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Explosive avian radiations and multi-directional dispersal across Wallacea: Evidence from the Campephagidae and other Crown Corvida (Aves)

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Abstract

The systematic relationships among avian families within Crown Corvida have been poorly studied so far and as such been of limited use for biogeographic interpretations. The group has its origin in Australia and is thought to have colonized Africa and the New World via Asia beginning some 35 Mya when terranes of Australian origin approached Asian landmasses. Recent detailed tectonic mapping of the origin of land masses in the region around Wallace's line have revealed a particularly complex movement of terranes over the last 20–30 Myr. Thus the biogeographic dispersal pattern of Crown Corvida is a particularly exciting case for linking vicariance and dispersal events with Earth history. Here we examine phylogenetic affinities among 72 taxa covering a broad range of genera in the basal radiations within Crown Corvida with an emphasis on Campephagidae and Pachycephalidae. Bayesian analyses of nuclear DNA sequence data identified the family Campephagidae as monophyletic but the large genus *Coracina* is not. Within the family Pachycephalidae the genera *Pachycephala* and *Colluricincla* are paraphyletic with respect to each other. The resulting phylogeny suggests that patterns of dispersal across Wallace's line are complex and began at least 25 Mya. We find evidence of explosive radiations and multi-directional dispersal within the last 10 Myr, and three independent long distance ocean dispersal events between Wallacea and Africa at 10–15 Mya. Furthermore, the study reveals that in the Campephagidae a complex series of dispersal events rather than vicariance is the most likely explanation for the current biogeographic pattern in the region.

Keywords: Passeriformes; Crown Corvida; Campephagidae; Dispersal; Vicariance; Radiation; Wallacea; Indian Ocean

1. Introduction

The marked difference in fauna and flora between Asia and Australia has fascinated biologists for centuries. Alfred

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Russell Wallace was the first to make detailed accounts of these differences and the zoogeographical boundary between Asia and Australia known as Wallace's line (Wallace, 1876). Wallace himself changed this boundary several times, in particular as Sulawesi contained fauna and flora belonging to both western and eastern regions. Today we know that major plates have collided in the Sulawesi area (Hall, 1998, 2002; Holloway, 1998; Moss and Wilson, 1998; Fig. 1) and it is no surprise that Wallace found it difficult to decide whether this island belonged to one region or the other. Another important aspect of the plate tectonics is that island arcs on the boundary towards the Pacific Ocean were squeezed between the advancing Australian/Papuan plate and the Ontong Java plateau in the Pacific, and moved rapidly to the west, just in front of New Guinea, creating opportunities for dispersal of birds within the archipelagos from Melanesia to the Philippines. Molecular phylogenies of several taxonomic groups (examples in Hall and Holloway, 1998; Barber et al., 2000) have been undertaken to elucidate biogeographic patterns within and across Wallacea. However, without robust phylogenies it has been very difficult to assess dispersal and differentiation patterns and the importance of vicariance linked with the movement of plate fragments within this region.

Based on analysis of protein allozymes, Christidis and Schodde (1991) suggested that the large oscine radiation (songbirds) originated in eastern Gondwana (proto-Australasia-Antarctica). There is now significant DNA sequence support for the view that the basal oscine lineages (Menuroidea and Meliphagoidea of Sibley and Ahlquist, 1990) originated in the Australo-Papuan region (and probably East Antarctica as well, considering the early Tertiary climate) (Barker et al., 2002; Ericson et al., 2002a,b) and radiated there, mostly as resident forest birds. These and other studies also indicate that more terminal groups, the Crown Corvida, dispersed out of Australia to other continents (Barker et al., 2002, 2004; Ericson et al., 2002a; Fuchs et al., 2006a; Jønsson and Fjeldså, 2006a) beginning 35 Mya. The basal clades within Crown Corvida are among the most understudied groups of passerine birds today (Jønsson and Fjeldså, 2006b). These include Campephagidae, Pachycephalidae, Oriolidae and Vireonidae. Apart from Vireonidae, these families are distributed mainly in Australia, Southeast Asia and Africa. Fuchs et al. (2007) developed a preliminary phylogenetic hypothesis for the Campephagidae (cuckoo-shrikes and allies) but focused on the biogeographic affinities of African and Indo-Malayan lineages. Consequently, many Wallacean and Australo-Papuan taxa were not examined. In the present study we focus on aspects of two assemblages that have large radiations within the Australo-Asian region: the geographically widespread family Campephagidae which comprises 6 genera and 87 species (Gill and Wright, 2006 disregarding the genus *Hemipus* see discussion further down) and the Australo-Papuan centered genus *Pachycephala*.

The aim of this study is: (1) to further establish relationships among and within the Crown Corvida assemblages, most notably Campephagidae and Pachycephalidae; (2) to provide a more detailed picture of the biogeographic and dispersal patterns of Crown Corvida across and within Wallacea supported by time estimates; and (3) to assess the relative roles of vicariance and dispersal in shaping oscine diversification in the region.

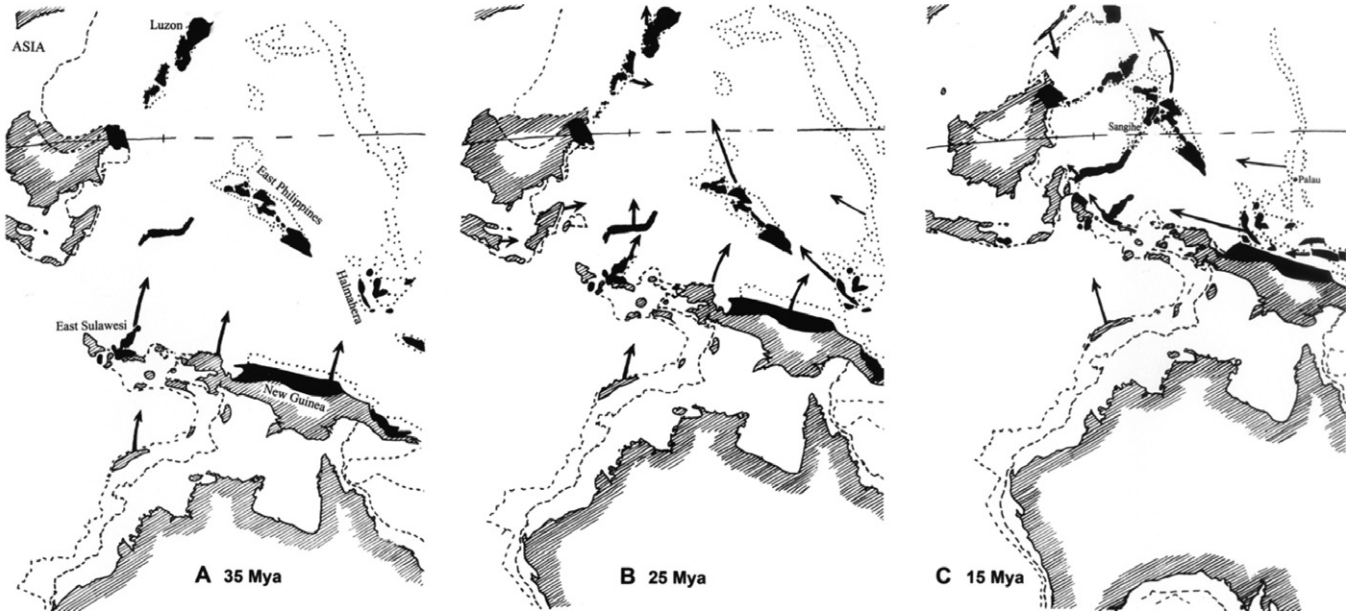

Fig. 1. Plate tectonics of the Indo-Australian region: reconstruction of major land-masses and archipelagos at 35, 25 and 15 Mya (redrawn from Hall, 2002). Present land masses (those belonging to old plates shaded, and new land of ophiolytic and calcareous origin in black) are surrounded by stippled lines indicating continental shelf and plate margins. Arrows indicate directions and rates of movements of geological structures at a particular time.

2. Material and methods

2.1. Taxon sampling and laboratory procedures

The lack of fresh tissue samples for DNA extraction has probably been the major reason that few studies have focused on these radiations so far. With careful primer design we have been able to obtain DNA sequences from old museum specimens (e.g. Irestedt et al., 2006) enabling us to obtain a broad taxon sampling of Campephagidae and *Pachycephala*. We also include several taxa whose affinities remain controversial e.g. *Hylocitrea bonensis*, *Platylophus galericulatus*, *Colluricincla tenebrosa*, *Coracornis raveni* and *Campochaera sloetti*, but exclude *Hemipus* and *Tephrodornis*, which are not directly related to Campephagidae (Fuchs et al., 2006). Altogether, we obtained data for 72 taxa encompassing 26 genera including multiple species within *Pericrocotus*, *Coracina*, *Lalage*, *Colluricincla*, *Pachycephala* and *Oriolus* (Table 1). Several members of the Passerida and basal oscine radiation were included as outgroups.

