Molecular Phylogenetics and Evolution 120 (2018) 248–258

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

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

Recovering the evolutionary history of crowned pigeons (Columbidae: *Goura*): Implications for the biogeography and conservation of New Guinean lowland birds

Jade Bruxaux[a,*], Maëva Gabrielli[a], Hidayat Ashari[b], Robert Prŷs-Jones[c], Leo Joseph[d], Borja Milá[e], Guillaume Besnard[a,1], Christophe Thébaud[a,1,*]

[a] Laboratoire Evolution & Diversité Biologique (EDB, UMR 5174), CNRS/ENSFEA/IRD/Université Toulouse III, 118 route de Narbonne, 31062 Toulouse, France
[b] Research Center for Biology, Museum Zoologicum Bogoriense, Cibinong 16911, Indonesia
[c] Bird Group, Department of Life Sciences, Natural History Museum, Tring, Herts HP23 6AP, England, United Kingdom
[d] CSIRO, National Research Collections Australia, Australian National Wildlife Collection, Canberra, ACT, Australia
[e] Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas (CSIC), Madrid 28006, Spain

ARTICLE INFO

Keywords:
New Guinea
Goura
Crowned pigeons
Molecular phylogeny
Biogeography

ABSTRACT

Assessing the relative contributions of immigration and diversification into the buildup of species diversity is key to understanding the role of historical processes in driving biogeographical and diversification patterns in species-rich regions. Here, we investigated how colonization, *in situ* speciation, and extinction history may have generated the present-day distribution and diversity of *Goura* crowned pigeons (Columbidae), a group of large forest-dwelling pigeons comprising four recognized species that are all endemic to New Guinea. We used a comprehensive geographical and taxonomic sampling based mostly on historical museum samples, and shallow shotgun sequencing, to generate complete mitogenomes, nuclear ribosomal clusters and independent nuclear conserved DNA elements. We used these datasets independently to reconstruct molecular phylogenies. Divergence time estimates were obtained using mitochondrial data only. All analyses revealed similar genetic divisions within the genus *Goura* and recovered as monophyletic groups the four species currently recognized, providing support for recent taxonomic changes based on differences in plumage characters. These four species are grouped into two pairs of strongly supported sister species, which were previously not recognized as close relatives: *Goura sclaterii* with *Goura cristata*, and *Goura victoria* with *Goura scheepmakeri*. While the geographical origin of the *Goura* lineage remains elusive, the crown age of 5.73 Ma is consistent with present-day species diversity being the result of a recent diversification within New Guinea. Although the orogeny of New Guinea's central cordillera must have played a role in driving diversification in *Goura*, cross-barrier dispersal seems more likely than vicariance to explain the speciation events having led to the four current species. Our results also have important conservation implications. Future assessments of the conservation status of *Goura* species should consider threat levels following the taxonomic revision proposed by del Hoyo and Collar (HBW and BirdLife International illustrated checklist of the birds of the world 1: non-passerines, 2014), which we show to be fully supported by genomic data. In particular, distinguishing *G. sclaterii* from *G. scheepmakeri* seems to be particularly relevant.

1. Introduction

New Guinea supports the richest lowland rainforest avifauna in Australasia, and a high proportion of species occurs nowhere else in the world (Beehler and Pratt, 2016; Mack and Dumbacher, 2007; Mayr, 1941). However, we still know little about the origin of New Guinean bird diversity, in particular how it evolved through immigration and/or diversification within the archipelago (Deiner et al., 2011; Jønsson et al., 2011; Moyle et al., 2016). While a large proportion of New Guinean avifauna shows close relationships to Australian lineages [*e.g.* Ptilonorhynchidae (Irestedt et al., 2015), Meliphagidae (Marki et al., 2017)], suggesting that Australia was the source area of many lineages (Moyle et al., 2016; Schodde, 2006; Heinsohn and Hope, 2006), the origin of a significant fraction of the region's avifauna remains unclear.

* Corresponding authors.
E-mail addresses: bruxaux.jade@gmail.com (J. Bruxaux), christophe.thebaud@univ-tlse3.fr (C. Thébaud).
[1] Co-senior authors.

https://doi.org/10.1016/j.ympev.2017.11.022
Received 7 June 2017; Received in revised form 28 November 2017; Accepted 29 November 2017
Available online 01 December 2017
1055-7903/

Particularly enigmatic is the biogeographical and temporal diversification of lineages containing multiple species endemic to New Guinea, with no close relatives elsewhere, such as crowned pigeons (*Goura*), berrypeckers (*Melanocharis*), and true pitohuis (*Pitohui*) (Jønsson et al., 2011, 2016; Moyle et al., 2016; Schodde and Christidis, 2014).

Four important factors underlie the buildup of present day species diversity in this area. First, New Guinea is a geologically recent island that became available for colonization by terrestrial species about 5–15 million years ago (Ma) (Hill and Hall, 2003; van Ufford and Cloos, 2005), implying recent colonization and diversification. Second, much of New Guinea and Australia are part of the same continental shelf, the former being the tectonically deformed northern margin of the latter. Thus, they are separated by very shallow seas and have been intermittently connected during sea-level lowstands (Voris, 2000), making biotic interchange especially likely for lowland organisms and of potential significance to understand the colonization patterns of New Guinea (Beehler et al., 1986; Deiner et al., 2011; Jønsson et al., 2011; Moyle et al., 2016; Schodde, 2006; Toussaint et al., 2015; Heinsohn and Hope, 2006). By contrast, New Guinea is separated from the continental shelf of Asia by deep-water channels (Hall, 2013) that have acted as barriers to dispersal for most but not all Asian bird lineages, as noted early on by Alfred Russel Wallace (Wallace, 1869, 1905). Third, since the Miocene, Australia has undergone an extensive aridification that led to a dramatic decline of the tropical rainforest biota, now restricted to northeastern Australia in close proximity to New Guinea (Byrne et al., 2011). Such large-scale aridification may have caused the extinction of many rainforest-adapted species, some of which are now geographically restricted to New Guinea. Finally, in light of new data on the major geological features of the region, a number of recent studies have emphasized that mountain and island uplift in a proto-Papuan archipelago may have played the role of a "species pump" (*e.g.* Aggerbeck et al., 2014; Jønsson et al., 2011, 2017; Toussaint et al., 2014). Recently, however, in a study on diversification patterns in songbirds, Moyle et al. (2016) suggested that New Guinea may have served mainly as an "evolutionary refuge" for Australian lineages, with diversification taking place prior to immigration out of their ancestral range (see also Schodde, 2006; Heinsohn and Hope, 2006). Thus, a major challenge for understanding the evolution of New Guinea's avian diversity is to decipher the relative contributions of immigration into the region, *in situ* speciation, and extinction history. This can be done by testing hypotheses regarding both the spatial and temporal scales of diversification events in lineages that host multiple New Guinean endemics.

Crowned pigeons (Columbidae: *Goura*) are large, lowland forest-dwelling species endemic to New Guinea, that differ markedly from any other species of pigeons by their size, a spectacularly large laterally compressed fan-like crest held erect over the head, and no oil gland (Darwin, 1868; Gibbs et al., 2001; Wallace, 1876). They occupy the extensive alluvial basins covered by vast areas of lowland rainforests that surround the main mountain massifs (Pratt and Beehler, 2015) as well as several neighboring islands (Aru Islands, Misool, Salawati, Batanta, Waigeo, and Yapen) lying in shallow water on the New Guinean continental shelf and formerly connected to the New Guinea mainland during sea-level lowstands in the Pleistocene (Beehler and Pratt, 2016; Voris, 2000). Populations found on the oceanic islands of Biak and Supiori in Cenderawasih (Geelvink) Bay and on the large Moluccan island of Seram were almost certainly introduced by humans (Beehler and Pratt, 2016; Gibbs et al., 2001). The genus *Goura* is distributed across lowland habitats forming a continuous ring around the island, and four allopatric or parapatric species have been recently recognized (del Hoyo and Collar, 2014) (Fig. 1). This raises the possibility that discontinuities among lowland basins due to presently eroded mountain ranges, inland bays, or more complex geological processes may have promoted speciation within New Guinean lowlands, as suggested by Mack and Dumbacher (2007). However, no comprehensive species-level phylogeny is currently available, and published evidence on genetic divergence (Besnard et al., 2016) is too incomplete to recognize taxa with a unique evolutionary history. In addition, two species recently recognized by del Hoyo and Collar (2014), i.e. Sclater's Crowned Pigeon *G. sclaterii* and Scheepmaker's Crowned Pigeon *G. scheepmakeri,* have long been considered as subspecies on the basis of plumage color similarities (Mayr, 1941; Gibbs et al., 2001; Rand and Gilliard, 1968), but this species split based on overall phenotypic divergence awaits confirmation. A phylogenomic and phylogeographic framework is needed to clarify the relationships among crowned pigeons and to document the biogeographical and temporal diversification of this lineage. In particular, such a phylogenomic and temporal framework should allow relevant comparisons with the major geological and climatic features that could have played a role in shaping the New Guinean biota in space and time.

A major obstacle to phylogenomic studies of taxa restricted to large and remote areas such as New Guinea is the difficulty of obtaining comprehensive geographic and taxonomic sampling of materials for DNA extraction and analysis. With all species of *Goura* becoming increasingly scarce in all but the most remote lowland rainforests (Gibbs et al., 2001), museum collections provide today the main source of DNA for addressing their evolutionary history while accounting for the range of variation found across New Guinea. However, most specimens are > 50 years old, have not been maintained so as to prevent DNA damage, and are therefore expected to contain degraded DNA that consists mostly of 100–200 base-pair fragments (Irestedt et al., 2006). Fortunately, many limitations due to low quality DNA can now be overcome using next generation sequencing (NGS) (*e.g.* Besnard et al., 2016; McCormack et al., 2016). In particular, genomic regions with high sequencing coverage (> 30×) such as complete mitogenomes can now be confidently assembled from old museum specimens (*e.g.* Besnard et al., 2016; Guschanski et al., 2013). However, phylogenetic reconstruction based on mitochondrial data alone may only partly reflect the evolutionary history of a group of species/populations, so that a multi-locus approach based on mitochondrial as well as nuclear genes is often necessary to increase the likelihood that the true species tree has been recovered (*e.g.* Ballard and Whitlock, 2004). Following recent advances in NGS analyses of museum samples (*e.g.* McCormack et al., 2016; Olofsson et al., 2016), it has become possible to recover nuclear markers that can be used in phylogenetic analyses even from relatively old specimens, thus providing excellent opportunities to assess and overcome the potential bias introduced by the use of mitochondrial markers alone.

