Macroevolutionary patterns in the diversification of parrots: effects of climate change, geological events and key innovations

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ABSTRACT

Aim Parrots are thought to have originated on Gondwana during the Cretaceous. The initial split within crown group parrots separated the New Zealand taxa from the remaining extant species and was considered to coincide with the separation of New Zealand from Gondwana 82–85 Ma, assuming that the diversification of parrots was mainly shaped by vicariance. However, the distribution patterns of several extant parrot groups cannot be explained without invoking transoceanic dispersal, challenging this assumption. Here, we present a temporal and spatial framework for the diversification of parrots using external avian fossils as calibration points in order to evaluate the relative importance of the influences of past climate change, plate tectonics and ecological opportunity.

Location Australasian, African, Indo Malayan and Neotropical regions.

Methods Phylogenetic relationships were investigated using partial sequences of the nuclear genes *c-mos*, *RAG-1* and *ZenK* of 75 parrot and 21 other avian taxa. Divergence dates and confidence intervals were estimated using a Bayesian relaxed molecular clock approach. Biogeographic patterns were evaluated taking temporal connectivity between areas into account. We tested whether diversification remained constant over time and if some parrot groups were more species rich than expected given their age.

Results Crown group diversification of parrots started only about 58 Ma, in the Palaeogene, significantly later than previously thought. The Australasian lorries and possibly also the Neotropical Arini were found to be unexpectedly species rich. Diversification rates probably increased around the Eocene/Oligocene boundary and in the middle Miocene, during two periods of major global climatic aberrations characterized by global cooling.

Main conclusions The diversification of parrots was shaped by climatic and geological events as well as by key innovations. Initial vicariance events caused by continental break up were followed by transoceanic dispersal and local radiations. Habitat shifts caused by climate change and mountain orogenesis may have acted as a catalyst to the diversification by providing new ecological opportunities and challenges as well as by causing isolation as a result of habitat fragmentation. The lorries constitute the only highly nectarivorous parrot clade, and their diet shift, associated with morphological innovation, may have acted as an evolutionary key innovation, allowing them to explore underutilized niches and promoting their diversification.

Keywords

Climate change, dispersal, diversification, Gondwana, historical biogeography, key innovation, molecular clock, molecular phylogeny, Psittaciformes, vicariance.

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INTRODUCTION

A robust temporal and spatial framework for the speciation events in a group of organisms is a prerequisite for understanding the evolutionary dynamics responsible for its current diversity. In this context, an assessment of the relative influences of plate tectonics, past climate change and ecological opportunity on the diversification process is especially important. Despite the eminent efforts that have been made to reconstruct the phylogenies of major vertebrate groups such as birds and mammals, the time scale of their radiations is still a matter of controversy. In the past, the strict interpretation of the fossil record led to the hypothesis that modern birds evolved in an explosive radiation paralleling that of mammals after the global perturbations that caused mass extinctions at the Cretaceous–Palaeogene (K–Pg) boundary 65 Ma. In this scenario, birds and mammals inherited practically the entirety of the terrestrial vertebrate adaptive landscape from the other dinosaur groups and the pterosaurs, and rapidly filled the many recently vacant ecological niches (Feduccia, 1995, 2003). However, several recent molecular phylogenetic studies have dated the origin of modern birds before the K–Pg boundary (Hedges *et al.*, 1996; Cooper & Penny, 1997; Pereira & Baker, 2006; Slack *et al.*, 2006; Brown *et al.*, 2007, 2008; Pratt *et al.*, 2009). Furthermore, the description of a well preserved fossil anseriform (*Vegavis*) from the very late Cretaceous pushed at least five basal avian splits back into the Cretaceous (Clarke *et al.*, 2005; Brown *et al.*, 2008).

The integration of molecular phylogenetic data with the geological context resulted in the conclusion that the continental break up of Gondwana during the Cretaceous shaped the diversification not only of the deep lineages of birds, but also those of mammals (Hedges *et al.*, 1996; Cracraft, 2001; Nishihara *et al.*, 2009). Within birds, the ratites (Palaeognathae) have played a crucial role in the arguments surrounding the biogeography of Gondwana. They were mainly thought to have diverged as a result of vicariance in the late Cretaceous caused by continental drift – with the exception of the kiwi (*Apteryx*) and the ostrich (*Struthio*), which dispersed later (Cooper *et al.*, 2001; Cracraft, 2001; Haddrath & Baker, 2001). However, the causal relationship between these geological and biological events has been called into question because assessment of evidence in favour of the temporal congruence of the two phenomena has often suffered from non independence, and dispersal has been neglected as a potential mechanism to explain current distribution patterns (Waters & Craw, 2006; Upchurch, 2008). Indeed, discordance between molecular phylogenies, in combination with divergence time estimates and patterns of continental break up, has recently been shown for the palaeognath birds, and vicariance alone is no longer considered the best explanation for ratite distribution patterns (Harshman *et al.*, 2008; Phillips *et al.*, 2010).

Another group of birds that is thought to have originated in Gondwana is the parrots (Psittaciformes). While several recently published molecular studies shed light on the phylogenetic relationships within parrots (de Kloet & de Kloet, 2005; Tavares *et al.*, 2006; Wright *et al.*, 2008; Schweizer

et al., 2010), the temporal patterns of their diversification remain controversial. The finding that the New Zealand taxa *Nestor* and *Strigops* formed the monophyletic sister group of the remaining taxa led to the assumption that the separation of New Zealand from Gondwana 82–85 Ma coincided with this early split within modern parrots (de Kloet & de Kloet, 2005). This bio- and palaeogeographic evidence was used to calibrate the diversification of several groups of Neotropical parrots (Ribas *et al.*, 2005, 2009; Tavares *et al.*, 2006). However, such calibrations based on New Zealand biogeography have been criticized as being a case in which geological and biological evidence lacked independence and always rely on implicit assumptions about vicariance and dispersal (Waters & Craw, 2006; Ho & Phillips, 2009; Treweek & Gibb, 2010). It was argued in the case of parrots, however, that the diversification of these today mostly non migratory birds was shaped primarily by vicariance and in fact not much influenced by dispersal. Following the same reasoning, Wright *et al.* (2008) considered a Palaeogene origin of modern parrots to be less likely than a Cretaceous origin, because a Palaeogene scenario would require several transoceanic dispersal events to explain current distribution patterns. In contrast, Schweizer *et al.* (2010) demonstrated that transoceanic dispersal between the Afrotropical, Indo Malayan, Neotropical and Australasian regions as well as Antarctica has to be invoked to explain the distribution patterns of parrots, no matter if they originated in the Palaeogene or in the Cretaceous. This in turn challenged the value of taking the separation of New Zealand from Gondwana as a calibration point for the initial split within parrots. Indeed, molecular dating based on complete mitochondrial genomes, involving fossil calibrations outside the parrots, dated the split of *Strigops* from two (*Agapornis*, *Melopsittacus*) (Pratt *et al.*, 2009) to six (*Agapornis*, *Aratinga*, *Brotogeris*, *Forpus*, *Melopsittacus*, *Nymphicus*) (Pacheco *et al.*, 2011) other genera of parrots after the K–Pg boundary.

In the present work, we generated a comprehensive temporal framework for the diversification of parrots based on a robust phylogenetic hypothesis, independent calibration points and a relaxed molecular clock approach (Drummond *et al.*, 2006) to test the hypothesis that the initial split within crown group parrots coincided with the separation of New Zealand from Australia. In addition, we aimed at establishing a detailed hypothesis of biogeographic and dispersal patterns and tested whether the rates of diversification remained constant over time or if there was indeed the hypothesized early burst after the K–Pg boundary in response to the extinction of other taxa. Finally, we asked if some groups within the parrots were more species rich than expected given their age.

MATERIALS AND METHODS

Sampling

Our sample comprised a total of 75 out of 353 extant parrot species and included representatives of all the major groups of this taxon (Table 1, Appendix S1 in Supporting Information)

Table 1 Tribal membership and distribution of the parrot taxa sampled for this study following Collar (1998) and Rowley (1998). Note that recent phylogenetic studies have revealed *Melopsittacus* to cluster together with the Loriini and the Cyclopsittacini, away from the remaining Platycercini. *Agapornis* and *Loriculus* form the sister group to those taxa, away from the remaining Psittaculini (Schweizer *et al.*, 2010; Wright *et al.*, 2008). The name Loricol oriinae has been proposed for this clade (Mayr, 2008). Compare this traditional taxonomic treatment with the relationship of *Bolbopsittacus*, *Coracopsis*, *Psittacella* and *Psittrichas* as revealed in this study.

Tribe	Species included	Range
Nestorini	<i>Nestor notabilis</i>	Australasian
Cacatuini	<i>Cacatua galerita fitzroyi</i>	Australasian
	<i>Cacatua moluccensis</i>	Australasian
	<i>Calyptrorhynchus funereus</i>	Australasian
	<i>Calyptrorhynchus latirostris</i>	Australasian
Psittrichadini 'Psittacini'	<i>Psittrichas fulgidus</i>	Australasian
	<i>Coracopsis nigra</i>	Malagasy
	<i>Coracopsis vasa</i>	Malagasy
	<i>Poicephalus gulielmi</i>	Afrotropical
	<i>Poicephalus meyeri</i>	Afrotropical
	<i>Poicephalus rufiventris</i>	Afrotropical
	<i>Poicephalus senegalus</i>	Afrotropical
	<i>Psittacus erithacus erithacus</i>	Afrotropical
	<i>Ara macao</i>	Neotropical
	<i>Amazona aestiva</i>	Neotropical
Arini	<i>Amazona dufresniana</i>	Neotropical
	<i>Amazona pretrei</i>	Neotropical
	<i>Derophtus accipitrinus</i>	Neotropical
	<i>Guarouba guarouba</i>	Neotropical
'Psittaculini'	<i>Pionus menstruus</i>	Neotropical
	<i>Triclaria malachitacea</i>	Neotropical
	<i>Agapornis canus</i>	Malagasy
	<i>Agapornis fischeri</i>	Afrotropical
	<i>Agapornis lilianae</i>	Afrotropical
	<i>Agapornis nigrigenis</i>	Afrotropical
	<i>Agapornis roseicollis</i>	Afrotropical
	<i>Alisterus chloropterus</i>	Australasian
	<i>Alisterus scapularis</i>	Australasian
	<i>Aprosmictus jonquillaceus</i>	Australasian
	<i>Eclectus roratus</i>	Australasian
	<i>Loriculus catamene</i>	Australasian
	<i>Loriculus galgulus</i>	Indo Malayan
	<i>Loriculus philippensis</i>	Indo Malayan
	<i>Polytelis alexandrae</i>	Australasian
	<i>Polytelis anthopeplus</i>	Australasian
	<i>Prioniturus discurus</i>	Indo Malayan
	<i>Prioniturus luconensis</i>	Indo Malayan
	<i>Prioniturus montanus</i>	Indo Malayan
	<i>Psittacella brehmii</i>	Australasian
Micropsittini	<i>Psittacula eupatria</i>	Indo Malayan
	<i>Psittinus cyanurus</i>	Indo Malayan
	<i>Tanygnathus megalorhynchus</i>	Australasian
	<i>Micropsitta finschii tristrami</i>	Australasian
'Platycercini'	<i>Micropsitta pusio</i>	Australasian
	<i>Barnardius zonarius</i>	Australasian
	<i>Cyanoramphus auriceps</i>	Australasian
	<i>Cyanoramphus novaezelandiae</i>	Australasian

