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Mitochondrial and nuclear DNA phylogenies reveal a complex evolutionary history in the Australasian robins (Passeriformes: Petroicidae)

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ABSTRACT

The Australasian robins (Petroicidae) comprise a relatively homogeneous group of small to medium-sized insectivorous birds. Their center of diversity is Australia and New Guinea (40 species) but seven species have managed to colonize geographically distant islands such as Tanimbar, New Britain, New Zealand, New Caledonia, Norfolk Island, Vanuatu, Solomon Islands, Fiji and Samoa. To resolve the evolutionary relationships within the Petroicidae, we here present the results of a phylogenetic analysis of sequence data from two mitochondrial genes (ND2, CO1) and one nuclear intron (β-Fibrinogen intron 5) for all 14 genera and 40 of the 46 currently recognized species. All phylogenetic analyses identified six primary lineages, treated here as subfamilies, within the Petroicidae: (1) Eopsaltriinae comprising *Eopsaltria* (excluding *E. flaviventris*), *Tregellasia*, *Peneothello*, *Melanodryas*, *Poecilodryas* and *Heteromyias*; (2) Drymodinae comprising *Drymodes*; (3) Microecinae comprising *Microeca*, *Monachella* and *Eopsaltria flaviventris*; (4) Petroicinae comprising *Petroica* and *Eugerygone*; (5) Pachycephalopsinae comprising *Pachycephalopsis*; and (6) Amalocichlinae comprising *Amalocichla*. The genera *Eopsaltria*, *Microeca*, *Peneothello* and *Poecilodryas* were found to be paraphyletic. Based on assessments of phylogenetic branching patterns and/or DNA divergence it also was apparent that *Eopsaltria australis*, *Tregellasia leucops*, *Melanodryas cucullata*, *Heteromyias albispecularis*, *Drymodes supercilious* and *Microeca flavigaster* may each comprise more than one species. The Petroicidae display a complex biogeographical history involving repeated radiations both within, and across Australia and New Guinea. It appears that dispersal into smaller islands such as New Britain, Tanimbar and the South Pacific has only been undertaken by species with a "flycatcher" body form.

1. Introduction

The Australasian robins (Petroicidae) comprise a relatively homogeneous group of small to medium-sized insectivorous birds. They occur in all wooded habitats from rainforest through temperate woodland to arid scrub, as well as treeless alpine regions. Most are somewhat plump, upright perching birds that employ a 'sit and pounce' foraging technique, but some are more flycatcher-like and a few resemble larger thrushes or small warblers. Their center of diversity is Australia and New Guinea where 40 of the 46 species, and all 14 genera occur (based on Boles (2007)). Three species occur in New Zealand, with one each in New Caledonia and Tanimbar, and one extending from Norfolk Island through Vanuatu and the Solomon Islands to Fiji and Samoa.

DNA–DNA hybridization data (Sibley and Ahlquist, 1990) aligned the Petroicidae (=Eopsaltriidae) with the Australasian centered Corvoidea (crows, whistlers, cuckoo-shrikes, fantails and allies), while allozyme data (Christidis and Schodde, 1991) instead, identified closer affinities with the Australasian Meliphagoidea (honeyeaters, fairy-wrens and Australasian warblers). Both placements were consistent with the distributional center of the Petroicidae. However, several DNA sequence studies (Ericson et al., 2002a; Barker et al., 2002, 2004; Beresford et al., 2005; Irestedt and Ohlson, 2008) indicate that the Petroicidae occupies a basal position in the largely northern hemisphere centered Passerida assemblage (warblers, swallows, finches, thrushes and allies). Such a basal phylogenetic position for the Australasian Petroicidae suggests that the family has had a long evolutionary history. Elucidating the phylogenetic and biogeographical history of the

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Petroicidae takes on additional significance, as Australasia is established as the center of origin for the world's oscine songbirds (Barker et al., 2002; Ericson et al., 2002b; Jønsson et al., 2011).

Based on plumages, eggs, skull characters and behavior, Schodde and Mason (1999) divided the family into three subfamilies: Drymodinae (*Drymodes*); Petroicinae (*Petroica*, *Eugerygone*, *Microeca*, *Monachella* and possibly *Pachycephalopsis*); and Eopsaltriinae (*Eopsaltria*, *Tregellasia*, *Peneoenanthe*, *Peneothello*, *Melanodryas*, *Heteromyias*, *Poecilodryas*). *Amalocichla* was included in the Acanthizidae, but DNA sequence data (Norman et al., 2009) firmly place this genus within the Petroicidae. Apart from the configuration of a single skull character, the vomer in the Eopsaltriinae, there were few characters identified by Schodde and Mason (1999) that defined the subfamilies from a phylogenetic perspective, and relationships within each subfamily were also poorly resolved.

A multi-locus DNA phylogenetic study on the Petroicidae by Loynes et al. (2009) was partially congruent with the taxonomy of Schodde and Mason (1999). The DNA data supported recognition of the Eopsaltriinae and Drymodinae, but the Petroicinae was found to be paraphyletic. Phylogenetic relationships of the enigmatic species *Peneoenanthe pulverulenta* and *Eopsaltria flaviventris* were also resolved. Although the study of Loynes et al. (2009) had good coverage of Australian taxa, it lacked the New Guinean genera *Monachella*, *Eugerygone* and *Amalocichla*, and representation from *Microeca*, *Poecilodryas, Petroica* and *Heteromyias* was restricted to Australian species. A DNA study by Miller and Lambert (2006) only examined relationships among the New Zealand species of *Petroica*.

To resolve the evolutionary relationships within the Petroicidae, we here present the results of a phylogenetic analysis of sequence data from two mitochondrial genes (ND2, CO1) and one nuclear intron (β-fibrinogen intron 5) for all 14 genera and 40 of the 46 currently recognized species. We use the phylogeny to better elucidate the biogeographical history of the family and to assess the patterns of ecological diversity.

2. Materials and methods

2.1. Taxon sampling

We sampled all 14 genera and 40 of the 46 of the currently recognized species (Boles, 2007). For several species multiple individuals and subspecies were examined (Table 1). No DNA data were obtained for the following six species: *Poecilodryas brachyura*, *Peneothello cryptoleuca*, *Microeca hemixantha*, *Petroica traversi*, *Petroica archboldi* and *P. bivittata*. The absence of these species from the analysis has differing effects on the phylogenetic and biogeographical conclusions. *M. hemixantha* is generally regarded to be an island representative of *M. flavigaster* (Boles, 2007), while DNA analysis has revealed a sister relationship between *P. traversi* and *P. macrocephala* (Miller and Lambert, 2006). The affinities of *P. brachyura* are less clear, but it is most similar to *P. hypoleuca* in overall appearance. *P. cryptoleuca* is believed to be a sister species of *P. cyanus* (Boles, 2007). More significant are the absence of *P. archboldi* and *P. bivittata* from the analyses as their affinities are very poorly understood (Schodde and Mason, 1999), and their restriction to the montane regions of New Guinea increases their importance in understanding the biogeographical history of the genus *Petroica*.

The taxon sampling also included representatives from Callaeatidae (*Callaeas cinerea*), Picathartidae (*Picathartes gymnocephalus*) and the large Passerida radiation (Hirundinidae: *Hirundo rustica*, Paridae: *Parus major*, Passeridae: *Passer montanus* and Sturnidae: *Sturnus vulgaris*), as these lineages have been suggested to be closely related to Petroicidae (Barker et al., 2002, 2004; Ericson et al., 2002a; Irestedt and Ohlson, 2008). The trees were rooted with Corvidae (*Corvus corone*). All sequences obtained in the present study have been lodged on GenBank with the accession numbers JN597010 to JN597237 and JN607437 TO JN607440.

As sequence data for all three genes were not obtained from all specimens included in this study, the taxon sampling for the analysis of the concatenated data was slightly reduced. Specimens from which both nuclear and mitochondrial sequences where available were generally included in the combined analysis. However, when the sequences from multiple specimens of the same taxon were found to be identical (or almost identical), some of these individuals were excluded from the analysis (mainly to reduce the amount of data for the time consuming phylogenetic analyses). In three cases (*Petroica multicolor*, *Petroica australis* and *E. flaviventris*), species were included in the combined analysis based on sequence data from only a single gene.

