CONVENTION ON INTERNATIONAL TRADE IN ENDANGERED SPECIES
OF WILD FAUNA AND FLORA

Twenty-eighth meeting of the Animals Committee
Tel Aviv (Israel), 30 August-3 September 2015

Interpretation and implementation of the convention

Species trade and conservation

Standard nomenclature

REVISED NOMENCLATURE FOR FOUR SPECIES OF BIRDS-OF-PARADISE (PARADISAEIDAE)

1. This document has been submitted by the United States of America.[1]

2. On March 25, 2015 the Ornithological Council (OC), a non-governmental organization in the United States, requested that the United States recommend changes to the taxonomy/nomenclature for four species found in the birds-of-paradise (Paradisaeidae) family. These nomenclature changes would no longer place these four bird species in the Paradisaeidae family.

3. The species are: Macgregor's bird-of-paradise (*Macgregoria pulchra*), Loria's bird-of-paradise or Loria's cnemophilus (*Cnemophilus loriae)*, the Crested bird-of-paradise or crested cnemophilus (*Cnemophilus macgregorii*), and the yellow-breasted bird-of-paradise or yellow-breasted cnemophilus (*Loboparadisea sericea*). The first three species occur in Indonesia and Papua New Guinea, while the Crested bird-of-paradise or yellow-breasted cnemophilus occurs only in Papua New Guinea.

4. The recommended new taxonomy would place Macgregor's Bird of Paradise in the Meliphagidae family (Honeyeaters), and the other three species in the Cnemophilidae family (Satinbirds).

5. The standard CITES nomenclature for the species included in the family Paradiseidae is : Morony, J.J., Bock, W.J. & Farrand, J., Jr. (1975): Reference List of the Birds of the World. American Museum of Natural History. 207 pp. For determining the correct spellings of the scientific names of the species in the family Paradiseidae, the standard CITES reference is: Dickinson, E.C. (ed.) (2003): The Howard and Moore Complete Checklist of the Birds of the World. Revised and enlarged 3rd Edition. 1039 pp. London (Christopher Helm).

6. OC cited the following published scientific papers to support its request:

   - Aggerbeck, M., J. Fjeldså, L. Christidis, P.-H. Fabre, and K.A. Jønsson. 2013. Resolving deep lineage divergences in core corvoid passerine birds supports a proto-Papuan island origin. *Molecular Phylogenetics and Evolution* 70: 272-285.

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[1] *The geographical designations employed in this document do not imply the expression of any opinion whatsoever on the part of the CITES Secretariat (or the United Nations Environment Programme) concerning the legal status of any country, territory, or area, or concerning the delimitation of its frontiers or boundaries. The responsibility for the contents of the document rests exclusively with its author.*

- Clements, J.F., T. S. Schulenberg, M.J. Iliff, D. Roberson, T.A. Fredericks, B. L. Sullivan, and C. L. Wood. 2014. The eBird/Clements checklist of birds of the world: Version 6.9. Online at [http://www.birds.cornell.edu/clementschecklist/download/]. Last accessed 22 March 2015.

- Cracraft, J., and J. Feinstein. 2000. What is not a bird of paradise? Molecular and morphological evidence places Macgregoria in the Meliphagidae and the Cnemophilinae near the base of the corvoid tree. *Proc. R. Soc. London B.* 267: 233-241.

- Gill, F. & D. Donsker (Eds). 2014. IOC World Bird List (v 4.4). doi : 10.14344/IOC.ML.4.4. Online at [http://www.worldbirdnames.org/bow/au_babblers/]. Last accessed 22 March 2015

- Irestedt, M., K.A. Jønsson, J. Fjeldså, L. Christidis, and P.G.P. Ericson. 2009. An unexpectedly long history of sexual selection in birds-of-paradise. BMC Evolutionary Biology 9: 235.

Three of the above publications that may not be readily available on the internet are attached in an Annex to this document.

7. The United States contacted the CITES Authorities of Indonesia and Papua New Guinea to seek their views on this nomenclatural issue but, as of June 30, 2015, has not received a response.

8. The United States requests the CITES Nomenclature Specialist to evaluate the nomenclature changes recommended by the OC and provide guidance on this nomenclature matter.

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Resolving deep lineage divergences in core corvoid passerine birds supports a proto-Papuan island origin

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ABSTRACT

It is well established that the global expansion of songbirds (Oscines) originated in East Gondwana (present day Australo-Papua), and it has been postulated that one of the main constituent groups, the "core Corvoidea", with more than 750 species, originated in the first islands that emerged where New Guinea is now located. However, several polytomous relationships remained within the clade, obstructing detailed biogeographical interpretations. This study presents a well-resolved family-level phylogeny, based on a dataset of 22 nuclear loci and using a suite of partitioning schemes and Maximum Likelihood and Bayesian inference methods. Resolving the relationships within the core Corvoidea provides evidence for three well-supported main clades, which are in turn sister to the New Zealand genus *Mohoua*. Some monotypic lineages, which have previously been considered *Incertae sedis*, are also placed in a phylogenetic context. The well-resolved phylogeny provides a robust framework for biogeographical analyses, and provides further support for the hypothesis that core corvoids originated in the proto-Papuan island region that emerged north of Australia in the late Oligocene/early Miocene. Thus, the core Corvoidea appear to represent a true island radiation, which successfully colonized all continents except Antarctica.

1. Introduction

Passerine birds (Passeriformes) comprise more than half of all extant bird species (>5300 sp., Gill and Donsker, 2012). They are divided into two major groups, Suboscines (Tyranni) and Oscines (Passeri), based on morphology (Raikow, 1982), anatomy (Ames, 1971) and molecular data (Sibley and Ahlquist, 1990; Barker et al., 2004; Hackett et al., 2008). The most basal oscine lineages occur in Australia (Christidis and Schodde, 1991; Ericson et al., 2002; Barker et al., 2004), with some sub-radiations in adjacent island regions, whereas the more terminal oscine lineages underwent extensive diversification and geographical expansions leading to their contemporary global distribution (Ericson et al., 2002; Barker et al., 2004). The two largest clades within the oscines are the Passerida (>3500 species) and an assemblage referred to as the "core Corvoidea" in recent publications. The present study focuses on the core Corvoidea that includes more than 750 species divided in 24 families (Gill and Donsker, 2012).

Core corvoids occur worldwide, and include species-rich families with almost cosmopolitan distributions as well as species poor or even monotypic lineages, most of which are endemic to the rainforests of New Guinea. The large Passerida radiation is nested within a small assemblage of "transitional oscines", which appear to be rooted in New Guinea. The strong contemporary signature of New Guinean taxa at the base of both the Passerida and the core Corvoidea recently led to the proposal of an origin of these radiations in a proto-Papuan archipelago, which later rose to become present-day New Guinea (Jønsson et al., 2011).

Two dispersal scenarios have been proposed: (i) Basal oscines colonised New Guinea from Australia during the Eocene–Oligocene, 25–45 million years ago (Mya), and gave rise to an early insular core corvoid radiation, which subsequently dispersed to Asia and onwards to other continents (Jønsson et al., 2011), or (ii) the core corvoids originally evolved in Australia and spread all other the world, by using the Malesian archipelagos as stepping stones to reach Eurasia (Ericson et al., 2002). The latter however, would imply a greater diversity of core corvoid taxa in Australia than can be seen today, although we may envisage a significant diversity loss due to extinction (Hawkins et al., 2005; Byrne et al., 2011) as most of Australia changed from mesic to arid

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climatic conditions in the course of the upper Tertiary (Fujioka and Chappell, 2010).

Both dispersal scenarios are plausible in view of the plate tectonic models for the region. Australia was once part of the supercontinent Gondwana. This broke up around 80 Mya, and the Australian landmass started moving northwards ca 40 Mya and collided with the Eurasian plate some 10–20 Mya (Hall, 2002, 2009). These movements caused an uplift of the proto-Papuan islands in the epicontinental seas over the northern part of the Australasian plate, and the appearance of a volcanic arc (the Sunda Arc) along the plate subduction zone, with a string of islands emerging west of New Guinea towards Eurasia (Hall, 2009). These new islands provided new habitats and may have acted both as a driver for speciation and as stepping-stones for dispersal between Australo-Papua and Asia. In this process, numerous new evolutionary lineages emerged within a relatively short time frame (Jønsson et al., 2011; Kennedy et al., 2012), causing substantial difficulty in defining clades and relationships among them. Some phylogenetic structure has been determined, but a polytomy, or multifurcating phylogenetic node of several core corvoid families has remained (Norman et al., 2009; Jønsson et al., 2011), and some species have still not been assigned to any family.

Polytomies significantly impede reliable assessments of ancestral areas of origin (Ree et al., 2005), and a better resolution of the basal branching pattern of the core Corvoidea was therefore needed to understand historical biogeographical patterns and processes. Polytomies may reflect insufficient data (“soft polytomy”), but they may also be real (“hard polytomy”) and reflect conflicting signals in the data as a result of differences among gene trees due to incomplete lineage sorting (Maddison, 1997). A hard polytomy could arise if ancestral populations diversified simultaneously and were non-dichotomously broken up into several daughter species, which could well be the case during a colonization sweep across an archipelago. It is interesting to understand whether the core corvoid families did in fact radiate so fast as to produce a star-like polytomy, or whether a more robust bifurcating phylogeny can be generated, allowing us to determine a specific sequence of vicariance and dispersal events.

In this study we used 22 nuclear markers for 45 passerine bird (32 core corvoids) taxa representing all deep lineages of the core Corvoidea in an attempt to robustly resolve systematic relationships. Analysed within an explicit spatio-temporal framework we use the phylogeny to elucidate biogeographical patterns of dispersal and diversification within core corvoid passerine birds.

2. Methods

2.1. Taxonomic sampling and laboratory procedures

Taxon sampling included 45 taxa of passerine birds (43 oscines) (Table 1), which were chosen to represent all core corvoid family branches identified by previous, more densely sampled studies. 32 taxa represent the 24 families within the core Corvoidea and all *Incertae sedis* taxa, and 11 other taxa represent the Passerida (6 taxa) and the basal oscines (5 taxa). *Acanthisitta chloris* is well established as the sister group to all other passerine birds (Ericson et al., 2002) and was used to root the tree.

22 nuclear loci were chosen as markers (*ALDOB*, *BDNF*, *BRAM*, *CHZ*, *CLTC*, *CRYAA*, *c-MOS*, *c-MYC*, *EEF2*, *EGR1*, *Fib-5*, *GAPDH*, *IRF2*, *Myo2*, *NTF3*, *ODC*, *PCBD1*, *RAG1*, *RAG2*, *RHO*, *TGFb2*, *TPM1*), relying largely on the markers used by Hackett et al. (2008) and some other markers that have proven useful for resolving avian phylogenies. As such, molecular data (19–22 loci) for 8 taxa included in the study by Hackett et al. (2008) were readily available from GenBank. Two nuclear protein-coding loci, RAG1 and RAG2, were sourced from Barker et al., (2004). Additionally, molecular data (6–8 loci) for 3 taxa (*Melampitta*, *Rhagologus* and *Pityriasis*) available on Genbank were included. All other sequences (2–20 loci for 35 species) were generated *de novo* for this study.

Fresh tissue samples were obtained for 35 taxa, and the DNA extracted using a standard Qiagen® kit and sequenced by capillary electrophoresis. Primers were selected based on previous studies (Table 2). A standard protocol of 10 μl dNTPs (10 μM), 6.5 μl ddH_2O, 2.5 μl buffer, 2 μl forward primer (10 μM), 2 μl reverse primer (10 μM) and 0.1–0.2 μl enzyme (AmpliTaq® DNA Polymerase) was employed, using standard kit reagents and buffers from Invitrogen®. All DNA sequences were deposited on GenBank (Table 3).

2.2. Sequence alignment

PCR products were sequenced in both directions by Macrogen Inc., using an ABI 3730xl sequencing machine. The raw sequences obtained were assembled into contigs using Sequencher 5.0 (GeneCodes Corp.) and along with additional sequences downloaded from GenBank aligned in SeaView (Gouy et al., 2010), using the MUSCLE alignment algorithm. (Edgar, 2004). We repeated the alignment process using MAFFT v6 (Katoh et al., 2002 and Katoh and Toh, 2008, http://www.ebi.ac.uk/Tools/msa/mafft/). All analyses were run using both alignments. Inspecting each individual alignment did not reveal any unusual misalignments and we therefore did not modify any of the alignments further. All sequences were examined using the BLAST tool in GenBank (Altschul et al., 1990), and coding regions were checked for the presence of indels or stop codons that may have disrupted the reading frame.

2.3. Data partitioning

We used Modeltest 3.7 (Posada and Crandall, 1998) to determine the most appropriate model of nucleotide evolution for each locus following the Akaike Information Criterion (AIC). A supermatrix was then constructed for the entire dataset, which resulted in a concatenated alignment of 22 loci for 45 taxa with a total length of 19,782 base pairs (bp) (Table 4). A preliminary analysis of 20 million generations in MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was run for each gene partition to provide an initial notion of the resolution of the phylogenies, as well as identifying any misidentified taxa or spurious sequences.

We separated exons from introns and trimmed these to GenBank annotations, as well as codon-aligning separate exons, to produce a concatenated exon alignment and a concatenated intron alignment, which were analysed separately. Modeltest was used to determine the most appropriate model for each partition in the two datasets. Because exons code for amino acids, we translated the bases of the exon alignment into an amino acid alignment, by way of the align-by-codons direct translation option in MEGA 5.0 (Tamura et al., 2011). This allows for a direct detection of stop-codons, which suggests that the gene is non-functional and therefore should not be used in the phylogenetic analysis. It also allows for analysing the exon data both by base pairs and by amino acids.

2.4. Testing for selection

The individual and the concatenated exon alignments were tested for traces of positive or negative selection using MEGA 5.0 (Tamura et al., 2011) and the implemented HyPhy application (Pond and Muse, 2005), set up with codon-aligned alignments, using all sites, and a neighbour-joining starting tree. We tested this to avoid using any exons under positive or purifying selection (Seabury et al., 2004), as such exons might cause a biased phylogenetic signal (Swanson et al., 2001).

Table 1
Taxa included in this study. Each taxon represents a number of species in one or more families following Gill and Donsker (2012). Voucher and tissue numbers (AIM = Auckland Institute and Museum; AMNH = American Museum of Natural History, New York; ANWC = Australian National Wildlife Collection, Canberra; CMC = Canterbury Museum, Christchurch; MV = Museum Victoria, Melbourne; ZMUC = Natural History Museum of Denmark, University of Copenhagen.) are indicated for taxa that were sequenced for this study. Additional vouchers in parentheses indicate field vouchers. Asterisks indicate taxa for which all sequences were sourced from GenBank. All family relationships are based on the IOC master list, 2012 – exceptions (in italics) are referenced in comments.

Taxa included in this study	Families represented in this study	Number of species represented	Voucher/tissue numbers	Taxonomic comments
Core Corvoidea				
Aegithina tiphia	Aegithinidae	4	ZMUC 139604	
Artamus cinereus	Artamidae	11	MV Z1288	
Batis crypta	Platysteridae	30	ZMUC 145955	
Cinclosoma punctatum	*Incertae Sedis*	9	ANWC B34989	*Cinclosoma* removed from Psophodidae, along with *Ptilorrhoa*
Coracina salomonis	Campephagidae	92	ZMUC 139341	
Corcorax melanorhamphos	Corcoracidae	2	ANWCB31070	
Corvus corone	Corvidae	129	*	
Daphoenositta chrysoptera	Neosittidae	3	ANWC B29699	
Dicrurus ludwigii	Dicruridae	25	ZMUC 143102	Excluding *Chaetorhyncus*
Dryoscopus cubla	Malaconotidae	50	ZMUC 142936	
Eulacestoma nigropectus	*Incertae sedis*	1	ANWC B24552 (MV E192)	
Falcunculus frontatus	Pachycephalidae	1	ANWC B49341	
Gymnorhina tibicen	Cracticidae	10	MV Z2776	
Ifrita kowaldi	*Incertae Sedis*	1	ANWC B24226 (MV E297)	
Lanius collaris	Laniidae	33	ZMUC 128600	
Machaerirhynchus flaviventer	Machaerirhyncidae	2	ANWC B31507	
Melampitta gigantea	*Incertae sedis*	2	*	
Mohoua albicilla	*Incertae sedis*	2	AIM 04-011	
Monarcha castaneiventris	Monarchidae	94	ZMUC 139475	
Oreocharis arfaki	Paramythiidae	2	ANWC B26914 (MV E373)	
Oreoica gutturalis	Oreocidae	3	ANWC B32777	Including *Aleadryas* rufinucha and *Ornorectes cristatus*
Oriolus oriolus	Oriolidae	35	ZMUC 138401	
Pachycephala pectoralis	Pachycephalidae	50	ZMUC 139478	
Peltops blainvillii	Cracticidae	2	ANWC B26510 (MV C204)	
Pityriasis gymnocephala	Pityriaseidae	1	*	
Platylophus galericulatus	Corvidae	1	ZMUC 139719	
Prionops retzii	Prionopidae, Tephrodornithidae, Vangidae	39	ZMUC 117527	
Psophodes olivaceus	Psophodidae	5	ANWC B31492	
Ptiloris magnificus	Paradisaeadae	41	ANWC B29761	
Rhagologus leucostigma	*Incertae sedis*	1	*	
Rhipidura cockerellii	Rhipiduridae	46	ZMUC 138568	Including *Chaetorhyncus*
Vireolanius leucotis	Vireonidae	63	ZMUC 120284	
Other Oscines				
Bombycilla garrulus	All Passerida	~3500	*	
Climacteris sp.	Climacteridae, Ptilonorhynchidae	27	*	
Cnemophilus loriae	Cnemophilidae	3	ANWC B26861 (MV E283)	
Malurus sp.	Acanthizidae, Dasyornithidae, Maluridae, Meliphagidae, Pardalotidae,	283	*	
Melanocharis nigra	Melanocharitidae	10	ANWC B15334 (MV E610)	
Menura novaehollandiae	Atrichornitidae, Menuridae	4	*	
Orthonyx teminckii	Orthonycidae	3	ANWC B46353	
Petroica multicolor	Petroicidae	46	ZMUC 139505	
Philesturnus carunculatus	Callaeidae, Notiomystidae	5	AMNH DOT11059	
Picathartes gymnocephalus	Chaetopidae, Eupetidae, Picathartidae	5	*	
Pomatostomus halli	Pomatostomidae	2	ANWC B28760	
Suboscines and Acanthisittidae				
Acanthisitta chloris	Acanthisittidae	2	CMC 41302	
Pitta sp.	All suboscines	~1300	*	

Table 2
Primer information. All Polymerase chain reactions (PCRs) were run for 40 cycles. Touchdown (TD) PCRs were run by running five cycles using the highest annealing temperature indicated, followed by five cycles with an annealing temperature one degree below and so on. The lowest indicated annealing temperature was used for the remaining PCR cycles. Bold characters indicate the avian chromosome on which the gene is positioned.

