



A supermatrix phylogeny of corvid passerine birds (Aves: Corvides)[☆]



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ABSTRACT

The Corvides (previously referred to as the core Corvoidea) are a morphologically diverse clade of passerine birds comprising nearly 800 species. The group originated some 30 million years ago in the proto-Papuan archipelago, to the north of Australia, from where lineages have dispersed and colonized all of the world's major continental and insular landmasses (except Antarctica). During the last decade multiple species-level phylogenies have been generated for individual corvid families and more recently the inter-familial relationships have been resolved, based on phylogenetic analyses using multiple nuclear loci. In the current study we analyse eight nuclear and four mitochondrial loci to generate a dated phylogeny for the majority of corvid species. This phylogeny includes 667 out of 780 species (85.5%), 141 out of 143 genera (98.6%) and all 31 currently recognized families, thus providing a baseline for comprehensive macroecological, macroevolutionary and biogeographical analyses. Using this phylogeny we assess the temporal consistency of the current taxonomic classification of families and genera. By adopting an approach that enforces temporal consistency by causing the fewest possible taxonomic changes to currently recognized families and genera, we find the current familial classification to be largely temporally consistent, whereas that of genera is not.

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1. Introduction

Oscine passerine birds comprise more than one third of global avian species diversity. The group is comprised of basal lineages (Menuroides, Climacterides, Meliphagides and Orthonychides) largely confined to Australasia, in addition to two cosmopolitan groups, the Passerides (>3500 species) and the Corvides (c. 800 species; Cracraft, 2014). Both the Passerides and the Corvides likely underwent rapid radiation early in their evolution, which has led to great difficulty in resolving the sequence of the oldest diversification events. Recent work has, however, provided a more refined picture of the deeper (inter-familial) systematic relationships within the Corvides (Aggerbeck et al., 2014). In addition, some taxonomically broader studies have included some new species into the Corvides, such as the genera *Ptilorrhoa* (Norman et al., 2009b), *Mohoua* (Norman et al., 2009b), *Erpornis* (Barker et al., 2004) and *Pteruthius* (Reddy and Cracraft, 2007), while others have

been excluded, such as *Hylocitrea* (Jønsson et al., 2008a), *Pachycare* (Norman et al., 2009a) and *Chelidorhynch* (Nyári et al., 2009).

The highest current diversity of Corvides is on the island of New Guinea, where a maximum of 93 species co-occur within a single 110 × 110 km grid-cell. This observation, in concordance with spatio-temporal biogeographical analyses, suggests that the group originated on islands in the area that now forms modern day New Guinea, probably in the Oligocene/Eocene era (Jønsson et al., 2011; Aggerbeck et al., 2014). From here, some ancestral lineages dispersed, resulting in global colonization and radiation (Jønsson et al., 2011; Aggerbeck et al., 2014). The occurrence of a number of species-poor corvid families endemic to New Guinea (e.g. Eulacestomatidae, Ifritidae, Paramythiidae and Melampittidae) suggests that the island might have served as a refugium during periods of climatic and environmental change. Thus, it appears that New Guinea may represent both a cradle and a species pump for the Indo-Pacific island region.

Members of the Corvides show high adaptational diversity, including some species-poor ancient clades of highly specialized species (e.g. *Ifrita*, *Eulacestoma* and *Daphoenositta*) as well as some dispersive and widely distributed groups that have diversified extensively (e.g. Monarchidae, Pachycephalidae, Corvidae).

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Members of the Corvidae have colonized all continental (except the Antarctica) landmasses, and can be found in all terrestrial habitats. Within the group there are multiple examples of both continental and insular radiations that are seemingly non-adaptive (e.g. Monarchidae, Vireonidae and Pachycephalidae), where the lineages have diversified and expanded over large geographic areas, without significant morphological divergence. Conversely, other clades are suggested to represent adaptive radiations (the Madagascan vanga family; Jønsson et al., 2012a) or reflect the consequence of strong sexual selection (birds-of-paradise; Irestedt et al. (2009). However, despite the proposed differences in diversification dynamics among corvid lineages, there is yet no general assessment of the relative importance of adaptive and non-adaptive processes in the evolution of the clade; this is mainly due to the lack of a broad species-level phylogenetic hypothesis.

