Molecular Phylogenetics and Evolution 64 (2012) 93–105

Contents lists available at SciVerse ScienceDirect

Molecular Phylogenetics and Evolution

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

Molecular phylogeny of African bush-shrikes and allies: Tracing the biogeographic history of an explosive radiation of corvoid birds

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ARTICLE INFO

Article history:
Received 9 September 2011
Revised 9 March 2012
Accepted 13 March 2012
Available online 28 March 2012

Keywords:
Biogeography
Dispersal
Malaconotidea
Multi-locus phylogeny
Radiation

ABSTRACT

The Malaconotidea (e.g., butcherbirds, bush-shrikes, batises, vangas) represent an Old World assemblage of corvoid passerines that encompass many different foraging techniques (e.g., typical flycatchers, flycatcher-shrikes, canopy creepers, undergrowth skulkers). At present, relationships among the primary Malaconotidea clades are poorly resolved, a result that could either be attributed to a rapid accumulation of lineages over a short period of time (hard polytomy) or to an insufficient amount of data having been brought to bear on the problem (soft polytomy). Our objective was to resolve the phylogenetic relationships and biogeographic history of the Malaconotidea using DNA sequences gathered from 10 loci with different evolutionary properties. Given the range of substitution rates of molecular markers we sequenced (mitochondrial, sex-linked, autosomal), we also sought to explore the effect of altering the branch-length prior in Bayesian tree estimation analyses. We found that changing the branch-length priors had no major effect on topology, but clearly improved mixing of the chains for some loci. Our phylogenetic analyses clarified the relationships of several genera (e.g., *Pityriasis*, *Machaerirhynchus*) and provide for the first time strong support for a sister-group relationship between core platysteirids and core vangids. Our biogeographic reconstruction somewhat unexpectedly suggests that the large African radiation of malaconotids originated after a single over-water dispersal from Australasia around 45–33.7 mya, shedding new light on the origins of the Afrotropical avifauna.

1. Introduction

Biological radiations that result in the rapid accumulation of lineages over a short period of time present many challenges for phylogenetic reconstruction because lineage sorting of polymorphic alleles and introgression/hybridization among diverging lineages may obscure the link between gene trees and the species tree (Maddison, 1997; Buckley et al., 2006; Maddison and Knowles, 2006; Carstens and Knowles, 2007; Knowles and Carstens, 2007; Liu and Pearl, 2007). Indeed, under certain combinations of ancestral population sizes and time between speciation events, the most likely gene tree may not correspond to the species tree (Degnan and Rosenberg, 2006; Kubatko and Degnan, 2007; Rosenberg and Tao, 2008). Such effects are expected in adaptive radiations, where ecological and phenotypic diversity appear within a rapidly diversifying lineage (e.g., Darwin's finches or cichlid fishes); they may also occur in non-adaptive radiations, where diversification is not directly related to ecological differentiation (e.g., multiple vicariant events over a short period of time due to climatic or tectonic changes, or as a consequence of geographical expansion).

The Malaconotidea (*sensu* Cracraft et al., 2004, 7 families, 40 genera and 134 species; Table 1) represents an Old World assemblage of corvoid passerines with their center of diversity in Africa. This clade includes birds that forage using several different techniques: typical flycatchers (e.g., *Batis*), flycatcher-shrikes (e.g., *Megabyas*), canopy creepers (e.g., *Malaconotus*), undergrowth skulkers (e.g., *Laniarius*) or foliage-gleaners (e.g., *Aegithina*, *Tephrodornis*). Recent molecular studies have indicated that some taxa included in traditionally recognized families (e.g. Malaconotidae, Platysteiridae) have been misplaced (Barker et al., 2004; Fuchs et al., 2004, 2006b; Moyle et al., 2006; Njabo et al., 2008). For

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http://dx.doi.org/10.1016/j.ympev.2012.03.007

Table 1
Taxonomic diversity (following Dickinson 2003) within each of the primary Malaconotidea lineages.

Familiy	Distribution	Genera/species	Genera/species sampled
Malaconotidae	Africa	10/52	10/18
Platysteiridae	Africa	6/28	6/14
Vangidae	Madagascar	15/22	3/3
Aegithinidae	Indo-Malaya	1/4	1/1
Pytiriasidae	Indo-Malaya	1/1	1/1
Cracticidae	Australasia	4/13	4/4
Artamidae	Australasia/Indo-Malaya	1/10	1/3
Philentoma (ex Monarchidae)	Indo-Malaya	1/2	1/2
Tephrodornis (ex Campephagidae)	Indo-Malaya	1/2	1/2
Rhagologus	Australasia	1/1	1/1
Peltops	Australasia	1/2	1/1
Machaerirhynchus (ex Monarchidae)	Australasia	1/2	1/2

instance, analyses of mitochondrial and nuclear sequence data have demonstrated that the genera *Bias*, *Megabyas* (*ex* Platysteiridae) and *Prionops* (*ex* Malaconotidae), as well as three Indo-Malayan genera, *Philentoma* (*ex* Monarchidae), *Hemipus* (*ex* Campephagidae), and *Tephrodornis* (*ex* Campephagidae) cluster with the Malagasy Vangidae and together form a third and previously unrecognized assemblage ('core Vangids' sensu Fuchs et al., 2004). Relationships among these three mainly African clades (hereafter 'core Malaconotids', 'core Platysteirids' and 'core Vangids'), as well as their relationships with the Indo-Malayan Aegithinidae and Pityriasidae, and Australasian Cracticidae and Artamidae, remain less well resolved. Indeed, almost all possible topologies have been recovered concerning the relationships among these clades (Sibley and Ahlquist, 1990; Barker et al., 2004; Fuchs et al., 2004, 2006b; Moyle et al., 2006; Reddy et al., 2012).

The relationships among the six primary clades (core Malaconotids, Platysteirids, Vangids, Aegithinidae, Pityriasidae and Artamidae–Cracticidae) recovered in previous molecular analyses are characterized by low support values and/or small branch-lengths, indicative of either the occurrence of a 'soft polytomy' or a burst of diversification. The latter scenario is expected to produce two results: (1) geographically isolated lineages (non-adaptive radiation) in Africa, Indo-Malaya and Australasia (sensu Newton 2003; Malesia and Australia); (2) three primary clades with very different foraging techniques and divergent bill morphologies in Africa (adaptive radiation). Corvoid passerines likely originated in the proto-Papuan archipelago, and probably were strong dispersers (Jønsson et al., 2011). The exact pattern of dispersal within Malaconotidea remains uncertain, although some data suggest a gradual colonization of the Afrotropics from Australasia via Indo-Malaya (Fuchs et al., 2006b). The uncertain topology at the base of the Malaconotidea tree (Fuchs et al., 2006b; Moyle et al., 2006), and the recent establishment of additional genera (e.g. *Pityriasis*, *Machaerirhynchus*, *Peltops*, *Rhagologus*) with a Malaconotidea affinity, prompt the need for additional studies with exhaustive taxonomic sampling and increased sampling of loci.

The Malaconotidea and allies, with several potentially nested radiations, constitute an ideal case study with which to assess the impact of larger sequence data sets on node robustness (i.e., to distinguish between 'soft' and 'hard' polytomies in some clades) and ascertain the impact of newly developed species tree reconstruction methods on topology. The addition of new data will also help to resolve the biogeographic history of this clade and determine whether there was a gradual expansion over land, or multiple long-distance oceanic dispersal events. To address these questions, we analyzed DNA sequence data from 10 loci for 49 Malaconotidea taxa.

2. Material and methods

2.1. Taxonomic sampling

We obtained DNA sequences for 54 species of corvoid passerines (Table 2), representing all genera included in Malaconotidea (Aegithinidae, Artamidae, Cracticidae, Malaconotidae, Platysteiridae, Pityriasidae, Vangidae) by Cracraft et al. (2004), with the exception of a most genera in the monophyletic Malagasy Vangidae (Reddy et al., 2012; Jønsson et al., 2012 three genera were included in the present study). We also included the Australasian genera *Machaerirhynchus, Peltops* and *Rhagologus* that were recently shown to be part of the Malaconotidea (Norman et al., 2009; Jønsson et al., 2011). As outgroups, we used sequences from representatives of the major corvoid linages (e.g. Barker et al., 2004; Fuchs et al., 2004, 2007): *Lanius collaris* (Laniidae), *Corvus corone* (Corvidae), *Terpsiphone viridis* (Monarchidae) and *Coracina melaschista* and *Campephaga flava* (Campephagidae).

2.2. Laboratory procedure and sequence alignment

DNA was isolated using a CTAB-based extraction (Winnepenninckx et al., 1993) or by using Qiagen DNeasy extraction kits (Qiagen Inc., Hilden, Germany). We sequenced 10 loci that were mapped to at least seven distinct chromosomes of the chicken and zebra finch genomes: two mitochondrial genes, one Z-linked locus, and seven autosomal loci (five introns and two exons) (Table 3). Amplification of target sequences was performed using the polymerase chain reaction with the primer pairs identified in Table 2. PCR products were purified using shrimp phosphatase and exonuclease (exoSAPit, Amersham Pharmacia). We sequenced the purified PCR products using Big Dye Terminator 3.1 sequencing reaction mix (Applied Biosystems, Foster, CA). Cycle-sequencing products were visualized on an AB 3730 automated sequencer. New DNA sequences generated for this study were deposited in GenBank (accession numbers JQ744638-JQ744995, JQ754306). Since we used toe-pad samples as a DNA source for some taxa, we were unable to obtain sequences from some loci for certain taxa (e.g., *Machaerirhynchus*), due to the degraded nature of the DNA.

