

## Phylogeny and biogeography of Oriolidae (Aves: Passeriformes)

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Understanding oscine passerine dispersal patterns out of their Australian area of origin is hampered by a paucity of robust phylogenies. We constructed a molecular phylogeny of the oscine family, Oriolidae, which is distributed from Australia through to the Old World. We used the phylogeny to assess direction and timing of dispersal and whether dispersal can be linked with the well-documented movements of geological terranes in the Indonesian Archipelago. We sampled 29 of 33 species of Oriolidae from fresh tissue and from toe pads from museum specimens, and examined two nuclear introns and two mitochondrial genes. Model-based phylogenetic analyses yielded strong support for clades that generally mirrored classical systematics. Biogeographical analyses and divergence time estimates demonstrated that the family originated in the Australo-Papuan region from where it dispersed first to Asia and then onwards to Africa and the Philippines before back-colonising Asia and the Indonesian archipelago. Thus, contrary to several other avian families in the region, Oriolidae represents a sequential dispersal pattern from Australia to Africa via Asia. However, it is noteworthy that the Pacific islands and archipelagos remain uncolonised and that members inhabiting Wallacea are recent colonisers suggesting that Oriolidae are poorly adapted to island life.

The faunal transition between Asia and Australia has received much attention since Wallace (1860, 1863) noted the remarkable species turnover between the western and eastern Indonesian islands (either side of Wallace's line). Most noticeable was the replacement of placental mammals to the west (except for bats and rodents) with marsupials to the east. Several avian examples are also known, e.g. woodpeckers to the west and cockatoos to the east (MacKinnon and Phillipps 1993, Coates and Bishop 1997). Today the geological history of the region is well-established. Wallacea is of mixed origin consisting of Australo-Papuan and Asian plate fragments as well as new volcanic islands (Hall 1998, 2002), and these land masses consequently harbour biota of different origins. Originally Australo-Papua was part of Gondwana, from which it was separated in the Late Cretaceous at around 80 Mya (Metcalf 1998). About 40 Mya the Australo-Papuan plate started to drift rapidly towards the north, and 10–20 Mya plate fragments began to intermingle in the seas between the two continental areas (Hall 1998, 2002). Although no land connection is yet established, we would expect that volant

organisms such as birds, bats and insects could take advantage of these stepping-stone islands and disperse across the gap.

Biogeographical patterns differ substantially among passerine bird groups, reflecting different times of origin and radiation and probably also different ecological adaptations and life-history strategies. However, it is becoming increasingly apparent that understanding geological history is an essential prerequisite for understanding patterns of present species distributions. For example, several studies have examined vertebrate speciation and biogeographical patterns in Indo-Pacific archipelagos (e.g. mammals in the Philippine archipelago, Steppan et al. 2003, Heaney 2005, Jansa et al. 2006, and passerine birds in Pacific archipelagos, Filardi and Moyle 2005, Cibois et al. 2007). However, few studies have yet encompassed the whole region on both sides of Wallace's line (exceptions exist for amphibians Evans et al. 2003 and passerine birds Jønsson et al. 2008a, Moyle et al. 2009). As robust phylogenetic hypotheses become available, it is now a great challenge to interpret evolutionary relationships in light of

the detailed knowledge of plate tectonics that is available for the region.

Evidence supports the origin of passerine birds (Passeriformes) within the Gondwanan supercontinent around the time of the K/T boundary (Barker et al. 2002, 2004, Ericson et al. 2002). Two major lineages within Passeriformes are recognized: the suboscines (Tyranni), which are mainly South American, and the oscines (Passeri), with an Australian origin. The basal lineages within oscines are more or less restricted to the Australo-Papuan region, which thus is assumed to be the area of origin for this diverse radiation (Christidis 1991, Barker et al. 2002, Edwards and Boles 2002, Ericson et al. 2002). Within oscines, the core Corvoidea comprises a group of corvoid birds, which includes such diverse families as cuckoo-shrikes (Campephagidae), African bush-shrikes (Malaconotidae), Old World orioles (Oriolidae), whistlers (Pachycephalidae), vireos (Vireonidae), fantails (Rhipudiridae), birds-of-paradise (Paradisaeae), shrikes (Lanidae) and crows (Corvoidea). Core Corvoidea has recently been established to be Australian of origin (Barker et al. 2004, Jönsson and Fjeldså 2006) and some of the families have dispersed to all other continents (except the Antarctica) and to remote oceanic islands and, in the process, evolved high species diversity (ca 750 spp., sensu Monroe and Sibley 1993). Other families such as birds-of-paradise have restricted ranges in Australo-Papua and adjacent islands, possibly because of constraints linked to their unique reproductive strategy (Irestedt et al. 2009).

Within the core Corvoidea, systematics of the Oriolidae (Old World orioles) has received little attention. Orioles are broadly distributed in Australia, Asia and Africa. Several species occur in the Indonesian and Philippine archipelagos on both sides of Wallace's line, and they therefore form an ideal group for investigating biogeographical history and dispersal patterns out of Australia. In this study we present the first molecular phylogeny of the family Oriolidae, based on both nuclear and mitochondrial DNA sequence data. We use the phylogeny to examine the mode, tempo and timing of biogeographical dispersal patterns out of Australia.

## Material and methods

### Taxon sampling and laboratory procedures

Orioles are medium-sized, mostly fruit-eating birds confined to mature forest and forest edges. Members of this fairly homogenous bird family, are traditionally defined to comprise the genera *Oriolus* and *Sphecothebes*. However, a recent study by Jönsson et al. (2008b) revealed that two species of *Pitohui* (*P. dicrous* and *P. kirbocephalus*) are closely associated with Oriolidae. Thus in the present study we included all species within Oriolidae except *O. crassirostris* of Sao Tome, which is morphologically very similar to *O. brachyrhynchus*, and *O. tenuirostris* from southeast Asia which is closely related to *O. chinensis diffusus*. Within the genus *Sphecothebes* we lack the two species endemic to Wetar and Timor, which are closely related to the Australo-Papuan *Sphecothebes vieilloti* (Monroe and Sibley 1993). We included four subspecies of the *Oriolus chinensis* complex.