In this study, we combine existing molecular data into a single supermatrix to produce a phylogenetic hypothesis that encompasses the vast majority of corvid species (667 species out of 780 species; Gill et al., 2010). This phylogeny provides a baseline for future macroecological, macroevolutionary and biogeographical analyses. Additionally, we delimit hierarchical taxonomic groups based on the temporal banding approach proposed by *Avice and Johns (1999)* and *Holt and Jønsson (2014)*. This allows for a temporally consistent delimitation of higher taxonomic hierarchical groups (families and genera).

2. Methods

2.1. Taxonomic sampling and sequence data

The taxonomy follows the IOC World Bird List version 2.7 (766 Corvidae species) (Gill et al., 2010) with the addition of taxa that have been established to belong within the Corvidae: *Cinclosoma* (5 species), *Ptilorrhoa* (4 species), *Paramythia montium*, *Oreocharis arfaki* and *Turnagra capensis*. Additionally, we included a further two taxa: *Hypothymis puella* previously considered a subspecies of *Hypthymis azurea* and *Cracticus argenteus* previously considered a subspecies of *Cracticus torquatus*. In total, we consider 780 Corvidae taxa in the current study (Table 1 and S1).

To collect suitable genes for the supermatrix assembly, DNA sequences of Corvid species were downloaded from GenBank. We focused on eight nuclear (c-mos, Fib-5, GAPDH, Myo2, ODC, RAG-1, RAG-2 and TGFb2) and four mitochondrial (COI, cyt-b, ND2 and ND3) genes, which have been used extensively to infer corvid phylogenies in recent years (e.g. Cicero and Johnson, 2001; Pasquet et al., 2002, 2007; Cibois et al., 2004; Fuchs et al., 2004, 2006, 2007, 2012; Ericson et al., 2005; Filardi and Moyle, 2005; Reddy and Cracraft, 2007; Irestedt et al., 2008, 2009; Jønsson et al., 2008a, 2008b, 2008c, 2010a, 2010b, 2010c, 2010d, 2011, 2012a, 2012b, 2014; Fabre et al., 2012, 2014; Norman et al., 2009b; Nyári et al., 2009; Kennedy et al., 2012; Toon et al., 2012, 2013; Kearns et al., 2013; Aggerbeck et al., 2014; Slager et al., 2014; Andersen et al., 2015). When possible, we selected sequences from the same vouchered specimens, including all sequences available to us as of December 2014. In addition, we included 12 newly generated sequences (deposited on Genbank: KP726920–KP726931). Finally, 13 outgroup taxa spanning all other major passerine lineages were included (Barker et al., 2004; Ericson et al., 2002; Aggerbeck et al., 2014): *Acanthisitta*, *Bombicilla*, *Callaenas*, *Climacteris*, *Cnemophilus*, *Malurus*, *Melanocharis*, *Menura*, *Orthonyx*, *Petroica*, *Picathartes*, *Pitta*, *Pomatostomus*.

We estimated the partial decisiveness of the supermatrix as the percentage of possible trees for which the supermatrix is decisive (Sanderson et al., 2010). The decisiveness quantifies the degree to which multiple loci with incomplete taxon coverage supplement

Table 1
Taxonomic coverage at family-level.

Families according to Gill et al. (2010)	N species	N species in tree	% Species in tree
Corvidae	127	114	89.8
Laniidae	33	29	87.9
Ifritidae	1	1	100.0
Monarchidae	93	88	94.6
Melampittidae	2	2	100.0
Paradisaeidae	41	40	97.6
Corcoracidae	2	2	100.0
Rhipiduridae	46	33	71.7
Dicruridae	22	19	86.4
Vangidae	31	29	93.5
Prionopidae	8	3	37.5
Platysteriidae	30	20	66.7
Malaconotidae	48	30	62.5
Pityriaseidae	1	1	100.0
Aegithinidae	4	1	25.0
Cracticidae	13	12	92.3
Artamidae	11	7	63.6
Machaerirhynchidae	2	2	100.0
Rhagologidae	1	1	100.0
Campephagidae	92	76	82.6
Neosittidae	3	1	33.3
Pachycephalidae	51	46	90.2
Oriolidae	35	35	100.0
Cinclosomatidae	9	8	88.9
Falcunculidae	1	1	100.0
Psophodidae	5	5	100.0
Oreoicidae	3	3	100.0
Vireonidae	59	52	88.1
Paramythiidae	2	2	100.0
Eulacestomatidae	1	1	100.0
Mohouidae	3	3	100
Corvidae	780	667	85.51

