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Resolving deep lineage divergences in core corvoid passerine birds supports a proto-Papuan island origin

Marie Aggerbeck [a,*], Jon Fjeldså [a], Les Christidis [b,c], Pierre-Henri Fabre [a,d], Knud Andreas Jønsson [a,e]

[a] Center for Macroecology, Evolution and Climate at the Natural History Museum of Denmark, University of Copenhagen, Universitetsparken, DK-2100 Copenhagen, Denmark
[b] National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW 2455, Australia
[c] Department of Genetics, University of Melbourne, Parkville, Vic. 3052, Australia
[d] Harvard Museum of Comparative Zoology, 26 Oxford Street, Cambridge, MA 02138, USA
[e] Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot SL5 7PY, UK

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ABSTRACT

It is well established that the global expansion of songbirds (Oscines) originated in East Gondwana (present day Australo-Papua), and it has been postulated that one of the main constituent groups, the "core Corvoidea", with more than 750 species, originated in the first islands that emerged where New Guinea is now located. However, several polytomous relationships remained within the clade, obstructing detailed biogeographical interpretations. This study presents a well-resolved family-level phylogeny, based on a dataset of 22 nuclear loci and using a suite of partitioning schemes and Maximum Likelihood and Bayesian inference methods. Resolving the relationships within the core Corvoidea provides evidence for three well-supported main clades, which are in turn sister to the New Zealand genus *Mohoua*. Some monotypic lineages, which have previously been considered *Incertae sedis*, are also placed in a phylogenetic context. The well-resolved phylogeny provides a robust framework for biogeographical analyses, and provides further support for the hypothesis that core corvoids originated in the proto-Papuan island region that emerged north of Australia in the late Oligocene/early Miocene. Thus, the core Corvoidea appear to represent a true island radiation, which successfully colonized all continents except Antarctica.

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1. Introduction

Passerine birds (Passeriformes) comprise more than half of all extant bird species (>5300 sp., Gill and Donsker, 2012). They are divided into two major groups, Suboscines (Tyranni) and Oscines (Passeri), based on morphology (Raikow, 1982), anatomy (Ames, 1971) and molecular data (Sibley and Ahlquist, 1990; Barker et al., 2004; Hackett et al., 2008). The most basal oscine lineages occur in Australia (Christidis and Schodde, 1991; Ericson et al., 2002; Barker et al., 2004), with some sub-radiations in adjacent island regions, whereas the more terminal oscine lineages underwent extensive diversification and geographical expansions leading to their contemporary global distribution (Ericson et al., 2002; Barker et al., 2004). The two largest clades within the oscines are the Passerida (>3500 species) and an assemblage referred to as the "core Corvoidea" in recent publications. The present study focuses on the core Corvoidea that includes more than 750 species divided in 24 families (Gill and Donsker, 2012).

Core corvoids occur worldwide, and include species-rich families with almost cosmopolitan distributions as well as species poor or even monotypic lineages, most of which are endemic to the rainforests of New Guinea. The large Passerida radiation is nested within a small assemblage of "transitional oscines", which appear to be rooted in New Guinea. The strong contemporary signature of New Guinean taxa at the base of both the Passerida and the core Corvoidea recently led to the proposal of an origin of these radiations in a proto-Papuan archipelago, which later rose to become present-day New Guinea (Jønsson et al., 2011).

Two dispersal scenarios have been proposed: (i) Basal oscines colonised New Guinea from Australia during the Eocene–Oligocene, 25–45 million years ago (Mya), and gave rise to an early insular core corvoid radiation, which subsequently dispersed to Asia and onwards to other continents (Jønsson et al., 2011), or (ii) the core corvoids originally evolved in Australia and spread all other the world, by using the Malesian archipelagos as stepping stones to reach Eurasia (Ericson et al., 2002). The latter however, would imply a greater diversity of core corvoid taxa in Australia than can be seen today, although we may envisage a significant diversity loss due to extinction (Hawkins et al., 2005; Byrne et al., 2011) as most of Australia changed from mesic to arid

* Corresponding author. Address: Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark.
E-mail address: marieag10@gmail.com (M. Aggerbeck).

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climatic conditions in the course of the upper Tertiary (Fujioka and Chappell, 2010).

Both dispersal scenarios are plausible in view of the plate tectonic models for the region. Australia was once part of the supercontinent Gondwana. This broke up around 80 Mya, and the Australian landmass started moving northwards ca 40 Mya and collided with the Eurasian plate some 10–20 Mya (Hall, 2002, 2009). These movements caused an uplift of the proto-Papuan islands in the epicontinental seas over the northern part of the Australasian plate, and the appearance of a volcanic arc (the Sunda Arc) along the plate subduction zone, with a string of islands emerging west of New Guinea towards Eurasia (Hall, 2009). These new islands provided new habitats and may have acted both as a driver for speciation and as stepping-stones for dispersal between Australo-Papua and Asia. In this process, numerous new evolutionary lineages emerged within a relatively short time frame (Jønsson et al., 2011; Kennedy et al., 2012), causing substantial difficulty in defining clades and relationships among them. Some phylogenetic structure has been determined, but a polytomy, or multifurcating phylogenetic node of several core corvoid families has remained (Norman et al., 2009; Jønsson et al., 2011), and some species have still not been assigned to any family.

