Molecular Phylogenetics and Evolution 110 (2017) 19–26

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

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

Phylogeny and biogeography of the imperial pigeons (Aves: Columbidae) in the Pacific Ocean

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ARTICLE INFO

Article history:
Received 4 October 2016
Revised 16 February 2017
Accepted 24 February 2017
Available online 27 February 2017

Keywords:
Island biogeography
Molecular phylogeny
Pacific Ocean
Polynesia
Ducula

ABSTRACT

We reconstruct the phylogeny of imperial pigeons (genus *Ducula*) using mitochondrial and nuclear sequence data. We evaluate the most likely biogeographic scenario for the evolution of this group that colonized many islands of the Pacific Ocean. The divergence time analysis suggests that the basal divergences within *Ducula* occurred more recently than in the fruit doves (genus *Ptilinopus*), a group that is also well diversified in Oceania. The imperial pigeons colonized the Melanesian region several times independently, and the diversification within this region led to several species in sympatry, in particular in the Bismarck archipelago. Central Polynesia was also colonized several times, first by a lineage during the Miocene that led to the large *D. latrans*, sister to the New Caledonian endemic *D. goliath*, then more recently by the widespread *D. pacifica*, during the Pleistocene. The phylogenetic pattern obtained with the extant *Ducula* species showed that the Eastern Polynesian endemics do not form a monophyletic group, with the Pacific Imperial Pigeon *D. pacifica* sister species with good support to the Polynesian Imperial Pigeon *D. aurorae*. However, the impact of recent anthropic extinctions has been important for the imperial pigeons, more than for the smaller fruit doves, suggesting that several *Ducula* lineages might be missing today.

1. Introduction

The Columbidae constitutes one of the most widespread and remarkable families of landbirds on tropical Pacific islands. Within this family, fruit doves (*Ptilinopus*) and imperial pigeons (*Ducula*) represent the bulk of the columbid diversification in Oceania. Both are forest-dwelling birds, mostly frugivorous that play a tremendous role in seed dispersal for many insular plants (McConkey et al., 2004). Together with several Australasian genera (*Hemiphaga*, *Lopholaimus*, *Gymnophaps*), they form a large clade within the Columbidae (Gibb and Penny, 2010; Pereira et al., 2007; Shapiro et al., 2002). *Ducula* are on average larger than *Ptilinopus*, with fewer species (36 vs. 50 for fruit doves) restricted to the Asian-Pacific region (marginally in the Indian Ocean, with a single *Ducula* species endemic to Christmas Island). *Ducula* and *Ptilinopus* co-exist in sympatry on many islands (Gibbs et al., 2001). *Ducula* imperial pigeons are widespread in the islands of the Pacific Ocean, with a high proportion of species occurring in New Guinea (22%), like the *Ptilinopus* fruit doves (24%), although an even larger proportion of imperial pigeons are found in the Wallacean region (39%, Fig. 1). Like many other groups of landbird, *Ducula* suffered from human colonization of the Pacific islands, because of predation by humans and introduced predators, and of habitat changes. Several imperial pigeons have become extinct, *Ducula lakeba* on Lakeba (Lau group, Fiji), *D. david* on Uvea (Wallis Group), *D. harrisoni* on Henderson (Pitcairn Group), and several undescribed imperial pigeons (*Ducula* or cf. *Ducula*) from the Austral Islands, Gambier Islands and Tonga (Balouet and Olson, 1987; Steadman, 2006; Tennyson and Anderson, 2012; Worthy and Tennyson, 2004; Wragg and Worthy, 2006). In addition, several populations vanished in Eastern Polynesia, leading to a drastic restriction of the area of several species (Fig. 1; see synthesis in Thibault and Cibois, 2017). Previous work on *Ptilinopus* showed that the diversification of this group within the Pacific has been complex, with several independent colonizations of the most remote eastern islands (Cibois et al., 2014). In this study, we reconstruct the biogeographic and temporal diversification of the imperial pigeons to discern possible colonization patterns of this group in Oceania.

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http://dx.doi.org/10.1016/j.ympev.2017.02.016
1055-7903/