each other to fully resolve phylogenetic relationships among species. A pattern of taxon coverage is decisive if the underlying true tree can be uniquely defined by combining the partially resolved subtrees generated from each locus. As the decisiveness of a given taxon coverage depends on the topology of the underlying true tree, which is not known, the decisiveness must be estimated as a probability. We used the program Decisivor (available from <https://github.com/josephwb/Decisivor> accessed on 3 June 2015) to calculate the partial decisiveness based on 1,000 random trees, using a binary matrix as an input with information regarding the presence or absence of loci.

2.2. Phylogenetic analyses

DNA sequences were aligned for each gene individually using MAFFT (Katoh et al., 2002), with the resulting alignments manually checked and where necessary corrected, in SEAVIEW (Gouy et al., 2010). Each of the 12 gene partitions were then analyzed separately in BEAST (Drummond et al., 2012) applying the best fitting model of nucleotide evolution as determined by the Akaike Information Criterion (AIC) in Modeltest 3.7 (Posada and Crandall, 1998) (Table 2). Analyses of the individual gene partitions were run for 100 million generations using a relaxed uncorrelated log-normal distribution for the molecular clock model, and assuming a Yule speciation process as a tree prior. These analyses allowed for an initial quality check of the sequence data, enabling us to detect any spurious sequences.

For analyses of the complete dataset, we generated a concatenated alignment of all 12 genes that included a total of 10,601 base pairs. Our initial analysis was run for 40 million generations after which we generated a maximum clade credibility (MCC) tree,

Table 2

Alignment details. Length of the alignments, the number of taxa available for each alignment and the best models of nucleotide substitution, as estimated using Modeltest following the Akaike Information Criterion.

Genes	N base pairs	N taxa (ingroup)	Substitution model (AIC)	Chromosome
<i>Mitochondrial genes</i>	3,187	654		
Cytochrome b (<i>cyt-b</i>)	1,143	344	TVM + I + Γ	Mitochondrial
Cytochrome oxidase subunit 1 (<i>COI</i>)	652	119	GTR + I + Γ	Mitochondrial
NADH dehydrogenase 2 (<i>ND2</i>)	1,041	580	GTR + I + Γ	Mitochondrial
NADH dehydrogenase 3 (<i>ND3</i>)	351	262	GTR + I + Γ	Mitochondrial
<i>Nuclear non-coding (introns)</i>	2,778	503		
Beta-fibrinogen intron-5 (<i>fib5</i>)	596	175	GTR + Γ	4
Glyceraldehyde-3-phosphodehydrogenase intron-11 (<i>GAPDH</i>)	297	375	TVM + Γ	1
Myoglobin intron-2 (<i>Myo2</i>)	675	331	TVM + Γ	1
Ornithine decarboxylase introns 6–7 (<i>ODC</i>)	638	319	GTR + I + Γ	2
Transforming growth factor, beta 2 intron-5 (<i>TGFb2</i>)	572	196	GTR + Γ	3
<i>Nuclear coding (exons)</i>	4,636	200		
Oocyte maturation factor Mos (<i>c-mos</i>)	603	136	TrN + I + Γ	4
Recombination activating protein 1 (<i>RAG1</i>)	2,881	139	GTR + I + Γ	11
Recombination activating protein 2 (<i>RAG2</i>)	1,152	63	TVM + I + Γ	11
<i>Nuclear</i>	7,514	511		
Concatenated	10,601	667		

which was then used as a starting tree in the subsequent analyses. As in the analyses of the individual loci we implemented a relaxed uncorrelated lognormal distribution for the molecular clock model, and assumed a Yule speciation process as a tree prior. We considered three nucleotide substitution partitions, one for the mitochondrial genes (GTR + I + Γ), one for the nuclear coding (exon) genes (GTR + I + Γ) and one for the nuclear non-coding (intron) genes (GTR + I + Γ). The final analysis was run for 1 billion generations. Convergence diagnostics were assessed in Tracer (Rambaut and Drummond, 2007), by determining the Effective Sample Size (ESS) and mean distribution values. The final output tree was summarized in TreeAnnotator (Drummond and Rambaut, 2007) as an MCC tree after discarding 75 million generations as burnin. Several of these analyses were run on the Cipres Science Gateway at <http://www.phylo.org> (Miller et al., 2011).