In this study, we use a "genome skimming" approach (Straub et al., 2012) to retrieve complete mitogenomes and nuclear DNA sequences, including ribosomal regions, 391 independent nuclear loci, and 1336 ultraconserved elements (UCEs) previously used for reconstructing global avian phylogenies (McCormack et al., 2013; Prum et al., 2015). This yields one mitochondrial and two nuclear datasets that allow us to examine the relationships among recognized species of *Goura* and to reconstruct the diversification history of the group in space and time, in order to infer the processes that may have shaped its evolution. Finally, we discuss the implications of our results for the taxonomy and conservation of *Goura* species.

2. Material and methods

2.1. Sampling

We sampled a total of 39 *Goura* individuals, comprising 37 museum specimens (toe-pads) and two samples of fresh tissues obtained in the field, distributed over most of the known distribution range of each recognized species (Fig. 1; Supplementary Table 1). Samples include ten individuals of Western Crowned Pigeon *Goura cristata*, six of *G. scheepmakeri*, seven of *G. sclaterii* and 16 of Victoria Crowned Pigeon *G. victoria* [following the taxonomy in del Hoyo and Collar (2014)]. Thirteen specimens were more than 100-years old, including one *G. cristata* sample from Alfred Russel Wallace's collection obtained by

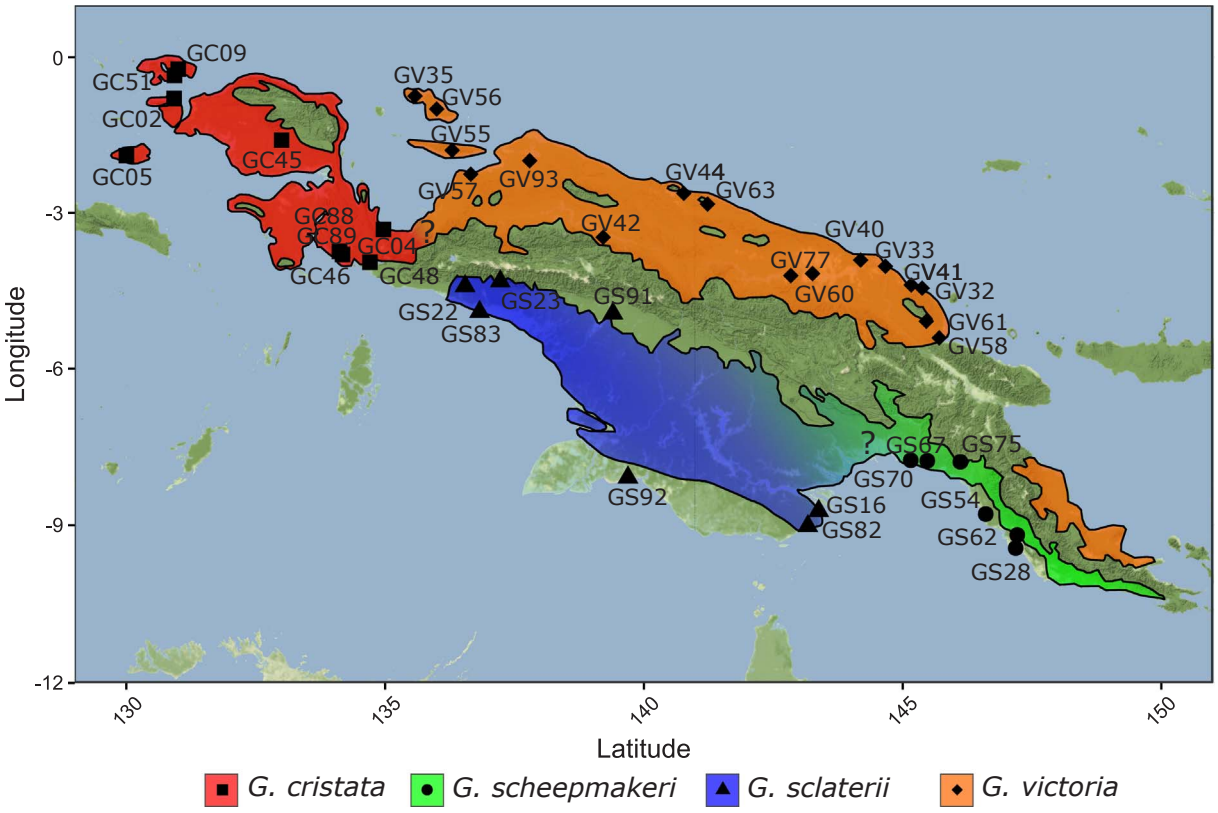

Fig. 1. Sampling localities of *Goura* crowned pigeons in New Guinea. Species distribution ranges are based on del Hoyo and Collar (2014) and Pratt and Beehler (2015) and are distinguished by specific colors and symbols. Question marks are added where distribution limits are unclear. Fading colors indicate uncertainty in distribution limits between species.

Charles Allen on the island of Misool, most probably in 1860 (van Wyhe and Rookmaaker, 2013). We also included four species belonging to the extant genera reported as the most closely related to crowned pigeons (Shapiro et al., 2002): *Didunculus strigirostris* (Tooth-billed Pigeon from Samoa; toe-pad museum sample), *Caloenas nicobarica* (Nicobar Pigeon from islands off south-east Asia to Solomon Islands; toe-pad museum sample), *Trugon terrestris* (Thick-billed Ground-Pigeon from New Guinea; tissue sample), and *Otidiphaps nobilis* (Pheasant Pigeon from New Guinea; tissue sample). In addition, *Geopelia striata* (Zebra Dove from Indonesia and the Malay peninsula; blood sample obtained on Reunion where the species has been introduced) was used as a more distant relative (Pereira et al., 2007). We finally added to this sampling the mitogenome data from two extinct relatives that were recently released in GenBank (Soares et al., 2016): *Raphus cucullatus* (the Dodo from the island of Mauritius; GenBank accession NC_031864.1) and *Pezophaps solitaria* (the Rodrigues Solitaire from the island of Rodrigues; GenBank accession KX902238.1).

Museum samples were kindly provided by the Natural History Museum, UK, (NHMUK), the American Museum of Natural History (AMNH), the Australian National Wildlife Collection (ANWC), the Museum Zoologicum Bogoriense (MZB), and the Zoological Museum University of Copenhagen (ZMUC). Details about specimens and collection localities are available in Supplementary Table 1.

2.2. DNA extraction and sequencing

Precautions were taken to avoid contamination of museum samples with modern DNA (*i.e.* use of a room where no fresh bird samples had ever been manipulated, laminar flow hood and sterilized materials; Besnard et al., 2016). In addition, DNA extractions and the first steps of library preparation were all performed in rooms where no amplified DNA was handled.

For toe-pad samples, we used around 1 mm^3 of tissue, as described in Besnard et al. (2016). When possible, we tried to use internal parts of the sample to avoid contamination with microbial or human DNA present on the surface of the sample. We used the Qiagen DNeasy Blood and Tissue kit (Qiagen Inc., Texas) following manufacturer recommendations, adding more proteinase K and DTT when tissue lysis was not easily obtained. The extracted DNA was eluted in a 120-µL volume of Buffer AE. Double stranded DNA concentration was measured using a Qubit 2.0 Fluorometer (Thermo Fisher Scientific, Delaware). For fresh samples (blood, tissue or feather), extractions were performed in a separate room following manufacturer's recommendations.

Fifty-four µL of each sample (9.2–929 ng of double stranded DNA) were used to prepare the sequencing library with the Illumina TruSeq Nano DNA Sample Prep kit following the instructions of the supplier (Illumina Inc., San Diego). DNA extracted from museum specimens was not sonicated since mean DNA fragment size was expected to be below 200 bp (Besnard et al., 2016). Libraries were multiplexed (24 per flow cell lane), and inserts were then sequenced from both ends on a HiSeq 2000, 2500 or 3000 sequencer (Illumina Inc., San Diego). Library preparation and sequencing were performed at the GeT-PlaGe core facility, hosted by INRA (Toulouse, France).

2.3. Mitogenome assembly

For each sample we first tried to assemble the mitogenome *de novo* using the organelle assembler Org.Asm v0.2.03 (http://pythonhosted.org/ORG.asm/). We used all the mitochondrial protein sequences of a rock pigeon (*Columbia livia*) as seeds (GenBank accession NC_013978.1). Read trimming was done automatically at the onset of the assembly to remove adaptor ends when the insert size was shorter than the read sequence. When the sequence obtained was incomplete, complete mitogenomes were obtained by mapping the individual reads against a good quality reference successfully built by Org.Asm from

another individual of the same species (GC02, GS22, GS28 and GV32 were used as references for *G. cristata*, *G. sclaterii*, *G. scheepmakeri* and *G. victoria*, respectively). At this stage, we first used Trimmomatic v0.32 (Bolger et al., 2014) to remove the adaptors and all reads shorter than 36 bp. GMAP-GSNAP v2015-11-20 (Wu and Nacu, 2010) and Samtools v1.1 (Li et al., 2009) were then used to map the reads against the reference mitogenome, remove PCR duplicates, reconstruct the consensus sequence and obtain alignment statistics. We filtered the results in relation to the quality of the alignment, keeping only alternative alleles called with an error probability of less than 1% (Phred quality score > 20 in the samtools vcf output). We used mapDamage v2.0.2 (Jónsson et al., 2013) to evaluate the number of errors likely due to the age of samples (via post-mortem deamination). The quality score was thus modified accordingly before the construction of the consensus sequence with Samtools (Li et al., 2009). We also manually checked final assemblies and scrutinized all positions showing polymorphisms that were due to the presence of two alternative sequences [*e.g.* heteroplasmy or nuclear mitochondrial copies (numts); more details in Supplementary Methods 1].

2.4. Nuclear data retrieval

Two strategies were applied to reconstruct nuclear DNA datasets from a subsample of specimens representative of each *Goura* species, *Didunculus* and *Caloenas*. First, we assembled the nuclear ribosomal cluster, and we then retrieved low copy DNA regions using read mapping on reference sequences.

2.4.1. Nuclear ribosomal cluster assembly

Nuclear ribosomal DNA (nrDNA) regions have rarely been used to reconstruct phylogenies in animals and particularly in birds (*e.g.* Chikuni et al., 1996; Paśko et al., 2011). This is mainly because the Internal Transcribed Spacer (ITS) is too long (*i.e.* 4–5 kb) to be amplified with PCR methods. However, the repeated nature of the nrDNA cluster is putatively an advantage to assemble this nuclear genomic region from NGS data, even with shallow sequencing of highly fragmented DNA from museum specimens. Here, we aimed to assemble nrDNA sequences (ca. 10 kb) that included the complete 18S gene, ITS1, 5.8S gene, ITS2, and 28S gene, plus 5′ and 3′ ends of the external transcribed spacer (ETS). To achieve this, we first used the 18S gene of *Columba livia* (1,737 bp; GenBank accession AF173630.1) as a seed to start the nrDNA cluster assembly of *G. cristata* sample GC02 [*Goura* sample used as reference in Besnard et al. (2016)], *C. nicobarica,* and *D. strigirostris*. The 18S sequence was extended using Geneious v. 9.0.5 (Biomatters Ltd., Auckland, New Zealand) by mapping reads with reiterations until sequence ends could not be properly elongated (due to numerous indels in the ETS). The consensus sequence of GC02 was then used to reconstruct the nrDNA sequence of other *Goura* individuals by mapping reads onto this reference (as described for the mitogenome reconstruction). A consensus sequence was reconstructed for each accession, and a site was considered to be polymorphic (using IUPAC codes) when two nucleotides or indels were supported by at least 25% of reads, such ambiguities likely resulting from the presence of different nrDNA paralogues in the genome. Sites covered with only 1× were considered as unknown bases (N). Since this marker did not provide true (unambiguous) intra-specific polymorphisms (see below), we chose to analyze 18 *Goura* samples only (four or five accessions per species, among those that rendered the best nuclear DNA/mitochondrial DNA ratio; see Supplementary Methods).

