Ocean islands can be comprehensively sampled.

We acknowledge that molecular phylogenetics is in a period of transition from single to multilocus studies (Barker *et al.* 2004; Hackett *et al.* 2008) and from sequence to genomic data (Balakrishnan *et al.* 2010; Suh *et al.* 2011; McCormack *et al.* 2012, 2013). We hope that this study will grow the foundation upon which later work can apply genomic technologies to further study the evolutionary biology of the Meliphagidae.

Materials and methods

Sampling

We harvested from GenBank sequence data from four mtDNA loci (12SRNA, ND2, Cytb and COI) and four

nuclear loci (RAG 1, GAPDH, and introns 5 and 7 of the beta-fibrinogen gene; Table S1). Representative individuals from 25 species were sequenced to increase the sampling of RAG1 (Barker *et al.* 2002; primers: RAG-1-F1b 5′-AAAAACAGCCTCTGATGACAGT-3′ and RAG-1-R2 5′-TCCCACTTCTGTGTTAGTGGA-3′), GADPH (Primmer *et al.* 2002; primers: exon11 ACCTTTCATG CGGGTGCTGGCATTGC and exon 12 5′-CATCAAG TCCACAACACGGTTGCTGTA-3′) and FIB-BI7 (Prychitko & Moore 1997; primers: FIB-BI7U (5′-GGA GAAAACAGGACAATGACAATTCAC-3′ and FIB-BI7L 5′-TCCCCAGTAGTATCTGCCATTAGGGTT-3′) for a total of 40 additional sequences. The Australian species *Xanthotis macleayanus* (not previously sampled) was also sequenced for ND2 (Sorenson *et al.* 1999; primers: L5216 and H6313 5′-ACTCTTRTTTAAGGCTTTGAAGGC-3′), RAG1, GADPH and FIB-BI7, and two Indonesian species *Myza celebensis* and *M. sarasinorum* (not previously sampled) were sequenced for ND2 (Sorenson *et al.* 1999; primers: L5143 5′-GAACCTACACARAAGRGATCAAA AC-3′ and H6313) beta-fibrinogen5 (Marini & Hackett 2002; primers: Fib5 5′-CGCCATACAGAGTATACTG TGACAT-3′ and Fib6 5′-GCCATCCTGGCGATTCT GAA-3′). PCR amplifications were carried out in 12 μl reaction volumes containing, 2 mM MgCl, 0.25 mM each dNTP, 1 × PCR buffer (Astral Scientific, Sydney, New South Wales, Australia), 0.2 μM of each primer and 0.2 U of Taq (Astral Scientific). PCR amplification was performed using a touchdown approach with an initial denaturation at 95°C for 3 min followed by 25 cycles of 95°C for 30 s, touchdown annealing step 60°C −50°C for 30 s, 72°C for 45 s and a final extension step at 72°C for 7 min. The PCR product was cleaned prior to sequencing with exoSAP (ThermoFisher Scientific, Melbourne, Victoria, Australia) following Werle *et al.* (1994). Sequencing reactions were performed in both directions and cleaned with ethanol/EDTA precipitation. Capillary electrophoresis was on a 3130 × l Genetic Analyser at the Griffith University sequencing facility. Raw sequence data were edited in Sequencher 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). Nuclear sequences with indels were phased by visually separating the chromatograms in forward and reverse directions.

Data matrix and phylogenetic analysis

Each dataset was aligned in Mafft v6 (Katoh *et al.* 2002; Katoh & Toh 2008, http://mafft.cbrc.jp/alignment/server/index.html, Accessed 10 February 2014) using the FFT-NS-2 method. A large indel present in some Fib5 *Meliphaga* sequences was excised prior to phylogenetic analysis (see Gardner *et al.* 2010; Nyári & Joseph 2011). Where heterozygous sequences included an indel, we randomly selected one allele to include in the analysis (e.g., *Lichmera indistincta* GADPH).

ModelTest 3.7 (Posada & Crandall 1998) was used to determine the most appropriate model of sequence evolution of each locus via the Akaike Information Criterion (AIC). A maximum likelihood tree was estimated for each gene dataset using GARLI 2.0 (Zwickl 2008) with the appropriate model of sequence evolution. Nodal support was estimated via 200 nonparametric bootstrap replicates. Nodal support was compared among gene trees to identify any supported conflict. The only conflict identified among genes was in the placement of *Melithreptus albogularis* and *M. brevirostris*. This conflict has been analysed further using species tree analysis in an earlier paper (Toon *et al.* 2010). We conclude that for the accessions, we have used from GenBank or derived afresh ourselves all genes appear to have the same history and can validly be concatenated to estimate an organism-level phylogeny (Table S1).

A concatenated ML analysis was performed by partitioning the dataset by locus with the respective models of evolution and parameter values estimated from the data. Two separate runs were performed and nodal support was assessed via 200 nonparametric bootstrap replicates.

Trees were also reconstructed using Bayesian analysis in MrBayes 3.2 (Yang 1997; Ronquist & Huelsenbeck 2003). The sequence alignment was partitioned by locus with the respective model of sequence evolution applied to each partition and run for 2×10^7 generations. Search parameters included an increase to 8 chains, unlinking of all partition-specific rates and models of evolution, adjustment of chain heating conditions (temp = 0.1–0.05) for improved chain swap acceptance rates, and sampling every 100 generations. The analysis was run three times starting from random trees. Convergence and mixing was assessed for all the parameters in TRACER v1.5 (Drummond & Rambaut 2007). Each run was also evaluated for stationarity by comparing log-likelihood values over time, and 10% of generations (2×10^6) were discarded as burn-in. The individual trees were compared for congruence and then combined to estimate posterior probabilities for individual clades (Huelsenbeck & Imennov 2002; Huelsenbeck *et al.* 2002). Analyses were run on the CIPRES 2.0 portal (Miller *et al.* 2010).

