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The evolutionary history of cockatoos (Aves: Psittaciformes: Cacatuidae)

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ABSTRACT

Cockatoos are the distinctive family Cacatuidae, a major lineage of the order of parrots (Psittaciformes) and distributed throughout the Australasian region of the world. However, the evolutionary history of cockatoos is not well understood. We investigated the phylogeny of cockatoos based on three mitochondrial and three nuclear DNA genes obtained from 16 of 21 species of Cacatuidae. In addition, five novel mitochondrial genomes were used to estimate time of divergence and our estimates indicate Cacatuidae diverged from Psittacidae approximately 40.7 million years ago (95% CI 51.6–30.3 Ma) during the Eocene. Our data shows Cacatuidae began to diversify approximately 27.9 Ma (95% CI 38.1–18.3 Ma) during the Oligocene. The early to middle Miocene (20–10 Ma) was a significant period in the evolution of modern Australian environments and vegetation, in which a transformation from mainly mesic to xeric habitats (e.g., fire-adapted sclerophyll vegetation and grasslands) occurred. We hypothesize that this environmental transformation was a driving force behind the diversification of cockatoos. A detailed multi-locus molecular phylogeny enabled us to resolve the phylogenetic placements of the Palm Cockatoo (*Probosciger aterrimus*), Galah (*Eolophus roseicapillus*), Gang-gang Cockatoo (*Callocephalon fimbriatum*) and Cockatiel (*Nymphicus hollandicus*), which have historically been difficult to place within Cacatuidae. When the molecular evidence is analysed in concert with morphology, it is clear that many of the cockatoo species' diagnostic phenotypic traits such as plumage colour, body size, wing shape and bill morphology have evolved in parallel or convergently across lineages.

1. Introduction

Psittaciformes is a large and diverse avian order currently classified into three families: Nestoridae (New Zealand parrots), Cacatuidae (cockatoos) and Psittacidae (all remaining parrots) (Christidis and Boles, 2008). The order contains over 370 species placed within ~74 genera, most of which are concentrated in the tropical parts of the Southern Hemisphere (Christidis et al., 1991a; Homberger, 2006). The birds range in length from 9 cm to 1 m and are noted for their colourful plumage, lifelong capacity for learning, vocalization ability, and charismatic character, which make them popular aviary birds. Anthropogenic habitat modifications, poaching and illegal trade are significant threats: 85 species are listed as critical, endangered or vulnerable and 19 species as extinct by the International Union for the Conservation of Nature (IUCN, 2010). Although Cacatuidae is a major linage of Psittaciformes, the genetic relationships among cockatoos have not been well scrutinized using molecular data. Brown and Toft (1999), employing a single mitochondrial gene (433 base pairs (bp) of 12s rRNA), has been the only attempt at constructing a phylogeny for the Cacatuidae.

The 21 currently accepted cockatoo species (Table 1) are noted for their variation in plumage (Fig. 1) and differ from Nestoridae and Psittacidae in a number of characteristics. Cacatuids possess a moveable head-crest, are larger than most nestorids and psittacids, and lack the Dyck feather texture which Nestorids and Psittacids have for bright blue and green plumage (Higgins, 1999). Cockatoos are restricted to the Australasian region (excepting New Zealand), ranging from the Philippines and eastern Indonesian islands of Wallacea to New Guinea, the Solomon Islands and Australia (Cameron, 2008). Numerous classifications for Cacatuidae have been proposed since Gmelin described *Psittacus aterrimus* (Palm Cockatoo) in 1788 (Higgins, 1999). The classification of cockatoos has been based on characters drawn from anatomy (Smith, 1975), biochemistry (Adams et al., 1984; Sibley and Ahlquist, 1990; Christidis et al., 1991a), biomechanics (Homberger, 2003), behaviour (Courtney, 1996), chromosomal structure (Christidis et al., 1991b) and single-locus molecular data (Brown and Toft,

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Table 1
Description of the 21 cockatoo species, habitat and distribution throughout the Australasian region and conservation status by the International Union for the Conservation of Nature Red List (IUCN, 2010). For detailed descriptions see Table S1. Nomenclature follows Christidis and Boles (2008).

Genus and species	Common name	Colour; body length; habitat type; landmass/country; conservation status
Probosciger aterrimus	Palm Cockatoo	Black; 49–68 cm; tropical woodland and rainforest; PNG and Australia; least concern
Calyptorhynchus banksii	Red-tailed BC	Black; 55–60 cm; diverse forest and woodland habitats; Australia; least concern
Calyptorhynchus lathami	Glossy BC	Black; 48 cm; dependant on Allocasuarina woodland; Australia; least concern
Calyptorhynchus funereus	Yellow-tailed BC	Black; 55–65 cm; sclerophyll forest and woodland; Australia; least concern
Calyptorhynchus latirostris	Carnaby's BC (WTBC)	Black; 54–56 cm; Eucalyptus woodlands; Australia; endangered
Calyptorhynchus baudinii	Baudin's BC (WTBC)	Black; 52–57 cm; Marri, Karri and Jarrah forests; Australia; endangered
Callocephalon fimbriatum	Gang-gang Cockatoo	Black; 32–37 cm; sclerophyll forest and woodland; Australia; least concern
Eolophus roseicapillus	Galah	Grey and pink; 35 cm; grassland and agriculture areas; Australia; least concern
Lophochroa leadbeateri	Major Mitchell's Cockatoo	Pink and white; 39 cm; semi-arid, arid dry woodlands; Australia; least concern
Cacatua alba	Umbrella Cockatoo	White; 46 cm; diverse habitats with primary forest preferred; North Moluccas; vulnerable
[b]*Cacatua moluccensis*	Salmon-crested Cockatoo	White; 50 cm; undisturbed lowland forest; South Moluccas; vulnerable
[a]*Cacatua ophthalmica*	Blue-eyed Cockatoo	White; 50 cm; lowland and montane rainforest; Island of New Britain; vulnerable
Cacatua galerita	Sulphur-crested Cockatoo	White; 48–55 cm; diverse forests and woodland habitats; PNG and Australia; least concern
Cacatua sulphrea	Yellow-crested Cockatoo	White; 35 cm; diverse lowland habitats; numerous southeast Asian islands; critically endangered
Cacatua sanguinea	Little Corella	White; 35–40 cm; farmland, grassland, sedge-plains, saltbush; PNG and Australia; least concern
Cacatua pastinator	Western Corella	White; 40–45 cm; Eucalyptus woodlands and grasslands; Australia; least concern
[b]*Cacatua tenuirostris*	Long-billed Corella	White; 40 cm; sclerophyll woodlands and grasslands; Australia; least concern
[a]*Cacatua ducorpsii*	Solomon Corella	White; 30 cm; lowland environments; Solomon islands; least concern
Cacatua goffini	Goffin's Cockatoo	White; 31 cm; diverse habitats and agriculture areas; Tenimbar islands; near threatened
[a]*Cacatua haematuropygia*	Red-vented Cockatoo	White; 31 cm; mangrove and extreme lowland forest; Philippines; critically endangered
Nymphicus hollandicus	Cockatiel	Grey; 29–32 cm; savanna, open woodlands and forests; Australia; least concern

[a] Not sampled in this study.
[b] Not included in Fig. 2; BC: Black-cockatoo; PNG: Papua New Guinea; WTBC: White-tailed Black-cockatoo.

