Molecular Phylogenetics and Evolution 52 (2009) 488–497

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

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

A multi-gene phylogeny reveals novel relationships for aberrant genera of Australo-Papuan core Corvoidea and polyphyly of the Pachycephalidae and Psophodidae (Aves: Passeriformes)

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ARTICLE INFO

Article history:
Received 15 December 2008
Revised 20 March 2009
Accepted 23 March 2009
Available online 31 March 2009

Keywords:
Core Corvoidea
Pachycephalidae
Psophodidae
Australo-Papuan radiation

ABSTRACT

The core Corvoidea is the largest and most diverse oscine assemblage within the Australo-Papuan region. Although central to an understanding of the evolutionary history and biogeography of the group the composition and intergeneric relationships of the Australo-Papuan radiation remain poorly understood. Here we analysed DNA sequence data from two nuclear gene regions and the mitochondrial cytochrome *b* gene, for 40 species of core Corvoidea to test the systematic affinities of key Australo-Papuan lineages. The families Pachycephalidae (whistlers, shrike-thrushes and allies) and Psophodidae (whipbirds, quail-thrush and allies) were both recovered as polyphyletic assemblages. The core pachycephaline assemblage comprised *Pachycephala*, *Colluricincla*, parts of *Pitohui*, and *Falcunculus* with the remaining genera resolving as four divergent lineages with no clearly defined affinities. *Ptilorrhoa* and *Cinclosoma* (Cinclosomatidae) formed a clade separate from *Psophodes* (Psophodidae) but neither clade showed clear affinities to any other taxa. Novel relationships were also identified for three aberrant New Guinean genera; ditypic *Machaerirhynchus* and monotypic *Rhagologus* were both nested within an assemblage that included the Artamidae and African malaconotoids (bush-shrikes and allies) while the enigmatic *Ifrita* was found to be part of an assemblage that included the Monarchidae and Paradisaeidae.

1. Introduction

A range of molecular datasets have identified the Australo-Papuan region as the centre of diversification for the oscine passerines (e.g. Sibley and Ahlquist, 1990; Christidis and Schodde, 1991; Barker et al., 2002, 2004; Ericson et al., 2002a). The key assemblages within the region include the Menurae, Ptilonorhynchidae, Climacteridae, Meliphagoidea, Orthonychidae, Pomatostomidae and core Corvoidea (sensu Barker et al., 2004). The core Corvoidea is the largest and most diverse assemblage within the Australo-Papuan region and also has major radiations within Africa and Asia (Beresford et al., 2005; Jønsson and Fjeldså, 2006). The circumscription of many genera and families within the core Corvoidea, as well as their phylogenetic affinities, remain unresolved. Molecular analyses have revealed that some taxa placed within the core Corvoidea are members of other assemblages (examples in Pasquet et al., 2002; Jønsson et al., 2007, 2008a) while some genera have been shown to be polyphyletic (Jønsson et al., 2007, 2008a). Nevertheless the emerging picture is of an African-centred radiation comprising bush-shrikes, vangas and allies (malaconotoids), and an Australo-Papuan radiation comprising the monarchs, fantails and birds-of-paradise among others (Barker et al., 2004; Fuchs et al., 2004; Moyle et al., 2006).

Within the Australo-Papuan region the Pachycephalidae has not been examined in detail. This assemblage (the Pachycephalinae of Sibley and Ahlquist, 1990) has previously been considered to include sitellas (*Daphoenositta*), the New Zealand endemic genus *Mohoua*, whistlers (*Pachycephala*), shrike-thrushes (*Colluricincla*), crested bellbird (*Oreoica*), shrike-tit (*Falcunculus*), pitohuis (*Pitohui*) and mottled whistler (*Rhagologus*). Several monotypic genera – goldenface (*Pachycare*), olive-flanked whistler (*Hylocitrea*), maroon-backed whistler (*Coracornis*) and wattled plough-bill (*Eulacestoma*) – were also assigned to the Pachycephalinae (Sibley and Ahlquist, 1990) although DNA–DNA hybridization data was lacking. Preliminary molecular analyses employing multi-gene datasets have since shown that *Pitohui* is polyphyletic (Jønsson et al., 2008b; Dumbacher et al., 2008) and that *Hylocitrea* is a member of the Passerida (Jønsson et al., 2008a; Spellman et al., 2008),

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doi:10.1016/j.ympev.2009.03.019

while Norman et al. (in press) have shown that *Pachycare* also lies outside the core Corvoidea and is a member of the Acanthizidae. The presumed monophyly of the remaining pachycephalines requires examination.

Another controversial assemblage within the Australo-Papuan core Corvoidea is the Psophodidae. The family currently comprises five genera restricted to Australia and New Guinea (*Androphobus*, *Cinclosoma*, *Ifrita*, *Psophodes*, *Ptilorrhoa*) following the demonstration that neither southeast Asian *Eupetes* (Jønsson et al., 2007) nor New Guinean *Melampitta* (Barker et al., 2004) are members of this assemblage as previously suggested (reviewed in Boles, 2007). The monophyly of the remaining members of the Psophodidae requires examination, in particular the affinities of the enigmatic New Guinean *Ifrita* which has proven difficult to place (see Dickinson, 2003). The relationships of the Australo-Papuan boatbills (*Machaerirhynchus*) also require examination. Although it is traditionally placed within the Monarchidae, microcomplement fixation data (Baverstock et al., 1992) and osteological comparisons (Schodde and Mason, 1999) indicate that this genus is a highly divergent flycatcher lineage or placed outside the Monarchidae. Irestedt et al. (2008) have recently shown that the Fijian endemic silktail *Lamprolia victoriae* is not a member of the Monarchidae (Olson, 1980; Sibley and Ahlquist, 1990) or Dicruridae (Sibley and Monroe, 1990; Dickinson, 2003) as traditionally accepted but is closely aligned with the Rhipiduridae.

The composition of the Artamidae (woodswallows, butcherbirds and allies) has also been revised recently. The study of Moyle et al. (2006) indicates that the Bornean bristlehead (*Pityriasis*) is not a member of the Artamidae as proposed by Sibley and Ahlquist (1990), but is aligned with the larger artamid–malaconotoid assemblage. The remaining artamid genera are generally regarded as comprising three lineages: (1) *Cracticus, Gymnorhina, Strepera* (traditionally segregated as the family Cracticidae); (2) *Peltops*; (3) *Artamus* (Schodde and Mason, 1999; Manegold, 2008) although Christidis and Boles (2008) include monotypic *Gymnorhina* in *Cracticus*. Dickinson (2003) proposed resegregating *Artamus* into a family on its own implying a closer affinity between *Peltops* and the remaining genera.