Molecular dating

Divergence times and confidence intervals were estimated using a Bayesian MCMC approach implemented in BEAST v1.7.4 (Drummond *et al.* 2012). To minimize missing data, which affects estimates of branch length and therefore estimates of time divergence, we used only the ND2 and the beta-fibrinogen5 gene datasets and included only those taxa sampled for both genes. The final alignment was of 102 in group taxa and 1541 bp.

Although the honeyeater fossil record is sparse, there are a few fossils dated from the Middle to Late Miocene and Pliocene (Boles 2005). The placement of these fossils within honeyeaters is undetermined and thus we used a molecular rate to estimate dates for the honeyeater radiation and divergences. We calculated a molecular rate for ND2 empirically using pairwise divergence between honeyeaters to determine a conversion factor for the passerine Cytb (GTR+G) rate of Weir & Schluter (2008). Corrected p-distances (GTR + G) between honeyeaters for Cytb and ND2 datasets were calculated in PAUP (Swofford 2002). We calculated a conversion factor of 1.8 using the regression of pairwise comparisons of Cytb and ND2 and then multiplied the conversion factor by 2.07% divergence per million years (standard deviation 0.006) (Weir & Schluter 2008) to obtain 3.73% divergence per million years between lineages or a substitution rate of 0.0186 per site per million years (standard deviation 0.005). Our rates are comparable to recent estimates suggesting that ND2 has a substitution rate that is ~1.75 to 2 times faster than Cytb in passerines (Norman *et al.* 2007; Lerner *et al.* 2011).

In initial runs, posterior estimates of the standard deviation of the uncorrelated lognormal relaxed clock parameter (ucld.stdev) were greater than zero, indicating rate heterogeneity. In all subsequent runs, we used a lognormal relaxed clock (uncorrelated). A birth–death incomplete sampling speciation tree prior (Stadler 2009) and a random starting tree were selected.

We selected a GTR + G model of evolution to be consistent with the molecular rate we employed. A normal prior was selected for the ND2 rate (0.0186 per site per million years, standard deviation 0.005), which was used to estimate the substitution rate for the beta-fibrinogen5 gene partition. Two final BEAST searches were run for 3×10^7 generations, sampling every 1000 generations. Stationarity and mixing was assessed for parameters in TRACER v1.5 and a maximum clade credibility tree was selected in TREEANNOTATOR (Drummond & Rambaut 2007) with the first 3000 trees discarded as burn-in.

Results

Thirty-three additional sequences were collected and aligned with sequences obtained from GenBank. A complete listing of taxa and GenBank accession numbers is in Table S1. No unexpected stop codons or frameshift mutations were detected in the coding regions (e.g. RAG1) of these new sequences. The final matrix comprised 85 nominal species (five represented by two nominal subspecies) aligned across 9246 positions spanning eight genes. Of those positions, 9215 are suitable for phylogenetic analysis. Of the four mitochondrial loci included in this study, ND2 had the highest number of informative characters; Fib5 was the most informative nuclear locus (Table 1).

Phylogenetic overview

The earliest divergence within meliphagids was consistently resolved as between *Myza* and all others (Figs 1 and 2; Fig. S1). Both analyses recovered the same 12 monophyletic groups, but relationships among them varied. For ease of presentation, we anchor discussion to the five major clades recovered in the Bayesian analysis as I, II, III, IV and V and subclades within these as Ia, Ib, Ic, or Va, Vb, and so on (Fig. 1); full and simplified results of the BEAST analysis of divergence times are shown in Figs S1 and S2, respectively).

Given our taxon sampling, conventionally recognized genera in Meliphagidae were mostly recovered as monophyletic apart from the now expected exceptions such as *Lichenostomus*, *Certhionyx* and *Phylidonyris* (*sensu lato* for all); their circumscriptions will be considered further in the Discussion.

Clade I, the largest and most consistently recovered clade across analyses comprised three subclades: Ia (*Acanthagenys*,

Table 1 Summary of the eight loci included in the present study

Locus	Length (aligned bp)	Category, chromosome No.*	Substitution model	A,C,G,T frequency	Variable sites (% total)	Informative sites (% total/% variable)
Fib5	531	Intron, 4	TVM+G	0.30, 0.17, 0.20, 0.33	335 (63.1)	219 (41.7/65.4)
Fib7	938	Intron, 4	TrN+G	0.32, 0.18, 0.19, 0.31	117 (12.5)	50 (5.4/42.7)
G3PDH	331	Intron, 1	TrN+G	0.21, 0.20, 0.32, 0.27	69 (20.8)	24 (7.3/34.8)
RAG1	2872	Exon, 5	TrN+G	0.31, 0.21, 0.24, 0.24	461 (16.1)	134 (4.7/29.1)
ND2	1009	Mitochondrial	GTR+I+G	0.29, 0.34, 0.12, 0.25	656 (65.0)	584 (58.5/89)
Cytb	1143	Mitochondrial	TVM+I+G	0.28, 0.34, 0.14, 0.24	535 (46.8)	463 (40.9/86.5)
COI	1430	Mitochondrial	GTR+I+G	0.27, 0.31, 0.17, 0.25	447 (31.3)	312 (22/69.8)
12S	930	Mitochondrial	GTR+I+G	0.30, 0.26, 0.22, 0.22	330 (35.5)	208 (22.6/63)

*Locus information and chromosome number was inferred from the genome map of the chicken genome on GenBank.

