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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.

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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 cockerelli/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

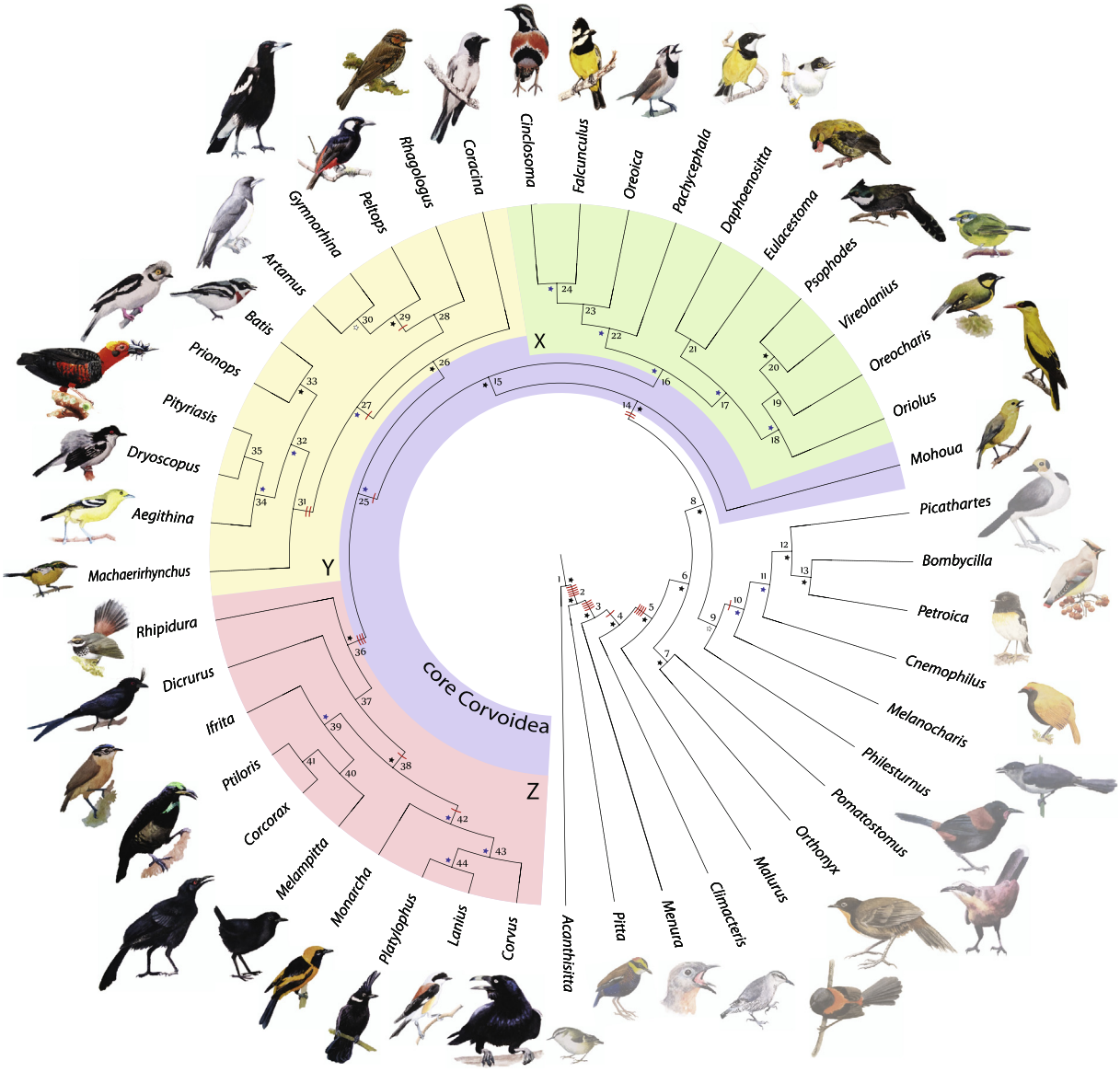

Fig. 1. 50% Majority rule consensus tree of the concatenated dataset (19,782 base pairs) of the core Corvoidea based on 100 million generations in MrBayes (branch lengths not representative) with illustrations representing the taxa included in the study. Core corvoid lineages are highlighted in colours. 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),