Multiple alignments were generated using Seal v2.0AL (Sequence Alignment Editor Version 1.0 alpha 1; Rambaut, 2007). Insertion–deletion events were treated as missing data. We used Sequencher 4.1 (Gene Codes Corporation) to assemble contigs from raw chromatograms and to ensure that the protein-coding gene sequences (RAG1, mos, ATP6, and ND2) had no stop codons or indels. We treated allelic polymorphisms in the nuclear loci using the appropriate IUPAC codes. The total aligned data set was 7230 base pairs (bp).

Table 2
List of taxa studied (following Dickinson 2003), tissue or voucher numbers and GenBank accession numbers.

Species	Tissue/voucher	ND2	ATP6	MB	FGB	GAPDH	mos	TGFb2	RAG1	BRM15	ODC
Aegithina tiphia	AMNH PRS691 (DOT9616)*	AY816232	JQ744677	AY816225	JQ744717	DQ406650	AY056905	JQ744818	AY799819	JQ744928	JQ744978
Artamus cinereus	ANSP10628*	JQ744638	JQ744688	JQ744693	JQ744724	JQ744729	JQ744787	JQ744841	JQ744887	JQ744939	JQ744990
Artamus cyanoupterus	ZMUC 135911* (TP)	DQ096728	No sequence	DQ406636	No sequence	DQ406661	No sequence	No sequence	AY799819	JQ744921	No sequence
Artamus maximus	NRM 569599* (TP)	No sequence	No sequence	JQ744694	JQ744708	JQ744730	JQ744762	JQ744793	No sequence	JQ744891	JQ744944
Batis capensis	MVZ RCKB W50910	DQ662008	JQ744671	JQ744695	JQ744713	JQ744731, JQ744732	JQ744779	JQ744828	JQ744875	JQ744920	JQ744972
Batis diops	FMNH 355976/ZMUC123048	JQ744639	JQ744669	JQ744696	JQ744712	JQ744733, JQ744734	JQ744775	JQ744832	JQ744870	JQ744916	JQ744986
Batis molitor	ZMUC123485/ZMUC121747	JQ744640	JQ744672	JQ744697	No sequence	JQ744735	JQ744783	JQ744846	JQ744877	JQ744934	JQ744984
Batis poensis occulta	MNHN 1998-783*	AY529941	JQ744663	AY529907	AY529974	DQ406665	EF052698	JQ744835	JQ744865	JQ744910	JQ744962
Batis pririt	MNHN 8-99	JQ744641	JQ744668	JQ744698	JQ744711	JQ744736	JQ744774	JQ744831	JQ744869	JQ744915	JQ744968
Batis soror	ZMUC 122568	DQ602086	JQ744684	JQ744699	No sequence	JQ744737	JQ744791	JQ744845	No sequence	JQ744935	JQ744985
Bias musicus	MNHN 03-23	AY529942	JQ744665	AY529908	AY529975	DQ406646	EF052699	JQ744808	JQ744867	JQ744912	JQ744964
Bocagia minuta	ZMUC 128533*/ZMUC 128785*	AY529943	JQ744658	AY529909	JQ744710	JQ744738	JQ744769	JQ744801	JQ744860	JQ744903	JQ744955
Campephaga flava	MVZ RCKB613	AY529944	JQ744682	DQ125949	AY529977	DQ406639	EF052700	JQ744825, JQ744826	JQ744883	JQ744909	JQ744961
Chlorophoneus dohertyi	FMNH 358005*	AY529945	JQ744669	AY529910	AY529978	DQ406644	JQ744777	JQ744812	JQ744872	JQ744918	JQ744970
Chlorophoneus nigrifrons	ZMUC 120151	AY529946	JQ744653	AY529911	AY529979	JQ744739, JQ744740	JQ744764	JQ744797	JQ744854	JQ744897	JQ744949
Chlorophoneus sulfureopectus	MNHN CG 1998-823*	AY529947	JQ744648	AY529912	AY529980	DQ406648	EF052701	JQ744795	JQ744848	JQ744892	GQ369669
Coracina melaschista	MNHN 06-69	AY529948	JQ744667	AY529913	AY529981	EF052807	EF052702	JQ744810	JQ744868	JQ744914	JQ744967
Corvus corone	MNHN CG 1995-41*	AY529949	HQ996673	AY529914	AY529982	DQ406663	EF052706	HQ996879	JQ744874	HQ996959	FJ358080
Cracticus nigrogularis	ANSP 11075*	JQ744642	JQ744691	JQ744700	JQ744727	JQ744741	JQ744790	JQ744844	JQ744890	JQ744942	JQ744993
Cyanolanius madagascarinus	MNHN E117	AY529950	JQ744681	AY529915	AY529983	DQ406649	EF052709	JQ744824	No sequence	JQ744933	No sequence
Dryoscopus cubla	ZMUC 116780	AY529952	JQ744656	AY529917	AY529985	JQ744742	JQ744767	JQ744802	JQ744858	JQ744901	JQ744953
Dryoscopus gambensis	ZMUC 124320/ZMUC 124413	AY529953	JQ744657	AY529918	AY529986	DQ406664	JQ744768	JQ744803	JQ744859	JQ744902	JQ744954
Dyaphorophyia castanea	MNHN 02-23	JQ744995	JQ744649	JQ744701, JQ744702	JQ744709	JQ744743, JQ744744	JQ744763	JQ744829	JQ744850	JQ744893	JQ744945
Dyaphorophyia chalybea	MNHN CG 1998-779*/MNHN 03-19	AY529954	JQ744664	AY529919	AY529987	DQ406666	JQ744773	JQ744836, JQ744837	JQ744866	JQ744911	JQ744963
Dyaprophyia jamesoni	FMNH 391788*	JQ744643	JQ744686	JQ744703	JQ744723	JQ744745, JQ744746	JQ744785	JQ744839	JQ744885	JQ744937	JQ744988
Gymnorhina tibicen	ANSP 10854*	JQ744644	JQ744690	JQ744704	JQ744726	JQ744747	JQ744789	JQ744843	JQ744889	JQ744941	JQ744992
Hemipus picatus	MNHN 33-6A (JF109, DV)	DQ411309	JQ744674	DQ406637	JQ744714	DQ406647	EF052710	JQ744815	JQ744879	JQ744922	JQ744973
Laniarius aethopicus	FMNH 356738*	AY529955	EU554464	AY529920	AY529988	JQ744748, JQ744749	JQ744776	JQ744811	JQ744871	JQ744917	JQ744969
Laniarius barbarus	ZMUC 116792	AY529956	JQ744654	AY529921	AY529989	DQ406656	EF052705	JQ744798	JQ744855	JQ744898	JQ744950
Laniarius funebris	ZMUC 123466/ZMUC 124175	AY529957	JQ744655	AY529922	AY529990	JQ744750	JQ744765	JQ744799	JQ744856	JQ744899	JQ744951
Laniarius luehderi	ZMUC 119044	AY529958	EU554461	AY529923	AY529991	JQ744751	JQ744766	JQ744800	JQ744857	JQ744900	JQ744952
Lanioturdus torquatus	US001	AY529959	JQ744675	AY529924	AY529992	JQ744752	JQ744780	JQ744833, JQ744834	AY799819	JQ744923	JQ744974
Lanius collaris	MNHN 02-26	AY529960	HQ996672	AY529925	AY529993	DQ406662	EF052707	HQ996837	JQ744849	HQ996907	FJ358081
Machaerirhynchus nigripectus	NRM 543672* (TP)	DQ084072	No sequence	FJ821090	JQ744715	JQ744753	JQ744781	JQ744816	No sequence	JQ744925	JQ744975
Malaconotus blanchoti	ZMUC 116824/ZMUC 122549	AY529961	JQ744652	AY529926	AY529994	DQ406651	EF052711	JQ744796	JQ744853	JQ744896	JQ744948
Megabyas flammulatus	MNHN 1968-1160* (TP)	A529962	JQ744680	AY529927	AY529995	DQ406652	EF052712	JQ744822	JQ744882	JQ744931	JQ744981
Nilaus afer	FMNH uncatalogued	AY529963	EU554446	AY529928	AY529996	DQ406638	JQ744778	JQ744813, JQ744814	JQ744873	JQ744919	JQ744971
Peltops blainvillii		No sequence	No sequence	FJ821099	No sequence	No sequence	No sequence	No sequence	No sequence	No sequence	No sequence

(*continued on next page*)

Table 2 (*continued*)

