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The evolution of the Indian Ocean parrots (Psittaciformes): Extinction, adaptive radiation and eustacy

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ABSTRACT

Parrots are among the most recognisable and widely distributed of all bird groups occupying major parts of the tropics. The evolution of the genera that are found in and around the Indian Ocean region is particularly interesting as they show a high degree of heterogeneity in distribution and levels of speciation. Here we present a molecular phylogenetic analysis of Indian Ocean parrots, identifying the possible geological and geographical factors that influenced their evolution. We hypothesise that the Indian Ocean islands acted as stepping stones in the radiation of the Old-World parrots, and that sea-level changes may have been an important determinant of current distributions and differences in speciation. A multi-locus phylogeny showing the evolutionary relationships among genera highlights the interesting position of the monotypic *Psittrichas*, which shares a common ancestor with the geographically distant *Coracopsis*. An extensive species-level molecular phylogeny indicates a complex pattern of radiation including evidence for colonisation of Africa, Asia and the Indian Ocean islands from Australasia via multiple routes, and of island populations 'seeding' continents. Moreover, comparison of estimated divergence dates and sea-level changes points to the latter as a factor in parrot speciation. This is the first study to include the extinct parrot taxa, *Mascarinus mascarinus* and *Psittacula wardi* which, respectively, appear closely related to *Coracopsis nigra* and *Psittacula eupatria*.

1. Introduction

The Indian Ocean islands are remarkable for their high levels of biodiversity and endemism, and the region has become an important focus for evolutionary research. This high biodiversity is explained by the ecological diversity and the complex geological history (Hall, 1996, 1997) of the region. In particular, the Indian Ocean islands have diverse avifauna, and available fossil data and historical documentation suggests that they may have been especially rich in parrot species; virtually all Indian Ocean island systems currently support or have supported parrot taxa (Hume, 2007). The surrounding continents also have many parrot species, suggesting that the islands may have been important stepping stones in the adaptive radiation of these birds.

1.1. The parrots, order Psittaciformes

In an extensive review of anatomical, morphological and behavioural evidence, Smith (1975) suggested a single parrot family subdivided into four subfamilies – the Platycercinae (with four tribes), Loriinae (with five tribes), Arinae and Psittacinae. Forshaw (1989) largely accepted Smith's tribal arrangements but redistributed them among three subfamilies, the Loriinae (no tribes), Cacatuinae (three tribes) and Psittacinae (nine tribes). Recent reviews (Collar, 1997; Forshaw, 2006) split the parrots into two families, Cacatuidae (cockatoos) and Psittacidae ('true parrots'), the latter of which is itself divided into Loriinae (lorikeets), Psittacinae (parrots and macaws), Strigopinae (New Zealand parrots), Psittrichadinae (the vulturine parrot) and Micropsittinae (the pygmy parrots) subfamilies. Further studies indicated that the Strigopinae parrots actually form a third family, Strigopidae (de Kloet and de Kloet, 2005; Wright et al., 2008). Analyses have also cast doubt on Forshaw's placement of *Psittrichas fulgidas* as the sole member of Psittrichadinae. Whilst these molecular phylogenetic analyses have not unambiguously identified the evolutionary position of *Psittrichas*, they do suggest a close relationship with *Coracopsis*, a genus belonging

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to Psittacinae (de Kloet and de Kloet, 2005; Schweizer et al., 2009; Wright et al., 2008). Forshaw (2006) split Psittacinae into six tribes: Psittacini (Afrotropical parrots), Psittaculini (psittaculine parrots), Arini (Neotropical parrots), Cyclopsittacini (fig parrots), Polytelini and Platycercini (broad-tailed parrots). Most of the parrots distributed in Africa and Asia, including those found on Indian Ocean islands and some from Australia, have been referred to Psittacini and Psittaculini. Psittacini includes *Coracopsis*, *Poicephalus* and *Psittacus*; Psittaculini, which is found in Australasia, Africa and Asia, comprises *Agapornis*, *Alisterus*, *Aprosmictus*, *Eclectus*, *Geoffroyus*, *Loriculus*, *Polytelis*, *Prioniturus*, *Psittacella*, *Psittacula*, *Psittinus* and *Tanygnathus*.

The parrots occurring in the Indian Ocean region show considerable range and population heterogeneity. Some genera are highly speciose and widely dispersed across islands and continents (Groombridge et al., 2004), whilst others show strong geographical restriction (Fig. 1) and little morphological diversification (Forshaw, 2006; Juniper and Parr, 1998). These striking contrasts make the parrots of this region an excellent system in which to answer questions about the biogeographic factors that influence speciation and adaptation. Numerous studies have attempted to resolve parrot systematics using both morphological and molecular techniques (Astuti et al., 2006; Birt et al., 1992; de Kloet and de Kloet, 2005; Hume, 2007; Mayr, 2010; Sibley and Ahlquist, 1990; Wright et al., 2008). Most recent molecular phylogenetic studies (Astuti et al., 2006; de Kloet and de Kloet, 2005; Schweizer et al., 2009; Wright et al., 2008) have encompassed parrot genera from across the clade's distribution giving a perspective of the broad evolutionary trends. However, sampling from within each genus has been comparatively restricted, particularly for *Coracopsis* and *Psittacula* which are important in the context of parrot evolution in the Indian Ocean. Here we seek to understand the species and subspecies relationships that underpin the adaptive radiation of Old-World parrots in and around the Indian Ocean islands. Specifically, by comparing the evolutionary history of island parrots (*Coracopsis*, *Eclectus* and *Tanygnathus*) with that of continental taxa (*Agapornis*, *Aprosmictus*, *Poicephalus*, *Polytelis* and *Psittacus*) and with those distributed both continentally and on islands (*Loriculus* and *Psittacula*), we aim to identify the biogeographical factors that influenced the adaptive radiation of parrots. This selected group of taxa also encompasses a range of species richness – *Aprosmictus*, *Eclectus*, *Psittacus* and *Tanygnathus* are monotypic, *Psittacula* is highly speciose; *Agapornis*, *Coracopsis*, *Loriculus*, *Poicephalus* and *Polytelis* show intermediate levels of diversity. Initially, we seek to confirm the genus-level relationships identified by previous studies (Schweizer et al., 2009; Wright et al., 2008) through a multi-locus phylogeny of genera in this region: *Agapornis*, *Aprosmictus*, *Coracopsis*, *Eclectus*, *Loriculus*, *Poicephalus*, *Polytelis*, *Psittacula* and *Psittacus*. We then establish species-level relationships to understand the radiation of these genera and the role of Indian Ocean islands. We substantially increase the sampling of parrot species and subspecies over that in previous studies. In particular, we