2.2. DNA extraction, PCR and sequencing

DNA was extracted from frozen and ethanol-preserved tissue using the salt-chloroform extraction procedure of Gemmell and Akiyama (1996). Primers for the amplification of the mitochondrial ND2 (Hackett, 1996; Kirchman et al., 2001) and CO1 (Christidis et al., 2010) genes, and the nuclear gene region β-fibrinogen intron 5 (Driskell and Christidis, 2004) were sourced from the literature. The choice of genes was largely based on previous success in elucidating intrageneric and intergeneric relationships in Australasian songbirds (e.g. Driskell and Christidis, 2004; Norman et al., 2007; Christidis et al., 2010).

PCR amplifications were performed in 25 μL reaction volumes using standard conditions as described in Norman et al. (1998), or in the presence of GoTaq Green Mastermix (Promega Corp., Wisconsin USA) with a final $MgCl_2$ concentration of 3 mM. Annealing temperatures ranged from 48 °C to 52 °C, while extension times ranged from 45 to 80 s depending on the product length. Amplified products were purified using AMPure (Beckman Coulter Inc., Massachusetts, USA), magnetic bead separation or the GFX Gel Band and PCR Purification Kit (Amersham Bioscience Corp., Piscataway, New Jersey, USA). Cycle sequencing reactions and purifications were performed as described in Norman et al. (2007). Sequenced products were separated on a MegaBACE 1000 capillary DNA sequencer as described in Norman et al. (2007). Sequences were aligned and edited using the program Sequencher v4.1.4 (Gene Codes Corp., Michigan, USA) or ProSeq 3 (Filatov, 2002).

2.3. Phylogenetic analysis

We used Bayesian inference and Maximum Likelihood to estimate phylogenetic relationships. All phylogenetic analyses were performed at the CIPRES Science Gateway [http://www.phylo.org/portal2/login!input.action] (Miller et al., 2010). The models for nucleotide substitutions used in the analyses were selected for each gene individually, and by codon position for the two mitochondrial genes by applying the Akaike Information Criterion using the program MrModeltest 2.2 (Nylander, 2004) in conjunction with PAUP* (Swofford, 1998).

In the Bayesian analyses, posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MrBayes 3.1.1 (Ronquist and Huelsenbeck, 2003). Analyses were performed for the individual genes separately and for the concatenated data set of all genes. For the concatenated data set, three different partitioning strategies were compared: (1) two partitions – one for β-fibrinogen intron 5 and one for the mitochondrial DNA; (2) four

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Table 1
Species and subspecies examined along with their distributions (Distr): NG = New Guinea; Aust = Australia; NZ = New Zealand; SI = Solomon Islands; NC = New Caledonia. Specimens examined are listed under the individual genes sequenced. Those specimens that were not included in the combined analysis are underlined. Tissue samples are listed according to their museum voucher field numbers. Prefixes for the various museums are: MV = Museum Victoria; AM = Australian Museum; UC = University of Copenhagen; NTAMAG = Northern Territory Museum and Art Gallery; SRI = Massey University. All other tissue samples are from the Australian National Wildlife Collection (CSIRO). More detailed locality and voucher information can be provided on request.

Taxon	Distr	ND2	CO1	Fib5
Amalocichla incerta brevicauda	NG		E325, C176	E325
A. sclateriana sclateriana	NG	E425	E425	E425
Drymodes brunneopygia	Aust	MV2640, MV2639	MV2640, D470	D470, MV2639
D. superciliaris superciliaris	Aust		C773	C773
D. s. brevirostris	NG	E641	E641	E641
Eopsaltria australis australis	Aust		B554	B554
E. a. chrysorrhos	Aust	C316, C500	C500, 49256	C316, C500
E. flaviventris	NC		AM072075	
E. georgiana	Aust	MV324, MV298	MV324, MV298	MV324
E. griseogularis griseogularis	Aust	MV293	MV271	
E. g. rosinae	Aust	MV352	MV352	
Eugerygone rubra saturatior	NG	C030		C030
Heteromyias albispecularis armiti	NG	E452		E452
H. a. centralis	NG	AMFB115	AMFB115	AMFB115
H. cinereifrons	Aust	C605, C688		C604, C605, C688
Melanodryas cucullata cucullata	Aust	031, MVF052		031, MVF052
M. c. picata	Aust	C953	C953	C953
M. c. westralensis	Aust	MV1079, MV1093	MV1079, MV1093	MV1079
M. vittata vittata	Aust	B763, B705		B763, B705
Microeca fascinans fascinans	Aust	D493, C940	D493,C940, MV3451	B648, D493, C940, C944
M. f. assimilis	Aust	MV1359	D349, MV1359	
M. f. pallida	Aust	MV1325	MV1325	C27
M. flavigaster flavigaster	Aust	MV3922, MV1244	MV3922, MV1244	D014, MV1241, MV3922
M. f. flavissima	Aust	JCW083	JCW083	JCW083, C723
M. f. flavissima	NG	E006		C007
M. f. laetissima	Aust		C527	C527
M. flavovirescens cuicui	NG	AMZ94, E659	E687	E687
M. griseoceps kempi	Aust	C732	C732	C732
M. papuana	NG	C064, E301	C064, E301	C051, C064
Monachella muelleriana muelleriana	NG	AML23, E058	E058, E060	L23, E060
Pachycephalopsis hattamensis lecroyae	NG	AMG76		
P. poliosoma poliosoma	NG	C033, E136, E743	C033, E136, E743	C033
Peneonanthe pulverulenta alligator	Aust	MV3918	MV3915, MV3918	
Peneothello bimaculata bimaculata	NG	360, AMS82	360, AMP58	360, AMP58
P. cyanus subcyanea	NG	C036, E187	E135, E187, CO36	C022, E135
P. sigillata sigillata	NG	E415, E455	E417, E455	E417
Petroica australis australis	NZ			SIR45
P. boodang boodang	Aust	081, B883	B398, B883	081
P. b. campbelli	Aust	MV263	MV263	
P. b. leggii		B676	B676	
P. goodenovii	Aust	MV1021, MV2589, D275	MV1021, MV2589, D275	B480, B919, D275
P. macrocephala toitoi	NZ	MV4240	MV4240	
P. multicolor polymorpha	SI		UCJF1	
P. phoenicea	Aust	Pph3, B695, MV4140	Pph3 B695, MV4140	B695
P. rodinogaster rodinogaster	Aust	B666, B683	B666, B683	B666, B683
P. r. inexpectata	Aust			B222
P. rosea	Aust	MV2742, C292	MV2742, C292	B832, C292
Poecilodryas albonotata griseiventris	NG	C168, E269, AMMP36	C168, E269, AMMP36	C168, AMMP36
P. cerviniventris	Aust	NTMAGA91	NTMAGA91	NTMAGA91
P. hypoleuca hypoleuca	NG	E680, AMZ97	E680, AMZ97	E680
P. placens	NG	E682	E682	364, E681, E682
P. superciliosa	Aust	C676	C672, C676	C672, C676
Tregellasia capito capito	Aust	B848	B820	B820, B848
T. c. nana	Aust	C571	C571, C603	C560, C571
T. leucops albifacies	NG	E020, E735	E735, E746	E735, E746, E020
T. l. albigularis	Aust	C736	C735	C735, C736
T. l. nigriceps	NG	AMG87	AMG87	AMG87

partitions – one for β-fibrinogen intron 5 and one for each codon position in the mitochondrial DNA; and (3) seven partitions – one for β-fibrinogen intron 5 and one for each codon position in ND2 and CO1 separately. To select the best partitioning strategy, we compared the log of Bayes Factors as suggested by Kass and Raftery (1995). Tracer v1.5 (Rambaut and Drummond, 2009) was used to calculate, and to compare, the Bayes Factors. For all partitions, two analyses, each with four Metropolis-coupled Markov Chain Monte Carlo simulations (one cold and three heated), were performed. We ran 10 million generations for the individual genes