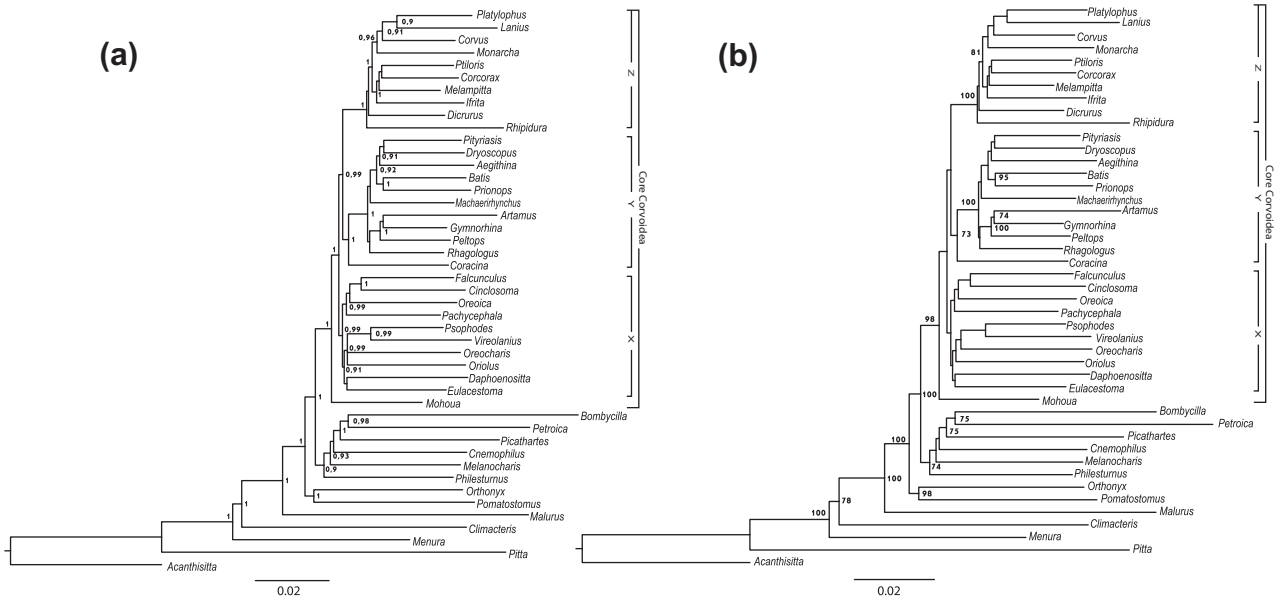

Fig. 2. Phylogenies based on analyses of the full concatenated dataset in (a) MrBayes, and (b) RAxML, with posterior probabilities above 0.90 (MrBayes) or bootstrap values above 70 (RAxML) shown. Core corvoid clades X, Y and Z are discussed in the main text.

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

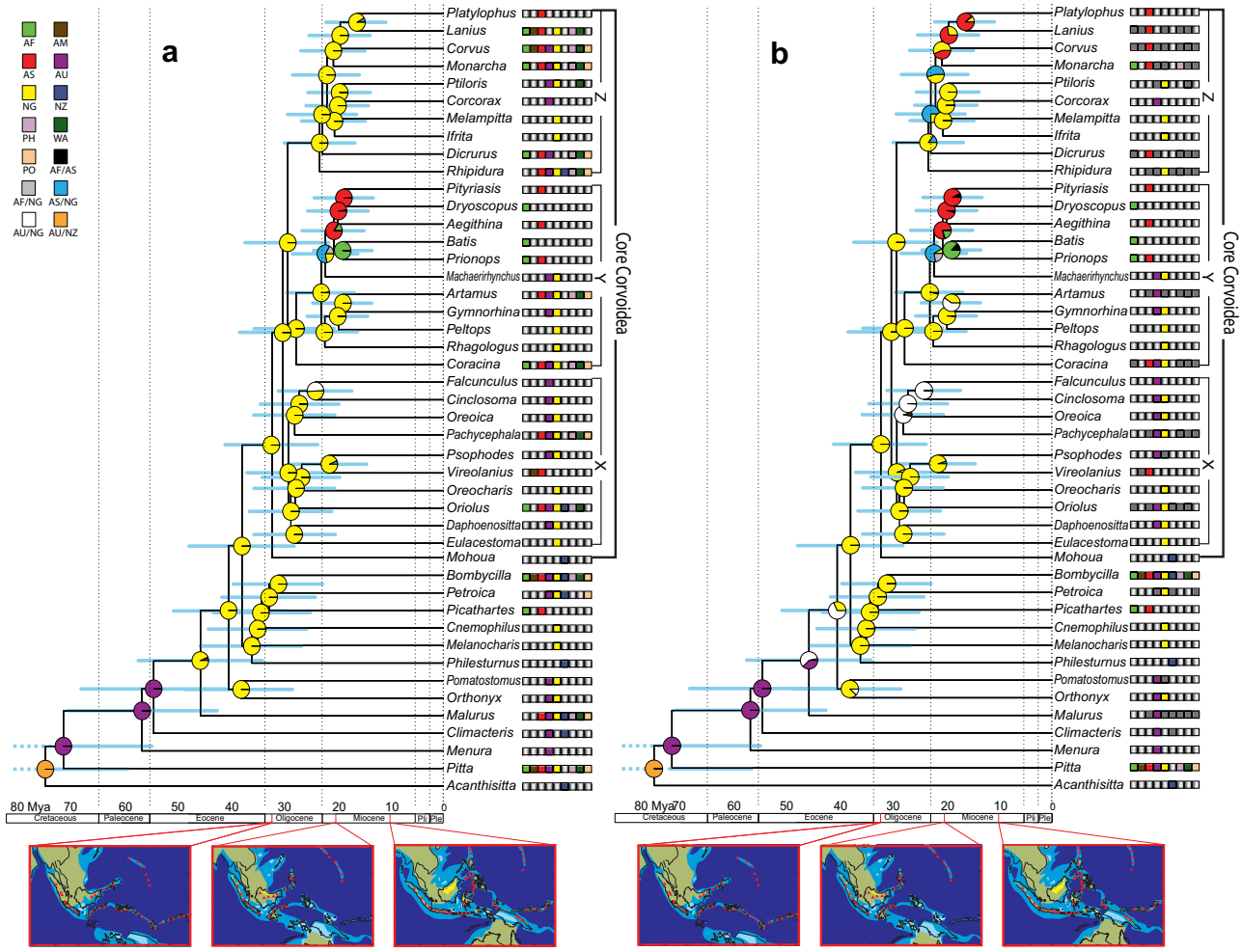

Fig. 3. Estimated ancestral areas using LAGRANGE, mapped onto the total evidence tree dated in BEAST. (a) Ancestral areas as estimated using the complete distributions (Table 5). (b) Ancestral areas as estimated using the constrained distributions (Table 5). Pie charts at internodes indicate the probability 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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