Table 1 Continued

Tribe	Species included	Range
'Cyclopsittini'	<i>Eunymphicus cornutus cornutus</i>	Australasian
	<i>Eunymphicus cornutus uvaensis</i>	Australasian
	<i>Lathamus discolor</i>	Australasian
	<i>Melopsittacus undulatus</i>	Australasian
	<i>Neophema chrysogaster</i>	Australasian
	<i>Neophema chrysostoma</i>	Australasian
	<i>Neophema pulchella</i>	Australasian
	<i>Neophema splendida</i>	Australasian
	<i>Neopsephotes bourkii</i>	Australasian
	<i>Northiella haematogaster</i>	Australasian
	<i>Platycercus caledonicus</i>	Australasian
	<i>Platycercus eximius</i>	Australasian
	<i>Platycercus flaveolus</i>	Australasian
	<i>Platycercus venustus</i>	Australasian
	<i>Prosopieia tabuensis</i>	Australasian
	<i>Psephotus chrysoterygius</i>	Australasian
	<i>Psephotus dissimilis</i>	Australasian
	<i>Psephotus varius</i>	Australasian
	<i>Purpureicephalus spurius</i>	Australasian
	<i>Bolbopsittacus lunulatus</i>	Indo Malayan
Lorini	<i>Cyclopsitta diophthalma</i>	Australasian
	<i>Psittaculirostris desmarestii</i>	Australasian
	<i>Psittaculirostris edwardsii</i>	Australasian
	<i>Trichoglossus johnstoniae</i>	Indo Malayan
	<i>Lorius garrulus</i>	Australasian
	<i>Psitteuteles goldiei</i>	Australasian
	<i>Eos cyanogenia</i>	Australasian
	<i>Charmosyna pulchella</i>	Australasian

[nomenclature follows Collar (1998) and Rowley (1998)]. Compared to a previous paper (Schweizer *et al.*, 2010), we added species of the genera *Poicephalus*, *Prioniturus* and *Psephotus*, the Neotropical taxon Arini, the Philippine endemic *Bolbopsittacus lunulatus*, the Australasian *Northiella haematogaster* and the genus *Psittacella*, which is analysed here for the first time in a molecular genetic study. To be able to date the phylogeny of parrots with external fossils as calibration points, we added sequences taken from GenBank of 20 avian species belonging to the Neognathae (Appendix S1). We further used *Struthio* as the outgroup for all analyses to account for the well accepted split between Palaeognathae and Neognathae (e.g. Livezey & Zusi, 2007; Hackett *et al.*, 2008). Partial sequences of the three nuclear genes *c-mos*, *RAG 1* and *ZenK* (second exon) were generated following the laboratory protocol described in Schweizer *et al.* (2010) (Appendix S2). The alignment of the sequences was done manually after translation into amino acids with BioEdit 7.0.5.2 (Hall, 1999).

Phylogenetic analyses

Phylogenetic hypotheses were established using Bayesian inference (BI), maximum likelihood (ML) and maximum parsimony (MP). BI was conducted with MrBAYES 3.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) using a mixed

model approach. We evaluated alternative biologically relevant parameter settings for our concatenated data corresponding to separate models with varying base frequencies, rate matrix, shape parameters and proportion of invariable sites for the various genes and/or their codon positions. Models were selected based on Akaike information criterion (AIC) values using MRMODELTEST 2.3 (Nylander, 2004). We performed two independent runs of Metropolis coupled Markov chain Monte Carlo (MCMC) analyses, each consisting of one cold chain and three heated chains with a default temperature of 0.2. The chains were run for 10 million generations with sampling every 100 generations. We checked that the average standard deviation of split frequencies converged towards zero, and the length of the 'burn in' period was calculated by visually inspecting trace files with TRACER 1.4.1 (Rambaut & Drummond, 2007) and by monitoring the change in cumulative split frequencies using AWTY (Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008). The first 25% of samples were then discarded as burn in (25,000 trees) well after the chains reached stationarity. We further compared likelihoods and posterior probabilities of all splits to assess convergence among the two independent runs using TRACER and AWTY. When the chains did not mix appropriately, the temperature was set to 0.1. The relevance of the different parameter settings was evaluated using the Bayes factor (BF) (Kass & Raftery, 1995; Brown & Lemmon, 2007). The harmonic mean calculated by MRBAYES was used as an estimation of the marginal likelihood of the data (Kass & Raftery, 1995). A more complicated model was favoured over a simpler model if $2\ln\text{BF}$ was greater than 10 (Brown & Lemmon, 2007). Indels were treated as missing data; however, based on the best fitting model (see Results, Phylogeny) MRBAYES was rerun with alignment gaps coded as binary characters and appended to the matrix using simple gap coding (Simmons & Ochoterena, 2000) as implemented in SEQSTATE 1.4.1 (Muller, 2005, 2006). The ML search was performed using RAXML 7.0.4 (Stamatakis, 2006) on the web server with 100 rapid bootstrap inferences, with all free model parameters estimated by the software (substitution rates, gamma shape parameter, base frequencies) based on the best parameter settings found by MRBAYES (Stamatakis *et al.*, 2008). The MP analyses for the concatenated data were conducted using PAUP* (Swafford, 2001) (heuristic search, 1000 random taxon addition replicates, tree bisection reconnection (TBR) branch swapping, gaps as fifth character state or missing data). Nodal support was estimated with a MP bootstrap analysis (1000 pseudo replicates, heuristic search, 10 random taxon addition replicates, TBR branch swapping, number of max trees limited to 100). Clades were considered as supported when clade credibility values of the BI were ≥ 0.95 (Huelsenbeck & Ronquist, 2001) and when bootstrap values were ≥ 70 (Hillis & Bull, 1993).

Molecular dating

We used BEAST 1.4.8 (Drummond & Rambaut, 2007) to estimate divergence times, applying a relaxed molecular clock with an uncorrelated lognormal distribution of branch lengths and a Yule tree prior with linked trees and clock models using

the best parameter settings as found by the MRBAYES analyses (different substitution models for the genes and their codon positions, see below). As no representative of crown group Psittaciformes is known from Palaeogene fossil deposits (Mayr, 2009), we used well accepted fossils outside the parrots as calibration points. We incorporated the earliest known penguin fossil, *Waimanu*, into our dating analyses and used a mean estimate of 66 Ma with a normal distribution ($95\% \pm 6$ Ma or $\text{SD} = 3.06$) for the split between Sphenisciformes (penguins) and other seabird lineages (Slack *et al.*, 2006; Pratt *et al.*, 2009). *Waimanu* has been considered as particularly useful for providing prior information for the calibration of molecular phylogenies (Pratt *et al.*, 2009). First, aquatic birds such as penguins can be expected to have a better fossil record than land animals. Furthermore, penguins are rather large compared with other birds and have more solid and not hollow bones. Moreover, penguins are distinct and thus easier to identify than other bird groups. All these points minimize the potential problem of the oldest fossil potentially underestimating the correct age of a group. The lower bound of the prior chosen accounts for potential dating errors of the fossil, and the upper bound takes into account that two putative members of the Gaviiformes have been described from the late Cretaceous (cf. Mayr, 2009). Nevertheless, we tested the influence of using more conservative priors for this split between penguins and other seabird lineages. We additionally used a uniform prior distribution with a lower bound of 60 Ma and an upper bound of 124 Ma (see below for justification of this upper bound). We also tested a lognormal prior distribution for the same split with a zero offset at 60 Ma (mean = 1, SD = 1.5). The sister group of Sphenisciformes is not yet unambiguously resolved, so two alternative hypotheses on their phylogenetic relationships were analysed separately with BEAST. First, we treated the penguins as a monophyletic clade with Procellariiformes (tubenoses), as suggested by Hackett *et al.* (2008) and Pratt *et al.* (2009). Second, we defined the penguins as the sister group of a clade consisting of Gaviiformes (loons), Procellariiformes, Pelecaniformes and Suliformes, based on our results (see below). As a second fossil calibration point we used a minimum age of 30 Ma for the stem Phoenicopteriformes (flamingos) (Ericson *et al.*, 2006; Brown *et al.*, 2008). Podicipediformes (grebes) are well supported as the sister group of Phoenicopteriformes, both by molecular and morphological data (Mayr, 2005; Brown *et al.*, 2008; Hackett *et al.*, 2008; Pratt *et al.*, 2009) and by our data (see below). In our BEAST analyses we thus defined these two groups as monophyletic. We used a uniform prior for their split, with a lower bound at 30 Ma accounting for stem group Phoenicopteriformes from the late Eocene/early Oligocene (Ericson *et al.*, 2006; Brown *et al.*, 2008; Mayr, 2009). Putative stem group Phoenicopteriformes have also been described from the middle Eocene (cf. Mayr, 2009) and even some, albeit doubtful, remains from the late Cretaceous (Olson & Feduccia, 1980). Given this uncertainty, we used a conservative upper bound of 124 Ma, which considers that well sampled fossil sites stemming from up to 124 Ma are not

described to contain any fossils of modern birds (cf. Pratt *et al.*, 2009). In addition, we used a uniform prior distribution, again with an upper bound of 124 Ma and a lower bound of 66 Ma for the split between Galloanserae and Neoaves. The lower bound was chosen considering that the fossil *Vegavis* belonged to Galloanserae at 66 Ma (Clarke *et al.*, 2005; Pratt *et al.*, 2009). Default prior distributions were chosen for all other parameters, and the MCMC was run for 25 million generations with sampling every 1000 generations. TRACER was used to confirm appropriate burn in and the adequate effective sample sizes of the posterior distribution. Three independent chains were run for each of the topological constraints and each prior setting, and we compared likelihoods and posterior probabilities of all splits to assess convergence among the runs using TRACER and AWTY. The resulting maximum clade credibility tree and the 95% highest posterior density (HPD) distributions of each estimated node were analysed with FIGTREE 1.2.1 (Rambaut, 2008). The relevance of the two topological constraints was evaluated with the Bayes factor (BF) in TRACER, with the marginal likelihood of the data estimated using the approach proposed by Suchard *et al.* (2001) (smoothed estimate method, 1000 bootstrap replicates).

