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ORIGINAL ARTICLE

Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): transoceanic colonization of Africa from Australo-Papua

Knud A. Jønsson[1,2]*, Rauri C. K. Bowie[2], Johan A. A. Nylander[3], Les Christidis[4,5], Janette A. Norman[5,6] and Jon Fjeldså[1]

[1]Vertebrate Department, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark, [2]Museum of Vertebrate Zoology and Department of Integrative Biology, 3101 Valley Life Science Building, University of California, Berkeley, CA 94720-3160, USA, [3]Department of Botany, Stockholm University, S-106 91 Stockholm, Sweden, [4]National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW 2450, Australia, [5]Department of Genetics, University of Melbourne, Parkville, Vic. 3052, Australia, [6]Sciences Department, Museum Victoria, GPO Box 666, Melbourne, Vic. 3001, Australia

*Correspondence: Knud A. Jønsson, Vertebrate Department, Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.
E-mail: kajonsson@snm.ku.dk

ABSTRACT

Aim Cuckoo-shrikes and allies (Campephagidae) form a radiation of birds widely distributed in the Indo-Pacific and Africa. Recent studies on the group have been hampered by poor taxon sampling, causing inferences about systematics and biogeography to be rather speculative. With improved taxon sampling and analyses within an explicit spatiotemporal framework, we elucidate biogeographical patterns of dispersal and diversification within this diverse clade of passerine birds.

Location Africa, Asia, Australo-Papua, the Pacific, the Philippines and Wallacea.

Methods We use model-based phylogenetic methods (MrBayes and garli) to construct a phylogenetic hypothesis of the core Campephagidae (Campephagidae with the exclusion of *Pericrocotus*). The phylogeny is used to assess the biogeographical history of the group with a newly developed Bayesian approach to dispersal–vicariance analysis (Bayes-diva). We also made use of a partitioned beast analysis, with several calibration points taken from island ages, passerine mitochondrial substitution rates and secondary calibration points for passerine birds, to assess the timing of diversification and dispersal.

Results We present a robust molecular phylogeny that includes all genera and 84% of the species within the core Campephagidae. Furthermore, we estimate divergence dates and ancestral area relationships. We demonstrate that Campephagidae originated in Australo-Papua with a single lineage (*Pericrocotus*) dispersing to Asia early. Later, there was further extensive transoceanic dispersal from Australo-Papua to Africa involving lineages within the core Campephagidae radiation.

Main conclusions The phylogenetic relationships, along with the results of the ancestral area analysis and the timing of dispersal events, support a transoceanic dispersal scenario from Australo-Papua to Africa by the core Campephagidae. The sister group to core Campephagidae, *Pericrocotus*, dispersed to mainland Asia in the late Oligocene. Asia remained uncolonized by the core Campephagidae until the Pliocene. Transoceanic dispersal is by no means an unknown phenomenon, but our results represent a convincing case of colonization over a significant water gap of thousands of kilometres from Australo-Papua to Africa.

Keywords
Africa, Australia, biogeography, birds, Campephagidae, cuckoo-shrikes, Indo-Pacific, Passeriformes, phylogeny, transoceanic dispersal.

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INTRODUCTION

Recent advances in our understanding of biological dynamics within islands and archipelagos, and between archipelagos and continents, have demonstrated a greater complexity than thought by earlier biogeographers (reviewed by Whittaker & Fernández-Palacios, 2007; Bellemain & Ricklefs, 2008; Emerson & Gillespie, 2008; Gillespie *et al.*, 2008). In particular, the increasing significance of reverse colonizations, whereby island systems are sources for continental biodiversity, has challenged a fundamental biogeographical paradigm (Filardi & Moyle, 2005; Bellemain & Ricklefs, 2008).

A second paradigm within biogeography that is receiving renewed attention is the determination of the relative importance of dispersal and vicariance in shaping distribution patterns of organisms across the globe (de Queiroz, 2005; Heaney, 2007). Dispersal and vicariance are often considered competing hypotheses when explaining present distribution patterns (de Queiroz, 2005). For example, disjunctly distributed sister-species can be explained either by dispersal or by postulating that an ancestral taxon was historically widespread, and that the present distribution pattern is a consequence of the extinction of populations from the intervening area. The advent of molecular-based phylogenies with corresponding divergence time estimates, however, has started to provide data sets with which one can explicitly test the underlying historical biogeographical pattern (e.g. Sanmartín & Ronquist, 2004; Brown *et al.*, 2006; Nylander *et al.*, 2008b; Voelker *et al.*, 2009).

The avian family Campephagidae (cuckoo-shrikes and allies) is distributed throughout Africa, Asia and Australia, as well as within the archipelagos of both the Indian and Pacific Oceans. Consequently, gaining an understanding of the origin, pattern and timing of dispersal that have led to the present cuckoo-shrike radiation is likely to be integral to interpreting broader regional biogeographical patterns and processes across continents and archipelagos.

The origin of passerine birds (Passeriformes) has been demonstrated to be within the Gondwanan supercontinent and ranges back to the Cretaceous/Tertiary (K/T) boundary (Barker *et al.*, 2002, 2004; Ericson *et al.*, 2002). Two major lineages within Passeriformes are recognized: the suboscines (Tyranni), which occur primarily in South America; and the oscines (Passeri), with a putative Australian origin. The basal lineages within oscines all occur in Australia, thus it is likely that Australia is the place of origin for this highly diverse radiation (Christidis, 1991; Barker *et al.*, 2002; Edwards & Boles, 2002; Ericson *et al.*, 2002).

One of the major avian biogeographical questions in recent years has been how oscines dispersed out of Australia. One sub-group, the Passerida, which has been very successful in terms of diversity (*c.* 3500 species), is thought to have originated in Africa (Fuchs *et al.*, 2006; Jønsson & Fjeldså, 2006; Johansson *et al.*, 2008). For this hypothesis to be correct, it would require transoceanic dispersal from Australia to Africa of an early Passerida ancestor, a scenario perhaps more parsimonious than assuming a partial extinction of a once widespread common ancestor/s.

Another large radiation within the Passeri is the core Corvoidea (*c.* 750 species, *sensu* Monroe & Sibley, 1993). The Campephagidae is the most species-rich family of birds both within the core Corvoidea complex, and in the Indo-Pacific region. The core Campephagidae, which excludes *Pericrocrotus* (minivets), but includes the cuckoo-shrikes and trillers belonging to the genera *Coracina*, *Lalage*, *Campochaera*, *Campephaga* and *Lobotos*, numbers 70 species, 57 of which are distributed from India (including Sri Lanka) in the west to Australia and the Pacific Islands in the east. A further 11 species occur in tropical Africa (including Madagascar and the Comoros), and two species occur on the Indian Ocean islands of Mauritius and Réunion. The systematic relationships within this group are poorly studied, and consequently inferences made on the biogeographical history are highly speculative.

It has been argued that the cradle of campephagid diversification was within the Australo-Papuan region (Jønsson *et al.*, 2008). However, the alternative hypothesis – that Asia could be the area of origin from where colonization of Africa and Australo-Papua could be explained by one radiation going west to Africa and another going east to Australo-Papua – could not be excluded. Recent work by Fuchs *et al.* (2007) and Jønsson *et al.* (2008) has suggested close affinities between African and Australian/Wallacean cuckoo-shrike species, leading the authors to speculate that dispersal directly between the two continents was a likely scenario. These studies, however, suffered from relatively poor taxon sampling hampering a more substantiated biogeographical investigation of the group.

