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Our evolving view of the kakapo (*Strigops habroptilus*) and its allies

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Abstract This paper surveys molecular and morphological work on parrots over the last 20 years and we show how it has re-shaped popular and scientific views regarding endemic New Zealand taxa. Recent research has shown the kakapo (*Strigops habroptilus*) is not closely related to apparent counterparts in Australia but in fact is a member of an ancient and exclusively New Zealand clade together with the kea and the kaka (*Nestor* spp.). Superficially similar Australian nocturnal taxa, the night (*Pezoporus occidentalis)* and the ground parrot (*P. wallicus)* are members of an altogether different family. At the same time, the parrots as a worldwide group have more or less retained their sense of Gondwanan ancestry, but with an increased focus on Australasia as a centre of origin. The previous paradigm explaining contemporary parrot diversity that suggested evolution was brought about exclusively by vicariant speciation has been supplanted with a synergistic model of dispersal and vicariance following the demonstration that multiple dispersal events have occurred, for example from Australia across the chain of Indian Ocean Islands to Africa.

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INTRODUCTION

Taxonomy and systematics both play pivotal roles in ornithology. The first is important because it gives stable scientific and common names to species and thereby facilitates communication. The second arranges species in ways that give them a sense of wider identity and affinity. Therefore, it works best when systematics reliably places species close to their nearest relatives. Increasingly, determining a species' nearest relatives is achieved by using DNA sequence based methods. For example, those species commonly known as '*robins*' and '*sparrows*' around the world include many different, and often quite unrelated, types of birds. These common names are of historical derivation and reflect a mixture of biological ignorance and nostalgia. As a result, it is important that scientific names of birds are: 1) well differentiated and, 2) preferably convey a sense of their identity.

For the past 20 years, the Chambers laboratory at Victoria University has used molecular methods to better understand the origins and affinities of the kakapo (*Strigops habroptilus*). This work has been considerably enhanced by studies in many overseas centres (de Kloet & de Kloet 2005; Astuti *et al.* 2006; Tokita *et al.* 2007; Wright *et al.* 2008). In the early stages these efforts were marked by rather piecemeal achievements and incremental advances. More recently they have converged on an overwhelming consensus. A key question has been the relationship of the kakapo to the 2 Australian nocturnal parrots. The possibility of a close relationship between the Australian nocturnal

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parrots, the night parrot (*Pezoporus occidentalis)* and the ground parrot (*P. wallicus*), and the kakapo is strongly suggested by their common possession of green stripy plumage. However, is this a shared derived trait, or merely a consequence of convergence selected by factors associated with their lifestyle? A second, but equally important, question concerns the relationship between kakapo and the other endemic New Zealand parrots and their relationship(s) with parrots from other parts of the world. This paper attempts to answer these questions and provide links to the original works upon which our views are now based.

A survey of recent data on parrot systematics

The recent OSNZ *Checklist of the Birds of New Zealand* (Gill *et al*. 2010) gives Gray (1845) as the first author to give the scientific name of *Strigops habroptilus* to the kakapo, and listed the genus *Strigops* under the subfamily Strigopinae and family Strigopidae. Gill *et al.* (2010) attributed the family and subfamily names to Gray (1848), which was later recognised as incorrect by Worthy *et al*. (2011), as Gray placed *Strigops* within Psittacidae, and the name Strigopidae was first erected by Bonaparte (1849), who in doing so was the first to segregate the New Zealand *Strigops* and *Nestor* species from all other parrots globally. Joseph *et al.* (2012) have recently proposed raising the family to superfamily level as the Strigopoidea (see later). Since the original naming of *Strigops habroptilus,* the genus was emended, unnecessarily, several times between 1849 and 1867 and a further species and 2 subspecies erected between 1849 and 1913. Nonetheless, Gray's original circumscription of the species has survived, and at present no subspecies are recognised (Gill *et al.* 2010).

Our earliest attempts (J. Hellewell & G.K. Chambers, *unpubl. data*) to probe the identity and relationship of the kakapo began with an investigation of short mitochondrial DNA sequences (*mt*DNA) from a ribosomal RNA gene target (12S). We were quickly able to conclude that *S. habroptilus* was closely related to *Nestor* species and that parrots as a whole were an old, Gondwanan, assemblage. These data were unable to answer questions regarding the possible relationships between *Strigops* and the Australian nocturnal genus, *Pezoporus.* This gap was rapidly filled by Leeton *et al.* (1994) who used *mt*DNA cytochrome *b* gene sequences to show that the night parrot (then known as *Geopsittacus occidentalis*) was closely related to the ground parrot (*Pezoporus wallicus*). In fact, the former has since reverted to *Pezoporus occidentalis* as used by Finsch (1867), at least partly in recognition of this relationship. However, neither of them were close to *Strigops*; the mean corrected genetic distance was 15.2% compared with just 9.03% between *Geopsittacus* and *Pezoporus*. Thus, one may make a preliminary diagnosis of morphological convergence of plumage characters between *Strigops* and the *Pezoporus* species contingent upon shared features of their ecological niches. There were caveats with this conclusion, as the study only looked at a single gene and it was known to cast up confounding artefacts known as *numts* (nuclear copies of mitochondrial genes). Further, the topological placement of *Strigops* in the Leeton *et al.* (1994) tree was uncertain and the tree itself was undated and unrooted (*i.e.,* outgroups were not used to identify the earliest branches on the tree). However, the basic finding has stood the test of time and many subsequent studies (Wright *et al.* 2008) have returned the same answer regarding the deep evolutionary divide between New Zealand and Australian nocturnal parrots.