Biogeographic reconstruction

We used the software LAGRANGE to reconstruct the biogeographic history of the parrots (Snapshot version for web configuration tool at <http://www.reelab.net/lagrange>) (Ree *et al.*, 2005; Ree & Smith, 2008) based on the maximum clade credibility tree from the best fitting model in BEAST. LAGRANGE treats dispersal and local extinctions as stochastic processes, incorporating a continuous time model for geographic range evolution through dispersal, extinction and cladogenesis (the DEC model), and can take connectivity between areas into account (Ree *et al.*, 2005; Ree & Smith, 2008; Ree & Sanmartin, 2009). According to their current distribution (Collar, 1998; Rowley, 1998), the terminal taxa were assigned to the Afrotropical, Australasian, Indo Malayan, Neotropical or Malagasy region (Table 1; Newton, 2003; Schweizer *et al.*, 2010). As the current distributions of parrot genera only exceptionally span over more than a single biogeographic area, the maximum range size was restricted to two areas, and all combinations of areas were allowed in the adjacency matrix. Baseline rates of dispersal and local extinction were estimated by the software. We considered two models of dispersal opportunities in our analyses. The first did not constrain dispersal between areas over time (dispersal rate between all areas set to 1). The second incorporated the following geographical information that may have facilitated dispersal among areas: the connection between Australasia and the Neotropical region via Antarctica until about 40 Ma, and the connection between Australasia and the Indo Malayan region from about 20 Ma (Li & Powell, 2001; Hall, 2002). All other break up events of Gondwana took place before the initial split within the parrots. The dispersal rate between Australasia and the Neotropical region was set to 1 before

40 Ma, and that between Australasia and the Indo Malayan region was set to 1 after 20 Ma. All other dispersal rates were set to 0.1.

Rates of diversification

Rates of diversification were analysed using the R packages 'Laser' 2.3 (Rabosky, 2006a) and 'Geiger' 1.3.1 (Harmon *et al.*, 2008). Temporal variation in diversification rates was visualized using semi logarithmic lineage through time (LTT) plots. The 1000 last trees from the posterior of the best fitting BEAST model were used with the root node set to 58.587 Myr (mean value recovered with the best fitting BEAST model), and all non parrot taxa and one subspecies of *Eunymphicus cornutus* were pruned. We plotted the mean LTT from these 1000 trees along with the 95% confidence intervals. To compute these, we used the intervals of node ages over the 1000 trees at every lineage added to the tree, starting from the root node. We compared the results with two null models of constant rate diversification under two extreme relative extinction rates, with speciation (λ) set to 0.2 and extinction (μ) set either to 0 (relative extinction rate $a = \mu/\lambda = 0$, pure birth model) or to 0.18 ($a = \mu/\lambda = 0.9$) (Couvreur *et al.*, 2010). One thousand phylogenetic trees with each diversification rate were simulated in MESQUITE 2.72 (Maddison & Maddison, 2009) to generate the null distributions. To account for incomplete taxon sampling, the simulated phylogenies contained 353 tips representing the current species diversity of parrots (Collar, 1998; Rowley, 1998) and were then pruned to 74 taxa in reflection of our taxon sampling. As our taxon sampling is not random, but biased towards the inclusion of more deeply diverging lineages (phylogenetically over dispersed sampling), the pruning of missing taxa was done non randomly using the method of Brock *et al.* (in press). This method incorporates a scaling parameter α to control the degree to which the sampling is phylogenetically over dispersed. When $\alpha = 0$, pruning of taxa from a phylogenetic tree is completely random. When $\alpha = 1$, a higher proportion of taxa with shorter tip branches are pruned, resulting in a higher number of tip branches that attach to the tree at deeper nodes. Higher values of α lead to an increase of the sampling bias towards the root, and only the oldest nodes are retained. We used various values between 0.1 and 10 for α to non randomly prune taxa from our simulated trees. The root node of the resulting trees was set to 58.587 Ma, and mean LTT curves were computed. The mean LTT curve from the posterior distribution of the BEAST analyses was compared with the mean curves of the two null models for various values of α by carrying out a Kolmogorov Smirnov goodness of fit test.

To test for temporal variation in diversification rates, the birth death likelihood (BDL) approach of Rabosky (2006b) and the (γ) statistic of Pybus & Harvey (2000) are often applied. However, it has recently been shown that rate downturns should not be inferred with these methods unless > 80% of species in a particular clade have been sampled (Cusimano & Renner, 2010). We therefore applied the recently

developed comparative method MEDUSA (Alfaro *et al.*, 2009). This uses a diversity tree as its basis, which corresponds to a time calibrated phylogeny with a species richness value assigned at each tip of the tree. MEDUSA first fits a single birth death model to the entire diversity tree based on the likelihood function of Rabosky *et al.* (2007). Then a model with two birth rates and two death rates, including a shift location parameter, is fitted to the diversity tree and its AIC score is compared with that of the first model. This process is continued until the AIC score of a more complex model with additional rate shifts and rate parameters is not less than a defined threshold number. The maximum clade credibility tree from the best fitting model in BEAST was used for the diversity tree and pruned down to 31 tips to account for missing species. These tips represented clades that were well supported in our phylogenetic inference and to which missing species could be assigned based on the results of other molecular phylogenetic studies (Tavares *et al.*, 2006; Wright *et al.*, 2008). The genera *Callocephalon*, *Ognorhynchus*, *Oreopsittacus* and *Psilopsiagon*, which were not included in these earlier studies, were assigned to clades based on taxonomic information (Forshaw, 1973). *Pezoporus* and *Geopsittacus* were included, together with *Psittacella*, as sister taxa of Platycercini (cf. Leeton *et al.*, 1994).

RESULTS

Sequence characteristics

The final alignment consisted of 3222 bp (c mos, 603 bp; RAG 1, 1461 bp; Zenk 1158 bp; Appendix S3). The alignment of RAG 1 contained one indel of three amino acids, two indels of one amino acid, and one indel of two amino acids. For c mos, the alignment contained one indel of four amino acids, while for Zenk there were six indels of one amino acid, one indel of three amino acids and one indel of two amino acids. There were no ambiguously aligned amino acids.

Phylogeny

No conflict was detected between the topologies of the trees resulting from the different parameter settings with MRBAYES (Appendix S3). After calculation of the Bayes factors, the parameter setting using different models of sequence evolution for the three genes and three codon positions with temperature set to 0.1 was chosen as the best fitting model (Fig. 1). Based on this parameter setting, we reran the MRBAYES analyses using 20 million generations with sampling every 100 generations; however, this had no influence on the results. The coding of gaps as binary characters had no impact on the tree topology and did not significantly influence node support values. The topologies of the best scoring trees obtained with BEAST, MRBAYES and RAXML were highly congruent with the strict consensus MP tree (Figs 1 & 2, Appendix S4). The ML and BI trees were even identical for the parrots (Fig. 1, Appendix S3). In the MP analyses, there was no difference in the topology of the

strict consensus trees when gaps were treated either as a fifth character state or as missing data.

Galliformes were found to be the sister group to Neoaves. However, the phylogenetic relationships within Neoaves could not be robustly resolved. Phoenicopteriformes and Podicipediformes always clustered together. Sphenisciformes were found to be the sister taxon of the seabird lineages (Gaviiformes, Procellariiformes, Pelecaniformes, Suliformes) with no robust support. The monophyly of Passeriformes was well supported, as was the sister group position of Acanthisitti (New Zealand wrens) to a clade containing the suboscines and the oscines. Psittaciformes formed an unresolved, not robustly supported clade with the Coraciiformes + *Falco* in the Bayesian and ML analyses. The BEAST and MP analyses revealed a clade consisting of the parrots and Coraciiformes, while *Falco* was the sister group to all the remaining Neoaves.

We confirmed the sister group relationship between the African Psittacini and the Neotropical Arini as proposed by Schweizer *et al.* (2010). The division of the Arini into two well supported clades is in congruence with other molecular analyses (Tavares *et al.*, 2006; Wright *et al.*, 2008). *Psittacella* clustered together with Platycercini without robust support in the ML and Bayesian analyses, while its position in a clade together with Platycercini and Loricoloriinae was not resolved in the MP analyses. The monophyly of the Platycercini was not robustly supported either. *Bolbopsittacus* was found to be the sister taxon of *Agapornis* and *Loriculus*. The sister group relationship between *Psittarchas* from Australasia and *Coracopsis* from the Malagasy region was robustly supported. This relationship was first proposed by de Kloet & de Kloet (2005), but either not confirmed (Wright *et al.*, 2008) or not robustly supported (Schweizer *et al.*, 2010). The cluster of *Coracopsis* and *Psittarchas* was found to be the sister group of the Arini and the Psittacini in the MP analyses. In contrast, MRBAYES and RAXML revealed it as the sister group of a cluster containing all Old World parrots except the Psittacini, Arini, Cacatuidae and *Nestor*, but with no robust support. BEAST found it to be the sister group of the cluster of *Psittacella* + Platycercini (Fig. 2).