Resolution of the composition and relationships within the Australo-Papuan core Corvoidea is essential to our understanding of the biogeographical patterns across the pan-tropical region of Africa, Asia and Australasia. In order to provide better clarity on the composition and phylogenetic relationships of Australo-Papuan genera within the core Corvoidea, we analysed DNA sequence data from the nuclear recombination activating gene-1 (RAG-1), myoglobin intron II (Myo2), and the mitochondrial cytochrome *b* (Cyt *b*) gene for 61 species. The dataset included representatives of the major Australo-Papuan lineages of core Corvoidea along with several aberrant genera from this region Representatives from other Australo-Papuan centred assemblages, along with the African malaconotoids, the Vireonidae and Passerida, were included in the study to assist in better defining the phylogenetic placement of these aberrant genera and species. In particular we aimed to test (1) monophyly of the Pachycephalidae, especially the placement of *Eulacestoma, Falcunculus, Mohoua* and *Rhagologus* within this group, and the affinities of *Daphoenositta* (Neosittidae), (2) monophyly of the Psophodidae and placement of the enigmatic *Ifrita*, (3) affinities of *Machaerirhynchus* to the Monarchidae and (4) relationships among the three lineages of the Artamidae.

2. Materials and methods

2.1. Taxon sampling

Our dataset comprised 61 ingroup taxa (Table 1) and included 39 species of core Corvoidea spanning the entire radiation within the Australo-Papuan region, three representatives of the African malaconotoid radiation and a member of the Vireonidae. The remaining 20 species comprised representatives from the other major lineages of Australo-Papuan oscines [Ptilonorhynchidae, Climacteridae, Meliphagoidea (Acanthizidae, Maluridae, Meliphagidae), Menuridae, Orthonychidae, Petroicidae and Pomatostomidae], along with representatives of the Passerida. The suboscines (Pittidae) *Pitta versicolor* (for Myo2) and *Hydronornis (Pitta) baudii* (for RAG-1 and Cyt *b*) were chosen as outgroups. Taxonomic nomenclature follows Christidis and Boles (2008) for Australian taxa and Dickinson (2003) for the others. Specimen details are provided in Table 1 for the 38 taxa sequenced as part of this study. DNA sequences for the remaining taxa were sourced from the literature (Cicero and Johnson, 2001; Ericson et al., 2002b and sources therein; Ericson and Johansson, 2003; Barker et al., 2004; Fuchs et al., 2004; Alström et al., 2006; Gonzalez et al., 2008) with associated GenBank accession numbers provided in Table 1.

2.2. DNA extraction and sequencing

Genomic DNA was prepared from tissue or blood samples using the QIAamp DNA Mini Kit (QIAGEN) or by the salt-chloroform extraction method of Gemmell and Akiyama (1996). Nucleotide sequence data were obtained from the nuclear gene regions RAG-1 and Myo2, and from the mitochondrial Cyt *b* gene. Irestedt et al. (2001) and Johansson et al. (2001) describe protocols for the PCR amplification and sequencing of RAG-1. Myo2 was amplified as a single fragment and sequenced using primers and conditions described by Heslewood et al. (1998) and Irestedt et al. (2002). The amplification and sequencing of Cyt *b* followed Johansson et al. (2002). A subset of samples was purified and sequenced using the procedures described in Norman et al. (2007). GenBank accession numbers for these newly derived sequences are provided in Table 1.

2.3. Phylogenetic analysis

As there were relatively few insertions in the Myo2 intron, the combined sequences could easily be aligned by eye with all gaps treated as missing data in the subsequent analyses. Bayesian inference (BI: Holder and Lewis, 2003; Huelsenbeck et al., 2001), maximum likelihood (ML) and maximum parsimony (MP) were used to estimate the phylogenetic relationships. The models for nucleotide substitutions used in the Bayesian analyses were selected for each gene individually by applying the Akaike Information Criterion (AIC, Akaike, 1973) and the program MrModeltest 2.2 (Nylander, 2005) in conjunction with PAUP∗ (Swofford, 1998). Parameters were estimated separately for each codon position of Cyt *b*. 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).

Two runs were conducted, each with one cold and three heated chains. For each gene region, we ran an analysis of 10 million generations with trees sampled every 500 generations. After discarding the trees saved during the “burn-in phase” (determined graphically), the topologies of the 50% majority-rule consensus trees, based on the remaining 20,001 trees, were compared and in all cases found to be identical. The analysis of the combined dataset was conducted in the same manner as for the individual genes with the analysis run for 15 million generations. The 50% majority-rule consensus trees were also identical in these runs and the posterior probabilities are based on a total of 30,001 saved trees. The burn-in was graphically estimated using AWTY (Wilgenbusch et al., 2004; Nylander et al., 2008). We also used the program AWTY to graphically assess whether the MCMC analysis had run long enough, such that tree topologies being sampled are in proportion to their true posterior probability distribution.

Table 1

Details of the species and families of Australo-Papuan core Corvoidea and other lineages used in the study. Full specimen details (tissue number, voucher information, locality and GenBank accession numbers) are provided for samples sequenced as part of this study. Species for which we obtained sequences from GenBank are referred to by their accession numbers only. AMNZ, Auckland Museum (New Zealand); ANWC, Australian National Wildlife Collection, CSIRO; MV, Museum Victoria; SAMA, South Australian Museum; n/a, voucher not available; AUS, Australia; NG, New Guinea. GenBank accession numbers are for RAG-1, Myo2 and Cyt *b*, respectively. Where GenBank sequences for a taxon were obtained from different species, both names are listed.