	Primer name	Primer sequence	Annealing T (°C)	Chromosome	Reference
1	AlDOB (ca 2000 bp)			**Z**	
	AldB.3F	GCCATTTCCAGCTCTCATCAAAG	58		Hackett et al. (2008)
	AldB.7R	AGCAGTGTCCCTTCCAGGTASAC			Hackett et al. (2008)
	AldB.6F	GAGCCAGAAGTCTTACCTGAYGG	50		Cox et al. (2007)
	AldB.8R	GCTCKCCCGTATGAGAAGGTCAGYTT			Hackett et al. (2008)
2	BDNF (602 bp)		55	**5**	
	ChickBDNF5	ATGACCATCCTTTTCCTTACTATG			Sehgal and Lovette. (2003)
	ChickBDNF3	TCTTCCCCTTTTAATGGTTAATGTAC			Sehgal and Lovette (2003)
3	BRAM (500–600 bp)		47–49	**3**	
	BRM15F	AGCACCTTTGAACAGTGGTT	TD		Goodwin (1997)
	BRM15R	TACTTTATGGAGACGACGGA			Goodwin (1997)
4	CHZ (500–600 bp)		39–45	**2**	
	CHDZ-E16	GACATCCTGGCAGAGTATCT	TD		Griffiths and Korn (1997)
	CHDZ-E15	TAGAGAGATTGAGAACTACAGT			Griffiths and Korn (1997)
5	CLTC (1392 bp)		63–55	**19**	
	CLTC.e6Fnew	CTACATGAACAGAATCAGTGGAGAGAC	TD		Chojnowski et al. (2008)
	CLTC.e7Rnew	GCTGCCACTTTTGCTGCCTCTGAATA			Chojnowski et al. (2008)
6	CRYAA (ca 1200)		63	**1**	
	CRY.1F	TTACTATYCAGCACCCCTGGTTCAA			Hackett et al. (2008)
	CRY.2R	CTGTCTTTCACTGTGCTTGCCRTGRAT			Hackett et al. (2008)
7	*c*-mos (607 bp)		44	**4**	
	944	GCCTGGTGCTCCATCGACTGG			Cooper and Penny. (1997)
	1550	GCAAATGAGTAGATGTCTGCT			Cooper and Penny (1997)
8	c-MYC (ca 1100 bp)		53	**2**	
	MYC-F-01	TAATTAAGGGCAGCTTGAGTC			Harshman et al. (2003)
	MYC-R-01	CCAAAGTATCAATTATGAGGCA			Harshman et al. (2003)
9	EEF2 (1743)			**28**	
	EEF2.5F	GAAACAGTTTGCTGAGATGTATGTTGC	60		Hackett et al. (2008)
	EEF2.7R	GGTTTGCCCTCCTTGTCCTTATC			Hackett et al. (2008)
	EEF2.6F	CCTTGAYCCCATCTTYAAGGT	58		Hackett et al. (2008)
	EEF2.9R	CCATGATYCTGACTTTCARGCCAGT			Hackett et al. (2008)
10	EGR1(ZENK) (1200 bp) exon		48	**13**	
	Z1F	AGAAACCAGCTATCCCAAYCAA			Chubb (2004)
	Z9R	CTCAATTGTCCTTGGAGAAAAGG			Chubb (2004)
	Z7R (ONLY FOR SEQUENCING)	CGTGAAAACCTCCGGTCACAG			Chubb (2004)
	Z3F (ONLY FOR SEQUENCING)	CCCTATGCCTGCCCAGTGGAGTCC			Chubb (2004)
11	Fib5 (500–600 bp)		52–56	**4**	
	Fib5	CGCCATACAGAGTATACTGTGACAT	TD		Fuchs et al. (2004)
	Fib6	GCCATCCTGGCGATTCTGAA			Fuchs et al. (2004)
12	GAPDH (ca 300 bp)		63	**1**	
	G3PL890	ACCTTTAATGCGGGTGCTGGCATTGC			Friesen et al. (1997)
	G3PH950	CATCAAGTCCACAACACGGTTGCTGTA			Friesen et al. (1997)
13	IRF2 (632)		55–56	**4**	
	IRF2.2F	ATGTCTTTGGGTCGGGTTTA	TD		Hackett et al. (2008)
	IRF2.3R	GAAACTGGGCAATTCACACA			Hackett et al. (2008)
14	Myo2 (ca 800 bp) introns		54	**1**	
	Myo2	GCCACCAAGCACAAGATCCC			Slade et al. (1993)
	Myo3	CGGAAGAGCTCCAGGGCCTT			Slade et al. (1993)
	Myo3F	TTCAGCAAGGACCTTGATAATGACTT			Heslewood et al. (2005)
15	NTF3 (695 bp)		55	**1**	
	ChickNT3F	ATGTCCATCTTGTTTTATGTG			Sehgal and Lovette (2003)
	and ChickNT3R	GTTCTTCCTATTTTTCTTGAC			Sehgal and Lovette (2003)
16	ODC (ca 600 bp) introns		59	**2**	
	OD6	GACTCCAAAGCAGTTTGTCGTCTCAGTGT			Allen et al. (2003)
	OD8R	TCTTCAGAGCCAGGGAAGCCACCACCAAT			Allen et al. (2003)
17	PCBD1 (936 bp)		64	**6**	
	PCBD.2F	AGAGCTGTGGGGTGGAACGAGGTGGA			Hackett et al. (2008)
	PCBD.4R	TCRTGGGTGCTCAAGGTGATGTGAAC			Hackett et al. (2008)
18	RHO (1057)		57–55	**12**	
	Rhod1F	GAACGGGTACTTTGTCTTTGGAGTAAC	TD		Cox et al. (2007)
	Rhod1R	CCCATGATGGCGTGGTTCTCCCC			Cox et al. (2007)
19	TGFb2 (500–600 bp)		54–55	**3**	
	TGFb2-5F	TTGTTACCCTCCTACAGACTTGAGTC	TD		Sorenson et al. (2004)
	TGFb2-6R	GACGCAGGCAGCAATTATCC			Sorenson et al. (2004)
20	TPM1 (489 bp)		60	**10**	
	F	AATGGCTGCAGAGGATAA			Primmer et al. (2002)
	R	TCCTCTTCAAGCTCAGCACA			Primmer et al. (2002)

2.5. Taxon partitioning

For a number of species, only some of the 22 loci amplified. Although, it has been suggested that missing data has little impact on Bayesian phylogenetic tree estimation and corresponding support values (Wiens and Moen, 2008), we ran additional Bayesian and Maximum likelihood analyses on a concatenated alignment that only included taxa for which we had more than 11 loci

Table 3

Taxon sampling. Asterisks after taxon names indicate that sequences from different species were used. Voucher numbers (AIM = Auckland Institute and Museum; AMNH = American Museum of Natural History, New York; ANWC = Australian National Wildlife Collection, Canberra; CMC = Canterbury Museum, Christchurch, MV = Museum Victoria, Melbourne, ZMUC = Natural History Museum of Denmark, University of Copenhagen) are indicated for the taxa that were sequenced *de novo* for this study. GB denotes that all sequences for this taxon were sourced from GenBank. Blank cells indicate that no sequence is available.

Taxon	*Voucher*	AIDOB	BDNF	*BRAM*	*CHZ*	CLTC	CRYAA	*c*-MOS	*c-MYC*	EEF2	EGR1	*Fib5*	GAPDH	IRF2	Myo2	NTF3	ODC	PCBD1	RAG1	RAG2	RHO	*TGFb2*	TPM1
Core Corvoidea																							
Aegithina tiphia	ZMUC 139604	KF690844	KF679174	KF690932	KF690750	KF691121	KF691093	KF679228	KF679285	KF690958	KF679201	KF690828	KF691063	KF690771	KF690870	KF679255	KF690798	KF690984	AY056977	AY443104	KF691007	KF690899	
Artamus cinereus	MV Z1288	KF690843	KF679173	KF690931	KF690749	KF691120	KF691092	KF679227	KF679284	KF690957	KF679200	KF690827	KF691062	KF690770	KF690869	KF679254	KF690797	KF690983	AY443262*	AY443108*	KF691006	KF690898	
*Batis crypta/mixta**	ZMUC 145955	KF690846	KF679176	KF690934		KF691123	KF691095	KF679230	KF679287	KF690960	KF679203	KF690830	KF691065	KF690773	KF690872	KF679257	KF690800	KF690986	AY443263*	AY443110*	KF691009	KF690901	KF691029
Cinclosoma punctatum	ANWC B34989		KF679157			KF691105		KF679213	KF679267	KF690944	KF679187	KF690810	KF691043		KF690850		KF690780		FJ821043				
*Coracina salomonis/ineata**	ZMUC 139341		KF679172	KF690930	KF690748		KF691091	KF679226	KF679283	KF690956	KF679199	KF690826	KF691061	KF690769	KF690868	KF679253	KF690796	KF690982	AY056988*	AY443127*		KF690897	KF691027
Corcorax melanorhamphos	ANWC B31070		KF679156	KF690914	KF690734	KF691104	KF691077	KF679212	KF679266		KF679186	KF690809	KF691042		KF690849	KF679239	KF690779		AY443273	AY443129	KF690994	KF690883	KF691016
Corvus corone	GB	EU737787	EU737948	KF690911	KF691040	EU302717	EU737634	AY056918	AF377274	EU738568	EU738890	EU739199	FJ357914	EU739593	EU739909	EU740235	FJ358080	EU738404	AY056989	AY443132	EU737161	EU737319	EU737488
Daphoenositta chrysoptera	ANWC B29699		KF679158	KF690915	KF690735	KF691106	KF691078		KF679268	KF690945	KF679188	KF690811	KF691044	KF690758	KF690851	KF679240		KF690969	AY443281	AY443138		KF690884	
*Dicrurus ludwigii/adsimilis**	ZMUC 143102	KF690841	KF679168	KF690926	KF690744	KF691116	KF691088	KF679222	KF679279	KF690953	KF679196	KF690822	KF691056	KF690766	KF690863	KF679250	KF690792	KF690979	AY056991*	AY443140*	KF691003	KF690895	KF691024
Dryoscopus cubla	ZMUC 142936		KF679177	KF690935	KF690752	KF691124	KF691096	KF679231	KF679288	KF690961	KF679204	KF690831	KF691066	KF690774	KF690873	KF679258	KF690801	KF690987		AY443142	KF691010	KF690902	KF691030
Eulacestoma nigropectus	ANWC B24552	KF690847	KF679180	KF690938		KF691127	KF691099	KF679234	KF679291	KF690963	KF679206	KF690834	KF691069	KF690775	KF690876	KF679261	KF690804	KF690989	FJ821051		KF691012	KF690904	KF691033
Falcunculus frontatus	ANWC B49341	EF592332	KF679159	KF690916	KF690736	KF691107	KF691079	KF679214	KF679269	KF690946	KF679189	KF690812	KF691045	KF690759	KF690852	KF679241	KF690781	KF690970	AY443287	AY443146	KF690995	KF690886	KF691017
Gymnorhina tibicen	MV Z2776		KF679178	KF690936		KF691125	KF691097	KF679232	KF679289		KF679205	KF690832	KF691067		KF690874	KF679259	KF690802		AY443289	AY443153		KF690903	KF691031
Ifrita kowaldi	ANWC B24226	EF592333	KF679181	KF690939	KF690754	KF691128	KF691100	KF679235	KF679292	KF690964	KF679207	KF690835	KF691070		KF690877	KF679262	KF690805	KF690990	FJ821054			KF690905	
*Lanius collaris/excubitor**	ZMUC 128600	KF690842	KF679170	KF690928	KF690746	KF691118	KF691090	KF679224	KF679281	KF690955	KF679198	KF690824	KF691058	KF690768	KF690865	KF679252	KF690794	KF690981	AY443293	AY443160*	KF691005	KF690896	
Machaerirhynchus flaviventer	ANWC B31507		KF679162	KF690919		KF691109	KF691082	KF679216	KF679271	KF690947	KF679191	KF690815	KF691048	KF690761	KF690855	KF679244	KF690784	KF690973	FJ821057		KF690998	KF690888	KF691020
*Melampitta gigantea/lugubris**	GB	EF592334											EU726203		EU726213		EU726221		AY443297	AY443165			
Mohoua albicilla	AIM 04-011		KF679185	KF690943		KF691132		HM159212	KF679297		KF679211	KF690839	KF691075		KF690882				FJ821058				KF691035
*Monarcha castaneiventris/ axillaris**	ZMUC 139475		KF679171	KF690929	KF690747	KF691119		KF679225	KF679282			KF690825	KF691059		KF690866		KF690795		AY057006*	AY443176*		GQ145461	KF691026
*Oreocharis arfaki/Paramythia montium**	ANWC B26914		KF679183	KF690941	KF690756	KF691130	KF691102	KF679237	KF679294	KF690966	KF679209	KF690837	KF691072	KF690777	KF690879	KF679264	KF690807	KF690992	AY443312	AY443192	KF691014	KF690907	
Oreoica gutturalis	ANWC B32777	EF592336	KF679160	KF690917	KF690737	KF691108	KF691080	KF679215	KF679270		KF679190	KF690813	KF691046	KF690760	KF690853	KF679242	KF690782	KF690971	AY443307	AY443183	KF690996		KF691018
Oriolus oriolus/larvatus/ chinensis***	ZMUC 138401	KF690840	KF679166	KF690924	KF690742	KF691114	KF691087	KF679220	KF679276	KF690952	KF679194	KF690820	KF691053	KF690765	KF690860	KF679249	KF690789	KF690978	AY057011*	AY443184*	KF691002	KF690893	KF691023
*Pachycephala pectoralis/ hyperythra**	ZMUC 139478	EF592340	KF679167	KF690925	KF690743	KF691115		KF679221	KF679278		KF679195	KF690821	KF691055		KF690862		KF690791		AY443310*	AY443188*		KF690894	
Peltops blainvillii	ANWC B26510	KF690848	KF679184	KF690942	KF690757	KF691131	KF691103	KF679238	KF679295	KF690967	KF679210	KF690838	KF691073	KF690778	KF690880	KF679265	KF690808	KF690993	FJ821065		KF691015	KF690908	
Pityriasis gymnocephala	GB			JQ744932				JQ744792				JQ744721	JQ744756		JQ744706		JQ744982		DQ376524			JQ744823	
Platylophus galericulatus	ZMUC 139719												KF691060		KF690867		EU380456						
*Prionops retzii/plumatus**	ZMUC 117527	KF690845	KF679175	KF690933	KF690751	KF691122	KF691094	KF679229	KF679286	KF690959	KF679202	KF690829	KF691064	KF690772	KF690871	KF679256	KF690799	KF690985	AY443322*	AY443211*	KF691008	KF690900	KF691028
Psophodes olivaceus	ANWC B31492	EF592376	KF679164	KF690922	KF690741	KF691112	KF691085	KF679219	KF679274	KF690950	KF679192	KF690818	KF691051	KF690763	KF690858	KF679247	KF690787	KF690976	FJ821069		KF691000	KF690891	
Ptiloris magnificus	ANWC B29761		KF679163	KF690920	KF690739	KF691110	KF691083	KF679217	KF679272	KF690948		KF690816	KF691049	KF690762	KF690856	KF679245	KF690785	KF690974	AY443325	AY443217		KF690889	
Rhagologus leucostigma	GB			JQ744943								JQ744728	JQ744757		EU273416		JQ744994		JQ744878			JQ744847	
*Rhipidura cockerellii/hyperthra**	ZMUC 138568		KF679169	KF690927	KF690745	KF691117	KF691089	KF679223	KF679280	KF690954	KF679197	KF690823	KF691057	KF690767	KF690864	KF679251	KF690793	KF690980	AY443329*	AY443223*	KF691004	GQ145469	KF691025
*Vireolanius leucotis/Hylophilus poicilotis**	ZMUC 120284								KF679277				KF691054		KF690861		KF690790		AY443291*	AY443156*			
Other oscines																							
Bombycilla garrulus	GB	EU737805	EU737967	KF690910	KF691038	EU738121	EU737652	AY329375	EF568201	EU738715	EU738908	EU739216	EU272099	EU739610	EU739927	EU740252	EU680709	EU738423	AY056981	AY443111	EU737179	EU737338	
Climacteris erythrops/ picumnus/rufa**/ Cormobates placens****	GB	EU737819	EU737982			EU738135	EU737667	AY056915*	AY037839**	EU738600	EU738765	EU739231	EF441215***	EU739625	EU739941	EU740267	EF441237***	EU738438	AY443268	AY443121	EU737194	EU737353	
Cnemophilus loriae	ANWC B26861		KF679179	KF690937	KF690753	KF691126	KF691098	KF679233	KF679290	KF690962		KF690833	KF691068		KF690875	KF679260	KF690803	KF690988	AY443269	AY443123	KF691011		KF691032
Malurus melanocephalus/ amabilis/leucopterus***	GB	EU737860	EU738027			EU738167	EU737707	AY056931	AY037840*	EU738717	EU738968	EU739272	EF441219*	EU739669	EU739983	EU740310	EF441241*	EU738481	AY057001	AY443162	EU737235	FJ422094	EU737551
Melanocharis nigra	ANWC B15334		KF679182	KF690940	KF690755	KF691129	KF691101	KF679236	KF679293	KF690965	KF679208	KF690836	KF691071	KF690776	KF690878	KF679263	KF690806	KF690991	AY057002	AY443167	KF691013	KF690906	KF691034
Menura novaehollandiae	GB	EU737863	EU738030	KF690912	KF691037	EU738170	EU737710	AY056934	AF295169	EU738643	EU738971		EF441220	EU739672	EU739986	EU740313	EF441242	EU738484	AF295191	AY443171	EU737238	EU737401	EU737554
Orthonyx temminckii	ANWCB46353			KF690921	KF690740	KF691111	KF691084	KF679218	KF679273	KF690949		KF690817	KF691050		KF690857	KF679246	KF690786	KF690975	AY443309	AY443187	KF690999	KF690890	KF691021
*Petroica multicolor/ Pachycephalopsis poliosoma**	ZMUC 139505	EF592348	KF679165	KF690923		KF691113	KF691086		KF679275	KF690951	KF679193	KF690819	KF691052	KF690764	KF690859	KF679248	KF690788	KF690977	AY443311*	AY443190*	KF691001	KF690892	KF691022
*Philesturnus carunculatus/ Callaeas cinerea**	AMNH DOT11059				KF691039*			HM159201	KF679296	KF690968		KF691036*	KF691074		KF690881		EU272124*		AY443317*	AY443202*		KF690885*	
Picathartes gymnocephalus	GB	EU737893	EU738062	KF690913	KF691041	EU738196	EU737736	AY056950	EF568199	EU738673	EU739003	EU739303	EF441225	EU739702	EU740018	EU740344	EF441247	EU738515	AY057019	AY443203	EU737265	EU737433	EU737580
Pomatostomus halli	ANWCB28760		KF679161	KF690918	KF690738		KF691081		AY064288			KF690814	KF691047		KF690854	KF679243	KF690783	KF690972	AY443321	AY443209	KF690997	KF690887	KF691019
Outgroup																							
Acanthisitta chloris	CMC 41302	EU737790	EU737951	KF690909		EU738109	KF691076	AY056903	AY037838	EU738714	EU738893	EU739202	EU726202	EU739596	EU739911		EU726220	EU738407	AY056975	AY443102	EU737164	EU737322	
*Pitta guajana/sordida**	GB	EU737895	EU738064			EU738198	EU737738	AY056952	EF568186*	EU738675	EU739005	EU739305	DQ78592	EU739704	DQ785986	EU740346	DQ785950	EU738517	DQ320611	DQ320575	EU737267	EU737435	EU737582

Table 4
Alignment details. Length of alignments, the best models of nucleotide substitution as estimated by Modeltest following the Akaike Information Criterion Details, invariant sites and indels. Synapomorphic indels are highlighted in bold and are mapped onto Fig. 1 in the main text. Homoplasic indels are in italics, while autamorphic indels are in plain text.