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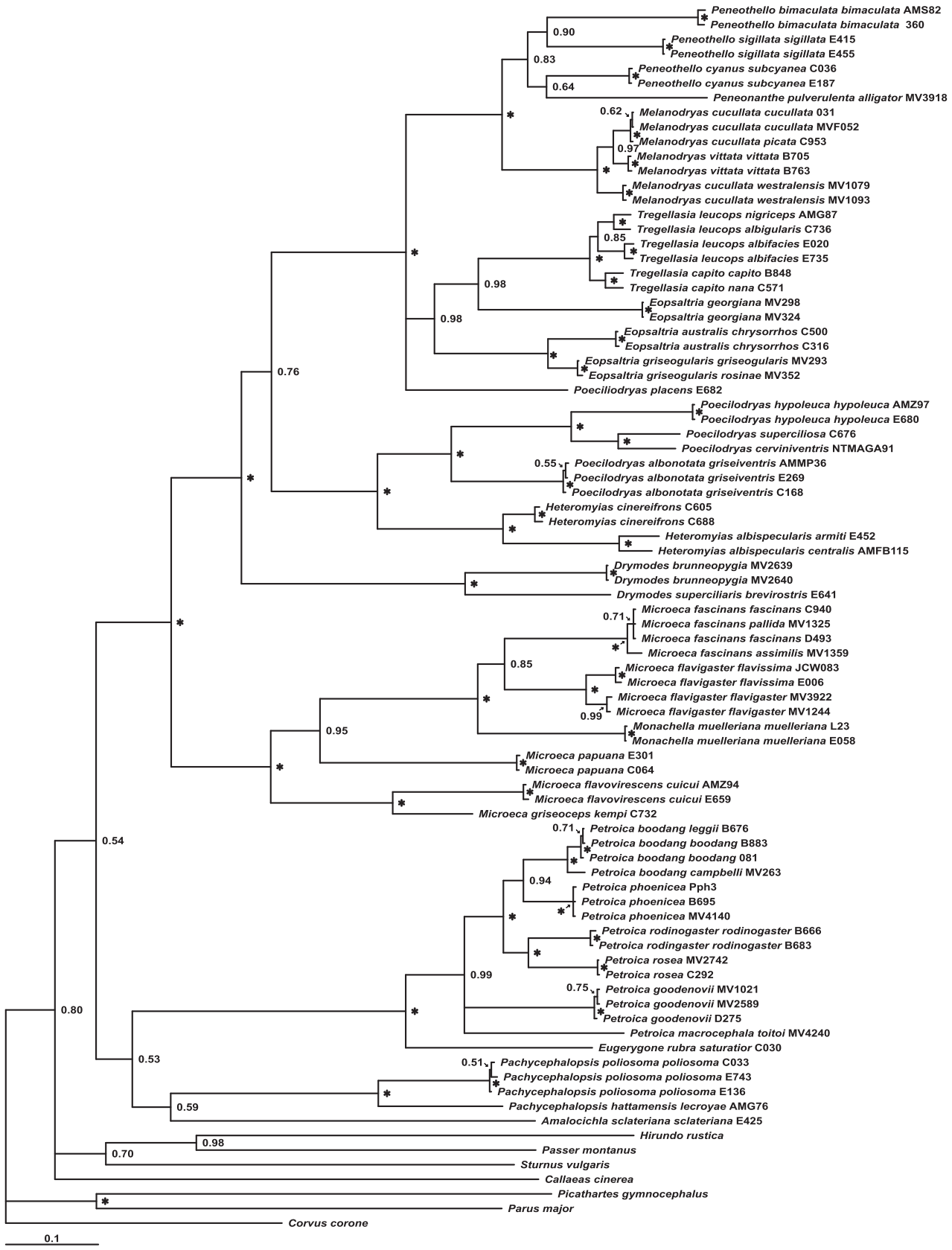

Fig. 1. Bayesian tree (with branch lengths) based on the ND2 sequences. Posterior probabilities are shown at the nodes; values of 1.00 are indicated with an asterisk. Specimen details are listed in Table 1.

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Fig. 2. Bayesian tree (with branch lengths) based on the CO1 sequences. Posterior probabilities are shown at the nodes; values of 1.00 are indicated with an asterisk. Specimen details are listed in Table 1.

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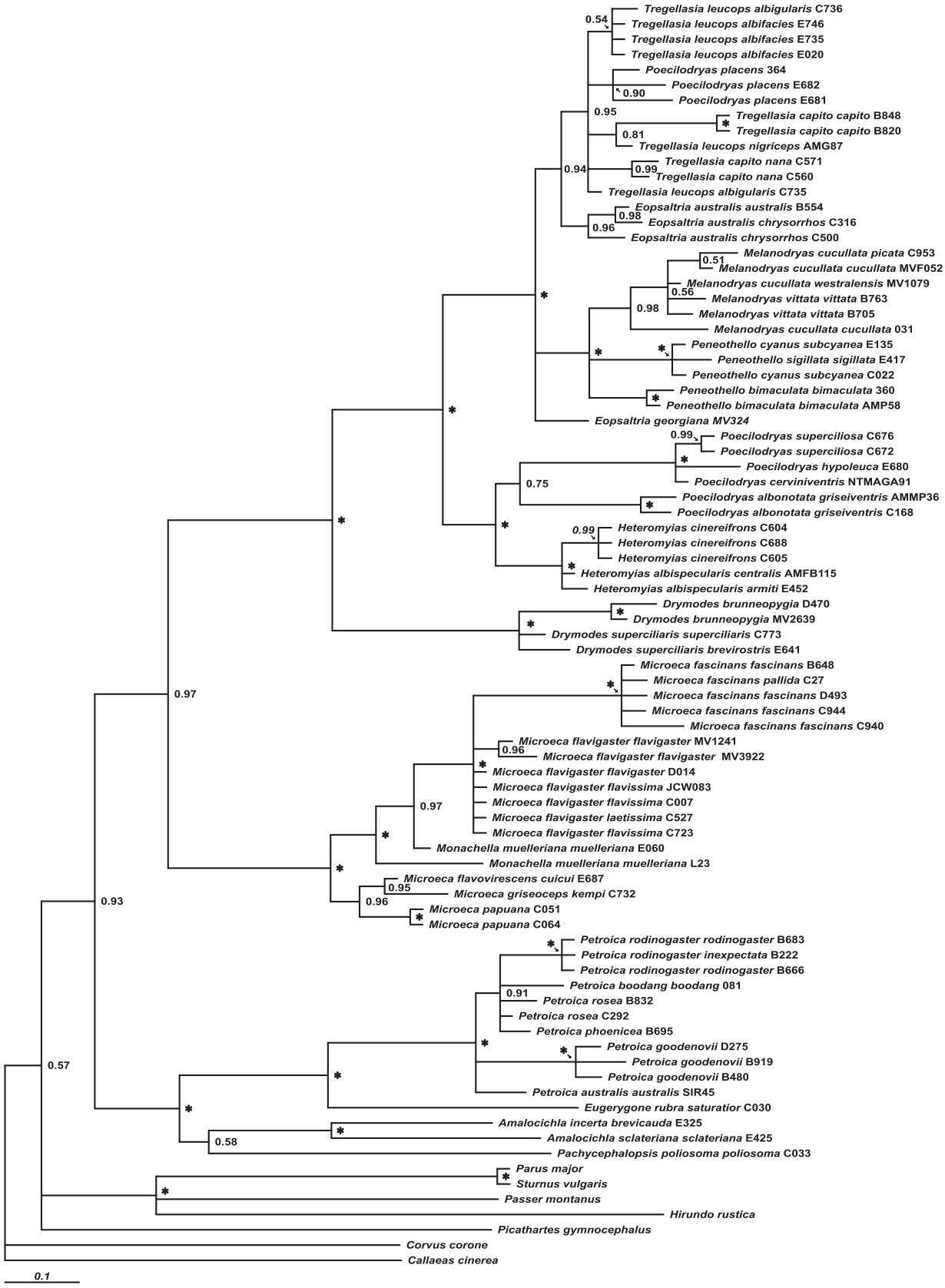

Fig. 3. Bayesian tree (with branch lengths) based on the β-fibrinogen intron 5 sequences. Posterior probabilities are shown at the nodes; values of 1.00 are indicated with an asterisk. Specimen details are listed in Table 1.

and 25 million generations for the concatenated data set, with trees sampled every 1000 generations. We used Tracer v1.5 (Rambaut and Drummond, 2009) to estimate when the chains had reached the apparent target and to ensure that the ESS for each

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parameter was appropriate. Trees sampled during the burn-in phase were discarded.