This species is widespread in Asia from India to Indonesia and has many distinct subspecies throughout its range. We also included *Oriolus kundoo* from southern Asia, which was recently separated from *O. oriolus* (Walter and Jones 2008). In total 29 species were included in the ingroup (including *O. kundoo*).

DNA from fresh tissue (blood, liver, muscle) was extracted using the Quiagen Dneasy Extraction kit (Quiagen, Valencia, CA), following the manufacturers' protocol. Two nuclear gene regions, ornithine decarboxylase (ODC) introns 6 to 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 and Johnson 2001); ND3: ND3-L10755/ND3-H11151 (Chesser 1999); ODC: OD6/OD8 (Allen and Omland 2003), G3P13/G3P14b (Fjeldså et al. 2003).

The thermocycling conditions included a hotstart 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 microliter 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. 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) in both directions with the same primers 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 in Irestedt et al. (2006). Additional internal primers for study skins are specified in Jönsson et al. (2008a) for GAPDH and in Irestedt et al. (2006) for ODC in addition to two new internal primers for ND2 specifically designed for this study, ND2per330F: ATTCCACTTYTGATTCC-CAGAAGT; ND2per340R: CCTTGTAGTACTTCTGG-GAATCA; ND2ori500F: AGCYTTAGGRGGATGAT-TRGGRCT; ND2ori530R: GARGAGAARGCYATRAT-YTTTCG; ND2ori790F: CAGGCTTCCTCCCAAAAT-GACT; ND2ori773R: AGTCATTTTGGGAGGAAGC-CTG.

Sequences were assembled with SeqMan II (DNASTAR). 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 with some minor manual adjustments. The concatenated alignment consisted of 2365 bp and the lengths of the individual alignments were GAPDH: 317 bp, ODC intron-6 and 7: 612 bp, NADH dehydrogenase subunit 2: 1041 (for some species we only obtained 525 bp) and NADH dehydrogenase subunit 3: 397 bp. Coding genes (ND2 and ND3)

Table 1. List of taxa included in the study. Acronyms are: AMNH, American Museum of Natural History, USA; ANWC, Australian National Wildlife Collection, Canberra, Australia; FMNH, Field Museum of Natural History, Chicago, USA; KU, Univ. of Kansas, Lawrence, USA; LSU, Louisiana State Univ., USA; MCSNC, Museo Civico di Storia Naturale di Carmagnola, Italy; MNHN, Muséum National d'histoire Naturelle, Paris, France; MV, Museum Victoria, Australia; MVZ, Museum of Vertebrate Zoology, UC Berkeley, USA; NRM, Naturhistoriska Riksmuseet, Stockholm, Sweden; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands; UMMZ, Univ. of Michigan Museum of Zoology; UWBM, Univ. of Washington, Burke Museum, Seattle, USA; ZMUC, Zoological Museum, Univ. of Copenhagen, Denmark.