Single gene alignmen	Base pairs	Taxa	Model (AIC)	Base pairs	Model (AIC)	Base pairs	Model (AIC)	Invariant sites	Convergence (Million generations)	Indels larger than 2 Base pairs
				Introns		Exons				
AlDOB	1328	23	TVM + G	904	TVM + G	423	K81 + I + G	792	2	172–176, 330–333, *437–459*, 699–701, 756–765, 786–791, **1165–1178**
BDNF	690	38	GTR + I + G	–		692	TIM + I + G	549	2	–
BRAM	442	37	TVM + G	377	TVM + G	64	TIM + I + G	130	2	118–131, 181–236, *288–294*
c-MOS	615	38	TrN + I + G	–		614	TrN + I + G	388	2	306–317
c-MYC	501	41	HKY + I + G	–		501	HKY + I + G	374	2	51–53
CHZ	542	29	GTR + G	542	TVM + G	–		157	2	33–35, *52–69*, **91–94,** 172–181, 176–185, 192–195, **204–207**, **223–262**, 272–281, 423–426, 474–504
CLTC	845	37	GTR + G	697	GTR + G	141	K80 + G	272	2	351–358, *441–448, 485–488,* 490–493, 550–558, 563–566, **585–594**, **598–601**, 707–711
CRYAA	1244	35	TrN + G	1130	HKY + G	116		387	2	123–132, **207–218, 235–243**, 256–259, 410–413, 445–450, *462–464,* 492–497, 527–530, **574–581**, *608–616,* 782–794, *947–1006*, **1122–1129**, 1176–1212
EEF2	1467	33	F81uf + I + G	1292	HKY + G	181	GTR + I + G	592	2	48–111, 117–136, **232–234**, 266–271, 479–500, 733–735, 914–925, 961–963, 1055–1059, 1105–1107, 1149–1153, 1274–1279, 1282–1289, **1317–1319,** 1355–1370, 1386–1390, 1414–1417
EGR1	1215	34	GTR + I + G	–		1215	GTR + I + G	837	2	*163–168*, 607–611
Fib5	630	41	TVM + G	601	GTR + G	28		153	2	37–46, **59–63**, 164–167, 217–219, 254–268, 412–429, 474–479
GAPDH	443	45	GTR + G	392	GTR + G	51		132	2	47–56, 80–84, **118–120**, **143–163**, 156–158, 173–180, 214–216, 242–246, 267–311, 358–362
IRF2	657	29	GTR + G	657	GTR + G	–		295	2	**119–121**, 130–134, 292–297, 409–414, **523–547**
Myo2	616	44	K80 + G	609	K80 + G	–		266	2	20–22, 192–195, 203–205, 359–365
NTF3	673	34	GTR + I + G	–		672	GTR + I + G	530	2	–
ODC	799	43	F81uf + G	679	TVM + G	120	K80 + G	221	2	**51–59**, 162–172, 392–405, 430–432, **443–446**, 455–537, **592–597**, 624–632, 683–724, 753–767
PCBD1	887	33	GTR + I + G	808	GTR + G	81	F81 + G	271	2	**187–196**, *222–226*, 282–284, **292–305**, 439–441, 474–476, **589–592**, 702–704, 784–790, 797–814
RAG1	2935	42	GTR + I + G	–		2934	GTR + I + G	1937	2	51–110
RAG2	1152	35	TVM + I + G	–		1152	TVM + I + G	727	2	–
RHO	980	28	K80 + G	965	K80 + G	18		370	2	10–16, 23–27, 136–138, **400–413**, 646–651, 777–785, 951–953
TGFb2	643	38	GTR + G	626	GTR + G	15		189	2	149–151, **211–216**, 282–284, **333–336**, 440–449, 566–587, **621–624**
TPM1	478	25	TrN + G	474	TrN + G	3		347	2	127–131
Concatenated datasets										
Full dataset	19782	45							20	
Taxa with min 12 loci	19782	37							12	
Introns	10761	45							2	
Exons (aminos)	9021	45							40	
11 *Mohoua* loci	9410	45							2	

(50%). This concatenated alignment included 37 (21 out of 32 core corvoids) taxa, thereby excluding *Cinclosoma*, *Melampitta*, *Mohoua*, *Vireolanius*, *Philesturnus*, *Pityriasis, Platylophus*, and *Rhagologus*. Of the eight taxa for which we only had sequence data of 11 loci or fewer, one taxon is not a core corvoid (*Philesturnus*) and six other taxa did not present any major systematic surprises. However, our finding that the New Zealand *Mohoua* represents the sister taxon of all other core corvoids led us to further investigate the data underlying the determination of its systematic position. We therefore, ran additional analyses in MrBayes, BEAST and RAxML on a concatenated dataset of the 11 genes, we had successfully sequenced for *Mohoua*, to investigate if missing data had any impact on its systematic placement.

2.6. Phylogenetic analyses and dating

Maximum Likelihood and Bayesian inference were used to generate phylogenetic hypotheses. Maximum Likelihood analyses in RAxML 7.3.0 (Stamatakis et al., 2008) were run on all gene partitions as well as on the concatenated alignment. The GTRGAMMA model was used for both tree inference and bootstrapping, with 1000 nonparametric bootstrap pseudoreplicates.

For Bayesian inference we used MrBayes v 3.1.2 (Ronquist and Huelsenbeck, 2003) and BEAST 1.6 (Drummond and Rambaut, 2007). The individual gene partition analyses were run for 20 million generations, the concatenated alignment, the exon alignment, and the intron alignment were run for 100 million generations, using the models specified by Modeltest. In all analyses, gene partitions were unlinked and a posterior distribution of trees was approximated by Bayesian MC^3 (Metropolis-Coupled Markov Chain Monte Carlo), with two runs each with four chains (three cold and one heated). Convergence of the Monte Carlo runs was graphically checked by monitoring cumulative posterior split probabilities and among-run variability using AWTY (Wilgenbusch et al., 2004). The generations before the chains reached apparent stationarity were discarded as burnin. We used a standard burnin of 10% of the run for all analyses, and altered in concordance with convergence diagnostics. As such, burnins for various analyses varied between 2 and 12 million generations for most analyses, but 20 million generations for the full dataset analysis, and 40 million generations for the amino acid partition (Table 4). For each data partition (single genes, exons, introns) as well as for the concatenated dataset, phylogenetic analyses were summarised as 50% majority-rule consensus trees.

Analyses in BEAST were run for 50 million generations for the complete concatenated alignment, the exon alignment, and the intron alignment, unlinking models, and using a relaxed uncorrelated lognormal distribution for the molecular clock model and assuming a Yule speciation process for the tree prior. We also used BEAST to estimate divergence times. Taxon sets were defined following the results of analyses in MrBayes and RaxML, and to establish an absolute chronology of diversification events we used one geological and one secondary calibration point. We used normal distributed priors and set the Time of the Most Recent Common Ancestor (TMRCA) at 76 Mya ± 8 standard deviations (SD) (95% confidence interval = 62.8–89.2 Mya) for the split between *Acanthisitta* and all other passerines, and TMRCA at 63 Mya, ±2 SD (95% confidence interval = 59.7–66.3 Mya) for the split between *Menura* and all other oscine passerine birds (Barker et al., 2004). Using these secondary calibration points may not be ideal. In particular, the assumption that the origin of the New Zealand endemic taxon *Acanthisitta* dates back to the origin of New Zealand some 80 Mya may be an overestimate leading to inflated age estimates of node ages (Worthy et al., 2010). However, because early passerine fossils cannot be placed confidently within the passerine crown group (Mayr, 2009), these calibrations appear to be among the few existing options for obtaining absolute date estimates. Ultimately, comparing the dated phylogeny with tectonic events and other studies using different means of dating may provide some assessment of the validity of the age estimates. All analyses in BEAST were repeated multiple times and convergence diagnostics were checked in Tracer (Rambaut and Drummond, 2007), determining convergence success by ESS and mean distribution values. An output tree was summarized in TreeAnnotator (Drummond and Rambaut, 2007) and burnin was set to five million generations.

The MrBayes and RAxML analyses were run on the internet portal, The CIPRES Gateway (Miller et al., 2011), and RAxML was also run directly on the Exelixis lab tool, RAxML BlackBox (Stamatakis et al., 2008).

2.7. Indel mapping

All individual alignments were checked for indels larger than 2 basepairs, and present in more than two species (Table 4) and the phylogenetic information compared to the phylogenetic structure obtained from the model based phylogenetic analyses.

2.8. Ancestral area reconstruction

LAGRANGE was used to compute ancestral areas (Ree et al., 2005; Ree and Smith, 2008; Smith, 2009). We randomly selected 1000 trees from the posterior distribution of the BEAST analysis of the concatenated dataset and ran LAGRANGE on each of these trees. The frequency of the most likely ancestral areas for clades was plotted as marginal distributions on the tree derived from the BEAST MCMC, recording the area (maxareas = 2) with the highest relative probability for each node. We repeated the analysis with maxareas = 3 to accommodate for the fact that some taxa have contemporary distributions that span more than two regions. This however, did not have any significant impact on the results of the ancestral state reconstruction and the strong "New Guinea origin" signal remained unaffected. In our ancestral area reconstruction analysis, the distribution of each taxon in the phylogeny represents the distribution of all members belonging to the particular clade (Table 1). Additionally, we performed an ancestral area analysis using only a constrained core distribution of the members of a clade, disregarding recent secondary colonization events. For example, if a group of eight species has seven species in Australia and one in New Guinea, the constrained distribution was considered Australian. We also relied on published papers, which have explicitly assessed the area of origin for a family. Based on contemporary species distributions obtained from the IOC world bird species list (Gill and Donsker, 2012) we assigned nine areas: AF: Africa, AM: Americas, AS: Eurasia, AU: Australia, NG: New Guinea, NZ: New Zealand, PH: Philippines, WA: Wallacea, and PO: Pacific Ocean islands.

3. Results

3.1. Analyses of the concatenated dataset

A total of 541 gene sequences were sequenced *de novo* (Table 3) and an additional 246 sequences were obtained from GenBank, providing an overall dataset of 787 gene sequences for 45 taxa. For locus details, see Table 4. Analyses of the molecular data aligned using MUSCLE and MAFFT did not reveal any significant topological differences.

Analysing the concatenated dataset in MrBayes and BEAST produced identical trees (Figs. 1–3). Both analyses converged after preliminary runs of 20 million generation but were run for 100 million generations to reduce the risk of any additional chain swaps. ESS values were all higher than 100 suggesting little

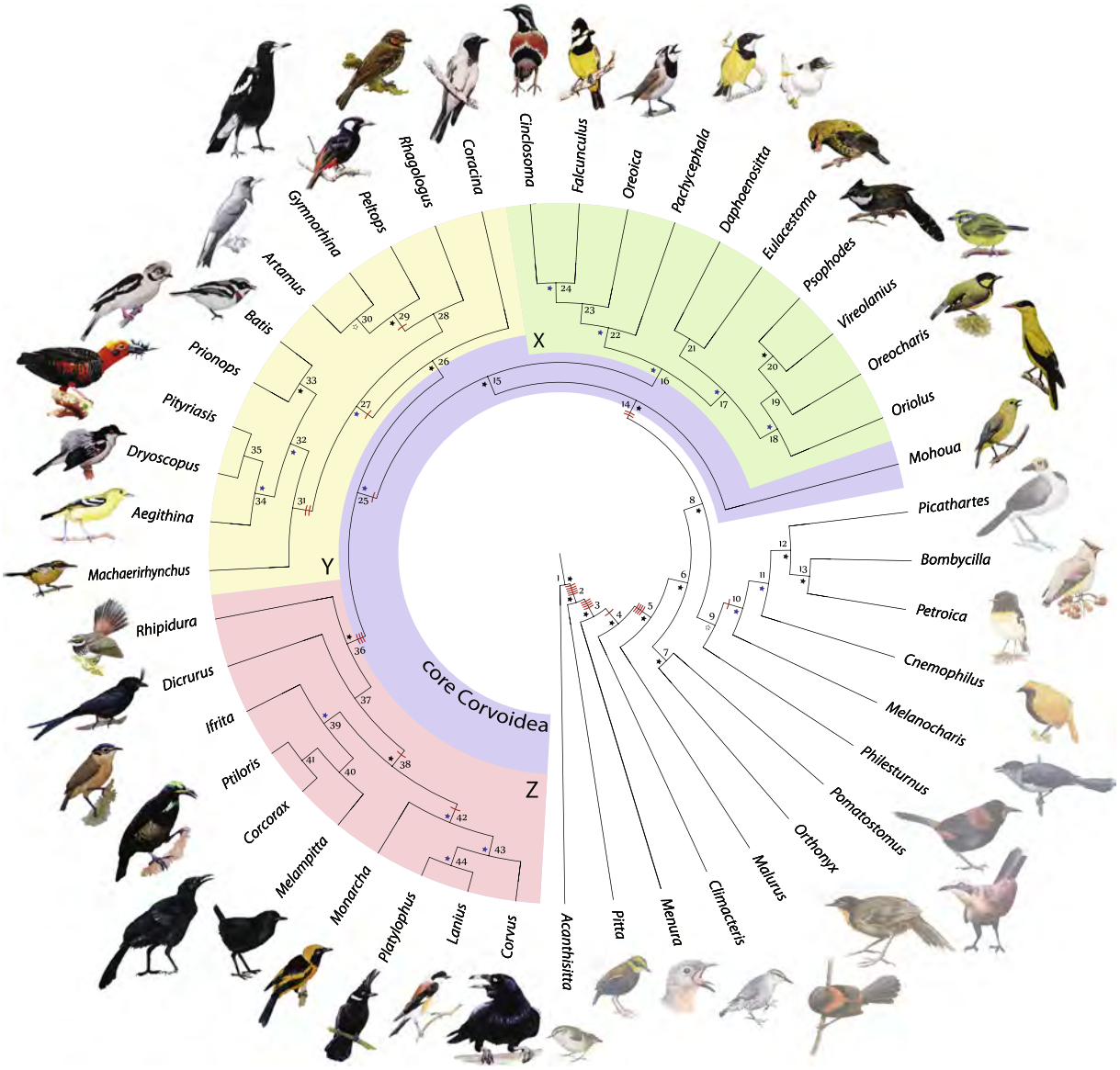

Fig. 1. 50% Majority rule consensus tree of the concatenated dataset (19,782 base pairs) of the core Corvoidea based on 100 million generations in MrBayes (branch lengths not representative) with illustrations representing the taxa included in the study. Core corvoid lineages are highlighted in colours. The coloured areas frame the individual clades; blue denoting the entire core Corvoidea, and green, yellow and pink denoting the clades X, Y and Z, respectively. Red bars indicate the position of one or more synapomorphic indels (Table 4). Stars indicate supported nodes. Black stars indicate well-supported relationships across all analyses. Blue stars indicate Bayesian support (MrBayes and/or BEAST) and white stars indicate maximum likelihood support (RAxML).

auto-correlation between the samples. 20 million generations were discarded as burnin from the MrBayes run, and 10 million generations were discarded as burnin from the BEAST run. We consider nodes well supported when posterior probabilities are $\geqslant 0.95$ and when bootstrap support values are $\geqslant 70$. All other nodes are considered unsupported. The maximum likelihood topology resulting from analysis using RAxML was identical to the two other topologies, but with fewer well-supported nodes (Fig. 2b).

Our analyses in MrBayes, BEAST and RaxML (Figs. 2 and 3) corroborate previous findings of a monophyletic core Corvoidea (PP = 1 and bootstrap = 98). The most basal lineage within the core corvoid clade is *Mohoua*. After this divergence, the core corvoids split into three well-supported clades, which we refer to as clades X (PP = 0.99), Y (PP = 1, bootstrap = 73) and Z (PP = 1, bootstrap = 100). Relationships among these clades are well supported in the Bayesian analysis (but not in the Maximum Likelihood analysis) such that clades Y and Z are sister (PP = 0.99), and these two clades together are sister to clade X (PP = 1).

Clade X (PP = 0.99) comprises *Falcunculus*, *Cinclosoma*, *Oreoica*, *Pachycephala*, *Psophodes*, *Vireolanius*, *Oreocharis*, *Oriolus*, *Daphoenositta* and *Eulacestoma*. This clade is further split in two subclades. One subclade (PP = 0.99) with *Cinclosoma* as sister to *Falcunculus* (PP = 1) is sequentially sister to *Oreoica* and *Pachycephala*. The other subclade (not supported) consists of the sister groups of *Daphoenositta* and *Eulacestoma* (not supported), diverging from a group with *Oriolus*, *Oreocharis* and sister taxa *Psophodes* and *Vireolanius* (PP = 0.99).

The next major clade (clade Y; PP = 1, bootstrap = 73) within the core Corvoidea consists of *Coracina*, *Rhagologus*, *Peltops*, *Gymnorhina*, *Artamus*, *Machaerirhynchus*, *Batis*, *Prionops*, *Aegithina*, *Dryoscopus* and *Pityriasis*. *Coracina* is sister to all other members of the clade, which splits into another two subclades. One consists of *Peltops*, *Gymnorhina* and *Artamus* (PP = 1, bootstrap = 100), which is in turn sister to *Rhagologus* (not supported). The other subclade (not supported) has *Machaerirhynchus* sister to two smaller groups – a relationship between *Batis* and *Prionops* (PP = 1, bootstrap = 95),

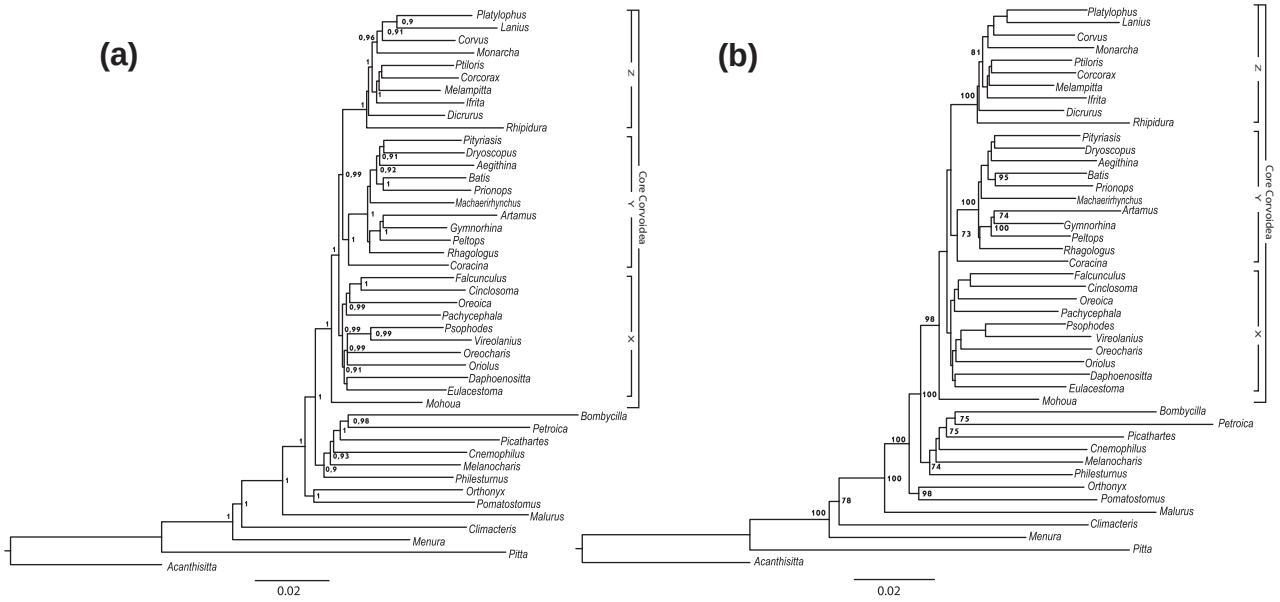

Fig. 2. Phylogenies based on analyses of the full concatenated dataset in (a) MrBayes, and (b) RAxML, with posterior probabilities above 0.90 (MrBayes) or bootstrap values above 70 (RAxML) shown. Core corvoid clades X, Y and Z are discussed in the main text.

and a clade including *Aegithina*, *Dryoscopus* and *Pityriasis* (not supported).

The last major clade (clade Z; PP = 1, bootstrap = 100) comprises *Rhipidura* and *Dicrurus* as the most basal lineages. These are sister to two subclades, one consisting of *Ifrita*, *Melampitta*, *Corcorax* and *Ptiloris* (PP = 1), and the other subclade consisting of *Monarcha*, *Corvus*, *Lanius* and *Platylophus* (PP = 0.96).

Excluding taxa for which less than 12 genes were available, did not change any well-supported relationships, suggesting that missing data does not adversely impact phylogenetic estimates.

3.2. Partitioned analyses

All analyses of the individual gene partitions produced trees (not shown) with low resolution and support values.

The Bayesian intron analysis (not shown) converged after 1 million generations. The analysis provided a robust basal part of the phylogeny, supporting all outgroup taxon relationships, and three monophyletic groups to some extent corresponding to the core corvoid clades X, Y and Z. The first clade Y has *Coracina* as the sister (PP = 1) to a polytomy of three lineages, one consisting of *Rhagologus*, a second clade comprising *Peltops*, which is sister (PP = 1) to *Gymnorhina* and *Artamus*, and a third subclade of *Machaerirhynchus* as the sister (not supported) to two smaller groups – *Prionops* and *Batis* (PP = 1), and *Aegithina* sister to *Dryoscopus* and *Pityriasis* (not supported). The second large clade X consists of *Falcunculus* and *Oreoica* (PP = 1) as the sister group of a large polytomy of *Daphoenositta*, *Oriolus*, *Vireolanius*, *Eulacestoma* and a sister group of *Psophodes* and *Oreocharis* (PP = 1). The last clade Z consists of mostly unsupported bifurcations, with *Pachycephala* as the most basal taxon. *Rhipidura* is the sister of *Melampitta* and *Dicrurus* (PP = 1), and an unsupported clade of *Monarcha* sister to two subclades, a clade of *Corvus*, *Lanius* and *Platylophus* (no support) and a clade of *Ifrita* sister (PP = 1) to *Corcorax* and *Ptiloris*.