Divergence time estimate

The comparison of the three independent runs for all BEAST analyses revealed high convergence among the various parameters, and effective samples sizes were > 293 for all parameters. The analyses based on two different topological constraints resulted in very similar divergence time estimates (Table 2). The mean values indicated that the initial split within the extant parrots occurred after the K Pg boundary (Fig. 3). The Bayes factors revealed the topological constraint based on the relationships of Sphenisciformes found with MRBAYES as the best fitting model. The mean value for the separation of *Nestor* from the remaining parrots was dated at 58.6 Ma (95% HPD: 44.9–72), and the Cacatuidae split at 47.4 Ma (36.3–59.4). The subsequent splitting events between the remaining major recent groups of parrots occurred

Figure 1 A 50% majority rule consensus tree of the Bayesian inference of parrots and other avian taxa. Clade credibility values and bootstrap values of the maximum likelihood inference above 50 are indicated at each node. The notation used in the text for the various parrot clades is indicated to the right of the tree.

between 32 and 40 Ma (Fig. 2, Table 2). The use of two different more conservative priors for the split between the penguins and the other seabird lineages (based on the topological constraint found to be the best fitting model) resulted in highly similar time estimates for the different splits, and our results can thus be considered as robust (Table 2).

Reconstruction of historical biogeography

The global ML at the root node for the unconstrained model was -64.87 (dispersal rate = 0.002237, extinction rate = 0.001918), while the constrained model had a global ML at the root node of -63.94 (dispersal rate = 0.008502, extinction rate = 0.001623). Of the 149 splits at nodes, 136

Figure 2 Maximum clade credibility tree of the dating analysis of parrots and other avian taxa using BEAST based on the best fitting model. Mean node ages and the 95% highest posterior density distributions are shown. Posterior summaries were only calculated for the nodes in the tree that had a posterior probability greater than 0.5. The nodes used for calibration are indicated by circles.

were unambiguously resolved between the two models. With regard to the 13 remaining nodes, however, the models either yielded different splits between areas (nodes 1, 2 and 7, Table 3, Fig. 4) or considered the same splits as most likely but revealed more than one split within two log likelihood units of the maximum for the respective node (Table 3, Fig. 4). At nodes 1 and 2, the two models differed in that the constrained model included, in addition to Australasia, the Neotropical region in the range of a common ancestor of these taxa. At node 7, the unconstrained model favoured a split between the Indo Malayan and Australasian + Indo Malayan realms, while the constrained model found a split between Australasia and Indo Malaysia as more likely.

Rates of diversification

When an improvement of the AIC score of ≥ 4 was considered as a significant increase in model fit (Burnham & Anderson, 2002; Alfaro *et al.*, 2009), MEDUSA found one period in which the tempo of diversification changed and led to the exceptionally species rich clade of the lorries (Loriinae) (Fig. 5). When models with an improvement of the AIC score of ≥ 2 were considered as supported (Burnham & Anderson, 2002), we had an indication for a second event of increased diversification rate for the clade leading to the Arini ($\Delta\text{AIC} = 3.4$). Both these increased diversification rates were associated with rather high species turnover, with death rates being 95.4% and 89.4%, respectively, of the birth rate. The

Table 2 Divergence dates of parrots and other avian taxa for various nodes estimated with a Bayesian relaxed clock approach. The mean values and the 95% highest posterior density (HPD) distributions are given for two topological constraints and for different prior distributions for the calibration of the split between penguins and other seabird lineages. The first topological constraint defined Sphe nisciformes (penguins) as the sister group of a clade consisting of Gaviiformes (loons), Procellariiformes (tubenoses), Pelecaniformes and Suliformes, based on our results, whereas the second one treated Sphenisciformes as a monophyletic clade with Procellariiformes, as suggested by Hackett *et al.* (2008) and Pratt *et al.* (2009). Node numbers refer to those in Fig. 2.

Node number	Topological constraints and prior for the calibration of the split between penguins and the other seabird lineages:							
	This study		Hackett <i>et al.</i> (2008), Pratt		This study		This study	
	Normal prior		Normal prior		Uniform prior		Lognormal prior	
	Mean	95% HPD (Ma)	Mean	95% HPD (Ma)	Mean	95% HPD (Ma)	Mean	95% HPD (Ma)
1	58.587	44.869 71.961	61.734	49.414 75.350	58.769	(45.375 72.343)	56.991	(44.104 70.470)
2	47.381	36.264 59.395	49.853	39.283 61.394	47.612	(36.779 58.826)	46.043	(35.349 57.082)
3	40.760	31.763 51.280	42.920	33.954 53.016	40.851	(31.625 49.997)	39.631	(30.608 49.006)
4	35.135	26.004 45.069	36.944	27.537 46.270	35.193	(26.631 44.636)	34.306	(25.863 43.498)
5	25.260	17.256 34.267	26.471	18.235 35.431	25.316	(17.421 34.087)	24.638	(17.266 33.053)
6	12.922	7.028 19.634	13.491	7.082 20.609	13.243	(6.821 20.253)	12.671	(6.924 19.249)
7	38.817	31.763 51.2799	40.851	32.157 50.418	38.903	(30.319 47.923)	37.728	(29.019 46.597)
8	36.137	27.429 45.009	38.036	29.672 47.233	36.210	(27.937 44.594)	35.004	(26.753 43.539)
9	27.609	17.792 37.948	29.342	18.122 40.053	27.945	(17.185 37.986)	26.851	(16.559 36.870)
10	31.130	22.278 40.249	33.023	24.264 41.708	31.253	(23.143 39.007)	30.223	(21.958 38.610)
11	18.465	10.765 26.496	19.574	11.258 28.475	18.665	(11.003 26.657)	18.005	(10.484 25.861)
12	19.850	12.722 27.802	20.888	13.106 28.743	19.817	(13.042 27.340)	19.220	(12.676 26.596)
13	14.016	7.730 20.959	14.605	8.094 21.421	13.889	(7.791 20.368)	13.451	(7.671 20.134)
14	9.802	5.816 14.327	10.331	5.996 14.876	9.856	(5.919 14.405)	9.471	(5.540 13.600)
15	32.650	24.179 41.281	34.176	25.606 42.752	32.600	(24.457 40.860)	31.449	(23.241 39.676)
16	18.589	11.715 26.352	19.587	12.482 27.706	18.662	(11.842 26.103)	18.034	(11.309 25.101)
17	14.165	8.213 20.884	14.899	8.559 21.829	14.168	(8.406 20.709)	13.720	(8.036 19.924)
18	28.526	20.680 36.727	29.928	21.862 38.675	28.513	(20.742 38.883)	27.531	(19.553 35.697)
19	23.672	16.328 31.230	24.701	17.241 32.363	23.614	(16.393 31.059)	22.808	(15.706 30.348)
20	13.832	8.072 20.270	14.352	8.356 20.705	13.776	(7.830 20.271)	13.409	(7.677 20.005)
21	33.193	23.547 42.683	35.008	25.442 44.404	33.335	(24.598 42.941)	32.279	(23.065 41.142)
22	25.242	17.249 33.480	26.751	18.466 35.562	25.470	(17.055 33.768)	24.552	(17.053 32.882)
23	112.902	97.157 124.000	115.412	101.975 123.999	112.749	(96.133 123.999)	110.942	(93.829 124.00)
24	80.650	58.979 101.899	81.717	61.759 100.406	78.833	(56.939 97.689)	78.867	(59.013 98.364)
25	95.638	79.197 111.523	98.647	84.511 112.247	95.753	(79.004 111.979)	93.390	(76.338 110.109)
26	70.362	52.600 88.130	73.081	57.364 90.358	71.165	(53.926 89.449)	69.299	(52.555 87.724)
27	62.406	45.517 79.743	65.177	48.929 81.072	63.357	(45.441 80.813)	61.963	(44.955 78.725)
28	49.148	31.177 66.126	48.901	30.817 65.317	49.250	(31.496 66.187)	47.044	(30.423 63.090)
29	64.527	58.715 70.421	64.083	58.229 69.790	65.387	(60.000 74.930)	62.302	(60.013 67.589)

background diversification rate was characterized instead by a low turnover, with the death rate only accounting for 1.9% of the birth rate (Fig. 5).

The LTT plot, too, indicated that the diversification rate of the parrots was not constant over time (Fig. 5). The first change occurred in the upper Eocene (around 40 Ma), with an acceleration in the diversification rate that lasted until the early Oligocene (around 30 Ma). A second increase in the diversification rate started in the middle Miocene (after 15 Ma). The decrease towards the present is probably influenced by incomplete lineage sampling, with some genera and many species missing (cf. Ricklefs *et al.*, 2007) and is not discussed further. The mean LTT curve differed significantly from the expectations under the null model based on a constant diversification rate and no extinction for any value of α tested

(Kolmogorov–Smirnov test, $P = 0.0002$). However, it was only significantly different from a null model based on a constant diversification rate and a rather high extinction rate for $\alpha > 1.08$, and the simulated mean LTT curves then showed an excess of younger branching events. However, the effects of extinction can be difficult to separate from those of increased speciation towards the present, a phenomenon termed the ‘pull of the present’ (Nee *et al.*, 1994). Extinction may not have had any dominant effect in our case, as the diversification of the species rich lorries started at the same time as the second indicated increase in diversification rate and probably influenced overall net diversification rates. Furthermore, MEDUSA identified a rather low turnover for the background diversification rate. As it is problematic to infer extinction rates from molecular phylogenies in the absence of fossil data (Rabosky,

Figure 3 Relative posterior density of the time estimate for the initial splits within crown group parrots generated using BEAST on the basis of two calibrations based on different topological constraints. K Pg, Cretaceous Palaeogene boundary.

2010), this has to be interpreted with caution. Although the evidence is somewhat inconclusive, we have an indication for two periods of increased net diversification rates for the parrots as a whole.

