



## The origin and phylogenetic relationships of the New Zealand ravens



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### ABSTRACT

The relationships of the extinct New Zealand ravens (*Corvus* spp.) are poorly understood. We sequenced the mitogenomes of the two currently recognised species and found they were sister-taxa to a clade comprising the Australian raven, little raven, and forest raven (*C. coronoides*, *C. mellori* and *C. tasmanicus* respectively). The divergence between the New Zealand ravens and Australian raven clade occurred in the latest Pliocene, which coincides with the onset of glacial deforestation. We also found that the divergence between the two putative New Zealand species *C. antipodum* and *C. moriorum* probably occurred in the late Pleistocene making their separation as species untenable. Consequently, we consider *Corax antipodum* (Forbes, 1893) to be a subspecies of *Corvus moriorum* Forbes, 1892. We re-examine the osteological evidence that led 19th century researchers to assign the New Zealand taxa to a separate genus, and re-assess these features in light of our new phylogenetic hypotheses. Like previous researchers, we conclude that the morphology of the palate of *C. moriorum* is unique among the genus *Corvus*, and suggest this may be an adaptation for a specialist diet.

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### 1. Introduction

Recent studies have argued that the core Corvoidea (crows, jays, and magpies) originated in what is now Wallacea in the late Oligocene/early Miocene and dispersed via the Indo-Pacific archipelago to the rest of the world (Jønsson et al., 2011). Subsequent work has concluded that the crows (genus *Corvus*) originated in the Palaearctic in the early Miocene and dispersed to North America and the Caribbean, Africa and Australasia (Jønsson et al., 2012). The colonization of Wallacea by the crows is likely to have taken place in the late Miocene, leading to further colonization of Australo-Papua around 5 Ma (Jønsson et al., 2012, 2016). Evidence for four colonization events of the Pacific from Asia and Australia have been found (Jønsson et al., 2012).

Following the work of Jønsson and colleagues, two clades of the genus *Corvus* are now recognised in Australia: the Australian ravens, comprising the Australian raven (*C. coronoides*), little raven (*C. mellori*), and forest raven (*C. tasmanicus*); and the Australian crows, which include the little crow (*Corvus bennetti*), Torresian crow (*Corvus orru*), along with the Bismarck crow (*Corvus insularis*).

All the recent genetic work on the evolution of the genus *Corvus*, however, has been based on the extant species. The status of the recently extinct New Zealand ravens remains unresolved.

The New Zealand (NZ) ravens have received little study since two species were described by Henry Ogg Forbes (Forbes, 1892a, c, 1893) based on partial sub-fossil skeletons. The two species, one found on the main islands of New Zealand (*Corvus antipodum*) and the other on the Chatham Islands (*Corvus moriorum*), appear to have been slightly smaller than the common raven (*Corvus corax*) but larger than the Australian raven of southern and eastern Australia. Forbes (1892b) suggested that supposedly unique characters of the cranium warranted separating the NZ ravens into their own genus, which he named *Palaeocorax*. Although the distinctiveness of some of Forbes' cranial features were questioned (Pycraft, 1911), no author formally recommended the synonymy of *Palaeocorax* and *Corvus* until Brodtkorb (1978). However, this recommendation was not widely accepted until Gill (2003) reviewed the New Zealand taxa and concluded that *Palaeocorax* should be regarded as a junior synonym of *Corvus*. Further, Gill's (2003) analyses of overall proportions and osteology led him to conclude that "New Zealand ravens probably evolved following the invasion of New Zealand by *C. coronoides* or a population of crows ancestral to *C. coronoides*."

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Very little is known about the biology of NZ ravens. Pycraft (1911) found that Chatham Island ravens, in addition to having smaller wings than northern ravens, had a shallower sternal keel and smaller pygostyle, indicating a slightly reduced flight capacity. Brooke (2000) suggested that damage found on the shells of snails of the genus *Placostylus* in the Far North of New Zealand may have been due to raven predation. Tennyson and Martinson (2007) proposed that the coastal nature of the majority of NZ raven fossil sites and the prevalence of raven bones with the bones of adult and immature sealion (*Phocarcctos hookeri*) may have meant a predator-prey relationship between the two taxa.

In the present study, we use molecular, osteological and distributional data to resolve the origins and phylogenetic relationships of these mysterious extinct New Zealand birds and to give further insight into the palaeobiology and distribution of ravens on the mainland of New Zealand.

## 2. Methods

### 2.1. Ancient DNA extraction and sequencing

We obtained bone samples of both *Corvus antipodum* (CM Av 12546, Marfells Beach, Marlborough) and *Corvus moriorum* (CM Av5468, Chatham Island) from the collections of the Canterbury Museum, New Zealand. Both samples are from dune deposits and are of late Holocene age. All DNA extraction and library preparation steps were performed in a purpose-built, physically isolated, ancient DNA laboratory at the Australian Centre for Ancient DNA, University of Adelaide.

Digestion of bone samples and DNA extraction were performed exactly as described by Mitchell et al. (2014b). Extracted DNA was enzymatically blunt-ended, and truncated Illumina adapters (see Mitchell et al., 2014b) were ligated according to the protocol of Meyer and Kircher (2010). The custom P5 and P7 adapter sequences each included a 7mer barcode to allow downstream identification of library molecules and exclusion of cross-contamination between DNA libraries. The libraries were amplified, enriched for bird mtDNA, quality controlled, and prepared for sequencing following the procedure outlined in (Mitchell et al., 2014b). We diluted the enriched libraries to 2 nM and ran them on an Illumina MiSeq using 2 × 150 bp (paired-end) sequencing chemistry.