Species	Tissue/voucher	ND2	ATP6	MB	FGB	GAPDH	mos	TGFb2	RAG1	BRM15	ODC
Philentoma pyrhoptera	LSUMNS B-38572*	AY816231	JQ744678	AY816224	JQ744718, JQ744719	DQ406668	EF052716	JQ744819	DQ376525	JQ744929	JQ744979
Philentoma velata	LSUMNS B-38542*	AY816228	JQ744679	AY816221	JQ744720	DQ406667	JQ744782	JQ744820, JQ744821	JQ744881	JQ744930	JQ744980
Pityriasis gymnocephala	NRM 569565* (TP)/ LSUMNS B-50309*	JQ744646	JQ744673	JQ744706	JQ744721	JQ744756	JQ744792	JQ744823	DQ376524	JQ744932	JQ744982
Platysteira cyanea	MNHN 02-22	AY529965	JQ744650	AY529930	AY529998	DQ406658	EF052717	JQ744830	JQ744851	JQ744894	JQ744946
Platysteira peltata	FMNH439393*	JQ744645	JQ744685	JQ744705	JQ744722	JQ744754, JQ744755	JQ744784	JQ744838	JQ744884	JQ744936	JQ744987
Prionops retzii	ZMUC 117524/ZMUC 119500	AY529966	JQ744661	AY529931	AY529999	DQ406654	EF052718	JQ744806	JQ744863	JQ744906	JQ744959
Prionops scopifrons	ZMUC 117528/ZMUC 117537	AY529967	JQ744662	AY529932	AY530000	DQ406653	JQ744771	JQ744807	JQ744864	JQ744907	JQ744960
Pseudobias wardi	FMNH 356702*	AY529968	JQ744666	AY529933	AY530001	DQ406642	EF052704	JQ744809	DQ376530	JQ744913	JQ744965, JQ744966
Rhagologus leucostigma	CAS AM1099	EF592323	JQ744692	EU273416	JQ744728	JQ744757, JQ744758	No sequence	JQ744847	JQ744878	JQ744943	JQ744994
Rhodophoneus cruentus	US002	AY529970	JQ744687	AY529935	AY530003		JQ744786	JQ744840	JQ744886	JQ744938	JQ744989
Strepera versicolor	ANSP 10670*	JQ744647	JQ744689	JQ744707	JQ744725	JQ744759	JQ744788	JQ744842	JQ744888	JQ744940	JQ744991
Tchagra australis	ZMUC 116831/ZMUC 124437	AY529971	JQ744659	AY529936	AY530004	JQ744760, JQ744761	JQ744770	JQ744804	JQ744861	JQ744904	JQ744956
Tchagra senegalus	ZMUC 116834	AY529972	JQ744660	AY529937	AY530005	DQ406657	EF052719	JQ744805	JQ744862	JQ744905	JQ744957, JQ744958
Telophorus zeylonus	FMNH390107*/MVZ JF1076 (DV)/MVZ RCKB1566	AY529973	JQ744683	AY529938	AY530006	DQ406655	JQ744772	JQ744827	JQ744876	JQ744908	JQ744983
Tephrodornis pondicerianus	USNM B-2140*	EF052689	JQ744676	EF052762	JQ744716	EF052751	EF052742	JQ744817	JQ744880	JQ744926	JQ744976
Tephrodornis virgatus	MNHN CG 1989-76* (TP)	AY816226	No sequence	AY816220	No sequence	DQ406643	EF052703	No sequence	DQ356526	JQ744924	No sequence
Terpsiphone viridis	MNHN 02-20	DQ125996	JQ744651	AY529939	AY530007	DQ406641	EF052708	JQ744794	JQ744852	JQ744895	JQ744947
Vanga curvirostris	MNHN CH 364A*	AY701508	No sequence	AY701505	No sequence	DQ406640	AY056972	No sequence	AY057040	JQ744927	JQ744977

Abbreviations: AMNH, American Museum of Natural History, New York, USA; ANSP, Academy of National Sciences, Philadelphia; FMNH, Field Museum of Natural History, Chicago, USA; LSUMNS, Louisiana State University Museum of Natural Sciences, Baton-Rouge, USA; MNHN, Museum National d'Histoire Naturelle, Paris, France; MVZ, Museum of Vertebrate Zoology, Berkeley, USA; NRM, Swedish Museum of Natural History, Stockholm, ZMUC, Zoological Museum University of Copenhagen, Denmark.

* Tissue with voucher specimens. DV indicate that a digital voucher is available. TP refers to species for which DNA was obtained from toe-pads.

Table 3
List of loci sequenced, location on the *Gallus gallus* (Chicken) and *Taeniopyga guttata* (Zebra Finch) genomes and primer sequences.

Locus	Genome and location	Primers	References
ND2	Mitochondrion	L5219: CCCATACCCCGAAAATGATG, H6313: CTCTTATTTAAGGCTTTGAAGGC	Sorenson et al. (1999)
ATP6	Mitochondrion	L9245: CCTGAACCTGACCATGAAC, H9947: CATGGGCTGGGGTCRACTATGTG	Eberhard and Bermingham (2004)
GAPDH intron-11 (GAPDH)	Nuclear: chromosome 1	G3P14b: AAGTCCACAACACGGTTGCTGTA, G3PintL1: GAACGACCATTTTGTCAAGCTGGTT, G3P13:TCCACCTTTGATGCGGGTGCTGGCAT	Fjeldså et al. (2003)
Myoglobin intron-2 (MB)	Nuclear: chromosome 1	Myo2: GCCACCAAGCACAAGATCCC, Myo3F: GCAAGGACCTTGATAATGACTT	Slade et al. (1993), Heslewood et al. (1998)
Cmos (*mos*)	Nuclear: chromosome 2	944F: CCTGGTGCTCCATCGACTGG, 1550R: GCAAATGAGTAGATGTCTGCT	Cooper and Penny (1997)
TGFB2 intron-5 (TGFb2)	Nuclear: chromosome 3	TGF5: GAAGCGTGCTCTAGATGCTG, TGF6: AGGCAGCAATTATCCTGCAC	Primmer et al. (2002)
ODC gene region introns 6 to 8 (ODC)	Nuclear: chromosome 3	OD6: GACTCCAAAGCAGTTTGTCGTCTCAGTGT, OD8r: CTTCAGAGCCAGGGAAGCCACCACCAAT	Primmer et al. (2002)
Beta-Fibrinogen intron-5 (FGB)	Nuclear: chromosome 4	Fib5: CGCCATACAGAGTATACTGTGACAT, Fib6: GCCATCCTGGCGATTCTGAA	Fuchs et al. (2004)
RAG1 (RAG1)	Nuclear: chromosome 5	R13: TCTGAATGGAAATTCAAGCTGTT R16: GTTTGGGGAGTGGGGTTGCCA R15: TCGCTAAGGTTTTCAAGATTGA R18: GATGCTGCCTCGGTCGGCCACCTT	Groth and Barrowclough (1999)
BRM intron-15 (BRM)	Nuclear: chromosome Z	BRM15F: AGCACCTTTGAACAGTGGTT, BRM15R: TACTTTATGGAGACGACGGA	Goodwin (1997)

2.3. Model selection

We determined the models for our different analytical partitions using the decision-theoretic (DT) approach implemented in DT_Modsel (Minin et al., 2003). We also compared the model selected using this criterion with the ones selected under the AIC. Ripplinger and Sullivan (2008) demonstrated that even if the topologies are not strictly identical when using the models selected under the different criteria (AIC and DT), the topologies are usually not statistically different from each other as the differences involve poorly supported nodes. When the best-fit model selected by DT_Modsel was not implemented in MrBayes (seven cases), we used the nearest and most parameter rich model for subsequent analyses. Although, over-parameterization may lead to non-identifiable parameters (Huelsenbeck and Rannala, 2004; Lemmon and Moriarty, 2004), its effect on modelling the magnitude of evolutionary changes and phylogenetic reconstruction is less dramatic than when using under-parameterized models (Gaut and Lewis, 1995; Sullivan and Swofford, 2001).

2.4. Phylogenetic analyses

Molecular phylogenies were estimated using Maximum Likelihood and Bayesian inference, as implemented in RAxML v7.0.4 (Stamatakis, 2006; Stamatakis et al., 2008, http://phylobench.vital-it.ch/raxml-bb/), MrBayes 3.1 (Huelsenbeck and Ronquist, 2003; Ronquist and Huelsenbeck, 2003) and Beast v.1.6.0 (Drummond et al., 2002, 2006; Drummond and Rambaut, 2007). Maximum likelihood and 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 among partitions (Ronquist and Huelsenbeck, 2003; Nylander et al., 2004). For each data set, two independent ML analyses were performed and log-likelihood values were compared to help ensure that convergence had taken place. For Bayesian analyses, four Metropolis-coupled MCMC chains (one cold and three heated) were run for 5–30 million iterations with trees sampled every 1000 iterations. The number of iterations discarded before posterior probabilities varied among analyses. We used default priors for all parameters with the exception of the branch-length prior. For the later we used exponential means of 10, 50, 100, 150, 200 and 500 because this prior has some effect on mixing and convergence (Brown et al., 2010; Marshall, 2010). We checked that the potential scale reduction factor (PSRF) approached 1.0 for all parameters and that the average standard deviation of split frequencies converged towards zero. We also used Tracer v1.5 (Rambaut and Drummond, 2007) to ascertain that our sampling of the posterior distribution had reached a sufficient effective sample size (ESS).