For the Maximum Likelihood analysis of the concatenated data we used RaxML v7.04 (Stamatakis, 2008) and seven partitions; one for β-fibrinogen intron 5, and one for each codon position in the two mitochondrial genes. In the RaxML analyses we used default parameters and 100 tree search replicates. Node stability on partitioned data sets was estimated with 100 non-parametric bootstrap replicates (Felsenstein, 1985).

3. Results

3.1. Sequence variation and selection of substitution models

Except for a few cases where species lacked a short segment of a studied gene region, the aligned sequences from the mitochondrial ND2 and CO1 genes were 1041 and 653 bp, respectively. The non-coding nuclear β-fibrinogen intron 5 sequences could be easily aligned by eye, due to the low number of insertions/deletions. All gaps were treated as missing data in the analyses. The alignment of the nuclear β-fibrinogen intron 5 consisted of 572 bp (the individual sequences ranged between 548 and 569 bp), while the concatenated data set of all three gene regions consisted of 2266 bp. Uncorrected p-distances among the ingroup taxa (Petroicidae) revealed sequence divergences of 0–26% for ND2, 0–19% for CO1, and 0–15% for β-fibrinogen intron 5.

Most of the indels (insertions or deletions) in the alignment of β-fibrinogen intron 5 were observed in comparisons between the outgroup and ingroup taxa. Within the ingroup taxa, some indels were restricted to single species or consisted of single nucleotides in highly repetitive regions. There were five phylogenetically informative indels among the ingroup taxa: (1) a 20 bp deletion shared between *Amalocichla incerta* and *Amalocichla sclateriana*; (2) a 12 bp deletion shared between the genera *Drymodes*, *Heteromyias*, *Poecilodryas*, *Melanodryas*, *Peneothello*, *Eopsaltria* and *Tregellasia* (β-fibrinogen intron 5 data was lacking for *Peneonanthe*); (3) a 7 bp deletion shared between the genera *Monachella* and *Microeca* (β-fibrinogen intron 5 data was lacking for *E. flaviventris*); (4) a 5 bp deletion shared between all species in the genus *Petroica*; and (5) a 1 bp deletion shared between *Melanodryas*, *Peneothello*, *Eopsaltria*, *Tregellasia* and *Poecilodryas placens* (β-fibrinogen intron 5 data was lacking for *Peneonanthe*). The alignment for the β-fibrinogen intron 5 sequences is provided as online Supplementary material (Supplementary Table 1).

The prior selection of substitution models selected the GTR + I + Γ model for the total ND2 and CO1 sequences, the 1st, 2nd and 3rd codon positions in ND2, and the 1st codon position in CO1. The HKY + Γ model was selected for the 2nd codon position in CO1 and for β-fibrinogen intron 5, while the GTR + Γ model was selected for the 3rd codon position in CO1. Assessment of the log of Bayes Factors indicated that the best partition strategy for the concatenated data set of all genes was seven partitions (one for β-fibrinogen intron 5, and one for each codon position in ND2 and CO1). This was the partition strategy employed for the concatenated data set. After discarding the burn-in phase, the final inference was based on total samples of 16,000 and 18,000 (concatenated from two runs each) from the posterior for the individual loci, and 32,000 samples (concatenated from two runs) from the total concatenated data set.

The GTR + I + Γ model was used for all partitions in the Maximum Likelihood analysis of the concatenated data using RaxML v.7.0.4 (Stamatakis et al., 2008).

3.2. Phylogenetics

The trees obtained from the Bayesian analyses of the individual gene partitions (Figs. 1–3) exhibit different degrees of resolution and are not topologically fully congruent. Overall, the ND2 tree contains the most strongly supported nodes (above 0.95 posterior probability) while the CO1 and β-fibrinogen intron 5 tree are less resolved and have fewer strongly supported nodes. Basal nodes are generally most strongly supported in the β-fibrinogen intron 5 tree. Even though the topologies from the individual gene trees are somewhat difficult to compare, the topological conflicts almost exclusively concern weakly supported nodes (<0.95 posterior probability). It is also noticeable that nodes that receive strong support values in the tree obtained from the concatenated data set (Fig. 4), are generally supported by both the mitochondrial genes (most often the ND2 tree) and the nuclear β-fibrinogen intron 5 tree (although several terminal nodes in the latter tree are not recovered).

The tree obtained from the Maximum Likelihood analysis of the concatenated data set (not depicted) is almost fully congruent with the Bayesian concatenated tree (Fig. 4). Only three topological differences occur and they all involve nodes that are weakly supported by posterior probabilities (⩽0.80) and bootstrap support values (⩽60%). The topologies of both concatenated trees are also in good congruence with the less taxon dense phylogeny presented by Loynes et al. (2009).

4. Discussion

4.1. Phylogenetic relationships

All phylogenetic analyses identified six primary lineages within the Petroicidae: (1) Eopsaltriines comprising *Eopsaltria* (excluding *E. flaviventris*), *Tregellasia*, *Peneothello*, *Melanodryas*, *Poecilodryas* and *Heteromyias*; (2) Drymodines comprising *Drymodes*; (3) Microecines comprising *Microeca*, *Monachella* and *E. flaviventris*; (4) Petroicines comprising *Petroica* and *Eugerygone*; (5) Pachycephalopsines comprising *Pachycephalopsis*; and (6) Amalocichlines comprising *Amalocichla*. In the concatenated tree (Fig. 4), each of these received posterior probabilities of 1.00 and bootstrap support of 100%. These lineages are consistent with results from the taxonomically limited DNA-based study of Loynes et al. (2009), which did not include *Monachella*, *Eugerygone* or *Amalocichla* or any non-Australian representatives of *Microeca*, *Petroica*, *Poecilodryas* and *Heteromyias*.

These DNA-based assessments of relationships are similar to the morphological-based treatment of Schodde and Mason (1999) which recognized three subfamilies (Eopsaltriinae, Petroicinae, Drymodinae). However, several major differences also exist between the DNA-based phylogenies and the treatment of Schodde and Mason (1999). Whereas, Schodde and Mason (1999) combined the petroicines and microecines in a single subfamily, the DNA data clearly suggests that they are not each other's closest relatives. *Amalocichla* was considered by Schodde and Mason (1999) to be a member of the Acanthizidae, but Norman et al. (2009) and the present study confirm that it is in fact part of the Petroicidae.

Here we treat the six primary lineages as subfamilies: Eopsaltriinae Mathews, 1946; Drymodinae Wolters, 1975–1982; Microecinae Loynes et al., 2009; Petroicinae Mathews, 1920; Pachycephalopsinae subfam. nov.; and Amalocichlinae subfam. nov. The new subfamily names Pachycephalopsinae and Amalocichlinae are proposed in accordance with Article 11.7 of the International Commission on Zoological Nomenclature (1999). Pachycephalopsinae: one genus *Pachycephalopsis* Salvadori, 1879, with two species, *Pachycephalopsis poliosoma* (Sharpe, 1882) [type] and *Pachycephalopsis hattamensis* (Meyer, 1874). Amalocichlinae: one genus *Amalocichla* De Vis, 1892, with two species, *A. sclateriana* De Vis, 1892 [type] and *A. incerta* (Salvadori, 1875).