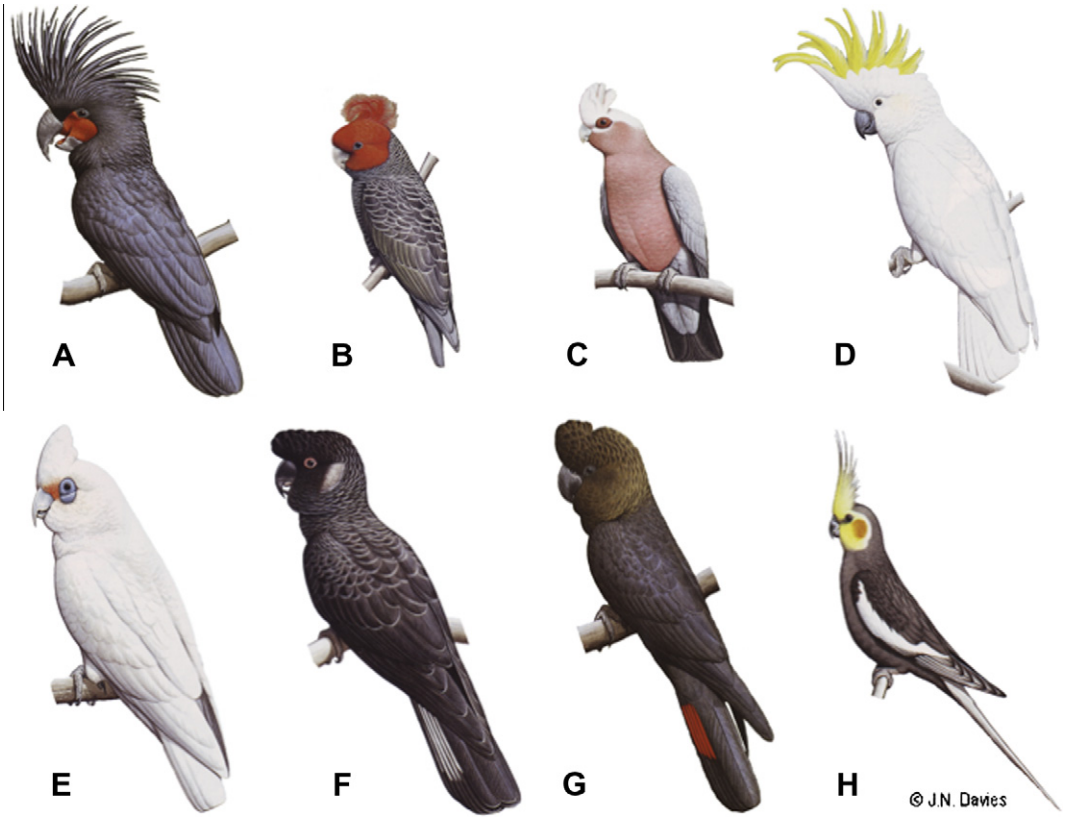

Fig. 1. Illustrations of eight adult male cockatoo species showing variation in plumage and morphology; (A) Palm Cockatoo (*Probosciger aterrimus*); (B) Gang-gang Cockatoo (*Callocephalon fimbriatum*); (C) Galah (*Eolophus roseicapillus*); (D) Sulphur-crested Cockatoo (*Cacatua galerita*); (E) Western Corella (*Cacatua pastinator*); (F) Baudin's Black-cockatoo (*Calyptorhynchus baudinii*); (G) Glossy Black-cockatoo (*Calyptorhynchus lathami*); and (H) Cockatiel (*Nymphicus hollandicus*). Images provided by artist J.N. Davies (with permission).

1999). Reaching a consensus classification and phylogeny for the Cacatudiae using morphological characters has been challenging (Homberger, 2006). Australasia has been identified as the region of origin for Psittaciformes (Wright et al., 2008; Schweizer et al., 2010). Therefore, an in-depth molecular study of cockatoos is overdue and presents an opportunity to develop a comprehensive understanding of Psittaciform evolution.

Dating the radiation of Psittaciformes is a point of contention in the literature, with the fossil record and molecular approaches yielding different estimates. Using the fossil record, a tertiary

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origin for most lineages has been hypothesized (Schweizer et al., 2010), although some have suggested the late Cretaceous (Stidham, 1998; Waterhouse, 2006). Waterhouse (2006) stated the need for additional Cretaceous fossils before any certainty can be brought to the debate (Waterhouse, 2006). A few molecular approaches have also hypothesized a late Cretaceous (Brown et al., 2007, 2008) and therefore Gondwanan origin (de Kloet and de Kloet, 2005; Tavares et al., 2006; Wright et al., 2008). Recent studies using appropriately modelled and calibrated mitochondrial genomes (mtg) and nuclear data have helped clarify the timing of diversification in other avian groups including ratites (Hackett et al., 2008; Phillips et al., 2010).

In this study we use 40 mitochondrial genomes, including five new cockatoo mitochondrial genomes, together with multiple fossil calibrations to estimate the timing of radiation for Nestoridae, Cacatuidae and Psittacidae. In addition, three mitochondrial and three nuclear DNA genes with near-complete taxon sampling from the four recognized subfamilies of Cacatuidae (Microglossinae, Calyptorhynchinae, Cacatuninae and Nymphicinae) (Schodde, 1997) facilitated an examination of the phylogenetic relationships and divergence dates of cockatoos, as well as the mode and tempo of their evolution. Lastly, upon examination of the historical timescale and biogeography of the Australasian region, the potential environmental influence that may have led to the diversification of Cacatuidae is discussed.

2. Materials and methods

2.1. Samples, DNA extractions, PCR and sequencing of cockatoos

A detailed list of the samples used in this study, together with extraction methods, PCR conditions and primer sequences can be found in the Supplementary information text (Tables S2 and S3). Briefly, DNA was isolated from each of the samples and PCR was used to amplify six genes: mitochondrial (mt) Cytochrome oxidase I (COI; ~720 bp; Genbank ID JF414274–JF414301), Cytochrome B (CytB; ~450 bp; Genbank ID JF414302–JF414327), NADH dehydrogenase subunit 2 (ND2; ~1020 bp; Genbank ID JF414328–JF414356) and nuclear (nu) Eukaryotic translation elongation factor 2 (EEF; ~830 bp; Genbank ID JF414357–JF414385) on chromosome 28, a non-histone chromosomal protein know as the High mobility group (HMG; ~470 bp; Genbank ID JF414386–JF414415) on chromosome 23 and the Transforming growth factor beta 2 (TGFB2; ~585 bp; Genbank ID JF414244–JF414273) on chromosome 3 (Table S2). PCR amplicons were sequenced using BigDye v3.1 (Applied Biosystems) at Macrogen facilities in Korea. The edited and concatenated alignment of mitochondrial and nuclear data totaled 4047 bp and will be hereafter referred to as the mt + nu4047 dataset (see Supplementary information). All major representatives within the subfamilies Microglossinae, Calyptorhynchinae, Cacatuninae and Nymphicinae were sampled for this study, including 29 individuals from 16 species (Table S3) and one budgerigar (*Melopsittacus undulatus*).