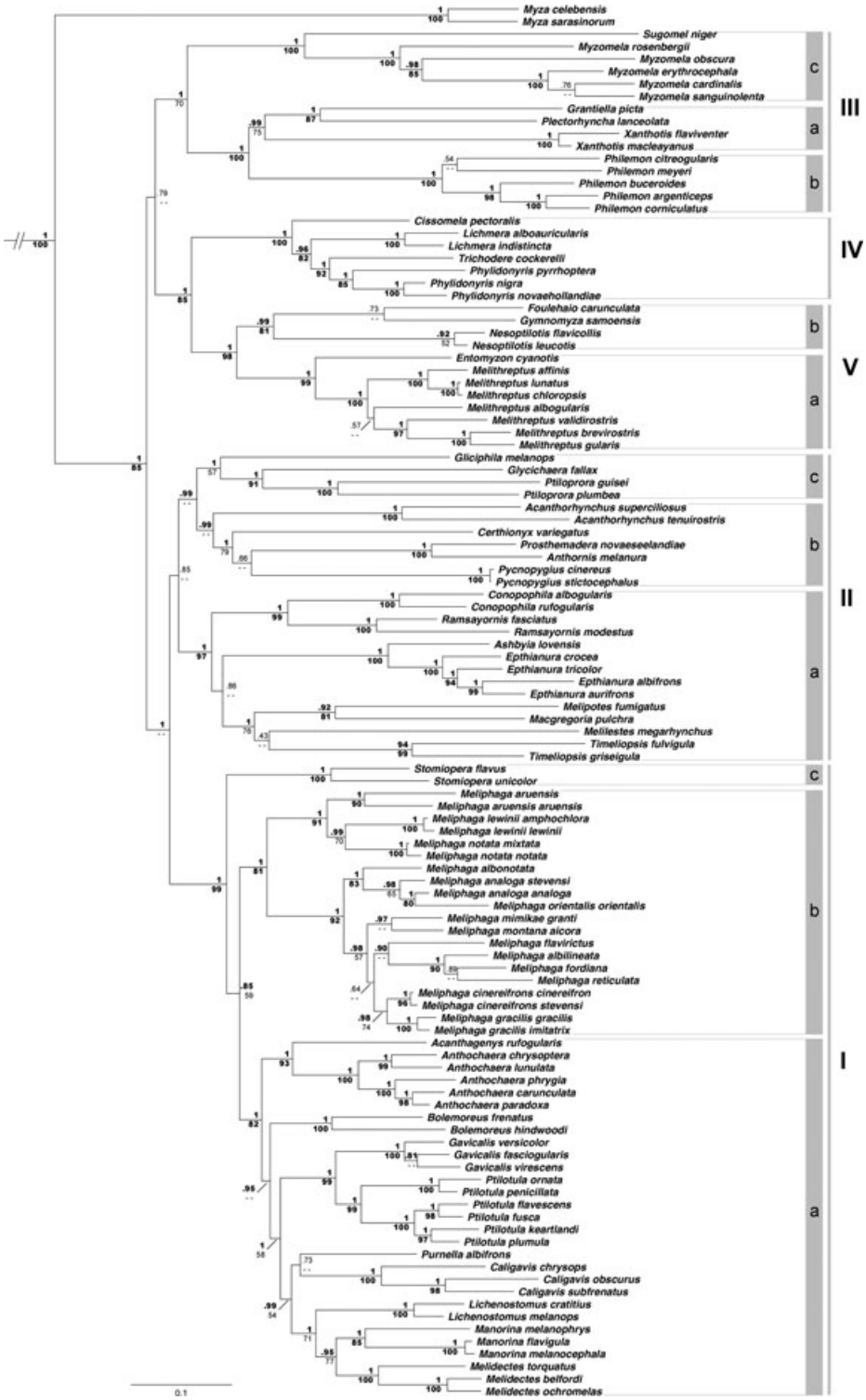

Fig. 1 Bayesian phylogeny representing the relationships within the Meliphagidae using the full dataset (outgroups have been pruned for brevity). Posterior probabilities >0.95 (Bayesian) and bootstrap values >80 (ML) are given on nodes in bold. In case of ML support lower than 50, nodes have - - to indicate a collapsed node under the ML search criterion. Clade numbering (I – V) and subclade lettering (a–c) are as in the text.