2.5. Partitioning strategy

The appropriateness of partitioning the data set (e.g. protein coding genes by codon position) was determined using the Bayes factor (B_F) (Nylander et al., 2004; Brown and Lemmon, 2007) as implemented in Tracer v1.5 (Rambaut and Drummond, 2007). A value greater than 4.6 for $\ln B_F$ was considered as strong evidence against the simpler model (Jeffreys, 1961).

2.6. Clock-like behavior

We compared the likelihood of the posterior distribution of trees assuming a strict clock with the likelihood of the posterior distribution of a tree assuming an uncorrelated lognormal clock using the Bayes factor. We arbitrarily set the basal divergence time of the Malaconotidea to 10 time units and used the best-fit nucleotide substitution model for the analyses. Analyses were run in Beast v1.6.0 (Drummond et al., 2002, 2006; Drummond and Rambaut, 2007) for 5 million iterations with trees sampled every 1000 iterations.

2.7. Species tree approaches

Methodologies in parsimony (Page and Charleston, 1997), likelihood (Maddison, 1997; Maddison and Knowles, 2006; Kubatko et al., 2009) and a Bayesian framework (Liu and Pearl, 2007; Liu et al., 2008; Kubatko et al., 2009; Heled and Drummond, 2010) have been developed to better accommodate the stochasticity of lineage sorting for phylogenetic reconstruction. We here used three species tree methods: *Beast (Heled and Drummond, 2010), Best 2.2 (Liu et al., 2008) and STEM v1.1 (Kubatko et al., 2009).

Table 4
Properties of each locus analyzed in the present study.

	ND2	ATP6	MB	GAPDH	mos	TGFb2	ODC	FGB	RAG1	BRM
Number of base pairs	1041	684	750	406	605	626	700	1011	1034	373
Model	GTR + Γ + I	GTR + Γ + I	K80 + Γ	K81uf + I	TrNef + Γ + I	TrNef + Γ	TrN + Γ	HKY + Γ	HKY + Γ	HKY + Γ
Clock model	Lognormal	Clock	Clock	Clock	Clock	Clock	Clock	Clock	Lognormal	Clock
Brlens prior	10	10	50	100	150	100	100	100	100	100
BI harmonic	21647.97	11653.95	4245.98	2647.36	2828.98	4223.74	3765.09	4644.32	4696.97	2554.12
BI partitioned harmonic	21144.56*	11210.59*	NA	NA	2727.49*	NA	NA	NA	4648.03*	NA

* Partitioning strategy that was supported by the Bayes factor.

STEM uses a coalescent model to estimate a ML species tree using gene trees for multiple independent loci (Kubatko et al., 2009). To obtain the ultrametric trees, we used Beast v.1.6.0 (Drummond et al., 2002, 2006; Drummond and Rambaut, 2007). We assigned the best fitting model, as estimated by DT_Modsel, to each of the nine loci (mitochondrial genes were considered a single unit). We assumed a Yule Tree prior, and an Uncorrelated Lognormal distribution for the molecular clock model for all loci (Drummond et al., 2006). We used default prior distributions for all other parameters and ran MCMC chains for 10 million generations. The program TreeAnnotator v.1.6.0 (Drummond and Rambaut, 2007) was used to create a single summary tree for each locus, and these trees were used as the input for STEM. Relative rates were based on the comparison of the mean rate output from Beast v.1.6.0. We used different prior values for the theta parameter (from 0.1 to 0.001) and checked for differences in topology.

We also used the Bayesian phylogenetic analyses under the coalescence model implemented in Best 2.2 (Liu et al., 2008). The chain was run between 100 million and 500 million iterations and we sampled every 2000 trees. The log likelihood was used to monitor the convergence of the algorithm. The species trees sampled from the Markov chain before the log-likelihood reached stationarity were discarded as burn-in. We evaluated several values for the prior distribution of population sizes (Leaché, 2009).

We also estimated the species tree using *Beast (Drummond et al., 2006; Drummond and Rambaut, 2007; Heled and Drummond, 2010). We assumed an the best fit molecular clock model for all loci and used the best-fit model for each partition, as determined with DT_Modsel; each locus was specified with its own model and clock rate. For Best 2.2 and *Beast, we ran the chains for 100 and 500 million iterations.

For all species tree analyses, we only used species for which sequence data was available for all loci ($n = 46$).

2.8. Biogeographic analyses

We used the maximum likelihood method implemented in Lagrange (Ree et al., 2005; Ree and Smith, 2008) to reconstruct the biogeographic history of the Malaconotidea. In Lagrange 2.0, transitions between discrete states (ranges) along phylogenetic branches are modeled as a function of time, thus enabling maximum likelihood estimation of the ancestral states at cladogeneic events. The program Lagrange finds the most-likely ancestral areas at a node and the split of the areas in the two descendant lineages, and also calculates the probabilities of these most-likely areas at each node (Ree and Smith, 2008). We defined four areas for the analyses: Afrotropics, Indo-Malaya, Australasia and Madagascar, and used the Maximum Clade Credibility tree from the Beast concatenated analyses. We set the root age at 45 million years (Barker et al., 2004; Fuchs et al., 2006b) or 35 million years (Jønsson et al., 2011). We performed analyses assuming three models of dispersion across biogeographic regions: (1) a one rate model as direct dispersals across all these regions have been empirically suggested; (2) a two rate model with the probability of direct dispersal between Australasia and Africa being half that of a dispersal event from Australasia to Indo-Malayan and Madagascar; and (3) a two rate model with the probability of direct dispersal between Australasia and Africa/Madagascar being half that of a dispersal event from Australasia to Indo-Malaya. The latter two models differ in whether Madagascar could be considered a stepping-stone for dispersal from Australasia to Africa. All matrices were considered symmetric, and outgroups were coded as of Australasian origin, reflecting the origin of the Corvoidea radiation (Jønsson et al., 2011).

3. Results

3.1. Model selection

The DT approach selected a simpler model than the AIC in 13 of the 22 different gene partitions (59%; Table 4), exactly the same model in eight (36%), and a different model but with the same number of parameters in one (4.5%). The tendency of DT to select simpler models than the AIC has been reported previously (Abdo et al., 2005; Minin et al., 2003; Ripplinger and Sullivan, 2008).

3.2. Effect of the branch-length prior

Altering the branch-length prior had a very strong effect on the likelihood scores, with overall tree length getting shorter as the prior distribution centered on shorter branch-lengths. The default value in MrBayes (0.1), implying relatively long branches, was favoured for mitochondrial loci. In contrast, a branch-length prior of 0.01 (exponential mean 100) was strongly favoured for all nuclear loci, offering a clear improvement in likelihood score. Under an extremely short branch-length prior (exponential mean 500), the likelihood of the tree was worse than with the default prior value. Interestingly though, topological arrangements and posterior probability values were usually not affected by the branch-length prior used. Exceptions involved nodes recovered with posterior probabilities of 0.51–0.55, which were sometimes in polytomy when altering the branch-length prior. For example the African clade plus *Pityriasis* was monophyletic in the FGB locus with exponential mean of 100, but formed a polytomy with an exponential mean of 10. However, none of these topological differences were significantly supported.

3.3. Clock-like behavior

Clock-like evolution was only rejected for two loci, ND2 and RAG1; all other loci appear to be evolving in a clock-like manner (Table 4).

3.4. Mitochondrial data set

The analyzed fragments of the mitochondrial genome correspond to the positions 4007 to 5047 (ND2) and 8024 to 8707 (ATP6) of the *Corvus frugilegus* mitochondrial genome (Härlid and Arnason, 1999), resulting in an alignment of 1725 bp. No insertions