2.4.2. Construction of the reference sequence for low copy nuclear DNA regions and mapping of reads

A common strategy to recover nuclear markers is to target particular regions of the genome and to enrich and sequence them using specific probes (*e.g.* McCormack et al., 2013; Prum et al., 2015). As no nuclear genome is currently available to design probes for any of the *Goura* species or close relatives, we used an alternative strategy consisting in mapping the Illumina reads to a reference sequence. While we could have used the Rock Pigeon *Columba livia* reference genome (Shapiro et al., 2013), this species is not a close relative to *Goura* and we preferred an alternative strategy based on using two large sets of markers that were assembled recently for producing large-scale phylogenetic hypotheses in modern birds (McCormack et al., 2013; Prum et al., 2015). These two sets comprise markers which correspond to highly conserved regions in birds, increasing the probability of finding reads corresponding to homologous sequences.

The first set of genes is composed of 1,336 ultra-conserved elements (UCE) with an average length of 410 bp that were characterized in the Pink-necked Green Pigeon *Treron vernans* (McCormack et al., 2013), a pigeon presumed to be more closely related to *Goura* than *Columba livia* (Fulton et al., 2012; Johnson and Clayton, 2000; Pereira et al., 2007). The second set of genes is composed of 391 nuclear loci with an average length of 1,263 bp, which were defined from the Red Junglefowl *Gallus gallus* genome and used to draw genetic data from 198 species of birds, including five species of Columbidae (Prum et al., 2015). Both sets of genes were aligned in Geneious to check for shared genes between the two datasets with the "Map to reference" option and default parameters. One gene shared by both datasets was deleted, leading to a total of 1726 independent loci, which were concatenated to create a unique reference sequence of ca. 1 Mbp. The Illumina reads were first trimmed with Trimmomatic (Bolger et al., 2014), allowing removal of the adapters, removal of the bases at the beginning or the end of reads when their quality was below three, and removal of the reads that after those manipulations, were shorter than 36 bp (default parameters). Only the reads where both forward and reverse reads had survived the trimming were kept for the alignment. The remaining Illumina reads from the 39 *Goura* individuals and two outgroups (*D. strigirostris* and *C. nicobarica*) were aligned to the reference sequence using GMAP-GSNAP v2015-11-20 (Wu and Nacu, 2010). Finally, Samtools v1.1 (Li et al., 2009) was used to build the bam files from the read alignments after removing PCR duplicates and to obtain statistics on this process (*i.e.* number of mapped reads, sequencing depth). This alignment was analyzed with mapDamage v2.0.2. (Jónsson et al., 2013), so that we could lower the Phread base quality score of the sites were deamination was highly likely. Following the read mapping, fasta files were generated for each of the 39 *Goura* individuals and the two outgroups using the doFasta command of ANGSD (Korneliussen et al., 2014) and keeping the most frequent base at each site.

2.5. Phylogenomic analyses

2.5.1. Mitogenome data

All mitogenomes were annotated as reported in Besnard et al. (2016) using Geneious v9.0.5 (Biomatters Ltd., Auckland, New Zealand). We removed the repeated sequences in the control region and aligned each protein-coding gene, each transfer RNA gene (tRNA), each ribosomal RNA gene (rRNA) and each non-coding region separately using the Geneious aligner with default parameters. We concatenated these alignments with SeqCat.pl v1.0 (Bininda-Emonds, 2005) and obtained a final dataset of 15,694 bp.

We used PartitionFinder v2.1.1 (Lanfear et al., 2017) to find the best partition schemes and nucleotide substitution models for both RAxML (Stamatakis, 2014) and MrBayes (Ronquist et al., 2012) analyses, with the greedy algorithm and considering 64 potential partitions: the 12S rRNA, the 16S rRNA, each tRNA, all non-coding sequences, and the three codon positions in each of the 13 protein-coding genes. We unlinked branch lengths and used the Bayesian information criterion (BIC) to select the best-fitting model and partition scheme (Malé et al., 2014), which was then used for tree reconstructions.

The maximum-likelihood (ML) analyses were performed using RAxML v8.1.5 (Stamatakis, 2014). We used 20 alternative runs and 500 replicates of non-parametric bootstrapping to evaluate the reliability of

the resulting tree. The Bayesian tree reconstruction was performed with MrBayes v3.2.2 (Ronquist et al., 2012). Two independent runs of four Metropolis-coupled Markov chains (MCMC) for Monte Carlo simulations were run for 20,00,000 generations, with parameters and trees sampled every 100 generations, and a burn-in of 50,000 generations. Convergence of the chains was manually checked using Tracer v1.6 (Rambaut et al., 2014).

2.5.2. Nuclear data

2.5.2.1. Ribosomal cluster. We annotated our nrDNA clusters in Geneious using a complete nuclear ribosomal DNA sequence of *G. gallus* (GenBank accession KT445934.2) as a reference. The complete alignment was 11,347-bp long. To determine the best partition scheme and nucleotide substitution model, we used PartitionFinder v2.1.1 (Lanfear et al., 2017) after separating our data in seven potential partitions [*i.e.* three ribosomal genes (18S, 5.8S, and 28S) and four intergenic spacers (5′ETS, ITS1, ITS2, and 3′ETS)] and used the same parameters as described for mitochondrial analyses. Similarly, we used RAxML v8.1.5 (Stamatakis, 2014) with 20 alternative runs and 1000 replicates of non-parametric bootstrapping, and MrBayes v3.2.2 (Ronquist et al., 2012) with two independent runs of four MCMC for 2,00,000 generations sampled every 100 generations and a burn-in of 50,000 generations, and manually checked the chain convergence using Tracer v1.6 (Rambaut et al., 2014).

2.5.2.2. Low copy conserved regions. Since we obtained low quality nuclear DNA sequences for some individuals, reflected by a low number of mapped reads, we decided to keep data only from individuals which had at least 5,000 mapped reads to minimize any potential bias related to sequencing errors or DNA degradation. Thus, our dataset contained 19 *Goura* individuals, including seven *G. cristata*, four *G. sclaterii*, two *G. scheepmakeri* and six *G. victoria*.

We then performed a ML reconstruction using RAxML v8.1.5 (Stamatakis, 2014) with 20 alternative runs and 100 replicates of non-parametric bootstrapping, using a General Time Reversible model (Tavaré, 1986) with invariable sites and a gamma distributed rate variation among sites (GTR + I + G model).

2.6. Dating divergence events

Dating species divergences on an absolute time scale is challenging in groups such as *Goura* for which fossil data is lacking. One solution is to date mitochondrial phylogenies by using a mean divergence rate of 2.1% per million years (Weir and Schluter, 2008). While this approach is widely used (*e.g.* Carmi et al., 2016; Shipham et al., 2015), it is often criticized (*e.g.* Lovette, 2004) because gene divergence often precedes population divergence (Edwards and Beerli, 2000) and variation in divergence rate has been observed among lineages in relation to variation in life-history traits, such as body mass (Nabholz et al., 2016). For birds, coalescent dates for mitochondrial sequences have been found to generally precede population splitting by 0.2–0.3 million years (Moore, 1995; Weir, 2006); hence, it seems reasonable to approximate the date of species divergence with the coalescent date. To date the splits within the genus *Goura*, we used the standard mitochondrial substitution rate corrected for body mass, following recommendations in Nabholz et al. (2016) and using a value of 2200 g for all *Goura* species since they all have a similar body mass (Gibbs et al., 2001). Since the corrected substitution rate is derived from coding-gene positions, we only kept coding-genes for dating analyses and removed *ATP8* and *ND4L* due to their short length, and *ND6* due to its reverse sense, as done by Nabholz et al. (2016). We partitioned the data according to the results of a new PartitionFinder analysis run on this new dataset (including *Goura* sequences only), and linked partitions for the tree reconstruction. We used a strict clock for each partition, fixing the third codon position partition to a substitution rate of 0.00942646 substitutions per site per million years, following Nabholz et al. (2016), and used a uniform prior for all the substitution rates. The substitution rate of first and second codon positions was given a uniform prior of 0.01 [0.005–0.015], while others priors were kept at their default values. We ran the analysis with a birth-death model (Stadler, 2009) for 10 million generations, logging every 1000 generations. We discarded the first 10% of trees as burn-in and manually checked for convergence using Tracer v1.6 (Rambaut et al., 2014).

To date the stem age of the *Goura* lineage, we used two individuals per species: GC05 and GC45, GS16 and GS82, GS67 and GS70, GV42 and GV56 for *G. cristata*, *G. sclaterii*, *G. scheepmakeri* and *G. victoria*, respectively. Here we included all the outgroup sequences (*D. strigirostris*, *C. nicobarica*, *T. terrestris*, *O. nobilis*, *R. cucullatus*, *P. solitaria*, *G. striata*) in the analysis. Only coding genes were used but *ATP8*, *ND4L* and *ND6* were excluded as described above. We used the age of the oldest divergence event within the *Goura* lineage found in the previous dating analysis as a prior to calibrate the phylogenetic tree of the entire group. We added a normal calibration point at 24.7 ± 3.5 Ma for the diversification of Columbidae following Soares et al. (2016), whose dating result is in agreement with the one obtained by Prum et al. (2015) and with the calibration point used in Claramunt and Cracraft (2015). We used nucleotide substitution models selected by PartitionFinder, and linked the partitions for the tree reconstruction. We applied a log normal relaxed molecular clock for each partition (Drummond et al., 2006; Lepage et al., 2007) and uniform priors for each substitution rate. The three uncorrelated log-normal relaxed clock means were given an exponential prior, and invariant proportion, when applicable, was given a uniform prior at 0.5 [0–1]. All the unstated priors were kept with default values. We ran the analysis with a birth-death Model (Stadler, 2009) for 100 million generations, logging every 1000 generations. We discarded the first 20% of trees as burn-in and manually checked for convergence using Tracer v1.6 (Rambaut et al., 2014). All analyses were performed using BEAST2 v2.4.3 (Bouckaert et al., 2014).