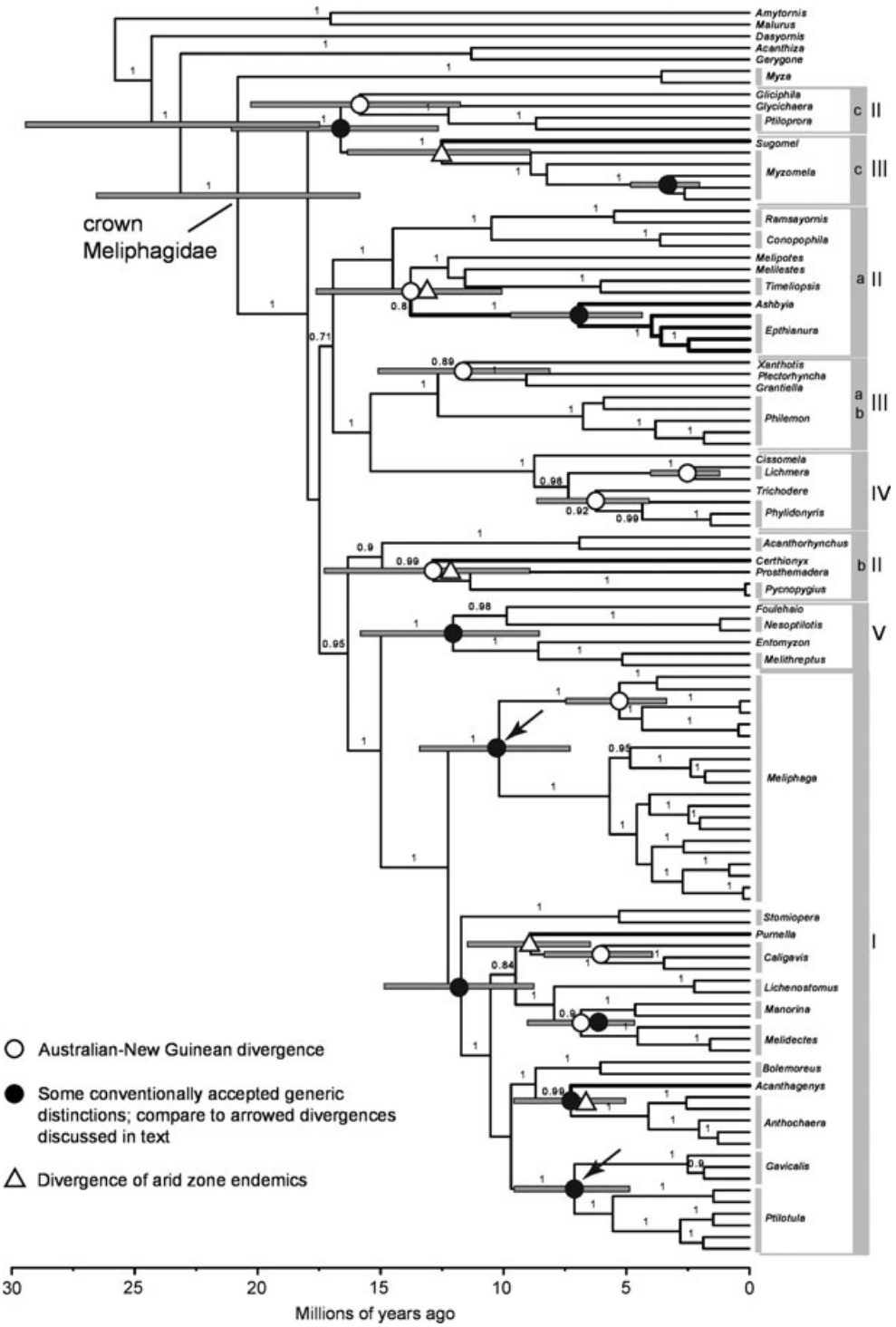

Fig. 2 Simplified presentation of full BEAST analysis showing only genera of Meliphagidae estimated in BEAST using ND2 and the beta-fibrinogen5 gene datasets. Fig. S1 shows all species names and all nodal support values from the BEAST analysis. Clade labels are as in Fig. 1. For key aspects of the analysis discussed in the text, 95% highest posterior intervals are here given as node bars, time on the scale bar is shown in millions of years ago and branch support is indicated by posterior probabilities above 0.95 at nodes. Open circles indicate a sampling of divergences between New Guinean and Australian taxa, closed circles indicate genus-level divisions referred to in the text for comparison with (a) proposed generic breakup of *Meliphaga* into two genera *Meliphaga* and *Microptilotis* and (b) *Gavicalis-Ptilotula*, and open triangles indicate divergence of Australian arid zone endemics.

Anthochaera, *Manorina*, *Melidectes*, *Lichenostomus* (*sensu stricto* of Nyári & Joseph 2011), *Purnella*, *Gavicalis*, *Bolemoreus*, *Caligavis* and *Ptilotula*), Ib (*Meliphaga*) and Ic (*Stomiopera*). Relationships among the three subclades were (Ic, (Ia, Ib)).

Clade II in the Bayesian analysis was poorly supported at PP = 0.79. Its three subclades were IIa (*Ramsayornis*, *Conopophila Melipotes*, *Melilestes*, *Timeliopsis* andthe chats *Epthianur*a and *Ashbyia*), IIb (*Acanthorhynchus*, *Certhionyx*, *Prosthemadera*, *Anthornis*, *Pycnopygius*) and IIc (*Glycichaera*, *Glyciphila*, *Ptiloprora*) and each had strong support (PP = 1). Clade II was the sister to Clade I.

Clade III comprised IIIa (*Xanthotis*, *Plectorhyncha*, *Grantiella*), IIIb (*Philemon*) and IIIc (*Myzomela*, *Sugomel*), and their relationships being (IIIc (IIIa,IIIb)). Within IIIa, *Grantiella* and *Plectorhyncha* were sister taxa, and *Xanthotis* was their sister. BEAST, however, placed IIIc as sister to Clade IIc.

Clade IV consistently comprised (*Cissomela*, (*Lichmera*, (*Trichodere*, *Phylidonyris s.s*))).

Clade V comprised subclade Va (*Melithreptus*, *Entomyzon*) and Vb (*Foulehaio*, *Gymnomyza*, *Nesoptilotis*) (*Gymnomyza* was excluded from the BEAST analysis due to missing data).

Relationships among these five clades and their subclades (*Myza* being sister to all five main clades) were different in each analysis and are essentially unresolved. MrBayes recovered ((I,II)(III(IV,V))), whereas BEAST did not recover Clades II and III and thus resulted in a more complex pattern of relationships (Fig. 2).

Timing of the radiation

Earliest divergences in Meliphagidae are estimated to be in the early Miocene around 20 million years ago (mya) (crown age HPD 26.6–15.9 Ma) (see Fig. 2). Most diversification at the genus and species level took place in the Miocene and Plio-Pleistocene, respectively.

Discussion

We used existing and newly available DNA sequence data to update recent appraisals (Schodde & Mason 1999; Christidis & Boles 2008) of relationships within the mainly Australo-Papuan passerine family Meliphagidae, the honeyeaters. We also provide the first estimates of divergence times in the group's history. Overall, our results affirm many of the changes recently advocated in meliphagid systematics and nomenclature, stemming largely from the pioneering work of Driskell & Christidis (2004) and later syntheses and analyses (Schodde & Mason 1999; Norman *et al.* 2007; Christidis & Boles 2008; Gardner *et al.* 2010; Nyári & Joseph 2011). First, we highlight some key phylogenetic questions still to be resolved and then present an overview of implications for the group's systematics, ecology and historical biogeography.