Taxon	Tissue No.	Voucher	Locality	GenBank numbers
Australo-Papuan core Corvoidea				
Artamidae				
Artamus leucorynchus	S3010	ANWC 38389	Griffith, New South Wales (Aus.)	FJ821042 FJ821079 FJ821111
Cracticus tibicen				AY064263 AY064741 AF197867
Peltops blainvillii	C011	ANWC 26492	Vanapa River (NG)	FJ821065 FJ821099 FJ821135
Campephagidae				
Coracina lineata	JCW073	ANWC 39960	Mission Beach, Queensland (Aus.)	FJ821046 EU273398 FJ821115
Lalage leucomela	C302	ANWC 39258	Pottsville, New South Wales (Aus.)	FJ821055 FJ821088 FJ821124
Corcoracidae				
Corcorax melanorhamphos				AY037849 AY064737 AY064274
Struthidea cinerea				AY064270 AY064738 AY064277
Dicruridae				
Dicrurus bracteatus	MV1191	MV B.24956	Gunn Point, Northern Territory (Aus.)	FJ821049 FJ821084 FJ821118
Monarchidae				
Machaerirhynchus flaviventer	C568	ANWC 39520	Mission Beach, Queensland (Aus.)	FJ821057 FJ821090 FJ821126
Monarcha melanopsis	B541	ANWC 38669	Kiola, New South Wales (Aus.)	FJ821059 FJ821092 FJ821128
Myiagra alecto	E631	MV B.15286	Port Moresby district, Central Province (NG)	FJ821060 FJ821093 FJ821129
Neosittidae				
Daphoenositta c. chrysoptera	F034	MV B.15187	Bendigo, Victoria (Aus.)	FJ821048 FJ821083 FJ821116
Daphoenositta c. striata	MV1311	MV B.23906	Cape Crawford, Northern territory (Aus.)	FJ821047 FJ821082 FJ821117
Oriolidae				
Oriolus flavocinctus	MV1603	n/a	Gunn Point, Northern Territory (Aus.)	FJ821063 FJ821096 FJ821132
Sphecotheres vieilloti	C398	ANWC 39350	Agnes Water, Queensland (Aus.)	FJ821075 FJ821107 FJ821145
Pachycephalidae				
Aleadryas rufinucha	C126	ANWC 26564	Efogi, Central Province (NG)	FJ821040 FJ821098 FJ821110
Colluricincla harmonica	MV1422	MV B.19428	Mt Sebine, Victoria (Aus.)	FJ821045 EU273396 FJ821113
Colluricincla megarhyncha	B841	ANWC 39020	Cambridge Plateau, New South Wales (Aus.)	FJ821044 FJ821081 FJ821114
Eulacestoma nigropectus	E193	MV B.20041	Awoma Ridge, Gulf Province (NG)	FJ821051 EU273400 FJ821120
Falcunculus frontatus	MV1394	MV B.20737	Otway State Park, Victoria (Aus.)	FJ821052 FJ821086 FJ821121
Mohoua albicilla	AukMus7	AMNZ B.10838	New Zealand	FJ821058 FJ821091 FJ821127
Oreoica gutturalis	W055	SAM B.39217	Mabel Creek, South Australia (Aus.)	FJ821061 FJ821094 FJ821130
Pachycephala olivacea	B761	ANWC 38935	Strahan, Tasmania (Aus.)	FJ821064 FJ821097 FJ821133
Pachycephala pectoralis	MV1419	MV B19792	Otway Ranges, Victoria (Aus.)	AY064266 AY064727 FJ821134
Pitohui ferrugineus	E611	ANWC 27091	Kokoda district (NG)	FJ821067 FJ821101 FJ821138
Pitohui nigrescens	E246	ANWC 26846	Awoma Ridge, Gulf Province (NG)	FJ821068 EU273415 FJ821137
Rhagologus leucostigma	E338	ANWC 26897	Awoma Ridge, Gulf Province (NG)	FJ821071 EU273416 FJ821141
Paradisaeidae				
Epimachus albertisi/fastuosus				AY037850 AY064735 U15205
Ptiloris magnificus/paradiseus				AY443325 AY064740 AY228092
Psophodidae				
Cinclosoma punctatum	B885	ANWC 39061	Tenterfield, New South Wales (Aus.)	FJ821043 FJ821080 FJ821112
Ifrita kowaldi	E311	ANWC 26890	Awoma Ridge, Gulf Province (NG)	EU273402 FJ821123 FJ821054
	E297	ANWC 24226	Awoma Ridge, Gulf Province (NG)	
Psophodes olivaceus	C291	ANWC 39248	Mebbin State Forest, New South Wales (Aus.)	FJ821069 FJ821102 FJ821139
Ptilorrhoa leucosticta	E419	ANWC 26950	Owen Stanley Range, Gulf Province (NG)	FJ821070 FJ821103 FJ821140
Rhipiduridae				
Chaetorhynchus papuensis				AY443267 EU726214
Rhipidura albiscapa	MV1396	MV B.19384	Otway State Park, Victoria (Aus.)	FJ821072 FJ821105 FJ821143
Rhipidura rufifrons	C733	ANWC 39685	McIlwraith Range, Queensland (Aus.)	FJ821073 FJ821104 FJ821142
Other core Corvoidea				
Malaconotoids				
Batis mixta				DQ011860, DQ011862
Laniarius aethiopicus				AY529920, EF635022
Telophorus dohertyi				AY443336
Vireonidae				
Vireo huttoni	MEX371	n/a		FJ821076 FJ821108 FJ821146
Other Australo-Papuan lineages				
Acanthizidae				
Acanthiza chrysorrhoa	MV2604	MV B.24219	Yellowdine, Western Australia (Aus.)	FJ821039 FJ821077 FJ821109
Gerygone fusca	MV317	MV B.24871	Pemberton, Western Australia (Aus.)	FJ821053 FJ821087 FJ821122
Oreoscopus gutturalis	C598	ANWC 39550	Atherton, Queensland (Aus.)	FJ821062 FJ821095 FJ821131
Sericornis frontalis	42461	ANWC 42461	Kangaroo Island, South Australia (Aus.)	FJ821074 FJ821106 FJ821144

Table 1 (*continued*)

Taxon	Tissue No.	Voucher	Locality	GenBank numbers
Maluridae				
Amytornis striatus	D511	ANWC 40614	Chapman Bore, South Australia (Aus.)	FJ821041 FJ821078 AY488401
Malurus amabilis/cyaneus				AY037847 AY064729 AY228088
Meliphagidae				
Lichenostomus penicillatus	MV1424	MV B.19440	Abbotsford, Victoria (Aus.)	FJ821056 FJ821089 FJ821125
Manorina melanocephala				AY064264 AY064734 AF197859
Ptiloprora plumbea				AY037848 AY064736 AY228091
Climacteridae				
Climacteris rufa				AY037846 AY064733 U58501
Cormobates placens				AY064260 AY064731 AY064278
Menuridae				
Menura novaehollandiae				AF295191 AY064744 U58502
Orthonychidae				
Orthonyx temminckii				AY064265 AY064728 AY064275
Pomatostomidae				
Pomatostomus temporalis				AY064267 AY064730 AY228090
Ptilonorhynchidae				
Ailurodeus crassirostris/melanotis				AY064259 AY064739 X74257
Ptilonorhynchus violaceus				AY064268 AY064742 X74256
Petroicidae				
Eopsaltria australis				AY064262 AY064732 AY062473
Drymodes brunneopygia	MV2664	MV B.26663	Noresman, Western Australia (Aus.)	FJ821050 FJ821085 FJ821119
Petroica rosea	MV1389	MV B.19363	Otway State Park, Victoria (Aus.)	FJ821066 FJ821100 FJ821136
Passerida				
Hirundo rustica				AY064271 AY064258 AM040741
Passer montanus				AY228027 AY228311 AY030118
Suboscine outgroups				
Pittidae				
Hydronornis (Pitta) baudii				AF295198
Pitta versicolor				AF295198 AY064280

Maximum likelihood analyses were performed using GARLI 0.95 (Zwickl, 2006). Five independent analyses (20 million generations for the combined analysis and 10 million generations for the individual partitions) were performed using the nucleotide substitution model GTR+I+Γ. Nodal support was evaluated with 100 non-parametric bootstrap pseudoreplications and scores of the best likelihood trees were within 0.5 likelihood units of the best tree recovered in each of the other four GARLI runs, suggesting that the five runs had converged.