Species	Voucher	Origin	GAPDH	ODC	ND2	ND3
<i>Colluricincla megarhynca</i>	ANWC39343	Australia	EU273377	EU273357	GQ494092	GQ494126
<i>Colluricincla ferrugineus</i>	MV E506	New Guinea	EU273391	EU273372	GQ494089	GQ494123
<i>Coracina caesia</i>	ZMUC 123521	Tanzania	EF052797		EF052773	
<i>Coracina caesia</i>	ZMUC134772	Tanzania		GQ901708		GQ901732
<i>Corvus corone</i>	MNHN 13-16	France	DQ406663	EU272116	AY529949	
<i>Cyclarhis gujanensis</i>	ZMUC128105	Ecuador	EU380473	EU380435		
<i>Cyclarhis gujanensis</i>	LSUMZ103262	Bolivia			AY030129	
<i>Daphoenositta chrysoptera</i>	MV1311	Australia	EU380474			
<i>Dicrurus bracteatus</i>	UWBM68045	New Guinea	EF052813	EU272113	EF052784	
<i>Hylophilus ochraceiceps</i>	ZMUC127900	Ecuador	EU272087	EU272109		
<i>Hylophilus ochraceiceps</i>	LSUMZ125496	Bolivia			AY030133	
<i>Lanius collaris</i>	MNHN 2-26	Cameroon	DQ406662	EU272112	AY529960	
<i>Oriolus albiloris</i>	RMNH.AVES.80981	Philippines	GQ901805	GQ901723	GQ901778	GQ901749
<i>Oriolus auratus</i>	NRM552082	Sierra Leone	GQ901799	GQ901717	GQ901771	GQ901742
<i>Oriolus bouroensis</i>	AMNH111097	Buru			GQ901780	GQ901751
<i>Oriolus brachyrhynchus</i>	LSU B-45144	Ghana	GQ901791	GQ901709	GQ901762	GQ901733
<i>Oriolus chinensis chinensis</i>	KU10945	Philippines	GQ901798	GQ901716	GQ901769	GQ901740
<i>Oriolus chinensis diffusus</i>	AMNH366779	Korea	GQ901806	GQ901724	GQ901782	GQ901753
<i>Oriolus chinensis diffusus</i>	NRM569620	Vietnam	GQ901804	GQ901722	GQ901777	GQ901748
<i>Oriolus chinensis diffusus</i>	KU10450	China	GQ901797	GQ901715	GQ901768	GQ901739
<i>Oriolus chinensis maculatus</i>	NRM569617	Sumatra	GQ901801	GQ901719	GQ901773	GQ901744
<i>Oriolus chinensis melanisticus</i>	ZMUC123918	Talau, Indonesia	EU273382	EU273362		GQ901757
<i>Oriolus chlorocephalus</i>	NRM569622	Tanzania	GQ901800	GQ901718	GQ901772	GQ901743
<i>Oriolus cruentus</i>	LSU B-52617	Borneo	GQ901792	GQ901710	GQ901763	GQ901734
<i>Oriolus flavocinctus</i>	MV1603	Australia	EF441221	EF441243	GQ901758	GQ901728
<i>Oriolus forsteni</i>	RMNH.AVES.14761	Ceram			GQ901779	GQ901750
<i>Oriolus hosii</i>	AMNH671235	Borneo			GQ901783	GQ901754
<i>Oriolus isabellae</i>	AMNH768148	Luzon	GQ901807	GQ901725	GQ901784	GQ901755
<i>Oriolus kundoo</i>	NRM 570086	Uzbekistan	GQ901809	GQ901727	GQ901787	
<i>Oriolus larvatus</i>	MVZ uncat. JF527	South Africa	GQ901796	GQ901714	GQ901767	GQ901738
<i>Oriolus melanotis</i>	AMNH346175	Timor			GQ901781	GQ901752
<i>Oriolus mellianus</i>	MNHN 1931-1	China	GQ901810		GQ901786	
<i>Oriolus monacha persistens</i>	NRM569619	Ethiopia	GQ901802	GQ901720	GQ901774	GQ901745
<i>Oriolus nigripennis</i>	LSU B-45335	Ghana	GQ901793	GQ901711	GQ901764	GQ901735
<i>Oriolus oriolus</i>	MCSNC1415	Italy	EF052755	EU273363	EF052693	
<i>Oriolus oriolus</i>	ZMUC138401	Denmark				GQ494146
<i>Oriolus percivali</i>	NRM569618	Kenya	GQ901803	GQ901721	GQ901775	GQ901746
<i>Oriolus phaeochromus</i>	NRM553510	Indonesia			GQ901776	GQ901747
<i>Oriolus sagittatus</i>	MV1225	Aust	GQ901788	GQ901705	GQ901759	GQ901729
<i>Oriolus steerei</i>	ZMUC100057	Mindanao			GQ901770	GQ901741
<i>Oriolus steerei</i>	AMNH782012	Negros	GQ901808	GQ901726	GQ901785	GQ901756
<i>Oriolus szalayi</i>	ANWC27056	New Guinea	GQ901789	GQ901706	GQ901760	GQ901730
<i>Oriolus trailli</i>	MNHN JF484	Laos	GQ901795	GQ901713	GQ901766	GQ901737
<i>Oriolus xanthonotus</i>	LSU B-57419	Borneo	GQ901794	GQ901712	GQ901765	GQ901736
<i>Oriolus xanthornus</i>	MNHN 4-10D	Thailand	DQ406645	EU272111	AY529964	
<i>Ornorettes cristatus</i>	ANWC26733	New Guinea	EU273389	EU273370	GQ494087	GQ494121
<i>Pachycephala simplex</i>	MV1183	Australia	EU599245	EU599259	EU600814	EU600797
<i>Pitohui dichrous</i>	MV E545	New Guinea	EU273390	EU273371	GQ494088	GQ494122
<i>Pitohui kirhocephalus</i>	FMNH 280697	New Guinea	EU273392		GQ494100	GQ494134
<i>Sphecotheres vielloti</i>	MV2915	Australia	GQ901790	GQ901707	GQ901761	GQ901731
<i>Vireo olivaceus</i>	ZMUC124543	Panama	EU273394	EU273374		
<i>Vireo olivaceus</i>	UMMZ T978	USA			AY136614	
Outgroup						
<i>Menura novaehollandiae</i>	MV F722	Australia	EF441220	EF441242		
<i>Menura novaehollandiae</i>	not vouchered	Australia			NC_007883	NC_007883

were checked for the presence of stop codons or insertion/deletion events that would have disrupted the reading frame. We used Bayesian inference (Holder and Lewis 2003, Huelsenbeck and Ronquist 2003), as implemented in MrBayes 3.1.2 (Huelsenbeck et al. 2001, Ronquist and 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 and 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 six partitions (GAPDH, ODC, 1st, 2nd, 3rd codon

positions for mtDNA and tRNA), i.e. mixed-models analyses (Ronquist and Huelsenbeck 2003, Nylander 2004). In all MrBayes analyses, the Markov Chain Monte Carlo (MCMC) were run using Metropolis-coupling, with one cold and three heated chains, for 10 (individual analyses) to 20 million (combined analysis) iterations with trees sampled every 100 iterations. The number of iterations discarded before the posterior probabilities were calculated (i.e. the length of the “burn-in” period) was graphically estimated using AWTY (Wilgenbusch et al. 2004, Nylander et al. 2008) 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.

We used GARLI 0.95 (Zwickl 2006) to perform maximum likelihood analyses. Five independent analyses (20 million generations for the combined analysis, 10 million generations for individual partitions) were performed. Nodal support was evaluated with 100 nonparametric bootstrap pseudoreplications.

#### **Distributions and identification of ancestral areas**

Distributional data have been digitised as part of a global effort to map all avian distributions. The distributional data consist of range maps based on conservative interpolation between documented records and comprehensive literature review, entered in a grid corresponding to  $1 \times 1$  geographical degrees, using the WorldMap software (Williams 1996). The distributional data can be linked, through clade codes, to the topologies of phylogenetic trees. For a simple visual presentation, species richness maps can be produced for groups of species representing branch-length quartiles, based on number of nodes from the root of the phylogeny. Thus, the 1st quartile represents the 25% of species closest to the root (the least number of nodes from the root to the taxon), and the 4th quartile represents the 25% of most terminal taxa (the highest number of nodes from the root). Where several species are separated from the root by an equal number of nodes, the most recently diverged species according to the chronogram will be placed in the higher branch-length quartile.