Phylogeny

Driskell & Christidis (2004) found that the earliest divergence in the Meliphagidae was that between the *Acanthorhynchus* spinebills (two species in eastern, southern and south-western Australia – Higgins *et al.* 2001; Fig. S2) and all other meliphagids that they had sampled, which did not include *Myza*. Later analyses (Nyári & Joseph 2011) questioned this. Here, improved taxon sampling yields a strongly supported alternative finding that the earliest divergence in the family was between Wallacean *Myza* and all other meliphagids. This parallels patterns of relationships among phalangerid marsupials in which Sulawesi lineages diverged at a comparable time as *Myza* (Ruedas & Morales 2005; Raterman *et al.* 2006) and in some other bird groups though at shallower temporal and phylogenetic depths than in this case (e.g., *Rhipidura* fantails – Nyári *et al.* 2009; *Coracina* cuckoo-shrikes – Jønsson *et al.* 2010; *Prioniturus* parrots – Schweizer *et al.* 2012). We estimate that *Acanthorhynchus* evolved later at 14.94 mya (11.05–19.36) when it diverged from its closest relatives *Certhionyx* of the Australian arid zone, *Pycnopygius* of New Guinea and *Prosthemadera* and *Anthornis* of New Zealand. Driskell & Christidis (2004) also recovered a close relationship among three of these latter genera except *Anthornis*, which they were unable to sample. Previously referred to by Driskell & Christidis (2004) as a 'hodge-podge assemblage' with poorly resolved relationships, we are now confident that these last four genera in New Guinea, New Zealand and the Australian arid interior are each other's closest relatives. The stage is set for studying the details of their remarkable evolution.

Mostly, the twelve groups we recovered in five major clades were also found by Driskell & Christidis (2004), although differences in taxon sampling influenced overall results of the studies. They did not recover our IIb because *Acanthorhynchus* appeared in their study as sister to all other meliphagids; otherwise, its composition was consistent in the two studies. Further, Driskell & Christidis (2004) only sampled one of the 20 species of *Lichenostomus* as then construed (*L. flavescens*) and so did not recover Ic of the present analysis nor, obviously, the paraphyly of *Lichenostomus* that is now established (Nyári & Joseph 2011; present study). Different patterns of relationships among studies are due in large part to essentially still poorly resolved deeper nodes within the meliphagid tree. Their resolution remains a challenge for later study.

Systematics

Uptake of genus-level changes that have now been well argued (Schodde & Mason 1999; Christidis & Boles 2008; Higgins *et al.* 2008) has been remarkably slow, inconsistent (e.g., within a collection of papers published online over a

few years – *cf* Burbidge *et al.* 2010 and Johnstone *et al.* 2013 in George *et al.* 2009–13), or simply confused in popular field-guide literature (e.g., Simpson & Day 2010). We therefore see a need to reiterate these changes here. In doing so, we stress links between necessary taxonomic changes and the now clarified understanding of phylogenetic and phenotypic patterns. We recommend generic-level splits based on assessments of phenotypic, genetic and temporal divergences, especially where the latter are estimated to have been in the Miocene.

The case for dismantling *Certhionyx sensu lato* (e.g., Schodde & Mason 1999) into the Pied Honeyeater *Certhionyx variegatus* Lesson, 1830, the Black Honeyeater *Sugomel niger* (Gould, 1838) and Banded Honeyeater *Cissomela pectoralis* (Gould, 1841), which fall in three different clades, now appears unassailable (Driskell & Christidis 2004; Nyári & Joseph 2011; present study). Their at best superficially similar patterns of pied black-and-white male plumages and grey-brown adult female (*Certhionyx*, *Sugomel*) and juvenile (*Cissomela*) plumages are shown in Fig. S2a,b. Notably, *Certhionyx variegatus* uniquely has a subocular ring of blue skin in both sexes; weighing 27 g, it is much larger than the other two species (both 9.5 g; Higgins *et al.* 2001). *Certhionyx variegatus* and *Sugomel niger* are endemic to inland Australia; *Cissomela pectoralis* occurs in monsoonal savannas of Australia's tropical north.

Similarly, having confirmed non-monophyly of *Phylidonyris sensu lato*, we affirm the need to recognize the White-fronted Honeyeater and Tawny-crowned Honeyeater as *Purnella albifrons* and *Gliciphila melanops*, respectively. The two species currently in *Glycifohia* Mathews, 1929, from New Caledonia and Vanuatu, have at times been placed in *Phylidonyris*. Andersen *et al.* (2014; seen while this paper was in revision) were able to examine these two species and found that Australian *Gliciphila* is closer to *Glycifohia notabilis* than to *Glycifohia undulata*. They suggested the taxonomically valid and simplest course of merging all in *Gliciphila*. Retention of *Gliciphila* for the species *melanops* would require a new generic name for the New Caledonian species *undulata*. This is not without merit as it would highlight the morphological and biogeographical complexity of the three species.

More recently revealed has been the paraphyly of *Lichenostomus* as construed since Schodde's (1975) interim arrangement (Gardner *et al.* 2010; Nyári & Joseph 2011). The 20 species that had been united in *Lichenostomus* Cabanis, 1851 are not monophyletic but are scattered in seven clades recognizable as genera across the meliphagid phylogeny, the main points relevant to their nomenclature being summarized in Table 2. Of the seven genera, only *Ptilotula* and *Gavicalis* are sister taxa and so could validly be synonymized under *Ptilotula* (Table 2). We do not advocate this arrangement because of their phenotypic, genotypic and temporal divergence (see Nyári & Joseph 2011), the latter here estimated at around 7.12 mya (4.88–9.57 mya). This is closely comparable with divergences of other conventionally recognized and undisputed generic pairs such as *Ashbyia-Epthianura* and *Acanthagenys-Anthochaera* (Figs 1 and 2). Notably, monotypic *Oreornis* of New Guinea has been placed in *Lichenostomus* by some authors (Beehler *et al.* 1986) but is still to be included in a molecular analysis.