In the present study we construct a densely sampled molecular phylogeny, which we use to assess several *a priori* hypotheses in order to gain a better understanding of the biogeographical history of cuckoo-shrikes. If cuckoo-shrikes originated in Asia, we would expect Asian taxa to dominate the basal clade(s) within the phylogeny. Conversely, if the origin was in Australo-Papua, then these taxa would be expected to dominate the basal part of the tree. If dispersal took place from Australia to Africa via Asia, as the terranes of the Australian and Asian plates collided some 20 Ma (Hall, 1998, 2002; Holloway, 1998), we would expect to find multiple dispersal events reflecting the close proximity of the many larger and smaller islands in the Indonesian and Philippine archipelagos, which would have served as stepping stones between Australia and mainland Asia. This kind of dispersal pattern has been demonstrated for other groups of birds, for example, the Pachycephalidae (Jønsson *et al.*, 2010a). These Asian colonizers would, in turn, be expected to be the founders of African lineages, and we would expect to find African lineages at distal parts of the tree.

MATERIALS AND METHODS

Taxon sampling and laboratory procedures

Recent studies of higher-level relationships within the Campephagidae have demonstrated that the genera *Lobotos*,

Campephaga, *Campochaera* and *Lalage* are nested within the *Coracina* complex. *Pericrocotus*, on the other hand, is the monophyletic sister-group (Fuchs *et al.*, 2007; Jønsson *et al.*, 2008). Sister to the Campephagidae (comprising *Coracina* and *Pericrocotus*) is an African assemblage including the families Platysteiridae and Malaconotidae (Fuchs *et al.*, 2007; Jønsson *et al.*, 2008), which are intermingled with some Australasian species (Norman *et al.*, 2009). Although the primary emphasis in our current paper is on the *Coracina* complex, we included several taxa from known sister groups (e.g. *Pericrocotus* and Malaconotidae) in order to address biogeographical questions appropriately. With this in mind, we have sampled 59 of the 70 (84%) species included within the core Campephagidae (Taylor, 2005).

Fresh tissue (blood, liver or muscle) was extracted using the Qiagen DNeasy Extraction kit (Qiagen, Valencia, CA, USA), following the manufacturer's protocol. Three nuclear gene regions: myoglobin intron-2 (Myo2) (chromosome 1), ornithine decarboxylase (ODC) intron-6 to intron-7 (chromosome 3), and glyceraldehyde-3-phosphodehydrogenase (GAPDH) intron-11 (chromosome 1); and two mitochondrial markers: NADH dehydrogenase subunit 2 (ND2) and subunit 3 (ND3), were sequenced and used to estimate phylogenetic relationships. Primer pairs used for amplification were: ND2: Lmet (Hackett, 1996)/H6312 (Cicero & Johnson, 2001); ND3: ND3-L10755/ND3-H11151 (Chesser, 1999); myoglobin intron-2: Myo2 (Slade *et al.*, 1993)/Myo-cora2R (Jønsson *et al.*, 2008) and Myo-coraF1 (Jønsson *et al.*, 2008)/Myo3F (Heslewood *et al.*, 1998); ODC: OD6/OD8 (Allen & Omland, 2003) and G3P13/G3P14b (Fjeldså *et al.*, 2003).

The thermocycling conditions included a hot start at 95 °C for 5 min, followed by 32 cycles at 95 °C for 40 s, 54–63 °C for 40 s, and 72 °C for 60 s, and was completed by a final extension at 72 °C for 8 min. One microlitre of the amplification products was electrophoresed on a 1.5% agarose gel and revealed under UV light with ethidium bromide to check for correct fragment size and to control for the specificity of the amplifications. Polymerase chain reaction (PCR) products were purified using ExoSap enzymes (exonuclease and shrimp alkaline phosphatase). Purified PCR products were cycle-sequenced using the Big Dye terminator chemistry (ABI; Applied Biosystems, Foster City, CA, USA) in both directions with the same primers as were used for PCR amplifications, except for G3P13, which was replaced by G3PintL1 (Fjeldså *et al.*, 2003), and run on an automated ABI 3100 DNA sequencer.

Corresponding laboratory procedures for study skins are detailed by Irestedt *et al.* (2006). Additional internal primers for study skins are specified by Jønsson *et al.* (2008) for myoglobin and GAPDH, and by Irestedt *et al.* (2006) for ODC. In addition, two new primers were specifically designed for this study, ND2cor778R: ATGATGAGTCAT TTTGGGAGGAA and ND2cor795F: CAGGTTTCCTCCCAAAGTGACTC.

Sequences were assembled with SeqMan II (DNASTAR Inc., Madison, WI, USA). Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. GenBank accession numbers are provided in Table 1.

Alignment and phylogenetic analyses

Alignment was performed using MegAlign (DNASTAR Inc.) with some minor manual adjustments. The concatenated alignment consisted of 3069 bp. Coding genes (ND2 and ND3) were checked for the presence of stop codons or insertion/deletion events that would have disrupted the reading frame. We used Bayesian inference (e.g. Huelsenbeck *et al.*, 2001; Holder & Lewis, 2003), as implemented in MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2003; Ronquist & Huelsenbeck, 2003) to estimate phylogenetic relationships. The most appropriate substitution models were determined with MrModeltest 2.0 (Nylander, 2004), using the Akaike information criterion (Akaike, 1973; Posada & Buckley, 2004). Bayesian analyses for the concatenated data set were performed allowing the different parameters (base frequencies, rate matrix or transition/transversion ratio, shape parameter, proportion of invariable sites) to vary between the seven partitions (GAPDH, ODC, Myo2, 1st, 2nd, 3rd codon positions for mtDNA, and tRNA), i.e. mixed-models analyses (Ronquist & Huelsenbeck, 2003; Nylander *et al.*, 2004). In all MrBayes analyses, the Markov chain Monte Carlo (MCMC) was run using Metropolis-coupling, with one cold and three heated chains, for 5 million to 15 million iterations with trees sampled every 1000 iterations. The number of iterations discarded before the posterior probabilities were calculated (i.e. the length of the 'burn-in' period) was estimated graphically using AWTY (Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008a) by monitoring the change in cumulative split frequencies. Two independent runs initiated from random starting trees were performed for each data set, and the log-likelihood values and posterior probabilities for splits and model parameters were checked to ascertain that the chains had reached apparent stationarity.

Maximum-likelihood analyses were performed using garli 0.95 (Zwickl, 2006). Five independent analyses were performed (20 million generations for the combined analysis, 15 million generations for ND2, and 10 million generations for the nuclear partitions). Nodal support was evaluated with 500 nonparametric bootstrap pseudoreplications.

Establishing ancestral areas

In order to elucidate ancestral patterns we used the newly developed 'Bayes-diva' approach (Nylander *et al.*, 2008b). In a standard dispersal–vicariance analysis (Ronquist, 1997) as implemented in the software diva (Ronquist, 1996, 2001), ancestral areas are optimized onto internal nodes of a phylogeny by minimizing the number of dispersal and extinction events required to explain the terminal distributions (Ronquist, 2003). The basic assumption (null model) is allopatric speciation in response to vicariance, but diva also considers dispersal and extinction in the shaping of current

Table 1 List of taxa included in the study.