The selection tests did not reveal selection on any loci. Consequently, we included all exons in the phylogenetic analyses. However, the nuclear DNA exon MCMC-chains failed to converge after 100 million generations, despite several attempts with various parameter settings, codon partitioning and gene partitioning. A translated amino acid alignment converged after 40 million generations and produced a polytomy of the core Corvoidea, but without a single well-supported node. The Maximum Likelihood analyses provided a slightly more resolved phylogeny, confirming *Psophodes* and *Vireolanius* as sister groups, and this group as sister group to the Vangidae and Platysteridae (*Prionops* and *Batis*). *Cinclosoma* was supported as sister group to *Falcunculus*.

3.3. Indel mapping

A total of 128 indels (excluding single nucleotide gaps) were uncovered. Comparing these to the phylogenetic results obtained by the model-based phylogenetic analyses, 28 indels were synapomorphic (Fig. 1), 10 indels were homoplasic, and 90 indels were autapomorphic. All indel sites are indicated in Table 4.

3.4. Dating

Dating the phylogeny using secondary calibration points provided rough time estimates of branching events throughout the evolution of the core Corvoidea (Fig. 3). The most basal node of the core Corvoidea, the split between *Mohoua* and the three major clades, was estimated at ~32 Mya and divergences of core corvoid clades X, Y and Z were estimated took take place shortly after within a relatively narrow time span of a few million years.

Because of the poor fossil record for the early Tertiary in the southern hemisphere, divergence time estimates have mainly been based on calibration points relating to plate tectonic events during the early avian history (e. g. Barker et al., 2004; Jønsson et al., 2011). This remains controversial, but the estimated time of early divergence among core corvoid groups, in the late Oligocene, has been remarkably robust to changes in calibration points (e.g., whether the isolation of *Acanthisitta* in New Zealand is assumed to have taken place in the late Cretaceous or early Tertiary). Moreover, a recent study using both fossils and biogeographical events to date eight nodes distributed throughout the passerine tree agrees with this Oligocene origin of the core Corvoidea (Kennedy et al., 2012). The estimated time of origin of the core corvoids corresponds to the time when the Australian plate moved towards Asia, and the proto-Papuan front of the Australian plate, which

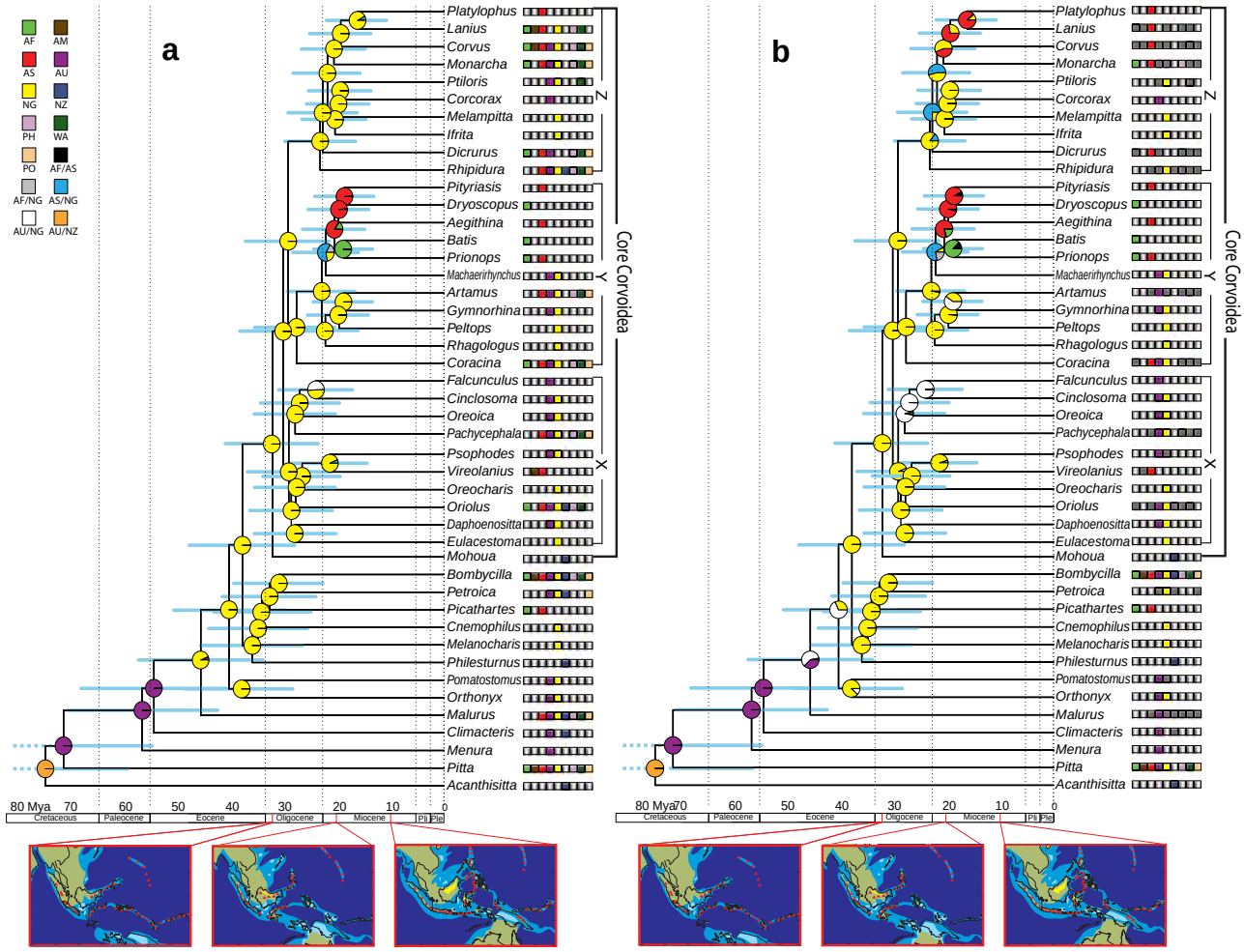

Fig. 3. Estimated ancestral areas using LAGRANGE, mapped onto the total evidence tree dated in BEAST. (a) Ancestral areas as estimated using the complete distributions (Table 5). (b) Ancestral areas as estimated using the constrained distributions (Table 5). Pie charts at internodes indicate the probability of the area of origin coloured according to the inset legend (AF = Africa, AM = Americas, AS = Asia, AU = Australia, NG = New Guinea, NZ = New Zealand, PH = Phillipines, WA = Wallacea, PO = Pacific Ocean Islands. AF/AS = Africa/Asia, AF/NG = Africa/New Guinea, AS/NG = Asia/New Guinea, AU/NG = Australia/New Guinea, AU/NZ = Australia/New Zealand). Distributions of the clades are indicated to the right of the taxon names. Empty squares indicate no presence in that area, coloured squares indicate presence in areas according to the inset legend, and dark grey squares (only in B) indicate areas omitted from the constrained distribution analysis. Inset maps from Hall (2009) at the bottom show the historical distribution of land in the Indo-Pacific (dark blue = deep sea, intermediate blue = carbonate platforms, light blue = shallow sea, green = land, yellow = highlands, red triangles = volcanoes).

had been submerged in the shallow epicontinental seas, emerged as an archipelago north of Australia (Hall, 2009).

3.5. Ancestral area reconstruction

Ancestral area reconstruction analysis using LAGRANGE (Fig. 3a and b) suggests that Basal oscine lineages (*Menura*, *Climacteris*) originated in Australia. More distal nodes branching off to *Malurus* and *Orthonyx*/*Pomatostomus* are equivocally determined to be of either Australian or Papuan origin. The Australian origin of basal oscine nodes (*Malurus* and *Orthonyx*/*Pomatostomus*) is stronger for the constrained analysis that disregards recent secondary dispersal events (Fig. 3b). The origin of the node that includes transitional oscine groups (*Philesturnus* to *Cnemophilus*), The Picathartidae, the Petroicidae, the Passerida (represented here only by *Bombycilla*) and the core Corvoidea appears to have originated in New Guinea. Most certainly the origin of the core Corvoidea and the origin of the three main core corvoid clades (X, Y and Z) is Papuan. Members of clade X occur mostly in New Guinea, with some back colonisation into Australia (e.g. *Falcunculus*). Clade Y, represents some of the exclusively African clades represented by *Dryoscopus*, *Batis* and *Prionops* and the ancestral area reconstruction suggests colonisation via Asia to Africa. Clade Z represents dispersal into Asia, at least if considering the ancestral area analysis of the constrained distributions (Fig. 3b).

4. Discussion

4.1. Towards a robust phylogeny of the core Corvoidea

The robustly resolved phylogeny of the core Corvoidea obtained in this study, based on several methodological approaches, subdivide the core Corvoidea into four major lineages, with *Mohoua* representing a deep branch, as sister to the remaining three clades (Fig. 2). Furthermore, many taxa that have traditionally been difficult to place are now placed in a phylogenetic context with high support. This provides an improved opportunity to more confidently assess the sequence of diversification and thus biogeographical events within the group.

The individual gene trees provided little well-supported resolution across the core Corvoidea. The intron (10,753 base pairs) and exon (9021 base pairs) trees produced some structure, although still with limited support. Analyses of the complete concatenated dataset (19,782 base pairs), however, produced congruent phylogenies across methodological phylogeny estimation approaches (Fig. 2), with the Bayesian approaches generating particularly high support values for most relationships (Fig. 2a and b). This leads us to believe that the systematic relationships within the core Corvoidea is largely resolved as presented in Figs. 1 and 2. The mapping of indels onto the phylogeny (Fig. 1), demonstrates that only some of them (22%) are synapomorphic, while 8% are homoplasic. The majority, 70%, are autapomorphic (restricted to single taxa), thus being phylogenetically uninformative. Most of the informative indels figure in the basal divergences, where genetic diversity is much greater between lineages than in the distal parts of the phylogeny. However, several indels support some of the corvoid clades, and because the proportion of synapomorphic indels are three times higher than that of the homoplasic indels, they appear to have some phylogenetic value, further confirming the position of these divergences.

4.2. Systematics of the core Corvoidea

While neither Norman et al. (2009) nor Jønsson et al. (2011) could resolve the position of *Mohoua*, this study places it as sister to all other core corvids. This adds to a growing number of examples of highly divergent songbird lineages restricted to New Zealand (Driskell et al., 2007). The remaining core corvoid taxa separated into three well supported clades referred to as X, Y and Z, as discussed below.

Clade X consists of the morphologically distinctive *Eulacestoma*, the Neosittidae, Paramythiidae, Oriolidae, Vireonidae and *Psophodes* as one subclade and a second subclade comprising *Falcunculus, Oreoica* and *Pachycephala* (previously all in the family Pachycephalidae) along with *Cinclosoma*. The present study confirms the earlier molecular findings of Norman et al. (2009) that *Psophodes* and *Cinclosoma* do not form a monophyletic clade. In the study by Norman et al. (2009), *Cinclosoma* was sister to *Ptilorrhoa* while *Psophodes* was not strongly aligned to other taxa. Following our analysis, *Cinclosoma* (*Ptilorrhoa* was not examined) is best considered a member of the pachycephalid complex, as a sister to *Falcunculus*. For *Cinclosoma*, only 11 loci amplified. Nonetheless, this relationship received high support in almost all analyses encompassing the taxon. The relationship between *Psophodes* and the Vireonidae needs further confirmation, but potentially holds a very interesting biogeographical scenario with an early dispersal to Asia (*Erpornis*, *Pteruthius*) and then onwards to the New World (Reddy and Cracraft, 2007; Jønsson et al., 2011).

Clade Y, consisting of the Campephagidae, Cracticidae, Artamidae, Machaerirhynchidae, Vangidae, Platysteiridae, Aegithinidae, Malaconotidae and Pityriaseidae is consistent with the findings of Jønsson et al. (2011) and Fuchs et al. (2012). Norman et al. (2009) was the first to demonstrate that *Rhagologus* and *Machaerirhynchus* were part of the Artamid–Malaconotid assemblage and that this cluster was sister to the Campephagidae. Our study and that of Fuchs et al. (2012) further corroborate this. However, our placement of *Rhagologus* as sister to the Cracticidae and Artamidae differs from Norman et al. (2009) and Fuchs et al. (2012). In Norman et al. (2009) there was no support for resolving the relationships within the Artamid–Malaconotid assemblage. Although also without support in Fuchs et al. (2012), *Rhagologus* is part of a polytomy, with *Machaerirhynchus* and *Aegithina* being more closely related to Artamidae and Cracticidae than to the Vangidae, Platysteiridae, Pityriaseidae and Malaconotidae as shown in this study.

Clade Z, which comprises the Rhipiduridae, Dicruridae, Paradisaeidae, Corcoracidae, Monarchidae, Corvidae, Laniidae and two *Incertae sedis* taxa, *Melampitta* and *Ifrita*, was also recovered by Norman et al. (2009) with high support. Whereas Norman et al. (2009) found strong support for *Ifrita* with the Monarchidae (see also Jønsson et al., 2011), our study places *Ifrita* with high support (PP = 1) in a clade with the Corcoracidae, Paradisaeidae and *Melampitta*. This is in concordance with Dumbacher et al. (2008), who demonstrated a well-supported relationship between *Ifrita* and *Melampitta*.

Comparing the molecular results with the basic morphology of the group, a significant divergence is apparent during the early core corvoid radiation, with clade X standing out as the most heterogeneous. This may suggest an adaptive radiation within Australasia, and apparently also in the African and Madagascan radiation (Jønsson et al., 2012). However, most of the species-rich families (such as Pachycephalidae, Rhipiduridae, Dicruridae, Monarchidae and Laniidae) just underwent great phylogenetic expansion with little morphological divergence.

4.3. New Guinea as a species pump

Ancestral area analyses in LAGRANGE (Fig. 3) based on contemporary distributions (Table 5) support an origin of the basal oscines in Australia. It is worth noting that within the large Meliphagoidea group (represented here by *Malurus*), the basal taxa are mainly found in Australia (Gardner et al., 2010). The ancestral area analysis supports an entirely New Guinean origin for the core corvoids, with three ancient dispersal events out of New Guinea resulting in colonization of Africa (*Batis*, *Prionops*, *Dryoscopus* in clade Y) and Asia (several members of clade Z as well as deep branches of the Vireonidae (Clade X, represented here only by the New World *Vireolanius*). Dispersal to Africa appears to represent dispersal via Asia. The sister taxa (*Pityriasis* and *Aegithina*) of the African families in clade Y both occur in Asia, and given that the Middle Eastern and Southern Asian regions between New Guinea and Africa were wooded throughout most of the Tertiary, as opposed to arid deserts nowadays (Janis, 1993), dispersal of core corvoids to Africa via Asia is plausible. Ancient dispersal events to Asia is represented by (1) *Platylophus, Lanius, Corvus, Monarcha, Dicrurus, Rhipidura* of which some groups have successfully colonised several other continents and (2) *Vireolanius*, which represents a subsequent colonization to the Americas. These ancient colonization patterns are particularly clear from the ancestral area analysis of the constrained distributions (Fig. 3b).

Contemporary distributions of all members of the core corvoid groups represented in the present study (present distributions in Fig. 3 and Jønsson et al., 2011) further suggest that numerous independent recent expansions have taken place. Our results confirm the hypothesis proposed by Jønsson et al. (2011), that Australian basal oscines colonized the Papuan area, adapted to island life, and diversified and ultimately dispersed through the adjacent archipelagos and onwards to new continents.

4.4. Time of origin, dispersal and diversification of the core Corvoidea

The timing of dispersal events is clearly surrounded by extensive error margins and should be regarded as a crude attempt to date the core corvoid phylogeny. We relied on secondary calibration points from Barker et al. (2004) as no relevant early corvoid fossils are known. Relying on secondary calibration points for the analysis may not be ideal but until more reliable calibration points are available this may be used as a very rough time estimate, and our estimates tie in with other studies that have attempted to date biogeographical events for the core Corvoidea (Kennedy et al., 2012). However, relative differences between clade ages can be

Table 5
Distributions used for the ancestral area analyses in LAGRANGE. Each taxon in the phylogeny represents a number of species belonging to one or more families. These families are indicated to the right and follow the taxonomy of the International Ornithological Committee (IOC) as referred to in the main text. Distributions represent the complete distribution of all members of the clade. AF = Africa, AM = Americas, AS = Eurasia, AU = Australia, NG = New Guinea, NZ = New Zealand, PH = Philippines, WA = Wallacea, PO = Pacific Ocean islands.

Taxa	Complete distribution									Constrained distribution									Taxonomic groups
	AF	AM	AS	AU	NG	NZ	PH	WA	PO	AF	AM	AS	AU	NG	NZ	PH	WA	PO	
Acanthisitta	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	Acanthisittidae
Aegithina	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	Aegithinidae
Artamus	0	0	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0	Artamidae
Batis	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	Platysteiridae
Bombycilla	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	ALL PASSERIDA
Cinclosoma	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	*Incertae Sedis*
Climacteris	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	Climacteridae, Ptilonorhynchidae
Cnemophilus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	Cnemophilidae
Coracina	1	0	1	1	1	0	1	1	1	0	0	1	1	1	0	0	0	0	Campephagidae
Corcorax	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Corcoracidae
Corvus	1	1	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	Corvidae
Daphoenositta	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	Neosittidae
Dicrurus	1	0	1	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	Dicruridae
Dryoscopus	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	Malaconotidae
Eulacestoma	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	*Incertae sedis*
Falcunculus	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Pachycephalidae
Gymnorhina	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	Cracticidae
Ifrita	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	*Incertae sedis*
Lanius	1	1	1	0	1	0	1	1	0	0	0	1	0	0	0	0	0	0	Laniidae
Machaerirhynchus	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	Machaerirhynchidae
Malurus	0	0	1	1	1	1	1	1	1	0	0	0	1	0	0	0	0	0	Acanthizidae, Dasyornithidae, Malurida, Meliphagidae, Pardalotidae
Melampitta	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	*Incertae sedis*
Melanocharis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	Melanocharitidae
Menura	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	Atrichornithidae, Menuridae
Mohoua	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	*Incertae sedis*
Monarcha	1	0	1	1	1	0	1	1	1	1	0	1	0	0	0	1	0	0	Monarchidae
Oreocharis	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	Paramythiidae
Oreoica	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	Oreocidae
Oriolus	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0	Oriolidae
Orthonyx	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	Orthonychidae
Pachycephala	0	0	1	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0	Pachycephalidae
Peltops	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	Cracticidae
Petroica	0	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	Petroicidae
Philesturnus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	Callaeidae, Notiomystidae
Picathartes	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	Chaetopidae, Eupetidae, Picathartidae
Pitta	1	1	1	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	ALL SUBOSCINES
Pityriasis	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	Pityriaseidae
Platylophus	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	Corvidae
Pomatostomus	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	Pomatostomidae
Prionops	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	Prionopidae, Tephrodornithidae, Vangidae
Psophodes	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	Psophodidae
Ptiloris	0	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	Paradisaeidae
Rhagologus	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	*Incertae sedis*
Rhipidura	0	0	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	Rhipiduridae
Vireolanius	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	Vireonidae

discussed without need for specific dates. What is most noteworthy in the dated phylogeny is the short time span of the origin of the main core corvoid clades. With *Mohoua* included as the most basal member of the core Corvoidea, this radiation dates back to the early Oligocene, at 32 Mya, which coincides with the geological evidence for the emergence of subaerial island habitats in the New Guinea area around 30–40 Mya (Hall, 2002, 2009). Although total submergence of New Zealand during the upper Tertiary has been suggested (Campbell and Landis, 2001; Waters and Craw, 2006; Campbell and Hutching, 2007), there are several lines of evidence suggesting that the inundation was never complete (Gibbs, 2006). The island-dwelling core Corvoidea took from around 32 Mya to 20 Mya to attain this rapid radiation, culminating in the events of the three major dispersals to Africa and Asia (and onwards to the Americas) within a relatively narrow time frame. These dispersal events coincide with the rise of the islands of the Sunda arc (Hall, 2009), thus providing a stepping stone island pathway to the Eurasian mainland. At the same time, the tectonic events leading to the creation of the Sunda arc will not have hindered core corvoids in back-colonising Australia, which is evident from the analyses (e.g. *Gymnorhina*, *Falcunculus*, *Cinclosoma*, *Oreoica*).