### 2.2. Data processing

We used 'sabre' v1.00 (<https://github.com/najoshi/sabre>) to identify paired forward and reverse reads that contained the 7mer barcode sequences corresponding to our libraries (no mismatches allowed). We then trimmed adapter sequences and merged the paired forward and reverse reads using Adapter-Removal v2.1.2 (Lindgreen, 2012). Low quality bases were trimmed (Phred < 20 --minquality 4) and merged reads shorter than 25 bp were discarded (--minlength 25). We visualised read quality using fastQC v0.10.1 (<http://www.bioinformatics.bbsrc.ac.uk/projects/fastqc>) before and after trimming to make sure the trimming of adapters was efficient.

We assembled mitochondrial genome sequences for *C. antipodum* and *C. moriorum* using an iterative mapping approach (see Mitchell et al., 2014a,b). We mapped successfully merged forward and reverse reads for both taxa against the mitochondrial genome sequence of the rook (*Corvus frugilegus*, GenBank accession Y18522) using BWA v0.7.8 (Li and Durbin, 2009) with parameters recommended for ancient DNA (aln -l 1024, -n 0.01, -o 2) (Schubert et al., 2012). We excluded reads with low mapping quality scores (Phred < 30) using SAMtools v1.4 (Li et al., 2009), and removed

duplicate reads using 'FilterUniqueSAMCons.py' (Kircher, 2012). A 50% consensus sequence was generated for both *C. antipodum* and *C. moriorum* from the remaining mapped reads using Geneious v8.1.6 (Biomatters; <http://www.geneious.com>), retaining the reference sequence for regions with no read coverage. These consensus sequences were then used for a subsequent round of mapping. This process was iterated until no additional reads could be mapped for either taxon (12 iterations for *C. antipodum* and nine iterations for *C. moriorum*). For the final consensus sequences, we called unambiguous bases only for sites with read depth  $\geq 2$  and where  $\geq 75\%$  of reads agreed, other sites were coded as IUPAC ambiguities.

Mean read depth across the 15,065-bp-long *C. antipodum* mitochondrial genome consensus sequence (GenBank accession KX822154) was 7.9x (standard deviation = 6.2x; coverage = 77.9%), based on 1848 reads of mean length 64.7 bp (standard deviation = 17.0 bp). The *C. moriorum* mitochondrial genome consensus sequence (GenBank accession KX822153) was 15,593 bp long, covered to a mean depth of 124.6x (standard deviation = 41.2x; coverage = 100%) by 26,626 reads of mean length 73.0 bp (standard deviation = 21.1 bp). We used the MUSCLE algorithm (as implemented in Geneious v8.1.6) to align the CO1, ND2, ND3, and CYTB loci of our new mitogenomes with a previously published, comprehensively sampled matrix of these four loci from corvid birds (Jönsson et al., 2016). We then used published mitogenome sequences to complete gaps in this alignment for (GenBank accession numbers in parentheses): *Corvus brachyrhynchos* (KP403809), *Corvus frugilegus* (Y18522), *Corvus hawaiiensis* (KP161620), *Corvus macrorhynchos* (KR072661), *Corvus splendens* (KJ766304), *Cyanopica cyanus* (JN108020), *Garrulus glandarius* (JN018413), *Nucifraga columbiana* (KF509923), *Pica pica* (HQ915867), *Podoces hendersoni* (GU592504), and *Urocissa erythrorhyncha* (JQ423932). From this alignment we selected taxa from the corvid sub-clade of interest for downstream phylogenetic analysis (Supplementary Information Tables 1 & 2).

### 2.3. Phylogenetic analysis and molecular dating

RAxML v8.2.0 (Stamatakis, 2006) was used to reconstruct a phylogeny from the dataset under a maximum likelihood framework. We divided the data into five partitions (Supplementary Information Table 3) based on the results of PartitionFinder v1.1.1 (Lanfear et al., 2012). Our partitioned RAxML analysis comprised a maximum likelihood search for the best-scoring tree from 1000 bootstrap replicates (-f a -m MULTIGAMMA -# 1000).

We used BEAST v1.8.2 (Drummond and Rambaut, 2007) to simultaneously infer the phylogeny and evolutionary timescale under a Bayesian framework. PartitionFinder was used to determine optimal partitioning and substitution models (Supplementary Information Table 4). Following Jönsson et al. (2016) we constrained the root of the tree to fall between the *Cissa/Urocissa* magpies and the clade comprising the remaining sampled taxa. We implemented a single lognormal relaxed clock model (with a rate multiplier parameter for each data partition), and constrained the age of two key nodes in accordance with the fossil record (Supplementary Information Table 7; using uniform distributions with hard minima and maxima):

- (1) We placed a minimum constraint of 5.3 Ma on the divergence between *Pica* and *Corvus* based on *Miopica paradoxa* from Belka and Novaya Emetovka in the Odessa Region of Ukraine. These sites are considered to belong to European fossil stage MN10 (Kurochkin and Sobolev, 2004) and thus be of Messinian (Pontian) age, between 5.3 and 7.2 Ma. *M. paradoxa* was described based on an incomplete ulna, and although similarities with jays were also noted, it is morphologically more similar to *Pica* magpies than to crows, ravens,

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