Table 2 Nomenclatural consequences of the breakup of *Lichenostomus* as construed since Schodde (1975)

Genera resulting from breakup of *Lichenostomus*	Composition
Bolemoreus, Nyári & Joseph 2011	Eungella and Bridled Honeyeater *B. hindwoodi* and *B. frenatus*, respectively
Stomiopera Reichenbach, 1852	Yellow Honeyeater *S. flava* and White-gaped Honeyeater *S. unicolor*, respectively
Caligavis Iredale, 1956	Yellow-faced, Obscure and Black-throated Honeyeaters, *C. chrysops, C. obscura* and *C. subfrenata*, respectively
Nesoptilotis Mathews, 1913	White-eared and Yellow-throated Honeyeaters, *N. leucotis* and *N. flavicollis*, respectively
Lichenostomus Cabanis, 1851	Purple-gaped and Yellow-tufted Honeyeater *L. cratitius* and *L. melanops*, respectively
Gavicalis, Schodde & Mason 1999	Singing, Mangrove and Varied Honeyeaters *G. virescens, G. fasciogularis* and *G. versicolor*, respectively
Ptilotula Mathews, 1912	Yellow tinted, Fuscous, White-plumed, Yellow-plumed Grey-fronted, and Grey-headed Honeyeaters *P. flavescens, P. fusca, P. penicillata, P. ornata, P. plumula*, and *P. keartlandi*, respectively

Myzomela is the largest meliphagid genus, 21–31 species having been recognized within it (Koopman 1957; Higgins *et al.* 2001). Schodde & Mason (1999) recognize two subgenera, *Myzomela* and *Cosmeteira*, for the sexually dimorphic and monomorphic species, respectively. To date, only four species (*M. sanguinolenta*, *M. erythrocephala*, *M. rosenbergii and M. cardinalis*) from subgenus *Myzomela* and one (*M. obscura*) from *Cosmeteira* have been examined phylogenetically (Driskell & Christidis 2004; present study), and non-monophyly of these two subgenera is apparent. Clearly, all species in *Myzomela* need to be analysed phylogenetically before the evolution of patterns of sexual dimorphism and monomorphism can be properly understood.

Concerning the well-established, familiar name *Meliphaga*, our analyses reinforce earlier findings (Driskell & Christidis 2004; Norman *et al.* 2007) that, surprisingly, have gone essentially unremarked (but see Schodde & Mason 1999). That is, within *Meliphaga* there are at least

two well-supported clades and that the phenotypically similar 'spotted' species of *Meliphaga* are not monophyletic (Fig. S2a,b). We question whether continued recognition of *Meliphaga* outweighs the benefit of taxonomically recognizing the substantial phylogenetic, biogeographic and even phenotypic diversity subsumed within it. The familiarity of *Meliphaga* as long construed can never be a *scientific* argument against considering the merit of dismantling it. Indeed, many long-established and never disputed generic distinctions elsewhere in meliphagids are of the same depth as in *Meliphaga* (Figs 1 and 2). Resistance to dismantling *Meliphaga* if applied across the entire meliphagid phylogeny could reasonably be taken to mean that only *Myza* and the 12 other clades and subclades consistently recovered by all analyses should be recognized as genera within the entire family.

The 'spotted' *Meliphaga* are cryptically similar species that are mostly monochromatic, green birds having a distinctive yellowish or whitish spot on their ear coverts. They occur in New Guinea and in Australia east of the Gulf of Carpentaria. They are not monophyletic because nested within them are three 'streaked' species (*albilineata*, *fordiana* and *reticulata*) (Christidis & Schodde 1993; Norman *et al.* 2007; present study Figs 1 and 2, S3a,b). The latter are predominantly grey with streaked underparts (Fig. S3a). They occur in Timor and Australia but only west of the Gulf of Carpentaria. We estimate the divergence time between a 'spotted' clade (*aruensis*, *notata*, *lewinii*) and the rest of *Meliphaga* at 10.19 mya (7.31–13.41). This divergence time closely approximates those we estimated for conventionally recognized generic distinctions (e.g., *Acanthagenys/Anthochaera*, *Ashbyia/Epthianura*, *Trichodere/Phylidonyris*, dismantled *Lichenostomus*). Further, they approximate divergences recognized subgenerically by Schodde & Mason (1999) within *Philemon*.

We argue that the weight of molecular data now suggests greater taxonomic merit in restricting *Meliphaga* Lewin, 1808 to the three relatively large 'spotted' species *aruensis*, *lewinii* and *notata* (type species *Meliphaga chrysotis* Lewin, 1808 = *Ptilotis lewinii* Swainson, 1837*)*, and placing all others in *Microptilotis* Mathews, 1912 (type species *Ptilotis gracilis* Gould, 1866). This taxonomy reflects the phylogenetic relationships, depths of temporal divergence and biogeographic patterns among the two clades as outlined above. It is consistent with generic distinctions in other clades of the meliphagid phylogenetic tree. It is also consistent with the trend in meliphagid systematics of recognizing more rather than fewer genera as their relationships and the temporal depths of many divergences become clearer (e.g., *Purnella*, *Gliciphila*, *Sugomel*, *Cissomela*, breakup of *Lichenostomus*). Most importantly, it provides a better framework for understanding the birds' biology and biogeography and for asking why they have diverged so little phenotypically. A taxonomically valid alternative is that of Schodde & Mason (1999) who recognized two subgenera, *Meliphaga* and *Microptilotis*, in *Meliphaga*.

Biogeography and ecology

Two broad results emerge from our analyses. First is that diversification of the extant lineages of the Meliphagidae may trace to the Miocene or even late Oligocene when the aridification of Australia began, as has been demonstrated in other Australian fauna and flora (Byrne *et al.* 2008, 2011; Toon *et al.* 2012). Second, as Driskell & Christidis (2004) argued, there has not been an Australian and a New Guinean radiation of meliphagids. We now examine specific results from our new synthesis that inform details of these broad findings.