2.3. Calibrating the tree

We used three fossils determined to be Corvidae as calibration points for dating the tree. All fossils were from the Miocene, and provide minimum ages for their respective lineages. We used offset exponential distributions as priors for these calibrations, following Ericson et al. (2014). The first fossil is considered an oriolid (Oriolidae) from the Early Miocene (16.3–23 Mya) deposits of Australia (Boles, 1999). This calibration point was used to date the divergence leading to members of the genera *Oriolus*, *Sphecotheres*, *Turnagra*, *Pitohui dichrous* and *Pitohui kirhocephalus* (offset = 16.3, mean = 2, 95% HPD interval = 16.35–23.68 Mya). The second fossil is considered a cracticid (Cracticidae), also from the Early Miocene (16.3–23 Mya) deposits of Australia (Nguyen et al., 2013). This calibration point was used to date the divergence leading to members of the genera *Peltops*, *Cracticus*, *Strepera* and *Gymnorhina* (offset = 16.3, mean = 2, 95% HPD interval = 16.35–23.68 Mya). The third fossil is considered a corvid (*Miocitta*, Corvidae) from the late Miocene (13.6–15.97 Mya) deposits of Colorado, USA (Brodkorb, 1972; Becker, 1987). This calibration point was used to date the divergence leading to members of the genera *Calocitta*, *Cyanocitta*, *Cyanocorax*, *Gymnorhinus* and *Aphelocoma* (offset = 13.6, mean = 1, 95% HPD interval = 13.63–17.29 Mya). These three fossil calibrations represent each of the three main Corvidae clades (denoted with a C in Fig. 1). In a separate analysis, we used a concatenated alignment of ND2 and *cyt-b* and applied a rate of 0.01 substitutions per site per lineage per million years, reflecting the “2% per-million-year rule” (Weir and Schluter, 2008).

To compare topological similarity to other recent avian super-trees, we extracted all members of the Corvidae from the phylogenies of Burleigh et al. (2015), Davis and Page (2014) and Jetz et al. (2012). We calculated Robinson-Foulds (RF) distances (Robinson and Foulds, 1981; Steel and Penny, 1993) using the *phangorn* package (Schliep, 2011) in R (R Development Core Team, 2014). Robinson-Foulds distances evaluate the number of topological changes between pairs of unrooted phylogenetic trees, in terms of the position of internal nodes required to convert one phylogeny into another. Inherent in this metric is that comparisons between trees that contain a larger number of taxa will require a greater number of changes, and hence generate higher RF values. Therefore, in addition to comparing the topology of our phylogeny to the alternative supertrees individually, we also pruned the trees to contain only species that were shared across all trees. For the Jetz et al. (2012) tree, we compared both the complete tree (which places some species based on taxonomic information rather than sequence data), and the “data only” tree (which considers only those species for which DNA sequence data was available).

2.4. Temporal banding to delimit consistent Corvidae families and genera

Building on work by Avise and Johns (1999) and Holt and Jönsson (2014), we used a temporal banding approach to suggest revisions to the higher taxonomic groups of the Corvidae. This approach creates temporally consistent higher taxonomic delimitations by splitting a dated phylogeny at specific points in time, such that the descendent species of the independent lineages form taxonomic units. While this approach delimits taxonomic groups in a transparent manner, there are currently no clear guidelines on how to select the most appropriate temporal cut-off points. We therefore adopted a “least disruption” approach to our taxonomic revision, aiming to make the fewest possible changes to current hierarchical taxonomic groups, while simultaneously enforcing temporal consistency. To do this, we tested all possible nodal cut-off points for the MCC tree (derived from the analyses of the concatenated dataset of all 12 genes), and compared the resulting independent clades to existing families and genera in the current taxonomy. We evaluated the extent of disruption as the “percentage consistency” with the original taxonomy, by considering pairwise comparisons of species and categorizing each species pair in one of the following categories: (1) “Splits”: pairs of species that were originally in the same taxonomic group are