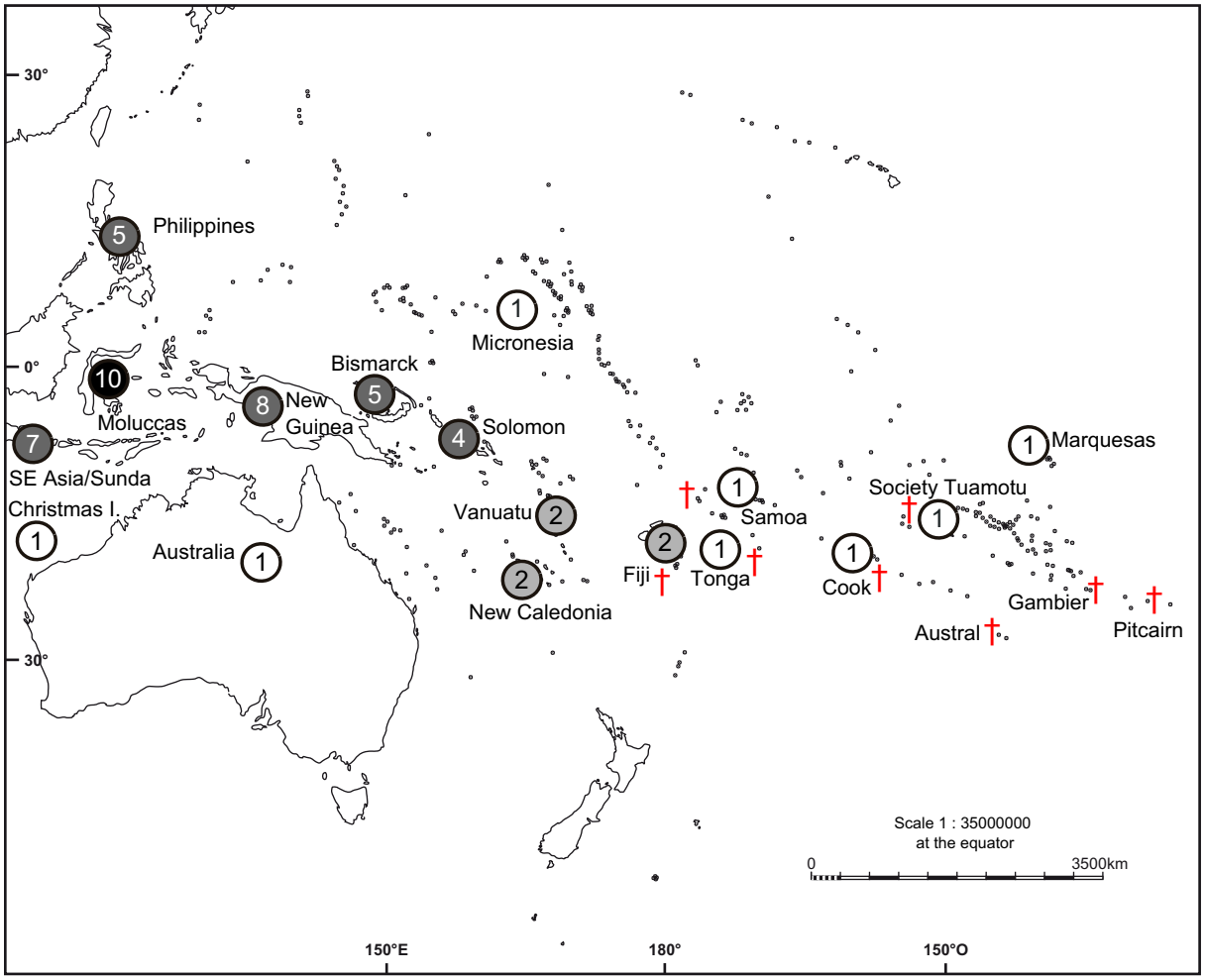

Fig. 1. Distribution of *Ducula* imperial pigeons. The number indicates the number of extant species found on each region or archipelago according to Dickinson and Remsen (2013). The red crosses indicate bone remains of extinct taxa or populations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Taxon sampling

We sampled 24 out of the 36 species recognized by Dickinson and Remsen (2013), with at least two individuals per species for most of them. 11 species were sequenced using museum specimens only as DNA source, while 13 species were sequenced from fresh tissue materials (see Table S1 for details on specimens and institutions). We were particularly interested in the imperial pigeons endemic to the Central and East Polynesian regions (5 taxa) for which we sequenced all subspecies and as many localities as possible. Although 12 species are not included in this study, we sequenced representatives of all plumage-based groups according to Goodwin (1967) and all geographic regions where imperial pigeons occur, from continental Asia to Polynesia, except the Philippines and Christmas Island in the Indian Ocean. We chose three genera for outgroups: *Ptilinopus* and *Alectroenas*, which are closely related and sister to the clade composed of *Ducula* and several related genera (see introduction), and one more distantly related pigeon, the Nicobar Pigeon *Caloenas nicobarica*.

2.2. DNA extraction, amplification and sequencing

Standard extraction protocols were followed except for extracts from toe-pads off museum specimens for which the time of digestion was increased from two to 12 h, and dithiothreitol (DTT 1 M, 20 μl) was added to the reaction. All tubes and reagents were UV-treated for 30 min before use and extraction tubes containing no sample were used as a control for contamination. We amplified portions of five genes, using the same primers as a previous study on fruit doves (Cibois et al., 2014): three mitochondrial genes, NADH dehydrogenase subunit 2 (ND2), cytochrome *c* oxidase subunit I (COI), and NADH subunit 3 (ND3) with flanking tRNAs; and two nuclear genes, Beta-fibrinogen (FGB), exons 5 to 6 and intron 5, and RAG-1 (RAG). PCR amplifications were performed in 25 μl reactions with 2 μl of template and 0.4 μM final concentration for primers. The thermocycling procedure started with an initial denaturation of 3 min at 95 °C, followed by 40 cycles of 30 s at 95 °C, 40 s at annealing temperature (46–55 °C), and 40 s at 72 °C for elongation. For museum specimens, PCR products were cycle sequenced in both directions at a contract sequencing facility (Macrogen, Amsterdam, The Netherlands) on an ABI3730 XL automatic DNA sequencer, using the same primers as used in PCR. Contiguous sequences derived from the set of sequence fragments were created using Sequencher (Genecodes, Ann Arbor, MI, USA). We carefully examined the sequences obtained from toe-pad extractions. Because amplifications could only be made for short fragments, the risks of obtaining pseudogenes or chimera are higher than when using fresh material (Moyle et al., 2013). To minimize these risks, we used specific primers designed to produce overlapping fragments, verified the absence of amplification in