DISCUSSION

Phylogeny

While the phylogenetic relationships within parrots as revealed in this study were mostly in congruence with previous results (de Kloet & de Kloet, 2005; Tavares *et al.*, 2006; Wright *et al.*, 2008; Schweizer *et al.*, 2010), we shed new light on the affinities of certain taxa. The relationships of the New Guinean genus *Psittacella* had not been analysed using DNA sequence data before. This genus has traditionally been treated as a member of the Psittaculini (Smith, 1975; Collar, 1998), although Christidis *et al.* (1991) suggested an affinity with the Platycercini on the basis of allozyme data. In our study, *Psittacella* formed the sister group of the Platycercini, but this relationship was not robustly supported. The monophyly of the Platycercini is still disputed. It only received robust support when *Psittacella* was not included in the analyses (Schweizer *et al.*, 2010), while Wright *et al.* (2008) could not resolve the position of the clade containing *Neophema* and *Neopsephotus* and the cluster of the remaining Platycercini. Resolution of this

part of the parrot phylogeny could probably be enhanced by the inclusion of *Pezoporus* and *Geopsittacus* in further molecular studies, as it was shown from cytochrome *b* data that these enigmatic genera may be linked with the platycercine parrots (Leeton *et al.*, 1994). The Philippine endemic *Bolbopsittacus* has traditionally been considered a member of either the Psittaculini (Smith, 1975) or the Cyclopsittacini (Smith, 1981; Collar, 1998), but we revealed it to be the sister taxon of *Agapornis* and *Loriculus*, in congruence with Wright *et al.* (2008).

Early diversification of parrots

While the stem lineage of parrots was probably already in existence in the Cretaceous, we have strong evidence that the crown group diversification of parrots probably started after the K Pg boundary at around 58 Ma, although the 95% HPD distribution included the late Cretaceous and ranged from 44.87 to 71.96 Ma. This is clearly later than the 80–85 Ma used in several previous studies as a calibration point for the initial split within the parrots (Tavares *et al.*, 2006; Ribas *et al.*, 2007, 2009; Wright *et al.*, 2008), coinciding with the separation of New Zealand from Gondwana. Our results are in congruence with the study of Pacheco *et al.* (2011), who estimated a node age for this split between 54.13 and 61.44 Ma, while Pratt *et al.* (2009) placed it even later, at 50.38 Ma (mean age). Clearly, even where geological and biological events appear to correspond, their temporal association ought to be corroborated by independent evidence to avoid circularity. However, as indicated by new geological evidence, a land bridge between New Zealand and Australia may have existed until the Early Eocene, up to 52 Ma (Gaina *et al.*, 1998; Tennyson, 2010). Hence, even if the initial split within the crown group of parrots occurred later than hitherto assumed, it could still have been caused by vicariant evolution after the final complete separation of New Zealand from Australia. However, it has to be considered that current endemic lineages such as *Nestor* and *Strigops* may have been more widely distributed in the past and/or may not have evolved in the area where they are found today. The avifauna of New Zealand is composite in nature and has repeatedly experienced colonization and extinction events leading to different degrees of isolation in different avifaunal elements (Trewick & Gibb, 2010; Goldberg *et al.*, 2011). Rather than being caused by long isolation, the impression of old endemism in *Nestor* and *Strigops* might also be a consequence of local survival or recent colonization in combination with extirpation elsewhere.

The age estimates for the various representatives of the outgroup were in agreement with other recently published studies (Hugall *et al.*, 2007; Brown *et al.*, 2008; Pratt *et al.*, 2009; Pacheco *et al.*, 2011). Our results support a growing body of evidence that the transition to modern birds occurred during the Cretaceous, with the parrots and other lineages likely to have been in existence well before the extinction of dinosaurs and pterosaurs (Hedges *et al.*, 1996; Cooper & Penny, 1997; Clarke *et al.*, 2005; Pereira & Baker, 2006; Slack

Table 3 Nodes for which the biogeographic reconstruction of parrots with LAGRANGE differed between the two models applied. The numbering of the nodes corresponds to that in Fig. 4. The split format reads as follows: [left|right], where 'left' and 'right' are the ranges inherited by each descendant branch, with 'left' corresponding to the upper branch, and 'right' to the lower branch in the phylogenetic tree in Fig. 4. All reconstructions within two log likelihood units (lnL) of the maximum for each node are shown, with the relative probability (Rel. Prob.) being the relative probability (fraction of the global likelihood) of a split. A, Australasian; AT, Afrotropical; IM, Indo Malayan; M, Madagascar; NT, Neotropical.

Node	Unconstrained model			Constrained model		
	Split	lnL	Rel. Prob.	Split	lnL	Rel. Prob.
1	[A A]	65.78	0.40	[A A+NT]	64.79	0.43
	[A A+NT]	66.06	0.31	[A A+AT]	65.05	0.33
	[A A+AT]	66.36	0.2262	[A A]	65.52	0.21
2	[A A]	65.88	0.36	[A+NT A]	64.73	0.46
	[A+NT A]	65.90	0.36	[A+AT A]	64.99	0.35
	[A+AT A]	66.2	0.26	[A A]	65.65	0.18
3	[A NT]	65.60	0.48	[A NT]	64.62	0.51
	[A AT]	65.91	0.35	[A AT]	64.89	0.39
	[A A]	67.33	0.09			
4	[AT NT]	65.44	0.56	[AT NT]	64.39	0.64
	[NT NT]	66.52	0.19	[NT NT]	65.67	0.18
	[A NT]	67.37	0.08			
5	[M A]	65.41	0.59	[M A]	64.38	0.65
	[A A]	65.93	0.35	[A A]	65.19	0.29
6	[A A]	65.24	0.69	[A A]	64.39	0.64
	[A IM]	66.64	0.17	[A IM]	65.3	0.26
7	[IM A+IM]	65.96	0.34	[IM A]	65.24	0.27
	[A A]	66.57	0.18	[IM IM]	65.35	0.25
	[IM A]	66.59	0.18	[A A]	65.38	0.24
	[IM IM]	66.65	0.17	[IM A+IM]	66.02	0.13
8	[A AT]	66.59	0.18	[A AT]	65.34	0.25
	[A+IM IM]	66.66	0.17	[A M]	65.42	0.23
	[A+IM A]	66.66	0.17	[IM AT]	65.98	0.13
	[A M]	66.66	0.17	[IM M]	66.06	0.12
	[IM AT]	67.15	0.10	[A A]	66.56	0.07
	[IM M]	67.31	0.09	[A+IM A]	66.73	0.06
	[A A]	67.62	0.06	[A+IM IM]	66.73	0.06
	[IM IM]	68.35	0.03	[IM IM]	67.25	0.04
	[M AT]	65.47	0.55	[M AT]	64.29	0.71
	[A AT]	67.05	0.11			
10	[A A]	65.15	0.76	[A A]	64.23	0.75
	[A A+IM]	66.28	0.2439	[A A+IM]	65.36	0.24
11	[A A]	65.14	0.76	[A A]	64.27	0.72
	[A A+IM]	66.42	0.21	[A A+IM]	65.55	0.20
12	[IM A+IM]	64.98	0.89	[IM A+IM]	64.29	0.71
				[IM A]	65.64	0.18
13	[A A+IM]	64.97	0.90	[A A+IM]	64.25	0.73
				[A A]	65.74	0.17

et al., 2006; Brown *et al.*, 2007, 2008; Pratt *et al.*, 2009; Pacheco *et al.*, 2011). A similar pattern has been found in mammals, and the mass extinction event at the K Pg boundary does not seem to have had a major influence on the diversification of today's mammals (Bininda Emonds *et al.*, 2007; Nishihara *et al.*, 2009). The diversification of the crown group of the parrots, however, did not start until the Palaeocene, and well after the K Pg boundary, but we cannot

exclude the possibility that earlier diversity within the group had gone extinct by the K Pg boundary.

Biogeography, species richness and temporal diversification patterns within parrots

The causes of diversification in the large and widely distributed clade of the parrots appear to be complex. However, our

Figure 4 Biogeographic reconstruction obtained using LAGRANGE of the area splits at the various nodes of parrots. The red circles indicate nodes either at which the reconstruction of the models yielded different splits between areas or where both models considered the same splits to be most likely but more than one split was revealed within two log likelihood units of the maximum for the respective node. The alternative reconstructions for these nodes are given in Table 3, along with the likelihood values.

analysis of temporal and spatial patterns in diversity allowed us to pinpoint some of the more important events in their evolutionary history.

It has been hypothesized that a common ancestor of the Arini and the Psittacini lived in Antarctica and became separated from the Australasian lineages when Antarctica began to split from Australia (Tavares *et al.*, 2006; Schweizer *et al.*, 2010). The two continents finally separated at about 40 Ma (Li & Powell, 2001), which corresponds well with our estimate for the split between those two groups (node 3, Figs 2 & 4). This agreement between geological and biological evidence indicates that vicariance may have been the major

force in this cladogenetic event. The constrained and unconstrained biogeographic models agreed in their reconstruction of the ranges of these two taxa, although different scenarios were revealed to be similarly likely (node 3, Table 3). Biogeographic reconstruction is hampered here by the fact that Antarctica cannot be implemented in the model as no recent taxa occur on this continent. As a result of climate change towards cooler conditions during the Eocene, continental ice sheets expanded rapidly on Antarctica in the earliest Oligocene (Zachos *et al.*, 2001). It was hypothesized that parrots then colonized the Neotropics and Africa from Antarctica, giving rise to the Arini and Psittacini (Tavares

Figure 5 Diversity tree and semi logarithmic lineage through time (LTT) plot for parrots. (a) Diversity tree of parrots used for the MEDUSA analyses. Clades for which we found an indication for an unusual diversification rate are assigned numbers that represent the order in which rate shifts were added by the stepwise Akaike information criterion (AIC) procedure. The estimated net diversification rates ($r = \lambda - \mu$) and relative extinction rates ($a = \mu/\lambda$) for the clades denoted by numbers and the background rates (Bg.) are indicated. We revealed the Loriinae to be exceptionally species rich and have an indication that the clade leading to the Arini showed an increased diversification rate. (b) Semi logarithmic LTT plot of the 1000 last trees from the posterior of the best fitting model obtained in BEAST showing the mean (Mean BEAST LTT) and the 5% and 95% confidence interval (CI) curves. In addition, the mean curves of the 1000 simulated trees for the two null models with constant diversification rates are given for two extreme values of the scaling parameter α (see text for further details). Arini clade 1 includes *Anadorhynchus*, *Ara*, *Aratinga*, *Cyanoliseus*, *Cyanopsitta*, *Deroptyus*, *Diopsittaca*, *Enicognathus*, *Guarouba*, *Leptosittaca*, *Nandayus*, *Pionites*, *Propyrrhura*, *Pyrrhura*, *Ognorhynchus*, *Orthopsittaca*, *Rhynchopsitta*. Arini clade 2 includes *Amazona*, *Bolborhynchus*, *Brotogeris*, *Forpus*, *Graydidascalus*, *Hapalopsittaca*, *Myopsitta*, *Nannopsittaca*, *Pionopsitta*, *Pionus*, *Psilopsiagon*, *Touit*, *Triclaria*. Loriinae clade 1 includes *Chalcopsitta*, *Eos*, *Glossopsitta*, *Lorius*, *Neopsittacus*, *Oreopsittacus*, *Pseudeos*, *Psitteteutes*, *Trichoglossus*. Loriinae clade 2 includes *Charmosyna*, *Phygis*, *Vini*.

et al., 2006; Schweizer *et al.*, 2010). We indeed found this divergence event to have occurred in the late Eocene or early Oligocene (at around 35 Ma) (node 4, Figs 2 & 4).