5. Conclusion

This paper presents a well-resolved phylogeny of the 24 families of the core Corvoidea. The study also succeeds in systematically placing four taxa (*Eulacestoma*, *Ifrita*, *Melampitta*, *Mohoua*), which have so far had *Incertae sedis* status. However, it remains to be decided whether they should be included in existing families or be classified as families in their own right. With a well-resolved phylogeny, we confirm that the core Corvoidea originated in the area where New Guinea is now located. Consequently, the core

Corvoidea with more than 750 extant species originated in an island environment and underwent further radiation in archipelagos of true oceanic origin, leading to successful colonisation of other continents.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2013.09.027.

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THE ROYAL SOCIETY

What is not a bird of paradise? Molecular and morphological evidence places *Macgregoria* in the Meliphagidae and the Cnemophilinae near the base of the corvoid tree

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The cnemophiline 'birds of paradise' (Cnemophilinae) and Macgregor's 'bird of paradise' (*Macgregoria*) have traditionally been included in the Paradisaeidae although their relationships within the group have been enigmatic and subject to repeated discussion in the literature. Here we use sequences from two mitochondrial genes, cytochrome *b* and cytochrome oxidase I, along with a suite of morphological characters, to investigate their relationships to paradisaeids and other members of the passerine Parvorder Corvida. The combined data strongly support the removal of both groups from the birds of paradise: the cnemophilines are basal members of the Corvoidea and *Macgregoria* is a member of the Meliphagoidea and embedded in the honeyeaters (Meliphagidae) close to the genus *Melipotes*. The amount of sequence divergence among basal passeriforms and members of the Corvida, as well as available fossil evidence for Australian corvidans, suggest that cnemophilines represent an ancient lineage within the corvoid radiation. Because cnemophilines and *Macgregoria* have been placed at the base of the paradisaeid tree, hypotheses of morphological, behavioural and ecological character-state transformations within the family will require reanalysis.

Keywords: Paradisaeidae; Corvida; Meliphagoidea; molecular systematics; *Macgregoria*; Cnemophilinae

1. INTRODUCTION

The birds of paradise (Corvida: Corvoidea: Paradisaeidae) encompass one of the more spectacular evolutionary radiations within the vertebrates. About 90 diagnosable phylogenetic species have diversified across New Guinea, nearby islands including the Northern Moluccas, and the eastern rainforests of Australia (Cracraft 1992; recognized as 42 biological species by Frith & Beehler (1998)). In the process, paradisaeids have evolved a stunning array of male plumage patterns and behavioural repertoires—classically explained by various models of sexual selection (Diamond 1986; Beehler 1987, 1989)—as well as diverse patterns of body size and bill morphology.

Because of this morphological and behavioural complexity, relationships among birds of paradise have long been uncertain, and most hypotheses have not been tested using modern phylogenetic methods. As a consequence, a variety of opinion about intergeneric relationships has arisen (Stonor 1936, 1938; Mayr 1945; Gilliard 1969; Diamond 1972; Schodde 1976; Nunn & Cracraft 1996; Frith & Beehler 1998), with much of the controversy centred around the systematic position of the manucodes (subfamily Manucodinae), the subfamily Cnemophilinae, and Macgregor's bird of paradise (*Macgregoria pulchra*). Previous molecular and morphological data have confirmed that the manucodines are indeed the sister group of the core birds of paradise, the Paradisaeinae (Helm-Bychowski & Cracraft 1993; Nunn & Cracraft 1996; Frith & Beehler 1998), and this is supported by new data in this paper.

Virtually all workers over the last 50 years have assumed the cnemophilines and *Macgregoria* to be members, albeit aberrant members, of the birds of paradise. This assumption has major implications for interpreting the evolutionary diversification of paradisaeids because both groups have typically been placed at the base of the family tree (e.g. Bock 1963; Frith & Beehler 1998), which creates a potential historical bias when reconstructing the evolutionary pathways of behaviour, plumage change, ecology and biogeography. That features of *Macgregoria* might be critical for interpreting paradisaeid evolution and behaviour has even found its way into the popular media (Attenborough 1996). Here we eliminate this bias by presenting molecular and morphological evidence that the cnemophilines and *Macgregoria* are not paradisaeids but instead are distantly related members of the corvidan assemblage.

2. METHODS

We sequenced the complete mitochondrial cytochrome *b* gene as well as the first 1020 bp (positions 6645–7661 in the *Gallus gallus* sequence; Desjardins & Morais 1990) of cytochrome oxidase I (COI) for all taxa, following methods previously described for fresh tissue (Nunn & Cracraft 1996; Lee *et al.* 1997) and for tissue taken from museum skins (Mundy *et al.* 1997). Some cytochrome *b* sequences were taken from previous studies (Helm-Bychowski & Cracraft 1993; Nunn & Cracraft 1996) and COI was sequenced for these taxa as well (in parentheses: GenBank accession numbers for cytochrome *b* and COI, respectively, and source of tissue (abbreviations: AM, Australian Museum; AMNH/PRS and AMNH/JC, Department of Ornithology frozen tissue collection, American Museum of Natural History; ANSP, Academy of Natural Sciences,

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Philadelphia; ANSP/AM, field number of Andy Mack (specimens from ANSP); FMNH, Field Museum of Natural History, Chicago; NHMLAC, Natural History Museum Los Angeles County; NYZP, New York Zoological Park (Wildlife Conservation Society); QM, Queensland Museum, Brisbane; MOV, Museum of Victoria, Melbourne; SP-J, field number of Stephen G. Pruett-Jones; SVE, field number of S. V. Edwards; ZSSD, Zoological Society San Diego)): trumpet manucode, *Phonygammus keraudrenii* (X74252, AF197826, NHMLAC LAK2010); curl-crested manucode, *Manucodia comrii* (U15207, AF197827, AM no number, from S. V. Edwards); raggiana bird of paradise, *Paradisaea (raggiana) augustaevictoriae* (U25738, AF197828, ZSSD A0489241); red bird of paradise, *Paradisaea rubra* (U25736, AF197829, NYZP, AMNH no number); Wilson's bird of paradise, *Diphyllodes respublica* (U15200, AF197830, AMNH 0053 from NYZP); king bird of paradise, *Cicinnurus regius* (U15201, AF197831, ZSSD A0489242); blue jay, *Cyanocitta cristata* (X74258, AF197832, AMNH/JC); satin bowerbird, *Ptilonorhynchus violaceus* (X74256, AF197833, QM 3119); and hermit thrush, *Catharus guttatus* (X74261, AF197834, FMNH 89–285). In addition, sequences of the following taxa are reported here for the first time: American robin, *Turdus migratorius* (AF197835, AF197836, FMNH 88–670 (cytochrome *b*), AMNH/PRS 1189 (COI); Australian raven, *Corvus coronoides* (AF197837, AF197838, AMNH/PRS 2285); Australian magpie, *Gymnorhina tibicen leuconotus* (AF197867, AF197868, AMNH/JC); lesser cuckoo-shrike, *Coracina fimbriata* (AF197839, AF197840, ANSP 1306); crested cnemophilus, *Cnemophilus macgregorii* (AF197841, AF197842, AMNH 816487); yellow-breasted cnemophilus, *Loboparadisea sericea sericea* (AF197843, AF197844, AMNH 809348); superb blue wren, *Malurus cyaneus* (AF197845, AF197846, AM FB625); straited pardalote, *Pardalotus striatus* (AF197847, AF197848, AM FB1062); white-browed scrubwren, *Sericornis frontalis* (AF197849, AF197850, SVE 1100); yellow-rumped thornbill, *Acanthiza chrysorrhoa* (AF197851, AF197852, AM FB780); white-naped honeyeater, *Melithreptus lunatus* (AF197853, AF197854, MOV 294); noisy friarbird, *Philemon corniculatus* (AF197855, AF197856, AM FB528); Lewin's honeyeater, *Meliphaga lewini* (AF197857, AF197858, AM FB226); noisy miner, *Manorina melanocephala* (AF197859, AF197860, AM FB1582); Macgregor's honeyeater, *Macgregoria pulchra* (AF197861, AF197862, AMNH 342052); common smoky honeyeater, *Melipotes fumigatus* (AF197863, AF197864, ANSP/AM 853); and red-throated myzomela, *Myzomela eques* (AF197865, AF197866, ANSP/AM 1023). Primers were those used in Nunn & Cracraft (1996), as well as many genus-specific primers designed from the sequences reported in that paper (available from authors).

Anatomical characters have long played an important role in paradisaeid systematic studies (e.g. Stonor 1938; Bock 1963; Frith & Beehler 1998) and therefore were included here. Osteological characters were scored for the cranium and humerus for each genus in the study and added to the molecular data set (see table 1 for list and description). Skeletons examined in collections of the American Museum of Natural History include (catalogue numbers in parentheses): glossy-mantled manucode, *Manucodia atra* (AMNH 3967, 3968); crinkle-collared manucode, *M. chalybata* (2832, 6785); *Phonygammus keraudrenii* (7690); *Paradisea rubra* (21600); lesser bird of paradise, *P. minor* (4927, 7652); *Cicinnurus regius* (2505); *Diphyllodes magnificus* (7510); *Cnemophilus macgregorii* (16517), *Loboparadisea sericea* (6467, 6783); variegated fairy wren, *Malurus assimilis* (9371); blue-and-white fairy wren, *M. leuconotus* (9370); brown thornbill, *Acanthiza pusilla* (9450); red-browed pardalote, *Pardalotus rubricatus* (9596), *P. striatus* (9461, 9480); large scrubwren, *Sericornis nouhuysi* (6794); perplexing scrubwren, *S. virgatus* (7350), *S. frontalis* (9415); white-plumed honeyeater, *Meliphaga penicillata* (9414); black-and-red honeyeater, *Myzomela rosenbergii* (7528); Papuan black honeyeater, *M. nigrita* (7624); black-headed honeyeater, *M. melanocephala* (23447); New Guinea friarbird, *Philemon novaeguineae* (7433); *P. corniculatus* (1410); white-rumped miner, *Manorina flavigula* (9659); *Melipotes fumigatus* (16073); *Macgregoria pulchra* (6465); brown-headed honeyeater, *Melithreptus brevirostris* (9654); *Ptilonorhynchus violaceus* (4188); *Turdus migratorius* (16067, 18803); *Catharus guttatus* (10569); *Cyanocitta cristata* (10283, 17939); house crow, *Corvus splendens* (22977); black-faced cuckoo-shrike, *Coracina novaehollandiae* (9304); and Australian magpie, *Gymnorhina tibicen* (11492).

χ^2-tests of base frequency homogeneity and character partition analyses (incongruence length difference test (ILD) of Farris *et al.* (1994)) were conducted on both the cytochrome *b* and COI sequences and on character partitions using PAUP* 4.0b2 (Swofford 1999) with 1000 replicates and heuristic searches on data with invariant characters removed to avoid problems with this test reported in the literature (Cunningham 1997; Allard *et al.* 1999). PAUP* was also used to generate all sequence distance measures (uncorrected *p*-distance and transversion distance), which were exported to JMP 3.2 (SAS Institute, Inc.) for analysis and plotting.

Global parsimony analyses of all the data were undertaken using PAUP* 4.0b2 (Swofford 1999). Based on previous molecular studies and palaeontological data (Sibley & Ahlquist 1990; Helm-Bychowski & Cracraft 1993; Boles 1995*a*,*b*, 1997), it was expected that the majority of the taxa investigated in this study would be relatively divergent from one another, with some representing lineages that presumably had originations early in the Tertiary. Many investigators have long believed this situation can lead to a severe transition bias at third positions and thus have the potential to confound phylogenetic resolution of deeper divergences (e.g. Irwin *et al.* 1991; Meyer 1994; although see Källersjö *et al.* 1999; Broughton *et al.* 1999). In order to explore this possible effect on phylogenetic structure, a parsimony analysis of first and second positions using all changes, along with third positions using transversional changes only (hereafter termed '3Tv parsimony analysis') was undertaken and then compared with the global parsimony analysis. This strategy takes advantage of transitional changes at first and second positions that, compared with third positions, are more conservative and typically result in amino-acid replacements. At the same time, this approach preserves character-state variation at third positions by sampling transversional change; other workers have emphasized the potential phylogenetic informativeness of transversional change in general, and third position transversions in particular (Miyamoto & Boyle 1989; Irwin *et al.* 1991; Yoder *et al.* 1996; Groth 1998; Matthee & Robinson 1999). Two genera of thrushes, *Turdus* and *Catharus* (Turdidae), were used as outgroups; turdids are members of the Parvorder Passerida (Sibley & Ahlquist 1990), which is the sister group to the Corvida. Phylogenetic signal was assessed by use of bootstrap (BS) resampling (500 replicates) using PAUP*'s heuristic-search algorithm (jackknife resampling produced similar results).

3. RESULTS

(a) *Sequence comparisons*

Both genes had proportional base frequencies typical of avian mitochondrial DNA (e.g. Nunn & Cracraft 1996):

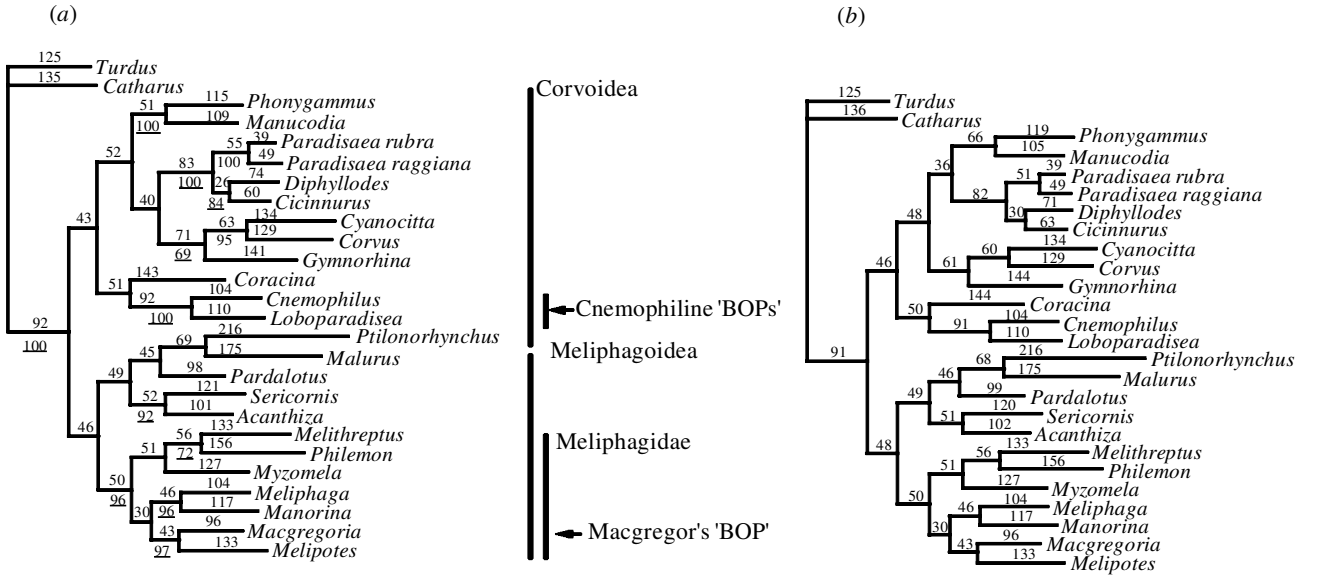

Figure 1. Two equally most parsimonious trees (4300 steps) of a global parsimony analysis (combined molecular and morphological data; morphological transformations treated as discussed in table 1) of corvidan ingroup taxa using two thrushes (Passerida) as outgroups. Numbers above branches are branch lengths; underlined numbers below branches are bootstrap values (500 replicates with heuristic search; only values $> 50\%$ shown). In both trees, the cnemophiline 'birds of paradise' and Macgregor's 'bird of paradise' are found to be distant relatives of paradisaeids.

cytochrome *b* (A, 28.7%; C, 33.1%; G, 13.1%; T, 25.1%), COI (A, 27.8%; C, 29.4%; G, 17.5%; T, 25.3%). Base frequencies were also found to be homogeneous across all taxa (cytochrome *b*, $\chi^2 = 42.092$, d.f. $= 69$, $p = 0.996$; COI, $\chi^2 = 46.107$, d.f. $= 69$, $p = 0.985$). These observations, the absence of any stop codons in the sequences, and the results from the phylogenetic comparisons are consistent with the amplified fragments being mitochondrial and not nuclear.

Pairwise *p*-distances and transversion distances were examined for each codon position as compared with overall divergence (data not shown). Because of the nature of the questions being asked in this study, relatively few closely related taxa were included; instead, the taxon sample spans the breadth of the corvidan passerines, many of which are distantly related (Sibley & Ahlquist 1990; Helm-Bychowski & Cracraft 1993). As a consequence, all pairwise comparisons—except for six within the Paradisaeinae—exhibit greater than 10.0% sequence divergence, and the majority are greater than 14.0%. These patterns are also seen in pairwise comparisons of transversion distances, only 11 comparisons exhibit transversion distances of less than 3.0%. Thus, as expected, third position transitions begin to show saturation near 10.0% *p*-distance (only six pairwise comparisons being below 10.0% *p*-distance).

(b) *Phylogenetic analysis*

Partition homogeneity tests on the two genes using the global and 3Tv parsimony strategies revealed that neither represented a significantly different partition (global analysis, $p = 0.387$; 3Tv analysis, $p = 0.597$). The data thus fit the criterion some workers have proposed that different data sets can be combined when they do not show evidence of biased phylogenetic signal (Bull *et al.* 1993). More interesting, however, is the observation that the 3Tv analysis increased the congruence between the two genes (see below).

Phylogenetic analyses were undertaken on 2163 bp of mitochondrial sequence and 17 morphological characters, for a total of 2180 characters. The results of a global parsimony analysis, giving all characters equal weight, yielded two equally parsimonious trees of 4300 steps (figure 1). Under each reconstruction both the cnemophilines and *Macgregoria* are removed from the birds of paradise. The cnemophilines have a surprising association with the campephagid *Coracina*, whereas *Macgregoria* is placed in the distantly related honeyeaters (Meliphagidae) near the genus *Melipotes*. The result for the cnemophilines is more ambiguous than for *Macgregoria* in that bootstrap values supporting the branch points between the cnemophilines and paradisaeids are below 50%. Those for *Macgregoria*, on the other hand, strongly support its placement within the meliphagids.

The global parsimony trees exhibit several highly unexpected results. First, in both trees the Meliphagoidea are not monophyletic because the bowerbird *Ptilonorhynchus* is clustered with the fairy wren *Malurus*, a relationship that is not supported by protein evidence (Christidis & Schodde 1991) or by DNA hybridization (Sibley & Ahlquist 1990). Furthermore, in one tree (figure 1*a*) the two lineages of the birds of paradise are not monophyletic despite a substantial amount of molecular and morphological evidence to the contrary (Sibley & Ahlquist 1990; Helm-Bychowski & Cracraft 1993; Frith & Beehler 1998). Other relationships are equally unexpected, including the cracticid *Gymnorhina* with the corvids, and *Pardalotus* with *Malurus* plus *Ptilonorhynchus* rather than with meliphagids and the acanthizids *Sericornis* and *Acanthiza* (Sibley & Ahlquist 1990; Christidis & Schodde 1991).