3. Results

3.1. Sequencing data

We obtained on average 11,317,165 paired-end reads per individual (range: 5,112,052–20,116,808; Supplementary Table 2) that were used to assemble the whole mitogenome and nuclear ribosomal DNA cluster, and to retrieve highly conserved nuclear regions spread across the genome.

3.2. Mitogenome assembly, and phylogenetic analyses

A complete mitogenome was reconstructed for all individuals. Despite evidence for some deamination, the consensus sequences were not modified by weighting the quality scores. This reflects the high mean sequencing depth of all mitogenomes, ranging from 16.74 to 7759.56×, with only one individual (GS91) showing a mean sequencing depth < 30× (Supplementary Table 2). Seventeen mitogenomes presented at least one site with two alternative nucleotides. In individuals with the lowest mean sequencing depth, we found some minor variants represented by very few reads (less than 10% of the mapped reads) and likely due to sequencing errors. Other minor variants were found (supported by 14–33% of the mapped reads) and were carefully examined in order to understand their origin, after the possibility of cross contamination had been ruled out (see Supplementary Methods 1). Two categories of individuals could be clearly differentiated, according to both the number of variable sites and the ratio of nuclear/mitochondrial DNA sequencing depth. This ratio, with an average of 0.06 in individuals without minor variant, ranged from 0.20 to 0.78 for all individuals with at least two variable sites except GC09 (see Supplementary Methods 1). A high ratio, which implies a higher nuclear coverage, allows the detection of mitochondrial genome copies

included in the nuclear genome [numts (Lopez et al., 1994)]. Therefore, the minor variants in this first case were likely numts. In contrast, a few individuals with one variable site and also GC09 did not show a particularly high ratio of nuclear/mitochondrial DNA sequencing depths. In such cases, we considered that apparent polymorphism was likely due to heteroplasmy. Phylogenetic relationships of major and minor variants also confirmed this difference: while minor variants considered as numts were sister to the whole species and showed short branches (pattern of "fossil" genome), supposed minor heteroplasmic sequences clustered with other mitochondrial sequences (see Supplementary Methods 1). For the rest of the analysis, we thus used majority-rule consensus sequences. All mitogenomes are deposited in GenBank (see Supplementary Table 2 for more details).

Following PartitionFinder results, we used a GTR + I + G model for the ML analysis, with the four partitions described in Supplementary Table 3. For the Bayesian analysis, PartitionFinder proposed the same partitions apart from the second codon position of *ATP8*. A GTR + I + G model was used for the first and third partitions, a Hasegawa-Kishino-Yano model (Hasegawa et al., 1985) with invariant sites and a gamma distributed rate variation (HKY + I + G model) was used for the second partition, and a GTR + G model (without invariant sites) was used for the fourth partition (Supplementary Table 3). All the Effective Sample Size (ESS) values were higher than 200, suggesting a good convergence of the Bayesian analysis.

We obtained very similar results with both the ML and Bayesian methods (Fig. 2A). These analyses highlighted four well supported monophyletic groups corresponding to the four recognized species, with reciprocal monophyly between *G. cristata/G. sclaterii* and *G. victoria/G. scheepmakeri* that were both recovered as well-supported monophyletic groups.

3.3. Nuclear ribosomal cluster assembly, and phylogenetic analyses

A partial nrDNA cluster of 10,397–10,738 bp was reconstructed for 18 *Goura* individuals, and two outgroups, *D. strigirostris* and *C. nicobarica*. The mean sequencing depth ranged from 13.39 to 356.62× (Supplementary Table 2). Four GC-rich regions in the ITS1 and 28S gene showed very low sequencing depth, and one to four of these parts were not covered in eight *Goura* individuals (for a total missing part ranging from 19 to 406 bp). In addition, a few sites (from 3 to 36 per individual) were considered to be polymorphic due to the presence of different nrDNA copies in the genome (see Material and Methods). Therefore, we checked visually all poorly covered regions and polymorphic sites. Manual adjustments (*e.g.* alignments in regions with insertions or deletions) were made before deciding which sites were polymorphic in the assembly. In the end, very low levels of polymorphism were observed within each recognized species, and no polymorphism was recovered from poorly covered regions, making us confident that the presence of different nrDNA copies in the genome did not lead to systematic errors in our analyses.

Following PartitionFinder results, ribosomal genes (*i.e.* 18S, 5.8S, and 28S) and intergenic spacers (*i.e.* ETS and ITS) were separately treated in two partitions. The selected nucleotide substitution models differ slightly between the ML and Bayesian analyses, probably due to the low number of models available in RAxML (Supplementary Table 4). In the ML analysis, we implemented a GTR + I + G model for the ribosomal gene partition, and a GTR + G model for the intergenic spacers. The Bayesian analysis was performed using a HKY + I model for ribosomal genes, and a HKY + G model for the intergenic spacers. All the ESS values were higher than 200, suggesting a good convergence of the Bayesian analysis.

The phylogenetic trees obtained with the ML and Bayesian methods are fully congruent with four different monophyletic groups corresponding to the four currently recognized species, with the two pairs of species, *G. cristata/G. sclaterii* and *G. victoria/G. scheepmakeri*, being recovered as well-supported monophyletic groups (Fig. 2B).

3.4. Low copy conserved regions assembly, and phylogenetic analyses

Among the 19 *Goura* individuals that were used in this analysis, Illumina reads effectively mapped against all 1,726 loci previously characterized by Prum et al. (2015) and McCormack et al. (2013). Therefore, our approach was successful in retrieving nuclear sequences from a large number of markers spread across the genome.

The number of mapped reads per individual ranged from 5,608 to 24,712, with an average number of 13,295 reads per individual. This corresponds to sequence lengths of 466,245 bp per individual on average (range: 240,318–804,043 bp). Given the size of the reference sequence (1,043,293 bp), the sequences generated showed a high level of missing data, as expected from shallow sequencing data (55.31% on average; range: 22.93–76.97%). The depth across the 1,726 genetic markers averaged over individuals was very low (3.11×) and ranged from 2.51 to 3.92× per individual. Despite this obvious limitation, our approach demonstrates that nuclear data can be relatively easily recovered from museum samples, as already suggested in a previous study (Besnard et al., 2016).

The nuclear phylogeny (Fig. 2C) supports the existence of four monophyletic groups with a topology which is fully congruent with those based on both mitochondrial and nuclear ribosomal DNA, with the two pairs of species, *G. cristata/G. sclaterii* and *G. victoria/G. scheepmakeri*, being again recovered as well-supported monophyletic groups.

3.5. Estimation of divergence times

For the mitochondrial dating analysis, we defined two partitions with PartitionFinder, the first one corresponding to the first two codon positions, and the second corresponding to the third position (Supplementary Table 5). A Tamura and Nei (1993) model with a gamma distributed rate variation among sites and estimated frequencies (TRN + G + X) was selected for the first partition, and a GTR model with estimated frequencies was selected for the second one (GTR + X). All the ESS values were higher than 200, as expected from a Bayesian analysis which had converged.

Taking into account body mass, we dated the crown age of the *Goura* genus at 5.90 Ma [median value with a 95% Highest Probability Density (HPD) of 5.32–6.50 Ma]. This result was used as a prior for the second calibration point of the larger phylogeny where we then found a slightly younger crown age at 5.73 Ma [HPD: 5.15–6.29] (Fig. 3). The split between *G. cristata* and *G. sclaterii* was dated at 1.94 Ma [HPD: 1.42–2.49], while the split between *G. scheepmakeri* and *G. victoria* was dated at 0.69 Ma [HPD: 0.46–0.95]. The stem age of the *Goura* genus was dated at 21.39 Ma [HPD: 17.32–25.44].

4. Discussion

4.1. On the use of museum specimens to obtain mitochondrial and nuclear genomic datasets

In this study, we used successfully museum study skins to acquire genomic data from both the nuclear and the mitochondrial genomes of several species of Columbidae. Our approach confirms once again that museum specimens are a valuable source of materials to obtain genomic information that can be used for phylogenetic analyses (Guschanski et al., 2013). In the course of this study, we developed new strategies to recover nuclear genetic data from a large number of markers spread across the genome. This should be particularly useful for forthcoming studies on the diversification of lineages for which recent collections are few or difficult to achieve, and existing museum collections are the only available source of DNA.

We found that the nuclear ribosomal DNA cluster can be assembled from the sequences obtained from poorly preserved DNAs. The long length of the internal transcribed spacer that appears to have limited