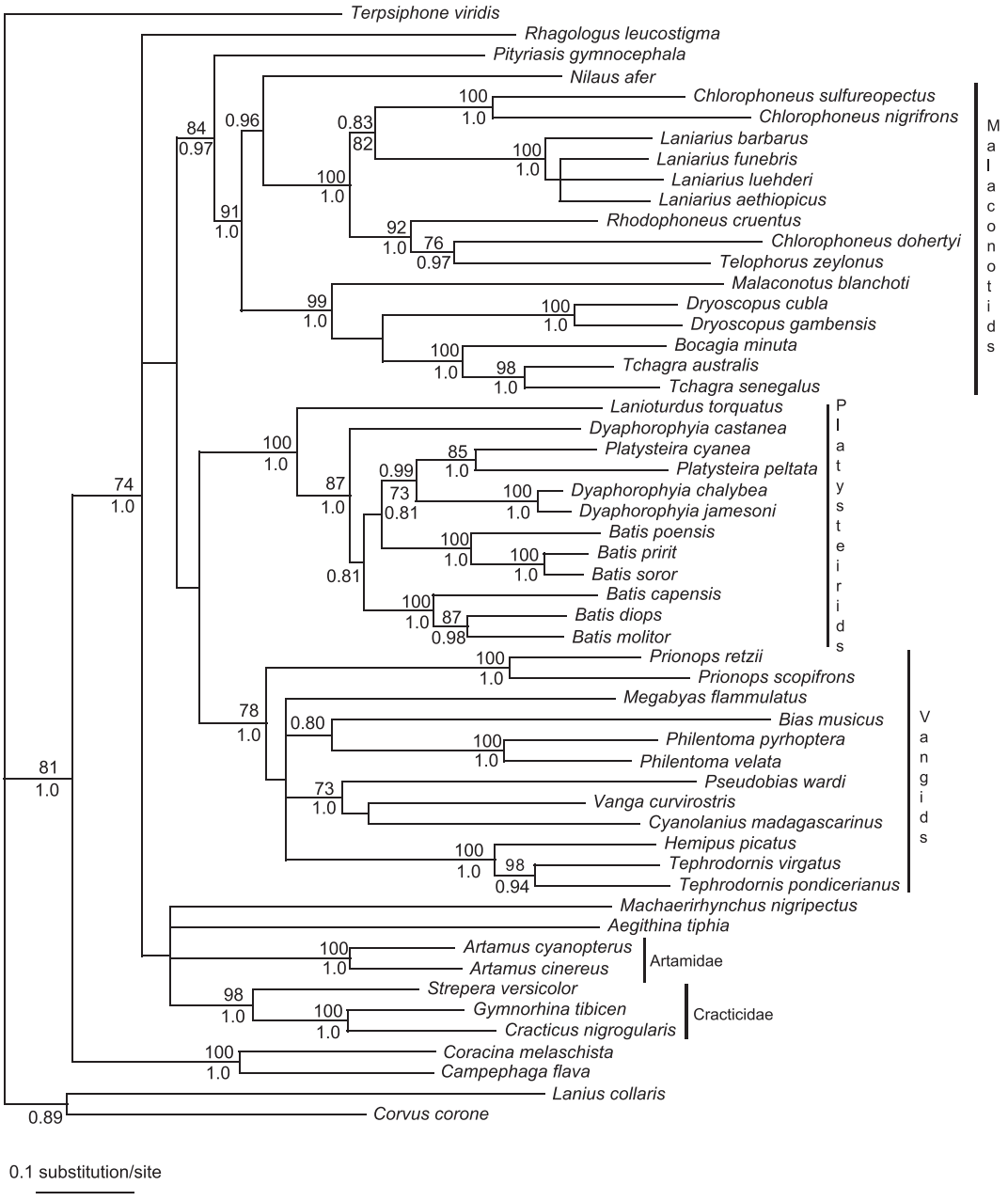

Fig. 1. 50% Majority rule consensus rule tree resulting from the Bayesian analyses of the mitochondrial data set (six partitions) using MrBayes 3.1.2. Numbers close to the nodes refer to posterior probabilities and maximum likelihood bootstrap support values higher than 0.80 and 60%, respectively.

or deletions were inferred from the alignment and all sequences translated to functional proteins. The Bayes factors strongly favoured a scheme with six partitions (first, second and third codon positions for both ND2 and ATP6) over three (first, second and third codon position, $B_F = 63.3$), two (ND2 and ATP, $B_F = 932.8$) and one ($B_F = 974.5$). Monophyly of the core malaconotids, platysteirids and vangids all received posterior probabilities (PP) of 1.0 and high bootstrap support (>85%) (Fig. 1). The monotypic Bornean *Pityriasis* clustered as the sister-group of the core malaconotids (PP = 1.0, $B = 90\%$). The Indo-Malayan *Aegithina* grouped with the Australasian taxa (Artamidae, Cracticidae *Machaerirhynchus*) in a fourth primary clade, although support for its monophyly was not significant (PP = 0.92, $B = 41\%$). Relationships among the four primary lineages did not receive significant support. Only one topological difference was found across the 50% majority rule consensus trees resulting from the different partitioning schemes. This involved the position of *Prionops* in the 'core Vangid' clade: it was sister to all other members of the core vangids in the one- and two-partitions analyses, PP: 0.62 and 0.64, but formed a polytomy with all other core vangid lineages in the three- and six-partition analyses. Further, there was no obvious change in relative branch-lengths across the consensus trees or in levels of support. Hence, partitioning the data set by gene and/or codon position only yielded a significant increase in likelihood without any change in topology, clade support, or branch-length.

3.5. Individual nuclear loci

The Bayes factors strongly favoured a codon partitioning scheme for the two nuclear exons (cmos: $B_F = 103.0$ and RAG1: $B_F = 47.6$). Individual gene trees showed similar levels of resolution and support (Supplementary Figs. 1–8). Twenty-one lineages, above the species level, that were supported by at least eight loci could be defined. Within the Malaconotidea, four lineages that

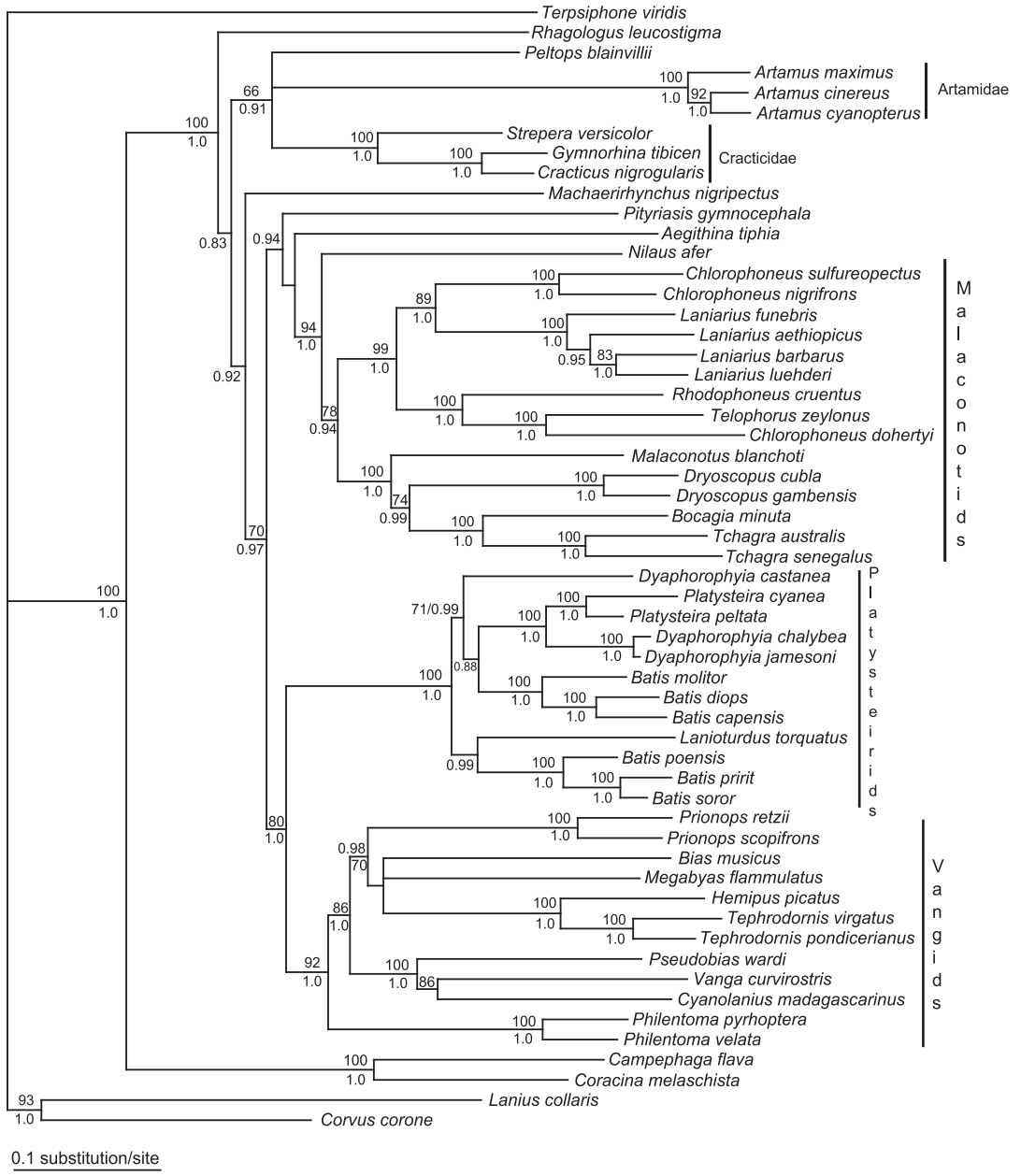

Fig. 2. 50% majority rule consensus rule tree resulting from the Bayesian analyses of the nuclear data set (eight partitions) using MrBayes 3.1.2. Numbers close to the nodes refer to posterior probabilities and maximum likelihood bootstrap support values higher than 0.80 and 60%, respectively.

include more than one genus were recovered across at least eight loci: *Laniarius*/*Chlorophoneus*/*Rhodophoneus*/*Telophorus*, *Malaconotus*/*Dryoscopus*/*Bocagia*/*Tchagra*, *Lanioturdus*/*Batis*/*Dyaphorophyia*/*Platysteira* ('core platysteirids'), and *Hemipus*/*Tephrodornis*. Relationships among some of these 21 lineages received support in only a few loci (e.g., 'core malaconotids' for MB, 'core vangids' for FGB), or were poorly supported. Conflicting nodes among the different nuclear loci were found in the 'core platysteirids' and involved the placement of the monotypic *Lanioturdus*, and some *Batis* species, and *Aegithina* (Supplementary Figs. 1–8).