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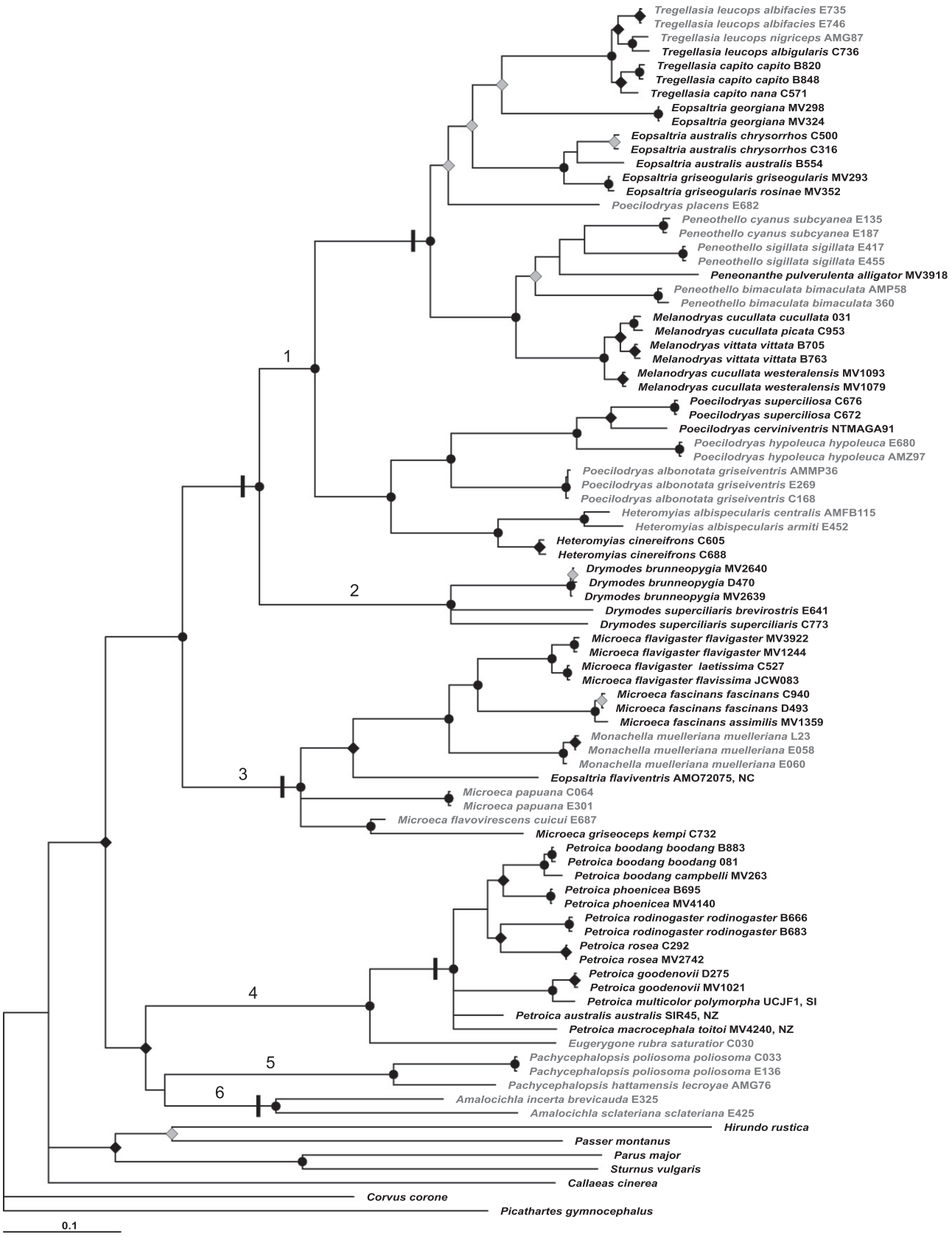

Fig. 4. Bayesian tree (with branch lengths) based on concatenated DNA sequences. Posterior probabilities and bootstrap support values from Maximum Likelihood analysis are indicated at the nodes: filled circles indicate 1.00 posterior probability and 100% bootstrap support; filled diamonds indicate ⩾0.95 posterior probability and ⩾75% bootstrap support; and open circles indicate ⩾0.75 posterior probability and ⩾50% bootstrap support. Specimen details are listed in Table 1. Phylogenetically informative indels are indicated by bars. Numbers refer to the subfamilies of Petroicidae recognized here: 1 = Eopsaltriinae; 2 = Drymodinae; 3 = Microecinae; 4 = Petroicinae; 5 = Pachycephalopsinae; 6 = Amalocichlinae. Species and subspecies in gray refer to those occurring in New Guinea. All other are from Australia unless followed by the following prefixes: NZ = New Zealand; NC = New Caledonia; SI = Solomon Islands.

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4.1.1. Eopsaltriinae

Within the Eopsaltriinae, two subclades were recovered in all analyses. The first comprised *Tregellasia*, *Eopsaltria*, *P. placens*, *Peneothello*, *Melanodryas* and *Peneoenanthe*, while the second comprised *Heteromyias* and *Poecilodryas* (less *placens*). These two clades were also recovered by Loynes et al. (2009). The first subclades further divided into two groups: (1) *Tregellasia*, *Eopsaltria*, *P. placens*; and (2) *Peneothello*, *Melanodryas*, *Peneoenanthe*.

The DNA trees did not recover *Eopsaltria* (*australis*, *griseogularis*, *georgiana*, *and flaviventris*) as a monophyletic genus. The concatenated (Fig. 4) and ND2 (Fig. 1) trees of the present study and that of Loynes et al. (2009) linked *Eopsaltria georgiana* with *Tregellasia*, while our CO1 (Fig. 2) and Fib 5 (Fig. 3) trees isolated the species as an independent lineage, as did the nuclear gene trees of Loynes et al. (2009). In considering the various tree topologies, *georgiana* is best segregated into monotypic *Quoyornis*. Even more divergent was New Caledonian *E. flaviventris*. Both the present study and Loynes et al. (2009) placed it within the Microecinae, and its affinities are discussed in the section dealing with that subfamily.

All trees (Figs. 1–4) linked New Guinean *P. placens* with *Eopsaltria* and *Tregellasia*. Boles (2007) suggested that with its strong yellow plumage it could be included in *Eopsaltria*. However, it is not sister to *Eopsaltria* so it is best segregated in its own genus, for which the names *Genneadryas* is available. Recognition of the four genera, *Eopsaltria* (*australis*, *griseogularis*), *Tregellasia* (*leucops*, *capito*), *Quoyornis* (*georgiana*) and *Genneadryas* (*placens*) is consistent with the relative depths of the nodes leading to each lineage.

The level of uncorrected ND2 sequence distance (6.5–6.9%) separating *Eopsaltria australis* (eastern Australia) and *E. griseogularis* (western Australia) is consistent with species-level separation, supporting current taxonomic treatments (e.g. Schodde and Mason, 1999; Boles, 2007; Christidis and Boles, 2008). Within *E. australis*, two mtDNA haplotype groups were identified which differed by uncorrected CO1 sequence distances of 5.7–5.8%. Loynes et al. (2009) recorded an ND2 distance of 5% between two *E. australis* haplotype groups. These divergences are comparable to those separating *E. australis* and *E. griseogularis*, thereby suggesting that each haplotype group warrants species level recognition. However, the two haplotype groups do not correspond to the two currently recognized subspecies *australis* and *chrysorrhos* (Schodde and Mason, 1999). Consequently, further phylogeographic work is required to ascertain the species limits within *E. australis*.

Ten subspecies of *Tregellasia leucops* are currently recognized (Boles, 2007), of which three were examined in this study: *albigularis* (far northeastern Australia), *nigriceps* (Southern Highlands of New Guinea) and *albifacies* (southeastern New Guinea). Two clades, differing by an average ND2 distance of 5.3% were identified: (1) *albigularis, nigriceps* and (2) *albifacies*. This value is higher than that recorded between the two subspecies of *Tregellasia capito* (ND2 distance of 2.9%) and is comparable to species level divergences in *Eopsaltria*. Although it apparent that additional species level diversity exists within *T. leucop*s, greater coverage of subspecies is required to elucidate species composition within the complex.