Ancestral areas for Oriolidae were estimated using DIVA (Dispersal-Vicariance Analysis) ver. 1.1 (Ronquist 1996, 1997). Five geographical regions were recognized: A: Australia/New Guinea; B: Wallacea; C: Eurasia; D: Philippines; E: Africa. Maxarea values were set to two. 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 ancestral ranges were similar in size to extant ranges (Sanmartín 2003, Nylander et al. 2008). Because DIVA can handle only fully bifurcating trees we were forced to deal with polytomies within clade I and a polytomy at the base of clade II, III/IV and *Oriolus xanthornus*. Taxa belonging to clade I occur in Wallacea and the Australo-Papuan region and relationships among many of the taxa were unresolved. We ran the analysis twice, once assuming an Australo-Papuan origin (A) of the clade and once assuming a more widespread Australo-Papuan/

Wallacean origin of the clade. For the other polytomy we ran three analyses reflecting the three possible relationships.

The analyses were carried out several times exploring the effect of changing the cost settings (codivergence = 0–5, duplication = 0–5, sorting = 0–5, switching = 0–5). None of these changes altered the outcome of the analysis suggesting a robust result.

#### **Dating analyses**

We used Beast V1.4.6 (Drummond et al. 2002, 2006, Drummond and Rambaut 2007), to estimate divergence dates within Oriolidae. We assigned the best fitting model, as estimated by MrModeltest2 to each of the partitions. We used ML corrected pairwise distances of ND2 for five well-supported nodes (PP  $\geq$  0.99 and ML bootstrap  $\geq$  95) and a recently published rate extrapolation (2.8% Myr<sup>-1</sup>) of evolution in ND2 for another family of passerine birds (Norman et al. 2007) to calibrate the tree. Needless to say that this sort of extrapolation carries with it a significant margin of error and thus we emphasize the importance of thinking of the time estimates only as a rough attempt to place diversification events within Oriolidae in a historical context. The following calibration points were used: 1) the split within clade I between *Oriolus flavocinctus/melanotis* and *O. szalayi* at 2.43 My  $\pm$  0.5 stdev (95% CI = 1.608–3.252 My); 2) the most basal split within clade III at 5.43 My  $\pm$  0.5 stdev (95% CI = 4.608–6.252 My); 3) the split in clade IV between *Oriolus chinensis diffusus* and *Oriolus kundoo/O. oriolus/O. chinensis melanisticus/O. c. chinensis* at 2.57 My  $\pm$  0.5 stdev (95% CI = 1.748–3.392 My); 4) the split in clade VI between *Oriolus albiloris/isabellae* and *O. steerei* (Negros) at 2.81 My  $\pm$  0.5 stdev (95% CI = 1.988–3.632 My) and 5) the split in clade VII between *Pitohui dichrous* and *P. kirhocephalus* at 5.04 My  $\pm$  0.5 stdev (95% CI = 4.218–5.862 My). 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 twice. We used the program Tracer (Rambaut and Drummond 2007) to assess convergence diagnostics.

## **Results**

### **Phylogenetic analyses**

Analyses performed on the concatenated data set (six partitions: GAPDH, ODC, 1st, 2nd, 3rd mtDNA codon positions and tRNA; ML: -ln 22590.74, BI harmonic mean -ln 21450.33) and on the individual partitions (GAPDH: AIC: GTR+ $\Gamma$ , ML: -ln 1820.18, BI harmonic mean -ln 1946.46; ODC: AIC: GTR+ $\Gamma$ , ML: -ln 2705.19, BI harmonic mean -ln 2801.14; ND3: AIC: GTR+I+ $\Gamma$ , ML: -ln 3835.97, BI harmonic mean -ln 3744.02; ND2: AIC: GTR+I+ $\Gamma$ , ML: -ln 12917.55, BI harmonic mean -ln 12540.15) yielded 50% majority-rule consensus trees that were topologically congruent for well-supported nodes (posterior probability  $>$  0.95 and bootstrap values  $>$  70%) for ODC, ND2 and ND3. GAPDH, however, does show

some differences in the basal part of the tree; placement of the Pitohui species is in conflict with the other gene trees. Relationships of the Pitohui species in the combined analysis, however, are also supported by Myoglobin sequence data in a study by Jönsson et al. (2008b). Thus we feel confident that *Pitohui dicrous* and *P. kirhocephalus* are in fact sister to *Sphecotheses vielloti* and that they in turn are part of the family Oriolidae. The nuclear gene trees (GAPDH and ODC) (not shown) generally provide few well-supported clades. This is not unexpected and reflects that the genes evolve too slowly to resolve closely related young species within Oriolidae. The nuclear data, however, provide evidence for the partition of some more basal clades. The ND2 and ND3 gene trees (not shown) provide better resolution in the distal part of the tree. The combined analysis (Fig. 1) of both mitochondrial and nuclear genes generates a robust, densely sampled phylogeny for the entire family Oriolidae.

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  $\geq 0.95$  and bootstrap values  $\geq 70$ ).