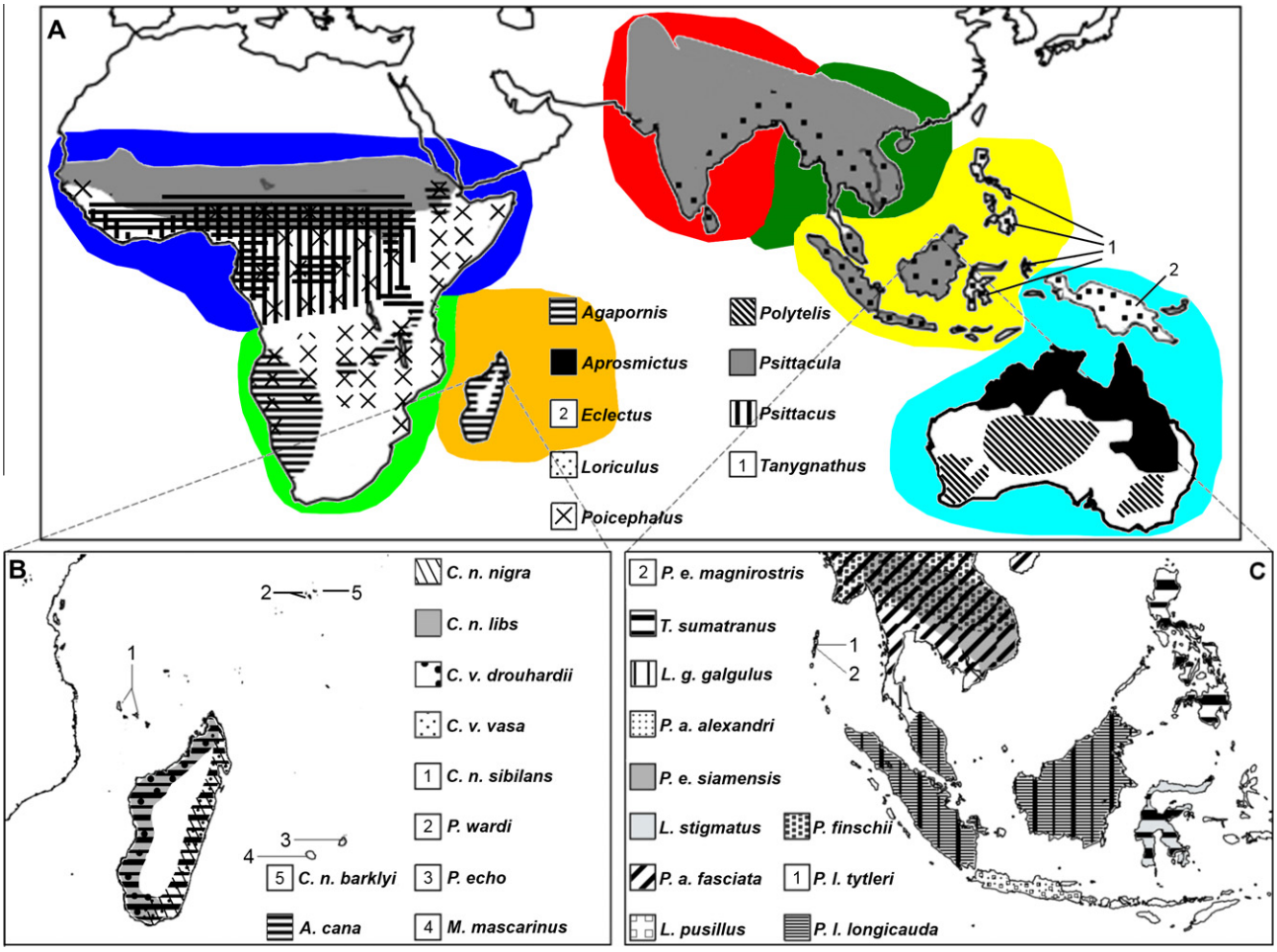

Fig. 1. The distribution of Old-World parrots in the Indian Ocean (Forshaw, 1989; Juniper and Parr, 1998). (A) Shows the distribution of a number of *Psittaculini* (Asian) and *Psittacini* (African) parrot genera. Several important regions are highlighted in colour. (B and C) highlight the distribution of these parrots on two major Indian Ocean regions, the Mascarene and Seychelles island groups, and the Indonesian Archipelago (B and C respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)