

## EVOLUTION

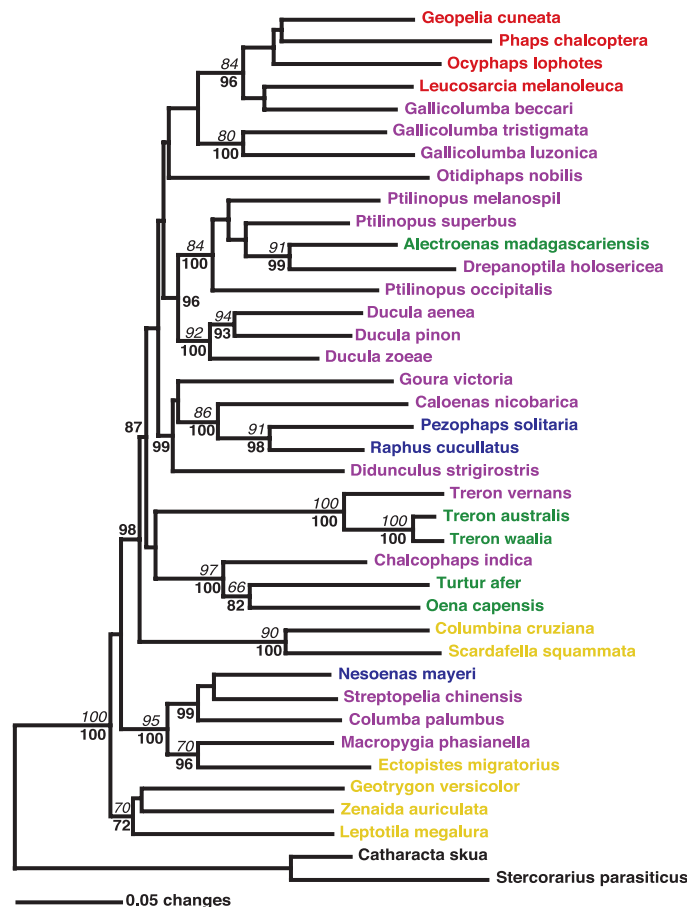
## Flight of the Dodo

Beth Shapiro,<sup>1,2</sup> Dean Sibthorpe,<sup>1</sup> Andrew Rambaut,<sup>1</sup>  
 Jeremy Austin,<sup>3</sup> Graham M. Wragg,<sup>1</sup> Olaf R. P. Bininda-Emonds,<sup>1</sup>  
 Patricia L. M. Lee,<sup>1</sup> Alan Cooper<sup>1,2\*</sup>

The evolutionary history of the dodo is very poorly understood. Like many avian island endemics, a high degree of morphological change associated with flightlessness and gigantism has obscured phylogenetic relationships, and historically the dodo has been linked with avian groups ranging from the ratites to the raptors (*1*). Since the mid-1800s, morphological studies have linked the dodo (initially *Didus ineptus*, now *Raphus cucullatus*) and its presumed close relative the solitaire (*Pezophaps solitaria*) with the Columbiformes (pigeons and doves), but their exact position is unresolved and they have been placed in many positions within the cosmopolitan Columbidae or in their own family, Raphidae, outside the Columbidae but within Columbiformes (*1, 2*). To answer these questions, we extracted DNA and amplified 1.4 kb of mitochondrial sequence [360–base pair (bp) 12S rRNA and 1050-bp cytochrome *b*] from 37 species of pigeons and doves, including the dodo, the solitaire, and multiple members of each of the five extant subfamilies (*3*). Short overlapping fragments were amplified by polymerase chain reaction (PCR), with museum specimens limited to 120 to 180 bp. Strict ancient DNA procedures were used to minimize contamination and detect nuclear mitochondrial copies (*4*), PCR products were cloned, and the solitaire sequences were independently replicated at the Natural History Museum, London.

The maximum likelihood (ML) tree for the combined data set (Fig. 1) reveals that the dodo and the solitaire are sister taxa. Despite the substantial morphological differences between the dodo, the solitaire, and other pigeons, the ML analysis shows them to be nested within the family Columbidae. The closest living relative is the monotypic Nicobar pigeon (*Caloenas nicobarica*) from the Nicobar Islands and nearby Southeast Asia, and the sister taxa to this clade are the crowned pigeons (*Goura*), from New Guinea. The unusual Samoan tooth-billed pigeon *Didunculus strigiro-*

*tris* (originally named for its dodolike beak) is the basal member of this strongly supported clade of large, generally ground-dwelling, island endemics. Furthermore, the phylogeographic distribution of this morphologically diverse clade suggests that the dodo and the sol-



**Fig. 1.** ML tree depicting the phylogenetic relationships of 37 species of pigeons and doves. Geographic distributions of the pigeons are as follows: Australian (red), African/Madagascan (green), Asian/Southeast Asian (purple), Mascarene Island (blue), and New World (yellow) taxa. The concentration of New World taxa at the base of the tree suggests that the initial radiation occurred in the New World. ML bootstrap consensus values for relationships with  $\geq 70\%$  support (italicized) and Bayesian posterior support values (bold) are given. Detailed phylogenetic analyses of potential outgroups identified Laridae, and consequently two species (Great Skua, *Catharacta skua*, and Parasitic Jaeger, *Stercorarius parasiticus*) were used (*3*).

itaire dispersed from Southeast Asia to the Mascarenes at some point in the past. Figure 1 indicates that a similar route was used by the Madagascan endemic *Alectroenas madagascariensis*, which is closely related to another Indo-Australian radiation.

Two external fossil calibrations were used in separate ML molecular clock calculations after tests found no violation of clocklike behavior (*3*). The analyses indicate that the dodo/solitaire and *Caloenas* diverged in the mid/late Eocene, around 42.6 million years ago (Ma) (95% confidence interval = 31.9 to 56.1 Ma), whereas the dodo and the solitaire separated in the late Oligocene, about 25.6 Ma (17.6 to 35.9 Ma). The latter date is biogeographically interesting as it is considerably older than the islands of Mauritius and Rodrigues. Geological evidence suggests that Mauritius emerged in a series of volcanic events, the earliest of which occurred around 6.8 to 7.8 Ma, whereas Rodrigues did not emerge until 1.5 Ma (*5*). Therefore, it seems highly unlikely that the large genetic distance between the dodo and the solitaire resulted from isolation on the two islands. Drilling projects have established that ridges surrounding the Mascarene Plateau were above sea level in the late Oligocene and have subsided slowly thereafter (*5*). The similarity between the timing of the dodo/solitaire divergence and the first geological evidence of land in the Mascarene island chain is striking and suggests that island stepping-stones may have been used before the two species eventually found their way to Mauritius and Rodrigues. Whether such dispersal was flighted or not cannot currently be determined, although the relatively isolated position and young age of Rodrigues would suggest that the solitaire, at least, may have retained a capacity for flight up until at least 1.5 Ma.

## References and Notes

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<sup>1</sup>Department of Zoology, University of Oxford, Oxford, OX1 3PS, UK. <sup>2</sup>Henry Wellcome Ancient Biomolecules Centre, University of Oxford, Oxford, OX1 3PS, UK. <sup>3</sup>Department of Zoology, The Natural History Museum, London SW7 5BD, UK.

\*To whom correspondence should be addressed. E-mail: alan.cooper@zoology.oxford.ac.uk