Taxon name	Voucher number	Origin	GAPDH	ODC	Myo	ND2
Aleadryas rufinucha	NRM 543658	New Guinea	EU273375	EU273355	EU273395	
Artamus cyanopterus	ZMUC 135911	Australia	DQ406661		DQ406636	DQ096728
Batis poensis	MNHN CG 1998-783	Cameroon	DQ406665	EU272120	AY529907	AY529941
Campephaga flava	RB 613	Kenya	DQ406639	EU380410	EF052822	AY529944
Campephaga petiti	FMNH 384855	Uganda	EF052795	EU380411	EF052823	EF052771
Campochaera sloetii	NRM 569328	New Guinea	EU380459	EU380412	EU380489	HM002951
Coracina abbotti	NRM 569468	Sulawesi	EU380460	EU380415	EU380491	HM002952
Coracina analis	AMNH 337784	New Caledonia	HM002899	HM002997		HM002953
Coracina atriceps	BMNH 1910.12.28.182	Ceram	EU272091	EU273118	EU272102	
Coracina azurea	ANSP 11901	Equatorial Guinea	EF052796	EU380416	EF052824	EF052772
Coracina bicolor	RMNH.AVES 61247	Sulawesi	HM002900	HM002998	HM002926	HM002954
Coracina boyeri	ANWC 27158	New Guinea	HM002901	HM002999	HM002927	HM002955
Coracina caeruleogrisea	ANWC 24169	New Guinea	HM002902	HM003000	HM002928	HM002956
Coracina caesia	ZMUC 123521	Tanzania	EF052797		EF052825	EF052773
Coracina caesia	ZMUC 134772	Africa		HM003001		
Coracina caledonica	FMNH 268458	Loyalty Isl	HM002903	HM003002	HM002929	HM002957
Coracina ceramensis	AMNH 562444	Ceram				HM002958
Coracina cinerea	FMNH 352837	Madagascar	EF052800	EU380417	EF052827	EF052685
Coracina coerulescens	USNM B3671	Philippines	EF052759	EU380418	EF052770	EF052697
Coracina dispar	AMNH 562297	Little Key				HM002959
Coracina dohertyi	RMNH.AVES 85029	Flores	HM002904	HM003003	HM002930	HM002960
Coracina fimbriata	RMNH.AVES 66951	Sumatra	HM002905	HM003004	HM002931	HM002961
Coracina graueri	RG 79-33-A-2	Congo	HM002906	HM003005	HM002932	HM002962
Coracina holopolia	AMNH MKL80	Solomon Islands	EF052801		EF052828	EF052775
Coracina incerta	ANWC 27044	New Guinea	HM002907	HM003006	HM002933	HM002963
Coracina ingens	AMNH 334884	Manus				HM002964
Coracina larvata normani	BMNH 1935.10.22.303	Borneo	EU380461	EU380419	EU380492	
Coracina leucopygia	RMNH.AVES 123485	Sulawesi	HM002908	HM003007	HM002934	HM002965
Coracina lineata lineata	ANWC 39960	Australia	HM002909	HM003008	HM002935	HM002966
Coracina lineata sublineata	ZMUC 95267	New Ireland	EU380462	EU380420	EU380493	
Coracina longicauda	ANWC 26970	New Guinea	HM002910	HM003009	HM002936	HM002967
Coracina macei larvivora	MNHN CG 1989-68	Thailand				EF052777
Coracina macei larvivora	ZMUC 95260	Thailand	EU380463	EU380421	EU380494	
Coracina maxima	ANWC 48004	Australia	HM002911	HM003010	HM002937	HM002968
Coracina mcgregori	FMNH 392259	Philippines	EF052805	EU380422	EF052831	EF052686
Coracina melanoptera	FMNH 233770	India	HM002912	HM003011	HM002938	HM002969
Coracina melaschistos	MNHN 6-69	Laos	EF052807	EU380423	AY529913	AY529948
Coracina mindanensis everetti	ZMUC 95262	Tawi Tawi	EU380464	EU380424	EU380495	HM002970
Coracina montana	ANWC 24172	New Guinea	HM002913	HM003012	HM002939	HM002971
Coracina morio	RMNH.AVES 61242	Sulawesi	HM002914	HM003013	HM002940	HM002972
Coracina newtoni	SEOR 001	Réunion	HM002915	HM003014	HM002941	HM002973
Coracina novaehollandiae	ANSP 10622	Australia	EF052808	EU380425	EF052834	EF052779
Coracina ostenta	AMNH 459820	Philippines	HM002916	HM003015		HM002974
Coracina papuensis artamoides	ANWC 39813	Australia	HM002917	HM003016	HM002942	HM002975
Coracina papuensis sclaterii	ZMUC 95265	New Britain	EU380465	EU380426	EU380496	HM002976
Coracina pectoralis	MNHN CG 1979-1352	South Africa	EF052810		EF052836	EF052781
Coracina polioptera	MNHN CG 1989-69	Thailand	EF052811		EF052837	EF052782
Coracina salomonis	ZMUC 139341	Makira	HM002918	HM003017	HM002943	HM002977
Coracina schistacea	AMNH 561078	Sula				HM002978
Coracina striata guillemardi	ZMUC 95261	Tawi Tawi	EU380466	EU380427	EU380497	HM002979
Coracina striata kochii	ZMUC 95258	Mindanao	EU380467	EU380428	EU380498	HM002980
Coracina sula	AMNH 562441	Sula				HM002981
Coracina temminckii	NRM 569324	Sulawesi	EU380468	EU380429	EU380499	HM002982
Coracina tenuirostris admiralitatis	ZMUC 95268	Manus Island	EU380469	EU380430	EU380500	HM002983
Coracina tenuirostris heinrothi	ZMUC 95264	New Britain	EU380470	EU380431	EU380501	HM002984
Coracina tenuirostris matthiae	ZMUC 95266	Mussau	EU380471	EU380432	EU380502	HM002985
Coracina tenuirostris remota	ZMUC 102478	New Hanover	HM002919	HM003018	HM002944	HM002986

Table 1 Continued

Taxon name	Voucher number	Origin	GAPDH	ODC	Myo	ND2
Coracina tenuirostris tenuirostris	ANWC 41992	Australia	HM002920	HM003019	HM002945	HM002987
Coracina typica	ZMUC 141101	Mauritius	HM002921	HM003020	HM002946	HM002988
Coracina welchmani	UWBM 60241	Solomon Islands	EF052799	EU380433	EF052826	EF052774
Daphoenositta chrysoptera	MV 1311	Australia	EU380474		EU380505	
Eopsaltria australis	MV 1390	Australia	EF441216	EF441238	AY064732	AY064749
Gymnorhina tibicen	MV AC78	Australia	DQ406669	EU272119	AY064741	AY064756
Lalage atrovirens	RMNH.AVES 84504	Tanimbar	HM002922	HM003021	HM002947	HM002989
Lalage leucomela	UWBM 57519	Australia	EF052814	EU380438	EF052840	EF052785
Lalage leucopyga	ZMUC 139386	Makira	HM002923	HM003022	HM002948	HM002990
Lalage leucopygialis	BMNH 1934.10.21137	Sulawesi	EU380477	EU380439	EU380507	HM002991
Lalage maculosa	AMNH 206135	British Samoa				HM002992
Lalage melanoleuca minor	ZMUC 95259	Mindanao	EU273381	EU273361	EU273403	HM002993
Lalage nigra	FMNH 344979	Philippines	EF052815	EU380440	EF052841	EF052786
Lalage sharpei	AMNH 206892	British Samoa				HM002994
Lalage sueurii	RMNH.AVES 65417	Roti, SW of Timor	HM002924	HM003023	HM002949	HM002995
Lalage tricolor	UWBM 57508	Australia	EF052816	EU380441	EF052842	EF052787
Lobotos oriolinus	RG 126479	Congo	HM002925	HM003024	HM002950	HM002996
Machaerirhynchus flaviventer	ANWC 39520	Australia			FJ821090	
Malaconotus blanchoti	ZMUC 116824	Kenya	DQ406651		AY529926	AY529961
Oreoica gutturalis	SAM B.39217	Australia			FJ821094	
Oriolus oriolus	MCSNC 1415	Italy	EF052755	EU273363	EF052766	EF052693
Ornorectes cristatus	ANWC 26733	New Guinea	EU273389	EU273370	EU273411	GQ494087
Orthonyx temminckii	MVB 831	Australia	EF441222	EF441244	AY064728	AY064755
Pachycephala pectoralis	MV 3477	Australia	EU273385	EU273366	EU273407	EU600813
Peltops blainvillii	ANWC 26492	New Guinea			FJ821099	
Pericrocotus divaricatus	UWBM 74728	Russia	EF052818	EU380450	EF052843	EF052788
Pericrocotus erythropygius	USNM B5659	Myanmar	EF052754	EU380451	EF052765	EF052692
Platysteira cyanea	MNHN 2-22	Cameroon	DQ406658		AY529930	AY529965
Prionops retzii	ZMUC 119500	Kenya	DQ406654	EU380457	AY529931	AY529966
Rhagologus leucostigma	ANWC 26897	New Guinea			EU273416	
Telophorus sulfureopectus	MNHN CG 1998-823	Malawi	DQ406648	EU380413	AY529912	AY529947
Outgroup						
Menura novaehollandiae	MVF 722	Australia	EF441220	EF441242	AY064744	AY064754