Searches for maximum parsimony trees in PAUP* (Swofford, 1998) were performed on the combined dataset only with all characters coded as unordered. To account for the effects of saturation at third codon positions in the rapidly evolving Cyt *b* gene a weighting scheme of Myo2 = 10, RAG-1 = 10, Cyt *b* 1st = 10, Cyt *b* 2nd = 10, and Cyt *b* 3rd = 1, was applied to the dataset. To reduce the risk of finding local optima only, multiple analyses were performed with taxa added in a randomized order (10 random addition replicates in each of three MP analyses). We employed the heuristic search option with tree bisection reconnection (TBR) branch swapping. Trees were rooted using Pittidae as the outgroup and bootstrap support values for internal nodes were calculated from 1000 replicates.

3. Results

3.1. Variation in the molecular dataset

The molecular dataset included 906 bp of sequence from the RAG-1 gene of which 321 sites (35%) were variable and 174 sites (19%) parsimony informative. Individual Cyt *b* sequences ranged from 806 to 999 bp in length. Overall, 492 sites (49%) were variable of which 444 (44%) were parsimony informative. For Myo2, we obtained 756 bp of aligned sequence (including indels) of which 435 sites (57%) were variable, and 245 sites (32%) parsimony informative. Individual Myo2 sequences varied in length from 709 bp (*Amytornis striatus*, *Climacteris rufa* and *Cormobates placens*) to 731 bp (*Ailurodeus crassirostris*). A total of 35 indels were observed in the Myo2 dataset of which 27 (77%) occurred within the 5′ region of the intron. Indels ranged in size from 1 to 19 bps and included 10 which varied in length and may represent multiple, independent, insertion/deletion events. Most indels were autapomorphic, occurring in a single taxon. However, several synapomorphic indels were identified when their distribution was mapped over the combined Bayesian phylogeny (Fig. 4). Two indels were also identified as homoplasies, occurring in lineages that resolved in distant parts of the tree. These were a 9 bp indel in the two species of *Colluricincla*, and the *Laniarius*–*Telophorus* clade; a 2 bp indel in the bowerbird–treecreeper clade (Climacteridae–Ptilonorhynchidae) paralleled by a similar indel in *Artamus*.

3.2. Model selection and phylogenetic relationships

A general time-reversible model with gamma-distributed rate variation and a proportion of invariable sites (GTR+I+Γ) was found to have the best fit for RAG-1 and each of the Cyt *b* codon partitions, while a general time-reversible model with gamma-distributed rate variation (GTR+Γ) was selected for the Myo2 dataset. Model parameters estimated using MrModeltest (Nylander, 2005) are available from the corresponding author on request. The selected models were used in the Bayesian analyses of the individual genes as well as in the combined analysis with individual model parameters (base composition, gamma shape parameter, proportion of invariant sites) estimated during the run. The trees obtained from the Bayesian analyses of the individual gene partitions (Figs.

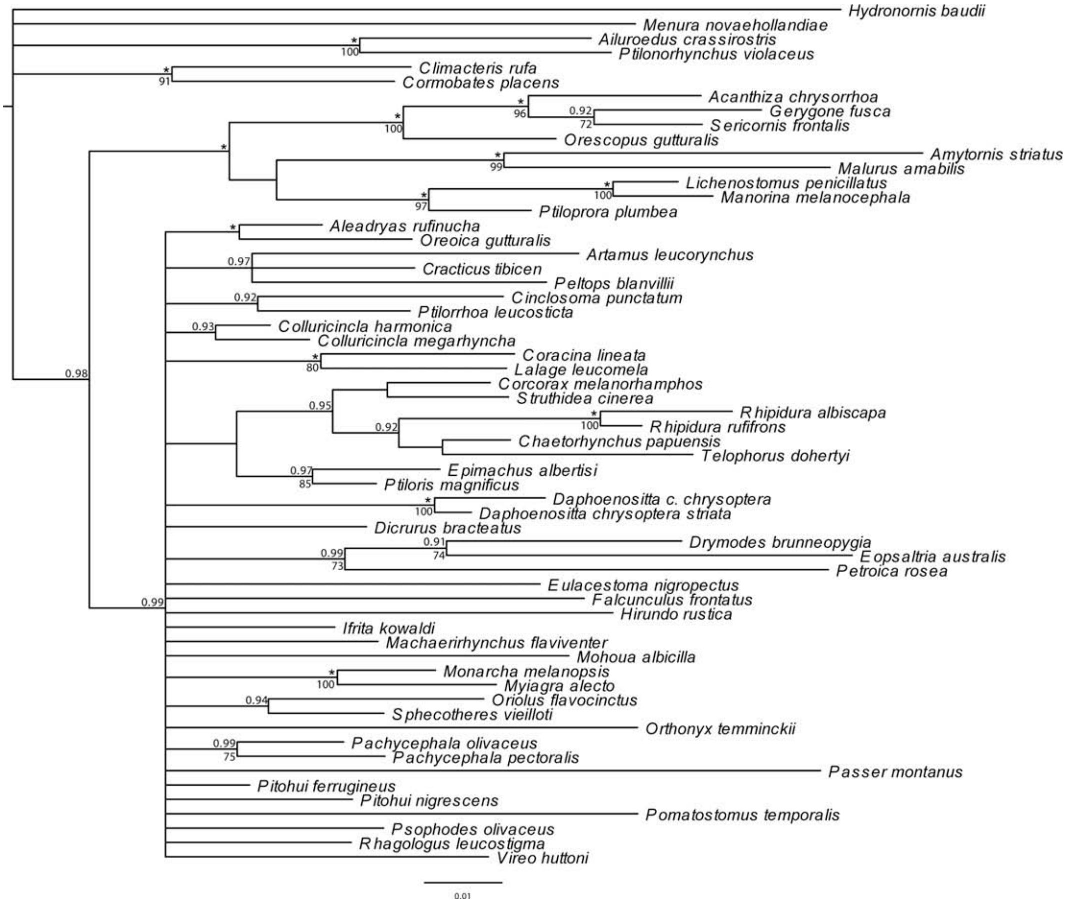

Fig. 1. The 50% majority-rule consensus tree (with branch lengths) obtained from the Bayesian analysis of RAG-1 sequences (AIC: GTR+I+Γ, ML: $-\ln = 5297.85$, BI harmonic mean $-\ln = 5485.16$). BI posterior probabilities $\geqslant 0.90$ are indicated above the nodes with * denoting a posterior probability of 1.00. ML bootstrap support values $\geqslant 75\%$ are indicated below the nodes.

1–3) and the combined dataset (Fig. 4) are topologically similar and the non-congruent relationships mostly involve nodes with low posterior probabilities (i.e., PP < 0.95). ML analyses provided high support for the majority of nodes with high posterior probabilities (PP > 0.95 and bootstrap values > 75). Nodes receiving support from only one of these analyses are aggregated at the base of the tree and additional sequence data and denser taxon sampling will be needed to confirm relationships. The 50% majority-rule consensus tree from the MP analysis of the combined dataset contained fewer well-resolved clades; however, those that were present were also recovered in the Bayesian and ML analyses (Fig. 4). Additional support for several clades was observed in the distribution of synapomorphic indels. These include the core Corvoidea families Monarchidae, Neosittidae and Paradisaeidae, as well as the Climacteridae, Meliphagidae and Ptilonorhynchidae (Fig. 4.)