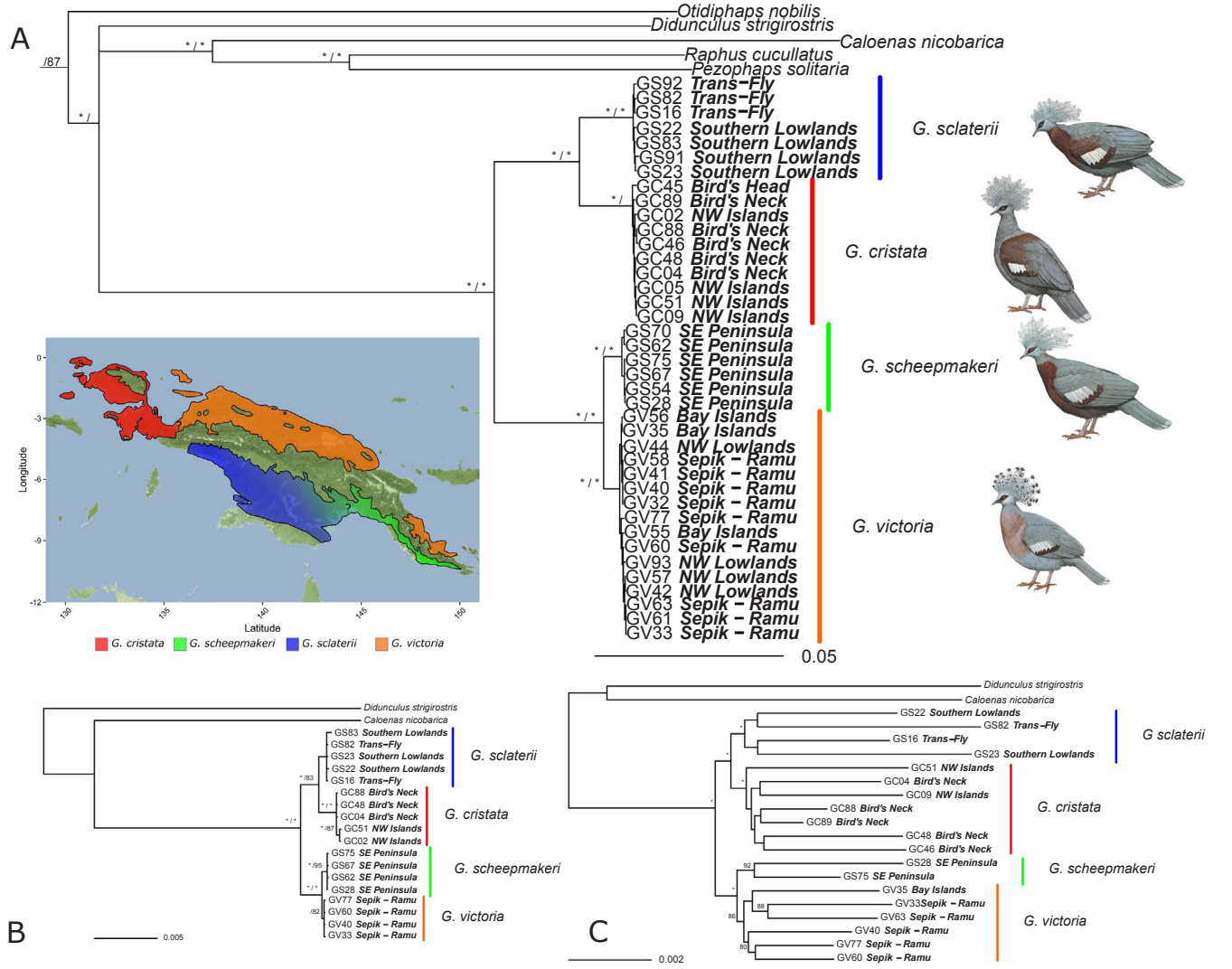

Fig. 2. Phylogenetic trees obtained from the entire mitogenome (A), nuclear ribosomal cluster (B), and conserved nuclear regions (C). Branch lengths were obtained from maximum likelihood analyses. Numbers at the nodes represent Bayesian posterior probabilities (PP) on the left, and maximum likelihood bootstrap values on the right. Stars correspond to 1.0 in PP, and 100% in bootstrap. Support values lower than 0.95 in PP and 70% in bootstrap are not included. Intra-specific support values are removed for clarity in (A). All images are reproduced from del Hoyo and Collar (2014) with permission of Lynx Edicions.

the use of this marker in avian phylogenetics (Chikuni et al., 1996; Paśko et al., 2011) can be overcome with a shotgun sequencing approach. However, variable intra-genomic sites require caution during the assembly process. We also showed that it is possible to recover low copy nuclear regions by mapping reads onto reference sequences, as expected from our previous work (Besnard et al., 2016) and already demonstrated in other taxa like plants (*e.g.* Olofsson et al., 2016). However, we found that not all individuals were amenable to nuclear genome analyses. For some specimens for which a very high quality mitogenome was recovered, we obtained a very low sequencing depth for the nuclear genome (*e.g.* GS70, GV41, GV42, GV56, more details in Supplementary methods 1) that prevented their inclusion in our datasets. This highly variable ratio could be linked to sample storage conditions before and after being accessioned at a museum (Binladen et al., 2006).

Phylogenetic analyses revealed entirely congruent topologies among the three genomic datasets, but terminal branches are longer and nodal support is lower in the analysis based on low copy conserved nuclear regions, especially at the intra-species level (see Fig. 2). This pattern on nuclear single-copy regions is likely due to post-mortem damages like cytosine deamination, even if the levels of deamination are much lower in museum samples than those typically found in ancient DNA samples (Sawyer et al., 2012). To minimize the impact of sequencing errors that result from this process, all sites that showed signs of degradation received a lower quality value [through mapDamage (Jónsson et al., 2013)] prior to analysis. To further minimize the impact of sequencing errors, we could also have removed all low coverage sites (*e.g.* less than 2–3×) from the dataset prior to analysis. We chose not to do so since this would have drastically reduced the dataset (28% for a threshold at 2×, 72% at 3×; see Supplementary Methods 2 for filtered data phylogenies). Higher nuclear genome coverage may alleviate some of the limitations we encountered but our analyses suggest that even low coverage data from conserved regions can prove very useful to infer phylogenetic relationships.

4.2. Unexpected phylogenetic relationships

All three phylogenetic analyses (*i.e.* based on mitogenome, nrDNA, and low-copy nuclear markers) resolved *Goura* into four main monophyletic groups, corresponding to the four species recently recognized by del Hoyo and Collar (2014). They are further grouped into two pairs of strongly supported sister species: the first pair comprises *Goura cristata* (western New Guinea) and *G. sclaterii* (southern New Guinea), while the second pair includes *G. victoria* (northern New Guinea) and *G.*

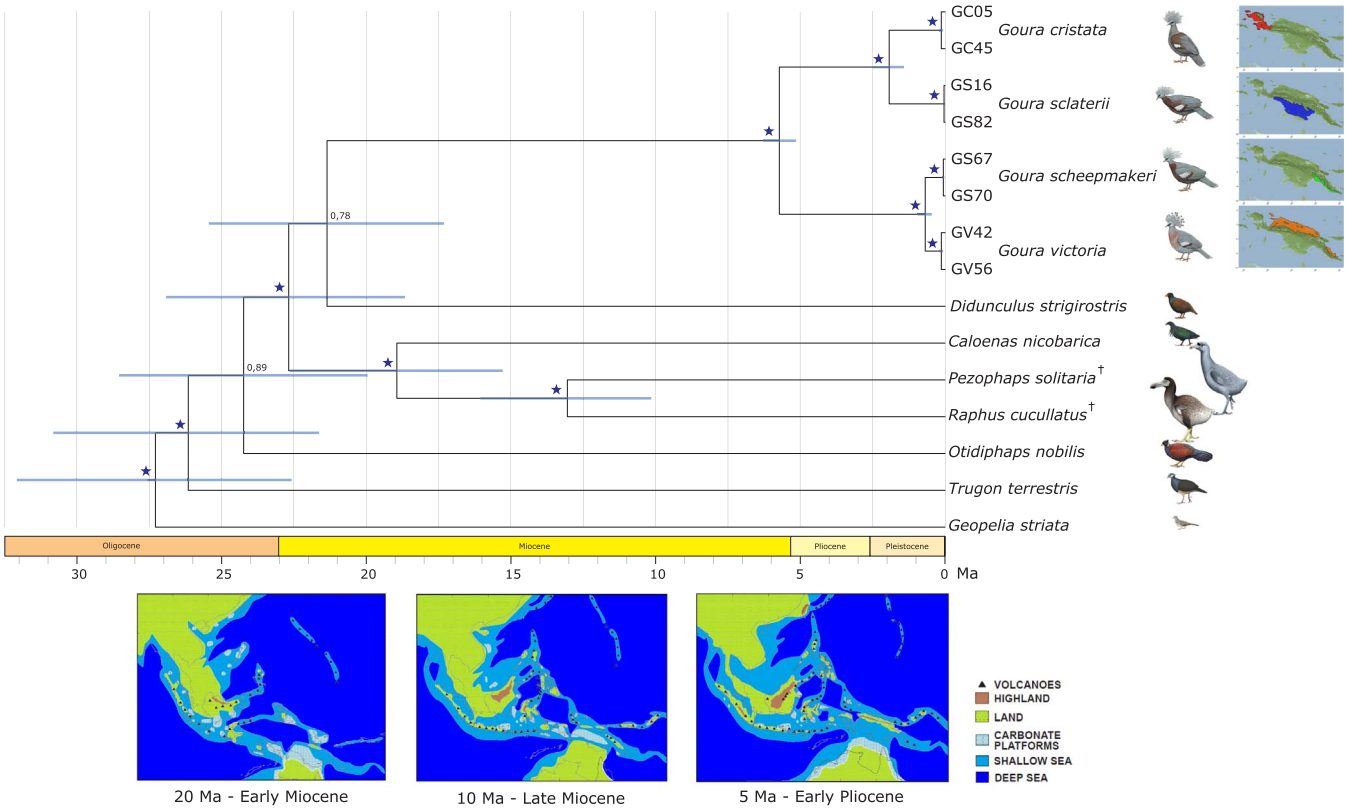

Fig. 3. Dated tree of *Goura* and its closest known relatives. Nodes are placed at median ages with 95% Highest Probability Density in blue. Values at nodes show posterior probabilities, and stars represent a probability of 1. Geological maps of the region [based on Hall (1998)] are shown at different ages (20, 10 and 5 million years ago). All Columbidae images are reproduced from del Hoyo and Collar (2014) with permission of Lynx Edicions.

scheepmakeri (southeastern New Guinea).

Our research confirms the distinction between *G. scheepmakeri* and *G. sclaterii* that was first proposed by del Hoyo and Collar (2014) mainly on the basis of morphology and plumage coloration, rather than previous taxonomic treatments that considered both taxa as subspecies of *G. scheepmakeri* [see Beehler and Pratt (2016) for discussion]. Moreover, *G. cristata* and *G. victoria*, whose distributions seem to abut along the Siriwo River on the eastern side of Cenderawasih (Geelvink) Bay, where they have been described as possibly hybridizing (Mayr, 1941), are also not each other's closest relatives.

Species with known or apparent contact zones are therefore not each other's closest relatives, which suggests a non-trivial scenario of speciation. Distributional contact zones among non-sister taxa such as those observed in *Goura* have been characterized in other New Guinea bird species complex (*e.g.* Deiner et al., 2011; Heads, 2001; Irestedt et al., 2015) and also in other taxa such as turtles (Georges et al., 2014), plants, mammals or snakes (reviewed in Heads, 2001), possibly implying a series of shared historical events responsible for the diversification of New Guinean fauna and flora. Investigating the speciation process in relation to past or recent gene flow between the diverging species would thus be of great interest. Unfortunately, in this study the low sequencing depth of nuclear data (leading to a high amount of missing data and a heterogeneous sequencing error rate among samples) prevented us from using population genomic analyses to evaluate alternative demographic models. Intraspecific analyses would also be interesting regarding possible geographic patterns in *G. sclaterii* for mitogenomes (Fig. 2A), and in *G. cristata* for nrDNA data (Fig. 2B). This second clustering, separating island and mainland individuals, is consistent with the proposal that *G. cristata* may comprise two subspecies (del Hoyo and Collar, 2014; Mayr, 1941; Rand and Gilliard, 1968). It is, however, weakly supported and since these subspecies do not clearly differ phenotypically (Beehler and Pratt, 2016), this warrants further exploration. Interestingly, the species with the largest distribution (*G. victoria*) does not seem to present any geographic clustering in spite of also containing two described subspecies, one smaller restricted to the islands of Cenderawasih (Geelvink) Bay, and the other larger and widely distributed across northern New Guinea from the Siriwo River to Astrolabe Bay (Beehler and Pratt, 2016).