3.6. Concatenated nuclear data

The 50% majority rule consensus tree resulting from the Bayesian analyses of the nuclear data was well resolved with 41 of the 46 nodes within the Malaconotidea receiving posterior probabilities greater than 0.95 (Fig. 2). All primary clades were recovered as monophyletic with very strong support: Artamidae, Cracticidae, Artamidae/Cracticidae, 'core platysteirids', 'core vangids' and 'core malaconotids'. The Indo-Malayan Aegithinidae and Pityriasidae were closely related to the 'core malaconotids' (PP = 0.94, *B* = 50%), but their relative position is uncertain (PP = 0.64, *B* = 45%). All Australasian lineages (Artamidae/Cracticidae, *Machaerirhynchus*) were recovered in a basal clade (*B* = 68%) or as a paraphyletic assemblage in our BI topology, but no strong conflict was detected among methods. Within the 'core vangids', *Philentoma* was the first taxon to diverge (PP = 1.0, *B* = 86%), followed by the Vangidae (PP = 0.98, B = 69%) and then by a clade including the Afrotropical *Prionops*, *Bias* and *Megabyas*, as well as the genera *Hemipus* and *Tephrodornis* (PP = 0.98, *B* = 69%). The 'core vangids' were recovered as sister to the 'core platysteirids' (PP = 1.0, *B* = 80%). Overall there are very strong topological similarities between the mitochondrial tree and the nuclear tree obtained from the concatenated analyses (Fig. 2).

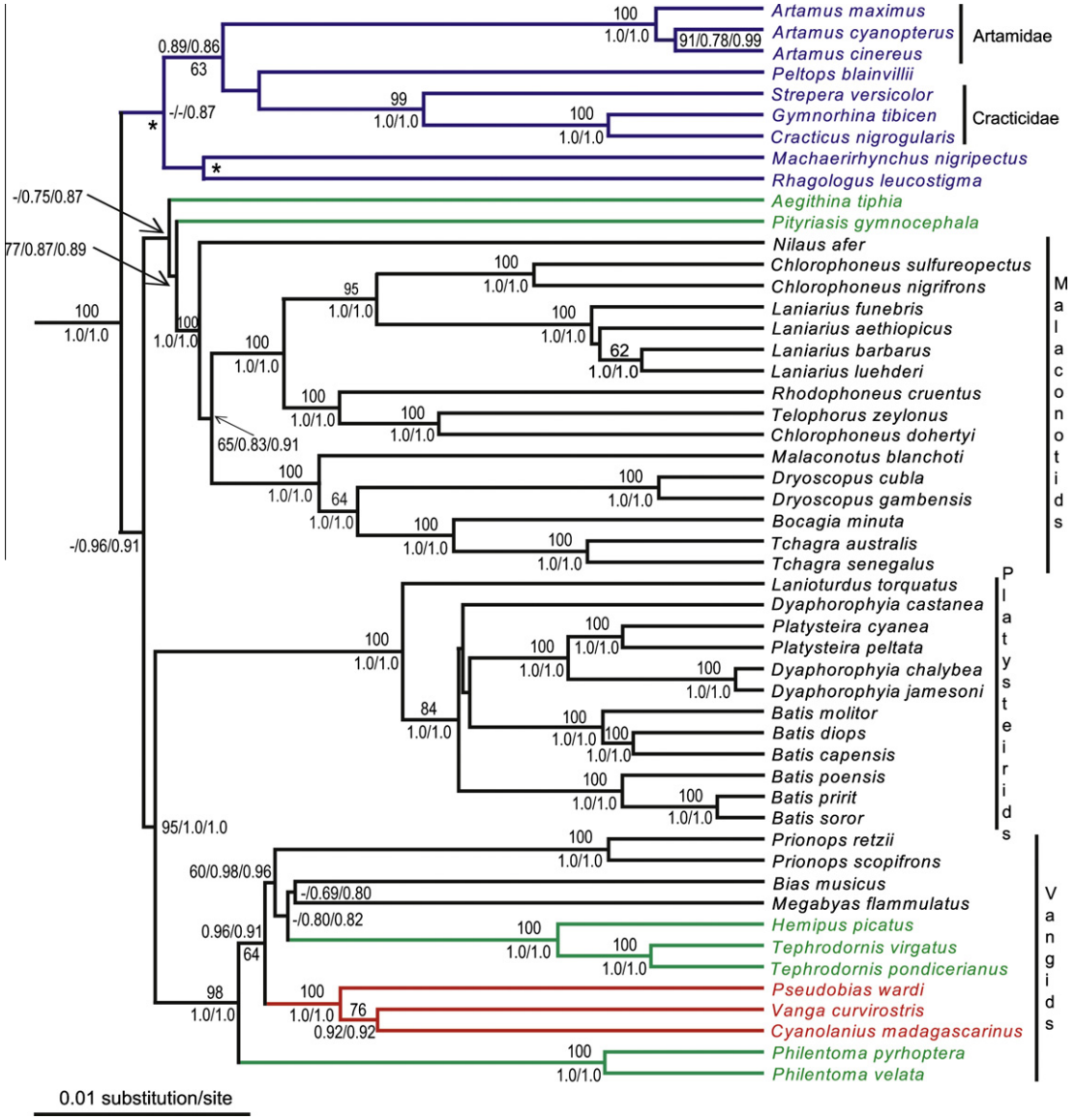

Fig. 3. Maximum Clade Credibility tree obtained using Beast v.1.6.0 (concatenation of the mitochondrial and nuclear data set, ten partitions). Numbers close to the nodes refer to maximum likelihood bootstrap values and posterior probabilities higher than 60% and 0.80 (MrBayes/Beast), respectively. Each locus was specified with its own specific substitution model. Color codes refer to the biogeographic origin of the terminal taxa. The asterisks indicate two nodes that were not recovered in the MrBayes analyses; the Australian lineage was paraphyletic with *Rhagologus* being the first lineage to branch off in the Malaconotidea (PP = 0.67), with *Machaerirhynchus* being sister to the clade formed by all non-Australasian taxa (PP = 0.72).

3.7. Incongruence between the mitochondrial and nuclear trees

Only a few contradictory nodes with support, were detected between the mitochondrial and nuclear data sets. The position of *Laniorturdus* was at the base of the 'core platysteirids' in the mitochondrial tree whereas it was in a more terminal position in this group in the nuclear tree. The position of *Aegithina* also varied between the two trees, but its position was not supported in the mitochondrial tree.

3.8. All data concatenated

We achieved satisfactory mixing and convergence for the concatenated data set for all parameters using MrBayes 3.1.2 with four chains run for 500 million iterations, a temperature of 0.1 and an exponential branch-length prior with a mean of 50. Problems in achieving convergence for large data sets, or the need to run very long analyses, have been reported for other large multi-locus datasets (Hackett et al., 2008; Lovette et al., 2010). We also obtained satisfactory mixing and effective sample sizes greater than 200 for all parameters using Beast v.1.6.0. The topology recovered in the Maximum Clade Credibility tree from the Beast analyses (Fig. 3) was very similar to the topology recovered in the partitioned by locus ML and MrBayes analyses, with differences mostly involving poorly supported nodes. The exception was *Aegithina,* which was the sister group of the *Pityriasis*/'core Malaconotids' clade in the Bayesian analyses (PP = 0.97), but sister to the Artamidae/Cracticidae clade in the ML analyses (B = 54%). The tree resulting from the MrBayes analyses only differ from that generated from the Beast analyses with respect to the placement of *Rhagologus* and *Machaerirhynchus*. In the MrBayes analyses *Rhagologus* was the first lineage to split off in the Malaconotidea (P = 0.67) whereas *Machaerirhynchus* was the sister group of all non-Australasian taxa (P = 0.72). The posterior

Table 5
Results of the biogeographic analyses using Lagrange for some selected clades. The Australasian clade includes the Artamidae, Cracticidae, as well as the genera: *Peltops*, *Machaerirhynchus* and *Rhagologus*. Acronyms: Af, Afrotropics; Au, Australasia; I, Indo-Malaya; M, Madagascar. When probabilities are equivocal ($P = 0.4–0.6$), the next most likely scenario is also indicated.