4. Discussion

4.1. Phylogenetic relationships among Australo-Papuan oscine passerines

The combined analysis (Fig. 4) recovered the major oscine assemblages that have been evident in previous molecular phylogenetic studies (Ericson et al., 2002a,b; Barker et al., 2002, 2004). There was strong support for the Meliphagoidea (Acanthizidae, Meliphagidae, Maluridae) and Petroicidae with the latter forming a strongly supported clade with the Passerida. The Ptilonorhynchidae, Climacteridae and Menuridae resolved as the basal lineages. In agreement with previous studies (e.g. Barker et al., 2002, 2004; Ericson et al., 2002b) the Orthonychidae and Pomatostomidae were not recovered as part of the core Corvoidea. Monophyly of the remaining genera as members of the core Corvoidea was evident but only received strong support from the combined Bayesian analysis (PP 1.00). Although Sibley and Ahlquist (1990) identified the Corcoracidae (*Corcorax*, *Struthidea*) and Psophodidae (*Psophodes*, *Ptilorrhoa*, *Cinclosoma*) as being outlying lineages of the corvine assemblage, our ML analysis of the combined dataset and Bayesian analysis of RAG-1 shows that they are most likely nested within the core Corvoidea.

Within the core Corvoidea, well established taxonomic groups were recovered with high support in the combined Bayesian analysis and in most gene trees. These included the Campephagidae (*Coracina*, *Lalage*), Paradisaeidae (*Epimachus*, *Ptiloris*), Corcoracidae (*Corcorax*, *Struthidea*), Monarchidae (*Monarcha*, *Myiagra*), and Oriolidae (*Oriolus*, *Sphecotheres*). Our analysis did not support the DNA–DNA hybridisation data of Sibley and Ahlquist (1990) in treating Dicruridae, Rhipiduridae and Monarchidae as a single family or as separate families in sequence (Dickinson, 2003; Christidis and Boles, 2008) a finding also evident in the study of Irestedt et al. (2008). With the exception of *Pitohui* congeneric taxa were also recovered as clades (*Rhipidura*, *Pachycephala*, *Colluricincla*, *Daphoenositta*) in the combined analysis and most gene trees. The phylogenetic signal in the dataset is sufficient to recover clades comprising closely related lineages as well as resolving deeper nodes (i.e., families and some supra-familial relationships). Although our phylogenetic analyses did not recover a fully resolved topology for the Australo-Papuan core Corvoidea the resolution is sufficient to identify (1) genera that associate together as clades,

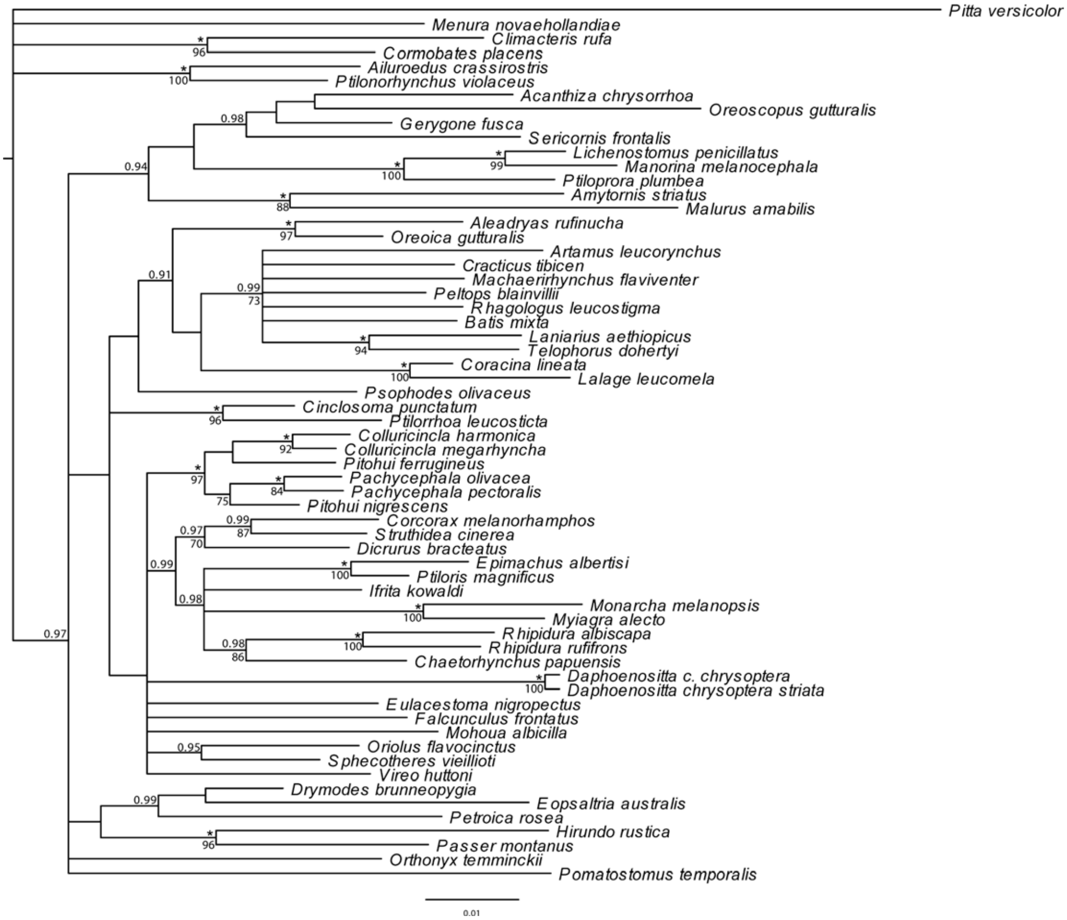

Fig. 2. The 50% majority-rule consensus tree (with branch lengths) obtained from the Bayesian analysis of Myo2 sequences (AIC: GTR+Γ, ML: −ln = 6355.09, BI harmonic mean −ln = 6478.04). BI posterior probabilities ⩾0.90 are indicated above the nodes with * denoting a posterior probability of 1.00. ML bootstrap support values ⩾75% are indicated below the nodes.

and (2) those genera that are assumed to be closely related but do not form clades in our analyses and require further investigation to determine phylogenetic affinities.

4.2. Monophyly of the Pachycephalidae and phylogenetic affinities of Eulacestoma, Falcunculus, Mohoua and Rhagologus

The pachycephaline assemblage of Sibley and Ahlquist (1990) did not resolve as a monophyletic clade in our analyses. Four distinct clades are evident, dispersed throughout the core Corvoidea, but their affinities remain largely unresolved. A large clade of core pachycephalines comprising *Colluricincla*, *Pachycephala* and *Pitohui* was recovered (Fig. 4) with *Falcunculus* as the sister lineage (PP 0.98). Jønsson et al. (2008a) previously showed that *Coracornis* is related to *Pachycephala* and therefore should be included within this clade of core pachycephalines. Jønsson et al. (2008b), and subsequently Dumbacher et al. (2008), found *Pitohui* to be polyphyletic and its members interspersed across the corvine assemblage. The only species retained as part of the core pachycephaline clade were *P. ferrugineus* and *P. nigrescens* (the two species included in the present study) but they did not resolve as sister taxa in any of the studies.