Three nuclear gene regions, myoglobin intron-2, ornithine decarboxylase (ODC) introns 6–7, and glyceraldehyde-3-phosphodehydrogenase (G3PDH) intron-11, were sequenced and used to estimate phylogenetic relationships among the Crown Corvida.

Procedures for extractions, amplifications, and sequencing of fresh tissue/blood samples are detailed in Irestedt et al. (2002), Allen and Omland (2003), Fjeldså et al. (2003) and Fuchs et al. (2007). Corresponding laboratory procedures for study skins are detailed in Irestedt et al. (2006). In addition nine new primers, Myo-coraF1 (5′-TGT CAG TGA CGT GAC ACA AGG GA-3′), Myo-cora2R (5′-TCC TCC AGG GCT TAC TCT AAA ACT G-3′), Myo-cora2Rb (5′-TCC TCC AGG GCT TAC TCT AAA ATT G-3′), Myo-cora159L (5′-GTA CAA GCA GGA GGA GGC ACA GA-3′), Myo-cora182H (5′-CAC ATA CCA TTT GCA TAC CAT GAG-3′), Myo-cora491L (5′-CAG ATC AGC ATC AGA GCT AGG A-3′), Myo-cora525H (5′-AGG AGC CTG GGC TAG GCA GAA GCA-3′), G3Pcora1F (5′-TAC TGC TGG TGA TCC AGG TGG ATA-3′) and G3Pcora1R (5′-TTC TTC CTG CTC CTC TGC CCC AT-3′) were designed to amplify myoglobin intron-2 and G3PDH intron-11 from study skins. For each gene and taxon, multiple sequence fragments were obtained by sequencing with different primers. These sequences were assembled into contigs with SEQMAN II™ (DNASTAR Inc.) or SEQUENCHER (Gene Codes Corporation). The occurrence of allelic polymorphisms in the three nuclear loci was suggested by the presence of double peaks. These double peaks were coded using the appropriate IUPAC codes. GenBank accession numbers are given in Table 1.

We were able to sequence the three gene regions almost completely for all included taxa except *Coracina caesia*, *C.pectoralis* and *Daphoenositta chrysoptera* for which we were not able to obtain ODC, and for *Platylophus galericulatus* and *Lalage leucopygialis* we were only able to sequence ODC intron-7 (232 bp). For *Colluricincla tenebrosa* the G3PDH sequence is lacking. Taken into account that we were unable to sequence ODC intron-7 for a few taxa and that some taxa lack some base pairs primarily in the 3′ or 5′ ends of the sequences, the sequences obtained varied in length between 680bp (*Lanius collaris*) to (716 bp (*Ptilonorhynchus violaceus*) for the myoglobin intron-2; between 230 bp (*Chaetops frenatus* and*Lanius collaris*) to 266 bp (*Cormobates placens*) for the G3PDH intron-11 and between 540 and 621 bp for the vast majority of the ODC sequences (but some large insertions/deletions made some sequences considerably longer, e.g. 650 bp in *Rhipidura rufifrons*, or shorter e.g. 424 bp in *Corvus corone*). For details of indels, see Table 2.

2.2. Sequence alignment

Multiple alignments were accomplished using SEAL v1.0AL (Sequence Alignment Editor Version 1.0 alpha 1; Rambaut, 1996). Insertion–deletion events were commonly inferred and were treated as missing data. Two regions from G3PDH intron-11 (nucleotides 191–214 and 268–287 in the complete alignment) were excluded from the phylogenetic analyses due to uncertainty in homology. The concatenated alignment consists of 1784 bp. The alignments for the individual genes could be requested from the corresponding author.

2.3. Model selection and phylogenetic inference

Molecular phylogenies were estimated using model-based approaches (maximum likelihood, ML and Bayesian inferences, BI), using PHYML v2.4 (Guindon and Gascuel, 2003) and MRBAYES 3.1.1 (Huelsenbeck and Ronquist, 2003; Ronquist and Huelsenbeck, 2003), respectively. All gaps were treated as missing data. Clade supports for the ML analyses was assessed using 100 replicates of non-parametric bootstrapping (Felsenstein, 1985). The models for nucleotide substitutions were selected for each gene individually by applying the Akaike Information Criterion (AIC, Akaike, 1973) and the program MRMODELTEST 2.2 (Nylander, 2005) in conjunction with PAUP*4b10 (Swofford, 1998).

Bayesian analyses of the concatenated data set were performed by freeing the different model parameters (base frequencies, rate matrix, shape parameter, proportion of invariable sites but not the topology) to vary between the three partitions using the *unlink* and *prset* commands. Two runs (four chains each), of three million generations were performed for the individual gene partitions and for the concatenated data set, with trees sampled every 100 generations. The priori selection of nucleotide substitution models suggested that the GTR + Γ model had the best fit for all three gene regions, but as the values of the model parameters differed between the partitions (see Table 3), we only performed mixed-model analyses for the concate-