Schweizer *et al.* (2010) proposed two further major dispersal events during the evolutionary diversification of parrots, namely the colonization of Madagascar from Australasia by a

common ancestor of *Coracopsis*, and the colonization of Madagascar and later Africa, again from Australasia, by a common ancestor of *Agapornis*. We found that a common ancestor of *Coracopsis* dispersed to Madagascar and split from *Psittirichas* at around 28 Ma, in the middle Oligocene (node 5, Fig. 4, Table 3; node 9, Fig. 2, Table 3). The split between *Agapornis* and *Loriculus* was found to have taken place later, at around 24 Ma (node 19, Fig. 2, Table 2). The biogeographic reconstruction revealed several colonization scenarios of Madagascar and Africa by ancestors of *Agapornis* as almost equally likely. We hypothesize that a colonization of Madagascar from Australasia followed by dispersal from Madagascar to Africa (Schweizer *et al.*, 2010) is most probable, as the Madagascan endemic *Agapornis canus* is the sister group to the African mainland *Agapornis* species (nodes 8 and 9, Fig. 4, Table 3). Thus, *Coracopsis* and *Agapornis* have independently colonized Africa/Madagascar through long distance dispersal across the Indian Ocean from Australasia. Within birds, such a biogeographic pattern has so far only been convincingly proposed for the cuckoo shrikes (Campephagidae) (Jonsson *et al.*, 2010).

Colonization of Indo Malaysia from Australasia occurred independently several times. *Bolbopsittacus*, which is endemic to the Philippines, split from its closest relatives in Australasia about 28 Ma, which probably represents the first colonization of the Indo Malayan region (node 18, Fig. 2, Table 2). This was perhaps facilitated by the East Philippines Halmahera South Caroline Arc, which was approaching the Australian plate at this time (Hall, 2002). Australasia reached its present position relative to Indo Malaysia around 20–25 Ma (Li & Powell, 2001; Hall, 2002), and all other splits between Australasian and Indo Malayan taxa seem to have occurred after the two realms came into close contact. The proximity of these two regions in combination with a complex pattern of tectonic movement and the development of archipelagos in this area could have provided new dispersal opportunities and facilitated faunal exchange between them (Hall, 1998, 2002). However, the exact pattern of colonization of the Indo Malayan region by ancestors of *Loriculus*, *Prioniturus*, *Psittinus*, *Psittacula* and *Tanygnathus* could not be inferred unambiguously with our biogeographic reconstruction. It possibly included dispersal back to Wallacea by *Prioniturus* and *Tanygnathus* in a way similar to that shown for the cuckoo shrikes (Campephagidae) (Jonsson *et al.*, 2008). Groombridge *et al.* (2004) dated the split of *Psittacula* from other parrots between 3.4 and 9.7 Ma using cytochrome *b* rates estimated for other avian species. This is consistent with our estimate regarding the split between *Psittacula* and *Psittinus/Tanygnathus* at a mean value of 6.25 Ma.

The analyses using MEDUSA found the loriests to be unexpectedly species rich given their age (Fig. 5). The loriests split from their closest relatives in the middle Miocene and are thought to have radiated through the islands off northern Australia and colonized areas west to Sulawesi and Bali, north to the Philippines, east to several Pacific islands and south to Australia (Christidis *et al.*, 1991; Collar, 1998; Schodde, 2006).

They differ from the remaining parrots in being highly specialized to a nectarivorous diet and are characterized by several morphological specializations of their feeding tract to nectarivory, including a modified gizzard musculature and a brush tip tongue allowing them to harvest nectar rapidly (Gunter, 1981; Richardson & Wooller, 1990; Collar, 1998). Their diet shift and the associated anatomy may represent a key innovation that promoted their radiation and account for their large species richness. The other highly nectarivorous bird group of Australasia comprises the honeyeaters (Meliphagidae), which are among the most species rich and most diverse group of birds in this region (Newton, 2003). The ecological relationships of the loriests and the honeyeaters with plants are not as species specific as they are in some other nectarivorous birds such as the Neotropical hummingbirds or the sunbirds in Africa (Fleming & Muchhala, 2008). Adaptation to and coevolution with individual plant species may thus not have been a primary driving force of the diversification of the loriests. However, nectar may have provided a spatially widespread underutilized niche, which would have allowed loriests to expand their geographical ranges and successfully establish populations on oceanic islands, which was often followed by allopatric speciation, and eventually followed by secondary sympatry through range expansion. Even today, however, congeneric species of the loriests occur generally in allopatry (Collar, 1998).

The radiation of the loriests started at a time when the LTT plots indicate an accelerated diversification rate for the parrots as a whole, from the middle Miocene onwards and contemporaneous with a period of gradual cooling following the middle Miocene climate transition (MMCT) (Zachos *et al.*, 2001; Shevenell *et al.*, 2004). During this period, the majority of the extant genera of parrots arose, similar to the case of other bird groups such as toucans (Ramphastidae) (Patane *et al.*, 2009), buteonines (Accipitridae) (do Amaral *et al.*, 2009) and some Passeriformes such as tapaculos, cuckoo shrikes and other crown Corvidae (Jonsson *et al.*, 2008; Mata *et al.*, 2009). A major change in vegetation began to take place contemporaneously in the middle/late Miocene, associated with the shrinking of rain forests and an increase in areas of open vegetation in Australia, Africa and South America (Jacobs *et al.*, 1999; Martin, 2006). While this led to a fragmentation of forest habitat into refugia, the newly opened savanna areas provided new ecological opportunities and may have been colonized by parrots from forests through niche expansion, prompting ecological speciation (Tavares *et al.*, 2006; Fjeldså & Bowie, 2008). The mechanisms of such ecological speciation across forest savanna ecotones have been demonstrated in other bird species (Smith *et al.*, 2001, 2005). We indeed found that several dry adapted Australasian lineages emerged at this time (*Melopsittacus*, *Polytelis alexandrae*, *Northiella/Psephotus*). In Africa, *Poicephalus*, a genus that includes several dry landscape taxa, split from *Psittacus*, a bird of lowland forests, then, and this was followed by diversification of *Poicephalus* (Collar, 1998). In South America, the uplift of southern portions of the Andes (Fariás *et al.*, 2008) followed by the

uplift of the Central Andean plateau, beginning in the late Miocene (Garzone *et al.*, 2008), led to further habitat change and fragmentation at around the same time, and could have promoted the radiation of Neotropical parrots (see below). Finally, environmental changes in Asia following the increased uplift of the Tibetan plateau and the onset of the Indian and east Asian monsoons during the late Miocene (Ruddiman & Kutzbach, 1990; Zhisheng *et al.*, 2001) probably also prompted the diversification of parrots there, as was proposed for the early diversification of the genus *Psittacula* in south and Southeast Asia by Groombridge *et al.* (2004).

A much earlier possible increase of net diversification rates for the parrots as a whole took place around the Eocene/Oligocene boundary and again coincided with a major global climatic aberration. It was characterized by cooler conditions just above the Eocene/Oligocene boundary and Antarctica becoming increasingly ice encrusted (Zachos *et al.*, 2001). Diversification around the Eocene/Oligocene boundary has also been found in other bird groups, including auks (Pereira & Baker, 2008), penguins (Baker *et al.*, 2006), trogons (Moyle, 2005), pigeons and doves (Pereira *et al.*, 2007). During this period, the major lineages of parrots emerged, and Africa and South America were colonized (see above). These newly colonized areas may have provided several ecological opportunities for the facilitation of diversification. We indeed have an indication based on the analyses with MEDUSA that the clade leading to the Neotropical Arini showed an increased diversification rate and that the Arini may be exceptionally species rich given their age. However, there seems to have been a time lag between the arrival in South America and the beginning of the diversification, although this needs to be corroborated with a broader taxon sampling. More generally, avian species richness is higher in South America than in any other continent, and almost one third of the world's bird species occur there (Price, 2008). High speciation rates in the Neotropics are probably caused by a spatially and temporally heterogeneous combination of mechanisms, with a strong influence from the uplift of the Andes and from Pleistocene glacial cycles in the Andes (Weir, 2006; Price, 2008; Thomas *et al.*, 2008). The beginning of the uplift of the Andes probably also promoted the generic diversification of Neotropical parrots (see above), and mountain uplift has indeed been suggested to have driven the diversification of *Pionus* parrots (Ribas *et al.*, 2007).

In summary, we found the diversification of parrots to be correlated with extrinsic mechanisms, namely climatic and geological events, but also to be associated with the evolution of a key innovation. It thus corresponds to a taxon pulse model (Erwin, 1981; Halas *et al.*, 2005). Initial vicariance events caused by continental break up were followed by dispersal, range expansion and local radiations. Vegetation shifts in combination with mountain orogenesis may have acted as a catalyst for the diversification of parrots by providing new ecological opportunities and challenges that facilitated ecological speciation, as well as by causing habitat fragmentation that resulted in vicariance events. To better understand the

influence of climate driven habitat change and geological events, especially from the middle Miocene onwards, on the speciation processes of parrots, future studies should attempt to integrate knowledge of phylogenetic relationships of closely related species into a spatial and temporal framework.