The complete mtDNA genomes of a Carnaby's Black-cockatoo (*Calyptorhynchus latirostris*; Genbank ID JF414243), Baudin's Black-cockatoo (*Calyptorhynchus baudinii*; Genbank ID JF414242), Glossy Black-cockatoo (*Calyptorhynchus lathami*; Genbank ID JF414241), Western Corella (*Cacatua pastinator butleri*; Genbank ID JF414240) and Salmon-crested Cockatoo (*Cacatua moluccensis*; Genbank ID JF414239) were generated through Roche (454) FLX sequencing of PCR amplicons. In brief, the mtDNA genome was first PCR-amplified in two overlapping 9 kb fragments. Subsequently the PCR products were purified, fragmented through nebulization, converted into MID-tagged sequencing libraries and sequenced as a partial fraction of an LR70 GS-FLX (Roche) run. The generated sequences were assembled into the complete mtDNA genome using the budgerigar (*M. undulatus*, Genbank ID EF450826) and kakapo (*Strigops habroptilus*, Genbank ID AY309456) mtDNA genomes as reference sequences (see Supplementary information).

2.2. Phylogenetic analysis

Phylogenetic reconstruction and molecular dating employed a three-step approach. First, following the avian mitochondrial study of Morgan-Richards et al. (2008), initial data exploration in PAUP v4.0b10 (Swofford, 2002) was conducted to determine whether RY-coding (A, G → R; C, T → Y) might be beneficial for reducing saturation and nucleotide compositional bias. Second, primary phylogenetic reconstructions were performed in MrBayes v3.1.2 (Huelsenbeck and Ronquist, 2001) and RaxML vGUI093 (Stamatakis, 2006). Third, a timescale for cacatuid evolution was estimated using BEAST v.1.5.3 (Drummond and Rambaut, 2007).

2.2.1. Nucleotide composition and saturation analysis of mitochondrial genomes

Manual alignment was performed in Se–Al v2.0a9 (Rambaut, 1996). The data set included complete mtDNA protein-coding genes, as well as ribosomal and transfer RNA gene sequences, totaling 14,534 nucleotides (after exclusion of sequences with ambiguous homology). Hereafter, this dataset is referred to as mtg14534. In addition to the five cockatoo genomes generated for this study, genomes of a further 35 bird species were included in the analysis (Table S5). We followed the detailed methodology of Phillips (2009) and Phillips et al., 2010. Four alignments were generated, two protein-coding alignments and two RNA alignments (nucleotide coding and RY-coding), to examine the nucleotide composition bias of first-, second- and third-codon positions (protein alignment) and stems and loops (RNA alignment). Compositional chi-square and relative composition variability (RCV) analyses were performed within PAUP v4.0b10 (Swofford, 2002) on all four alignments (Table S4) to assess the influence of compositional heterogeneity on phylogenetic reconstruction. This is of particular concern when saturation erodes the phylogenetic signal. The 'stemminess' (proportion of internal branch length contributing to total tree length) of minimum evolution trees inferred from *p*-distances was evaluated for third-codon positions and RNA loop sites in the mtg14538 data set. Stemminess increased from 0.108 to 0.213 in third positions and from 0.169 to 0.212 in loop sites upon RY-coding (Table S4). The higher 'stemminess' of the RY-coded data indicates greater phylogenetic signal retention and reduced potential for composition variability to mislead phylogenetic reconstruction (Phillips et al., 2010). RY-coding also reduced the compositional variability among taxa (Table S4), hence we used RY-coding for third-codon and RNA-loop positions.

2.2.2. Analysis of mtg14534 and mt+nu4047 datasets

The mtg14534 dataset (Table S5) was partitioned as standard nucleotide coding for first- and second-codon positions and RNA-stems, and RY-coded nucleotides for third-codon positions and RNA-loops. The program jModelTest v0.1.1 (Posada, 2008) favored GTR+G+I for each of the standard nucleotide partitions and the 2-state F81-equivalent+G+I was employed for the RY-coded partitions, as recommended by Phillips et al., 2010. The mt+nu4047 dataset employed standard nucleotide coding, given the decreased saturation and composition bias among cockatoos, relative to birds as a whole (e.g. mtg14534). For the mt+nu4047 dataset jModelTest v0.1.1 (Posada, 2008) recommended GTR+G for the mitochondrial protein-coding genes and HKY+G for the nuclear genes. Bayesian analyses were run in MrBayes v3.1.2 and maximum likelihood analyses in RAxML vGUI093, with the full substitution model and branch-length rate multipliers unlinked among codons and RNA structural partitions. In the MrBayes analysis, two independent

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replicates with three Markov Chain Monte Carlo (MCMC) chains were each run for 5,000,000 generations, with trees sampled every 5000 generations. The burn-in for each MrBayes run was determined *a posteriori* to maximize the tree set included for analysis, while ensuring that –ln*L* had plateaued, clade frequencies had converged between runs (clade frequency standard deviations < 0.01), and estimated sample sizes (ESS) for substitution parameter estimates were above 200. These parameters were monitored using Tracer v1.5, LogCombiner v1.5.3 and Treeannotator v1.5.3 (Drummond and Rambaut, 2007). Once burn-in (10%) was removed, FigTree v1.2.2 (Rambaut, 2009) was used to generate the consensus tree.

For the maximum likelihood analysis in RAxML, 1000 pseudoreplicates were run under the full bootstrapping option. In order to reduce computational time, topological constraints were applied to the nodes that were deemed uncontroversial and had received >0.99 posterior probabilities in the MrBayes analysis. These include Galliformes, Anseriformes, Neoaves, Falconidae, Accipitridae, Apodiformes, Coraciiformes+Trogoniformes, Charadriiformes, Podicipediformes, Procellariiformes, Sphenisciformes, Cuculiformes, Passeriformes, Oscines and Suboscines.

