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evolution using secondary calibrations derived from studies with broader taxon sampling using these deep fossils rather than biogeographic calibrations (Pratt et al. 2009; Schweizer et al. 2011; White et al. 2011).

Passerines have also been difficult to resolve morphologically, because convergent evolution in life history traits in this

nuclear contigs, as these gave scores lower than 150 when aligned to the mitochondrial reference genomes. For all species, Geneious 6.1.7 (Biomatters Ltd, www.geneious.com, last accessed July 2015), was used to align the assembled contigs against reference genomes (supplementary tables S2 and S3, Supplementary Material online), typically using "map to reference" with medium-low sensitivity. Contig overlaps were identified and contigs were

adjacent to gaps, the ND6 (light-strand encoded), noncoding regions, and stop codons (often incomplete in the DNA sequence), were excluded from the alignment. Conserved amino acids or stem columns were used to define the boundaries of ambiguous regions next to gaps. The third position of protein-coding genes have been coded as RY. RY recoding of third codons increases the proportion of observable changes on internal branches of the tree (treeness) and decreases the differences in nucleotide composition (relative compositional variability; e.g., Harrison et al. 2004; Gibb et al. 2007; Phillips et al. 2010). The full data set is 13,837 bp long and is separated into five partitions: three codon positions, and RNA stems and loops. The best partitioning and models were found using Bayesian information criterion model selection with a greedy search scheme and unlinked branch lengths in PartitionFinder (Lanfear et al. 2012), which recommended three final partitions: first codons plus loops, second codons plus stems, and third codons. These three partitions were used in all subsequent analyses. Alignments and trees can be downloaded from TreeBASE (TB2:15732).

Data were analyzed using maximum likelihood (ML) methods implemented in RAxML (Stamatakis et al. 2008), using a general time reversible model with gamma distribution (GTR + G). Bayesian analyses were performed using MrBayes (Huelsenbeck and Ronquist 2001) using GTR + I + G. Data sets were run for 10 million generations, and sampled every 2,500 generations after a burnin of 1,000,000 generations. Independent runs were checked for convergence, and trace files analyzed using Tracer (Rambaut and Drummond 2003) to ensure effective sample size (ESS) values greater than 200. Trees were viewed using Figtree v1.4 (http://tree.bio.ed.ac.uk/software/figtree/ [accessed June 2015]).

The data were also analyzed using the CAT–GTR mixture model of PhyloBayes-MPI 1.5a (Lartillot et al. 2013) with no RY coding, and constant sites removed. Two independent chains were run for 26,700 iterations and checked for convergence in likelihood and model parameters (tracecomp subprogram) and clade posterior probability (bpcomp subprogram). The first 10% of trees were discarded as burnin and a 50% majority rule Bayesian consensus tree with associated posterior probabilities was computed from the remaining trees using bpcomp.

Dating

Dated analyses were performed using BEAST and BEAUTI v1.8.0 (Drummond et al. 2012) with the data set partitioned as above. An uncorrelated relaxed clock model was used with rates among branches distributed according to a lognormal distribution. The tree prior used a speciation birth–death process. Nucleotide partitions used an estimated GTR + I + G model with the at-gc scale operators and delta exchange removed for the RY coded partition. To circumvent the use of the problematic *A* biogeographic calibration, we chose indirect calibrations from recent published data sets that also included some passerines and used widely accepted fossil calibrations. The root prior had a normal distribution with mean 70 Ma, SD 9 Ma. All passerines excluding *A* had a normal distribution with mean 62 Ma, SD 10 Ma. These calibrations are based on the results of Schweizer et al. (2011) and are very similar to other recent publications (White et al. 2011; Jetz et al. 2012). Schweizer et al. (2011) used the penguin fossil *W* as a calibration for the split between Sphenisciformes and other seabirds (Slack et al. 2007). This calibration used a mean of 66 Ma (SD 3.06) with normal distribution. The lower bound takes into account potential dating errors of the fossil, and the upper bound allows for putative members of Gaviiformes (loons) from the late Cretaceous. In addition they tested uniform and

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Passerine Radiation Dates and Calibrations Used in a Selection of Recent Studies

Avian Studies							
Pratt et al. (2009)	61.05	50–70[a]	57.26	48–67[a]	Y	N	Focused on broad range of birds including passerines
Schweizer et al. (2011)	70.36	52.6–88.13	62.4	45.5–79.7	Y	N	Focused on parrots but uses broad range of birds for dating including passerines.
White et al. (2011)	68.03	55–82[a]	63.95	51–78[a]	Y	N	Focused on parrots but uses broad range of birds for dating including passerines.
Pacheco et al. (2011)	78.5	71–85[a]	74.9	—	Y	Y	Includes broad range of birds. Dating includes NZ wrens calibration
Jetz et al. (2012)	70[a]	—	66.8	—	Y	N	Supertree study. Soft maximum bounds on most calibrations of 110 Ma.
Jarvis et al. (2014)	39[a]	32–43[a]	32[a]	27–36[a]	Y	N	Primarily uses conservative (i.e. young) minimum bounds with no maximum. The surprisingly young passerine split requires further investigation.
Passerine Studies							
Barker et al. (2004)	82	—	77–76	—	NA	Y	Dating primarily calibrated using NZ wrens split.
Jønsson et al. (2011)	—	—	80[a]	—	NA	Y	Calibrations based on Barker et al. (2004).
Kennedy et al. (2012)	44[a]	—	4 t		0	5 . 6 0 3 8 4	

avian evolution improves, so will our calibrations for the timing of passerine evolution. The basic structure of the passerine tree appears to be consistent across many studies, and as different calibrations are applied to the tree, the branch lengths will shrink or expand proportionately. The recent work of Jarvis et al. (2014) used 1,156 clocklike exons to examine avian evolution, and found a much more recent timing for the radiation of Passerines (~39 Ma, table 2).

Many studies of passerines have been calibrated using the rifting of New Zealand and Australia around 82 Ma for the separation of Acanthisittidae from other passerines (table 2). We find no evidence to support this suggestion. Our study, which calibrates passerine evolution using secondary calibrations of the basal nodes from previous more widely sampled studies that used well-defined fossil calibrations, avoids this problem and allows us to more realistically begin to interpret passerine evolution and biogeography. We find crown group Passeriformes began diverging in the early Paleocene, with major expansion of the speciose oscine lineages during the Oligocene.

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