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REFERENCES

- Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L., Carnevale, G. & Harmon, L.J. (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences USA*, **106**, 13410–13414.
- do Amaral, F.R., Sheldon, F.H., Gamauf, A., Haring, E., Riesing, M., Silveira, L.F. & Wajntal, A. (2009) Patterns and processes of diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). *Molecular Phylogenetics and Evolution*, **53**, 703–715.
- Baker, A.J., Pereira, S.L., Haddrath, O.P. & Edge, K.A. (2006) Multiple gene evidence for expansion of extant penguins out of Antarctica due to global cooling. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 11–17.
- Bininda Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007) The delayed rise of present day mammals. *Nature*, **446**, 507–512.
- Brock, C.D., Harmon, L.J. & Alfaro, M.E. (in press) Testing for temporal variation in diversification rates when sampling is incomplete and nonrandom. *Systematic Biology*.
- Brown, J.M. & Lemmon, A.R. (2007) The importance of data partitioning and the utility of Bayes factors in Bayesian phylogenetics. *Systematic Biology*, **56**, 643–655.
- 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**, 257–259.
- 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.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference*, 2nd edn. Springer Verlag, New York.
- Christidis, L., Schodde, R., Shaw, D.D. & Maynes, S.F. (1991) Relationships among the Australo Papuan parrots, lorikeets, and cockatoos (Aves, Psittaciformes): protein evidence. *Condor*, **93**, 302–317.
- Clarke, J.A., Tambussi, C.P., Noriega, J.I., Erickson, G.M. & Ketchum, R.A. (2005) Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature*, **433**, 305–308.
- Collar, N.J. (1998) Family Psittacidae (parrots). *Handbook of the birds of the world*, Vol. 4 (ed. by J. del Hoyo, A. Elliott and J. Sargatal), pp. 280–477. Lynx Edicions, Barcelona.
- Cooper, A. & Penny, D. (1997) Mass survival of birds across the Cretaceous Tertiary boundary: molecular evidence. *Science*, **275**, 1109–1113.
- Cooper, A., Lalueza Fox, C., Anderson, S., Rambaut, A., Austin, J. & Ward, R. (2001) Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature*, **409**, 704–707.
- Couvreur, T.L.P., Franzke, A., Al Shehbaz, I.A., Bakker, F.T., Koch, M.A. & Mummenhoff, K. (2010) Molecular phylogenetics, temporal diversification, and principles of evolution in the mustard family (Brassicaceae). *Molecular Biology and Evolution*, **27**, 55–71.
- Cracraft, J. (2001) Avian evolution, Gondwana biogeography and the Cretaceous Tertiary mass extinction event. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 459–469.
- Cusimano, N. & Renner, S.S. (2010) Slowdowns in diversification rates from real phylogenies may not be real. *Systematic Biology*, **59**, 458–464.
- 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**, 699–710.
- Ericson, P.G.P., Anderson, C.L., Britton, T., Elzanowski, A., Johansson, U.S., Kallersjö, 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.
- Erwin, T.L. (1981) Taxon pulses, vicariance, and dispersal: an evolutionary synthesis illustrated by carabid beetles. *Vicariance biogeography: a critique* (ed. by G. Nelson and D.E. Rosen), pp. 159–196. Columbia University Press, New York.
- Fariás, M., Charrier, R., Carretier, S., Martinod, J., Fock, A., Campbell, D., Caceres, J. & Comte, D. (2008) Late Miocene high and rapid surface uplift and its erosional response in the Andes of central Chile (33°–35° S). *Tectonics*, **27**, T1005. doi:10.1029/2006TC002046.
- Feduccia, A. (1995) Explosive evolution in Tertiary birds and mammals. *Science*, **267**, 637–638.
- Feduccia, A. (2003) 'Big bang' for tertiary birds? *Trends in Ecology and Evolution*, **18**, 172–176.
- Fjeldså, J. & Bowie, R.C.K. (2008) New perspectives on the origin and diversification of Africa's forest avifauna. *African Journal of Ecology*, **46**, 235–247.
- Fleming, T.H. & Muchhala, N. (2008) Nectar feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. *Journal of Biogeography*, **35**, 764–780.
- Forshaw, J.M. (1973) *Parrots of the world*. Landsdowne Press, Melbourne.
- Gaina, V., Roest, W.R., Muller, R.D. & Symonds, P. (1998) The opening of the Tasman sea: a gravity anomaly animation. *American Meteorological Society, AMS Journals Online, Earth Interactions*, **2**, 1–23.
- Garzone, C.N., Hoke, G.D., Libarkin, J.C., Withers, S., MacFadden, B., Eiler, J., Ghosh, P. & Mulch, A. (2008) Rise of the Andes. *Science*, **320**, 1304–1307.
- Goldberg, J., Trewick, S.A. & Powlesland, R.G. (2011) Population structure and biogeography of *Hemiphaga* pigeons (Aves: Columbidae) on islands in the New Zealand region. *Journal of Biogeography*, **38**, 285–298.
- Groombridge, J.J., Jones, C.G., Nichols, R.A., Carlton, M. & Bruford, M.W. (2004) Molecular phylogeny and morphological change in the *Psittacula* parakeets. *Molecular Phylogenetics and Evolution*, **31**, 96–108.
- Guntert, M. (1981) Morphologische Untersuchungen zur adaptiven Radiation des Verdauungstraktes bei Papageien (Psittaci). *Zoologische Jahrbucher. Abteilung für Anatomie und Ontogenie der Tiere*, **106**, 471–526.
- 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., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C. & Yuri, T. (2008) A phylogenomic study of birds reveals their evolutionary history. *Science*, **320**, 1763–1768.
- Haddrath, O. & Baker, A.J. (2001) Complete mitochondrial DNA genome sequences of extinct birds: ratite phylogenetics and the vicariance biogeography hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, **268**, 939–945.
- Halas, D., Zamparo, D. & Brooks, D.R. (2005) A historical biogeographical protocol for studying biotic diversification by taxon pulses. *Journal of Biogeography*, **32**, 249–260.
- Hall, R. (1998) The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. *Biogeography and geological evolution of SE Asia* (ed. by R. Hall and J.D. Holloway), pp. 99–131. Backhuys Publishers, Leiden.
- Hall, R. (2002) Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer based reconstructions, model and animations. *Journal of Asian Earth Sciences*, **20**, 353–431.
- Hall, T.A. (1999) BioEdit, a user friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, **41**, 95–98.

- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008) Geiger: investigating evolutionary radiations. *Bioinformatics*, **24**, 129–131.
- Harshman, J., Braun, E.L., Braun, M.J., Huddleston, C.J., Bowie, R.C.K., Chojnowski, J.L., Hackett, S.J., Han, K.L., Kimball, R.T., Marks, B.D., Miglia, K.J., Moore, W.S., Reddy, S., Sheldon, F.H., Steadman, D.W., Stepan, S.J., Witt, C.C. & Yuri, T. (2008) Phylogenomic evidence for multiple losses of flight in ratite birds. *Proceedings of the National Academy of Sciences USA*, **105**, 13462–13467.
- Hedges, S.B., Parker, P.H., Sibley, C.G. & Kumar, S. (1996) Continental breakup and the ordinal diversification of birds and mammals. *Nature*, **381**, 226–229.
- Hillis, D.M. & Bull, J.J. (1993) An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Systematic Biology*, **42**, 182–192.
- Ho, S.Y.W. & Phillips, M.J. (2009) Accounting for calibration uncertainty in phylogenetic estimation of evolutionary divergence times. *Systematic Biology*, **58**, 367–380.
- Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17**, 754–755.
- Hugall, A.F., Foster, R. & Lee, M.S.Y. (2007) Calibration choice, rate smoothing, and the pattern of tetrapod diversification according to the long nuclear gene RAG 1. *Systematic Biology*, **56**, 543–563.
- Jacobs, B.F., Kingston, J.D. & Jacobs, L.L. (1999) The origin of grass dominated ecosystems. *Annals of the Missouri Botanical Garden*, **86**, 590–643.
- Jonsson, K.A., Irestedt, M., Fuchs, J., Ericson, P.G.P., Christidis, L., Bowie, R.C.K., Norman, J.A., Pasquet, E. & Fjeldså, J. (2008) Explosive avian radiations and multi directional dispersal across Wallacea: evidence from the Campephagidae and other crown Corvidae (Aves). *Molecular Phylogenetics and Evolution*, **47**, 221–236.
- Jonsson, K.A., Bowie, R.C.K., Nylander, J.A.A., Christidis, L., Norman, J.A. & Fjeldså, J. (2010) Biogeographical history of cuckoo shrikes (Aves: Passeriformes): transoceanic colonization of Africa from Australo Papua. *Journal of Biogeography*, **37**, 1767–1781.
- Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773–795.
- 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.
- Leeton, P.R.J., Christidis, L., Westerman, M. & Boles, W.E. (1994) Molecular phylogenetic affinities of the night parrot (*Geopsittacus occidentalis*) and the ground parrot (*Pezoporus wallicus*). *The Auk*, **111**, 833–843.
- Li, Z.X. & Powell, C.M. (2001) An outline of the palaeogeographic evolution of the Australasian region since the beginning of the Neoproterozoic. *Earth Science Reviews*, **53**, 237–277.
- Livezey, B.C. & Zusi, R.L. (2007) Higher order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society*, **149**, 1–95.
- Maddison, W.P. & Maddison, D.R. (2009) *Mesquite: a modular system for evolutionary analysis. Version 2.72*. Available at: <http://mesquiteproject.org>.
- Martin, H.A. (2006) Cenozoic climatic change and the development of the arid vegetation in Australia. *Journal of Arid Environments*, **66**, 533–563.
- Mata, H., Fontana, C.S., Mauricio, G.N., Bornschein, M.R., de Vasconcelos, M.F. & Bonatto, S.L. (2009) Molecular phylogeny and biogeography of the eastern tapaculos (Aves: Rhinocryptidae: *Scytalopus*, *Eleoscytalopus*): cryptic diversification in Brazilian Atlantic Forest. *Molecular Phylogenetics and Evolution*, **53**, 450–462.
- Mayr, G. (2005) The Paleogene fossil record of birds in Europe. *Biological Reviews*, **80**, 515–542.
- Mayr, G. (2008) The phylogenetic affinities of the parrot taxa *Agapornis*, *Loriculus* and *Melopsittacus* (Aves: Psittaciformes): hypotarsal morphology supports the results of molecular analyses. *Emu*, **108**, 23–27.
- Mayr, G. (2009) *Paleogene fossil birds*. Springer Verlag, Berlin.
- Moyle, R.G. (2005) Phylogeny and biogeographical history of Trogoniformes, a pantropical bird order. *Biological Journal of the Linnean Society*, **84**, 725–738.
- Muller, K. (2005) SeqState: primer design and sequence statistics for phylogenetic DNA data sets. *Applied Bioinformatics*, **4**, 65–69.
- Muller, K. (2006) Incorporating information from length mutational events into phylogenetic analysis. *Molecular Phylogenetics and Evolution*, **38**, 667–676.
- Nee, S., Holmes, E.C., May, R.M. & Harvey, P.H. (1994) Extinction rates can be estimated from molecular phylogenies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **344**, 77–82.
- Newton, I. (2003) *The speciation and biogeography of birds*. Academic Press, London.
- Nishihara, H., Maruyama, S. & Okada, N. (2009) Retroposon analysis and recent geological data suggest near simultaneous divergence of the three superorders of mammals. *Proceedings of the National Academy of Sciences USA*, **106**, 5235–5240.
- Nylander, J.A.A. (2004) *MrModeltest v2*. Evolutionary Biology Centre, Uppsala University, Sweden.
- Nylander, J.A.A., Wilgenbusch, J.C., Warren, D.L. & Swofford, D.L. (2008) AWTY (are we there yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics*, **24**, 581–583.
- Olson, S.L. & Feduccia, A. (1980) Relationships and evolution of flamingos (Aves: Phoenicopteridae). *Smithsonian Contributions to Zoology*, **316**, 1–73.
- Pacheco, M.A., Battistuzzi, F.U., Lentino, M., Aguilar, R., Kumar, S. & Escalante, A.A. (2011) Evolution of modern birds revealed by mitogenomics: timing the radiation and origin of major orders. *Molecular Biology and Evolution*, **28**, 1927–1942.
- Patane, J.S.L., Weckstein, J.D., Aleixo, A. & Bates, J.M. (2009) Evolutionary history of *Ramphastos* toucans: molecular