AMNH, American Museum of Natural History, USA; ANSP, Academy of Natural Science, Philadelphia, USA; ANWC, Australian National Wildlife Collection, Canberra, Australia; BMNH, British Museum of Natural History, Tring, England; FMNH, Field Museum of Natural History, Chicago, USA; MCSNC, Museo Civico di Storia Naturale di Carmagnola, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MV, Museum Victoria, Australia; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; RB, Rauri Bowie, Museum of Vertebrate Zoology (MVZ), University of California, Berkeley; RG, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; RMNH, Rijksmuseum van Natuurlijke Histoire, Leiden, The Netherlands; SAM = South Australian Museum, Australia; SEOR, Société d'Etudes Ornithologiques de la Réunion; USNM, United States National Museum (Smithsonian), Washington DC, USA; UWBM, University of Washington, Burke Museum, Seattle, USA; ZMUC, Zoological Museum, University of Copenhagen, Denmark. All ingroup taxa are vouchered.

GAPDH, glyceraldehyde-3-phosphodehydrogenase; ODC, ornithine decarboxylase; Myo2, myoglobin intron-2; ND2, NADH dehydrogenase subunit 2.

distribution patterns (Ronquist, 1997), thus it has proven to be an appropriate and popular biogeographical reconstruction method. A limitation of the implementation of DIVA (and many other biogeographical optimization methods) is that it requires fully bifurcated trees, and that the method does not take into account the uncertainty in phylogenetic inference. In contrast, 'Bayes-DIVA' takes topological uncertainty into account. Rather than using a single fully resolved topology, which often is possible only by making certain assumptions about relationships in a given tree, we sampled 15,000 trees (by thinning the chain, i.e. sampling every *n*th generation) from the MCMC output and ran DIVA on all of them. The frequency of ancestral areas for clades was then recorded and plotted as marginal distributions on the majority-rule consensus tree derived from the MCMC. The major advantage of the Bayes-DIVA method is that the marginal distributions for the alternative ancestral areas at each node in the tree are the product of the phylogenetic uncertainty in the rest of the tree and the uncertainty in the biogeographical reconstruction of the node of interest.

In this study, which focuses on members of the core Campephagidae, we included several other groups known to be the closest relatives to Campephagidae, such that the basal part of core Campephagidae is no longer the root of the tree. This is

because ancestral reconstructions become increasingly unreliable towards the root of the tree, which can cause the ancestral distributions at the root to include all areas analysed (Ronquist, 1996). Ancestral reconstructions depend on both the nodes above (more distally) and below (more basally) the group of interest.

We assigned seven geographical areas for the DIVA analysis considering evidence of historical relationships of geological plates and terranes (Audley-Charles, 1981; Hall, 1998; Moss & Wilson, 1998): A) Australia/New Guinea (including the Bismarcks and the Admirality Islands, which, given their immediate proximity to New Guinea, have been easily colonizable in recent time); B) Wallacea (the area east of Borneo and Bali and west of New Guinea); C) the Pacific islands; D) the Philippine islands; E) Asia (including Sumatra, Borneo and Java, which are part of the Asian plate and have been connected to the Asian mainland on multiple occasions); F) Africa (including Madagascar); and G) the Indian Ocean islands of Réunion and Mauritius. The analysis was carried out constraining the maximum number of areas encompassed by the ancestral distributions to the maximum size of extant ranges using the maxareas (=2) option in DIVA. This is equivalent to assuming that the ancestors of the group in question have the same ability to disperse as their extant descendants and therefore that ancestral ranges were similar in size to extant ranges (Sanmartín, 2003; Nylander *et al.*, 2008b).

Dating analyses

We used BEAST v.1.4.6 (Drummond *et al.*, 2002, 2006; Drummond & Rambaut, 2007) to estimate the divergence dates within the Campephagidae. We assigned the best fitting model, as estimated by MrModeltest2, to each of the partitions. Because there are no fossils within or close to the Campephagidae, we used a combination of the island age of Réunion (2 Ma; see below) and a rate of 0.028 substitutions per site per lineage per million years for ND2 (corrected pairwise distances), which is derived from Galapagos mockingbirds (Drovetski *et al.*, 2004) and secondary calibration points from Barker *et al.* (2004). We assumed a Yule Speciation Process for the tree prior and an uncorrelated lognormal distribution for the molecular clock model (Drummond *et al.*, 2006; Ho, 2007). We used default prior distributions for all other parameters and ran MCMC chains for 50 million generations. The analysis was repeated three times. We used the program Tracer (Rambaut & Drummond, 2007) to assess convergence diagnostics.

Calibration points

The use of geological calibration points has been applied successfully for several avian groups, such as scops-owls (Fuchs *et al.*, 2008), sunbirds (Warren *et al.*, 2003) and whistlers (Jønsson *et al.*, 2010a). A general problem when using islands as calibration points is that colonization may have taken place long after their emergence. Thus, in order to use the age of an island as a calibration point, the island should be fairly young and as remote as possible. In the present study, the only islands that fit these criteria are Mauritius (7.8 Myr old; McDougall & Chamalaun, 1969) and Réunion (*c.* 2 Myr old; Chevallier & Vatin-Perignon, 1982) in the Indian Ocean. It is unknown what the error margins for these age estimates are, and using these exact ages would indeed be misleading. Therefore we applied to our data a recently published rate extrapolation (2.8% Myr^{-1}) of evolution in ND2 for another family of passerine birds (Norman *et al.*, 2007). This provides an age estimate for the split between *Coracina newtoni* (Réunion) and *Coracina typica* (Mauritius) at 1.35 Ma. Given the younger age of Réunion compared with Mauritius, it makes sense to assume that Mauritius was colonized before the emergence of Réunion, and that Mauritius would have acted as the source of colonists to Réunion once it emerged. So the combination of island age and ND2 evolution suggests that the split of these two species of cuckoo-shrike took place sometime around 1.5 Ma. Thus, for this calibration we chose a normally distributed prior at 1.5 Ma ± 0.25 SD (age within 95% confidence intervals (CI) = 1.089–1.911 Ma). Because it is important to have calibration points both basally and distally in the phylogenetic tree, we also used secondary calibration points from Barker *et al.* (2004). Barker *et al.* (2004) used a nonparametric rate-smoothing (NPRS) and a penalized-likelihood (PL) approach, as well as a calculation based on the DNA–DNA hybridization study of Sibley & Ahlquist (1990). The split of *Acanthisitta* from all other passerines is estimated at *c.* 82 Ma and was used to calibrate the tree. We used the age of two of the oscine splits (nodes 7 and 11 in Barker *et al.*, 2004). We used an average of the different age estimates presented by Barker *et al.* (2004). This translates into an estimate of the age of the split between *Artamus* and *Malaconotus* to be 27.5 Ma ± 1 SD (age within 95% CI = 25.86–29.14 Ma) and the split between *Menura* and all other oscines at 62.5 Ma ± 1 SD (age within 95% CI = 60.86–64.46 Ma).

Our chronogram can also be visualized as a relative-time chronogram (when removing the absolute age estimates). This is important because we are also interested in assessing whether dispersal events of certain clades are centred on a particular time that could be explained by discrete palaeogeographical events.

RESULTS

Phylogenetic analyses

The use of old museum specimens at times made amplification of some DNA segments rather difficult, thus a few sequence fragments are missing (Table 1).