Polytomies significantly impede reliable assessments of ancestral areas of origin (Ree et al., 2005), and a better resolution of the basal branching pattern of the core Corvoidea was therefore needed to understand historical biogeographical patterns and processes. Polytomies may reflect insufficient data (‘‘soft polytomy’’), but they may also be real (‘‘hard polytomy’’) and reflect conflicting signals in the data as a result of differences among gene trees due to incomplete lineage sorting (Maddison, 1997). A hard polytomy could arise if ancestral populations diversified simultaneously and were non-dichotomously broken up into several daughter species, which could well be the case during a colonization sweep across an archipelago. It is interesting to understand whether the core corvoid families did in fact radiate so fast as to produce a star-like polytomy, or whether a more robust bifurcating phylogeny can be generated, allowing us to determine a specific sequence of vicariance and dispersal events.

In this study we used 22 nuclear markers for 45 passerine bird (32 core corvoids) taxa representing all deep lineages of the core Corvoidea in an attempt to robustly resolve systematic relationships. Analysed within an explicit spatio-temporal framework we use the phylogeny to elucidate biogeographical patterns of dispersal and diversification within core corvoid passerine birds.

2. Methods

2.1. Taxonomic sampling and laboratory procedures

Taxon sampling included 45 taxa of passerine birds (43 oscines) (Table 1), which were chosen to represent all core corvoid family branches identified by previous, more densely sampled studies. 32 taxa represent the 24 families within the core Corvoidea and all *Incertae sedis* taxa, and 11 other taxa represent the Passerida (6 taxa) and the basal oscines (5 taxa). *Acanthisitta chloris* is well established as the sister group to all other passerine birds (Ericson et al., 2002) and was used to root the tree.

22 nuclear loci were chosen as markers (*ALDOB*, *BDNF*, *BRAM*, *CHZ*, *CLTC*, *CRYAA*, *c-MOS*, *c-MYC*, *EEF2*, *EGR1*, *Fib-5*, *GAPDH*, *IRF2*, *Myo2*, *NTF3*, *ODC*, *PCBD1*, *RAG1*, *RAG2*, *RHO*, *TGFb2*, *TPM1*), relying largely on the markers used by Hackett et al. (2008) and some other markers that have proven useful for resolving avian phylogenies. As such, molecular data (19–22 loci) for 8 taxa included in the study by Hackett et al. (2008) were readily available from GenBank. Two nuclear protein-coding loci, RAG1 and RAG2, were sourced from Barker et al., (2004). Additionally, molecular data (6–8 loci) for 3 taxa (*Melampitta*, *Rhagologus* and *Pityriasis*) available on Genbank were included. All other sequences (2–20 loci for 35 species) were generated *de novo* for this study.

Fresh tissue samples were obtained for 35 taxa, and the DNA extracted using a standard Qiagen® kit and sequenced by capillary electrophoresis. Primers were selected based on previous studies (Table 2). A standard protocol of 10 μl dNTPs (10 μM), 6.5 μl ddH_2O, 2.5 μl buffer, 2 μl forward primer (10 μM), 2 μl reverse primer (10 μM) and 0.1–0.2 μl enzyme (AmpliTaq® DNA Polymerase) was employed, using standard kit reagents and buffers from Invitrogen®. All DNA sequences were deposited on GenBank (Table 3).

2.2. Sequence alignment

PCR products were sequenced in both directions by Macrogen Inc., using an ABI 3730xl sequencing machine. The raw sequences obtained were assembled into contigs using Sequencher 5.0 (GeneCodes Corp.) and along with additional sequences downloaded from GenBank aligned in SeaView (Gouy et al., 2010), using the MUSCLE alignment algorithm. (Edgar, 2004). We repeated the alignment process using MAFFT v6 (Katoh et al., 2002 and Katoh and Toh, 2008, http://www.ebi.ac.uk/Tools/msa/mafft/). All analyses were run using both alignments. Inspecting each individual alignment did not reveal any unusual misalignments and we therefore did not modify any of the alignments further. All sequences were examined using the BLAST tool in GenBank (Altschul et al., 1990), and coding regions were checked for the presence of indels or stop codons that may have disrupted the reading frame.

2.3. Data partitioning

We used Modeltest 3.7 (Posada and Crandall, 1998) to determine the most appropriate model of nucleotide evolution for each locus following the Akaike Information Criterion (AIC). A supermatrix was then constructed for the entire dataset, which resulted in a concatenated alignment of 22 loci for 45 taxa with a total length of 19,782 base pairs (bp) (Table 4). A preliminary analysis of 20 million generations in MrBayes (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) was run for each gene partition to provide an initial notion of the resolution of the phylogenies, as well as identifying any misidentified taxa or spurious sequences.

We separated exons from introns and trimmed these to GenBank annotations, as well as codon-aligning separate exons, to produce a concatenated exon alignment and a concatenated intron alignment, which were analysed separately. Modeltest was used to determine the most appropriate model for each partition in the two datasets. Because exons code for amino acids, we translated the bases of the exon alignment into an amino acid alignment, by way of the align-by-codons direct translation option in MEGA 5.0 (Tamura et al., 2011). This allows for a direct detection of stop-codons, which suggests that the gene is non-functional and therefore should not be used in the phylogenetic analysis. It also allows for analysing the exon data both by base pairs and by amino acids.

2.4. Testing for selection

The individual and the concatenated exon alignments were tested for traces of positive or negative selection using MEGA 5.0 (Tamura et al., 2011) and the implemented HyPhy application (Pond and Muse, 2005), set up with codon-aligned alignments, using all sites, and a neighbour-joining starting tree. We tested this to avoid using any exons under positive or purifying selection (Seabury et al., 2004), as such exons might cause a biased phylogenetic signal (Swanson et al., 2001).

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