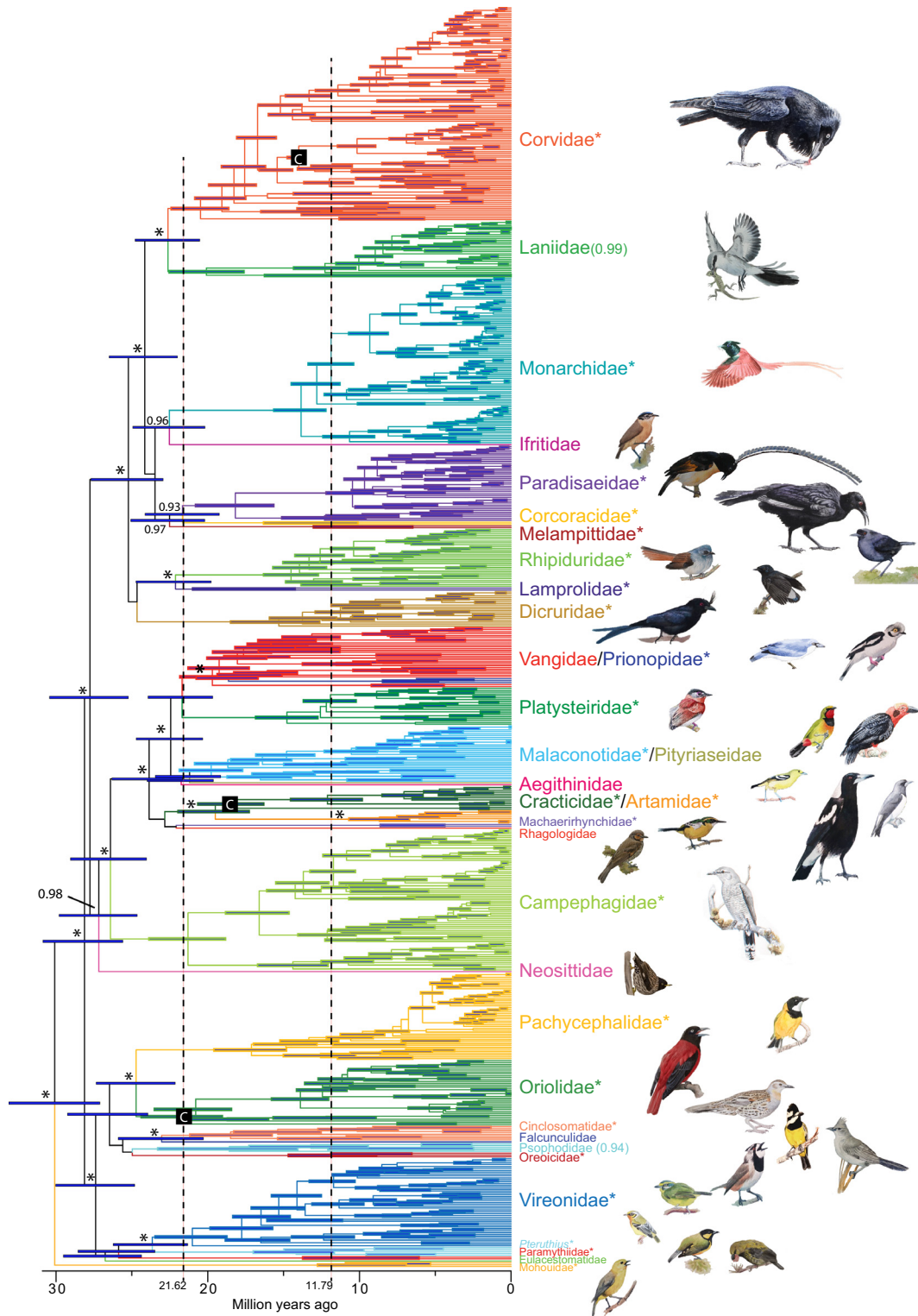


Fig. 1. Time calibrated maximum clade credibility (MCC) tree from the analyses of 12 genes (8 nuclear and 4 mitochondrial) including 667 out of 780 (85.5%) Corvidae species. Clades are colored according to currently considered families with names given to the right of clades. Posterior probabilities are provided for nodes at the base of the tree up to the level of families. Asterisks indicate a posterior probability of 1.00. Horizontal bars indicated 95% Highest Posterior Density (HPD) intervals. Dotted vertical lines indicate the least disruptive delimitation of families and genera. Currently recognized families to be lumped according to temporal banding are combined to the right. There are two cases in which currently recognized families should be split according to temporal banding. These cases involve the Vireonidae and the Oriolidae, where the clade to be split has been colored in a different tone. The three calibration points are indicated by a black box with a white C. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

now in a different groups, (2) “Lumps”: pairs of species that were originally in different groups are now in the same group, and (3) “Unchanged”: pairs of species in the same group that remain in

the same group. The final possibility, pairs of species in different groups that remain in different groups, was not considered. Total consistency was calculated as the proportion of the total of the

pairwise species comparisons in all categories (i.e. 1 + 2 + 3) that were assigned as “Unchanged” (i.e. 3). The R code to perform this analysis is uploaded on Dryad, doi:10.5061/dryad.v0np1.

3. Results

We included 3,038 DNA sequences for 667 out of 780 species (85.5%) of the Corvidae (Table 1 and S1). The dataset included four mitochondrial and eight nuclear genes with a mean of 4.6 (median = 4) loci and 3352 base pairs (median = 2,584, min = 257) analyzed per species. The resulting concatenated dataset included 10,601 nucleotides, with 62% of the matrix representing missing character states. This dataset contains members of all 31 families and 141 out of 143 genera (98.6%), missing only the monotypic *Eutrachomyias* and *Urolestes* (Gill et al., 2010). The partial decisiveness of the supermatrix for the 667 species was 0.933, suggesting it is decisive for 93.3% of all possible trees.