Subsequently, DNA sequencing methodology and phylogenetic data analysis have progressed and the scale and standard of molecular systematic work on parrots has been ramped up considerably. It is now typical for long sequences (often in excess of 1 kb per target) to be obtained from multiple nuclear and mitochondrial gene targets and for trees to be constructed using 4 or more computing procedures with statistical tests of support even for individual branches. These newer studies featured multiple outgroups, and were calibrated with respect to geological events and/or the fossil record and/or generalised molecular clocks based on rates of DNA sequence evolution for each gene (and even for each position in each gene).

The authors now present a brief synopsis of contemporary studies but one including references to all such work, so that readers may be able to construct the full story for themselves. Thus, Christina Miyaki's group at Universidade de São Paulo did several studies on neotropical parrots (Miyaki *et al.* 1998; Tavares *et al.* 2004, 2006). Brown and Toft (1999) tackled the cockatoos and Groombridge *et al.* (2004) covered the *Psittacula* parakeets. These were followed by 3 larger, more general, phylogenetic studies (de Kloet & de Kloet 2005; Astuti *et al.* 2007; Tokita *et al.* 2007). We note in passing that the last paper in this list marks the start of an era where morphological traits began to be mapped onto phylogenetic trees in an attempt to understand the chronology of novel anatomical developments in parrots. This programme has since seen further valuable contributions from Mayr (2008, 2010) and Schweizer *et al.* (2010, 2011).

A consensus on phylogenetic patterns began to emerge from the early work and culminated with the publication of the large multi-locus study of Wright *et al.* (2008) to which the Chambers laboratory contributed. The consistent grouping of *Nestor* with *Strigops* basal to all other parrots was sufficient to convince the OSNZ Checklist

Committee (Gill *et al.* 2010) regarding their placement ahead of the cockatoos in the systematic list of taxon names and to place *Nestor* in the same family with *Strigops*, as Bonaparte (1849) had long ago advocated. According to the conventional rules of zoological nomenclature this family must be called Strigopidae Bonaparte, 1849 as this name has precedence over Nestoridae, which is based on 'Nestorinae Bonaparte, 1849' which family-group name was listed under 'Strigopidae' by Bonaparte (1849). The kea (*N. notablis*) and kaka (*N. meridionalis*) do, however, remain in their own distinct sub-family the Nestorinae as first suggested by Bonaparte.

Across the rest of the parrots and at the level of phylogenetic resolution possible from the data, vicariance seems to be the rule; African parrots group with other African parrots and South American parrots group with other Neotropical species. The New Zealand group was shown to be very old compared with the other parrots and this early branching was soon followed by the cockatoos. Dating these events is tricky and Wright *et al.* (2008) explored 2 dating scenarios for the Strigopidae; the geological separation of Australia and New Zealand at 82 mya vs. the conservative method using dating based on the first recorded parrot fossil at 50 mya.

Further studies have since followed, directed at less resolved parts of the tree including *Psittacella* and *Pezopora* (Joseph *et al.* 2011) and Cacatuidae (White *et al.* 2011). Another thrust has been more detailed scrutiny of the dominant vicariant paradigm (Schweizer *et al.* 2010, 2011; Kundu *et al.* 2012). In large part, the vicariant radiation model has stood up well, but it is increasingly clear that it cannot account for all relationships. Fresh biogeographical hypotheses have sprung up to provide the missing explanations including trans-oceanic settlements across the Indian Ocean. To reflect all the recent advances in understanding of the hierarchical relationships among parrots globally, Joseph *et al.* (2012) presented a new systematic proposal wherein parrots were arranged in 6 families and 12 subfamilies rather than the traditional 1 family, or 3 families as in Gill *et al.* (2010). This is largely concerned with relabeling various hierarchical levels within the phylogeny in the interest of normalising genetic divergence between various groups. Most of the family-group names used by Joseph *et al.* (2012) were pre-existing, but these authors did introduce Coracopseinae for the Madagascan parrots and Psittacellinae for a clade of Australasian parrots. It remains to be seen how widely this proposal will be taken up, but it is a comprehensive hypothesis of parrot relationships which will doubtless become the focus of future research.

DISCUSSION AND CONCLUSION

The case for evolutionary convergence between *Strigops* and *Pezoporus* has certainly been made to the extent that to dissent from this view would be to ignore strong evidence. Equally, *Strigops* and *Nestor* group together as an early split from the main group of parrots. They were followed shortly afterwards by the now diverse, but monophyletic assemblage of cockatoos. It does, however, remain to be seen if *Strigops* and *Nestor* will remain as members of the family Strigopidae (as Gill *et al*. 2010 presently has them) or each become recognised at family rank within the superfamily Strigopoidea as Joseph *et al.* (2012) now suggest. The exact dating of this initial split from other parrots globally cannot be decided, but it is likely to be ancient and later divergence within Strigopidae is a strictly New Zealand phenomenon. As yet fossil data from the Early Miocene of New Zealand attest to only the presence of nestorine parrots in New Zealand (Worthy *et al*. 2011), but the relationships discussed above indicate that the *Strigops* lineage was present in New Zealand long before.

In summary, the last 20 years have seen great advances in our general understanding regarding the history, relationships and identity of the kakapo. It stands revealed as an extremely old endemic lineage whose superficial similarities to the Australian nocturnal parrots are just that, superficial products of evolutionary convergence. The new systematic arrangement has seen them change places to move ahead of the cockatoos in the systematic list and now have the genus *Nestor* as part of the same family. Ironically, this is exactly as Bonaparte (1849) had them.

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