Node	Equal rate			Differential rate (M = Af = 0.5)			Differential rate (Af = 0.5)		
	Inference	Ln	Relative probability	Inference	Ln	Relative probability	Inference	Ln	Relative probability
Campephagidae/Malaconotidea	[Au|Au]	−46.4	0.542	[Au|Au]	−46.0	0.569	[Au|Au]	−46.3	0.569
	[AfAu|Au]	−46.7	0.405	[AfAu|Au]	−46.4	0.370	[AfAu|Au]	−46.8	0.370
Malaconotidea	[Au|Af]	−46.0	0.860	[Au|Af]	−45.7	0.752	[Au|Af]	−46.0	0.760
Australasian clade	[Au|Au]	−45.8	0.996	[Au|Au]	−45.5	0.996	[Au|Au]	−45.8	0.996
Malaconotidea minus Australasian clade	[Af|Af]	−46.1	0.731	[Af|Af]	−45.9	0.661	[Af|Af]	−46.2	0.661
Core Platysteirids/core Vangids	[Af|Af]	−45.9	0.891	[Af|Af]	−45.9	0.859	[Af|Af]	−45.9	0.859
Core Vangids	[Afl|I]	−46.3	0.601	[Afl|I]	−46.1	0.550	[Afl|I]	−46.3	0.572
	[A|I]	−47.4	0.212	[Af|I]	−46.9	0.240	[Af|I]	−47.2	0.231
Core Vangids minus *Philentoma*	[M|Af]	−46.9	0.321	[M|Af]	−46.5	0.360	[M|Af]	−46.8	0.345
	[Af|Afl]	−47.0	0.303	[Af|Afl]	−46.7	0.270	[Af|Afl]	−47.0	0.285
	[I|Afl]	−47.0	0.303	[I|Afl]	−46.7	0.270	[I|Afl]	−47.0	0.285
Hemipus/*Tephrodornis*/*Prionops*/*Bias*/*Megabyas*	[Afl|Af]	−46.2	0.640	[Afl|Af]	−46.0	0.595	[Afl|Af]	−46.3	0.614
	[Af|Af]	−46.9	0.350	[Af|Af]	−46.4	0.396	[Af|Af]	−46.7	0.377
Hemipus/*Tephrodornis*/*Prionops*	[I|Af]	−46.1	0.756	[I|Af]	−45.8	0.727	[I|Af]	−46.3	0.740
Core Platysteirids	[Af|Af]	−45.8	0.996	[Af|Af]	−45.5	0.994	[Af|Af]	−45.8	0.995
Aegithina/*Pityriasis*/core Malaconotids	[Afl|I]	−45.9	0.937	[Afl|I]	−45.5	0.911	[Afl|I]	−45.9	0.916
Pityriasis/core Malaconotids	[I|Af]	−45.8	0.933	[I|Af]	−45.5	0.923	[I|Af]	−45.8	0.923
Core Malaconotids	[Af|Af]	−45.8	0.988	[Af|Af]	−45.5	0.985	[Af|Af]	−45.8	0.986

probabilities from the Beast and MrBayes analyses were very similar (Fig. 3). Differences between the ML and the Bayesian topologies were slight and never supported by strong bootstrap and posterior probabilities. One caveat to the ML analyses is that an over-parameterized substitution model had to be used for the eight nuclear loci, because RAxML only implements the GTR model of nucleotide substitution. This might explain the differences in topology.

We regard the topology generated in Beast v.1.6.0 as the best estimate of phylogeny under the concatenated approach because, unlike in MrBayes, deviation from a strict molecular clock can be taken into account. We performed the biogeographic analyses on the topology generated with Beast, although we note that our conclusions would be identical if we used the MrBayes topology, because only one ancient dispersal from Australasia is recovered (paraphyly of the Australasian lineage) and the relationships among the non-Australasian lineages are identical.

3.9. Species tree approaches

For the Bayesian methods Best 2.2 (Liu, 2008) and *Beast v1.5.4 (Heled and Drummond, 2010), we used different prior values for the species population size (Leaché, 2009) and ran the chains for a minimum of 100 million iterations and a maximum of 500 million iterations. We did not detect any sign of convergence of the Markov chains using these two methods, and ESSs for some parameters remained low (<50), despite further attempts to optimize *mcmc* settings (temperature, number of chains) or alter priors (e.g., branch-length prior). Hence, we do not present the results from these analyses.

The topology recovered using the maximum likelihood species tree approach implemented in Stem was not dependent on the value of the population size prior (0.01 to 0.0001). The topology (Supplementary Fig. 9) obtained differed in many ways from the topology recovered from the concatenated analyses. For examples, *Pityriasis* was nested within 'core malaconotids' and formed the sister group to *Nilaus*, and the first lineage branching off within Malaconotidea was the 'core vangids' and not Artamidae/Cracticidae. Running the analyses and sequentially deleting one locus indicated that the sister-group relationship between *Nilaus* and *Pityriasis* was mostly due to FGB, as also seen in the gene tree analyses.

3.10. Biogeographic analyses

Results of the biogeographic analyses using the maximum likelihood algorithm implemented in Lagrange are indicated in Table 5. The results did not depend on the time at the root node and changing the dispersal probabilities had little effect on the overall pattern (Table 5). The analyses indicate that members of Malaconotidea dispersed directly from Australia to Africa. This dispersal occurred between the divergence of Campephagidae and the Malaconotidea, and the divergence of the Australasian lineages from the remaining Malaconotidea. Five dispersal events between the Afrotropics, Indo-Malaya and Madagascar subsequently occurred, involving *Aegithina*/*Pytiriasias*, the 'core malaconotids', *Philentoma*, the Vangidae and *Hemipus*/*Tehprodornis*.

4. Discussion

We analyzed DNA sequence data obtained from 10 loci representing different inheritance modes (maternal, paternal or biparental) and different substitution rates (mitochondrial, nuclear introns and exons) for all Malaconotidea genera with the exception of some members of the Vangidae. The topologies we recovered were variable and differed considerably between concatenation *versus* species tree analyses. Below we discuss the implication of these topological differences in terms of biogeographical interpretations and what the limitations of each approach may be in the context of our study.

4.1. Phylogeny and biogeography of the Malaconotidea

4.1.1. Mitochondrial versus concatenated nuclear data

The topology resulting from the analyses of the mitochondrial and nuclear genomes had only one major conflict: the position of the monotypic *Lanioturdus*, an endemic of the Namibian desert. Both genomes supported the monophyly of the primary clades highlighted in Fuchs et al. (2004, 2006b): 'core Malaconotids, 'core

Platysteirids', 'core Vangids' and Artamidae/Cracticidae (including *Peltops*, Norman et al., 2009), as well as the relationships within the 'core malaconotids' and 'core platysteirids'.

4.1.2. Total evidence topology

Recently, three Australasian passerine genera with disputed affinities were shown to be part of the Malaconotidea: *Peltops*, *Machaerirhynchus* and *Rhagologus* (Norman et al., 2009). The Shieldbills (*Peltops*) were shown to be nested within Artamidae-Cracticidae (Norman et al., 2009). Our analyses, with more complete sampling, retrieved the same result. The genera *Machaerirhynchus* and *Rhagologus* were found to be each others closest relatives in the Beast concatenated analyses, although support was low. The *Machaerirhynchus-Rhagologus* clade was related to Artamidae-Cracticidae-*Peltops* with moderate support. The Australian lineage formed a clade (Beast concatenated) or a paraphyletic assemblage (concatenated MrBayes). Yet in each topological arrangement, only one ancient dispersal out of Australasia is likely to have taken place.

Our study also lends further evidence for the affinities of the Bornean Bristlehead (*Pityriasis*) being within the Malaconotidea, as the sister-group to the 'core malaconotids'. These results suggest that the biogeographic history of the Indo-Malayan and African lineages may be more complex than previously thought (Fuchs et al., 2006b). Unlike previous studies, our data provided strong support for a sister-group relationship between 'core Platysteirids' and 'core Vangids' and for the relationships within the 'core Vangids' Our biogeographic reconstructions indicate that the 'core Vangids' and Vangidae may be of African origin, as previously suggested (Fuchs et al., 2006b).

As expected from the high level of congruence found between the mitochondrial and nuclear genomes, relationships within the 'core Malaconotids' and 'core Platysteirids' are highly supported and highly congruent with Fuchs et al. (2004, 2006b) and Njabo et al. (2008), respectively. The conflict between the nuclear and mitochondrial genomes with respect to the placement of the genus *Lanioturdus* ('core platysteirids') remains a puzzle, and should be further explored.