Table 1
Taxonomic sampling

Species	Family/tribe	Voucher/tissue number	Origin	GAPDH	ODC	Myo
Batis poensis	Platysteiridae	MNHN CG 1998-783*	Cameroon	DQ406665	EU272120	AY529907
Campephaga flava	Campephagidae	RB613	Kenya	DQ406639	EU380410	EF052822
Campephaga petiti	Campephagidae	FMNH384855*	Uganda	EF052795	EU380411	EF052823
Campochaera sloetii	Campephagidae	NRM569328*, TP	New Guinea	EU380459	EU380412	EU380489
Chaetops frenatus	Picathartidae	PFI uncat.*	South Africa	EF441212	EF441234	AY228289
Chlorophoneus sulfureopectus	Malaconontidae	MNHN CG 1998-823*	Malawi	DQ406648	EU380413	AY529912
Colluricincla tenebrosa	Pachycephalidae	NRM569469*, TP	Palau		EU380414	EU380490
Colluricincla harmonica	Pachycephalidae	MV1422*	Australia	EU273376	EU273356	EU273396
Colluricincla sanghirensis	Pachycephalidae	ZMUC123921	Indonesia	EF441213	EF441235	EF441256
Coracina abbotti	Campephagidae	NRM569468*, TP	Sulawesi	EU380460	EU380415	EU380491
Coracina atriceps	Campephagidae	BMNH1910.12.28.182*, TP	Ceram	EU272091	EU272118	EU272102
Coracina azurea	Campephagidae	ANSP11901*	Equatorial Guinea	EF052796	EU380416	EF052824
Coracina caesia	Campephagidae	ZMUC 123521	Tanzania	EF052797		EF052825
Coracina cinerea	Campephagidae	FMNH 352837*	Madagascar	EF052800	EU380417	EF052827
Coracina coerulescens	Campephagidae	USNM B3671*	Philippines	EF052759	EU380418	EF052770
Coracina larvata	Campephagidae	BMNH1935.10.22.303*, TP	Borneo	EU380461	EU380419	EU380492
Coracina lineata	Campephagidae	ZMUC95267*, TP	New Ireland	EU380462	EU380420	EU380493
Coracina macei	Campephagidae	ZMUC95260*, TP	Siam	EU380463	EU380421	EU380494
Coracina mcgregori	Campephagidae	FMNH 392259*	Philippines	EF052805	EU380422	EF052831
Coracina melaschista	Campephagidae	MNHN 6–69	Laos	EF052807	EU380423	AY529913
Coracina mindanensis	Campephagidae	ZMUC95262*, TP	Tawi Tawi	EU380464	EU380424	EU380495
Coracina novaehollandiae	Campephagidae	ANSP 10622*	Australia	EF052808	EU380425	EF052834
Coracina papuensis	Campephagidae	ZMUC95265*, TP	New Britain	EU380465	EU380426	EU380496
Coracina pectoralis	Campephagidae	MNHN CG 1979-1352*, TP	South Africa	EF052810		EF052836
Coracina striata guillemardi	Campephagidae	ZMUC95261*, TP	Tawi Tawi	EU380466	EU380427	EU380497
Coracina striata kochii	Campephagidae	ZMUC95258*, TP	Mindanao	EU380467	EU380428	EU380498
Coracina temminckii	Campephagidae	NRM569324*, TP	Sulawesi	EU380468	EU380429	EU380499
Coracina tenuirostris admiralitatis	Campephagidae	ZMUC95268*, TP	Manus Island	EU380469	EU380430	EU380500
Coracina tenuirostris heinrothi	Campephagidae	ZMUC95264*, TP	New Britain	EU380470	EU380431	EU380501
Coracina tenuirostris matthiae	Campephagidae	ZMUC95266*, TP	Mussau	EU380471	EU380432	EU380502
Coracina welchmani	Campephagidae	UWBM 60241*	Solomon Islands	EF052799	EU380433	EF052826
Coracornis raveni	Pachycephalidae	NRM569472*, TP	Sulawesi	EU380472	EU380434	EU380503
Corcorax melanorhamphos	Corcoracidae	AM LAB1059*	Australia	EF441214	EF441236	AY064737
Cormobates placens	Climacteridae	MV E309*	New Guinea	EF441215	EF441237	AY064731
Corvus corone	Corvidae	MNHN 13-16*	France	DQ406663	EU272116	AY529914
Cyclarhis gujanensis	Vironidae	ZMUC128105	Ecuador	EU380473	EU380435	EU380504
Daphoenositta chrysoptera	Neosittidae	MV1311*	Australia	EU380474		EU380505
Dicrurus bracteatus	Dicruridae	UWBM 68045*	Australia	EF052813	EU272113	EF052839
Eopsaltria australis	Petroicidae	MV 1390*	Australia	EF441216	EF441238	AY064732
Epimachus albertisii	Paradisaeidae	MV C148*	Australia	EU380475	EU380436	AY064735
Gymnorhina tibicen	Cractidae	MV AC78*	Australia	DQ406669	EU272119	AY064741
Hirundo rustica	Hirundinidae	NRM 976238*	Sweden	EF441218	EF441240	AY064258
Hylocitrea bonensis	Pachycephalidae	BMNH1932.11.25.7*	Sulawesi	EU380476	EU380437	EU380506
Hylophilus ochraceiceps	Vireonidae	ZMUC127900	Ecuador	EU272087	EU272109	EU272100
Lalage leucomela	Campephagidae	UWBM 57519*	Australia	EF052814	EU380438	EF052840
Lalage leucopygialis	Campephagidae	BMNH1934.10.21137*, TP	Sulawesi	EU380477	EU380439	EU380507
Lalage melanoleuca	Campephagidae	ZMUC95259*, TP	Mindanao	EU273381	EU273361	EU273403
Lalage nigra	Campephagidae	FMNH 344979*	Philippines	EF052815	EU380440	EF052841
Lalage tricolor	Campephagidae	UWBM 57508*	Australia	EF052816	EU380441	EF052842
Lanius collaris	Laniidae	MNHN 02-26	Cameroon	DQ406662	EU272112	AY529925
Malurus amabilis	Maluridae	MV C803*	Australia	EF441219	EF441241	AY064729
Menura novaehollandiae	Menuridae	MV F722*	Australia	EF441220	EF441242	AY064744
Monarcha melanopsis	Monarchidae	MV B541*	Australia	EU272089	EU272114	DQ084110
Oriolus chinensis	Oriolidae	ZMUC123918	Indonesia	EU273382	EU273362	EU273404
Oriolus flavocinctus	Oriolidae	MV1603*	Australia	EF441221	EF441243	EF441258
Oriolus oriolus	Oriolidae	MCSNC1415*	Italy	EF052755	EU273363	EF052766
Oriolus xanthornus	Oriolidae	MNHN 4–10D*	Thailand	DQ406645	EU272111	AY529929
Orthonyx temminckii	Orthonychidae	MV B831*	Australia	EF441222	EF441244	AY064728
Pachycephala albiventris	Pachycephalidae	ZMUC117176	Philippines	EF441223	EF441245	EF441259
Pachycephala grisola	Pachycephalidae	ZMUC118870	Philippines	EU380478	EU380442	EU380508
Pachycephala pectoralis	Pachycephalidae	MV1419*	Australia	EU380479	EU380443	AY064727
Pachycephala philippensis	Pachycephalidae	ZMUC117169	Philippines	EU380480	EU380444	EU380509
Pachycephala rufiventris	Pachycephalidae	NRM543657*, TP	Australia	EU380481	EU380445	EU380510

(*continued on next page*)

Table 1 (*continued*)

Species	Family/tribe	Voucher/tissue number	Origin	GAPDH	ODC	Myo
Pachycephala schlegelii	Pachycephalidae	ZMUC26828*, TP	New Guinea	EU380482	EU380446	EU380511
Pachycephala soror	Pachycephalidae	ZMUC135468	New Guinea	EU380483	EU380447	EU380512
Pachycephala sulfuriventer	Pachycephalidae	NRM569473*, TP	Sulawesi	EU380484	EU380448	EU380513
Pachycephalopsis hattamensis	Petroicidae	NRM552153*, TP	New Guinea	EF441224	EF441246	EF441260
Pericrocotus cinnamomeus	Campephagidae	USNM B6146*	Myanmar	EF052753	EU272117	EF052764
Pericrocotus divaricatus	Campephagidae	NRM569470*, TP	Vietnam	EU380485	EU380449	EU380514
Pericrocotus divaricatus	Campephagidae	UWBM 74728*	Russia	EF052818	EU380450	EF052843
Pericrocotus erythropygius	Campephagidae	USNM B5659*	Myanmar	EF052754	EU380451	EF052765
Pericrocotus ethologus	Campephagidae	AMNHJGG991*	Nepal	EF052819	EU380452	EF052844
Pericrocotus flammeus	Campephagidae	MNHN CG 1989-75*, TP	Thailand	EF052821	EU380453	EF052845
Pericrocotus igneus	Campephagidae	ZMUC95263*, TP	Palawan	EU380486	EU380454	EU380515
Pericrocotus solaris	Campephagidae	BMNH1948.80.2191*, TP	Myanmar	EU380487	EU380455	EU380516
Picathartes gymnocephalus	Picathartidae	LSU B-19213*	West Africa	EF441225	EF441247	AY228314
Platylophus galericulatus	Corvidae	NRM569471*, TP	Malay Peninsula	EU380488	EU380456	EU380517
Pomatostomus temporalis	Pomatostomidae	MV D257*	Australia	EF441226	EF441248	AY064730
Prionops retzii	Malaconontidae	ZMUC 119500	Kenya	DQ406654	EU380457	AY529931
Prunella modularis	Prunellidae	NRM976138*	Sweden	EF441227	EF441249	AY228318
Ptilonorhynchus violaceus	Ptilonorhynchidae	MV B836*	Australia	EF441228	EF441250	AY064742
Ptiloprora plumbea	Meliphagidae	MV C173*	New Guinea	EF441229	EF441251	AY064736
Rhipidura rufifrons	Rhipiduridae	MV C733*	Australia	EU272090	EU272115	EU272115
Saltator atricollis	Cardinalidae	NRM 966978	Paraguay	EF441230	EF441252	AY228320
Sturnus vulgaris	Sturnidae	NRM966615*	Sweden	EF441231	EF441253	AY228322
Sylvia atricapilla	Sylviidae	NRM 976380*	Sweden	EF441232	EF441254	AY228323
Terpsiphone viridis	Monarchidae	MNHN 02-20	Cameroon	DQ406641	EU380458	AY529939
Vireo flavoviridis	Vireonidae	ZMUC124543	Panama	EU273394	EU273374	EU273417
Vireo olivaceus	Vireonidae	ZMUC120827	Bolivia	EU272088	EU272110	EU272101

Vouchered samples are indicated by an asterisk. Samples where DNA was extracted from toe-pads are marked TP. Acronyms are AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, ANSP, Academy of Natural Science, Philadelphia, USA; BMNH, British Museum of Natural History, UK; FMNH, Field Museum of Natural History, Chigaco, USA; LSU, Museum of Natural science, Louisiana State University; MCSNC, Museo Civico di Storia Naturale di Carmagnola, Italia;MV, Museum Victoria, Melbourne; MNHN, Muséum National d'histoire Naturelle, Paris, France; NRM, Swedish Museum of Natural History;PFI, Percy FitzPatrick Institute, Cape Town; RB, Rauri C. K. Bowie; USNM, University States National Museum, Washington, USA; UWBM, University of Washington, Burke Mseum, Seattle, USA; ZMUC Zoological Museum of Copenhagen; Rauri Bowie, University of Stellenbosch, South Africa.

nated data set. After checking for convergence (when the split frequency between the runs was below 0.01) the burn-in phase was discarded and the inference for the individual genes and the concatenated data set was based on a posterior sample of 25001 samples each.