2.2.3. Molecular dating

A timescale for avian evolution was estimated using BEAST v.1.5.3 with the mtg14534 data set (Tables S5 and S6) partitioned as for the phylogenetic analysis. Previous analyses have shown that rates of mitochondrial evolution between avian orders are not auto-correlated (Phillips et al., 2010). Among molecular dating programs BEAST is unique for incorporation of a combination of characteristics that are desirable for analysis of the present dataset: (a) separate model allocation across the protein-codon and RNA structure-data partitions, including the equivalent model for the RY-coded positions; (b) soft-bound calibration prior distributions; and (c) relaxation of the molecular clock without assuming rate-correlation among branches. Here the option for rates among branches to be distributed according to a lognormal distribution provided more flexibility than the exponential distribution (Drummond et al., 2006; Phillips et al., 2010). GTR+G+I (and 2-state equivalent for RY-coded data) models were allocated across the protein-codon and RNA structure-data partitions. In order to provide temporal calibration, prior height distributions for five nodes were employed. The minimum marks the first appearance of a generally agreed-upon member of the crown group, and the maximum marks the age of relatively well-sampled fossil assemblages in potential geographic regions of origin that contain no putative crown group members, but do contain stem members or ecological equivalents. Selection of uniform, normal or lognormal distributions for calibration priors followed Ho and Phillips (2009).

For the Galloanserae, a calibration range of 66–86 Ma (Clarke et al., 2005; Benton and Donoghue, 2007) was employed as a normally distributed prior. For the Sphenisciformes, a calibration minimum of 61 Ma (based on the penguin *Waimanu* Slack et al., 2006) was set for a log normal distribution as described by Ho and Phillips (2009). A mean of 65 Ma and an upper 95th percentile of 73 Ma were used to reflect expectations for a K/T boundary radiation, after the extinction of numerous stem seabirds and the possibility of seabirds evolving in the Southern Hemisphere during late Campanian to late Maastrichtian. Four divergences provided uniform calibration priors with minimum bounds as follows: Podicipedifrmes/Phoenicopteriformes (30 Ma; Mayr, 2005); Pandionidae/Accipitridae (37 Ma; Mayr, 2005); Apodidae/Trochilidae (47.5 Ma; Ericson et al., 2006); and Cacatuidae/Psittacinae (16 Ma; Boles, 1993). Conservative upper bounds were employed for each of these four divergences, reflecting the absence of any putative members of these groups or close relatives in the Maastrichtian. Based on the MrBayes analysis (described above), a user-specified starting tree was input manually into BEAST (XML file provided in Supplementary information). Twenty independent MCMC chains were run for 10 million generations each, with trees sampled every 5000 generations. The burn-in for each BEAST run was determined *a posteriori*.

A timescale for cacatuid evolution was estimated using BEAST v.1.5.3 with the mt+nu4047data set (Table S7) and standard nucleotide coding. jModelTest recommended a GTR+G for mitochondrial protein genes and a HKY+G model for the nuclear genes. An uncorrelated relaxed clock was used with a lognormal distribution of rates among branches (Drummond et al., 2006). To provide temporal calibration, prior height posterior distributions for three nodes using the corresponding posterior tree heights from the mtg14534 analysis (Table S7) were set as normally distributed priors. The calibration for the tree model root height was set with the range of 30–51 Ma. Ranges of 18–37 Ma and 4–17 Ma were employed for Cacatuidae and for *Calyptorhynchus*, respectively (Table S7). Based on the MrBayes analysis (see above) a user-specified starting tree was used in BEAST and ten independent MCMC chains were run for 20 million generations.

3. Results and discussion

3.1. Timing and topology of parrots and cockatoos

The primary focus of this study was to investigate the mode and tempo of cockatoo evolution. However, dating Cacatuidae using 40 mtDNA genomes and well-accepted fossil calibrations also provided insights into the broader debate regarding evolution of the Psittaciformes. Our molecular dating approach involved robust analytical techniques to detect modelling problems, such as saturation and compositional heterogeneity, often observed in deep-time phylogenies. The evolutionary reconstruction incorporating five new cockatoo mitochondrial genomes examined the timing of divergence for Nestoridae, Cacatuidae and Psittacidae. However, as with all molecular dating approaches it is important to be cognisant of the degree of error (95% credibility intervals; CI) associated with such aging estimates.

The calibrated analysis of the mtg14534 dataset supports an origin and radiation of Psittaciformes in the middle-late Eocene, consistent with other estimates (Ericson et al., 2006; Tavares et al., 2006; Brown et al., 2007; Pratt et al., 2009; Schweizer et al., 2010). During this time Australia was drifting west to north-west as it separated from Antarctica (Table 2). A calibration of 82 Ma for the separation of Australian and New Zealand was specifically avoided because it has been shown as inappropriate for dating the evolution of both volant and terrestrial bird lineages (Wright et al., 2008; Ho and Phillips, 2009; Trewick and Gibb, 2010). The relaxed molecular clock analysis estimated the most recent common ancestor (MRCA) of the Psittaciformes at ~47.4 Ma (95% CI; 59–36.4 Ma; Table 2). Our phylogenetic findings are in close agreement with previous molecular studies (de Kloet and de Kloet, 2005; Tavares et al., 2006; Gibb et al., 2007; Wright et al., 2008; Schweizer et al., 2010), in which Nestoridae (New Zealand parrots) form a sister clade to all other extant parrots and cockatoos (Table 2 and Fig. S1). Our dated phylogeny and those of others (Ericson et al., 2006; Brown et al., 2007, 2008) conflict with the hypothesis of a Gondwanan origin of all parrots during the Cretaceous (Wright et al., 2008). Our estimate of the origin and diversification of Psittaciformes in the Eocene (Table 2) seems consistent with the sparse fossil record (Mourer-Chauviré, 1992; Mayr and Daniels, 1998; Dyke and Cooper, 2000; Mayr, 2002; Waterhouse et al., 2008) and supports the multiple trans-oceanic dispersal events and local radiations advocated by Schweizer et al. (2010). Reassuringly, and taking a broader picture of avian evolution, the topology of our mtg14534 phylogeny generated using Bayesian or maximum likelihood frameworks (Figs. S1 and

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Table 2
Molecular dating estimates for key splits in the Psittaciformes. Most recent common ancestor (MRCA) date estimates were generated using 40 Aves whole mitochondrial genomes (mtg14534 dataset, see Section 2) with 95% credibility intervals (CI) of the highest posterior density. The consensus tree from which these estimates are derived can be found in the Supplementary information (Fig. S1). An overview of tertiary series with brief description of geological, climatic and biological events is included together with the MRCA estimates for comparative purposes.