### Geographical distributions of branch-length quartiles

A visual illustration of how the diversification of orioles changed in time and space (Fig. 2) presents geographical patterns of species richness for four groups defined from different phylogenetic branch-lengths. This approach is naïve in the sense that the timing of speciation events does not directly follow from the number of nodes on a branch, and therefore is not directly comparable across the phylogeny. Nevertheless, this approach provides a rough

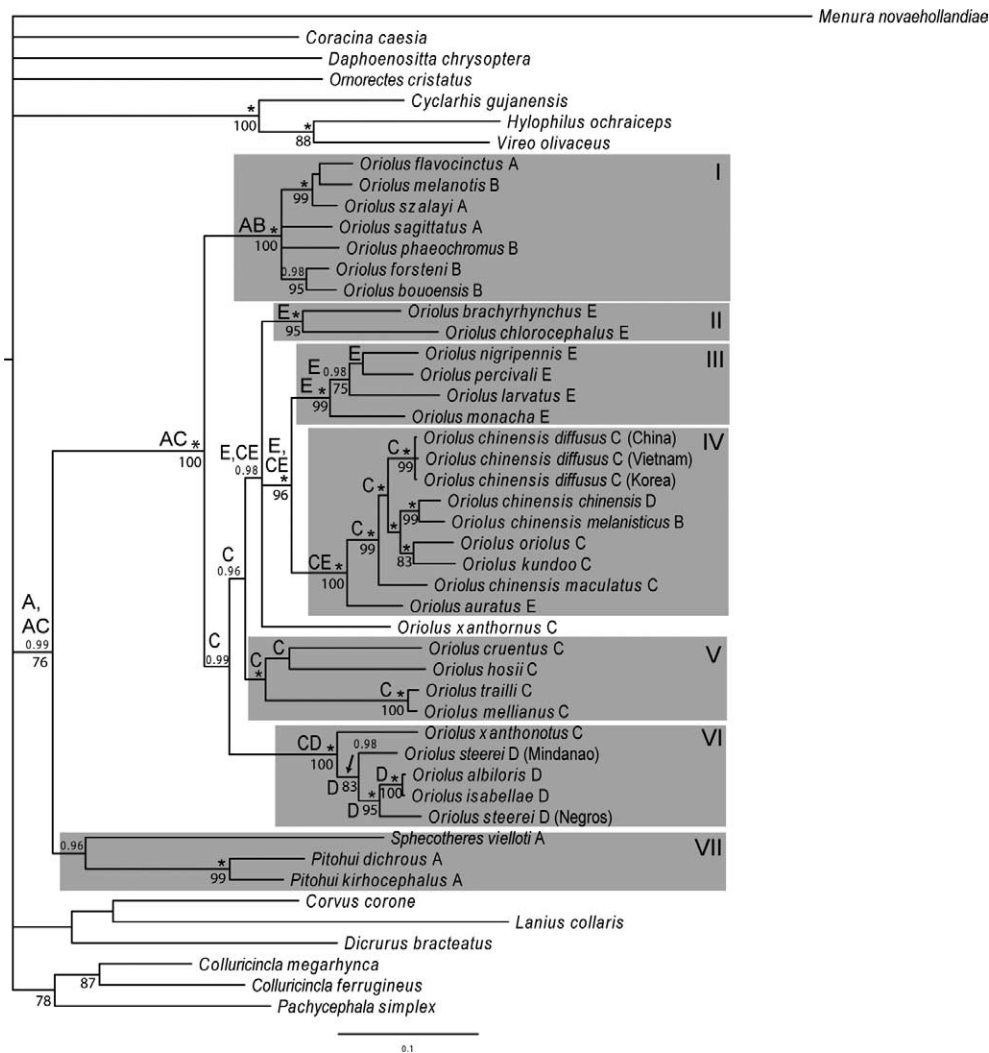


Figure 1. The 50% majority rule consensus tree of Oriolidae obtained from the Bayesian analysis of the combined dataset (GAPDH, ODC, ND2 and ND3). Support values are indicated to the left of the nodes. Above the branch is the posterior probability (only values above 0.95 are shown, asterisks indicate 1.00 posterior probabilities). Below the branch is the maximum likelihood bootstrap value (only values above 70 are shown) from 100 pseudoreplicates. Ancestral areas of origin according to the DIVA analysis are indicated to the left of nodes and present distributions of terminal taxa are indicated after the taxon names (A = Australo-Papua, B = Wallacea, C = Eurasia including, Sumatra, Java and Borneo, D = Philippines and E = Africa). Clades discussed in the text are indicated by roman numerals I–VII.