4.3. Biogeographical and temporal diversification of Goura in lowland rainforests of New Guinea

New Guinea has long been seen as a diversification center for some lineages, such as corvoid passerine birds (Jønsson et al., 2011, 2017). However, the fact that New Guinea has been available for dispersal and colonization by terrestrial organisms for less than 15 Ma, and perhaps as little as 5 Ma, makes this view difficult to generalize. Schodde (2006), Schodde and Christidis (2014), Moyle et al. (2016) and Heinsohn and Hope (2006) proposed that the island could have played a refugial role for tropical rainforest birds that 'escaped' from Australia when elements of their biota progressively disappeared. Early diversification could have thus occurred in Australia, possibly followed by more recent events in New Guinea, after it became available for colonization.

Our results, which highlight a first diversification event in the *Goura* lineage around 5.73 Ma [HPD: 5.32–6.50], are consistent with the view that current species diversity is best explained by speciation occurring within New Guinea, similarly to what has been described in other bird groups, such as lories and lorikeets (Schweizer et al., 2015), and woodland kingfishers and kookaburras (Andersen et al., 2017).

The continuity of lowland rainforests around the island of New Guinea implies a possibility of contact and gene flow between diverging species comprising this biota. However, distributional limits between congeneric species or subspecies, such as those observed in *Goura*,

located either in the Bird's Neck [the so called Zoogeographers' Gap (Hartert et al., 1936)] or in the south-eastern part of the central cordillera, have also been found in other species complexes (Mack and Dumbacher, 2007). Further, these limits appear to coincide with possible ancient and now disappeared physical barriers such as the Aure Trough, an inland sea filled by 3–4 Ma (Deiner et al., 2011), that now separates the distribution of *G. sclaterii* and *G. scheepmakeri*. Recent physical barriers could also be involved, such as the Bird's Neck isthmus that was formed between 3 and 5 Ma (Charlton, 2000) and now separates *G. cristata* from both *G. sclaterii* and *G. victoria*. The southeastern Peninsula that separates *G. victoria* and *G. scheepmakeri* may have existed for more than 5 Ma (Hill and Hall, 2003; van Ufford and Cloos, 2005) and be considered as another limit. While these barriers, in particular the Bird's Neck isthmus or the Aure Trough, might have led to the splitting of an ancestral population into the two main *Goura* lineages through vicariance, our dating results show divergence times < 2 Ma and strongly suggest that cross-barrier dispersal has been the primary event leading to speciation within these two lineages.

Geographically separated ranges abutting along common boundaries, as is the case between *G. cristata* and *G. victoria*, *G. cristata* and *G. sclaterii*, and *G. scheepmakeri* and *G. sclaterii*, can be associated with spatial changes in environmental factors, species interactions in areas of contact, or dispersal limitation even in the absence of physical barriers (Bull, 1991). Unfortunately, identifying the processes that may have led to differentiation in the first place, as well as the mechanisms that prevent range overlap in zones of contact, requires some knowledge of environmental niche differentiation among species. Such knowledge is currently not available, even though the different species of *Goura* are seen as ecologically similar (Gibbs et al., 2001), and will be difficult to acquire without obtaining much more data on the precise geographic distribution of the different species.

We estimated the stem age of the *Goura* lineage at 21.39 Ma [HPD: 17.32–25.44]. The interpretation of stem age is contingent upon taxon sampling and is highly sensitive to recently extinct taxa that were not sampled. The long temporal gap between stem and crown ages suggests a possible role of extinction history, especially since two of the closest relatives of *Goura* (*R. cucullatus* and *P. solitaria*) are indeed extinct (Shapiro et al., 2002). Known or presumed relatives live or lived mainly on islands from Mascarene Islands in the west to Samoan Islands in the east (Gibbs et al., 2001; Worthy, 2001). These islands, mainly of volcanic origin, are geologically unstable and that could have caused extinctions among close relatives (Heupink et al., 2014), in addition to the massive prehistoric and historic human-caused extinctions that have affected many landbirds, including pigeons, and are still and may remain largely undocumented (Steadman, 2006, 1995). Alternatively, it is also plausible that the *Goura* lineage originated and perhaps diversified in Australia before dispersing across to New Guinea, and then went extinct in Australia (Schodde, 2006); the absence of any known close relative of *Goura* in Australia and the lack of fossil data does not allow us to formally test the hypothesis, however.

4.4. Implications for conservation

Our results confirm the recent decision of del Hoyo and Collar (2014) to consider four species rather than three in the genus *Goura*. Current *ex situ* conservation measures such as breeding programs do not take this taxonomic change into account yet (*e.g.* EAZA, 2017). Most of the individuals kept in zoos as *G. scheepmakeri* probably belong to *G. sclaterii*. The distribution of *G. sclaterii* is much larger than that of *G. scheepmakeri,* for which only a few recent records are available, all in Lakekamu Basin where it may be rather common but is still hunted (B.M. Beehler, pers. comm.), and which may have already been extirpated long ago throughout most of its range in the southeastern peninsula (King and Nijboer, 1994). A review of digital images available on Google Images using MORPHIC (Leighton et al., 2016) using either "*Goura scheepmakeri*" or "Scheepmaker's Crowned Pigeon" as keywords did not yield a single picture corresponding to *G. scheepmakeri.* This raises important concerns regarding the conservation status of this species. Our study thus highlights that a rapid assessment of the populations throughout the known and presumed distribution range of *G. scheepmakeri* is of critical importance for the conservation of that species.

5. Conclusions

In this study, we confirmed the view that the *Goura* genus comprises four well separated lineages (del Hoyo and Collar, 2014), and two pairs of species that are sister groups (*i.e.*, *G. cristata* and *G. sclaterii* being the sister group to *G. victoria* and *G. scheepmakeri*). Interestingly, species with abutting geographic ranges are not each other's closest relatives, except *G. cristata* and *G. sclaterii*, which may meet somewhere between Etna Bay (Bird's Neck) and Mimika River (westernmost southern lowlands) (Mayr, 1941). Species diversification might have begun at the Miocene-Pliocene boundary, which suggests that it could have taken place within New Guinea. If so, our dating results show that an initial range expansion prior to barrier formation could have led to an early divergence due to vicariance associated with orogeny, but subsequent rounds of speciation were more likely due to cross-barrier dispersal events. Similar patterns appear to emerge from other recent studies of New Guinea complex lowland avian lineages, *e.g.* the Little Shrike-thrush *Colluricincla megarhyncha* (Deiner et al., 2011) and the White-eared Catbird *Ailuroedus buccoides* (Irestedt et al., 2015). This suggests that complicated phylogeographic processes have been at play in lowland regions of New Guinea, even though the vast expanses of forests occupying these regions form a continuous ring around the island with few apparent geographical and ecological isolating barriers (Mack and Dumbacher, 2007). We also found that the age of the *Goura* lineage itself accords with the hypothesis that Australia has been an important centre of diversification for Australasian bird lineages that dispersed to the island of New Guinea prior to extinction in Australia owing to post Miocene contraction of lowland rainforests (Schodde, 2006; Heinsohn and Hope, 2006). However, proving this connection may remain a difficult task in groups that are now restricted to New Guinea and for which the fossil record is scarce or even absent.

Acknowledgments

We are very grateful to Mark Adams (NHMUK), Paul Sweet and Thomas Trombone (AMNH), Robert Palmer (ANWC), and Jan Bolding Kristensen and Jon Fjeldså (ZMUC), for their invaluable contribution to this work through tissue loans. We are also grateful to Kadarusman, Gono Semiadi, Laurent Pouyaud, Régis Hocdé and Amos for encouraging us to conduct this study and for their invaluable help in the field, to Boris Delahaie, Joris Bertrand, and Yann Bourgeois for helping with toe-pad sampling at NHMUK, and to Jill Olofsson for enlightening discussions. We thank Hélène Holota for help with the laboratory work and Genotoul bioinformatics platform Toulouse Midi-Pyrenees for providing access to computing resources. We further thank Lynx Edicions for allowing us to reproduce paintings from the Handbook of the Birds of the World, and Staffan Widstrand and Fondation Iris for providing the picture used in the graphical abstract. We are also grateful to the reviewers for comments and suggestions that greatly improved the manuscript. The first author was supported by a Ministère de l'Enseignement Supérieur et de la Recherche PhD scholarship. Fieldwork and part of the museum work were supported by the Lengguru 2014 Project (www.lengguru.org), conducted by the French Institut de Recherche pour le Développement (IRD), the Indonesian Institute of Sciences (LIPI) with the Research Center for Biology (RCB) and the Research Center for Oceanography (RCO), the University of Papua (UNIPA), the University of Cendrawasih (UNCEN), the University of Musamus (UNMUS) and the Polytechnic School of Sorong (POLTEK) with corporate sponsorship from COLAS

Group, Veolia Water and the Total Foundation. Sequencing was supported by the 'Laboratoire d'Excellence' TULIP (ANR-10-LABX-41; ANR-11-IDEX-0002-02).

Data accessibility

In the NCBI nucleotide database, all newly assembled sequences are available under accessions MG590263 to MG590323.

Authors' contributions

C.T. and G.B. initiated, coordinated and supervised the project; J.B., CT. and G.B. conceived the study and designed the analyses; C.T., R.P-J., H.A., B.M., and L.J. coordinated the collection of field and museum samples; molecular data were obtained by J.B. with contributions from G.B; J.B., M.G. and G.B. analyzed the data, with contributions from C.T; J.B., M.G., G.B., and C.T. wrote the paper with comments from other authors.

Appendix A. Supplementary materials

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2017.11.022.

References

Aggerbeck, M., Fjeldså, J., Christidis, L., Fabre, P.-H., Jønsson, K.A., 2014. Resolving deep lineage divergences in core corvoid passerine birds supports a proto-Papuan island origin. Mol. Phylogenet. Evol. 70, 272–285. http://dx.doi.org/10.1016/j.ympev.2013.09.027.

Andersen, M.J., McCullough, J.M., Mauck, W.M., Smith, B.T., Moyle, R.G., 2017. A phylogeny of kingfishers reveals an Indomalayan origin and elevated rates of diversification on oceanic islands. J. Biogeogr. http://dx.doi.org/10.1111/jbi.13139. (in press).

Ballard, J.W.O., Whitlock, M.C., 2004. The incomplete natural history of mitochondria. Mol. Ecol. 13, 729–744. http://dx.doi.org/10.1046/j.1365-294X.2003.02063.x.

Beehler, B.M., Pratt, T.K., 2016. Birds of New Guinea: Distribution, Taxonomy, and Systematics. Princeton University Press, Princeton, NJ, USA.

Beehler, B.M., Pratt, T.K., Zimmerman, D.A., 1986. Birds of New Guinea. Princeton University Press, Princeton, NJ, USA.

Besnard, G., Bertrand, J.A.M., Delahaie, B., Bourgeois, Y.X.C., Lhuillier, E., Thébaud, C., 2016. Valuing museum specimens: high-throughput DNA sequencing on historical collections of New Guinea crowned pigeons (*Goura*). Biol. J. Linn. Soc. 117, 71–82. http://dx.doi.org/10.1111/bij.12494.