For GAPDH we sequenced between 272 and 298 bp, but managed to obtain only 215 bp from *Aleadryas rufinucha*, 197 bp from *Coracina analis*, 197 bp from *Coracina bicolor*, 197 bp from *Coracina caledonica*, 197 bp from *Coracina*

graueri, 197 bp from *Coracina leucopygia*, 235 bp from *Coracina longicauda*, 197 bp from *Coracina melanoptera*, 180 bp from *Coracina montana*, 197 from *Coracina ostenta*, 163 bp from *Coracina tenuirostris tenuirostris*, 197 bp from *Lalage sueurii*, and 197 bp from *Lobotos oriolinus*. The total GAPDH alignment was 321 bp.

For ODC intron-6 and intron-7 we obtained 540–615 bp, but managed to obtain ODC intron-6 (245–249 bp) only from *Coracina analis*, *Coracina bicolor*, *Coracina leucopygia*, *Coracina ostenta*, *Lalage leucopygialis* and *Lalage sueurii*. The total alignment of ODC intron-6 and intron-7 was 634 bp.

For myoglobin intron-2 we sequenced 669–708 bp; however, some of the sequences (mostly some accessed from GenBank) were shorter, ranging between 625 and 662 bp. These include *Telophorus sulfureopectus*, *Prionops retzii*, *Platysteira cyanea*, *Malaconotus blanchoti*, *Artamus cyanopterus*, *Coracina novaehollandiae*, *Coracina pectoralis*, *Lalage tricolor* and *Batis poensis*. The total alignment of myoglobin intron-2 was 716 bp.

For NADH dehydrogenase subunit 2 we typically obtained between 1023 and 1041 bp, but only 1013 bp from *Coracina pectoralis*, 960 bp from *Coracina boyeri*, 919 bp from *Coracina polioptera*, 827 bp from *Coracina typica*, 816 bp from *Coracina newtoni*, 772 bp from *Campochaera sloetti*, *Coracina bicolor*, *Coracina striata kochii* and *Coracina temminckii*, 669 bp from *Coracina ceramensis*, *Coracina ostenta* and *Coracina sula*, and 525 bp from *Coracina dispar*.

Analyses performed on the concatenated data set (six partitions: GAPDH, ODC, Myo2, 1st, 2nd, 3rd mtDNA codon positions; maximum likelihood (ML): −ln 30273.75, Bayesian inference (BI) harmonic mean −ln 28990.66) and on the individual partitions (GAPDH: AIC: HKY + Γ, ML: −ln 2177.63, BI harmonic mean −ln 2447.96; ODC: AIC: GTR + Γ, ML: −ln 3231.03, BI harmonic mean −ln 3567.96; Myo2: AIC: HKY + Γ, ML: −ln 3767.67, BI harmonic mean −ln 4163.17; ND2: AIC: TVM + Γ, ML: −ln 19497.81, BI harmonic mean −ln 19178.53) yielded 50% majority-rule consensus trees that were topologically congruent for well-supported nodes (posterior probability >0.95 and bootstrap values >70%). The nuclear gene trees (GAPDH, ODC and Myo2) (see Appendices S1–S3 in Supporting Information) provide only a few well-supported clades. This was not unexpected, and reflects the fact that the nuclear genes used evolve too slowly to resolve closely related young species within the Campephagidae. The nuclear data do, however, provide evidence for the partitioning of some basal clades. The ND2 gene tree (Appendix S4) provides better resolution in the distal part of the tree, and the combined analysis (Fig. 1) of both mitochondrial and nuclear genes generates a rather robust and densely sampled core Campephagidae phylogeny.

Scores of the best likelihood trees were within 0.5 likelihood units of the best tree recovered in each of the other four GARLI runs, suggesting that the five runs had converged. The ML tree topology was completely congruent with the BI topology for well-supported nodes (posterior probability >0.95 and bootstrap values >70).

Bayesian dispersal–vicariance analysis

The Bayes-DIVA analysis (Fig. 2) recovers the origin of oscines to be Australian (nodes 1–6) in concordance with several other studies (Christidis, 1991; Barker *et al.*, 2002; Edwards & Boles, 2002; Ericson *et al.*, 2002). The origin of the Campephagidae (node 7) including *Pericrocotus*, which occurs in Asia (including Borneo, Sumatra and Java), is also recovered as Australian/Asian (AE; >0.97 CI). Given that the origin of the next node (8) is Australian (A; >0.96 CI) and that nodes (9 and 10) further up in the tree are Australian/African in origin (AF; >0.99 and >0.96 CI, respectively), it is most parsimonious to assume that the initial dispersal event from Australia led to *Pericrocotus* colonizing Asia, where the genus subsequently radiated. *Pericrocotus* is distributed in mainland Asia, Borneo, Java, Sumatra and Palawan, but is absent from Wallacea (Jønsson *et al.*, 2010b). The absence of *Pericrocotus* from Wallacea suggests that direct dispersal from Australia to Asia, not island-hopping across the Wallacean archipelago, is the most likely scenario. The core Campephagidae, however, remained in Australo-Papua. Node 10 splits into an all-African group (four species) and another group more or less restricted to Australo-Papua with a few rather late dispersals to Asia. Node 9 also splits into an all-African group (three species) and a more heterogeneous group consisting of species belonging basally to Australo-Papua, Wallacea, the Philippines and the Pacific. It is noteworthy that there is no indication of lineage sharing between Australo-Papua and mainland Asia at this stage. Furthermore, there is a rather clear pattern of dispersal between Australia and Africa, bypassing Asia. Apart from *Pericrocotus*, there is no dispersal to Asia from Australo-Papua in the basal part of the Campephagidae phylogeny. In fact, all Asian members of the core Campephagidae are found at terminal points in the phylogeny. Ancestral area reconstructions in distal parts of the tree become somewhat ambiguous, probably due to a high exchange of species between various regions leading to an obscured biogeographical signal. It should be noted, though, that the two Indian Ocean species (*Coracina newtoni* and *Coracina typica*) have an Asian rather than an African origin.

Dating analyses

The results of the BEAST dating analysis (Fig. 3) indicate the origin of the Campephagidae to be in the Late Oligocene and the origin of the core Campephagidae to be in the Early Miocene. We are particularly interested in the timing of dispersal between Australia and Africa. Thus, the time of common ancestry for the African clade comprising *Coracina cinerea*, *C. graueri*, *C. pectoralis* and *C. caesia*, and its sister-group is found to be 14 Ma (95% highest posterior density (HPD) = 11.5–17 Ma) and the time of common ancestry for the African clade comprising *Campephaga* and *Lobotos* and its sister-group is 17 Ma (95% HPD = 14–20 Ma). *Coracina azurea* is a species that proves difficult to place in the phylogeny. Although *C. azurea* is sister to *C. abbotti* in both the Bayesian and the BEAST