2.4. Molecular dating

Bayesian approaches for divergence time estimates were performed using the MULTIDISTRIBUTE software package (Kishino et al., 2001; Thorne and Kishino, 2002). We estimated different branch length variance–covariance matrices for our three partitions using ESTBRANCHES after estimating the parameter values of the F84 + Γ model with the assistance of PAML (Yang, 1997). Output was then analyzed simultaneously by MULTIDIVTIME. We performed the dating analyses in both relative and absolute time frameworks. For the relative time analyses, we set the basal node to five time units and adopted as priors 0.0114 ± 0.0114 substitutions per site per time unit for the rate at the root node (estimated using the procedure described in the multidivtime.readme file and Wiegmann et al., 2003). Due to lack of robust fossil calibration points within the Passeriformes, we used a secondary calibration point for the absolute time dating analyses: the Crown Corvida/Passerida split. Previous divergence estimates for this node were based on different primary calibration points (*e.g.* Acanthisitta/Eupasseres—Ericson et al., 2002a; Barker et al., 2004, or a combination of multiple calibration points within the vertebrates, of which the *Acanthisitta*/Eupasseres were not a part,—Pereira and Baker, 2006). To minimize as much as possible the biases associated with secondary calibration points (e.g. Graur and Martin, 2004), we used the minimum and maximum values (taking account of standard deviations or confidence intervals resulting from these studies). The Crown Corvida/Passerida split was thus constrained to have occurred between 39.8 and 54.2 Myrs BP. For the absolute time analyses, we set the distance between the tip and the root to 65 ± 32.5 Myrs BP, corresponding to the split between the Menuridae and the remaining Oscines (Barker et al., 2004), and adopted as priors 0.0054 ± 0.0054 substitutions per site per million years for the rate at the root node. For all the dating analyses, we set the parameter "brownmean" (which affects the variation of rates of molecular evolution over time) to 0.2 ± 0.2. For the absolute-time dating analyses, actual values input into the program were adjusted so that one time unit equals 13 Myr, corresponding to five

Table 2
List of indels shared by the taxa for the three loci, with information on the number and sequences of involved nucleotides, position of the insertion/deletion event in the concatenated alignment, nature of the mutational event (insertion or deletion), homoplastic state of the indel with respect to the tree obtained from the concatenated mixed-model analyses, any peculiar information concerning its location (e.g. in a repeated zone) and name of all taxa that share the indel

Locus	*N* nucleotide	Position in the concatenated alignment	Insertion/ deletion	Homoplasic	Pattern	Indel shared by
Myoglobin	2 (GG)	17–18	Deletion	No		*Oriolus*
	3 (AGG)	155–157	Deletion	Yes	In a AGG repeated zone	*Chaetops*/*Picathartes*, *Hirundo*
	4 (AAGT)	405–408	Deletion	Yes		*Monarcha*, *Platylophus*
	2 (CT)	448–449	Insertion	No		*Chaetops*/*Picathartes*
ODC	2 (CA)	794–795	Deletion	Yes	In a CA repeated zone	Vireonidae, *Picathartes*, *Terpsiphone*
	1 (A)	841	Insertion	No	In A repeated zone	Oriolidae, Pachycephalidae
	1(T)	819	Deletion	No	In T repeated zone	*Coracina macei*, *C. larvata, C striata*
	3 (CTT)	906–908	Deletion	Yes	In a CTTCTT zone	*Lalage* apical, *Ptiloprora*
	4 (AGTT)	936–939	Deletion	Yes		*Coracina papuensis*, *C. caledonica*
	7	1063–1070	Deletion	No		*Oriolus oriolus, O. chinensis*
	59	1075–1151	Deletion	No		*Oriolus oriolus, O. chinensis*
	11	1109–1119	Deletion	No		*Pericrocotus*
	3 (TTG)	1166–1168	Deletion	Yes	TTGTTG	Vireonidae, *Hylocitrea, Campephaga flava, Corcorax, Hirundo*
	4 (TGAG)	1179–1183	Deletion	Yes		*Corvus, Terpsiphone, Monarcha, Lanius, Corcorax*
	7 (GTCCTGG)	1184–1190	Deletion	No		Campephagidae
	1 (T)	1285	Deletion	No		Oriolidae
	17	1305–1322	Deletion	No		*Prunella*/*Saltator*
	3 (TGA or CAA)	1365–1367	Insertion	No		All but Crown Corvida + Passerida
	2 (AG)	1370–1371	Deletion	Yes	AG	*Pachycephalopsis*/*Hirundo*
	15	1451–1465	Insertion	No		Passerida—*Chaetops*/*Picathartes*
G3P	8	1522–1529	Deletion	No		*Coracina tenuirostris heinrothi and matthiae and C. mindanensis*
	2 (AG)	1525–1526	Deletion	No		*Pericrocotus cinnamomeus, P. igneus*
	1 (G)	1520	Deletion	No		Clade B—*Campephaga*/*Campochaera*
	2 (TG)	1558–1559	Insertion	No		*Prunella*/*Saltator*
	1 (G)	1559	Insertion	No		Vireonidae
	18	1603–1623	Deletion	No		Passerida
	2 (CA)	1628–1629	Deletion	No		Vireonidae
	8	1631–1638	Deletion	No		Passerida
	1 (T)	1667	Insertion	Yes	T rich zone	Crown Corvida + Passerida
	1 (A)	1676	Insertion	No	A rich zone	All *Pericrocotus* but *erythropygius*
	2 (GT)	1698–1699	Insertion	No		Malaconotidae and allies
	6 (CTGCCT)	1683–1688	Deletion	Yes		All but *Menura*, *Ptiloprora* and Ptilonorhynchus and Lanius
	1 (T)	1716	Insertion	Yes	T rich zone	*Corvus* clade + *Eopsaltria*
	1 (G)	1754	Insertion	No	G rich zone	All*Pericrocotus* but *erythropygius*/*ethologus*
	1 (G)	1768	Deletion	No		*Prunella*/*Saltator*
	1 (G)	1776	Insertion	No		*Campephaga*

Most of the homoplastic indels involved repeated zones of variable lengths.

Table 3
Arithmetic mean estimates for the model parameters from the Bayesian analyses

	Myoglobin	G3PDH	ODC
Alignment length	732	294[a]	765
Model selected	GTR + Γ	GTR + Γ	GTR + Γ
−Ln	6096.14	3293.96	6381.32
Freq. A	0.277	0.191	0.277
Freq. C	0.226	0.195	0.164
Freq. G	0.231	0.351	0.217
Freq. T	0.265	0.261	0.342
A-C	0.083	0.056	0.084
A-G	0.355	0.298	0.366
A-T	0.052	0.062	0.042
C-G	0.104	0.106	0.138
C-T	0.337	0.414	0.288
G-T	0.069	0.065	0.082
Γ	1.540	0.463	1.229

[a] The length does not include the excluded characters.

time units, as the program achieves convergence of the Markov chain best when the prior for the time separating the ingroup node from the present is between 0.1 and 10 time units (multidivtime.readme file, Wiegmann et al., 2003). We used the topology obtained from the Bayesian mixed-model analyses (Fig. 2) as a template for all the dating analyses. The Markov Chain Monte Carlo analyses were run twice for 1,100,000 generations (burn-in period: 100,000 generations) and parameters were sampled every 100 generations.

3. Results

The trees obtained from the Bayesian analyses of the individual genes were generally topologically congruent (Figs. 3–5); only three nodes, mostly terminals, were recovered as incongruent (congruence being supported by bootstrap values or posterior probabilities greater than 70% and 0.95, respectively). These nodes involve: (1) the relationships of *P. solaris* and *P. ethologus* within *Pericrocotus*, with G3PDH favouring *solaris* with *cantonensis/divaricatus* (PP = 0.96) whereas myoglobin favors a sister-group relationship between *solaris* and *ethologus* (PP = 0.99); (2) the relationships of *C. atriceps* and *C. papuensis* within the large *Coracina* clade, ODC favors a sister-group relationship between the two taxa (PP = 0.99) whereas myoglobin suggests that *C. papuensis* is more closely related to the *C. striata/C. larvata/C. macei* clade than to *C. atriceps*; and (3) the phylogenetic position of *Coracina abbotti,* ODC favors a sister-group relationships with *C. melaschista* (PP = 0.99) whereas the analyses performed with the concatenated data set indicate that *C. abbotti* is sister-to *C. azurea* (PP = 1.0). It should be noted that a relationship between *C. cinerea* and *C. temminckii* (Fig. 4) was supported by ODC only, a gene region that was not available for *C. caesia* and *C. pectoralis*.