Melanodryas cucullata was not recovered as a monophyletic species with respect to its congener, *Melanodryas vittata*. The three individuals of *M. cucullata* from eastern Australia (subspecies *cucullata* and *picata*) and Tasmanian *M. vittata* formed one clade, while the two individuals of *M. cucullata* from western Australia (*westralensis*) comprised a second clade. Western *M. cucullata* differed by up to 4.3% ND2 distance from eastern *M. cucullata*, whereas the ND2 distance between the latter and *M. vittata* was only 2.6%. Such a pattern of relationships conflicts with the placement of *M. cucullata* and *M. vittata* into different subgenera by Schodde and Mason (1999). Given the paraphyly of *M. cucullata*, three species need to be recognized in *Melanodryas*: *M. vittata*, *M. westralensis* and *M. cucullata* (includes *picata*). We recommend that the English names Eastern Hooded Robin and Western Hooded Robin be applied to *M. cucullata* and *Melanodryas westralensis*, respectively.

Melanodryas is part of a clade that includes *Peneothello* (New Guinea) and *Peneonanthe* (coastal northern Australia and New Guinea). The three species of *Peneothello* examined (*cyanus*, *sigillata* and *bimaculata*) were not recovered as a monophyletic group with respect to *Peneoenanthe*, which is in agreement with the findings of Loynes et al. (2009). Consequently, we here treat *Peneonanthe* as a subgenus of *Peneothello*. *P. cryptoleuca* was not examined but is thought to form a sister pair with *P. cyanus* in the subgenus *Papualestes* (Wolters, 1975–1982; Boles, 2007). According to Wolters (1975–1982) and Boles (2007), *P. sigillata* and *P. bimaculata* are also sister species in the subgenus *Peneothello*. However, only the ND2 tree (Fig. 1) recovered a sister relationship between the two (c.f. Loynes et al., 2009). Further DNA analysis including *P. cryptoleuca* is required to resolve subgeneric limits within *Peneothello*.

The other clade of Eopsaltriinae comprises *Poecilodryas* (less *placens*) and *Heteromyias*. When Mayr (1941) rationalized the limits of *Poecilodryas*, he combined six species that had previously been placed in five genera by Mathews (1930). Mayr (1986) retained this arrangement, other than for the removal of *pulverulenta* to *Peneoenanthe*. Boles (2007) raised the possibility that *P. placens* and *Poecilodryas albonotata* might be better placed elsewhere. The DNA trees confirm that *placens* does not belong here and is part of the *Eopsaltria–Tregellasia* assemblage. The other four species in this genus examined (*P. hypoleuca*, *P. superciliosa*, *P. cerviniventris* and *P. albonotata*) were recovered as a monophyletic group. Although *P. brachyura* was not examined, it shares similar plumage patterns and foraging behavior with *P. hypoleuca*, *P. superciliosa* and *P. cerviniventris* (Boles, 2007). Conversely, *P. albonotata* lacks the facial and wing patterns of the others, has a more massive but flattened bill and forages primarily by the flycatching rather than pouncing. These morphological and behavioral differences are also reflected in the DNA-based trees, with *P. albonotata* being the most divergent member of *Poecilodryas*. As suggested by Boles (2007), it is here separated generically into monotypic *Plesiodryas*.

The relatively high ND2 distance (8.5%) between *Poecilodryas superciliosa* and *Poecilodryas cerviniventris* is consistent with the recent practice of treating them as separate species (Schodde and Mason, 1999; Boles, 2007; Christidis and Boles, 2008).

Although some authors have included *Heteromyias* in *Poecilodryas* (e.g. Schodde, 1975; Schodde and Mason, 1999; Dickinson, 2003), the relatively high level of ND2 distance (15.5–20.6%) is such, that retention of the two is the more appropriate treatment.

Heteromyias cinereifrons of northeastern Australia is sometimes included in New Guinean *Heteromyias albispecularis* (Schodde, 1975; Schodde and Mason, 1999; Dickinson, 2003). The level of ND2 distance between *H. cinereifrons* and *H. albispecularis* (10.5–11.3%) is more consistent with separate species treatment. The latter species has several forms which break up into three subspecies groups (Boles, 2007). Representatives from two of these groups were examined here: *H. a. armitii* (southeastern New Guinea) and *H. a. centralis* (northern and central New Guinea). The 5.7% ND2 sequence distance recorded between *armitii* and *centralis* suggests that *H. albispecularis* may comprise more than one species. Greater coverage of subspecies is required to elucidate species composition within the *H. albispecularis* complex.

4.1.2. Drymodinae

The CO1, β-fibrinogen intron 5 and concatenated trees (Figs. 2–4) recovered three deeply diverged lineages within *Drymodes*: *D. brunneopygia* (southern Australia); *D. superciliaris brevirostris* (New Guinea); and *D. s. superciliaris* (northeastern Australia).

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ND2 data were not obtained for last taxon. The New Guinean and Australian forms of *Drymodes superciliaris* are arguably best separated out as species. We the retain English name Northern Scrub-robin for the Australian form *D. superciliaris*, and refer the three New Guinean subspecies (*beccarii*, *nigriceps* and *brevirostris*) to *D. beccarii* Salvadori, 1876. The English name New Guinean Scrub-robin is applied to the latter.

4.1.3. Microecinae

Morphological assessments (e.g. Boles, 2007) have suggested a close association between *Monachella*, *E. flaviventris* and *Microeca*. All DNA trees (Figs. 1–4) not only confirmed this, but nested *Monachella* and *E. flaviventris* within *Microeca*. *Monachella* formed a clade with *Microeca fascinans* and *M. flavigaster*, which in turn was linked to *E. flaviventris* (only CO1 data were available for the latter). *Microeca flavovirescens* and *Microeca griseoceps* were recovered as sister taxa as were *M. fascinans* and. *M. flavigaster*. *Microeca papuana* is believed to represent the most divergent member of the genus (e.g. Schodde and Mason, 1999) and the DNA trees (Figs. 1–4) separated it as a monotypic lineage.

Because *Monachella* and *E. flaviventris* are embedded in *Microeca*, both could be included in a broader concept of that genus. However, the observed level of ND2 distances between major lineages within the Microecinae ranged from 17% to 20.3% which is comparable to the distance separating *Heteromyias* and *Poecilodryas*. Consequently, the action taken here is to divide *Microeca* into three genera, retain *Monachella* for *muelleriana*, and place *flaviventris* in a new monotypic genus. The name *Microeca* now applies to *M. fascinans*, *flavigaster* (and presumably *hemixantha*); *papuana* is segregated into *Deviocea*; while *flavovirescens* and *griseoceps* are placed in *Kempiella*. As no available generic name exists for *flaviventris*, we propose a new genus for this species.

Cryptomicroeca, gen. nov. Christidis, Irestedt, Rowe, Boles and Norman, this study

Type species: *Eopsaltria flaviventris* Sharpe, 1903.

The name is derived from *kryptos*, (Greek, hidden) and *Microeca* (the genus of petroicine robins to which this species is related); it alludes to this long undetected relationship.

Within *M. fascinans*, southeastern *fascinans* and northwestern *pallida* have sometimes been treated as a species, separate from southwestern *assimilis* (e.g. Sharpe, 1879). Representatives of all three forms were included in the present study. Both mitochondrial trees (Figs. 1 and 2) recovered *M. f. fascinans* and *M. f. pallida* as a clade separate from *M. f. assimilis*. Nevertheless, the ND2 distance between the two clades was low (c. 1.7%) supporting recognition of only one species.

There were, however, two deep lineages recovered in *Microeca flavigaster*: (1) *M. f. flavissima* (Cape York Australia and southeastern New Guinea) and *M. f. laetissima* (northeastern Australia); and (2) *M. f. flavigaster* (northern Australia). ND2 distances between the two clades were in the order of 4.2–4.3% ND2; comparable to other sister species level distances recorded within Petroicidae. Inclusion of DNA data on *M. f. tormenti* (northwestern Australia), *M. f. laeta* (northern New Guinea) and *M. f. tarara* (southwestern New Guinea) is critical to determining whether additional species should be recognized within the *M. flavigaster* complex. The low ND2 distance (0.7%) separating *M. f. flavissima* and *M. f. laetissima* is more consistent with the treatment of Mayr (1986) who only recognized one subspecies in eastern Australia (c.f. Schodde and Mason, 1999).