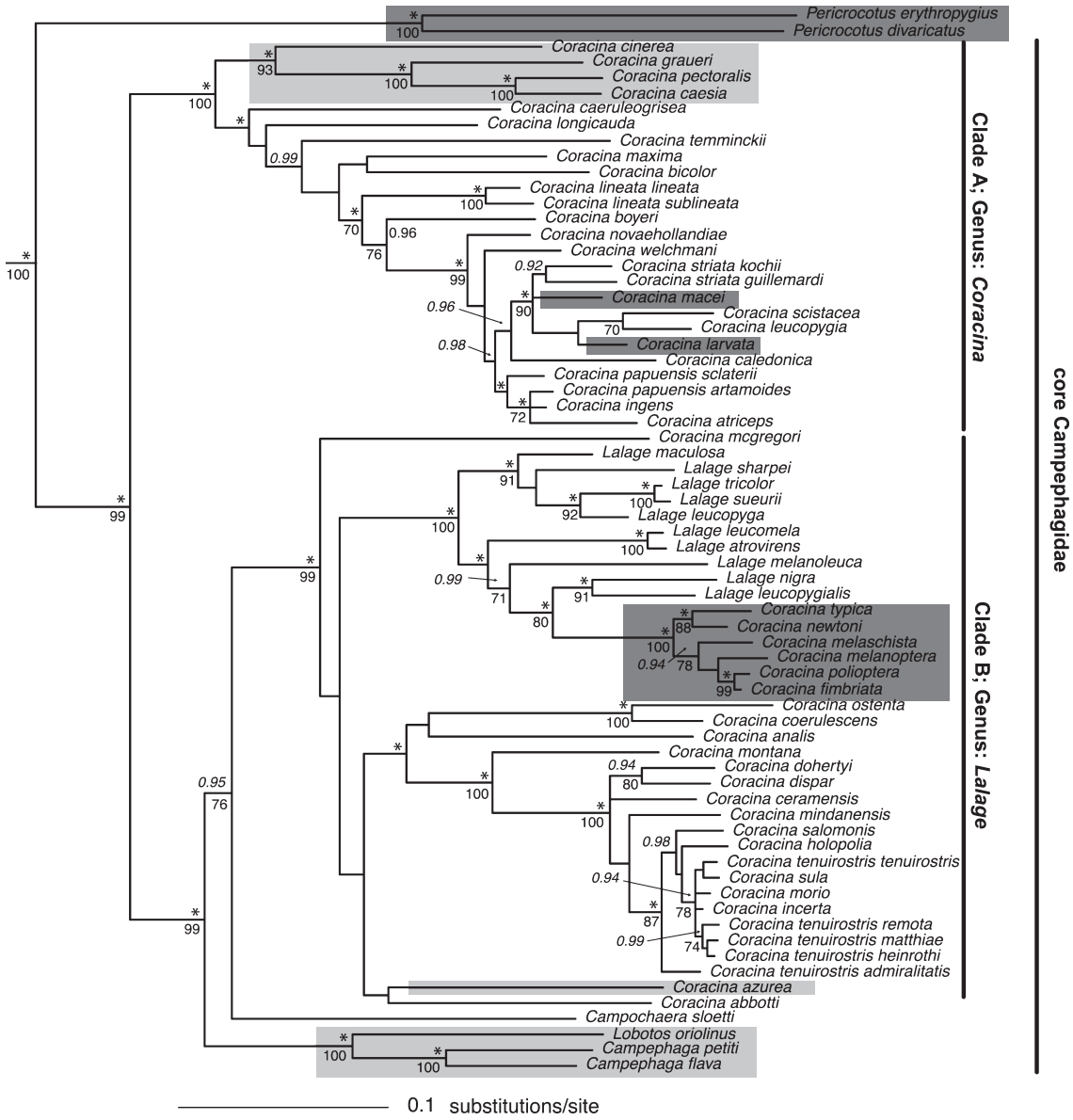
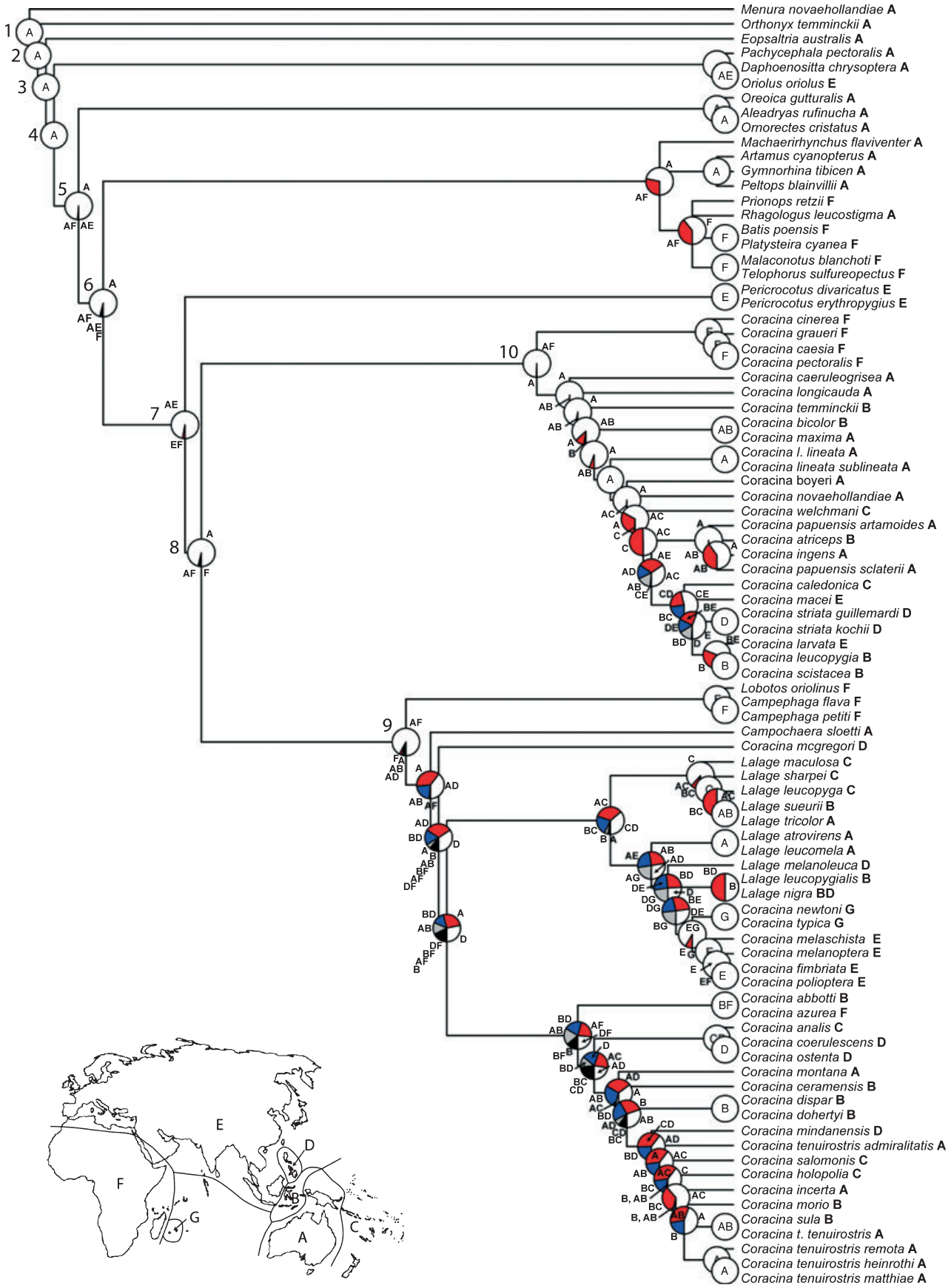


Figure 1 The 50% majority rule consensus tree of the core Campephagidae and close relatives obtained from the Bayesian analysis of the combined data set: glyceraldehyde-3-phosphodehydrogenase (GAPDH), ornithine decarboxylase (ODC), myoglobin intron-2 (Myo2), NADH dehydrogenase subunit 2 (ND2). Support values are indicated to the left of the nodes. Above the branch is the posterior probability (only values above 0.90 are shown, asterisks indicate posterior probabilities of 1.00). Below (or above to the right of) the branch is the maximum likelihood bootstrap value (only values above 70% are shown) from 500 pseudoreplicates. Terminal taxa distributed in Africa, light grey; terminal taxa distributed in Asia (and the Indian Ocean), dark grey. All other taxa are either Australo-Papuan, Wallacean, Philippine or Pacific in distribution.