The relationships between these four taxa could not be resolved with G3PDH intron-11 (Fig. 3) and myoglobin intron-2 (Fig. 5). Fuchs et al. (2007) sequenced four loci (nuclear cmos, G3PDH intron-11 and myoglobin intron-2 and mitochondrial ND2) and the relationships between *C. caesia/C. pectoralis* and *C. cinerea* were only resolved, and significantly supported, in their ND2 gene tree, where both clades appear sister-groups (all other loci involved polytomies for these taxa). Yet, unlike this study, *C. temminckii* was not sampled by Fuchs et al. (2007). Thus, it is not possible to decipher with the data we have in hand the relative position of *C. temminckii* with respect to *C. caesia/C. pectoralis* and *C. cinerea* as the two loci that bear information are not confronted to each other due to technical difficulties in amplifying ODC for *C. caesia* and *C. pectoralis*. This issue has no effect on the biogeographic interpretations as the African taxa would in any cases have their closest relatives in Wallacea.

The posterior distribution of topologies is presented as a 50% majority-rule consensus tree from the concatenated analysis (Fig. 2). Arithmetic means of the likelihood score was –ln = 15850.46. Several apparently synapomorphic indels were observed when mapping the data onto the tree topology. A few indels were also found to be incongruent with the phylogenetic tree. A summary of indels shared by at least two taxa is indicated in Table 2. Regions that were excluded from the phylogenetic analyses are not included here.

As already highlighted by Fuchs et al. (2007), *Pericrocotus* forms the sister group to the rest of the Campephagidae. Within the latter assemblage there is little support for the traditional generic subdivision. The large genus *Coracina* is polyphyletic with respect to the other smaller genera. Fuchs et al. (2007) placed *Coracina coerulescens* together with *C. azurea*, but with improved taxon sampling we place *C. azurea* (Africa) together with *C. abbotti* (Sulawesi) (PP = 0.98). *C. coerulescens* (Philippines) on the other hand forms a clade together with other species in adjacent archipelagos. Interestingly, *Campochaera sloetti* (New Guinea), which was suggested to be associated with the *Lalage* complex based on plumage characters by Fuchs et al. (2007) is placed with strong support with the African *Campephaga*.

The Campephagidae are not closely associated with Oriolidae, as suggested by Sibley and Ahlquist (1990) and *Hylocitrea bonensis* from Sulawesi, hitherto considered a pachycephalid (Monroe and Sibley, 1993) is placed in the Passerida in our study. This highlights how little is known about systematic affinities of many Wallacean taxa, which have simply been "dumped" in major groups of superficially similar birds in this biogeographic region without thorough character analysis.

Dating analyses (Fig. 6) show that the Campephagidae diverged from its sister group, the Australian Cracticidae and African Malaconotidae and allies at about 37 Mya (95% CI = 29.–45.1 Mya). Within the Campephagidae, *Pericrocotus* split from other Campephagids at about 26 Mya (95% CI = 18.8–34.3 Mya). This corresponds to a time when Australian plate fragments had moved close (400 km) to the nearest islands of the Asian plate in the

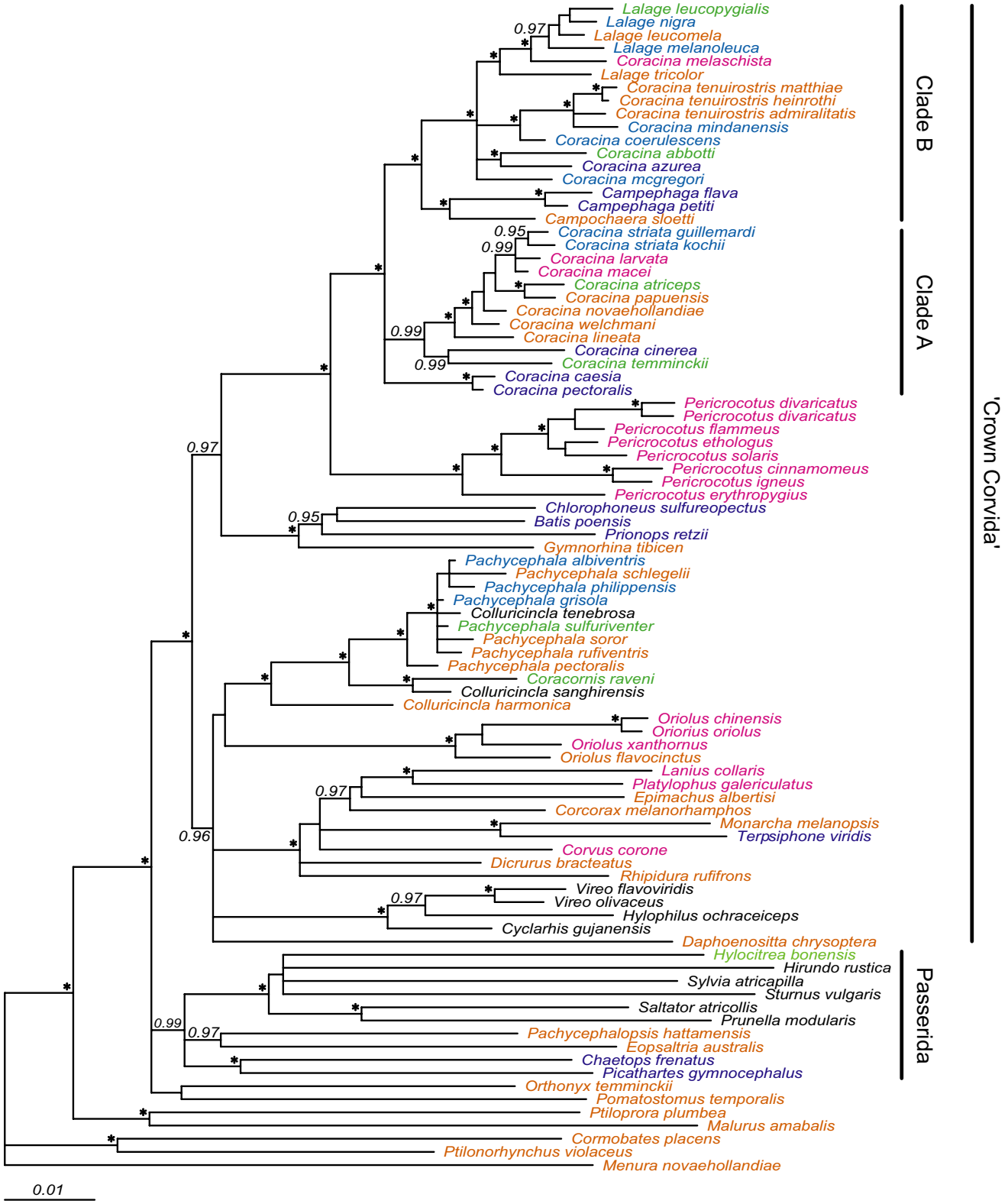

Fig. 2. Bayesian topology obtained from the combined dataset of Myo, ODC and G3PDH. Campephagidae includes *Coracina*, *Lalage*, *Campochaera* and *Campephaga* (clades A and B) as well as *Pericrocotus*. Pachycephalidae includes *Pachycephala*, *Colluricincla* and *Coracornis*. Posterior probabilities greater than 0.95 are shown. An asterisk indicates posterior probabilities of 1.0. The colours indicate present day distributions. Green: Wallacea, Blue: Philippines, Pink: Asia west of Wallace's line, Yellow: Australia/New Guinea, Dark blue: Africa. *Colluricincla tenebrosa* of Palau and *Colluricincla sanghirensis* of Sanghihe island are uncoloured as they are found on remote islands that cannot be assigned to any of the above mentioned geographical areas. Other taxa in black are vireos of America and the Passerida which are cosmopolitan.