In our analysis, *P. ferrugineus* grouped with the two species of *Colluricincla*. *P. incertus* is often associated with *P. ferrugineus* on morphological grounds (e.g. Wolters, 1975–1982), although DNA data are needed to confirm this. Until additional studies are undertaken we recommend that *P. ferrugineus* and *P. incertus* are included in *Colluricincla*. Should they be shown to comprise a distinct genus, *Pseudorectes* Sharpe 1877 is the available name. *Pitohui nigrescens* was found to be distantly related to *Pachycephala* and may represent a distinct genus taking the name *Melanorectes* Sharpe 1877. Other species previously found to be associated with *Pachycephala* are *Coracornis raveni* and *Colluricincla sanghirensis* (Jønsson et al., 2008a) which resolved as sister lineages. These taxa could be placed in *Pachycephala.* Finally, *Colluricincla tenebrosa* was nested within *Pachycephala* (Jønsson et al., 2008a) and is best treated as a member of that genus.

Falcunculus, recovered as the sister lineage to the core pachycephaline clade (as circumscribed here), is often aligned with *Eulacestoma* (Wolters, 1975–1982; Schodde and Mason, 1999; Dickinson, 2003) owing to their shared robust, laterally compressed bills. Similarities in foraging behaviour are also evident with members of both genera reported to tear at bark and break open twigs to search for insects. Despite these similarities, our DNA data do not support a sister relationship between them. Although *Eulacestoma* was recovered as the sister lineage to the assemblage comprising the core pachycephalines and *Falcunclulus* there is no support for this association in any of the data partitions. It is most likely that similarities between *Falcunculus* and *Eulacestoma* in bill morphology are convergent owing to similar foraging strategies. In contrast, there are some overall similarities between *Falcunculus* and species of *Pachycephala* in the patterns of yellow and black adult plumage and rufous juvenile plumages that support an association between these genera.

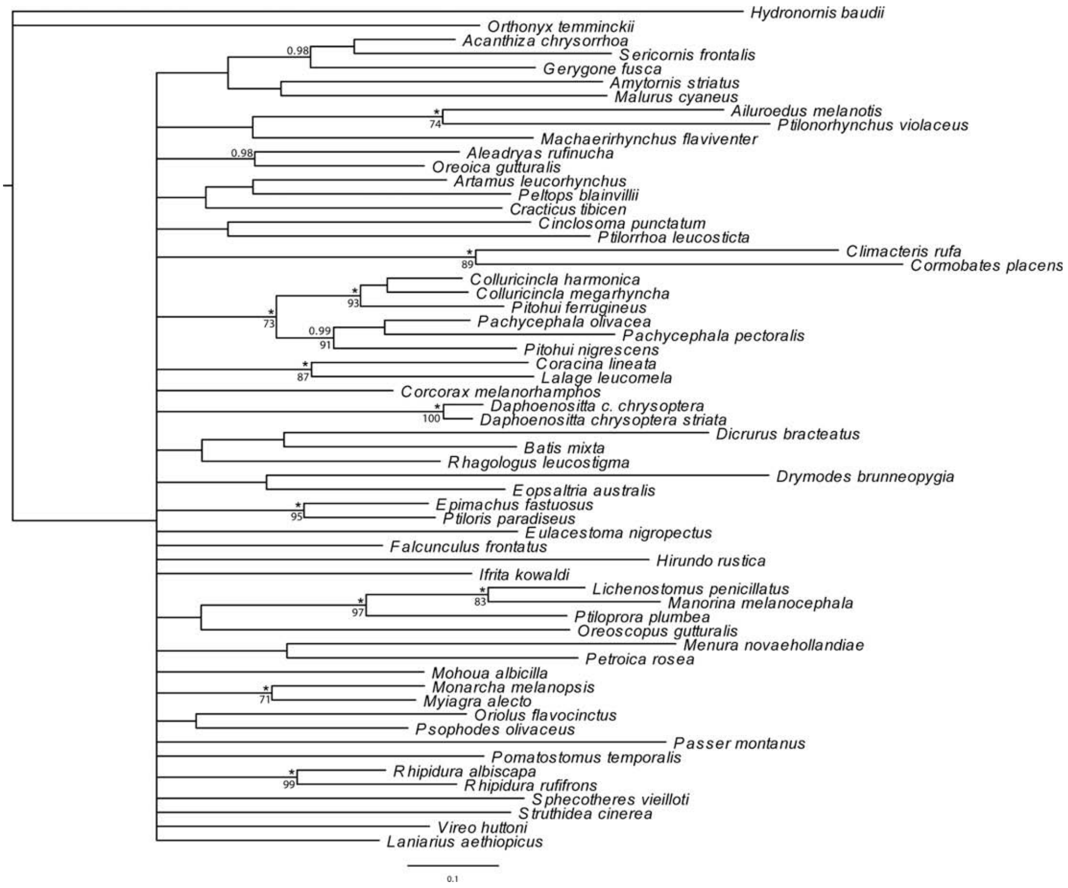

Fig. 3. The 50% majority-rule consensus tree (with branch lengths) obtained from the Bayesian analysis of Cyt *b* sequences (AIC: GTR+I+Γ, ML: −ln = 5297.85, BI harmonic mean −ln = 5485.16). BI posterior probabilities ⩾0.90 are indicated above the nodes with * denoting a posterior probability of 1.00. ML bootstrap support values ⩾75% are indicated below the nodes.

Although *Aleadryas rufinucha* is sometimes included within *Pachycephala* (e.g. Coates, 1990), all analyses identified it as the sister lineage to *Oreoica* and provided strong support for this association (PP 1.00, ML 100%). *Aleadryas rufinucha* occurs in the mountains of New Guinea (1670–2600 m) while *Oreoica* inhabits the arid scrublands of Australia indicating an unusual biogeographical association. Barker et al. (2004) found relatively strong support for a sister relationship between *Oreoica* and *Pitohui cristatus* (which occurs in the lowlands and hill country of New Guinea), while Jønsson et al. (2008b) identified a moderately supported sister relationship between *Aleadryas* and *P. cristatus* and this association was also observed in the DNA study of Dumbacher et al. (2008). Combining the findings of these two studies with those of the present one, it is clear that an assemblage exists that comprises *Oreoica*, *Aleadryas* and *Pitohui cristatus* (Oreoicidae). All three could be combined in the genus *Oreoica* Gould, 1838, which has priority over *Aleadryas* Iredale, 1956 and *Ornorectes* Iredale, 1956 (the subgenus erected for *Pitohui cristatus*). Alternately, they can be kept in three monotypic genera with *Ornorectes* resurrected for *P. cristatus*. Given the relatively large genetic divergences separating the three (Figs. 1–4) and their morphological distinctiveness, the latter treatment is recommended here.