First, our analysis brings into sharp relief the number of species, including several monotypic genera, that are now confined, or almost so, to the Australian arid zone and whose closest relatives inhabit much wetter zones (see Schodde 1982; Schodde 2006). Some of these, if only through their high vagility, have become specialized to the arid zone, most notably *Acanthagenys* and *Purnella* within Clade I, the chats *Epthianura* and most especially monotypic *Ashbyia* of Clade II, *Sugomel* from Clade III and *Certhionyx* from Clade II. Further, monotypic *Gliciphila* of Clade II is of semi-arid and temperate southern habitats. The sister pair of monotypic genera *Plectorhyncha* and *Grantiella* of Clade III also range widely in eastern Australian arid, semi-arid and temperate zones. *Sugomel* of Clade II is most closely related to tropical and subtropical *Myzomela*, also from Clade II. Similarly, the closest relatives of *Certhionyx* (Clade II) are in forested habitats of New Guinea, New Zealand and mesic eastern and south-western Australian woodlands. In this respect, they parallel two other genera that range widely in the Australian arid zone and which have closest relatives in more mesic zones (i.e., endemic monotypic parrot genus *Melopsittacus* – Joseph *et al.* 2011; and the monarchid Magpie-lark *Grallina cyanoleuca* (Schodde & Mason 1999).

Some of these species have evolved notable ecological specializations to the arid zone. *Sugomel* (Clade III) is highly specialized to feeding on tubular flowers of, and has perhaps co-evolved with, its arid-zone-endemic food plants *Eremophila* spp (Ford 1978; Higgins *et al.* 2001, 2008). *Grantiella* (Clade III) is a diet specialist on fruits of mistletoes (e.g., *Amyema* spp; Higgins *et al.* 2008) and *Purnella* (Clade I) is well known for its albeit less marked association with mistletoes (*Amyema*, *Lysiana* spp.; Watson 1997; Higgins *et al.* 2008). A more complete understanding of the evolutionary history of *Purnella* (Clade I) in the arid zone will require more detail on its relationships and

timing of likely Miocene divergences among its closest relatives, which include Australian and New Guinean *Caligavis* (Clade I), New Guinean *Melidectes* (Clade I), and Australian *Manorina* (Clade I) and *Lichenostomus sensu stricto* (Driskell & Christidis 2004; Nyári & Joseph 2011).

The Australian chats *Epthianura* (four species) and monotypic *Ashbyia* (in Clade III) are essentially a small radiation within the Meliphagidae (Sibley 1970; Parker 1973; Schodde 1982; Schodde & Mason 1999; Driskell & Christidis 2004; Gardner *et al.* 2010; Nyári & Joseph 2011; present study). Relative to most honeyeaters, they have diverged ecologically and behaviourally in being often gregarious, largely terrestrial insectivores that are sexually dichromatic. Sexual dichromatism is relatively uncommon in the Meliphagidae (but see *Certhionyx* (Clade II), *Sugomel* and *Myzomela* (Clade III), for examples). In common with more vagile honeyeater species, chats are territorial when breeding (Williams 1979; Schodde & Mason 1999). They range almost exclusively across largely treeless shrublands of the arid and semi-arid zones or subcoastal tropical wetlands (Higgins *et al.* 2001). The most extreme example is monotypic *Ashbyia* (Clade II), the Gibberbird, which is known for its association with treeless, stony desert ('gibber' or desert pavement) in inland eastern Australia. It is the most terrestrial honeyeater. Two species of *Epthianura*, the Crimson Chat *E. tricolor* and the Orange Chat *E. aurifrons* (Clade II), are nomadic mainly within the arid zone. The Yellow Chat *E. crocea* (Clade II) is primarily a species of tropical coastal marshes. At times, it has evidently dispersed hundreds of kilometres deep into the arid zone where it has been recorded in temporary reedbeds that developed since European settlement around artesian water sources (Ford & Parker 1974). The fourth species, the White-fronted Chat *E. albifrons* (Clade II), occurs in southern Australian semi-arid zones. Williams (1979) and Williams & Main (1976) studied the physiology of *Epthianura* (Clade II) and concluded that the species' ability to live in semi-arid and arid regions is explained by distributions and seasonal movements that complement the physiology of evaporative water loss and thermoregulation so as to enhance survival at high ambient temperatures.

Striking biogeographical patterns emerge following the dismantling of *Lichenostomus* (Table 2; Nyári & Joseph 2011). First is the disjunct distribution of the two southern Australian species of *Nesoptilotis* (Clade V), the Yellow-throated Honeyeater *N. flavicollis* and the White-eared Honeyeater *N. leucotis*, and the group now clearly among their closest relatives Pacific islands *Gymnomyza* and *Foulehaio*, and wide-ranging Australian *Melithreptus* and *Entomyzon* (all from Clade V). The extreme phenotypic diversity among these taxa is worth noting. *Gymnomyza* (Clade V) includes some of the largest species in the family and the shared blackish underparts of *N. leucotis* (Clade V) and *G. viridis*, which despite the size disparity in the birds themselves may be ancestral within the clade. Second concerns the five species comprising *Caligavis* and *Bolemoreus* (both Clade I). While broadly similar morphologically, these two genera appear not closely related to each other but are mainly confined to the Tumbunan (Schodde & Calaby 1972) rainforests of eastern Australia and New Guinea. The exception is one species, the Yellow-faced Honeyeater *C. chrysops*, which occurs mainly in temperate woodlands and forests of eastern Australia.