Figure 2 A summary of the Bayesian dispersal–vicariance analysis (Bayes-DIVA) of the core Campephagidae and close relatives. The tree is a chronogram based on a 50% majority-rule consensus tree of a Bayesian Markov chain Monte Carlo (MCMC) analysis of a combined data set of mitochondrial [NADH dehydrogenase subunit 2, (ND2)] and nuclear [glyceraldehyde-3-phosphodehydrogenase (GAPDH), ornithine decarboxylase (ODC) and myoglobin intron-2 (Myo)] DNA sequences. Breeding region for each taxon, as delimited in the map, is given after each taxon name. Pie charts at internal nodes represent the marginal probabilities for each alternative ancestral area derived using DIVA while integrating over tree topologies using MCMC. These probabilities account for the phylogenetic uncertainty in the rest of the tree and the biogeographical uncertainty (multiple equally parsimonious reconstructions) at each node, conditional on this node occurring in a given sampled topology. In the pie charts, the first four areas with highest probability are coloured according to relative probability in the following order: white > red > blue > grey, and any remaining areas are collectively coded in black. Some basal nodes have been assigned a number, which is referred to in the Discussion. Biogeographical regions: A, Australia/New Guinea; B, Wallacea; C, The Pacific Archipelago; D, The Philippine Archipelago; E, Asia (including Sumatra, Java and Borneo); F, Africa; G, Mauritius/Réunion.



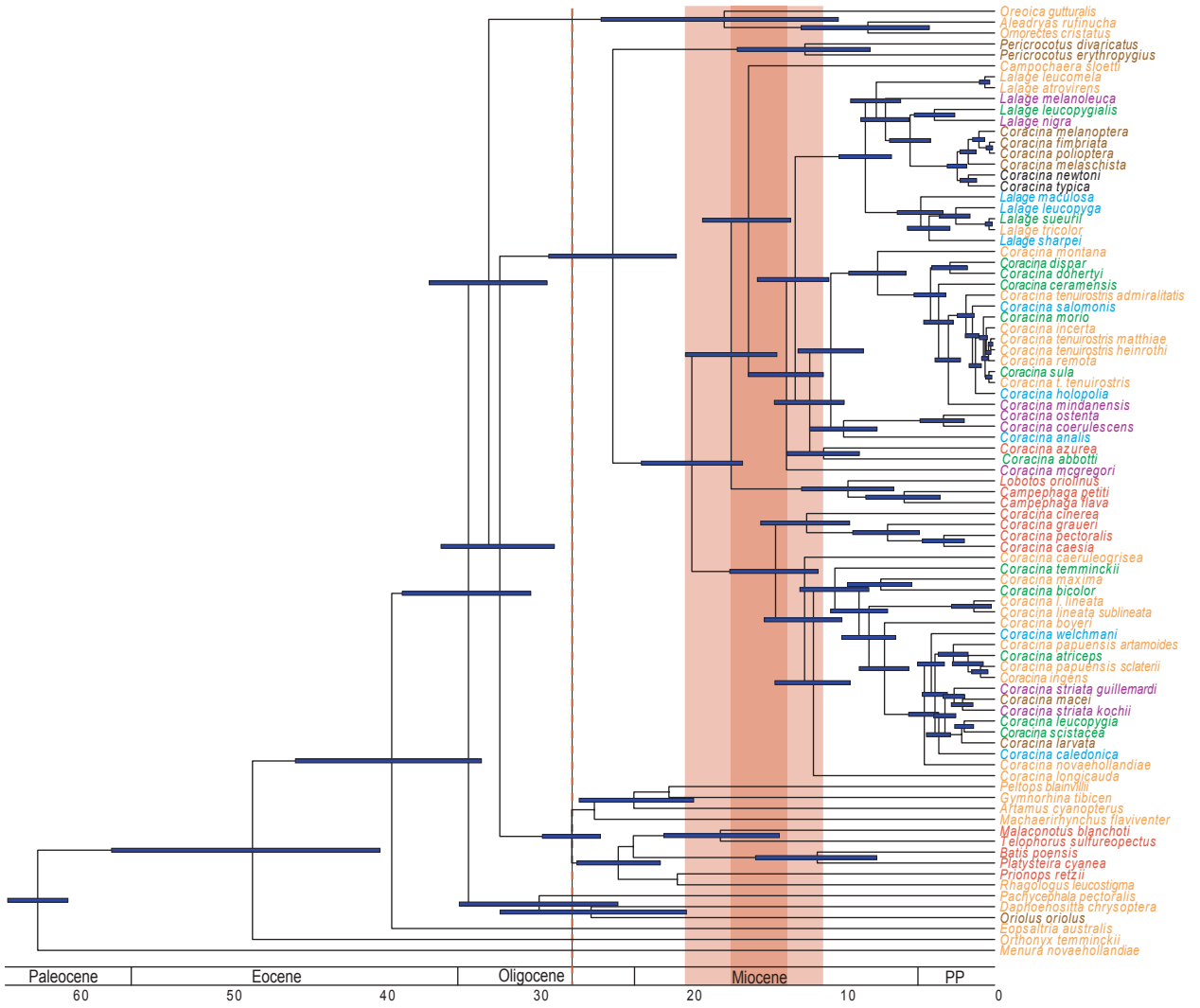


Figure 3 Chronogram of the core Campephagidae and close relatives based on the BEAST analysis. Blue bars represent 95% highest posterior density (HPD) intervals. Terminal taxa are coloured according to present distributions: yellow, Australia/New Guinea (including the Bismarck Archipelago); green, Wallacea; red, Africa; blue, Pacific Archipelago; purple, Philippine Archipelago; brown, Asia (including Sumatra, Java, Borneo); black, Mauritius and Réunion. The vertical red column indicates the time span when the three African clades dispersed from Australia to Africa; shaded red indicates 95% HPD intervals; red dotted line indicates putative dispersal between Australia and Africa in the Oligocene.

analyses, the relationship has no support and thus should be considered unresolved. Therefore, the split between *C. azurea* and any sister taxon is cautiously set to 13.5 Ma (95% HPD = 11–16 Ma). With these age estimates, it seems that the three dispersal events to Africa have taken place in a rather narrow time frame in the Miocene between 13.5 and 17 Ma (95% HPD = 11–20 Ma). Dispersal into mainland Asia, on the other hand, did not take place before the Pliocene.

DISCUSSION

Systematics and taxonomy

Our study presents the first robust phylogeny of the core Campephagidae (Campephagidae with the exclusion of *Pericrocotus*) including all genera, and lacks only a few species with restricted ranges (mainly on smaller islands in the archipelagos surrounding Australo-Papua). The missing island taxa are generally linked to taxa on larger nearby landmasses (Taylor, 2005). Therefore, we feel confident in recommending some preliminary taxonomic changes. Our study confirms the monophyly of the Campephagidae, with a core Campephagidae group consisting of the genera *Coracina*, *Lalage*, *Campephaga*, *Lobotos* and *Campochaera*. These genera, however, are not monophyletic. Two primary clades are apparent, as also noted by Fuchs *et al.* (2007) and Jønsson *et al.* (2008). One clade (A) comprises a subset of *Coracina* Vieillot, 1816 (including the type species for the genus, *Coracina papuensis*) and thus should maintain this name. Clade B contains species of two genera, *Lalage* and *Coracina*. The oldest name for this

assemblage is *Lalage* (*Lalage* Boie, 1826), and thus we propose that the whole clade be treated under the name *Lalage*. Whether or not the genus *Lobotos*, which is sister to the genus *Campephaga*, should be maintained as a separate genus, is debatable. Peters (1960) argued that there is little reason to maintain the genus *Lobotos* as it does not seem to differ substantially in morphology from *Campephaga*. However, mitochondrial ND2 sequence data differ by 11.62% between the genera, perhaps suggesting that genus status is valid. Based on the results of the present study, the family Campephagidae now contains five genera: *Pericrocotus*, *Coracina*, *Campephaga* (including *Lobotos*), *Campochaera* and *Lalage* (including several species previously assigned to *Coracina*) (Fig. 1).