4.1.4. Petroicinae

A close association between *Petroica* and monotypic *Eugerygone* was recovered in all the DNA trees and is consistent with morphologically-based assessments (Schodde and Mason, 1999; Boles, 2007). The levels of uncorrected ND2 sequence distance between *Eugerygone* and *Petroica* (14.1–17.0%) are consistent with generic recognition.

Schodde and Mason (1999) maintained four subgenera within *Petroica*: *Petroica* (*boodang*, *multicolor*, *goodenovii*, *macrocephala* and *bivittata*); *Littlera* (*phoenicea*); *Erythrodryas* (*rosea*, *rodinogaster*); and *Miro* (*australis*, *traversi*). The subgenus *Petroica* was not recovered in any of the DNA trees. A sister relationship between *P.* (*P.*) *boodang* and *P.* (*Littlera*) *phoenicea* was consistently recovered, though with low support. Although the combined tree of Loynes et al. (2009) identified P. (P.) *boodang* and P. (P.) *goodenovii* as sister species, this was influenced strongly by the two sharing identical B5 sequences. Their other gene trees were more consistent with the present study in identifying a closer relationship between *Petroica* boodang and *Petroica phoenicea*. In our study, *P. boodang* was not sister to *P. multicolor*, even though the two have been treated as either a single species (e.g. Mayr, 1986) or as sister species (Schodde and Mason, 1999). Our results, based on a single gene (CO1), instead, suggest a closer relationship between *P. multicolor* and *Petroica goodenovii*.

Within *P. boodang*, eastern Australian *boodang* and Tasmanian *leggii* were almost identical in DNA sequences while western Australian *campbelli* was more distant (Figs. 1, 3 and 4). Although Schodde and Mason (1999) tentatively separated *P. b. leggii* from *P. b boodang*, the DNA data are more consistent with the treatment of Mayr (1986) who only recognized one subspecies across eastern Australia and Tasmania.

Both mtDNA gene trees (Figs. 1 and 2) did not align *P. macrocephala* with other members of the subgenus *Petroica*, and instead recovered it as the first diverged lineage. Miller and Lambert (2006) recorded a sister relationship between *P. macrocephala* and *P.* (*Miro*) *traversi*, while *P.* (*Miro*) *australis* was either weakly linked to *P. multicolor* or to the *P. macrocephala–traversi* group, depending on the tree building algorithm used. In our study, only β-fibrinogen intron 5 was available for *P. australis* and this species was recovered as an early diverged lineage in the tree (Fig. 3).

Pink-breasted *P. rosea* and *P. rodinogaster* were recovered as sister species in the concatenated (Fig. 4) and ND2 (Fig. 1) trees, but not in the CO1 (Fig. 2) or β-fibrinogen intron 5 (Fig. 3) trees. Similarly, in the Loynes et al. (2009) study the nuclear gene trees did not recover the two as sister species. Although Schodde and Mason (1999) maintained the two in the subgenus *Erythrodryas* they noted that it may constitute a paraphyletic group.

The DNA data indicates that the subgeneric circumscription within *Petroica* requires a major re-assessment. Whether additional genera could be recognized is also worthy of further investigation. Better coverage of mitochondrial and nuclear DNA data across all species of *Petroica*, including New Guinean *P. archboldi* and *P. bivittata*, is needed before such taxonomic revision is possible.

4.2. Ecology

Christidis and Norman (2010) commented that within Australian songbirds, sympatric congeners were generally part of separate lineages and were rarely sister taxa. Examples included *Acanthiza* thornbills (Nicholls et al., 2000), *Amytornis* grasswrens (Christidis, 1999), *Malurus* fairy-wrens (Christidis and Schodde, 1997) and *Meliphaga* honeyeaters (Norman et al., 2007). Such a pattern is consistent with the conclusions of Grant and Grant (1997) and Peterson et al. (1999) that most speciation in birds occurs in geographical, not ecological dimensions. Nevertheless, examples of ecological speciation have been suggested in birds-of-paradise (Irestedt et al., 2009) and honeyeaters (Norman et al., 2007). Within the Microecinae, *Kempiella* (formerly *Microeca*) *flavovirescens* (lowland New Guinean rainforest) and *K. griseoceps*

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(lower montane New Guinean and northeastern Australian rainforest) were recovered as sister species. The two are generally considered to be altitudinally separated ecological counterparts (Diamond, 1972; Schodde and Mason, 1999) and they may represent another example of ecological speciation.

Loynes et al. (2009) noted that the *Petroica* robins of eastern Australia (*phoenicea*, *boodang*, *rodinogaster* and *rosea*) share breeding ranges and were strongly distinguished from one another in terms of genetic divergence, suggesting a long evolutionary history. Although the ND2 (Fig. 1) and concatenated (Fig. 4.) trees recovered *P. rosea* and *P. rodinogaster* as sister species (though statistical support was low), the two differ in foraging behavior. *Petroica rosea* is a warbler-like foliage gleaner while *P. rodinogaster* employs a typical robin 'perch and pounce' method and the two cannot be considered as ecological replacements. The woodland-adapted *P. phoenicea* has been considered to be one of the more divergent members of the genus (e.g. Schodde and Mason, 1999), but the mtDNA trees (Figs. 1 and 2) and combined tree (Fig. 4) recovered it as sister to *P. boodang*, though with low support. Further resolution of the interrelationships between the species of *Petroica* is needed to better assess the role of ecological differentiation in generating taxonomic diversity.

4.3. Biogeography

An examination of the deeper divergences within the Petroicidae indicates that most are centered within New Guinea. The Amalocichlinae and Pachycephalopsinae are restricted to New Guinea. Within the Microecinae, the basal taxa *Deviocea* (formerly *Microeca*) *papuana*, *Kempiella flavovirescens* and *Kempiella griseoceps* are largely restricted to New Guinea, with only the last species also occurring in Australia (Cape York Peninsula). The only other microecine species that occur in Australia, *M. flavigaster* and *M. fascinans* represent terminal branches. This suggests a New Guinean center of origin for the Microecinae. The Drymodinae are represented in both Australia and New Guinea and it is not possible, on current data, to determine their likely biogeographical origin. Although the Eopsaltriinae are distributed across New Guinea and Australia, basal lineages such as *Genneadryas* (formerly *Poecilodryas*) *placens* and *Plesiodryas* (formerly *Poecilodryas*) *albonotata* are restricted to New Guinea. Within the Petroicinae, *Eugerygone* is restricted to New Guinea, while *Petroica* is widespread across the Australo-Pacific region. Unfortunately, the New Guinean members of *Petroica* were not examined.

Christidis and Norman (2010) reviewed the role of several biogeographic barriers in generating species diversity within Australia. One of the most significant barriers identified was the Carpentarian Barrier in northern Australia. Several recent molecular studies have identified major taxonomic breaks coinciding with this barrier that do not correspond to variations in plumage patterns. Examples include fairy-wrens *Malurus melanocephalus* (Jennings and Edwards, 2005) and honeyeaters *Melithreptus albogularis* (Toon et al., 2010). In both these cases, plumage-based assessments identify a different subspecies in central-eastern Australia from that occurring in northeastern Australia and across northern Australia. DNA data instead, place the major taxonomic break as occurring between the northern Australian and northeastern Australian populations (Jennings and Edwards, 2005; Toon et al., 2010).