3.1. Phylogenetic analyses

Upon obtaining a suitable starting tree, analyses of the concatenated dataset converged after 60 million generations; however, we ran the analysis for a further 940 million generations to explore the likelihood surface and reduce the risk of being stuck on local optima. Effective Sample Size (ESS) values were all higher than 200, suggesting little auto-correlation between the samples. The alignment, MCC tree and 1,000 randomly selected trees from the post burn-in posterior distribution have been uploaded on Dryad, doi:10.5061/dryad.v0np1.

The resulting MCC tree (Fig. 1) was then compared with previous phylogenetic hypotheses of the Corvidae, most notably the backbone as per Aggerbeck et al. (2014) in addition to various family level trees (e.g. Cicero and Johnson, 2001; Pasquet et al., 2002, 2007; Cibois et al., 2004; Fuchs et al., 2004, 2006, 2007, 2012; Ericson et al., 2005; Filardi and Moyle, 2005; Reddy and Cracraft, 2007; Irestedt et al., 2008, 2009; Jönsson et al., 2008a, 2008b, 2008c, 2010a, 2010b, 2010c, 2010d, 2011, 2012a, 2012b, 2014; Fabre et al., 2012, 2014; Norman et al., 2009b; Nyári et al., 2009; Kennedy et al., 2012; Toon et al., 2012, 2013; Kearns et al., 2013; Aggerbeck et al., 2014; Slager et al., 2014; Andersen et al., 2015). Discrepancies involved poorly supported nodes and as such can be attributed to stochasticity in the phylogenetic analyses as well as lack of resolving power due to the number of loci included. We recovered the same three main clades as Aggerbeck et al. (2014), with Mohouidae as the sister clade to these. We note that

the phylogenetic position of some ancient New Guinean lineages remain contentious and can only be placed with little or no support (e.g. Iffitidae, Machaerirhynchidae, Cinclosomatidae, Falcunculidae, Psophodidae, Oreocidae, Eulacestomatidae). Dating analyses using the three fossil calibration points (see Fig. 1) provide similar results to those of Jönsson et al. (2011), Kennedy et al. (2012), Aggerbeck et al. (2014) and Ericson et al. (2014), with the origin of the Corvidae estimated to be at 30.1 Mya (95% HPD intervals 27.1–33.1 Mya). Dating estimates in concordance with the “2% rule” pushes the origin of the Corvidae back to 38.5 Mya (95% HPD intervals 33.6–43.4 Mya).