MRCA for the order, family and/or subfamily of Psittaciformes	Median molecular date (95% CI)	Tertiary series, major geological, climatic and/or biological events in Australasia (worldwide fossil discoveries and dating within the Psittaciformes)
MRCA of Psittaciformes (Nestoridae, Cacatuidae and Psittacidae)	47.4 Ma (59–36.4)	Eocene (55–34 Ma) Separation of Australia from Antarctica begins; drifting west to north-west; warm and wet conditions; (Psittaciforme fossil from London Clay of England) Oligocene (34–23 Ma)
MRCA of Cacatuidae and Psittacidae	40.7 Ma (51.6–30.3)	Final separation from Antarctica; Pacific and Australian plates start to collide in the New Guinea region; temperate rainforest types; sclerophyll plant communities developing; active volcanism; sea levels start to rise
MRCA of Cacatuidae	27.9 Ma (38.1–18.3)	Early Miocene (23–16 Ma) High sea levels; circum-polar circulation began; warm to high temperatures; high rainfall; temperate rainforests widespread; open plains were established; gymnosperms were dominant; Eucalyptus was present; abundant waterbirds and arboreal marsupials; (incomplete rostrum of *Cacatua* intermediate from Riversleigh deposit, Queensland, Australia)
MRCA of Cacatuninae (*Cacatua pastinator* and *C. moluccensis*)	11.4 Ma (19.2–5.6)	Middle Miocene (16–11 Ma) to late Miocene (11–5 Ma)
MRCA of Calyptorhynchinae (*Calyptorhynchus baudinii* and *C. lathami*)	10.1 Ma (17.5–4.6)	Seas retreated; volcanism in Queensland and west Kimberley region; uplift of East Papua Terrane; westerly winds increased; cooling; arid climate; rainforests present near Alice Springs; forests in northern Western Australia; dry sclerophyll, open woodland and grasslands; fire increased; browning of Australia

MRCA: most recent common ancestor; Ma: million years ago; CI: credibility interval.

S2), corroborates recent nuclear datasets (Hackett et al., 2008). Notably, Psittaciformes is sister to Falconiformes. It appears that increased taxon sampling has delivered consistency between mitochondrial and nuclear phylogenetic inferences; although an examination of the evolutionary history for the other avian orders (Figs. S1 and S2) were not the focus of this study.

3.2. Timing of the Australasian cockatoo radiation

The main rationale for conducting the mtg14534 analysis was to provide node height estimates, and associated errors (95% CI), for key split dates within the Cacatuidae. The mtg14534 reconstruction indicated that the MRCA for Cacatuidae and Psittacidae occurred in the Eocene at ~40.7 Ma (95% CI; 51.6–30.3 Ma; Table 2), consistent with the estimates of Ericson et al. (2006) and Brown et al. (2007). The five new cockatoo genomes enabled, for the first time, the base of Calyptorhynchinae (black cockatoos) to be estimated at ~10.1 Ma (95% CI; 17.5–4.6 Ma; Table 2) and that of Cacatuinae at ~11.4 Ma (95% CI; 19.2–5.6 Ma; Table 2). The posterior distributions of the three nodes were subsequently used to calibrate the nodes for the mt+nu4047 analysis (Table S7). Both of our datasets are consistent with the diversification of all cockatoo genera during the early Miocene to Pliocene (Fig. 2; Table 2), and with a *Cacatua* intermediate fossil from the Riversleigh deposits (Boles, 1993). The latter has been described as a small cockatoo with a rostrum consistent with a rainforest environment, although not contra-indicative of drier, more open habitats. The Miocene (23–5 Ma) was significant in the evolution of modern Australian vegetation and fauna, and we consider it likely that expansion of sclerophyll, eucalyptus, and grasslands (Table 2) was a driving force behind the speciation of cockatoos. During this time the Australian plate approached and collided with the Asian plate, causing an uplifting of the East Papua Terrane (White, 1994). Temperatures cooled and a more arid climate developed, with increased fire (White, 1994; Kershaw et al., 2002). The vegetation changed into a mosaic of different types which varied from remnant rainforests, and other broad-leaf forests, to dry sclerophyll communities; across the increasingly dry interior, open grassland and saltbush plains were present (White, 1994; Merrick et al., 2006). The early-middle Pliocene was a significant period for migration between south-east Asia and Australia, and we hypothesize that cockatoos migrated and diversified into dry habitats during this time.

The multi-locus mt+nu4047 dataset generated a robust phylogeny, with each gene producing a nearly identical topology when analysed individually (results not shown). Cacatuid phylogeny calibrated with the mtg14534 analysis, revealed a three-way split that occurred ~22.2 Ma (95% CI; 29.8–15.5 Ma; Fig. 2). The three cockatoo lineages are as follows: (1) a speciose cacatuine-type lineage of *Cacatua*, *Callocephalon*, *Eolophus, Lophochroa* and *Probosciger*; (2) a calyptorhynchine lineage of *Calyptorhynchus*; and (3) the monotypic *Nymphicus* (Fig. 2). A clear separation of 'black' and 'white' cockatoos, as described by Adams et al. (1984), was not found in our multi-locus phylogeny. Instead, the large 'cacatuine' lineage is a mixture of white, grey, pink and black cockatoos with at least five sub-lineages. We did not sample all south-east Asian cockatoos (Table 1).

The multi-locus phylogeny of cockatoos enables investigation of previously unrecognized affiliations and evaluation of the current taxonomy. The first unexpected result was the placement of *Probosciger aterrimus*, a large black cockatoo. All of our mtDNA (except CytB, discussed below) and nuDNA data, either as single genes or concatenated, placed *P. aterrimus* within the speciose 'cacatuinae' lineage. In contrast, previous studies identified *P. aterrimus* as the basal member of Cacatuidae (Brown and Toft, 1999; Astuti et al., 2006). Our evidence (provided in Supplementary information) suggests that these studies may have integrated a mitochondrial nuclear copy in their phylogenetic reconstructions, which artificially placed *P. aterrimus* in a basal position.

Callocephalon fimbriatum has been variously included in Cacatuinae and Calyptorhynchinae on the basis of allozymes (Adams et al., 1984), single-locus DNA sequences (Brown and Toft, 1999), bill biomechanics (Homberger, 2003) and behaviour (Forshaw and Cooper, 1981; Schodde, 1997). Likewise, the position of *Eolophus roseicapillus* has historically been problematic; it too has been variously included in *Cacatua* or separated as *Eolophus* (Christidis and Boles, 2008). Our results suggest *C. fimbriatum* and *E. roseicapillus* are sister taxa and reconsideration of their generic status may be warranted (Fig. 2). The taxonomic history of *Lophochroa leadbeateri* is similar; morphological analyses have led different authors to assign this species to *Lophocroa* or *Cacatua* (Christidis and Boles, 1994, 2008; Schodde, 1997; Brown and Toft,