Our results are in strong contradiction with recent osteological analyses in which none of the above clades (Malaconotidea, 'core malaconotids', 'platysteirids' and 'vangids') were recovered as monophyletic (Manegold, 2008). Cladistic analyses of morphological data supported a close relationship of most vangas with butcher-birds and woodswallows, whereas other vanga lineages were inferred to be closely related to some 'core platysteirids' (*Mystacornis*, *Newtonia*) or even drongos (*Calicalius*), and Old World orioles (*Tylas*). None of the relationships highlighted by Manegold (2008) were recovered by our data, although we did not sample all genera in the Vangidae. We never found a direct relationship between the vangas we sampled and butcher-birds/woodswallows in any of the gene trees. Further, Johansson et al. (2008) and Reddy et al. (2012) showed strong evidence for *Mystacornis* being closely related to the vangid genera we sampled. Manegold (2008) emphasized, above all, the strong bills with a massively ossified nasal region of butcher-birds, woodswallows and some vangas. However, some tendencies towards extraordinary amphirhinal ossification are seen in several species representing deep lineages in the corvoid assemblage (e.g., *Falcunculus*, *Struthidea*, *Aleadryas*, *Rhagologus*, *Oreoica* and *Grallina*, J. Fjeldså pers. obs.). Thus there may be a general disposition in core corvoids for such ossification (or calcification of cartilage) whenever there is strong selection for reinforcement of the bill. No recent molecular data (Barker et al., 2004; Fuchs et al., 2004, 2006b; Norman et al., 2009; Jønsson et al., 2011) are in agreement with the osteological analyses (Manegold, 2008). Our phylogeny suggests that flycatching and sally-gleaning was predominant in the 'core platysteirids'-'core vangids', and that only terminal vanga taxa (e.g. *Vanga*, *Euryceros*) developed strong bills for probing and tearing wood (Jønsson et al., 2012; Reddy et al., 2012). This situation contrasts with that encountered in the 'core malaconotids', where early lineages (e.g. *Pityriasis*, *Malaconotus*) had very robust bills.

4.1.3. Biogeography of the Malaconotidea

The topology from the concatenated analyses recovered a monophyletic Australo-Papuan clade including Artamidae (some *Artamus* species dispersed into the Indo-Malayan region), Cracticidae, and the monotypic *Machaerirhynchus*, *Peltops* and *Rhagologus* (Norman et al., 2009; Jønsson et al., 2011, 2012). This result suggests that only one ancient dispersal event out of Australasia occurred. Our biogeographic analyses revealed that members of Malaconotidea dispersed directly from Australasia to Africa during the late Eocene (ca. 45–33.7 mya, Fuchs et al., 2006b; Jønsson et al., 2011). Given the general tendency of dispersal during the early phylogenetic history of the core corvoids, this scenario appears plausible (Jønsson et al., 2011). The pattern and timing of colonization of Africa by the Malaconotidea match those described for Passerida (e.g., Old World Flycatchers, sparrows, warblers, thrushes) (Fuchs et al., 2006a) Passerida were assumed to have colonized Africa from Australasia through the now (mostly) submerged Broken Ridge, Kerguelen, Crozet and South Madagascar plateaus in the southern Indian Ocean c. 45 mya (Fuchs et al., 2006a; Johansson et al., 2008). Three further direct dispersals from Australasia to Africa have been detected in Campephagidae, although they likely occurred more recently (Fuchs et al., 2007; Jønsson et al., 2008, 2010).

The relationships of the Indo-Malayan and African lineages are more complex; some lineages (*Hemipus*, *Philentoma*, *Tephrodornis*) are nested within the 'core vangids', whereas others are either sister to the 'core malaconotids' (*Pityriasis*) or sister to the clade formed by the 'core malaconotids'-*Pityriasis* (*Aegithina*). This result would imply at least five dispersal events among Africa, Indo-Malaya and Madagascar. Our extended data set allowed us to resolve relationships of the Vangidae and clarify, to some extent, their biogeographic origin. A previous study supported an African origin for the Vangidae, although the relationships among the primary lineages of 'core vangids' formed a polytomy (Fuchs et al., 2006b). Adding more loci allowed us to resolve the relationships among genera in the 'core vangids' and infer an African origin of the Vangidae with strong support. The time window for the colonization of the Vangidae (Fuchs et al. 2006b) corresponds to the colonization of Madagascar by members of the Bernieridae and the *Streptopelia picturata*/*Nesoenas mayeri* doves (Fuchs et al., 2008), as well as by *Agapornis* (c. 24 mya) and *Coracopsis* (c. 28 mya) parrots (Schweizer et al., 2011) from the Australasian/Indo-Malayan regions. These results suggest that the avifauna of Madagascar underwent a major turnover during the Late Oligocene or early Miocene.

4.1.4. Species tree analyses and limitations of concatenated analyses

Over the past decade, concatenation of several gene regions together has been the primary approach used to reconstruct the evolutionary history of lineages using different types of data (e.g., DNA and morphology, mitochondrial and nuclear sequences). This approach is rooted in a 'total evidence' philosophy where all available data should be combined to provide the best estimate of the phylogeny. When applied to molecular data, this approach was considered appropriate because it allowed the combination of several loci with different evolutionary dynamics, enabling loci to bring robust information to bear on different parts of the total evidence tree. This approach has also gained some popularity with the development of model-based methods (e.g. MrBayes, Beast and RAxML) that allow the user to take into account the heterogeneity

of rates of molecular evolution across loci by enabling every locus to have its own substitution model.

We obtained satisfactory mixing and convergence for all parameters for the analyses of the partitioned mitochondrial and nuclear data sets. In contrast, the concatenated mitochondrial and nuclear data set showed very poor mixing for the rate multipliers in most of the analyses and analyses needed to be run for much longer. The different nuclear loci evolve at very similar rates. The fastest nuclear locus evolves about two times faster than the slowest locus. The mitochondrial data set evolve 32 times faster than the slowest nuclear locus in our data set. One factor that may have affected the mixing and convergence of the rate multipliers is the difference in the branch-length prior used. Indeed, changing the branch-length prior in our individual loci not only changed the overall tree length (as expected), but also the likelihood and degree of MCMC mixing. For example, for most nuclear loci, an exponential branch-length prior of 100 was a better fit than a branch-length prior of 10, whereas the opposite was true for the mitochondrial data. Hence, combining the two types of data sets with drastically different evolutionary rates may prevent the algorithm from converging on the target distribution.

We also noted that using an intermediate exponential branch-length prior of 50 did improve the mixing but only after running the analyses for 500 million generations. Hence, it seems that one of the most difficult parameters to deal with in concatenated analyses is the heterogeneity in tree length of individual gene trees (Edwards, 2009). Another, potential factor could be the non-clock-like behavior of the loci. In all but two loci, a strict molecular could not be rejected. Yet a visual inspection of individual gene trees suggests that lineages that have longer branches than their sister-groups vary across loci. For instance, *Artamus* has a very long branch in RAG1 and TGFb2 but has a short branch in the mitochondrial data set. Hence, it is possible that the differences in the rates of evolution across lineages and loci may prevent the rate parameter from converging.

4.1.5. Difficulties in achieving convergence in species tree analyses

Most species tree methods have been developed to reconstruct the relationships among recently diverged species with the idea of sampling multiple individuals/alleles per species (Belfiore et al., 2008; Brumfield et al., 2008; Fuchs et al., 2011). When the objective is to reconstruct relationships among different families, the sampling strategy is often very different, as usually not all species are sampled and only one individual per species is included. We tried two different Bayesian methods, Best and *Beast, and both failed to converge or mix satisfactorily even when changing several MCMC parameters. A lack of convergence for similar datasets has already been reported in several studies, even after running the analyses for a billion iterations (Cranston et al., 2009; Alström et al., 2011). The maximum likelihood method implemented in STEM is an alternative to Bayesian methods, but the robustness of the species tree is difficult to estimate because some relationships appeared that were barely supported in any of the gene trees. Moreover, the topology resulting from the STEM analyses was never recovered in any of the gene trees as exemplified by the relationship between *Nilaus* and *Pityriasis*.

5. Conclusions

The analysis of DNA sequences from 10 loci provided an updated robust phylogeny of Malaconotidea and helped clarify the relationships of several monotypic Australasian genera. Whereas some parts of the tree have now been resolved using more data ('soft polytomy'), some others have still not been resolved, suggesting that they may represent real rapid radiation events. We had hoped that the use of new species tree approaches would have enabled us to resolve these parts of the tree where 'discordant' signal could be due to deep coalescence. Yet, none of the Bayesian methods converged on the target distribution or mixed properly, suggesting that the use of these methods for phylogenetic analyses addressing relationships among genera or families may be difficult, or require a much larger dataset. Our analyses suggest that only one ancient dispersal event out of Australasia and directly to Africa occurred in Malaconotidea, whereas multiple faunistic exchanges occurred between the Afrotropics and Indo-Malaya.

Acknowledgments

We are very grateful to P. Sweet and J. Cracraft (AMNH), L. Joseph and N. Rice (ANSP), J. Dumbacher (CAS), J. Bates, S. Hackett, T. Gnoske and D. Willard (FMNH), R. Brumfield, D. Dittmann and F. Sheldon (LSUMZ), C. Cohen (PFIAO), M. Braun and J. Dean (USNM), for tissue loans. Laboratory work at MNHN was supported by the 'Service Commun de Systématique Moléculaire', IFR CNRS 101, MNHN and by the Plan Pluriformation 'Etat et structure phylogénétique de la biodiversité actuelle et fossile'. It is part of the agreement no. 2005/67 between the Genoscope and the Muséum National d'Histoire Naturelle on the project 'Macrophylogeny of life' directed by G. Lecointre. This research was supported by a postdoctoral fellowship to J. Fuchs from the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute and the University of California at Berkeley. J. Fjeldså acknowledges the Danish National Research Foundation for funding to the Center for Macroecology, Evolution and Climate. We are also very grateful to C. Krajewski, D. Mindell, J. Dumbacher and one anonymous for comments that improved this manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2012.03.007.

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