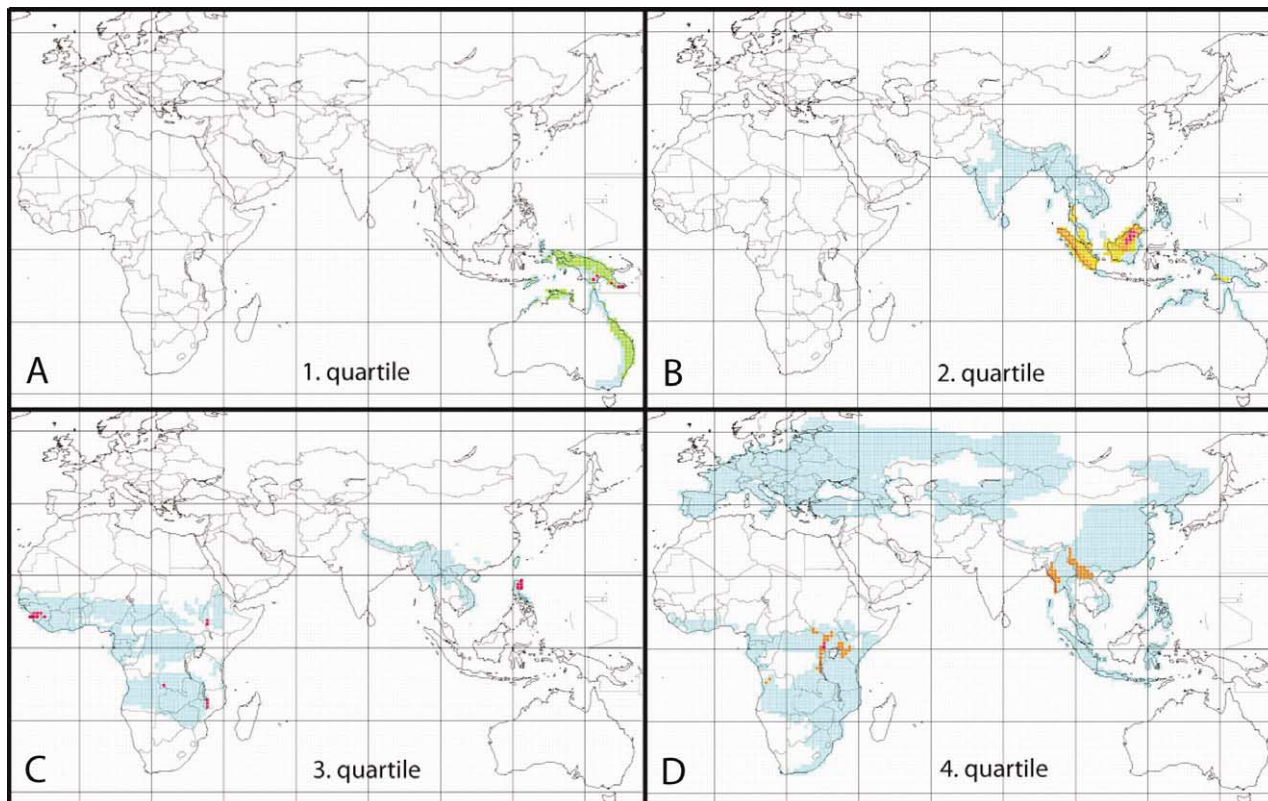


Figure 2. Richness patterns of Oriolidae, according to branch-length groups (number of nodes from the base of the phylogeny). (A) 1st quartile illustrates the distributions of the nine most basal species. (B–C) 2nd and 3rd quartiles illustrate the distribution of the intermediate species in the phylogeny, (D) 4th quartile illustrates the distribution of the nine most terminal species. Light blue colour represents one species, and the warmer colours represent the higher numbers of overlapping species. Highest number of species in one grid is: A: 4, B: 4, C: 2, D: 3.

illustration of an origin in the humid parts of the Australo-Papuan area and a rapid dispersal over to the Eurasian mainland, with diversification in the Greater Sundas (B), and further diversification in Africa (C) and the Orient and a recent back colonisation to Wallacea (D).

### Dispersal-Vicariance analysis

To run an ideal DIVA analysis one would want to include several taxa outside the focal group, such that the basal part of the ingroup is no longer the root of the tree. This is because the reliability of ancestral reconstructions becomes increasingly unreliable towards the root of the tree, which can cause the ancestral distributions at the root to include all areas analysed (Ronquist 1996). Basal relationships among corvid bird families, however, have proven hard to resolve (Jönsson et al. 2008a) and this somewhat confounds the DIVA analysis in this study because we are unable to determine the closest sister groups of Oriolidae. Thus the DIVA analysis presented is conducted exclusively on the ingroup.

The DIVA analysis (Fig. 1 and 3) suggests an Australo-Papuan or a more widespread Australo-Papuan/Eurasian origin of the basal nodes. The widespread Australo-Papuan/Eurasian result is most likely an artefact for the above mentioned reasons. Several other core Corvoidean families have been demonstrated to be of Australo-Papuan origin

(Jönsson et al. 2008a) and with several basal species within Oriolidae occurring in Australo-Papua it seems reasonable to assume that this is also the case for Oriolidae. Because the origin of clade I is hard to determine we present the results from the DIVA analysis where we assumed the origin of clade I to be Australian but we have indicated in the figure that the origin could be both Australo-Papuan and Wallacean.

From the Australo-Papuan region orioles colonised mainland Asia, as indicated by a Eurasian origin of nodes leading to clades II–VI and to clades II–V. Further up the tree we find a colonisation of Africa indicated by an African origin of the nodes leading to clades II, III and III/IV, and within clade IV there is a back-colonisation of Asia from Africa.

### Dating analyses

The results of the BEAST dating analysis (Fig. 3) indicate the origin of Oriolidae to be in the Miocene with a rather deep split 20 Mya between the *Sphecotheses/Pitohui* clade (VII) and all other orioles (clades I–VI). The origin of Oriolus (clades I–VI) is ca 13 Mya. The diversification within the group of Australian and Wallacean brown orioles (clade I) is determined to be rather young at 5 Mya and the origin of clades II–VI and clades II–V when orioles dispersed to Asia is determined to be 12 Mya and 11 Mya,