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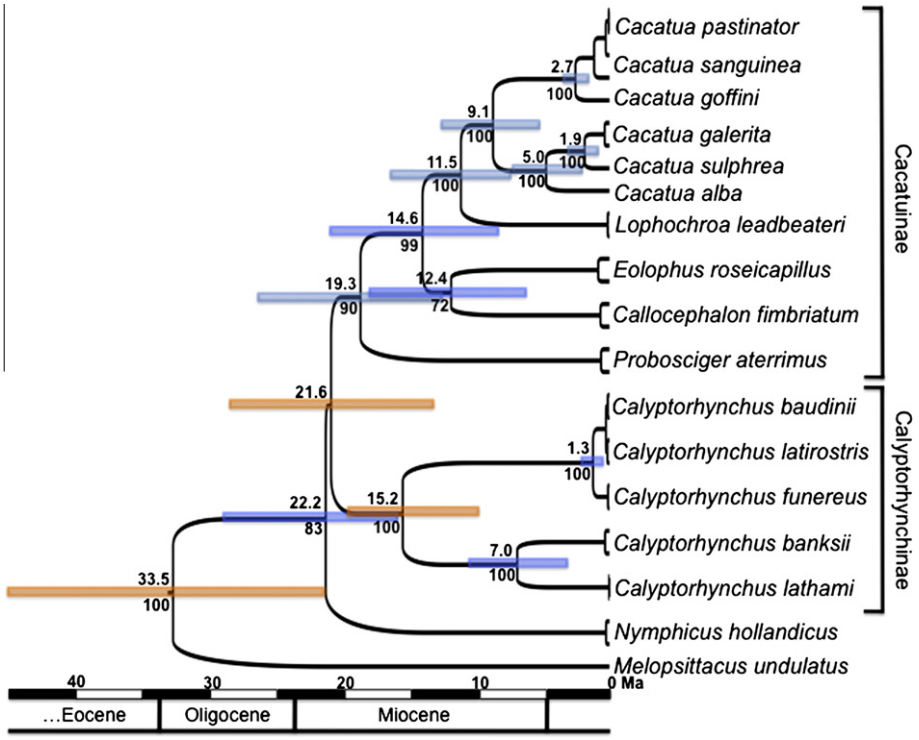

Fig. 2. Molecular phylogeny and date estimates of the cockatoo radiation generated from the mt+nu4047 dataset (three mitochondrial and three nuclear DNA genes; see Section 2). A consensus Bayesian inference tree generated in BEAST is shown with Bayesian posterior probability values (>70%) indicated below the nodes. Median age estimates are shown above nodes (Ma). Blue bars correspond to estimated node ages (95% highest posterior density; HPD) for split dates within Cacatuidae. Orange bars correspond to nodes with age priors, these were enforced based on the mtg14534 dataset (see Table 2 and Supplementary information). A scale bar (Ma) incorporating geological time periods is shown below the phylogeny. For further information regarding the phylogenetic analysis see Section 2 and Supplementary information. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1999). Our phylogeny firmly places *L. leadbeateri* as sister to *Cacatua,* and supports the generic status of *Lophocroa* (Schodde, 1997). Clearly, morphological plasticity of bills, body size, and plumage colour within Cacatuidae (Fig. 1) has generated some uncertainty towards previous systematics and taxonomy of cockatoos. Further work adopting a multi-locus approach would clarify the positions of the five cockatoos not included in our mt+nu4047 dataset: *C. moluccensis*, *C. tenuirostris, C. haematuropygia, C. ophthalmica* and *C. ducorpsii* (Table 1).

The second major lineage of Cacatuidae is Calyptorhynchinae, which includes the 'black' cockatoos of *Calyptorhynchus* (Fig. 2). According to our estimates Calyptorhynchinae radiated in the mid to late Miocene (mtg14534 estimate ~10.1 Ma; CI 95% 4.6–17.5 Ma; Table 2). We note that divergence within *Calyptorhynchus* is notably older than that within other cockatoo genera. The two lineages of Calyptorhynchinae in our multi-locus phylogeny support Schodde's (1997) recognition of subgenera *C.* (*Calyptorhynchus*) Desmarest, 1826 (*C. banksii* and *C. lathami*) and *C.* (*Zanda*) Mathews, 1913 (*C. funereus*, *C. baudinii* and *C. latirostris*). The divergence time within these subgenera is interesting; our molecular dating estimates indicate that *C.* (*Calyptorhynchus*) radiated in the late Miocene to early Pliocene (Fig. 2), whereas *C.* (*Zanda*) radiated during the Pleistocene (~1.3 Ma; Fig. 2). The radiation of *C.* (*Zanda*) agrees with expectations that the south-west corner of Australia became isolated from eastern parts by the arid Nullarbor Plain (White, 1994). The estimate of ~1.3 Ma (95% CI 2.3–0.6 Ma; Fig. 2) for the radiation of the closely-related *C. funereus*, *C. baudinii* and *C. latirostris* is consistent with numerous east–west splits observed in other Australian flora and fauna (King et al., 1978; Oliver et al., 1979; Hopper and Gioia, 2004). Such endemism has resulted in south-western Australia being listed as a global biodiversity hot spot (Myers et al., 2000).

The third major lineage at the base of the cockatoo radiation is *Nymphicus hollandicus* (Fig. 2) the sole member of Nymphicinae. Clearly this monotypic lineage is an important part of the evolutionary history of cockatoos, and, unlike most other cockatoos, *N. hollandicus* (Fig. 1) has an Australian-wide distribution. Our results support the biochemical analysis of Adams et al., 1984, and comparative analysis of the bill apparatus by Homberger (2003), who concluded that *N. hollandicus* branched off the main cacatuid stem 'early' and is the sole living member of a third root lineage. Our findings conflict with Brown and Toft (1999), who found a close association between *Nymphicus* and Calyptorhynchinae. This result highlights, once again, concerns associated with single-locus analysis, especially in genes (such as 12S rRNA), where rate heterogeneity impacts on the accuracy of reconstructions.

3.3. Evolutionary plasticity in cockatoos: implications for taxonomy

Prior to the advent of molecular techniques, biological classification methods were, through necessity, based on measurable phenotypic characters. As demonstrated in our phylogenetic reconstruction and many others (e.g., Lerner and Mindell, 2005 and Phillips et al., 2010), classification based solely on phenotypic attributes may be problematic for many species. For Cacatuidae, a case-in-point is the close genetic relationship between *C. fimbriatum* and *E. roseicapillus* (Fig. 2). Not only do they differ greatly in plumage (Fig. 1), they also posses different bill structures, which has resulted in them being classified in different genera (Condon, 1975; Homberger, 2003). An in-depth study of bill biomechanics by Homberger (2003) identified two types of bills: (1) the psittacid-type, a 'Swiss army knife' in its multi-functionality but highly specialized for shelling seeds intra-orally; and (2) the "calyptorhynchid"-type, also multi-functional but with reduced

transverse mobility of the mandibles, requiring the assistance of the foot while eating. *E. roseicapillus* was identified with the psittacid-type and *C. fimbriatum* with the "calyptorhynchid"-type, illustrating the adaptive radiation of bill morphology that has been documented since the description of Darwin's finches (West-Eberhard, 2003).

The diversification of cockatoos is believed to have been driven, in part, by bill adaptations and specializations, that allowed the lineage to move into previously unoccupied niches (West-Eberhard, 2003). Boles (1993) concluded "some characters of the rostrum appear more related to peculiarities of feeding and food choice than as clues to a taxon's phylogenetic background". Our phylogenetic reconstructions show that variation in bill morphology has little correlation with genetic distance within Calyptorhynchinae (*C. baudinii, C. latirostris, C. banksii*) or Cacatuinae (*C. pastinator* and *Cacatua sanguinea*). Likewise, it appears plumage and bauplan have specifically influenced the systematics for *Callocephalon*, *Lophochroa*, *Nymphicus* and *Probosciger* genera. Our molecular dating estimates suggest landscape change, especially during the Miocene–Pleistocene (White, 1994; Kershaw et al., 2002) have driven these phenotypic traits, and that plumage, wing and bill morphologies have evolved in parallel or convergently across lineages.