Bininda-Emonds, O.R.P., 2005. SeqCat.pl version 1.0. Program distributed by the author. AG Systematik und Evolutionsbiologie, IBU - Fakultät V, Carl von Ossietzky Universität Oldenburg.

Binladen, J., Wiuf, C., Gilbert, M.T.P., Bunce, M., Barnett, R., Larson, G., Greenwood, A.D., Haile, J., Ho, S.Y.W., Hansen, A.J., Willerslev, E., 2006. Assessing the fidelity of ancient DNA sequences amplified from nuclear genes. Genetics 172, 733–741. http://dx.doi.org/10.1534/genetics.105.049718.

Bolger, A.M., Lohse, M., Usadel, B., 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. Bioinformatics 30, 2114–2120. http://dx.doi.org/10.1093/bioinformatics/btu170.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A., Drummond, A.J., 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. PLoS Comput. Biol. 10, e1003537. http://dx.doi.org/10.1371/journal.pcbi.1003537.

Bull, C.M., 1991. Ecology of parapatric distributions. Annu. Rev. Ecol. Syst. 22, 19–36. http://dx.doi.org/10.1146/annurev.es.22.110191.000315.

Byrne, M., Steane, D.A., Joseph, L., Yeates, D.K., Jordan, G.J., Crayn, D., Aplin, K., Cantrill, D.J., Cook, L.G., Crisp, M.D., Keogh, J.S., Melville, J., Moritz, C., Porch, N., Sniderman, J.M.K., Sunnucks, P., Weston, P.H., 2011. Decline of a biome: evolution, contraction, fragmentation, extinction and invasion of the Australian mesic zone biota. J. Biogeogr. 38, 1635–1656. http://dx.doi.org/10.1111/j.1365-2699.2011.02535.x.

Carmi, O., Witt, C.C., Jaramillo, A., Dumbacher, J.P., 2016. Phylogeography of the Vermilion Flycatcher species complex: Multiple speciation events, shifts in migratory behavior, and an apparent extinction of a Galápagos-endemic bird species. Mol. Phylogenet. Evol. 102, 152–173. http://dx.doi.org/10.1016/j.ympev.2016.05.029.

Charlton, T.R., 2000. Tertiary evolution of the eastern Indonesia collision complex. J. Asian Earth Sci. 18, 603–631. http://dx.doi.org/10.1016/S1367-9120(99)00049-8.

Chikuni, K., Minaka, N., Ikenaga, H., 1996. Molecular phylogeny of some Passeriformes, based on cytochrome b sequences. J. Yamashina Inst. Ornithol. 28, 1–8. http://dx.doi.org/10.3312/jyio1952.28.1.

Claramunt, S., Cracraft, J., 2015. A new time tree reveals Earth history's imprint on the evolution of modern birds. Sci. Adv. 1, e1501005. http://dx.doi.org/10.1126/sciadv.1501005.

Darwin, C., 1868. The Variation of Animals and Plants under Domestication. In: John Murray, London, UK.

Deiner, K., Lemmon, A.R., Mack, A.L., Fleischer, R.C., Dumbacher, J.P., 2011. A passerine bird's evolution corroborates the geologic history of the island of New Guinea. PLoS ONE 6. http://dx.doi.org/10.1371/journal.pone.0019479.

del Hoyo, J., Collar, N.J., 2014. HBW and BirdLife International Illustrated Checklist of the Birds of the World 1: Non-passerines. In: Lynx Edicions, Barcelona.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4, e88. http://dx.doi.org/10.1371/journal.pbio.0040088.

EAZA, 2017. Specialist Programmes [WWW Document]. Eur. Assoc. Zoos Aquar, URL http://www.eaza.net/conservation/programmes/ (accessed 04.14.17).

Edwards, S.V., Beerli, P., 2000. Perspective: gene divergence, population divergence, and the variance incoalescence time in phylogeographic studies. Evolution 54, 1839–1854. http://dx.doi.org/10.1554/0014-3820(2000) 054[1839:PGDPDA]2.0.CO;2.

Fulton, T.L., Wagner, S.M., Fisher, C., Shapiro, B., 2012. Nuclear DNA from the extinct Passenger Pigeon (*Ectopistes migratorius*) confirms a single origin of New World pigeons. Ann. Anat. - Anat. Anz. Special Issue: Ancient DNA 194, 52–57. http://dx.doi.org/10.1016/j.aanat.2011.02.017.

Georges, A., Zhang, X., Unmack, P., Reid, B.N., Le, M., McCord, W.P., 2014. Contemporary genetic structure of an endemic freshwater turtle reflects Miocene orogenesis of New Guinea. Biol. J. Linn. Soc. 111, 192–208. http://dx.doi.org/10.1111/bij.12176.

Gibbs, D., Barnes, E., Cox, J., 2001. Pigeons and Doves: A Guide to the Pigeons and Doves of the World. Bloomsbury Publishing, London, UK.

Guschanski, K., Krause, J., Sawyer, S., Valente, L.M., Bailey, S., Finstermeier, K., Sabin, R., Gilissen, E., Sonet, G., Nagy, Z.T., Lenglet, G., Mayer, F., Savolainen, V., 2013. Next-generation museomics disentangles one of the largest primate radiations. Syst. Biol. 62, 539–554. http://dx.doi.org/10.1093/sysbio/syt018.

Hall, R., 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. J. Limnol. 72, 1.

Hall, R., 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: Hall, Robert, Holloway, Jeremy D. (Eds.), Biogeography and Geological Evolution of SE Asia. Backhuys Publishers, Leiden, The Netherlands, pp. 99–131.

Hartert, E., Paludan, K., Rothschild, Lord, Stresemann, E., 1936. Die Vögel des Weyland-Gebirges und seines Vorlandes. Mitteilungen Aus Dem Zool. Mus. Berl. 21, 165–240.

Hasegawa, M., Kishino, H., Yano, T., 1985. Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. J. Mol. Evol. 22, 160–174. http://dx.doi.org/10.1007/BF02101694.

Heads, M., 2001. Birds of paradise, biogeography and ecology in New Guinea: a review. J. Biogeogr. 28, 893–925. http://dx.doi.org/10.1046/j.1365-2699.2001.00600.x.

Heinsohn, T., Hope, G., 2006. The Torresian connections: zoogeography of New Guinea. In: Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y. (Eds.), Evolution and Biogeography of Australian Vertebrates. Australian Scientific Publishing, Oatlands, Australia.

Heupink, T.H., van Grouw, H., Lambert, D.M., 2014. The mysterious Spotted Green Pigeon and its relation to the Dodo and its kindred. BMC Evol. Biol. 14, 136. http://dx.doi.org/10.1186/1471-2148-14-136.

Hill, K.C., Hall, R., 2003. Mesozoic-Cenozoic evolution of Australia's New Guinea margin in a west Pacific context. Geol. Soc. Am. Spec. Pap. 372, 265–290. http://dx.doi.org/10.1130/0-8137-2372-8.265.

Irestedt, M., Batalha-Filho, H., Roselaar, C.S., Christidis, L., Ericson, P.G.P., 2015. Contrasting phylogeographic signatures in two Australo-Papuan bowerbird species complexes (Aves: *Ailuroedus*). Zool. Scr. 45, 365–379. http://dx.doi.org/10.1111/zsc.12163.

Irestedt, M., Ohlson, J.I., Zuccon, D., Källersjö, M., Ericson, P.G.P., 2006. Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). Zool. Scr. 35, 567–580. http://dx.doi.org/10.1111/j.1463-6409.2006.00249.x.

Johnson, K.P., Clayton, D.H., 2000. Nuclear and mitochondrial genes contain similar phylogenetic signal for pigeons and doves (Aves: Columbiformes). Mol. Phylogenet. Evol. 14, 141–151. http://dx.doi.org/10.1006/mpev.1999.0682.

Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P.L.F., Orlando, L., 2013. mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. Bioinformatics 29, 1682–1684. http://dx.doi.org/10.1093/bioinformatics/btt193.

Jønsson, K.A., Borregaard, M.K., Carstensen, D.W., Hansen, L.A., Kennedy, J.D., Machac, A., Marki, P.Z., Fjeldså, J., Rahbek, C., 2017. Biogeography and biotic assembly of indo-pacific corvoid passerine birds. Annu. Rev. Ecol. Evol. Syst. 48, 231–253. http://dx.doi.org/10.1146/annurev-ecolsys-110316-022813.

Jønsson, K.A., Fabre, P.-H., Kennedy, J.D., Holt, B.G., Borregaard, M.K., Rahbek, C., Fjeldså, J., 2016. A supermatrix phylogeny of corvoid passerine birds (Aves: Corvides). Mol. Phylogenet. Evol. 94, 87–94. http://dx.doi.org/10.1016/j.ympev.2015.08.020.

Jønsson, K.A., Fabre, P.-H., Ricklefs, R.E., Fjeldså, J., 2011. Major global radiation of corvoid birds originated in the proto-Papuan archipelago. Proc. Natl. Acad. Sci. U. S. A. 108, 2328–2333. http://dx.doi.org/10.1073/pnas.1018956108.

King, C.E., Nijboer, J., 1994. Conservation considerations for crowned pigeons, genus *Goura*. Oryx 28, 22–30. http://dx.doi.org/10.1017/S0030605300028258.

Korneliussen, T.S., Albrechtsen, A., Nielsen, R., 2014. ANGSD: Analysis of Next Generation Sequencing Data. BMC Bioinf. 15, 356. http://dx.doi.org/10.1186/s12859-014-0356-4.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T., Calcott, B., 2017. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. Mol. Biol. Evol. 34, 772–773. http://dx.doi.org/10.