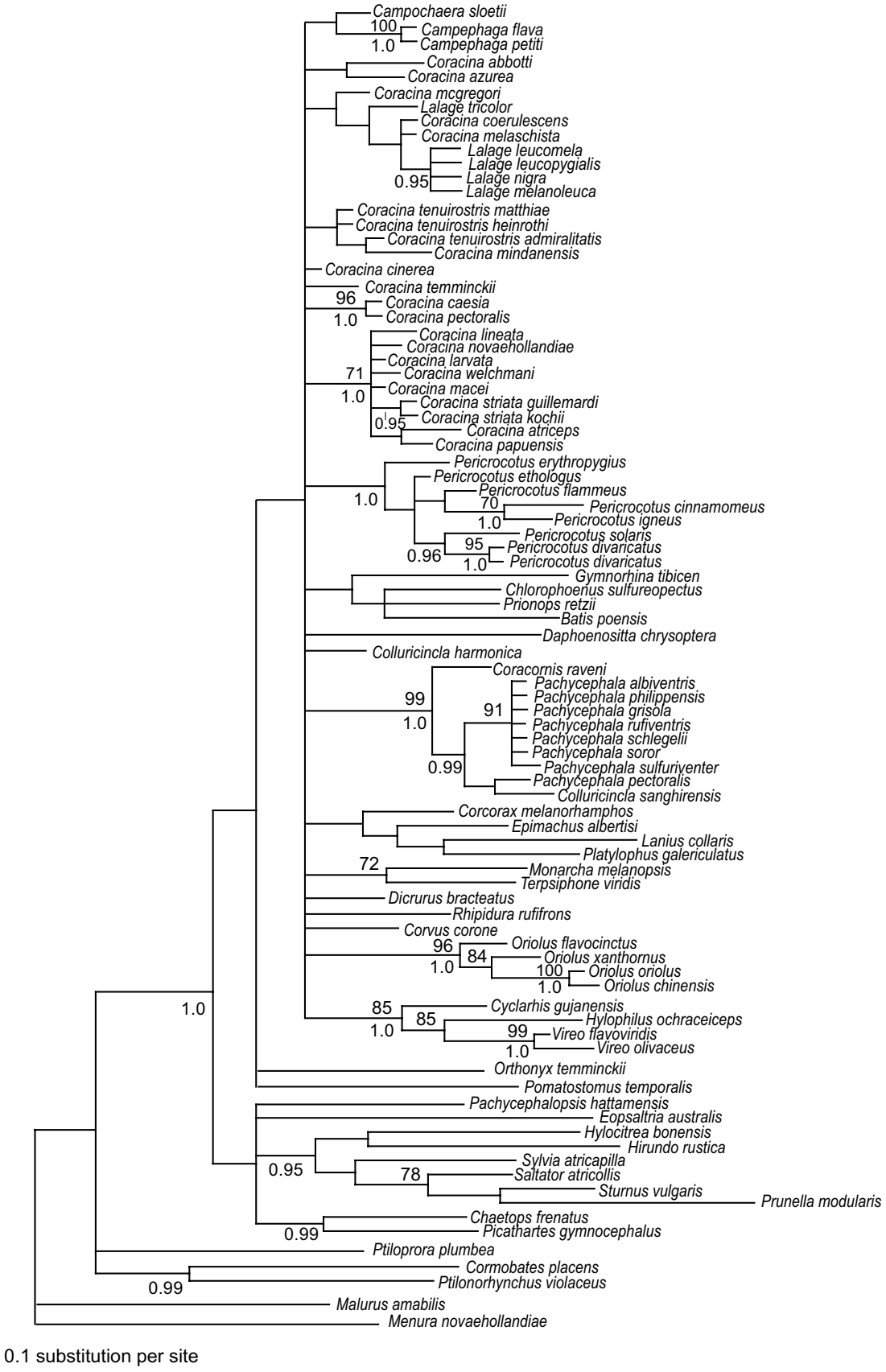

Fig. 3. Bayesian topology obtained from the G3PDH. Posterior probabilities greater than 0.95 are shown below the branch in front of the nodes. ML bootstrap supports are shown above the branch in front of the nodes.

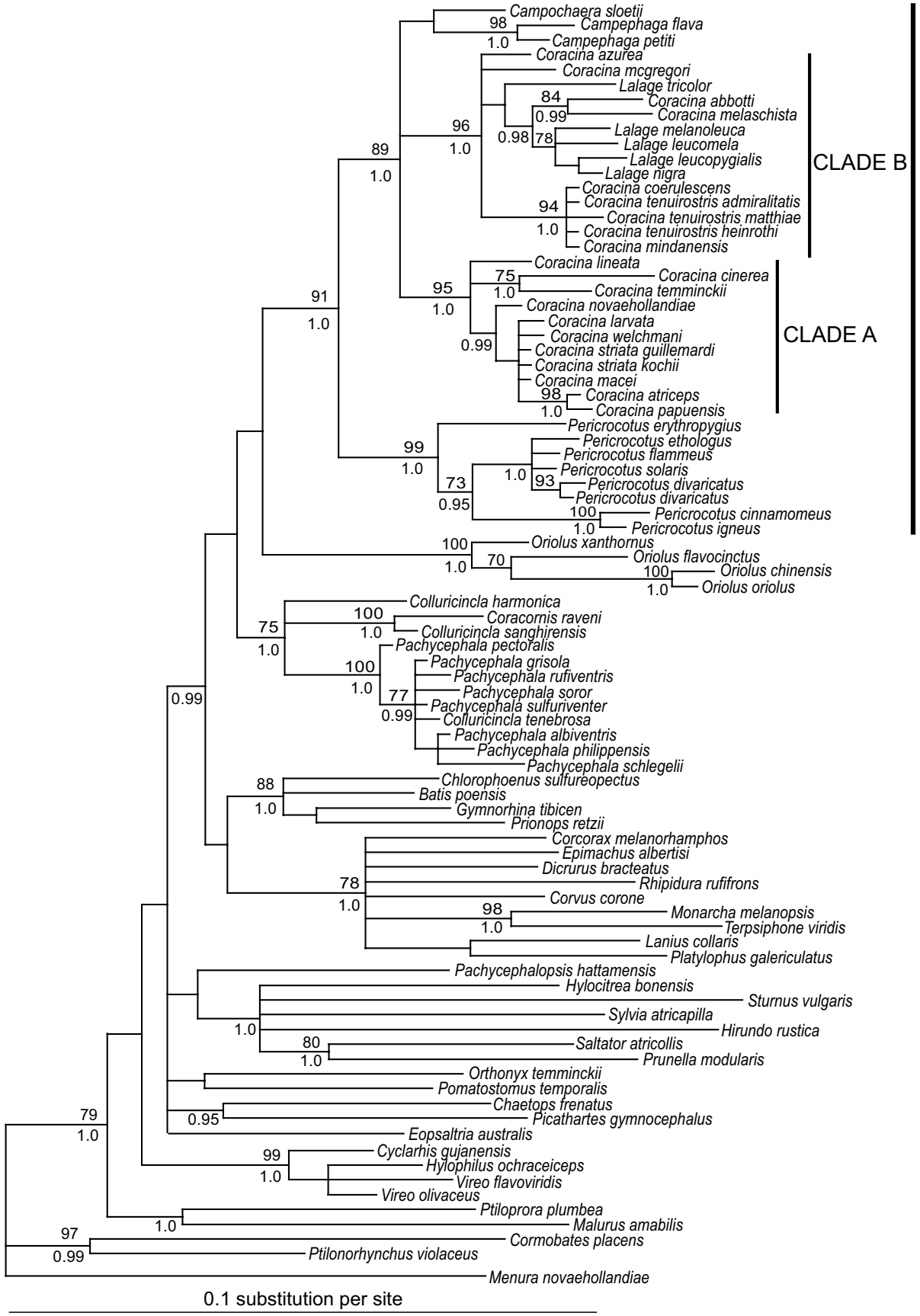

Fig. 4. Bayesian topology obtained from the ODC. Posterior probabilities greater than 0.95 are shown below the branch in front of the nodes. ML bootstrap supports are shown above the branch in front of the nodes.