3.4. Conclusion and conservation implications

Complete mtDNA genomes of 40 avian species (including five new cacatuid genomes), together with a ~4 kb multi-locus mtDNA and nuDNA dataset, have provided a number of insights into the evolutionary history of Cacatuidae which, to date, has received only a superficial interrogation by molecular methodologies. Using relaxed clock molecular methods that integrate errors associated with phylogeny and calibration, we have, for the first time, provided date estimates for key split dates within the radiation of the Cacatuidae. Dating the phylogeny using avian fossil calibrations, our dating estimate does not support a Gondwanan origin for Psittaciformes but rather an origin in the Eocene, and the Miocene–Pliocene as a significant period for cacatuid radiation in Australasia. As with all molecular dating and temporal reconstructions, they must be treated with caution and we expect additional data (mtDNA and nuclear genomes) will refine the estimates presented in this study.

Our phylogeny highlights a number of key deviations from previous classifications: (1) an absence of a clear monophyly of 'white' and 'black' cockatoos; (2) *Probosciger aterrimus* grouped within the Cacatuinae and was not identified as the first generic divergence for cockatoos; (3) *N. hollandicus* was not identified as most closely related to the calyptorhynchine lineage, but rather the sole member of a basal monotypic lineage; and (4) *E. roseicapillus* and *C. fimbriatum* were identified as sister taxa. Our dataset suggests a closer examination of the taxonomic relationship for some cockatoo species may be warranted, and we endorse a multidisciplinary approach to cacatuid systematics. The development of a robust phylogenetic and taxonomic framework is possibly more important for Psittaciformes than for any other bird lineage, because they have the largest number of threatened species in the world (Waterhouse, 2006) with 23% of conservation concern (IUCN, 2010). Importantly, the molecular framework presented here will facilitate future research and the assignment of evolutionarily significant units and/or management units within Cacatuidae.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2011.03.011.

References

Adams, M., Baverstock, P.R., Saunders, D.A., Schodde, R., Smith, G.T., 1984. Biochemical systematics of the Australian cockatoos (Psittaciformes: Cacatuinae). Australian Journal of Zoology 32, 363–378.

Astuti, D., Azuma, N., Suzuki, H., Higashi, S., 2006. Phylogenetic relationships within parrots (Psittacidae) inferred from mitochondrial cytochrome-b gene sequences. Zoological Science 23, 191–198.

Benton, M.J., Donoghue, P.C.J., 2007. Paleontological evidence to date the tree of life. Molecular Biology and Evolution 24, 26–53.

Boles, W.E., 1993. A new cockatoo (Psittaciformes: Cacatuidae) from the Tertiary of Riversleigh, north-western Queensland, and an evaluation of rostral characters in the systematics of parrots. Ibis 135, 8–18.

Brown, D.M., Toft, C.A., 1999. Molecular systematics and biogeography of the cockatoos (Psittaciformes: Cacatuidae). The Auk 116, 141–157.

Brown, J.W., Payne, R.B., Mindell, D.P., 2007. Nuclear DNA does not reconcile 'rocks' and 'clocks' in Neoaves: a comment on Ericson et al.. Biology Letters 3, 257–260.

Brown, J.W., Rest, J.S., Garcia-Moreno, J., Sorenson, M.D., Mindell, D.P., 2008. Strong mitochondrial DNA support for a Cretaceous origin of modern avian lineages. BMC Biology 6, 6.

Cameron, M., 2008. Cockatoos. CSIRO Publishing, Australia.

Christidis, L., Boles, W.E., 1994. The Taxonomy and Species of Birds of Australia and its Territories. Royal Australasian Ornithologists Union, Melbourne.

Christidis, L., Boles, W.E., 2008. Systematics and Taxonomy of Australian Birds. CSIRO Publishing, Australia.

Christidis, L., Schodde, R., Shaw, D.D., Maynes, S.F., 1991a. Relationships among the Australo-Papuan parrots, lorikeets, and cockatoos (Aves: Psittaciformes): protein evidence. The Condor 93, 302–317.

Christidis, L., Shaw, D.D., Schodde, R., 1991b. Chromosomal evolution in parrots, lorikeets and cockatoos (Aves: Psittaciformes). Hereditas 114, 47–56.

Clarke, J.A., Tambussi, C.P., Noriega, J.I., Erickson, G.M., Ketcham, R.A., 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. Nature 433, 305–308.

Condon, H.T., 1975. Checklist of the Birds of Australia, Part 1. Non-passerines. Royal Australasian Ornithologists Union, Melbourne.

Courtney, J., 1996. The juvenile food-begging calls, food-swallowing vocalisation and begging postures in Australian cockatoos. Australian Bird Watcher 16, 236–249.

De Kloet, R.S., de Kloet, S.R., 2005. The evolution of the spindlin gene in birds: Sequence analysis of an intron of the spindlin W and Z gene reveals four major divisions of the Psittaciformes. Molecular Phylogenetics and Evolution 36, 706–721.

Desmarest, A.G. 1826. Dictionnaire des Sciences Naturelles dans lequel on traite methodiquement des differens etres de la nature. F.G. Levrault, Strasbourg, pp. 21-117.

Drummond, A.J., Rambaut, A., 2007. BEAST: bayesian evolutionary analysis by sampling trees. BMC Evolutionary Biology 7, 214.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biology 4 (5), 699.

Dyke, G.J., Cooper, J.H., 2000. A new psittaciform bird from the London Clay (Lower Eocene) of England. Palaeontology 43, 271–285.

Ericson, P.G.P., Anderson, C.L., Britton, T., Elzanowski, A., Johansson, U.S., Källersjö, M., Ohlson, J.I., Parsons, T.J., Zuccon, D., Mayr, G., 2006. Diversification of Neoaves: integration of molecular sequence data and fossils. Biology Letters 2, 543–547.

Forshaw, J.M., Cooper, W.T., 1981. Australian Parrots. Lansdowne Press, Melbourne.

Gibb, G.C., Kardailsky, O., Kimball, R.T., Braun, E.L., Penny, D., 2007. Mitochondrial genomes and avian phylogeny: complex characters and resolvability without explosive radiations. Molecular Biology and Evolution 24, 269–280.

Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C.K., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, W.A., Han, K.L., Harshman, J., 2008. A phylogenomic study of birds reveals their evolutionary history. Science 320, 1763–1768.

Higgins, P.J., 1999. In: Handbook of Australian, New Zealand & Antarctic Birds. Vol. 4, Parrots to Dollarbird. Oxford University Press.