Biogeography

The Bayes-DIVA analysis indicates that the origin of the basal clades of oscine passerine birds (represented here by *Menura* and *Orthonyx* nodes 1 and 2), Petroicidae (represented by *Eopsaltria* node 3), and the basal part of the core Corvoidea (represented by all other taxa outside Campephagidae nodes 4–6) is Australo-Papuan. The Campephagidae (node 7), including *Pericrocotus*, has an Australian/Asian origin, whereas the origin of the core Campephagidae (node 8) is Australo-Papuan. This could be interpreted in one of two ways: (1) members of the Campephagidae were historically distributed throughout the Australo-Papuan and Asian region and later retracted to Australo-Papua when the core Campephagidae started radiating, or (2) a *Pericrocotus* ancestor dispersed out of Australia and colonized Asia as the first dispersal event within this group. We argue that the latter is the most likely scenario, given that there are no other Asian species in the basal part of the core Campephagidae phylogeny. At the time when *Pericrocotus* diverged from the core Campephagidae some 25 Ma, there was still a substantial body of water between Australia and Asia, and it is more parsimonious to assume that a single proto-*Pericrocotus* colonized Asia (which is also supported by the Bayes-DIVA analysis) than to assume a historical range expansion followed by a range retraction of the whole Campephagidae. A molecular study of *Pericrocotus* unequivocally demonstrates that the radiation is centred in mainland Asia, from where dispersal took place in a south-eastwards direction to the Indonesian archipelago (Jønsson *et al.*, 2010b). This dispersal pattern supports the idea that *Pericrocotus* colonized Asia by long-distance dispersal rather than by island hopping from Australia across Wallacea.

African species occur in two distinct basal clades within the core Campephagidae. One clade contains *Campephaga* and *Lobotos*. Another clade contains four species: *Coracina caesia*, *C. pectoralis*, *C. graueri* and *C. cinerea*. *Coracina azurea* is difficult to place, but is linked with low support to *C. abbotti* of Sulawesi. As *C. azurea* is not closely related to other African taxa, it seems to constitute an independent colonization of Africa at a relatively early time in the evolution of the core Campephagidae. Thus, we find three colonizations of Africa, none of which appears to be closely linked to the two very distal clades of mainland Asian taxa. This indicates that the Campephagidae did not colonize Africa via Asia, unless one assumes extinction of Asian representatives from all three dispersing clades.

To sum up, we find, based on the phylogeny and the Bayes-DIVA analysis, that the Campephagidae arose in Australo-Papua, from where one early dispersal event of *Pericrocotus* colonized mainland Asia. Africa was colonized twice (perhaps three times) directly from Australia at around 14–20 Ma. Within the past 10 Myr, no cuckoo-shrike has colonized Africa. Rather, within this time frame, there have been a number of multi-directional dispersal events taking place from Australo-Papua to the Pacific Islands, the Philippines, Wallacea and mainland Asia. The Indian Ocean Islands of Réunion and Mauritius were among the most recently colonized islands, and were colonized from Asia rather than Africa during the Plio/Pleistocene.

Given that there is no evidence for the core Campephagidae having colonized Asia at an early point, we find little reason to suspect that cuckoo-shrikes colonized Africa via Asia, as this would require numerous extinction events. On the other hand, at the time of the 'African colonization' in the mid-Miocene, Australia had collided with Asia, providing a stepping-stone colonization pathway across Wallacea; and from the Oligocene to the mid-Miocene, large expanses of forest covered a continuous area from Southeast Asia to Africa, creating a dispersal corridor for forest-associated taxa (Janis, 1993). Parts of this region became significantly drier towards the end of the Miocene and caused parts of western Asia, the Arabian Peninsula and north-eastern Africa to become arid grassland and desert (Jacobs *et al.*, 1999). With these climatic and tectonic changes in mind, it seems by no means impossible that members of the core Campephagidae dispersed via islands and forested land masses from Australia to Africa, and that Asian members subsequently went extinct. However, it does seem difficult to explain that *Pericrocotus* successfully radiated and still has many extant members throughout Asia, whereas all members of the core Campephagidae that expanded in the Miocene went extinct.

A number of recent studies have demonstrated transoceanic dispersal as a possible mechanism to explain present disjunct distribution patterns of various groups of vertebrates (Yoder *et al.*, 2003; Heinicke *et al.*, 2007; Pereira *et al.*, 2007). However, the evolutionary link between Australo-Papua and Africa/Madagascar remains rather unusual, although it has been suggested for several angiosperm families (Baum *et al.*, 1998; Davis *et al.*, 2002; Mummenhoff *et al.*, 2004). We know of only few terrestrial avian examples for which a link between Australia and Africa has been suggested (Fuchs *et al.*, 2006; Jønsson & Fjeldså, 2006; Jønsson *et al.*, 2008; Wright *et al.*, 2008; Schweizer *et al.*, 2010). For the Psittaciformes (Wright *et al.*, 2008; Schweizer *et al.*, 2010) the authors reach somewhat different conclusions regarding dispersal. It seems that Psittaciformes is rather old, and that the link could be explained by vicariance events associated with the break-up of Gondwana and perhaps some dispersal events over relatively short

distances. Thus, the present study is the most substantiated avian example of long-distance ocean dispersal and colonization of Africa across the Indian Ocean from Australo-Papua.

Jønsson & Fjeldså (2006) have previously suggested that land plateaux in the southern Indian Ocean could have facilitated dispersal from Australia to Africa at around 45–50 Ma. However, by the Miocene these large land plateaux had subsided markedly (Coffin *et al.*, 2002; Wallace *et al.*, 2002). Although the Kerguelen Archipelago had several subaerial islands, it was far to the south and is unlikely to have aided birds crossing the Indian Ocean. Rather, it seems that cuckoo-shrikes dispersed directly across the Indian Ocean to Africa during two or three individual colonizations within a narrow time frame between 13.5 and 17 Ma.

The majority of cuckoo-shrike species are rather sedentary forest-associated species, and the few real migratory members inhabit high-latitude regions in continental Asia. However, the general lack of movements probably reflects the fact that the birds inhabit regions where environmental conditions vary little by season. Clearly, cuckoo-shrikes disperse well because they have colonized isolated oceanic islands in Micronesia, Melanesia and the Indian Ocean (Taylor, 2005). It seems that mobility is very plastic among birds, probably best exemplified by another avian family, Rallidae, whose members are generally thought of as poor flyers but nevertheless have colonized a multitude of remote islands and archipelagos across the globe (Taylor, 1996).

Although other avian studies in the Indian Ocean have demonstrated that transoceanic dispersal is important for colonizing islands (Warren *et al.*, 2003; Fuchs *et al.*, 2008), the present study infers the occurrence of transoceanic dispersal over an unusually large body of water (the Indian Ocean). A recent study of *Turdus* thrushes found evidence for direct dispersal from Africa to the Caribbean (Voelker *et al.*, 2009), lending further support to the idea that long-distance ocean dispersal may be an important biogeographical force.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 The 50% majority rule consensus tree of the core Campephagidae obtained from the Bayesian analysis of glyceraldehyde-3-phosphodehydrogenase (GAPDH).

Appendix S2 The 50% majority rule consensus tree of the core Campephagidae obtained from the Bayesian analysis of ornithine decarboxylase (ODC).

Appendix S3 The 50% majority rule consensus tree of the core Campephagidae obtained from the Bayesian analysis of myoglobin intron-2 (Myo2).

Appendix S4 The 50% majority rule consensus tree of the core Campephagidae obtained from the Bayesian analysis of NADH dehydrogenase subunit 2 (ND2).

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BIOSKETCHES

Knud A. Jønsson is a PhD student at the Zoological Museum, University of Copenhagen, Denmark. His main interests include the systematics and historical biogeography of passerine birds with a particular emphasis on the Indo-Pacific region.

Jon Fjeldså is a professor at the Zoological Museum, University of Copenhagen, Denmark. He has broad interests in the phylogeny and systematics of birds as well as a general interest in several other aspects of ornithology, ecology and conservation.

Author contributions: K.A.J. and J.F. conceived the ideas; K.A.J. and J.A.A.N. collected and analysed the data. All authors took part in the writing process.

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