These results raise the conjecture that global parsimony is giving us a misleading signal; if so, what factors might

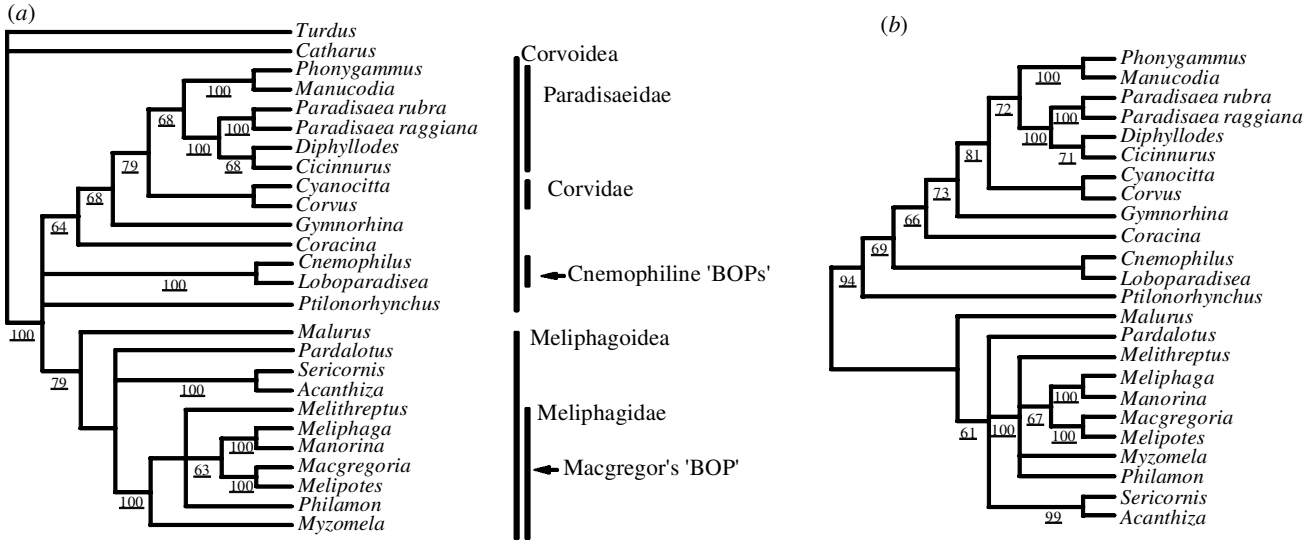

Figure 2. (*a*) A strict consensus tree produced by 3Tv parsimony analysis (morphological data treated as in the analysis of figure 1) of corvidan ingroup taxa using two thrushes (Passerida) as outgroups. Three equally parsimonious trees of 1845 steps were found. (*b*) Analysis of the corvidan ingroup using 3Tv parsimony analysis, with the thrush outgroups deleted and midpoint rooting used to place the root, produced two equally most parsimonious trees of 1682 steps. Underlined numbers below branches are bootstrap values (only values $> 50\%$ shown). In both analyses, the cnemophilines and *Macgregoria* are far removed from the paradisaeids.

be invoked to explain these results? One possible explanation is homoplasy in third positions due to an excess of transitional change. *Ptilonorhynchus* and *Malurus*, for example, could be clustering together (but with bootstrap support of less than 50%) due to having very long branches. One test of this (Siddall & Whiting 1999) is to see whether the two suspect taxa maintain their relative positions when the other is deleted. When *Ptilonorhynchus* is deleted, *Malurus* remains grouped with the pardalotids and acanthizids in the Meliphagoidea, which is relatively consistent with the work of others (e.g. Sibley & Ahlquist 1990); when *Malurus* is deleted, however, *Ptilonorhynchus* moves to the base of the corvoids. This suggests *Ptilonorhynchus* was attracted to *Malurus* for reasons other than a close relationship.

Second, compared with the relatively long terminal branches of the majority of taxa, internodal branch lengths are much shorter, thus making spurious associations among lineages more likely. Finally, when first and second positions, on the one hand, are compared with third positions using an ILD test, the two partitions are discovered to be weakly incongruent or very weakly congruent depending on the level of significance one is willing to accept ($p = 0.091$). The phylogenetic signal thus appears to be different in the two partitions. To test whether this weak incongruence might be related to an excess of third position transitions, an ILD test was performed on the 3Tv data set comparing all first and second position changes with that of third position transversions; congruence between the partitions now increases substantially ($p = 0.194$), thus implying that transitions in third positions are contributing to a different phylogenetic signal. Both ILD tests were undertaken to maximize their effectiveness (Cunningham 1997; Allard *et al*. 1999).

Because of a number of questionable phylogenetic associations produced under global parsimony and the suggestion from the ILD test that these might be due, at least in part, to homoplasy within third position transitions, an analysis was undertaken in which transitional changes were eliminated from third positions. In the 3Tv parsimony analysis, an assessment of phylogenetically informative variation of all the molecular and morphological data yielded three equally parsimonious trees of 1845 steps (figure 2*a*). In the strict consensus the Paradisaeidae are monophyletic and the corvids are their sister group, followed by the cracticid *Gymnorhina*, the campephagid *Coracina,* and then an unresolved polytomy involving the cnemophilines, bowerbirds and the meliphagoids. Within the meliphagoids, *Malurus* is at the base, the meliphagids are monophyletic, and *Sericornis* and *Acanthiza* are united but unresolved with respect to *Pardalotus*. Once again, *Macgregoria* is clustered with *Melipotes* with high bootstrap support. Overall, the tree is much more congruent with relationships inferred from other data such as DNA hybridization (Sibley & Ahlquist 1990) than are the results of the global parsimony analysis (figure 1).

In this analysis both the cnemophilines and *Macgregoria* are far removed from the Paradisaeidae. The Meliphagoidea are strongly monophyletic (with 79% BS) and separated from the other corvidans. Using this data set, the base of the corvoids and the placement of the root remain ambiguous, yet the data are consistent with the hypothesis that cnemophilines are basal corvoids along with bowerbirds.

The potential influence of a distant outgroup on the ingroup reconstruction was also evaluated in a separate analysis (figure 2*b*; two trees of 1682 steps). Eliminating the two thrushes and using midpoint rooting produced a result nearly identical to that of figure 2*a* except that now the cnemophilines are seen as the sister group of all corvoids except the bowerbirds. Moreover, eliminating the outgroup has resulted in strong support (94% BS) for

the separation of the meliphagoids and corvoids (assuming the root is correctly placed). Support for the placement of the cnemophilines near the base of the corvoid lineage and distant to the paradisaeids has increased over the results of figure 2*a*, as they are separated from paradisaeids by a series of nodes with moderate to high bootstrap values. *Macgregoria* is once again clustered with *Melipotes*.

The removal of the cnemophilines and *Macgregoria* from the paradisaeids is not merely a consequence of combining the molecular and morphological data. A 3Tv analysis of each gene separately, or combined, results in the cnemophilines being placed at or near the base of the corvoids (resulting multiple parsimonious trees preclude an exact placement), far removed from paradisaeids, and in having *Macgregoria* united with *Melipotes*.

(c) *Morphological evidence*

Corvidans exhibit a large amount of variation in skull morphology (Stonor 1938; Bock 1963), and some of that is relevant for understanding the phylogenetic position of the cnemophilines and *Macgregoria*. Following are new observations and interpretations relevant to the systematics of these two taxa based on 15 characters from the skull and two from the humerus (table 1).

Table 2 lists character-state changes optimized on, and common to, all three most parsimonious trees of figure 2*a* that are pertinent to the phylogenetic placement of the cnemophilines and *Macgregoria*. A total of ten morphological character-state changes exclude the cnemophilines from the paradisaeids and at the same time place them at the base of the corvidan tree. None of the changes are unique (i.e. have a consistency of 1.00) across the entire tree, but all but one (character 2) are unique within the corvoids above the level of the cnemophilines. Cnemophilines possess many features that are primitive relative to the derived condition of paradisaeids and their close relatives: delicate vomers that are barely expanded distally, and thin dorsoventrally (Bock 1963), absence of ossification in the floor of the nasal cavity (when viewed ventrally; Bock 1963, figs 4 and 5), absence of a nasal septum, maxillopalatines that are club-shaped at their distal end and excavated laterally (Bock 1963, fig. 1). Thus, the morphological data, like the molecular data, support the hypothesis that cnemophilines are not closely related to paradisaeids but are primitive corvidans with a skull much like that of bowerbirds.

The morphological data indicate that *Macgregoria* is nested deeply within the Meliphagoidea and is the sister taxon of the meliphagid *Melipotes*. This relationship is supported by 12 character-state changes on the three most parsimonious trees, and two of those character-state transformations, 16(2) and 10(1), are unique on the entire tree. Like the cnemophilines, *Macgregoria* lacks the derived corvoid characters mentioned above. Instead, it shares many characters of meliphagoids, and of meliphagids in particular, including long and narrow maxillopalatines that are club-shaped and highly excavated, a distinct and expanded foot of the ectethmoid that rests along the jugal bar (Bock 1963, fig. 9), very long transpalatine processes, and a derived condition of the pneumatic fossae of the humerus (see table 2 for others).

4. DISCUSSION

(a) *Systematics of* Macgregoria

Macgregoria was described as a paradisaeid without discussion (De Vis 1897), and Sharpe (1891–1898) soon thereafter suggested a close relationship between *Macgregoria* and the paradisaeid genus *Paradigalla*, presumably because both have nearly all black plumage. Since that time most workers have left *Macgregoria* within the paradisaeids, but with little supporting evidence; Iredale (1950), on the other hand, proposed removing *Macgregoria* from the Paradisaeidae, but again for no stated reason other than it was different from other paradisaeids. The only relevant data after that time were provided by Bock's (1963) discussion of cranial anatomy, and he proposed that *Macgregoria* was closer to the cnemophilines than to the paradisaeines. This conclusion was reached, however, largely because character variation was not examined across all corvidans, nor were character polarities understood within a cladistic framework. As demonstrated in this study, *Macgregoria* and the cnemophilines have a much more primitive skull than do paradisaeines, but this primitive resemblance cannot be used as evidence of their close relationship. Recently, Frith & Beehler (1998) examined 52 characters, mostly plumage, and placed *Macgregoria* as the sister group of the Paradisaeinae. Their sampling, however, was restricted to birds of paradise except for three outgroup taxa, none of them basal corvoids. Their conclusions regarding *Macgregoria* were based on a single osteological character, the supposed presence of an ossified nasal septum in *Macgregoria* and paradisaeines, but in fact *Macgregoria* lacks a nasal septum (as discussed above), a condition typical of basal corvoids and meliphagoids. Other characters noted by them are found elsewhere among the corvoids and thus do not specify a *Macgregoria* and Paradisaeinae relationship.

The molecular and morphological data strongly support the placement of *Macgregoria* within the Meliphagidae, and taking into account the small sample of meliphagid genera included here, *Macgregoria* is the sister group of *Melipotes*. This is a placement borne out by a more comprehensive sample of meliphagids currently under study (A. Driskell, personal communication). The three species of *Melipotes* all have a well-developed yellow facial apterium beginning anteriorly at the eye and which is wattle-like ventrally. This facial patch can flush red when the bird is excited. In *Macgregoria* the wattle is fully developed and anchored at the eye; unlike in *Melipotes* the wattle cannot flush red. Given the hypothesis that *Macgregoria* and *Melipotes* are sister taxa, the two conditions of the facial wattle should probably be considered homologous despite their differences. The apterium–wattle of *Melipotes* is probably the primitive condition.

The species of *Melipotes* are dark grey or black, with light mottling or spotting; the plumage of *Macgregoria* is deep black. The bill shape in the two genera is virtually identical. Both have a pinkish egg, with brown spotting that is more abundant at its large end (Rand 1940; Coates 1990, p. 266). Species in both genera are frugivores (Beehler 1983, 1988; Beehler *et al*. 1986). All of these data are consistent with the results of the molecular analysis. At the same time *Macgregoria* must be considered a highly derived meliphagid in being large and bulky, in having

Table 1. *Morphological characters and character-states for taxa in this study*

(Characters, character-states, and whether character was treated as ordered or unordered include the following. 1. Nasal septum: (0) absent; (1) present. Ordered. 2. Vomer: (0) relatively delicate, little expansion anteriorly, dorsoventrally flattened, with broad, shallow groove dorsally; (1) relatively delicate, flattened dorsoventrally, with lateral sides of distal end having short projections; (2) more robust, broadened distally, with distal end elaborated, with dorsal groove broad but deeper than in (0) or (1); (3) very robust, dorsal groove very deep and narrow; (4) robust, broadened distally, only moderately deep dorsal groove, braces nasal septum, distal end with robust anterior projections; (5) very broad distally, dorsal groove only moderately deep, braces nasal septum and mediopalatine process of premaxilla, robust anterior projections. Ordered, character-state tree: (((5)4,3)2,1)0. 3. Mediopalatine process of premaxilla: (0) absent; (1) present, does not extend posteriorly much beyond palatine–premaxilla junction; (2) extends well beyond junction. Ordered. 4. Maxillopalatine: (0) long, thin, delicate bone with expanded elongate club-shaped posterior end that is excavated laterally; (1) flat triangular or long narrow plate-like structure, not club-shaped and excavated. Ordered. 5. Zygomatic process and mandibular musculature: (0) zygomatic moderately well developed and tapering to point, does not divide temporal fossa; (1) zygomatic heavy, short, and blunt, separated from quadratocranial articulation, divides temporal fossa into two compartments, and is strongly excavated ventrally for muscles in lower compartment; (2) zygomatic long and thin, ends in sharp point, does not divide temporal fossa; (3) zygomatic short and blunt, does not divide temporal fossa; (4) zygomatic relatively short, excavated on lateral side for muscle attachment but does not divide temporal fossa. Unordered. 6. Temporal fossa: (0) relatively small, extends slightly beyond border of paroccipital process; (1) very small, confined anterior to border of process; (2) large, expands far posterior to border of process. Unordered. 7. Transpalatine processes: (0) relatively short and blunt at end; (1) relatively short and pointed at end; (2) very long, narrow, pointed at end. Unordered. 8. Interpalatine processes: (0) very short, blunt, nearly absent; (1) relatively long and thin. Unordered. 9. Palatine, ventral crest (= mediopalatine of Bock (1963)): (0) posterior end with sharp rise to level of articulation with pterygoids; (1) posterior end of crest grades smoothly to articulation. Ordered. 10. Ectethmoid, foot: (0) not well demarcated by strong constriction, not elongated and lying flat along jugal bar; (1) elongated, lying flat along jugal bar, with anterior projection. Ordered. 11. Ectethmoid, head: (0) not greatly expanded posteriorly or anteriorly, with relatively narrow articulation to frontal and, partially, to nasal–frontal hinge; (1) head not well developed, fused to frontal just posterior to nasal–frontal hinge by very narrow, neck-like connection; (2) head not connected to frontal, lacrimal intervenes; (3) head very large, expanded posteriorly along frontal and anteriorly along lateral nasal bar. Unordered. 12. Quadrate, orbital process: (0) tapers to end, foot poorly to only moderately developed and orientated more or less along axis of process; (1) foot well developed and orientated perpendicular to axis of process (T-shaped); (2) foot entirely absent, process tapers to blunt point. Unordered. 13. Quadrate, medial condyle: (0) projects ventrally to same degree as lateral condyle, or projects only slightly more ventrally; (1) medial condyle projects decidedly more ventrally relative to lateral condyle, which is strongly to moderately flatted, not rounded. Unordered. 14. Lacrimal: (0) absent or vestigial; (1) well developed, bracing lateral nasal bar and jugal. Ordered. 15. Ectethmoid, dorsal foramen in head: (0) absent; (1) present. Ordered. 16. Humerus, pneumatic and secondary pneumatic fossae: (0) secondary fossa present, deeply undercuts head of humerus, separated from pneumatic fossa by median crest (medial bar) so that two fossae are distinct and not broadly confluent; (1) secondary fossa absent, surface of bone external to internal tuberosity only slightly or moderately excavated for muscle attachment, attachment for supraspinatus not deep in pneumatic fossa, median crest well developed; (2) secondary fossa essentially absent but bone is moderately to strongly excavated, with median crest being reduced and present only proximally so that both pneumatic fossae are broadly confluent, supraspinatus attachment a very deep pit in pneumatic fossa. Unordered. 17. Humerus, attachment of brachialis: (0) triangular and shortened proximodistally, very deep pit; (1) elongated, tapering proximally, relatively shallow throughout. Ordered.)

taxon	character-states 00000000001111111 12345678901234567
Turdus	00000000000210000
Catharus	00000200000000000
Phonygammus	14111000001110010
Manucodia	14111000001110011
Paradisaea rubra	15211201001110011
Paradisaea raggiana	15211201001110011
Diphyllodes	15211201001111011
Cicinnurus	15211201101111011
Cyanocitta	02103001001011011
Corvus	02110001001111011
Coracina	02103201000011011
Gymnorhina	13012021003011011
Cnemophilus	00003000000100110
Loboparadisea	00003000000100110
Ptilonorhynchus	00014211002001010
Malurus	01012111100200010
Pardalotus	01014111100200020
Sericornis	00002101100200020
Acanthiza	00002111100200020
Melithreptus	01012120110210020
Meliphaga	01000121113200020
Macgregoria	01002120113100???
Melipotes	01002120110100020
Myzomela	01012120110200020
Philamon	01002120113210020
Manorina	01000120113210020

Table 2. *Morphological character transformations on trees of figure 2a that are relevant for the phylogenetic placement of the cnemophilines and* Macgregoria

(Number refers to characters in table 1 that diagnose the relevant clade on all three most parsimonious trees; number in parentheses refers to the derived character-state. The characters under the cnemophilines exclude them from higher hierarchical levels; the numbers under *Macgregoria* include it at higher hierarchical levels within the Meliphagoidea.)

cnemophilines		*Macgregoria*	
clade	derived characters lacking in cnemophilines	clade	derived characters possessed by *Macgregoria*
Coracina + higher corvoids	2(2), 3(1), 13(1), 17(1)	Meliphagoidea	2(1), 6(1), 9(1), 12(2)
Gymnorhina + higher corvoids	1(1), 11(1)	all meliphagoids but *Malurus*	16(2)[a]
corvids + paradisaeid	12(1)		
Paradisaeidae	2(4), 5(1), 14(0)	Meliphagidae branches within meliphagids	7(2), 8(0), 10(1)[a] 13(1), 4(0), 11(3)
		Macgregoria + *Melipotes*	12(1)

[a] Had a consistency on all trees of 1.00.

soft deep black plumage, and in having a large deep orange wing patch.

(b) *Systematics of the cnemophilines*

The cnemophilines have also had a somewhat confusing taxonomic history. In the days of their discovery many workers viewed the birds of paradise and bowerbirds to be very closely related and some united them in a single family. When *Cnemophilus macgregorii* was first described, DeVis (1891, pp. 39–40) placed this new genus and species in the Ptilonorhynchidae, presumably because their bright yellow and red pigments in their plumage resemble those of various bowerbirds, particularly *Amblyornis* and *Xanthomelus* (= *Sericulus*) to which he thought *Cnemophilus* to be closely allied. Likewise, early workers (Sclater 1895; W. Rothschild in Rothschild & Hartert (1896)) placed *Loria*, another cnemophiline, within ptilornorhynchids. At the same time, however, they were drawing attention to features they believed indicated a relationship between the cnemophilines and birds of paradise (Sclater 1891, 1895, p. 344). The preponderance of recent opinion, following Mayr (1962), Bock (1963), and Gilliard (1969), has placed cnemophilines with the birds of paradise.

Bock (1963, fig. 13) envisioned cnemophilines as being ancestral to both birds of paradise and bowerbirds, a conclusion that might be reached by a general phenetic analysis of morphological features but which cannot be supported by molecular and morphological data interpreted cladistically. The cnemophilines appear to be neither birds of paradise nor bowerbirds, but they share a primitive cranial anatomy with bowerbirds and, like bowerbirds, represent an early lineage of the corvoids.

(c) *Australasian avifaunal history*

Investigating the history of corvidans within Australia necessarily begins with an understanding of their phylogenetic relationships. This study, although by no means comprehensive in its taxon sampling, is consistent with the hypothesis that the corvidans can be separated into two major lineages, the Corvoidea and Meliphagoidea. These results further corroborate the hypothesis that bowerbirds are close to, or at the base of, the corvoids and postulate for the first time that the cnemophilines are the next oldest branch. This raises the issue of when the cnemophiline lineage might have originated.