Ho, S.Y.W., Phillips, M.J., 2009. Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. Society of Systematic Biologists 58, 367–380.

Homberger, D.G., 2003. The comparative biomechanics of a prey-predator relationship: the adaptive morphologies of the feeding apparatus of Australian black cockatoos and their foods as a basis for the reconstruction of the evolutionary history of the Psittaciformes. In: Vertebrate Biomechanics and Evolution. BIOS Scientific, Oxford, pp. 203–228.

Homberger, D.G., 2006. Classification and Status of Wild Populations of Parrots. Blackwell Publishing.

Hopper, S.D., Gioia, P., 2004. The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. Annual Review of Ecology Evolution and Systematics 35, 623–650.

Huelsenbeck, J., Ronquist, F., 2001. MrBayes: bayesian inference of phylogeny, version 3.1.2. Bioinformatics 17, 754–755.

IUCN, 2010. IUCN Red List of Threatened Species. Version 2010.4. <http://www.iucnredlist.org>.

Kershaw, A.P., Clark, J.S., Gill, A.M., D'Costa, D.M., 2002. A History of Fire in Australia. Cambridge University Press.

King, D.R., Oliver, A.J., Mead, R.J., 1978. The adaptation of some Western Australian mammals to food plants containing fluoroacetate. Australian Journal of Zoology 26, 699–712.

Lerner, H.R.L., Mindell, D.P., 2005. Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. Molecular Phylogenetics and Evolution 37, 327–346.

Mathews, G.M., 1913. New genera. Austral Avian Records 1, 195–196.

Mayr, G., 2002. On the osteology and phylogenetic affinities of the Pseudasturidae-Lower Eocene stem-group representatives of parrots (Aves, Psittaciformes). Zoological Journal of the Linnean Society 136, 715–729.

Mayr, G., 2005. The Paleogene fossil record of birds in Europe. Biological Reviews 80, 515–542.

Mayr, G., Daniels, M., 1998. Eocene parrots from Messel (Hessen, Germany) and the London Clay of Walton-on-the-Naze (Essex, England). Palaeobiodiversity and Palaeoenvironments 78, 157–177.

Merrick, J.R., Archer, M., Hickey, G.M., Lee, M.S.Y., 2006. Evolution and Biogeography of Australasian Vertebrates. Australian Scientific Publishing.

Morgan-Richards, M., Trewickm, S.A., Bartosch-Harlid, A., Kardalisky, O., Philips, M.J., McLenachan, P.A., Penny, D., 2008. Bird evolution: testing the Metaves clade with six new mitochondrial genomes. BMC Evolutionary Biology 8, 20–32.

Mourer-Chauviré, C., 1992. Une nouvelle famille de perroquets (Aves: Psittaciformes) dans l'Éocène Supérieur des phosphorites du Quercy, France. Geobios Mémoire Spécial 14, 169–177.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Oliver, A.J., King, D.R., Mead, R.J., 1979. Fluoroacetate tolerance, a genetic marker in some Australian mammals. Australian Journal of Zoology 27, 363–372.

Phillips, M.J., 2009. Branch-length estimation bias misleads molecular dating for a vertebrate mitochondrial phylogeny. Gene 441, 132–140.

Phillips, M.J., Gibb, G.C., Crimp, E.A., Penny, D., 2010. Tinamous and moa flock together: mitochondrial genome sequence analysis reveals independent losses of flight among ratites. Systematic Biology 59 (1), 90–107.

Posada, D., 2008. JModelTest: phylogenetic model averaging. Molecular Biology and Evolution 25 (7), 1253–1256.

Pratt, R.C., Gibb, G.C., Morgan-Richards, M., Phillips, M.J., Hendy, M.D., Penny, D., 2009. Toward resolving deep Neoaves phylogeny: data, signal enhancement, and priors. Molecular Biology and Evolution 26 (2), 313–326.

Rambaut, A., 1996. Se-Al: Sequence Alignment Editor. Version 2.0. Computer Program and Documentation Distributed by the Author. <http://iubio.bio.indiana.edu/soft/iubionew/molbio/dna/analysis/Pist/main.html>.

Rambaut, A., 2009. FigTree v1.2.2. Computer Program and Documentation Distributed by the Author. <http://tree.bio.ed.ac.uk/software/figtree>.

Schodde, R., 1997. Cacatuidae. In: Houston, W., Wells, A. (Eds.), Aves (Columbidae to Coraciidae). Zoological Catalogue of Australia. CSIRO Publishing, Melbourne, pp. 64–108.

Schweizer, M., Seehausen, O., Güntert, M., Hertwig, S.T., 2010. The evolutionary diversification of parrots supports a taxon pulse model with multiple trans-oceanic dispersal events and local radiations. Molecular Phylogenetics and Evolution 54, 984–994.

Sibley, C.G., Ahlquist, J.E., 1990. Phylogeny and Classification of Birds: A Study in Molecular Evolution. Yale University Press.

Slack, K.E., Jones, C.M., Ando, T., Harrision, G.L., Fordyce, R.E., Arnason, U., Penny, D., 2006. Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. Molecular Biology and Evolution 23 (6), 1144–1155.

Smith, G.A., 1975. Systematics of parrots. Ibis 117, 18–68.

Stamatakis, A., 2006. RAxML.xml-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690.

Stidham, T.A., 1998. A lower jaw from a Cretaceous parrot. Nature 396, 29–30.

Swofford, D.L., 2002. PAUP: Phylogenetic Analysis using Parsimony, Version 4.0 b10. Sinauer Associates, Sunderland, MA.

Tavares, E., Baker, A., Pereira, S., Miyaki, C., 2006. Phylogenetic relationships and historical biogeography of neotropical parrots (Psittaciformes: Psittacidae: Arini) inferred from mitochondrial and nuclear dna sequences. Systematic Biology 55, 454–470.

Trewick, S.A., Gibb, G.C., 2010. Vicars, tramps and assembly of the New Zealand avifauna: a review of molecular phylogenetic evidence. Ibis 152, 226–253.

Waterhouse, D.M., 2006. Parrots in a nutshell: the fossil record of Psittaciformes (Aves). Historical Biology: A Journal of Paleobiology 18, 223–234.

Waterhouse, D.M., Lindow, B.E.K., Zelenkov, N.V., Dyke, G.J., 2008. Two new parrots (Psittaciformes) from the Lower Eocene Fur Formation of Denmark. Palaeontology 51, 575–582.

West-Eberhard, M.J., 2003. Developmental Plasticity and Evolution. Oxford University Press, USA.

White, M.E., 1994. After the Greening: The Browning of Australia. Kangaroo Press, Sydney.

Wright, T.F., Schirtzinger, E.E., Matsumoto, T., Ebrehard, J.R., Graves, G.R., Sanches, J.J., Capelli, S., Muller, H., Scharpegge, J., Chambers, G.K., 2008. A multilocus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. Molecular Biology and Evolution 25, 2141–2156.

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