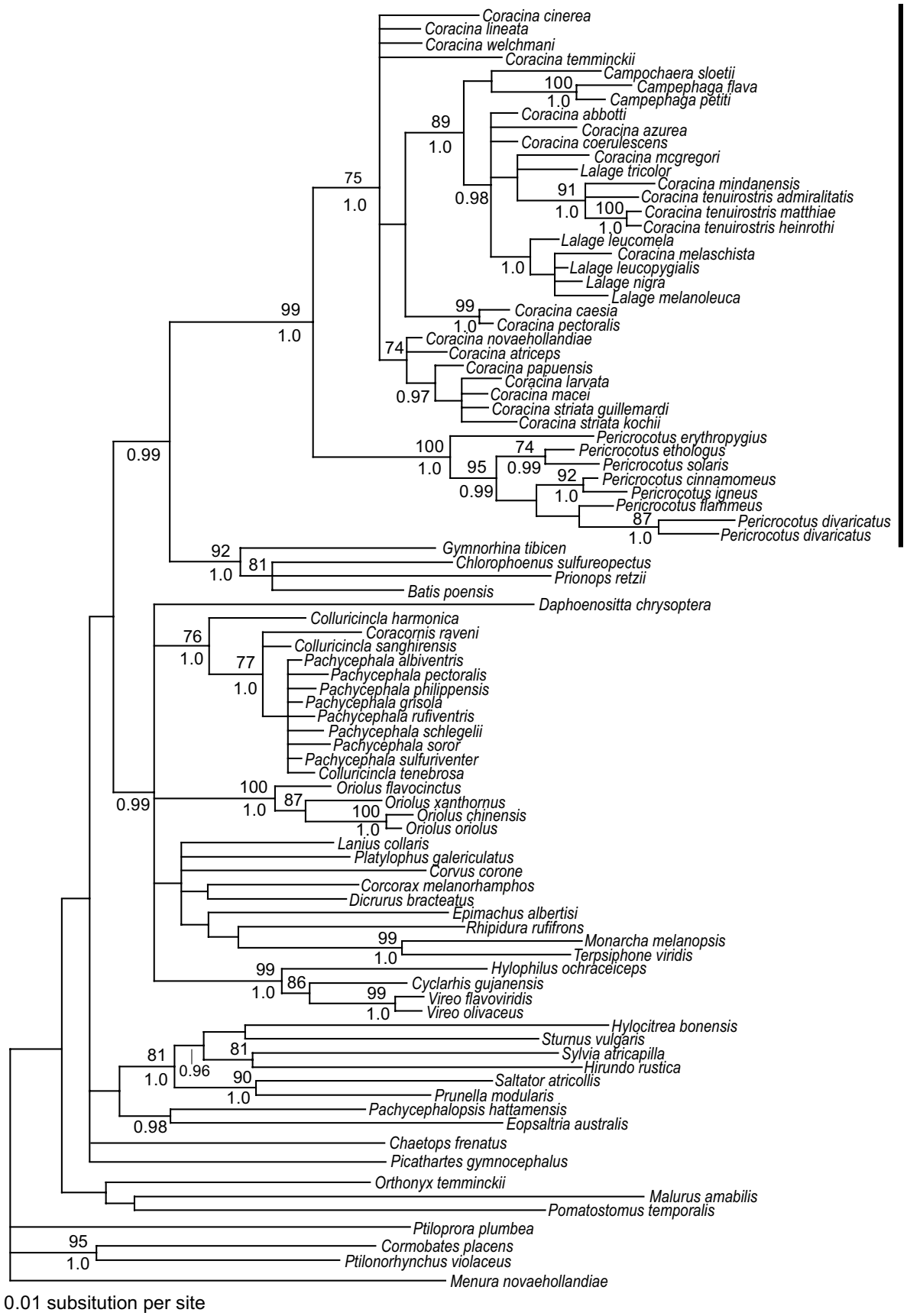

Fig. 5. Bayesian topology obtained from the Myo. Posterior probabilities greater than 0.95 are shown below the branch in front of the nodes. ML bootstrap supports are shown above the branch in front of the nodes.

area where Sulawesi is now (Fig. 1b), and it makes sense to believe that it was a one-time dispersal event that brought a *Pericrocotus* ancestor out of Australia. It then diverged within mainland Asia and the Greater Sunda area (with one species, *P. lansbergei*, assumed to be close to *P. cinnamomeus* and *P. igneus*, on the Lesser Sundas). The deep splits within the *Coracina/Lalage/Campephaga/Campochaera* clade, with three or four independent lineages in Africa and Madagascar, took place about 15–18 Mya. From about 12 Mya and onwards the large diversification of this clade took place within Wallacea coinciding with the highly dynamic movements of small plate fragments and volcanic and ophiolitic islands in this area and on the border towards the Pacific (Fig. 1).

For the *Pachycephala/Colluricincla* clade we find two early divergences; the split of *Colluricincla harmonica* at 25 Mya and subsequently the lineage with *Coracornis raveni* (Sulawesi) and *Colluricincla sanghirensis* (Sanghihe island, which is on the chain of volcanoes off the terminus of Sulawesi's northern peninsula) diverging at ca. 15 Mya. More recently (5 Mya) *Pachycephala* underwent an explosive radiation within Australia, New Guinea, Wallacea and adjacent archipelagos on the Pacific boundary. A much denser taxon sampling will be needed to sort out details of this radiation.

4. Discussion

Previous studies have confirmed an Australian/Papuan origin for the basal Crown Corvida radiation, including Campephagidae and Pachycephalidae (Barker et al., 2002; Ericson et al., 2002a,b; Fuchs et al., 2006a; Jønsson and Fjeldså, 2006b). The family Pachycephalidae is still mainly distributed within Australia/New Guinea and adjacent archipelagos. The Australo-Papuan centered *Colluricincla harmonica*, forms a deep branch in our phylogeny, in accordance with the Australo-Papuan origin of the group. Later (at 15 Mya) a clade diverged with *Coracornis raveni* (in Sulawesi) and the small, dull *Colluricincla sanghirensis* (in Sangihe Island further north). It is worth noting that eastern Sulawesi represents a terrane that was once connected with the Bird's Head Peninsula of New Guinea, and that the different parts of Sulawesi were pieced together at 10–15 Mya and connected with the volcanic chain of which Sangihe is part. *Pachycephala*, which is widely distributed from Western Indonesia and the Philippines in the West to Samoa and Tonga in the East, forms the terminal clade. *Colluricincla tenebrosa* (in the oceanic island Palau, located on the volcanic arc north of New Guinea) is nested within *Pachycephala*. We hypothesise that this radiation was possible because of the proximity to New Guinea of archipelagos of volcanic/ophiolitic island, including Halmahera and the East Philippines (Fig. 1c), and because of the rapid drifting of these islands near the end of the Miocene, whereby these birds could spread throughout the present Philippines (*P. philippensis*, *albiventris* and *plateni* in our phylogeny) and then onwards to the coastal mangroves of south-eastern Asia. Thus the biogeographic pattern may be explained through island-hopping with only moderate distances of dispersal.

The Campephagidae present a very different picture. The deep split between *Pericrocotus* and the other Campephagids at ca. 26 Mya suggests an early dispersal out of Australia/New Guinea at a time when the distance between the plate fragments at the north-western edge of the Australian plate and the Greater Sunda area of Asia was diminishing rapidly (Fig. 1b; Hall, 2002). Taking the Australian origin as well supported, the most parsimonious interpretation would be to assume a rapid dispersal into south-eastern Asia, where *Pericrocotus* then radiated (with secondary dispersal to the Philippines and lesser Sundas), The rest of the Campephagids then underwent a much more dynamic process of differentiation within Australasia and adjacent Indopacific archipelago. When examining the *Coracina-Campephaga-Lalage* assemblage in detail (Fig. 2) it is not easy to associate specific clades with biogeographic regions. For instance, the Sulawesi taxa do not cluster together, nor do those of the Philippines, or those from Africa. This argues against radiations centered within these regions. Rather there seems to be a complex mix of dispersal events across broader biogeographic regions.

It is particularly remarkable that three or four lineages in Africa/Madagascar (with altogether 13 species) represent deep branches (8–18 Mya, according to Fig. 6), while species inhabiting the Indian subcontinent are in much more terminal positions (2.5 and 7 Mya according to Fig. 6; *C. melaschista* in Clade B, and *C. macei* in Clade A). This does not suggest a progressive dispersal through the Oriental Region to Africa, but instead direct transoceanic dispersal during the early radiation of *Coracina*. In three cases a sister taxon of the Afrotropical lineage could be identified on islands which are wholly or partly part of the Australian plate. Thus, among the taxa included in this study, *C. abbotti* of Sulawesi is sister to *C. azurea* of the Guinea-Congolian rainforest of Africa. *Campochaera sloetti* of New Guinea is sister to the African genus *Campephaga*, which is widespread across Africa, and *C. temminckii* of Sulawesi is the sister of *C. cinerea* of Madagascar. Although we cannot exclude the possibility that *C. cinerea* could be more closely related to the African *C. caesia* and *C. pectoralis* (see Fuchs et al., 2007) because of incomplete taxon sampling, the African clade would still be associated with *C. temminickii*.

Overall, the low representation of Campephagid clades A and B in southern Asia, and the suggested relationships of African taxa with species in New Guinea and Sulawesi (the south-eastern part of which originated as part of the Australian plate) suggest that Africa may have been colonized across the Indian Ocean in the mid-Miocene (eventually by island hopping), rather than by dispersal across Wallace's line into Asia and so onwards, over land.