The DNA data obtained on the Petroicidae further demonstrate the significance of the Carpentarian Barrier in generating taxonomic diversity. Within *M. flavigaster*, the two major lineages identified by the DNA data corresponded to a northern Australian clade and a northeastern Australian clade (including eastern New Guinea). The genetic divergence between the two clades was suggestive of species level separation. The present study also substantiates the species level divergence between northern/northwestern *P. cerviniventris* and northeastern *P. superciliosa*. The other species of Petroicidae for which DNA are available for populations on either side of the Carpentarian Barrier is *Peneothello* (*Peneonanthe*) *pulverulenta*. Loynes et al. (2009) obtained ND2 sequence data from northeastern Australian *leucura*, while the present study examined *alligator* from the Northern Territory. In this instance the ND2 distance between the two (2.1%) was consistent with subspecies level differentiation.

Although the New Guinean populations of *M. flavigaster* were found to be closely related to those of northeastern Australia, there were examples in the Petroicidae where species level divergences were observed between Australian and New Guinean populations. The New Guinea and northern Australian forms of *D. superciliaris* were as diverged from one another as they were from *D. brunneopygia*. Separation of New Guinean and Australian populations of *Heteromyias* was confirmed by the DNA data and there was an indication that some New Guinean populations of *T. leucops* could be specifically separated from Australian populations. The honeyeater *Meliphaga gracilis* (Norman et al., 2007) and the logrunner *Orthonyx temminckii* (Norman et al., 2002) are additional examples of species that once were thought to be shared between Australia and New Guinea, but were revealed by DNA data to each comprise separate Australian and New Guinean species. Further study on other presumed shared species between Australia and New Guinea could reveal additional species level diversity.

Toon et al. (2010) identified another case in honeyeaters where plumage-based assessments of species limits did not accord with DNA data, this time in southern Australia. Eastern populations of *Melithreptus lunatus* formed a clade with Tasmanian *M. affinis* separate from western populations of *M. lunatus*. In the present study, an identical pattern of discordance between plumage pattern and DNA lineages was found in *Melanodryas*. Eastern *M. cucullata* and Tasmanian *M. vittata* formed one clade, while western populations of *M. cucullata* formed a separate clade. A closer evolutionary relationship between eastern Australian and Tasmanian taxa, relative to western ones, is common and established examples include honeyeaters (*Acanthorhynchus*, *Anthochaera*), finches (*Stagonopleura*), black-cockatoos (*Calyptorhynchus*) and *Petroica boodang* (present study: Fig. 1). In each of these cases, plumage patterns are consistent with an eastern Australian/Tasmanian clade and a western clade. Conversely, *Melithreptus* and *Melanodryas* add to a growing number of examples in which DNA differentiation does not track plumage patterns but is consistent with biogeographical barriers. Such patterns suggest that plumage may be more influenced by environmental factors than previously thought.

The situation in *Melanodryas* is particularly interesting. The Tasmanian form *M. vittata* is monomorphic with adults resembling females/immatures of dimorphic mainland forms of *M. cucullata*. Interestingly, two other species complexes have representatives in Tasmania that resemble mainland immatures. The adult Green Rosella (*Platycercus caledonicus*) from Tasmania resembles immature mainland Crimson Rosellas (*P. elegans*). Similarly, the Tasmanian Forty-spotted Pardalote (*Pardalotus quadragintus*) resembles immature mainland Spotted Pardalotes (*P. punctatus*). Why juvenile and immature plumages should be retained in these Tasmanian species is worthy of further research. Price (2007) has noted that in several species complexes, the "duller" plumaged species tend to occur on islands.

The present study has revealed that within the Petroicidae, vicariant barriers have played a significant role in generating taxonomic diversity in Australian and New Guinea, with dispersal playing a minor role. Miller and Lambert (2006) suggested that two invasions of *Petroica* from Australia gave rise to the 3–4 species currently found in New Zealand. Apart from New Zealand *Petroica*, only four other species have expanded away from Australia and

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New Guinea; *M. hemixantha* on Tanimbar, *Monachella muelleriana coultasi* on New Britain, *P. multicolor* in the south-west Pacific, and *Cryptomicroeca* (formerly *Eopsaltria*) *flaviventris* on New Caledonia. All four share a "flycatcher body-plan". Boles (2007) noted that unlike other members of the genus, populations of *P. multicolor*, from the Solomon Islands and south-west Pacific, are very similar to the microecines in foraging behavior and body proportions. One could surmise from this that a "flycatcher body-plan" has facilitated dispersal across water barriers. Dispersal as a generator of species diversity in the Indo-Pacific is now well documented in monarchine flycatchers (Filardi and Moyle, 2005), whistlers (Jønsson et al., 2008, 2010a), cuckoo-shrikes (Jønsson et al., 2010b) and white-eyes (Moyle et al., 2009). Christidis and Norman (2010) noted that the ability to adapt to mangrove habitats appeared linked to island dispersal in several Australasian songbird genera. Future studies need to consider the role of ecological adaptations in facilitating dispersal across water barriers.

4.4. Taxonomic revision of Petroicidae

A taxonomy based on the findings from the present study is detailed below. Three areas require comment. Firstly, within *Peneothello*, the composition of the subgenera *Peneothello* and *Papualestes* adopted here requires further confirmation. Secondly, whether *P. brachyura* could be separated into the subgenus *Leucophantes*, as advocated by Wolters (1975–1982), was not resolved as that species was not available for DNA analysis. Finally, subgenera clearly exist within *Petroica*, as judged by DNA distances between lineages, but their composition cannot be resolved at the present because: (1) DNA data is either lacking or minimal for key species; and (2) the DNA-based relationships are highly contradictory with regard to the existing subgeneric classification (e.g. Wolters, 1975–1982). Consequently, no subgenera are indicated here.

Family PETROICIDAE Mathews, 1920
- Subfamily EOPSALTRIINAE Mathews, 1946
  - *TREGELLASIA* Mathews, 1912 (*capito*, *leucops* [at least 2 species])
  - *QUOYORNIS* Mathews, 1912 (*georgiana*)
  - *EOPSALTRIA* Swainson, 1832 (*australis* [2 species], *griseogularis*)
  - *GENNAEODRYAS* Mathews, 1920 (*placens*)
  - *MELANODRYAS* Gould, 1865 (*cucullata*, *vittata*, *westralensis*)
  - *PENEOTHELLO* Mathews, 1920
    - Subgenus *Peneothello* Mathews, 1920 (*sigillata*, *bimaculata*)
    - Subgenus *Papualestes* Mathews, 1920 (*cyanus*, *cryptoleuca*)
    - Subgenus *Peneonanthe* Mathews, 1920 (*pulverulenta*)
  - *POECILODRYAS* Gould, 1865 (*cerviniventris*, *hypoleuca*, *superciliosa*, *brachyura*)
  - *PLESIODRYAS* Mathews, 1920 (*albonotata*)
  - *HETEROMYIAS* Sharpe, 1879 (*albispecularis* [probably at least 2 species], *cinereifrons*)
- Subfamily DRYMODINAE Wolters 1975–1982
  - *DRYMODES* Gould, 1840 (*brunneopygia*, *superciliaris*, *beccarii*)
- Subfamily MICROECINAE Loynes, Joseph and Keogh, 2009
  - *MICROECA* Gould, 1840 (*fascinans*, *flavigaster* [probably at least 2 species], *hemixantha*)
  - *MONACHELLA* Salvadori, 1874 (*muelleriana*)
  - *CRYPTOMICROECA* this work (*flaviventris*)
  - *KEMPIELLA* Mathews, 1913 (*griseoceps*, *flavovirescens*)
  - *DEVIOECA* Mathews, 1925 (*papuana*)
- Subfamily PETROICINAE Mathews, 1920
  - *EUGERYGONE* Finsch, 1901 (*rubra*)
  - *PETROICA* Swainson, '1829'
    - Subgeneric compositions still to be resolved (*boodang*, *phoenicea*, *multicolor*, *goodenovii*, *rodinogaster*, *rosea*, *macrocephala*, *traversi*, *australis*, *archboldi*, *bivittata*)
- Subfamily PACHYCEPHALOPSINAE this work
  - *PACHYCEPHALOPSIS* Salvadori, 1879 (*hattamensis*, *poliosoma*)
- Subfamily AMALOCICHLINAE this work
  - *AMALOCICHLA* De Vis, 1892 (*sclateriana*, *incerta*)

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.08.014.

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