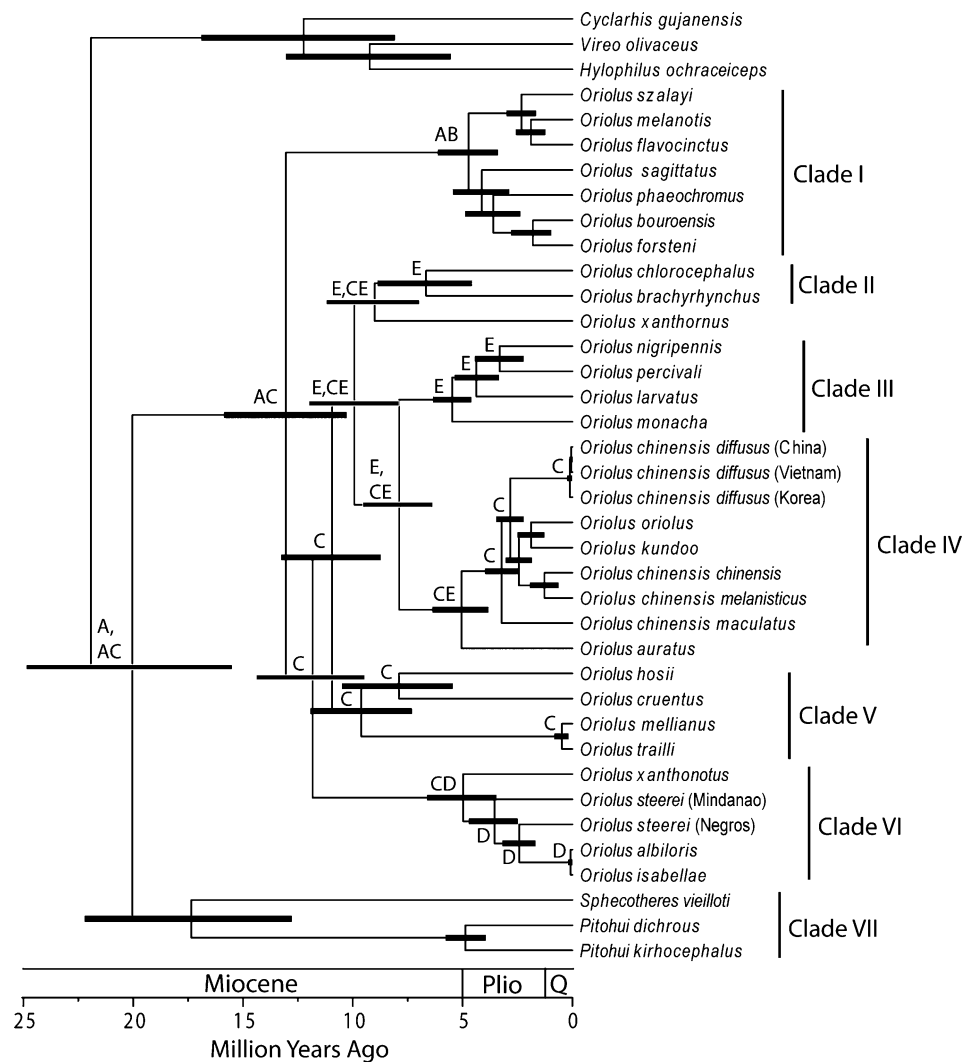


Figure 3. Chronogram based on the BEAST analysis of Oriolidae. ML corrected pairwise distances of ND2 and a recently published rate ( $2.8\% \text{ Myr}^{-1}$ ) of evolution in ND2 for passerine birds were used to calibrate the tree. Bars represent 95% HPD intervals. Ancestral areas of origin according to the DIVA analysis are indicated to the left of nodes (A = Australo-Papua, B = Wallacea, C = Eurasia including, Sumatra, Java and Borneo, D = Philippines and E = Africa). Clades discussed in the text are indicated to the right by roman numerals I–VII.

respectively, whereas dispersal to Africa from Asia (root of clades II–IV and clades III–IV, are found to be between 8 and 10 Mya. Back-colonisation of Asia from Africa (the split between *O. auratus* and *O. chinensis/oriolus/kundoo* is at 5 Mya but dispersal into the Indonesian and Philippine archipelagos by *O. chinensis melanisticus* and *O. c. maculatus* did not happen until 3 Mya. Dispersal to the Philippines from Asia (clade VI) took place at 5 Mya.

## Discussion

### Systematics

The study establishes that Oriolidae (with the inclusion of *Sphecotheres* and two *Pitohui* species) is monophyletic with seven well-supported clades (Fig. 1). Figbirds (*Sphecotheres*) and *Pitohui dichrous* and *P. kirhocephalus* form a clade (clade VII), and this clade is sister to the genus *Oriolus* (all other orioles). It should be mentioned that recent studies

have demonstrated that the genus *Pitohui* is in fact polyphyletic and that several members have been assigned to other genera. Thus the only species left in the genus *Pitohui* are the two species within the family Oriolidae (Jønsson et al. 2008b, 2010). A basal group within *Oriolus* (clade I) includes all the Wallacean brown oriole species and the three Australo-Papuan orioles. Within this assemblage, however, resolution is poor, which may reflect recent rapid radiation and colonisation of Wallacean islands from the Australo-Papuan region.

The “African black-headed orioles” are reconstructed in two distinct clades (clades II and III). The data are equivocal about the relationship between these two clades and they occur in a polytomy that also includes a largely Asian clade (IV) and *O. xanthornus*. One of the African clades (II) contains *O. brachyrhynchus* and the green-headed *O. chlorocephalus*. The rest of the “African black-headed orioles” fall in another clade (III). The golden orioles (including both African and Asian species) are found in the



same clade (IV) and we find clear evidence that *Oriolus chinensis* is polyphyletic. We did not sample all *O. chinensis* subspecies and therefore we can only state that *O. chinensis* populations in mainland Asia (*O. c. diffusus*), the Philippines (*O. c. chinensis* and *O. c. melanisticus*) and the Sunda Islands (*O. c. maculatus*), which are represented in this study, are rather divergent according to DNA data and that species status for at least these three taxa must be considered.

A clade of Philippine orioles (clade VI) has *O. xanthonotus* of Borneo at the base. Here we note that there is only a minor molecular differentiation between *O. albiloris* and *O. isabellae*, perhaps indicating that they should be treated as a single taxonomic unit. Finally, there is a clade (V) of Asian red and black orioles, which includes *O. cruentus*, *O. hosii*, *O. trailli* and *O. mellianus*.

All relationships recovered in the present analyses are in concordance with previously recognised superspecies, the only notable differences being possible polyphyly of the African black-headed assemblages, which fall out as two distinct clades. This, however, may simply be due to poor resolution between clades II, III and IV. Furthermore, *Oriolus xanthornus* has historically been considered part of the red and black Asian clade (V) (Walter and Jones 2008) although it resembles African black-headed orioles by plumage colours. Poor resolution in this part of the phylogeny makes us unable to determine with confidence where it belongs but it does seem to have a closer affinity with the African black-headed species. Evolutionary lability in plumage colours and patterns is seen within many other families of birds such as New World Orioles (Allen and Omland 2003), Minivets (Jönsson et al. 2010) and bush-shrikes (Nguembock et al. 2008). However, this is not the case for Old World orioles, where distinct plumages characterise different lineages.