Other taxa for which molecular dating has supported oceanic dispersal over tectonic vicariance in the Indian Ocean include carnivores (Yoder et al., 2003), amphibians

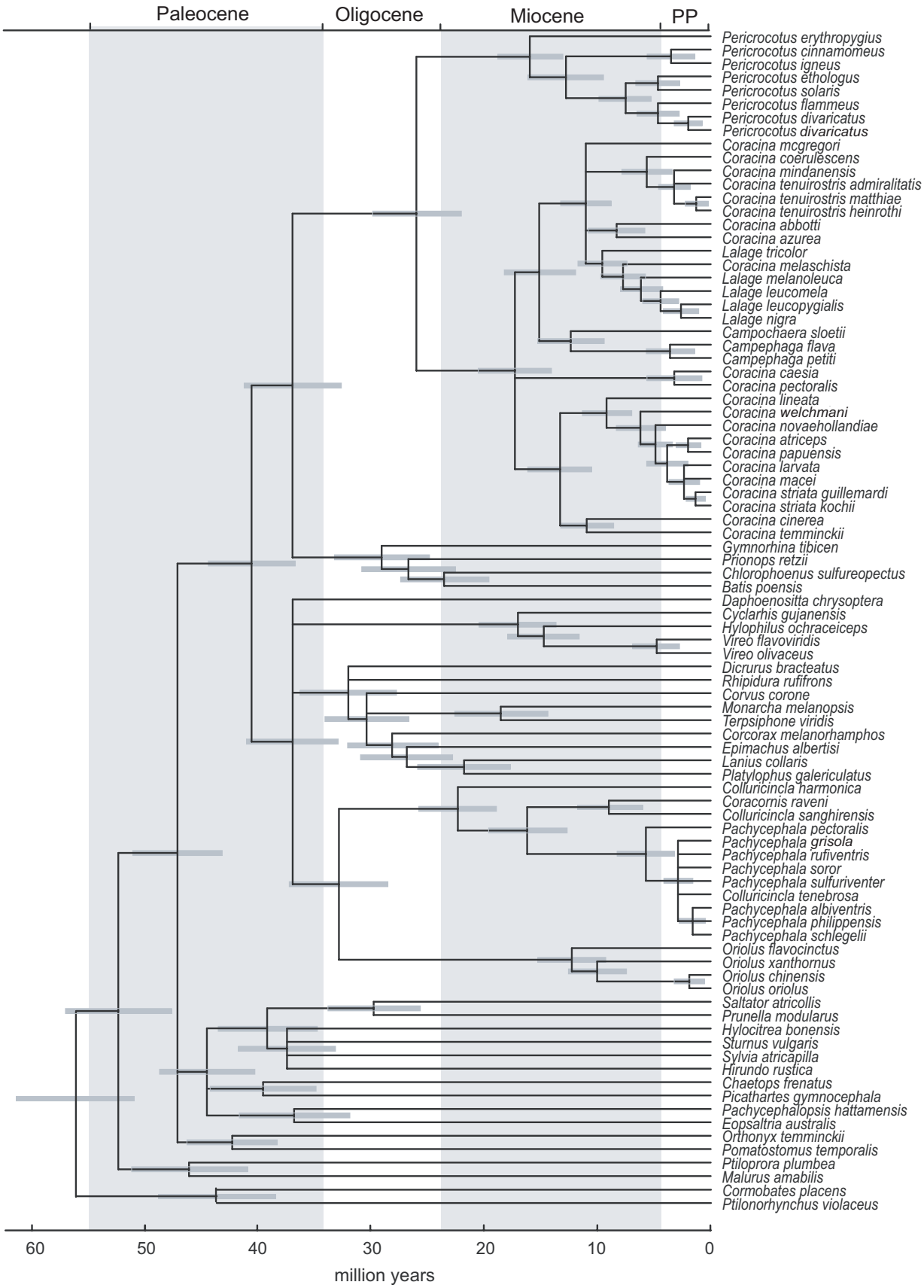

Fig. 6. Chronogram for Crown Corvida. The gray bars indicate standard deviations for the node ages.

(Vences et al., 2003) and reptiles (Raxworthy et al., 2002). These studies focus on dispersal between mainland Africa and Madagascar, but it is also possible that similar dispersal could have taken place between Australia/Wallacea and Africa/Madagascar, as suggested for several angiosperm families (Baum et al., 1998; Davis et al., 2002; Mummenhoff et al., 2004). Likewise several cases have been described where Australasian avian lineages colonized Mauritius or Madagascar via *trans*-oceanic dispersal from Australasia (e.g., colonization of Madagascar by *Alectroenas,* pigeons (Shapiro et al., 2002), by *Anas* dabbling ducks (Johnson and Sorenson, 1998, 1999) and by *Coracopsis* parrots, de Kloet and de Kloet, 2005). Unfortunately the reconstruction of plate tectonics are unable to tell to what extent the submarine arc regions and plateaus in the Indian Ocean had islands above sea level during the Tertiary (Fuchs et al., 2006b; Jønsson and Fjeldså, 2006a). Extensive land areas in the sub-Antarctic zone may have existed in the distant past (Jønsson and Fjeldså, 2006a) but the time of subsidence of these areas is unknown.

Within the cuckoo-shrike clade B (sensu Fuchs et al., 2007) a subclade is recovered including *C. tenuirostris heinrothi* (New Britain),*C. tenuirostris matthiae*, *C. tenuirostris admiralitatis* (Admirality Islands) and *C. mindanensis* and *C. coerulescens* (Philippines). This radiation would seem to have its centre of origin in the Philippines, but when interpreting this it is worth noting that through the Upper Tertiary the East Philippines were located north of New Guinea and closely associated with Halmahera and the Melanesian Arc (Fig. 1). Thus the most likely interpretation would be to assume a radiation within these island arcs, which were closely associated with the ophiolytic formations along the north coast of New Guinea. Similar patterns of diversification within archipelagos have recently been demonstrated for monarch flycatchers (another Crown Corvidan lineage) in the Pacific (Filardi and Moyle, 2005) and for rodents in the Philippines (Jansa et al., 2006).

The Campephagidae complex seems to illustrate very dynamic dispersal events across the Australo-Papuan and Wallacean Regions coinciding with the time, in the mid-Miocene, just before the collision of landmasses of Australian and Asian origin, and when there was also a very complex development of archipelagos on the transition towards the Pacific region. It is worth noting that somewhat earlier (at 40 Mya, corresponding to the early radiation of Crown Corvida groups) a large Melanesian archipelago developed close to the Papuan coast (Hall, 2002, Fig. 17) and this may have provided "empty" habitats on the newly formed islands and may thus have stimulated the evolution of r-selected, dispersal strategies (Diamond, 1974) (as opposed to the conservative non-dispersal strategy of the more basal Australo-Papuan lineages). Such strategies are characteristic of several lineages in the Crown Corvida, such as the monarch flycatchers, but may be particularly developed among the cuckoo-shrikes. Most of these species can form small groups, mostly family parties of 4–5 individuals, and sometimes larger flocks, and moving in groups may greatly enhance the success of long-distance dispersal. Although primarily adapted to forest habitat, most species readily adapt to edge habitats and thickets, and they have opportunistic feeding habits: although mostly known as caterpillar-eaters, they are indeed very versatile, and especially *Coracina* eat a broad range of arthropods and also take small vertebrates, fruits and berries, and even other plant material. Thus they are superbly suited to take advantage of the low levels of interspecific competition on islands. Further examination of the genus *Coracina*, including the morphologically distinct island forms from the Indian Ocean islands Reunion and Mauritius, would be interesting for biogeographic analysis.

Island radiations in "supertramp" groups such as the Campephagidae may also permit later "upstream" colonizations of mainlands to either side of the island sea. Thus the remarkable dispersal patterns in Campephagid clades A and B (Fig. 2) does not track the movement of main geological plates but seems instead to reflect an extraordinary ability to take advantage of the many new opportunities that arose off the continental margins, in connection with the dynamic development of island arcs. We found one case of "upstream" colonization for the *Coracina* radiation having dispersed into Wallacea and then back to the Moluccas and New Britain around "mainland" New Guinea (*C. tenuirostris*). We also highlight three trans-oceanic dispersal events between Sulawesi/New Guinea and Africa/Madagascar although as mentioned above the close relationship between *Coracina cinerea* and *C.temminckii* (Fig. 2) could be a result of character sampling bias wherefore we should be cautious about interpretations based on this relationship. Regarding *Pericrocotus*, our study supports an initial big leap dispersal event across Wallacea and a later diversification within Asia, with a final dispersal back into the Wallacean archipelago. Overall, vicariance has been of minor importance compared to dispersal in this avian family.

This study only presents the tip of the iceberg and there is no reason to doubt that a complete phylogenetic study will reveal even more complex dispersal patterns for the basal clades of Crown Corvida. It is an interesting challenge for future research to explore the biogeography of these groups in more detail, and to analyze relationships between ability to disperse and variation in life history tactics. It is also a challenge to explore the possible role of changes in life strategies in explaining the dichotomy between taxonomic groups where vicariance seems to be a predominant mode of speciatioin, and those with a more dynamic patterns of diversification incolving long distance dispersal.

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