Keast (1977) first proposed a relationship between *Mohoua* from New Zealand and the pachycephalines based on similarities in bill and nostril shapes, plumage patterns and nest structure. The DNA–DNA hybridization data of Sibley and Ahlquist (1990) also suggested an assemblage that included *Mohoua*, the pachycephalines and *Daphoenositta* (more recently treated as Neosittidae). The present DNA data do not support any such associations. Both *Mohoua* and *Daphoenositta*, while nested within the core Corvoidea, have no obvious links to any pachycephaline genera. Examination of osteological characters by Olson (1990) also failed to identify any obvious relationships for *Mohoua*. The present study identified both genera as part of a basal polytomy within the large Australo-Papuan assemblage and further studies will be required to determine their affinities. *Rhagologus*, the remaining member of the pachycephaline assemblage examined here, was recovered as a member of a strongly supported clade comprising the Artamidae and African malaconotoids.

4.3. Monophyly of the Psophodidae and phylogenetic affinities of *Ifrita*

One of the more controversial assemblages among Australo-Papuan songbirds has involved the members of the families Orthonychidae, Eupetidae and Psophodidae. Traditionally treated as a single assemblage (Deignan, 1964) several molecular studies showed *Orthonyx* to comprise a lineage (Orthonychidae) outside the core Corvoidea (Christidis and Schodde, 1991; Ericson et al., 2002a; Barker et al., 2002, 2004; Irestedt and Ohlson, 2008). *Eupetes* is part of a non-corvine African radiation that includes *Chaetops* and *Picathartes* (Jønsson et al., 2007) and *Melampitta* is linked with the monarchines (Barker et al., 2004) or paradisaedines (Sibley and Ahlquist, 1987). Psophodidae comprises the remaining five genera (*Androphobus*, *Cinclosoma*, *Ifrita*, *Psophodes* and *Ptilorrhoa*) of which all but *Androphobus* were included in the present study. *Androphobus* is generally thought to be closely related to *Psophodes* (e.g. Schodde and Mason, 1999) but this needs testing.

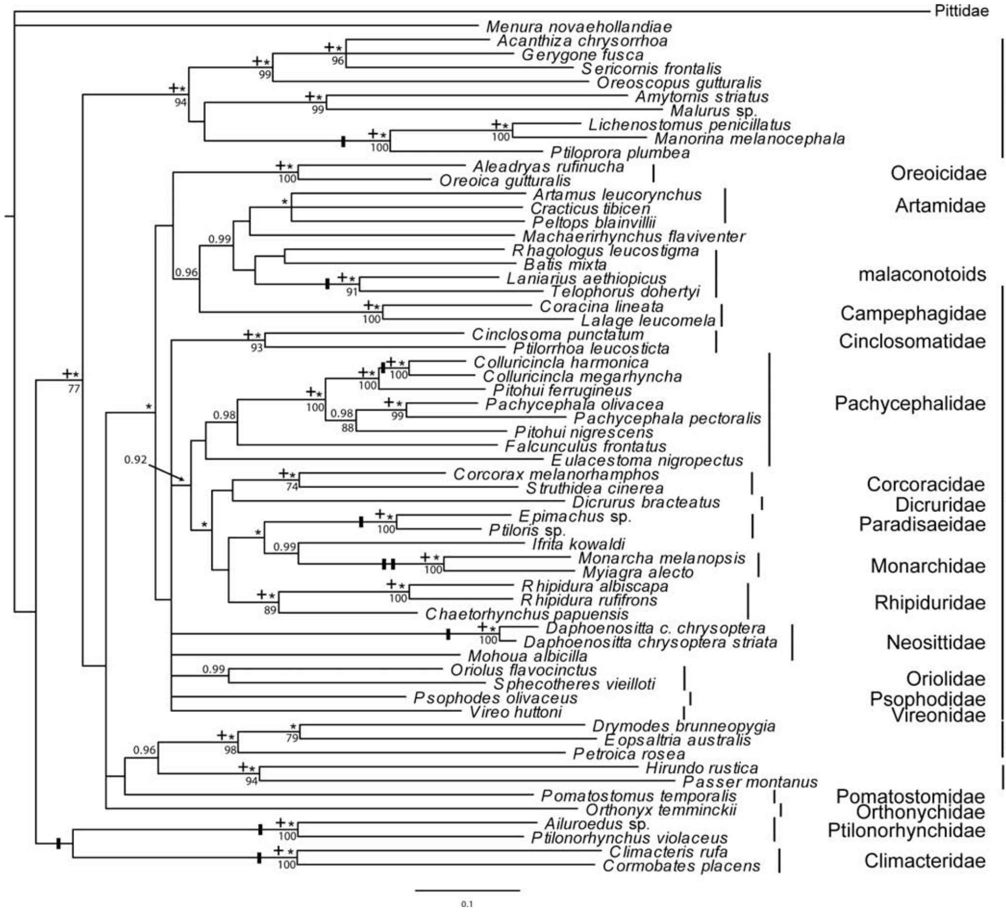

Fig. 4. The 50% majority-rule consensus tree (with branch lengths) obtained from the Bayesian analysis of the combined dataset (ML: −ln = 31334.06, BI harmonic mean −ln = 32149.73). BI posterior probabilities ⩾0.90 are indicated above the nodes with * denoting a posterior probability of 1.00. ML bootstrap support values ⩾75% are indicated below the nodes. ♦, indicates nodes receiving high MP bootstrap support (>70%) in the 50% majority-rule consensus tree (CI = 0.471, RI = 0.416). Vertical bars indicate the location of phylogenetically informative indels.

The Psophodidae was not recovered as a monophyletic assemblage. All analyses except the Cyt *b* single gene partition provided support for a sister relationship between the Australian quail-thrush (*Cinclosoma*) and New Guinean jewel-babblers (*Ptilorrhoa*). DNA–DNA hybridization data (Sibley and Ahlquist, 1990) also identified a close relationship between these two genera. There are similarities between the two in terms of behaviour, eggs and nests (summarised in Boles, 2007) and members of both are sexually dimorphic. No osteological characters have been found to differentiate between the two genera (Boles, 2007), further supporting a close association. Our analysis could not resolve the affinities of *Psophodes* but it is clearly not linked to *Cinclosoma* or *Ptilorrhoa* (contra arguments of Schodde and Mason, 1999). While *Androphobus* is generally thought to be closely related to *Psophodes* (e.g. Schodde and Mason, 1999), this needs testing. The species of *Psophodes* (whipbirds and wedgebills) have crests and resemble the Australo-Papuan babblers (Pomatostomidae) in habits and behaviour but there was no indication in the present study of an association between these lineages. On the basis of these results Psophodidae should be retained for *Psophodes* and *Androphobus* with Cinclosomatidae restricted to *Cinclosoma* and *Ptilorrhoa*.