- phylogenetics, temporal diversification, and biogeography. *Molecular Phylogenetics and Evolution*, **53**, 923–934.
- Pereira, S.L. & Baker, A.J. (2006) A mitogenomic timescale for birds detects variable phylogenetic rates of molecular evolution and refutes the standard molecular clock. *Molecular Biology and Evolution*, **23**, 1731–1740.
- Pereira, S.L. & Baker, A.J. (2008) DNA evidence for a Paleocene origin of the Alcidae (Aves: Charadriiformes) in the Pacific and multiple dispersals across northern oceans. *Molecular Phylogenetics and Evolution*, **46**, 430–445.
- Pereira, S.L., Johnson, K.P., Clayton, D.H. & Baker, A.J. (2007) Mitochondrial and nuclear DNA sequences support a cretaceous origin of Columbiformes and a dispersal driven radiation in the Paleogene. *Systematic Biology*, **56**, 656–672.
- 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**, 90–107.
- 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**, 313–326.
- Price, T. (2008) *Speciation in birds*. Roberts and Company, Greenwood Village, CO.
- Pybus, O.G. & Harvey, P.H. (2000) Testing macro evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 2267–2272.
- Rabosky, D.L. (2006a) Laser: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evolutionary Bioinformatics Online*, **2**, 257–260.
- Rabosky, D.L. (2006b) Likelihood methods for detecting temporal shifts in diversification rates. *Evolution*, **60**, 1152–1164.
- Rabosky, D.L. (2010) Extinction rates should not be estimated from molecular phylogenies. *Evolution*, **64**, 1816–1824.
- Rabosky, D.L., Donnellan, S.C., Talaba, A.L. & Lovette, I.J. (2007) Exceptional among lineage variation in diversification rates during the radiation of Australia's most diverse vertebrate clade. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2915–2923.
- Rambaut, A. (2008) *Figtree 1.2*. Published by the author. Available at: <http://tree.bio.ed.ac.uk/software/figtree/>.
- Rambaut, A. & Drummond, A.J. (2007) *Tracer v1.4*. Available at: <http://beast.bio.ed.ac.uk/tracer>.
- Ree, R.H. & Sanmartin, I. (2009) Prospects and challenges for parametric models in historical biogeographical inference. *Journal of Biogeography*, **36**, 1211–1220.
- Ree, R.H. & Smith, S.A. (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, **57**, 4–14.
- Ree, R.H., Moore, B.R., Webb, C.O. & Donoghue, M.J. (2005) A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, **59**, 2299–2311.
- Ribas, C.C., Gaban Lima, R., Miyaki, C.Y. & Cracraft, J. (2005) Historical biogeography and diversification within the Neotropical parrot genus *Pionopsitta* (Aves: Psittacidae). *Journal of Biogeography*, **32**, 1409–1427.
- Ribas, C.C., Moyle, R.G., Miyaki, C.Y. & Cracraft, J. (2007) The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2399–2408.
- Ribas, C.C., Miyaki, C.Y. & Cracraft, J. (2009) Phylogenetic relationships, diversification and biogeography in Neotropical *Brotogeris* parakeets. *Journal of Biogeography*, **36**, 1712–1729.
- Richardson, K.C. & Wooller, R.D. (1990) Adaptation of the alimentary tract of some Australian lorikeets to a diet of pollen and nectar. *Australian Journal of Zoology*, **38**, 581–586.
- Ricklefs, R.E., Losos, J.B. & Townsend, T.M. (2007) Evolutionary diversification of clades of squamate reptiles. *Journal of Evolutionary Biology*, **20**, 1751–1762.
- Ronquist, F. & Huelsenbeck, J.P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, **19**, 1572–1574.
- Rowley, I. (1998) Family Cacatuidae (cockatoos). *Handbook of the birds of the world* (ed. by J. del Hoyo, A. Elliott and J. Sargatal), pp. 246–279. Lynx Edicions, Barcelona.
- Ruddiman, W.F. & Kutzbach, J.E. (1990) Late Cenozoic plateau uplift and climate change. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **81**, 301–314.
- Schodde, R. (2006) Australia's bird fauna today: origins and evolutionary development. *Evolution and biogeography of Australasian vertebrates* (ed. by J.R. Merrick, M. Archer, G.M. Hickey and M.S.Y. Lee), pp. 413–458. Auscub, Sydney.
- Schweizer, M., Seehausen, O., Guntert, 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.
- Shevenell, A.E., Kennett, J.P. & Lea, D.W. (2004) Middle Miocene Southern Ocean cooling and Antarctic cryosphere expansion. *Science*, **305**, 1766–1770.
- Simmons, M.P. & Ochoterena, H. (2000) Gaps as characters in sequence based phylogenetic analyses. *Systematic Biology*, **49**, 369–381.
- Slack, K.E., Jones, C.M., Ando, T., Harrison, G.L., Fordyce, R.E., Arnason, U. & Penny, D. (2006) Early penguin fossils, plus mitochondrial genomes, calibrate avian evolution. *Molecular Biology and Evolution*, **23**, 1144–1155.
- Smith, G.A. (1975) Systematics of parrots. *Ibis*, **117**, 18–68.
- Smith, G.A. (1981) The origin of Philippine parrots and the relationships of the guaiabero *Bolbopsittacus lunulatus*. *Ibis*, **123**, 345–349.
- Smith, T.B., Schneider, C.J. & Holder, K. (2001) Refugial isolation versus ecological gradients. *Genetica*, **112**, 383–398.

- Smith, T.B., Calsbeek, R., Wayne, R.K., Holder, K.H., Pires, D. & Bardeleben, C. (2005) Testing alternative mechanisms of evolutionary divergence in an African rain forest passerine bird. *Journal of Evolutionary Biology*, **18**, 257–268.
- Stamatakis, A. (2006) RAxML VI HPC: maximum likelihood based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.
- Stamatakis, A., Hoover, P. & Rougemont, J. (2008) A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology*, **57**, 758–771.
- Suchard, M.A., Weiss, R.E. & Sinsheimer, J.S. (2001) Bayesian selection of continuous time Markov chain evolutionary models. *Molecular Biology and Evolution*, **18**, 1001–1013.
- Swofford, D.L. (2001) *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0*. Sinauer Associates, Sunderland, MA.
- Tavares, E.S., Baker, A.J., Pereira, S.L. & Miyaki, C.Y. (2006) Phylogenetic relationships and historical biogeography of Neotropical parrots (Psittaciformes: Psittacidae: Arini) inferred from mitochondrial and nuclear DNA sequences. *Systematic Biology*, **55**, 454–470.
- Tennyson, A.J.D. (2010) The origin and history of New Zealand's terrestrial vertebrates. *New Zealand Journal of Ecology*, **34**, 6–27.
- Thomas, G.H., Orme, C.D.L., Davies, R.G., Olson, V.A., Bennett, P.M., Gaston, K.J., Owens, I.P.F. & Blackburn, T.M. (2008) Regional variation in the historical components of global avian species richness. *Global Ecology and Biogeography*, **17**, 340–351.
- 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.
- Upchurch, P. (2008) Gondwanan break up: legacies of a lost world? *Trends in Ecology and Evolution*, **23**, 229–236.
- Waters, J.M. & Craw, D. (2006) Goodbye Gondwana? New Zealand biogeography, geology, and the problem of circularity. *Systematic Biology*, **55**, 351–356.
- Weir, J.T. (2006) Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. *Evolution*, **60**, 842–855.
- Wilgenbusch, J.C., Warren, D.L. & Swofford, D.L. (2004) AWTY: a system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. Available at: <http://ceb.csit.fsu.edu/awty> (accessed 31 January 2011).
- Wright, T.F., Schirtzinger, E.E., Matsumoto, T., Eberhard, J.R., Graves, G.R., Sanchez, J.J., Capelli, S., Mueller, H., Scharpegge, J., Chambers, G.K. & Fleischer, R.C. (2008) A multilocus molecular phylogeny of the parrots (Psittaciformes): support for a Gondwanan origin during the Cretaceous. *Molecular Biology and Evolution*, **25**, 2141–2156.

- Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.
- Zhisheng, A., Kutzbach, J.E., Prell, W.L. & Porter, S.C. (2001) Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since late Miocene times. *Nature*, **411**, 62–66.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Species sampled, museum and collection numbers, GenBank accession numbers for the three genes analysed, and sample type.

Appendix S2 Laboratory methods.

Appendix S3 Sequence characteristics and model parameters.

Appendix S4 Maximum parsimony tree of parrots and other avian taxa.

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