## Biogeography

Few studies have addressed biogeographical patterns of vertebrates across Wallacea (Hisheh et al. 1998: fruit bats; Evans et al. 2003: frogs), and the focus has mainly been on organisms that have colonised Wallacea from Asia and not vice versa. Michaux (1998) published a paper on birds, which is mostly an expanded list of birds occurring in certain defined subregions within the Indo-Pacific but that study did not include any analyses of colonisation patterns. More detailed studies of passerine birds of Australo-Papuan origin dispersing across and within Wallacea are now appearing (Jönsson et al. 2008c, 2010, Norman et al. 2009), and these studies have demonstrated a marked variation in dispersal patterns between families, reflecting differences in ecology and life-history strategies, and possibly also reflecting their respective times of dispersal.

Oriolidae is an example of a bird family that has colonised Asia from the Australo-Papuan region. Although the results of the DIVA analysis are somewhat ambiguous at the root of the Oriolidae phylogeny, it is most parsimonious to assume a rather restricted Australo-Papuan origin of the group based on the fact that several basal members are at present distributed in Australo-Papua (Fig. 1, 2). The distribution of the brown oriole species (clade I) within Wallacea comprises *O. forsteri* and *O. bouroensis* in the

Ceram-Buru area, part of a microplate that was once connected with the Vogelkop Peninsula of the western Papuan landmass, and *O. melanotis* of Timor/Wetar, which represents a microplate that detached from mainland Australia in the mid-Miocene and rose above sea-level in the late Pliocene (Hall 1998, 2002). Furthermore, *O. phaeochromus* inhabits the North Moluccas, and dates back to Late Pliocene/Pleistocene. These islands are of oceanic origin, but were located very close to the Vogelkop Peninsula at this time (Hall 1998, 2002). These ages and distributions suggest that, although several taxa occur on isolated islands within Wallacea, they may only have dispersed a short distance from New Guinea and then drifted to their current locations. No basal members of Oriolidae occur in Asia (Fig. 2A).

Poor resolution within clade I makes it difficult to evaluate if multiple colonisations of the Moluccas took place in the Plio/Pleistocene or if a historically widespread brown taxon diversified within the archipelago. It was suggested by Diamond (1982) that the brown orioles mimic the larger and rather aggressive friarbirds to avoid competition during feeding. If this were in fact so, convergent brown plumage evolution within the area where friarbirds exist would indeed seem an advantageous adaptation. These brown orioles are the only orioles that have been successful in maintaining populations on Wallacean islands apart from some subspecies of *Oriolus chinensis*, which occur in Talaud, Sulawesi and the Lesser Sunda Islands.

The origin of clades V and VI is Asian and thus the initial colonisation of Asia, did not leave any trace in Wallacea, suggesting long-distance dispersal or extinction of all intervening populations. The lineage diversity maps suggests an initial proliferation in Sundaland (Fig. 2B), and this was followed by large range expansions in Asia (Fig. 2C, D). The red and black orioles in clade V radiated within southeast Asia from around 10 Mya, and orioles in clade VI colonised the Philippines around 4 Mya (possibly via Palawan). From Asia there is evidence of colonisation of Africa in the Late Miocene by the two African black/green-headed clades (II and III), at a time when evergreen humid forest probably extended across northern and central Africa (Fjeldså and Bowie 2008) (Fig. 2C).

The colonisation pattern of Oriolidae is interesting in several ways. At first sight it seems a straight forward dispersal from Australia to Asia and onwards to Africa, which is the general pattern proposed for oscine passerine birds proposed by Barker et al. (2002) and Ericson et al. (2002). However, the initial leap across Wallacea without colonisation of the archipelago is puzzling. Orioles apparently have a great dispersal capacity over land, exemplified by their rapid colonisation of Asia and Africa but are absent from the Melanesian (and other oceanic) archipelagos, which were successfully colonised by several other corvid families (e.g. Pachycephalidae, Campephagidae, Monarchidae).

Colonisation of both the Philippine and Indonesian archipelagos took place in rather recent time and it is tempting to speculate that orioles are poorly adapted to archipelago life and that the recent archipelago colonisations from both Australia and Asia represent a source to sink spill-over from the mainland. It seems probable that when orioles colonised Asia in the Miocene it must have involved a series of island-hopping events within Wallacea



(Indonesian island chain), maybe followed by extinction of populations inhabiting small volcanic islands. Apart from the recent colonisations of the northern Moluccas and the Philippines, orioles are absent from ophiolitic islands (derived from oceanic crust that was uplifted above sea level mainly through volcanism).

Perhaps orioles require rather large and stable land areas with mature forests for the fruits they require, or a vegetation different from the pioneer communities of newly formed islands. They are therefore mostly restricted to the microplates that are close to mainlands and larger land-bridge islands. A better understanding of the ecological requirements of orioles may be essential for interpreting the general rarity of orioles within the Wallacean area.

Likewise there is no obvious reason why orioles have not colonised the Melanesian archipelagos. Orioles have radiated and dispersed to Asia and Africa already in the Miocene, whereas colonisation of the Philippine and the Indonesian archipelagos did not take place until the Pliocene when Palawan was in place as a landbridge between Borneo and Luzon. Competition with other species of frugivorous birds (the fruit pigeons of *Ptilinopus* and *Ducula* are widespread in the Pacific and may be competitors), may have made colonisation of the Philippine and the Indonesian archipelago difficult and also kept orioles completely out of the western Pacific archipelagos.

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