Ifrita kowaldi has been one of the most enigmatic birds in terms of resolving its phylogenetic affinities and it has often been treated as “genus incertae sedis” (e.g. Dickinson, 2003). *Ifrita* has generally been placed with the Timaliidae, Orthonychidae, Eupetidae or Psophodidae (reviewed in Boles, 2007), although others have argued for affinities with the Old World muscicapine flycatchers (Desfayes, 1967) or the Australo-Papuan malurine wrens (Harrison, 1967). These last two suggestions largely revolve around the blue plumages that typify *Ifrita* and are apparent in some genera of Maluridae and Muscicapidae. Our analysis did not recover *Ifrita* as a member of the Psophodidae or Cinclosomatidae, instead identifying a strong association with the Monarchidae in the combined Bayesian analysis (Fig. 4, PP 0.99). Blue plumage patterns are evident in various monarchine genera and future analyses on the relationships within the monarchine radiation should include *Ifrita* in order to better resolve its affinities.

4.4. Affinities of Machaerirhynchus and Rhagologus

The combined Bayesian analysis (Fig. 4) and Myo2 tree (Fig. 2) provided strong support for a clade that united *Machaerirhynchus* and *Rhagologus* with the artamid–malaconotoid assemblage (PP 0.99). *Machaerirhynchus* is generally considered to be part of the Monarchidae, albeit as a very distinct lineage (e.g. Schodde and Mason, 1999). An association with the Artamidae has not previously been postulated. Although the microcomplement fixation data of Baverstock et al. (1992) identified *Machaerirhynchus* as a highly distinctive lineage not closely linked to the Monarchidae and allies, their study did not include representatives of the Artamidae. Schodde and Mason (1999) noted several osteological feature of the skull of *Mach-*

aerirhynchus that were highly divergent from monarchines and accordingly segregated the genus into its own subfamily, later elevated to family status (Machaerirhynchidae) by Dickinson (2003). An association between *Machaerirhynchus* and the Artamidae does not seem unreasonable given that *Peltops*, a core member of the Artamidae (see below), was previously placed near the monarchid flycatchers (e.g. Mayr, 1941; Rand and Gilliard, 1960). Interestingly, both *Machaerirhynchus* and *Peltops* capture insects by "fly-catching" from an open perch, a typically monarchine-like behaviour. Another member of this larger clade are the ioras *Aegithina* (not included in this study), which have black and yellow plumages reminiscent of those of *Machaerirhynchus*. Further molecular phylogenetic analyses will be required to confirm these possible associations.

While there are some behavioural features that link *Peltops* and *Machaerirhynchus*, no such clues exist for suggesting an association between *Rhagologus* and any members of the Artamidae. While the affinities of *Rhagologus* could not be fully resolved, our analysis suggests that they may lie with the African malaconotoids rather than the Artamidae. Previously, *Rhagologus* has been placed near, or in, *Pachycephala* (e.g. Mayr, 1967; Wolters, 1975–1982), and Schodde and Mason (1999) included Sulawesian *Hylocitrea* within *Rhagologus* but without explanation. The DNA study of Jønsson et al. (2008a) demonstrated that *Hylocitrea* is not related to the Pachycephalidae and is in fact part of the Passerida, as a member of the Bombycillidae (Spellman et al., 2008). *Rhagologus* is superficially similar to the insectivorous pachycephalines, but has a dull mottled plumage and is highly frugivorous. A reappraisal and better understanding of its biology are needed in light of these new insights into its phylogenetic affinities.

4.5. Relationships within the Artamidae

The three lineages which comprise the Artamidae were recovered as a single clade in our analysis of the combined dataset (Fig. 4) and RAG-1 with strong support (PP 1.00 and 0.97). There was no support for the treatment adopted by Dickinson (2003) of separating *Artamus* as a family. Consistent with previous studies our analysis showed that the Artamidae are more closely related to the African bush-shrikes and allies (malaconotoids) than the Australo-Papuan-centred rhipidurines, paradisaedines and monarchines. A close association between the Artamidae and this African centred assemblage is also supported by recent morphological assessments (Manegold, 2008). Our analysis shows that *Machaerirhynchus* and *Rhagologus* are also associated with this large assemblage.

4.6. Biogeography

The novel insights provided on the phylogenetic affinities of genera of Australo-Papuan core Corvoidea offers an enhanced perspective on the biogeographical history of this assemblage. Within the Australo-Papuan region several divergent radiations are becoming apparent from the results of this and other studies (e.g. Barker et al., 2004; Moyle et al., 2006). One assemblage includes the Artamidae, together with *Machaerirhynchus* and *Rhagologus*, and has close links with the African centred bush-shrikes, vangas and allies. This assemblage has its greatest diversity within Africa and further taxon sampling should provide useful insights into the historical biogeographical connections between the Australo-Papuan and African avifauna. A second large radiation comprising the monarchines, rhipidurines, paradisaedines, corvines (sensu stricto) and corcoracines has its greatest diversity within the Australo-Papuan region and appears to be closely linked to a third radiation comprising the pachycephalines although further confirmation is needed.

The relationships of the Oriolidae, Campephagidae, Psophodidae, Cinclosomatidae and Oreoicidae (as delimited here) remain unresolved. Nevertheless, evidence of complex biogeographical patterns across Australia and New Guinea is emerging. The Cinclosomatidae is represented in New Guinea by 3–4 species of *Ptilorrhoa*, which replace each other altitudinally from the lowlands through to the high mountains. Within Australia, members of the genus *Cinclosoma* inhabit the arid regions of central Australia and the drier forests and woodlands of eastern and southern Australia with one species (*C. ajax*) in the lowlands and foothills of New Guinea. Thus, within the family there are representatives in the forests and mountains of New Guinea, lowlands of New Guinea and the drier regions of Australia. A similar pattern is observed in *Oreoica* and its allies. *Aleadryas rufinucha* occurs in the mountains of New Guinea, *Ornorectes cristatus* in the lowlands and hill country of New Guinea, and *Oreoica gutturalis* the arid scrublands of Australia. This pattern of affinities between the New Guinean mountain taxa and those of the drier regions of Australia is repeated in other families. Nicholls (2001) found that within *Acanthiza* (Acanthizidae) the New Guinean representative *A. murina*, restricted to the high mountains is most closely allied to *A. nana* and *A. lineata*, which largely inhabit the largely dry-forests of south-eastern Australia. The emerging picture is one where Australia and New Guinea share a single avifauna with complex connections that increasingly involve the dry central areas of Australia rather than the east-coast rainforests. Furthermore, there seems to be a shifting interplay between the roles of niche conservatism and niche evolution in defining the present macroecological patterns in Australian birds (e.g. Hawkins et al., 2005).

Acknowledgments

We thank V. White, M. Irestedt and D. Zuccon for laboratory assistance; W.E. Boles for editorial comments; and three anonymous reviewers for helpful comments on earlier versions of the manuscript. For the loan of tissue samples we thank the Auckland Museum (New Zealand), Australian National Wildlife Collection (Commonwealth Scientific and Industrial Research Organisation, Australia) and South Australian Museum (Australia). This research was supported by Swedish Research Council Grant No. 2007-5280 to P.G.P. Ericson.

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