Estimates of the Robinson-Foulds distances (Table S2) suggest that our phylogenetic hypothesis of the Corvidae is topologically most similar to the “data-only” MCC tree generated by Jetz et al. (2012). The next most similar tree is the tree generated by Davis and Page (2014), closely followed by the tree generated by Burleigh et al. (2015), which however has more species. Finally the tree generated by Jetz et al. (2012) with species included for which no data was available is the most dissimilar tree. To avoid the problem of uneven sampling, we calculated Robinson-Foulds distances for the same trees including only the 263 shared species. This analysis suggests that the “data only” tree generated by Jetz et al. (2012) is still the most similar, followed by the tree generated by Burleigh et al. (2015), which is in turn closely followed by the tree generated by Davis and Page (2014).

3.2. Temporal banding to determine consistent lineage-based families and genera

Fig. 2 shows the results of our temporal banding “least disruption” analysis, which resulted in the selection of cut-points producing 127 genera (splitting the phylogeny at 11.79 Mya) and 30 families (splitting the phylogeny at 21.62 Mya), with 51 genera and 22 families unchanged from the current taxonomy. Full details of the revised taxonomy are shown in Tables S3–S5. The temporal banding of the Corvidae supports recent work by Schodde and Christidis (2014), who proposed several new families (e.g., Iffitidae, Lamprolidae and Rhagologidae). In addition, temporal banding further suggests that *Pteruthius*, which is currently a genus within the Vireonidae, should be considered its own family. Furthermore, Prionopidae is nested within Vangidae, and Pityriaseidae may best be considered part of the Malaconotidae, although this relationship was recovered with low support. Finally, temporal banding suggests that Cracticidae and Artamidae should together be considered a single family.

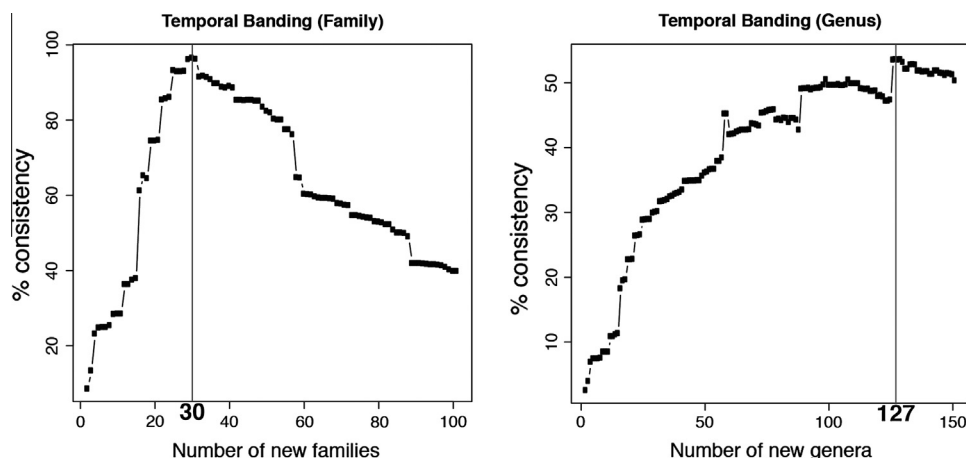


Fig. 2. Results determining the cut-off point for the least disruptive temporal banding for families and genera for the Corvidae. At family level the most consistent number of groups is 31 and the tree should be cut at 22.09 Mya. At the genus level the most consistent number of groups is 127 and the tree should be cut at 11.95 Mya.