1093/molbev/msw260.
Leighton, G.R.M., Hugo, P.S., Roulin, A., Amar, A., 2016. Just Google it: assessing the use of Google Images to describe geographical variation in visible traits of organisms. Methods Ecol. Evol. 7, 1060–1070. http://dx.doi.org/10.1111/2041-210X.12562.
Lepage, T., Bryant, D., Philippe, H., Lartillot, N., 2007. A general comparison of relaxed molecular clock models. Mol. Biol. Evol. 24, 2669–2680. http://dx.doi.org/10.1093/molbev/msm193.
Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G., Durbin, R., Subgroup, 1000 Genome Project Data Processing, 2009. The Sequence Alignment/Map format and SAMtools. Bioinformatics 25, pp. 2078–2079. https://doi.org/10.1093/bioinformatics/btp352.
Lopez, J.V., Yuhki, N., Masuda, R., Modi, W., O'Brien, S.J., 1994. Numt, a recent transfer and tandem amplification of mitochondrial DNA to the nuclear genome of the domestic cat. J. Mol. Evol. 39, 174–190. http://dx.doi.org/10.1007/BF00163806.
Lovette, I.J., 2004. Mitochondrial dating and mixed support for the "2% rule" in birds. Auk 121, 1–6. http://dx.doi.org/10.1642/0004-8038(2004) 121[0001:MDAMSF]2.0.CO;2.
Mack, A., Dumbacher, J., 2007. Birds of Papua. In: Marshall, Andrew J., Beehler, Bruce M. (Eds.), The Ecology of Papua, Part I. The Ecology of Indonesia Series VI. Periplus, Singapore, pp. 654–688.
Malé, P.-J.G., Bardon, L., Besnard, G., Coissac, E., Delsuc, F., Engel, J., Lhuillier, E., Scotti-Saintagne, C., Tinaut, A., Chave, J., 2014. Genome skimming by shotgun sequencing helps resolve the phylogeny of a pantropical tree family. Mol. Ecol. Resour. 14, 966–975. http://dx.doi.org/10.1111/1755-0998.12246.
Marki, P.Z., Jønsson, K.A., Irestedt, M., Nguyen, J.M.T., Rahbek, C., Fjeldså, J., 2017. Supermatrix phylogeny and biogeography of the Australasian Meliphagides radiation (Aves: Passeriformes). Mol. Phylogenet. Evol. 107, 516–529. http://dx.doi.org/10.1016/j.ympev.2016.12.021.
Mayr, E., 1941. List of New Guinea Birds: A Systematic and Faunal List of the Birds of New Guinea and Adjacent Islands. In: American Museum of Natural History, New-York, USA.
McCormack, J.E., Harvey, M.G., Faircloth, B.C., Crawford, N.G., Glenn, T.C., Brumfield, R.T., 2013. A phylogeny of birds based on over 1,500 loci collected by target enrichment and high-throughput sequencing. PLoS ONE 8, e54848. http://dx.doi.org/10.1371/journal.pone.0054848.
McCormack, J.E., Tsai, W.L.E., Faircloth, B.C., 2016. Sequence capture of ultraconserved elements from bird museum specimens. Mol. Ecol. Resour. 16, 1189–1203. http://dx.doi.org/10.1111/1755-0998.12466.
Moore, W.S., 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus nuclear-gene trees. Evolution 49, 718–726. http://dx.doi.org/10.1111/j.1558-5646.1995.tb02308.x.
Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M., Faircloth, B.C., 2016. Tectonic collision and uplift of Wallacea triggered the global songbird radiation. Nat. Commun. 7, 12709. http://dx.doi.org/10.1038/ncomms12709.
Nabholz, B., Lanfear, R., Fuchs, J., 2016. Body mass-corrected molecular rate for bird mitochondrial DNA. Mol. Ecol. 25, 4438–4449. http://dx.doi.org/10.1111/mec.13780.
Olofsson, J.K., Bianconi, M., Besnard, G., Dunning, L.T., Lundgren, M.R., Holota, H., Vorontsova, M.S., Hidalgo, O., Leitch, I.J., Nosil, P., Osborne, C.P., Christin, P.-A., 2016. Genome biogeography reveals the intraspecific spread of adaptive mutations for a complex trait. Mol. Ecol. 25, 6107–6123. http://dx.doi.org/10.1111/mec.13914.
Paśko, Ł., Ericson, P.G.P., Elzanowski, A., 2011. Phylogenetic utility and evolution of indels: A study in neognathous birds. Mol. Phylogenet. Evol. 61, 760–771. http://dx.doi.org/10.1016/j.ympev.2011.07.021.
Pereira, S.L., Johnson, K.P., Clayton, D.H., Baker, A.J., 2007. Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleogene. Biol. Syst. http://dx.doi.org/10.1080/10635150701549672.
Pratt, T.K., Beehler, B.M., 2015. Birds of New Guinea, second ed. Princeton University Press, Princeton, NJ, USA.
Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M., Lemmon, A.R., 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. Nature 526, 569–573. http://dx.doi.org/10.1038/nature15697.
Rambaut, A., Suchard, M., Xie, D., Drummond, A., 2014. Tracer v1.6, Available from http://beast.bio.ed.ac.uk/Tracer.
Rand, A.L., Gilliard, E.T., 1968. Handbook of New Guinea Birds. Weidenfeld & Nicolson, London, UK.
Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A., Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542. http://dx.doi.org/10.1093/sysbio/sys029.
Sawyer, S., Krause, J., Guschanski, K., Savolainen, V., Pääbo, S., 2012. Temporal patterns of nucleotide misincorporations and DNA fragmentation in ancient DNA. PLoS ONE 7, e34131. http://dx.doi.org/10.1371/journal.pone.0034131.
Schodde, R., 2006. Australia's bird fauna today–origins and evolutionary development. In: Merrick, J.R., Archer, G.M., Hickey, G.M., Lee, M.S.Y. (Eds.), Evolution and Biogeography of Australasian Vertebrates. Auscipub, Oatlands, Australia, pp. 413–458.
Schodde, R., Christidis, L., 2014. Relicts from Tertiary Australasia: undescribed families and subfamilies of songbirds (Passeriformes) and their zoogeographic signal. Zootaxa 3786, 501–522. https://doi.org/10.11646/zootaxa.3786.5.1.
Schweizer, M., Wright, T.F., Peñalba, J.V., Schirtzinger, E.E., Joseph, L., 2015. Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes). Mol. Phylogenet. Evol. 90, 34–48. http://dx.doi.org/10.1016/j.ympev.2015.04.021.
Shapiro, B., Sibthorpe, D., Rambaut, A., Austin, J., Wragg, G.M., Bininda-Emonds, O.R., Lee, P.L., Cooper, A., 2002. Flight of the dodo. Science 295. http://dx.doi.org/10.1126/science.295.5560.1683.
Shapiro, M.D., Kronenberg, Z., Li, C., Domyan, E.T., Pan, H., Campbell, M., Tan, H., Huff, C.D., Hu, H., Vickrey, A.I., Nielsen, S.C.A., Stringham, S.A., Hu, H., Willerslev, E., Gilbert, M.T.P., Yandell, M., Zhang, G., Wang, J., 2013. Genomic diversity and evolution of the head crest in the rock pigeon. Science 339, 1063–1067. http://dx.doi.org/10.1126/science.1230422.
Shipham, A., Schmidt, D.J., Joseph, L., Hughes, J.M., 2015. Phylogenetic analysis of the Australian rosella parrots (*Platycercus*) reveals discordance among molecules and plumage. Mol. Phylogenet. Evol. 91, 150–159. http://dx.doi.org/10.1016/j.ympev.2015.05.012.
Soares, A.E.R., Novak, B.J., Haile, J., Heupink, T.H., Fjeldså, J., Gilbert, M.T.P., Poinar, H., Church, G.M., Shapiro, B., 2016. Complete mitochondrial genomes of living and extinct pigeons revise the timing of the columbiform radiation. BMC Evol. Biol. 16, 230. http://dx.doi.org/10.1186/s12862-016-0800-3.
Stadler, T., 2009. On incomplete sampling under birth–death models and connections to the sampling-based coalescent. J. Theor. Biol. 261, 58–66. http://dx.doi.org/10.1016/j.jtbi.2009.07.018.
Stamatakis, A., 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30, 1312–1313. http://dx.doi.org/10.1093/bioinformatics/btu033.
Steadman, D.W., 2006. An extinct species of tooth-billed pigeon (*Didunculus*) from the Kingdom of Tonga, and the concept of endemism in insular landbirds. J. Zool. 268, 233–241. http://dx.doi.org/10.1111/j.1469-7998.2005.00010.x.
Steadman, D.W., 1995. Prehistoric extinctions of pacific island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131. http://dx.doi.org/10.1126/science.267.5201.1123.
Straub, S.C.K., Parks, M., Weitemier, K., Fishbein, M., Cronn, R.C., Liston, A., 2012. Navigating the tip of the genomic iceberg: next-generation sequencing for plant systematics. Am. J. Bot. 99, 349–364. http://dx.doi.org/10.3732/ajb.1100335.
Tamura, K., Nei, M., 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. Mol. Biol. Evol. 10, 512–526. http://dx.doi.org/10.1093/oxfordjournals.molbev.a040023.
Tavaré, S., 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. Lect. Math. Life Sci. 17, 57–86.
Toussaint, E.F.A., Hall, R., Monaghan, M.T., Sagata, K., Ibalim, S., Shaverdo, H.V., Vogler, A.P., Pons, J., Balke, M., 2014. The towering orogeny of New Guinea as a trigger for arthropod megadiversity. Nat. Commun. 5, 4001. http://dx.doi.org/10.1038/ncomms5001.
Toussaint, E.F.A., Shaverdo, H., Hendrich, L., Balke, M., 2015. Mosaic patterns of diversification dynamics following the colonization of Melanesian Islands. Sci. Rep. 5, 16016. http://dx.doi.org/10.1038/srep16016.
van Ufford, A.Q., Cloos, M., 2005. Cenozoic tectonics of New Guinea. AAPG Bull. 89, 119–140. http://dx.doi.org/10.1306/08300403073.
van Wyhe, J., Rookmaaker, K., 2013. Alfred Russel Wallace: Letters from the Malay Archipelago. Oxford University Press, Oxford, UK.
Voris, H.K., 2000. Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. J. Biogeogr. 27, 1153–1167. http://dx.doi.org/10.1046/j.1365-2699.2000.00489.x.
Wallace, A.R., 1905. My Life: A Record of Events and Opinions. Dodd, Mead & Company, New-York, USA.
Wallace, A.R., 1876. The Geographical Distribution of Animals: with a Study of the Relations of Living and Extinct Faunas as Elucidating the Past Changes of the Earth's Surface. Macmillan and Co, London, UK.
Wallace, A.R., 1869. The Malay Archipelago: The Land of the Orang-utan, and the Bird of paradise. A Narrative of Travel, with Studies of Man and Nature. Macmillan and Co, London, UK.
Weir, J.T., 2006. Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. Evolution 60, 842–855. http://dx.doi.org/10.1111/j.0014-3820.2006.tb01161.x.
Weir, J.T., Schluter, D., 2008. Calibrating the avian molecular clock. Mol. Ecol. 17, 2321–2328. http://dx.doi.org/10.1111/j.1365[HYPHEN]294X.2008.03742.x.
Worthy, T.H., 2001. A giant flightless pigeon gen. et sp. nov. and a new species of Ducula (Aves: Columbidae), from Quaternary deposits in Fiji. J. R. Soc. New Zealand 31 (4), 763–794. http://dx.doi.org/10.1080/03014223.2001.9517673.
Wu, T.D., Nacu, S., 2010. Fast and SNP-tolerant detection of complex variants and splicing in short reads. Bioinformatics 26, 873–881. http://dx.doi.org/10.1093/bioinformatics/btq057.