Ideally, an answer to this question would draw on fossil evidence, but in this case it is meagre. The oldest known passerine bird is from the early Eocene of Australia (about 54.6 million years before present (Myr BP); Boles 1995*a*, 1997), but its exact affinities cannot be resolved. If this fossil is related to either the Corvida or Passerida, it would set a minimum age for their divergence, and the age of the fossil is consistent with speculations that passeriforms began diverging at least 55 Myr BP (Sibley & Ahlquist 1985). Fossil evidence indicates that several distantly related corvidan lineages (menurids, orthonychids) had differentiated in Australia by about the early Miocene (Boles 1993, 1995*b*), thus implying a still more ancient origin for the group as a whole. Minimally, these observations suggest the Corvida have probably been in Australia since sometime in the early Tertiary. Using DNA hybridization data Sibley & Ahlquist (1985, 1990) proposed that the Corvida originated in Australia and asserted their separation from the remaining oscine passerines, the Passerida, to be 58–60 Myr BP (Sibley & Ahlquist 1985, p. 4). Considerable uncertainty must be ascribed to this conjecture as it derives from a dubious and poorly calibrated molecular clock.

The fossil evidence (reviewed in Boles (1997), and above) permits the inference that the major split between the Passerida and Corvida took place at least by the early Tertiary. That age therefore places a minimal boundary on interpreting the molecular data and their potential for inferring something about the temporal depth of the corvidan radiation within Australia. Because transversion distances are thought to be roughly linear with time (e.g. Miyamoto & Boyle 1989; Matthee & Robinson 1999), they can be employed as a general index to relative times of divergence. Transversion differences from the thrush (Passerida) outgroups to the corvine ingroups range from 5.8 to 7.9%; from meliphagoid taxa to the corvoids, 5.6 to 7.9%; from *Ptilonorhynchus* to other corvoids, 6.3 to 7.5%; and from cnemophilines to other corvoids (except *Ptilonorhynchus*), 5.6 to 6.9%. Conservatively, two conclusions might be drawn from these data. First, the variability in distances within and among these sister groups suggests the existence of variable evolutionary rates of

transversional change. The degree to which this is the case, however, cannot be investigated meaningfully until taxon samples are increased, as inadequate sampling itself could lead to apparent rate variability of some lineages. Second, the distances, especially the high values, indicate that the separation of the Passerida and Corvida, and the subsequent diversification of the basal lineages within the latter, appear to be nearly contemporaneous. This seems to be true of the cnemophilines as well, and thus these data suggest they represent a relatively old, possibly Eocene or Oligocene element, within the Australian avifauna.

Previous genetic studies have supported the hypothesis that honeyeaters (Meliphagidae) are also an ancient radiation within Australasia (Sibley & Ahlquist 1985, 1990; Christidis 1991; Christidis & Schodde 1991), a conclusion consistent with a maximal transversion distance within the family of 5.2% observed in the small sample of this study (table 1). *Macgregoria* is 2.6% transversional distance (10.5% uncorrected *p*-distance) from *Melipotes*, which indicates the two groups have been separated for a moderate amount of time.

(d) *Implications for understanding evolution of the birds of paradise*

Virtually all discussions of paradisaeid evolution—morphological, behavioural, ecological—have been predicated on the assumption that cnemophilines and *Macgregoria* are paradisaeids and occupy a primitive position within the family. But placing these two taxa near the base of the paradisaeid tree results in their characters having an influence on postulated evolutionary transformations within the family. This has been true for features such as mating systems, sexual dimorphism, ancestral plumage pattern, and ancestral distributions. Removing the cnemophilines and *Macgregoria* from the birds of paradise will necessitate a re-evaluation of their morphological and behavioural evolution once relationships within the family are better understood. Thus, although the manucodines are the strongly supported sister taxon to the paradisaeines, compelling evidence for basal relationships within the core birds of paradise (Paradisaeinae) has not yet been presented.

(e) *Vernacular names*

The removal of the cnemophilines and *Macgregoria* from the paradisaeids necessitates a change in their vernacular names since all are referred to as birds of paradise. The cnemophilines have no readily available vernacular name, hence it is proposed here that the three biological species be called Loria's cnemophilus (*Cnemophilus loriae*), crested cnemophilus (*C. macgregorii*), and yellow-breasted cnemophilus (*Loboparadisea sericea*). The word 'cnemophilus' refers to being a lover of the mountain slope (Frith & Beehler 1998, p. 178), which characterizes all the species. *Macgregoria pulchra* can now be called Macgregor's honeyeater.

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The division of the major songbird radiation into Passerida and 'core Corvoidea' (Aves: Passeriformes) — the species tree vs. gene trees

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The knowledge of evolutionary relationships among oscine songbirds has been largely improved in recent years by molecular phylogenetic studies. However, current knowledge is still largely based on sequence data from a limited number of loci. In this study, we re-evaluate relationships among basal lineages within the 'core Corvoidea' and Passerida radiations, by adding additional loci to previously published data. The trees obtained from the individual genes suggest incongruent topologies. Especially the positions of Callaeatidae (wattlebirds), Cnemophilidae (satinbirds) and Melanocharitidae (longbills and berrypeckers) vary among the trees, but RAG-1 is the only gene that unambiguously suggested a 'core Corvoidea' affinity for these taxa. Analyses of various combined data sets show that the phylogenetic positions for Callaeatidae, Cnemophilidae and Melanocharitidae largely depend on which genes that have been combined. As the RAG-1 gene has contributed to a majority of the phylogenetic information in previous studies, it has deeply influenced previous molecular affinities of these taxa. Based on the current data, we found a reasonable support for a Passerida affinity of Callaeatidae and Cnemophilidae, contrary to previous molecular studies. The position of Melanocharitidae is more unstable but a basal position among Passerida is congruent with a deletion observed in the glyceraldehyde-3-phosphodehydrogenase (GAPDH) loci. Molecular clock estimations conducted on the combined data sets were generally found to be similar, but for some divergences significant differences were found. These results illustrate the potential problem of phylogenies predominantly based on characters from one or a few loci, and exemplify the importance of well-supported phylogenies before reasonable time estimates of passerine divergences could be achieved.

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Introduction

Nearly half of the extant bird species in the world belong to the oscine (songbird) lineage which constitutes the majority of perching birds (Passeriformes), the linage is thus by far the most abundant avian radiation (Monroe & Sibley 1993). It includes many familiar birds; some of which are among the most well-studied birds in avian science. A robust phylogeny of oscines has therefore been highly desirable as a framework for various comparative studies and to better understand the biogeographical history of songbirds. Phylogenetic evidence from morphological studies (e.g. Beecher 1953; Ames 1971; Raikow 1978) has been limited, largely because convergent evolution to similar feeding specializations is commonly found in perching birds. During the 1980s, Charles G. Sibley and coworkers made the first serious molecular attempt, by using DNA–DNA hybridization data, to resolve the passerine tree and other avian relationships (Sibley & Ahlquist 1990). One main conclusion was that oscine birds could be divided in two reciprocally monophyletic clades: Corvida and Passerida. However, the avian DNA–DNA hybridization network by Sibley and coworkers has been heavily criticized on methodological grounds (Cracraft 1987; Houde 1987; Harshman 1994). Subsequent independent molecular studies (Barker *et al.* 2002, 2004; Ericson *et al.* 2002a,b) suggest that

Corvida *sensu* Sibley *et al*. is polyphyletic, as several deep lineages confined to the Australian region (e.g. Menuridae, Ptilonorhynchidae, Meliphagidae, Pomatostomidae and Orthonychidae) are subsequent sisters to all other oscines. The monophyly of Passerida on the other hand seems well supported as a lineage nested within Corvida *sensu* Sibley *et al*. (Barker *et al*. 2002, 2004; Ericson *et al*. 2002a).

Barker *et al*. (2002, 2004) were the first to publish a phylogeny of passerine birds based on DNA sequence data, with an almost complete family representation. Their results suggest that a majority of traditional corvidan birds form a clade that is the sister to Passerida (their 'core Corvoidea'). Furthermore, Barker *et al*. (2004) found that Callaeatidae (wattlebirds) in New Zeeland, Cnemophilidae (satinbirds) and Melanocharitidae (longbills and berrypeckers) in New Guinea, represent basal lineages in their 'core Corvoidea' radiation. Several studies have further shown that Petroicidae and Picathartidae are basal members of the Passerida radiation (Ericson *et al*. 2002b; Ericson & Johansson 2003; Barker *et al*. 2004; Jønsson *et al*. 2007). No morphological characters unambiguously support this subdivision, but an amino acid insertion in the c-*myc* gene has been proposed as a synapomorphy for Passerida (Ericson *et al*. 2000; Ericson & Johansson 2003).

Many internal relationships among 'core Corvoidea' and Passerida are poorly supported in the phylogeny by Barker *et al*. (2004). This is particularly the case for deeper relationships within the 'core Corvoidea'. However, independent studies based on other genes overall support the Barker *et al*. (2004) phylogeny, but relationships that are in topological conflict have also been found both within the 'core Corvoidea' (e.g. Fuchs *et al*. 2006) and Passerida (e.g. Ericson & Johansson 2003). Possibly the most intriguing of these is the amino acid insertion in c-*myc* (Ericson *et al*. 2000; Ericson & Johansson 2003) that is not supported as having a single unique origin in the Barker *et al*. (2004) phylogeny. However, that other studies find conflicting relationships to those suggested by Barker *et al*. (2004) is hardly surprising. The Barker *et al*. phylogeny in essence represents a RAG-1 gene tree (75% of the nucleotide data) and gene trees are not necessarily genealogically identical to the species tree (Maddison 1997). In this study, we evaluate the relationships of deep branches in 'core Corvoidea' and Passerida suggested by Barker *et al*. (2004), by adding independent DNA sequence data to their data set. We examine trees from individual genes and various combined data sets, as well as amino acid changes and indel events. We also examine how the phylogenetic results affect molecular clock estimates.

Materials and methods

Taxon sampling, amplification and sequencing

We examined the phylogenetic delimitation of Passerida and core Corvoidea, respectively, by analysing DNA sequence data from 36 taxa. The taxon sampling is based on previous molecular results (Barker *et al*. 2002, 2004; Ericson *et al*. 2002a; Ericson & Johansson 2003), and includes representatives from all recognized basal lineages within Passerida and 'core Corvoidea', as well as a selection of more terminal taxa within these two clades. The sampling also includes representatives from all lineages of oscines that have been suggested to be basal in relation to the 'core Corvoidea'–Passerida split. Five nuclear loci, RAG-1, RAG-2, myoglobin intron 2 (Myo), ornithine decarboxylase introns 6–7 (ODC) and glyceraldehyde-3-phosphodehydrogenase intron 11 (GAPDH), have been studied. The RAG-1 and RAG-2 sequences have been downloaded from GenBank, while sequences from Myo, ODC and GAPDH have either been sequenced for this study or downloaded from GenBank. The latter three have been chosen as they are easy to amplify from study skins (Irestedt *et al*. 2006), and have been shown to be useful to resolve avian relationships at this phylogenetic level (e.g. Jønsson *et al*. 2007). For extraction, amplification and sequencing procedures for fresh tissue/blood samples, see Irestedt *et al*. (2001, 2002), Fjeldså *et al*. (2003) and Allen & Omland (2003), while corresponding procedures for study skins are described in Irestedt *et al*. (2006) and Jønsson *et al*. (in prep). See Table 1 for the complete taxon sampling and GenBank accession numbers.

Phylogenetic inference and model selection

We used Bayesian inference (see, e.g. Huelsenbeck *et al*. 2001; Holder & Lewis 2003) to estimate the phylogenetic relationships. The models for nucleotide substitutions used in the analyses were selected for each gene individually by applying the Akaike Information Criterion (AIC, Akaike 1973) using the program MrModeltest 2.2 (Nylander 2005) in conjunction with PAUP* (Swofford 1998). Due to a rather low number of insertions in the studied genes/introns, the sequences could easily be aligned by eye. All gaps are treated as missing data in the 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 & Huelsenbeck 2003). Analyses were performed for (i) all the individual genes separately, (ii) the RAG-1 and RAG-2 genes combined, (iii) a concatenated data set with all genes, and (iv) a data set with all genes *except* the RAG-1 gene. In the analysis of concatenated data sets the models selected for the individual gene partition were used, but the topology was constrained to be the same. We used an unconstrained, exponential branch length prior. All chains were run for 10 million generations, with trees sampled every 100th generations. The trees sampled during the burn-in phase (i.e. before the chain had reached its apparent target distribution) were discarded, and after checking for convergence, final inference was made from the concatenated output from the two runs.

Table 1 Specimen data and GenBank accession numbers for samples used in the study.

Species	Sample ID	ODC	GAPDH	Myo	RAG-1	RAG-2	Species used in Barker *et al.* (2004)
Batis poensis	MNHN CG 1998-783	EU272120	DQ406665	AY529907	AY443263	AY443110	*B. mixta*
Bombycilla garrulus	NRM 986044	EU272128	EU272099	AY228286	AY056981	AY443111	
Callaeas cinerea	Ewen	EU272124	EU272097	EU272108	AY443317	AY443202	*Philesturnus carunculatus*
Chaetops frenatus	PFI uncat.	EF441234	EF441212	AY228289	AY443266	AY443116	
Colluricincla harmonica	MV1422	EU273356	EU273376	EU273396	AY443270	AY443124	
Coracina atriceps	WRZM1910.12.28.182	EU272118	EU272091	EU272102	AY056988	AY443127	*C. lineata*
Cormobates placens	MV E309	EF441237	EF441215	AY064731	AY443274	AY443130	*C. leucophaea*
Corvus corone	MNHN 13-16	EU272116	DQ406663	AY529914	AY056989	AY443132	
Dicrurus bracteatus	UWBM 68045	EU272113	EF052813	EF052839	AY056991	AY443140	*D. adsimilis*
Gymnorhina tibicen	MV AC78	EU272119	DQ406669	AY064741	AY443289	AY443153	
Hirundo rustica	NRM 976238	EF441240	EF441218	AY064258	AY443290	AY443155	
Hylophilus ochraceiceps	ZMUC127900	EU272109	EU272087	EU272100	AY443291	AY443156	*H. poicilotis*
Lanius collaris	MNHN 2-26	EU272112	DQ406662	AY529925	AY443293	AY443160	*L. excubitor*
Loboparadisaea sericea	NRM 566737	EU272125	EU272095	EU272106	AY443294	AY443161	
Cnemophilus loriae	NRM 569572	EU272126	EU272096	EU272107	AY443269	AY443123	
Malurus amabilis	MV C803	EF441241	EF441219	AY064729	AY057001	AY443162	*M. melanocephalus*
Melanocharis versteri	NRM 543385	EU272121	EU272092	EU272103	AY443299	AY443168	
Menura novaehollandiae	AM Lab1112	EF441242	EF441220	AY064744	AY057004	AY443171	
Monarcha melanopsis	B541, UWBM 62890	EU272114	EU272089	DQ084110	AY057006	AY443176	*M. axillaris*
Oedistoma pygmaeum	NRM 569569	EU272122	EU272093	EU272104	AY057010	AY443182	*O. iliolophum*
Oriolus xanthornus	MNHN 4–10D	EU272111	DQ406645	AY529929	AY057011	AY443184	*O. larvatus*
Orthonyx temminckii	MV B831	EF441244	EF441222	AY064728	AY443309	AY443187	
Pachycephala albiventris	ZMUC 117176	EF441245	EF441223	EF441259	AY443310	AY443188	*P. hyperythra*
Pachycephalopsis hattamensis	NRM 552153	EF441246	EF441224	EF441260	AY443311	AY443190	*P. poliosoma*
Parus major	NRM 956363	EU272127	EU272098	AY228310	AY443314	AY443197	
Pericrocotus cinnamomeus	USNM B6146	EU272117	EF052753	EF052764	AY443316	AY443200	*P. ethologus*
Picathartes gymnocephalus	LSUMZ B-19213	EF441247	EF441225	AY228314	AY057019	AY443203	
Pomatostomus temporalis	MV D257	EF441248	EF441226	AY064730	AY057023	AY443210	*P. isidorei*
Prunella modularis	NRM 976138	EF441249	EF441227	AY228318	AY057024	AY443213	*P. collaris*
Ptilonorhynchus violaceus	AM LAB1099	EF441250	EF441228	AY064742	AY057026	AY443216	
Ptilorrhoa leucosticta	NRM 84405	EF441255	EF441233	EF441261	AY443326	AY443218	*P. caerulescens*
Rhipidura rufifrons	C733, CEF239	EU272115	EU272090	DQ084100	AY443329	AY443223	*R. hyperythra*
Sturnus vulgaris	NRM 966615	EF441253	EF441231	AY228322	AY057032	AY443232	
Sylvia atricapilla	NRM 976380	EF441254	EF441232	AY228323	AY057033	AY443233	*S. nana*
Toxorhamphus poliopterus	NRM 543574	EU272123	EU272094	EU272105	AY057036	AY443238	*T. novaeguineae*
Vireo olivaceus	NRM 976766	EU272110	EU272088	EU272101	AY057041	AY443245	*V. philadelphia*

Acronyms: AM, Australian Museum, Sydney; LSUMZ, Louisiana State University, Museum of Natural Science; MNHN, Muséum National d'Histoire Naturelle, Paris; MV, Museum Victoria, Melbourne; NRM, Swedish Museum of Natural History, Stockholm; PFI, Percy Fitzpatrick Institute, Cape Town; USNM, National Museum of Natural History, Smithsonian Institution, Washington; UWBM, University of Washington, Burke Museum; WRZM, Walter Rothschild Zoological Museum, Tring; ZMUC, Zoological Museum of the University of Copenhagen.

Some Myo, GAPDH and ODC sequences, and all RAG-1 and RAG-2 sequences have been downloaded from GenBank. The RAG-1 and RAG-2 sequences that have been obtained from a different species than those used for Myo, GAPDH and ODC are indicated in the table.

All alignments of individual genes were also inspected for indel events, and the protein coding genes (RAG-1 and RAG-2) were also inspected for amino acid changes. One indel event was found to be of potential interest for the 'core Corvoidea'–Passerida split; a deletion in the GAPDH alignment. In order to examine the taxonomic distribution of this indel more carefully, all GAPDH sequences available (downloaded from GenBank and unpublished sequences by us and colleagues at the Swedish Museum of Natural History, data not shown) were inspected for this indel events. In totally 125 GAPDH sequences were examined.

Molecular rate smoothing estimates

Divergence times were estimated using the nonparametric rate smoothing method PATHd8 (Britton *et al.* 2007), which smoothes substitution rates sequentially by taking averages over paths lengths from an internode to all its descending terminals. The primary aim was not to make improved time estimates, but to investigate how different phylogenetic hypotheses affect the molecular clock estimates.

A reliable passerine calibration point based on fossil data is currently lacking, why the separation of New Zealand from Australia/Antarctica has been used as a calibration point for

the separation of *Acanthisitta* from the rest of the passerines in several studies (Barker *et al.* 2002, 2004; Ericson *et al.* 2002a)? As we lack sequences data from *Acanthisitta* for Myo, ODC and GAPDH, we arbitrary used the molecular estimate of the split of *Menura* from the rest of the oscines at 62 Mya (Barker *et al.* 2004). Divergence time estimates were made on the trees obtained from the (i) RAG-1 and RAG-2 data set, (ii) the data set with all genes, and (iii) the data set with all genes except the RAG-1 gene.

Results

Model selection and phylogenetic relationships

A priori selection of substitution models supported that the GTR + I + Γ model had the best fit for RAG-1 and RAG-2, and GTR + Γ for Myo, ODC and GAPDH. These models were used in the Bayesian analyses of the individual genes as well as in the combined analysis. After discarding the burn-in phase the inference were based on a total of 75 000–90 000 samples from the posterior for the individual genes and the combined data sets. For the phylogenetic inference, the mode of the posterior distribution of topologies was presented as a majority-rule consensus tree from each analysis (Figs 1 and 2).

