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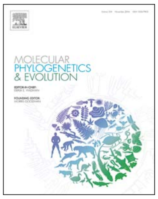

Recovering the evolutionary history of crowned pigeons (Columbidae: *Goura*): Implications for the biogeography and conservation of New Guinean lowland birds

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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.

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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