Supporting Driskell & Christidis's (2004) conclusion that there have not been separate Australian and New Guinean radiations are at least 10 independent divergence events between Australian and primarily New Guinean taxa (Fig. 2). Notable and among the oldest of these is that of *Gliciphila melanops* and its closest relatives. *G. melanops* (both Clade II) occurs exclusively in southern Australian heaths and shrublands, mainly in semi-arid zones. Notwithstanding scope for clarifying relationships of *Gliciphila* (Clade II), its lineage appears to have diverged in the mid-Miocene. Aside from *Glycifohia* of Vanuatu and New Caledonia (Andersen *et al.* 2014), its closest relatives in our analyses, *Glycichaera* and *Ptiloprora* (of Clade II), are almost entirely in New Guinean rainforests but for an isolated population of the former in riparian rainforests and woodlands of the tropical far north-eastern tip of Australia. Unravelling the ecology and biogeography underlying the evolution of these extraordinarily disjunct distributions, and particularly details of the timing of their origins, would be a rewarding comparative study. Possibly pertinent to the timing of the evolution in *G. melanops* (Clade II) is the finding reported by Dolman & Joseph (2012) that mitochondrial DNA diversity across its vast and highly fragmented range is remarkably unstructured and that its geographical disjunctions across southern Australia evolved very recently.

Finally, we note that the most significant of two Australian species yet to be included in any molecular analysis because of its rarity in collections, the Grey Honeyeater *Conopophila whitei*, is endemic to inland mulga *Acacia aneura* shrubland and woodland of the arid zone. If it is not sister to the two other species of *Conopophila* (Clade II), which occur across tropical woodlands in northern Australia and New Guinea, its retention in monotypic *Lacustroica* North, 1910 may be warranted.

Conclusions

The iconic Australo-Papuan family Meliphagidae (honeyeaters) constitutes a spectacular evolutionary radiation involving a remarkable diversity of phenotypic, ecological and behavioural traits. Well-supported clades consistently

comprise species that are phenotypically very divergent from one another and similar species are often not closely related. As a consequence, understanding the evolution of this radiation has been intractable until the integration of molecular data with morphology, ecology and behaviour. This has enabled recognition of a striking number of monotypic genera and justified genus-level rearrangements that better reflect the history of their diversification since the onset of Miocene aridity in Australia. The position of the mostly arid zone and semi-colonial Australian chats (Higgins *et al.* 2001) is a clear example. Furthermore, the broadly similar distributions and sometimes superficial phenotypic similarities shared by some of the arid zone species appear to have masked the evolutionary complexity of the group's radiation in the arid zone. As noted in a study of the superfamily Meliphagoidea, to which the honeyeaters belong, (Gardner *et al.* 2010), a long evolutionary history may have enhanced the difficulty of understanding relationships within the group.

Even with the data from Pacific Island taxa in Andersen *et al.* (2014; seen as this paper was revised) challenges remain for further work. Systematic clarification is still needed for some groups such as *Philemon* friarbirds, and there is a need for expanded taxon and gene sampling outside Australia and especially in New Guinea, and among Pacific Islands and Indonesia. Notable here is that there are key taxa for which no molecular data are available: Australian *Conopophila whitei*, New Guinean *Oreornis*, and some species of each of *Melilestes* (*sensu lato*), *Lichmera*, *Philemon* and *Myzomela*. The spatial and temporal dynamics of their historical biogeography also warrant closer study as resolution of clade relationships is enhanced through further work. Foremost here is the need for a complete, well-resolved species-level phylogeny to enable estimation of rates of extinction and speciation and thus more precise estimation of key drivers in environmental history (e.g., lineage-through-time analysis, Espeland & Murienne 2011; Brumfield 2012; Hawlitschek *et al.* 2012) as well as linkages with evolution of key food plants such as eucalypts, acacia and mistletoes. This would allow refinement of the observation made here that honeyeater lineages appear to have colonized the Australian arid zone on multiple, independent occasions and perhaps secondarily. We consider that a solid framework has now been achieved for the purpose of better understanding such facets of the evolution and ecology of honeyeaters, at least in Australia.

Acknowledgements

We acknowledge the prior workers before us whose work we have tried to build on and further synthesize. Alex Drew took the photographs. LJ thanks his co-authors for their patience. Comments from C. Pavey, R. Schodde and anonymous reviewers considerably sharpened the manuscript and corrected errors in it.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Full results of BEAST analysis. 95% highest posterior intervals are given as node bars. Time on the scale bar is shown in million years – see text for discussion of particular divergence times. Branch support is indicated by posterior probabilities above 0.95 at nodes.

Fig. S2. Ventral views of the *Acanthorhynchus* spinebills and species that have been placed in *Certhionyx sensu lato*. All specimens are from the Australian National Wildlife Collection. (a) Male specimens of, left to right: Pied Honeyeater *Certhionyx variegatus* (B47902); Black Honeyeater *Sugomel nig*er (B14783); Banded Honeyeater *Cissomela pectoralis* (B55103), Eastern Spinebill *Acanthorhynchus tenuirostris* (B46148); Western Spinebill *A. superciliosus* (B50347). (b) Sexual and age-related dichromatism in, left to right: Pied Honeyeater (male, B47902; female B36623); Black Honeyeater (male B14783, female B46628); Banded Honeyeater (male B 55103; juvenile B6778).

Fig. S3. (a) Ventral and (b) lateral views of specimens representing the 'spotted' and 'streaked' subgroups traditionally assigned to *Meliphaga* and the alternative genus-group nomenclature we recommend (see text for discussion). All specimens are from the Australian National Wildlife Collection. Left to right: 'Spotted' species: *Meliphaga lewinii* (B18956); *Microptilotis orientalis* (B 26043); *Microptilotis albonotata* (B25160); 'Streaked' species: *Microptilotis albilineata* (B13848); *Microptilotis reticulata* (B30276).

Table S1. Listing of all taxa studied and GenBank accession numbers of relevant sequences.