The trees obtained from the Bayesian analyses of the individual gene partitions are all more or less topologically incongruent (Fig. 1), but certain clades are supported by all gene regions. In general, certain regions in the trees are seemingly more congruent than other, while the incongruence is worse in other areas of the trees. Of interest for this study are the relative positions of Callaeatidae, Cnemophilidae, Melanocharitidae (*Toxorhamphus*, *Oedistoma* and *Melanocharis*), Picathartidae and Petroicidae (*Pachycephalopsis*). While the RAG-1 tree suggests that all of these taxa, except Petroicidae, are basal members of core Corvoidea, the position of these taxa are not that clear in the other genes. However, several of them are generally suggested to be basal members of the Passerida radiation, while others are principally unresolved or in some occasion basal to both the Passerida and 'core Corvoidea' radiations. Of all the individual gene trees, the RAG-1 tree is also the most resolved tree and has most nodes with posterior probability values > 95%, followed by the RAG-2 gene, while the trees obtain from the intron regions are the most unresolved and have lowest number of nodes with posterior probability values > 95%. However, this is merely a consequence of the how many phylogenetically informative characters these genes have, respectively.

Variation in the molecular data set

The alignments of the protein coding genes RAG-1 and RAG-2 consists of 2872 and 1152 bp, respectively. A few amino acid indels were observed in the two RAG alignments, all RAG-1 indels were found to be autapomorphic, while two deletions in RAG-2 were shared between *Cormobates*, *Ptilonorhynchus* and *Vireo*, and *Bombycilla* and *Hirundo*, respectively. However, as these indels are of no interest for the division of Passerida and 'core Corvoidea' they are not further discussed. The alignments of the non-coding intron regions were 338 bp for GAPDH, 750 bp for Myo and 758 bp for ODC. Most indels in these more variable regions were found to be short and autapomorphic (one exception is the ODC sequence from *Rhipidura* that has a 83-bp long insertion). Some indels were also found to be incongruent with the phylogenetic tree obtained from the analysis of the combined data sets. However, these were generally found in the most variable regions and some of the single base pair insertions actually consist of different bases. Most indel events congruent with any/all combined phylogenies were found to be of limited interest for the Passerida and 'core Corvoidea' division (e.g. supporting only minor terminal clades) and will not be further discussed. However, one indel was found to be of potential interest for the 'core Corvoidea'–Passerida split; a deletion of 18 bp in the GAPDH alignment were uniquely found in all traditional Passerida species (32 taxa), *Chaetops*, *Picathartes*, *Pachycephalopsis*, Callaeatidae, *Cnemophilus*, *Loboparadisaea*, *Toxorhamphus*, *Oedistoma* and *Melanocharis* (*Lanius* and *Ptilorrhoa* have partly overlapping autapomorphic deletions in GAPDH, but they start and end at different positions). If mapping this indel on the combined trees (Fig. 2), the GAPDH deletion has its most parsimonious distribution on the tree obtained from the analyses of the combined data set of all genes expect RAG-1 (tree C, Fig. 2). No amino acid substitutions were found in the protein coding genes RAG-1 and RAG-2 that could be of importance for the 'core Corvoidea'–Passerida split.

Molecular rate smoothing estimates

Divergence estimates from the RAG-1/RAG-2 tree and the tree based on all genes except RAG-1 are generally rather similar, but for some nodes the time estimates are strikingly different. The most noticeable, is that Callaeatidae is suggested to have diverged from other oscines 30.5 Mya in the estimate from the RAG-1/RAG-2 tree, while the corresponding estimate from the tree based on all genes except RAG-1 suggest the Callaeatidae diverged from the 'Passerida' linage as early as 46 Mya.

Discussion

Species tree, gene trees and the 'core Corvoidea'–Passerida split

The trees obtained from the Bayesian analyses of the individual gene partitions are more or less topologically incongruent (Fig. 1), especially regarding the positions of Callaeatidae, Cnemophilidae, Melanocharitidae and Picathartidae. The analyses of the combined data set (Fig. 2) also shows that the

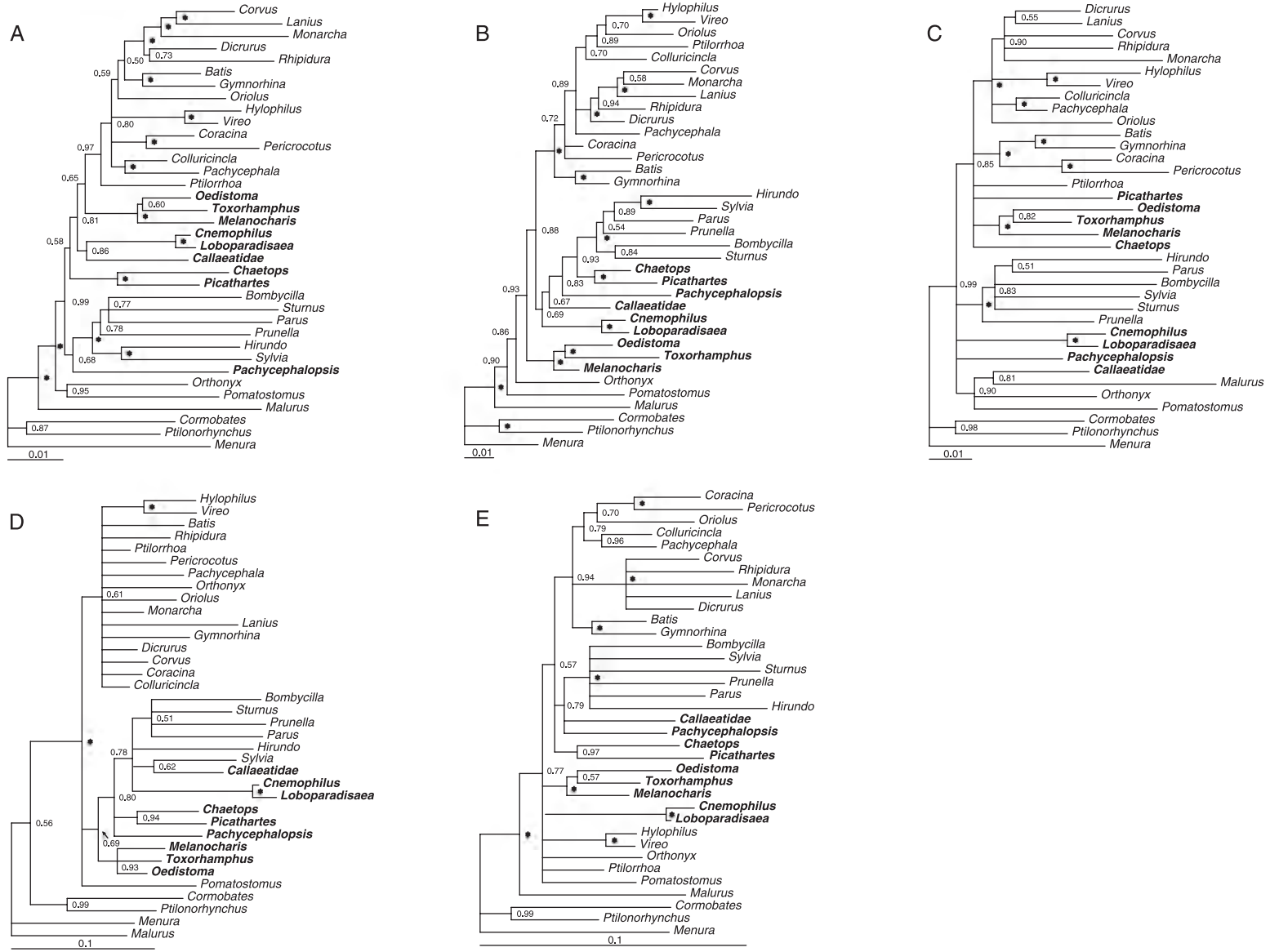

Fig. 1 A–E. The majority rule consensus trees obtained from the Bayesian analyses of the individual genes. —A. RAG-1. —B. RAG-2. —C. Myo. —D. GAPDH. —E. ODC. Posterior probability values are indicated at the node, posterior probability values of 1.00 are indicated with an asterisk. Lineages suggested by Barker *et al.* (2004) to be basal in 'core Corvoidea' (Callaeatidae, Cnemophilidae and Melanocharitidae) and in Passerida (Petroicidae and Picathartidae) are in bold type.

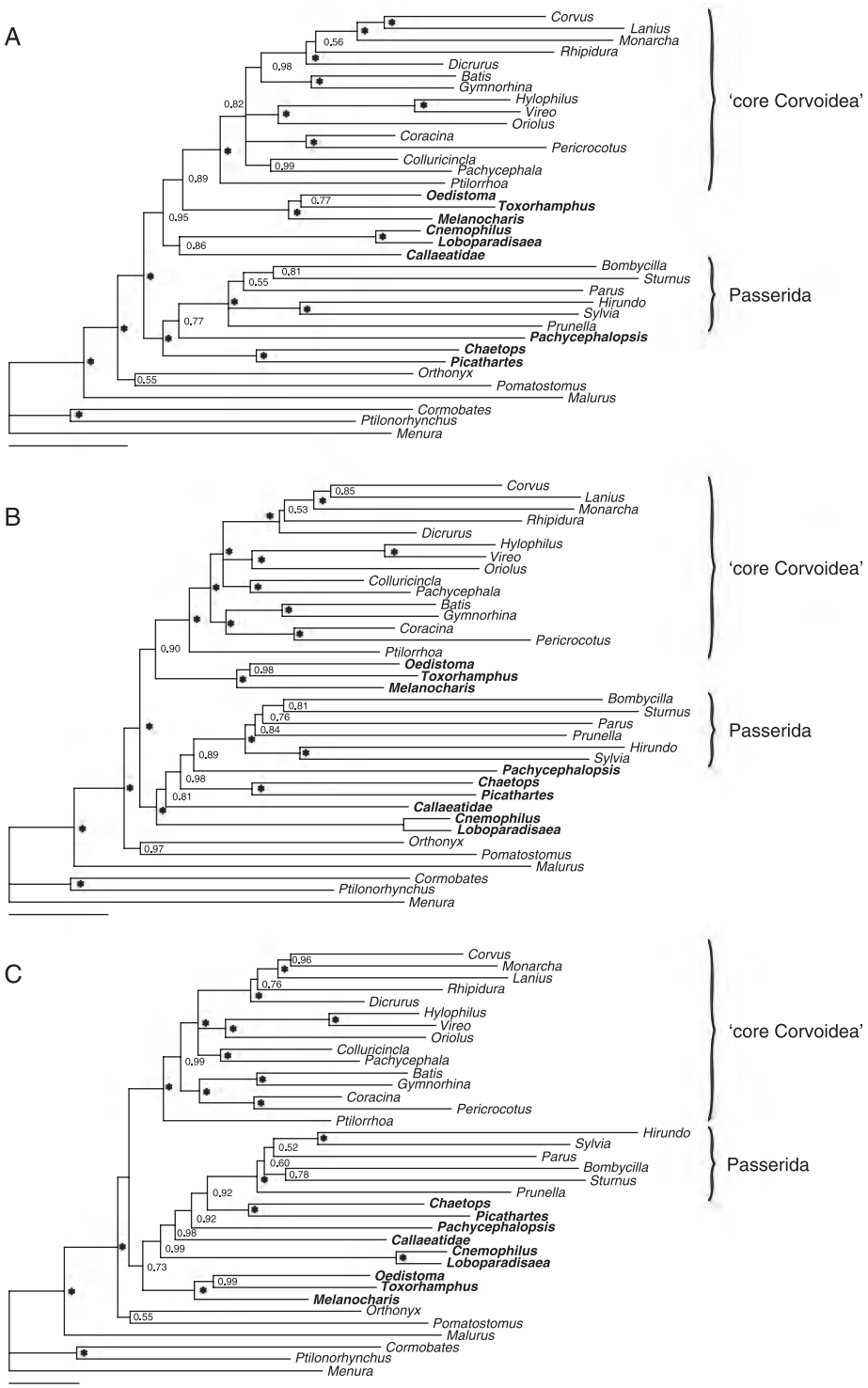

Fig. 2 A–C. The majority rule consensus trees obtained from the Bayesian analyses of combined data sets. —A. The tree obtained from the analyses of RAG-1 and RAG-2. —B. The tree obtained from the analyses of all genes (RAG-1, RAG-2, Myo, GAPDH and ODC). —C. The tree obtained from all genes except RAG-1. Posterior probability values are indicated at the node, posterior probability values of 1.00 are indicated with an asterisk. Lineages suggested by Barker *et al*. (2004) to be basal in 'core Corvoidea' (Callaeatidae, Cnemophilidae and Melanocharitidae) and in Passerida (Petroicidae and Picathartidae) are in bold type.

phylogenetic positions for these taxa largely depend on which genes that has been combined. It is therefore worth noticing that the phylogeny by Barker *et al.* (2004) is based on only two genes (RAG-1 and RAG-2) and that RAG-1 represents nearly 75% of the nucleotide data included in the study. In essence, the Barker *et al.* (2004) phylogeny is a RAG-1 gene tree, and gene trees are not necessarily topologically identical to the species tree (Maddison 1997). This is often neglected in avian molecular phylogenetics, although incongruence is a common phenomenon in molecular phylogenetic studies and has been reported at many avian levels (e.g. Degnan 1993; Alström & Ödeen 2002; Irestedt *et al.* 2004; Moyle 2004; Fjeldså *et al.* 2005; Fuchs *et al.* 2006). Observed incongruence between gene trees could be an effect of both biological processes (Maddison 1997), and various analytical factors such as the choice of optimality criterion (Huelsenbeck 1994) or taxon sampling (Graybeal 1998; Hedtke *et al.* 2006). It has also been found that current tests of incongruence are not always reliable (Sullivan 1996; Cunningham 1997). Therefore, in practice, incongruence between gene trees may be difficult to handle. Nevertheless, this is a problem that has to be considered in avian molecular systematics. Theoretically, a phylogeny based on DNA sequences from multiple independent loci should have a better chance of identifying the correct species tree than a single gene tree, by increasing the signal : noise ratio. Edwards *et al.* (2007) have demonstrated that there is a high probability of recovering the correct species tree (for eight taxa) with only three genes, if a large proportion of the genes have phylogenies that matches the species tree. On the other hand it was also shown that more than 100 genes might be needed to recover the correct species tree with reasonably high probability, if a low proportion of the gene trees are congruent with the species tree. Consequently, the information needed to resolve the correct species tree may differ significant among and within clades, due to factors such as the particular phylogenetic history (e.g. the occurrence of long and short branches within a tree and the relationship between them) and properties of the studied genes (e.g. number of variable sites, saturation, etc.).

As a consequence of this, many more loci than those available at present may be needed before a well-supported phylogeny of all oscine birds can be obtained. In the present era of genomics, it is technically possible to sequence hundreds of independent loci for all oscine families. However, in practice the funding in avian molecular systematics is limited and it is reasonable to believe that it will be long before a data set (with a sufficient number of independent loci) is available, that is satisfactorily powerful to resolve all nodes in the oscine species tree correctly. As branch lengths often vary considerably within a species tree, incongruence is likely to be more common in certain regions of a species tree (Rokas *et al.* 2003; Kubatko & Degnan 2007). It is also commonly observed that certain taxa often change positions in phylogenies when different markers are used while other taxa are more firmly placed regardless of the genes used. As most avian phylogenetic studies published at present use more than one gene, it is possible to compare individual gene trees for congruence and incongruence. Even with a data set with rather few genes, it should be possible to identify stable and unstable regions in a given species tree with some confidence. In Barker *et al.* (2004) phylogeny two genes were used, the RAG-1 and RAG-2. Although these genes are closely linked the phylogenies obtained from them are not topologically congruent. Especially, when considering the 'core Corvoidea'–Passerida split these two genes favour two different scenarios (trees A and B, Fig. 1), and if all gene trees in this study are considered (trees A–E, Fig. 1) it is obvious that the phylogenetic positions of Callaeatidae, Cnemophilidae and Melanocharitidae are difficult to assess. RAG-1 is the only gene that assigns these taxa to the 'core Corvoidea' radiation. The other gene trees are either virtually unresolved (Myo), place some of the taxa within Passerida (ODC) or place all of them within Passerida (RAG-2 and GAPDH).

When comparing the trees obtained from the combined data sets of RAG-1 and RAG-2, with the trees of all genes, and with the trees of all genes excluding RAG-1 (Fig. 2A–C), some interesting patterns are elucidated. First, the tree obtained from the RAG-1 and RAG-2 combined data set, is very similar to the individual tree from the RAG-1 gene. This is hardly surprising, as RAG-1 has more than two times, as many, parsimony informative sites as does RAG-2. In the tree obtained from the analyses of all genes, Callaeatidae and Cnemophilidae move from a basal position in the 'core Corvoidea' to become basal members of the Passerida and Melanocharitidae are placed as the basalmost clade in the 'core Corvoidea' (although with a posterior probability of only 0.90). Furthermore, the combined analysis of all genes except RAG-1, supports a tree where also the Melanocharitidae clade becomes a basal member of the Passerida, but again with low support (posterior probability 0.73). These results clearly illustrate that relationship that appear to be well supported (in this case by several thousand basepairs!) by one or a limited number of loci, could in fact be very unstable and that a few additional genes might alter the topology considerably. An obvious conclusion from these results is that many biological relationships based on molecular data from a limited number of loci need to be further substantiated by independent markers, before we can consider these phylogenetic hypotheses well supported.

The affinity of Callaeatidae, Cnemophilidae and Melanocharitidae, divergence date estimates and conclusions

The phylogenetic affinity of Callaeatidae, Cnemophilidae, Melanocharitidae and other basal passerida and 'core Corvoidea'

clades deserves further attention. Additional independent loci would most likely cast more light over this part of the oscine phylogeny. However, based on current data we believe that we have a reasonable support for a Passerida affinity of Callaeatidae and Cnemophilidae, while the affinity of Melanocharitidae is more uncertain. We consider the phylogeny based on all genes except RAG-1 as the most plausible hypothesis for this part of the oscine phylogeny as: (i) it is fully congruent with the unique deletion observed in GAPDH in core Passerida, Petroicidae, Picathartidae, Callaeatidae, Cnemophilidae and Melanocharitidae; (ii) the topology is consistent with a monophyletic origin of the amino acid insertion in c-*myc* found in core Passerida and Picathartidae; (iii) the position of Callaeatidae, Cnemophilidae and Melanocharitidae is most deviant in the RAG-1 gene tree; and (iv) it is the biogeographically most parsimonious hypothesis as it requires only one major dispersal event of the Passerida branch from the Australo-Papuan region to the Old World.

To understand the evolution and biogeographical history of oscines or other avian clades, molecular clock estimations on DNA sequence data is an important and commonly used tool. Many factors such as uncertainties in calibrations (e.g. Graur & Martin 2004) none clocklike evolution, or inconsistent use of the various calibrations methods available (Peterson 2006), could make these estimates less reliable. An additional, obvious but often overlooked problem with molecular time estimates is how well the phylogenies, on which the estimates are based, represent the species phylogeny. Herein, we have shown drastically topological changes for a group of taxa when different genes have been used to interpret their affinity, and this will obviously also affect the time estimates of the divergences of these taxa. When we compared some divergence estimates from the RAG-1/RAG-2 tree and the tree based on all genes except RAG-1 most estimates were found to be rather similar, but some nodes were found where the time estimates are strikingly different. The most noticeable is that Callaeatidae is suggested to have diverged from other oscines 30.5 Mya in the estimate from the RAG-1/RAG-2 tree, while the corresponding estimate from the tree based on all genes except RAG-1 suggest the Callaeatidae diverged from the 'Passerida' linage as early as 46 Mya. Such large discrepancy is an obvious source for incorrect interpretations of biogeography or evolutionary responses to habitat changes.

The results in this study illustrate the potential problem of using a small number of genes in avian systematics, and especially when a majority of the phylogenetic informative characters have been obtained from one (or a few) loci. We advocate that individual genes always should be analysed separately (apart for the combined analysis) and inspected for topological congruence/incongruence, as this makes it possible to discriminate, with some confidence, between parts of a tree that are well and poorly supported. When possible, we also advocate selecting multiple independent loci that contribute roughly equal to the phylogenetic information, rather than using very long sequences from single loci. The results also illustrate the importance of well-supported phylogenies before reasonable time estimates of passerine divergences could be achieved.

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