4. Discussion

4.1. Toward a complete species level phylogeny of the Corvidae

A decade ago, Jönsson and Fjeldså (2006) generated a supertree for oscine passerine birds, which included 171 species (<25%) belonging to Corvidae. This supertree had no branch lengths and provided no statistical support values for the proposed phylogenetic relationships. Since then phylogeneticists have generated substantial amounts of additional sequence data and recently Jetz et al. (2012) summarized the state of the avian tree of life in an analysis that included DNA sequence data for roughly two thirds of all bird species. For the Corvidae, Jetz et al. (2012) included data for 478 species, and subsequent supertrees have included 461 species (Burleigh et al., 2015) and 303 species (Davis and Page, 2014). Despite the Corvidae part of the tree generated by Jetz et al. (2012) being the most similar to our tree (Table S2), many relationships are inconsistent with those proposed herein based on a greater number of loci and DNA base pairs. These differences likely reflect the nature of the tree assembly methodology used by Jetz et al. (2012), which, while certainly an improvement from Jönsson and Fjeldså (2006), involved grafting clades onto a backbone tree, in addition to placing more than 3,000 out of the 10,000 species based on current taxonomy. These uncertainties have resulted in many spurious systematic relationships and dubious branch lengths across the tree (Ricklefs and Pagel, 2012).

In this study we have included 667 out of 780 species of the Corvidae proposed by Gill et al. (2010), representing 85.5% of the total diversity. This is a major increase in the number of species sampled in comparison with previous phylogenetic hypotheses, and this improvement should facilitate a variety of macroevolutionary and macroecological analyses at the species level. The tree is congruent with previous analyses of subsets (families and genera) within the Corvidae and is well sampled toward the root, such that the majority of the 113 missing species are nested within terminal radiations. The backbone (family-level interrelationships) of our Corvidae tree is similar to the backbone of the tree by Aggerbeck et al. (2014), who used 22 nuclear genes, but differs from the poorly resolved family-level tree generated by Selvatti et al. (2015), who used only five mitochondrial and four nuclear genes. The same four nuclear genes used by Selvatti et al. (2015) were also used by Jönsson et al. (2011). Both analyses clearly demonstrate that resolution of the relationships among corvid families cannot be achieved utilizing these genes alone.

4.2. Systematics and consistent taxonomy of the Corvidae

We used the Corvidae MCC tree to propose a temporally consistent delimitation of families and genera. Our results suggest that families within Corvidae are generally temporally consistent with only marginal changes required. These changes involve: (1) defining *Pteruthius*, which is currently part of the Vireonidae, as a separate family; (2) treating Lamprolidae as a separate family, including the genera *Lamprolia* and *Chaetorhynchus*, as already suggested by Schodde and Christidis (2014); (3) treating Prionopidae as part of the Vangidae, as already suggested by Fuchs et al. (2012); and (4) treating Cracticidae and Artamidae as a single family. Finally, we note that while a temporally consistent delimitation supports treating Pityriaseidae as part of the Malaconotidae, this relationship lacks statistical support. For genera the situation is more complex and requires a much greater amount of renaming, and possibly the addition of more molecular data to confidently establish phylogenetic relationships around the genus-level time limits.

These new hierarchical ranks improve on traditional taxonomic units in that each rank represents the same amount of evolutionary history across the clade, and that their definition is transparent and reproducible. Our analysis further demonstrates that this improvement can be achieved without major changes in the current taxonomy, by judiciously selecting the cutoff time for temporal banding. These new groups represent more objective comparable units for analyses of evolutionary trends, such as variation in diversification rates and phenotypic divergence. At the genus level it appears that, despite our aim to minimize taxonomic disruption, a greater number of changes are necessary to obtain a temporally consistent taxonomy. However, our temporally consistent taxonomy may stimulate a re-evaluation of certain genera within Corvidae, while highlighting that a consistent delineation at least at family level is both theoretically achievable, and practically feasible.

5. Conclusions

In this study we provide a phylogenetic hypothesis based on a supermatrix of 12 nuclear and mitochondrial genes including 85.5% of the species diversity of Corvidae. This phylogenetic tree provides a robust baseline for further macroecological, macroevolutionary and biogeographical analyses. Finally, these analyses highlight the potential to delimit temporally consistent families and genera, and suggest that the current familial classifications are largely temporally consistent, whereas those of genera are not.

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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.2015.08.020>.

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