Morphological Clocks in Paleontology, and a Mid-Cretaceous Origin of Crown Aves

MICHAEL S.Y. LEE[1,2,*], ANDREA CAU[3], DARREN NAISH[4], AND GARETH J. DYKE[4]

[1]*Earth Sciences Section, South Australian Museum, North Terrace, Adelaide 5000, Australia;* [2]*School of Earth and Environmental Sciences, University of Adelaide 5005, Australia;* [3]*Museo Geologico e Paleontologico "Giovanni Capellini", Via Zamboni 63, 40126 Bologna, Italy; and* [4]*Ocean and Earth Science, University of Southampton, Southampton SO14 3ZH, UK*
Correspondence to be sent to: E-mail: mike.lee@samuseum.sa.gov.au.

Birds are among the most diverse and intensively studied vertebrate groups, but many aspects of their higher-level phylogeny and evolution still remain controversial. One contentious issue concerns the antiquity of modern birds (=crown Aves): the age of the most recent common ancestor of all living birds (Gauthier 1986). Very few Mesozoic fossils are attributable to modern birds (e.g., Clarke et al. 2005; Dyke and Kaiser 2011; Brocklehurst et al. 2012; Ksepka and Boyd 2012) suggesting that they diversified largely or entirely in the early Paleogene, perhaps in the ecological vacuum created by the extinction of non-avian dinosaurs, pterosaurs, and many archaic (stem) birds (e.g., Longrich et al. 2011). In contrast, molecular studies indicate that modern birds commenced radiating deep within the Mesozoic, for example ∼130 Ma (Cooper and Penny 1997; Haddrath and Baker 2012) or ∼113 Ma (Jetz et al. 2012), with ratites, galliforms, anseriforms, shorebirds, and even passerines surviving across the KPg boundary (∼66 Ma). The oldest molecular dates further imply an extraordinarily rapid early bird evolution, with the modern birds appearing only 20 myr after *Archaeopteryx* (∼150 Ma). However, both approaches entail considerable uncertainties: for example, nonpreservation of fossils always underestimates the antiquity of lineages, whereas rate heterogeneity, saturation, and calibration uncertainty can strongly bias molecular divergence dating.

One major shortcoming of the paleontological approach to this debate has been subjective approaches for inferring divergence dates on fossil phylogenies. Typically, an undated tree topology is first inferred, often using parsimony, and then the oldest known fossils for various clade are used to set a (hard) minimum ages for those clades. Divergence times are then either: (i) enforced onto the rest of tree in order to minimize ghost lineages, or (ii) pushed slightly deeper in time based on a range of nonphylogenetic criteria. The first approach is repeatable but always results in the youngest possible divergence dates (e.g., see O'Leary et al. 2013),

an assumption which is frequently difficult to justify (Brusatte 2011). For instance, the divergence date of two 100 million-year-old fossil taxa would be set at 100 Ma—even though this implies zero-length branches and infinitely fast evolutionary rates (e.g., Hunt and Carrano 2010), and extreme phenotypic differences might suggest a rather earlier divergence. The second approach can be *ad hoc*, as there are several ways to extend lineage durations beyond the absolute minimum: often these extensions are arbitrary guesses, but newer methods use estimates based on sampling/preservation rates, or adding a constant interval to the base of every lineage or node, or "borrowing" time by extending selected divergences downwards with concomitant reduction of the duration of the immediately preceding stem lineages (Brusatte 2011; Bapst 2012). All dated bird chronograms based on the fossil record to date have been created using such methods (e.g., van Tuinen et al. 2006; Dyke and Kaiser 2011).

Methods originally developed for molecular divergence dating (Ronquist et al. 2012a) provide a quantitative means to infer divergence dates on paleontological trees, using explicitly phylogenetic information, but have rarely been used in the latter context. These Bayesian methods simultaneously infer best supported tree topologies, branch lengths, and divergence dates by using likelihood models of trait evolution, and relaxed-clock models to accommodate variation in evolutionary rates across branches. In a morphological/paleontological context, these methods can estimate divergence dates across trees by reconstructing the duration of "ghost" lineages (leading to each fossil or recent terminal taxon), using the rate and inferred amount of morphological evolution along that lineage. Thus, a divergence date between two 100 million-year-old fossil taxa would be estimated as only slightly earlier if they are morphologically similar, and substantially earlier if highly phenotypically distinct. In this article, we apply these new methods to an updated data set of living and fossil birds, in order to quantify

the paleontological signal for the age of modern (crown) birds.

Surprisingly, "total evidence dating" has until now been used exclusively to calibrate combined morphological and molecular data sets, containing fossil and living taxa (e.g., Pyron 2011; Ronquist et al. 2012a). However, the approach is obviously also applicable for data sets consisting of only morphological data—including those consisting mostly or entirely of fossil taxa. We employ a morphological clock analysis of a paleontological data set of Mesozoic and extant birds, to estimate divergence dates for modern (crown) Aves. We also test whether a key assumption of clock models and "total evidence dating"—that younger taxa should have undergone more anagenesis—holds in morphological data, which potentially undergoes much more episodic evolution than does molecular data.

Materials and Methods

Phylogenetic and Stratigraphic Data

The data set consists of 247 characters sampled across 64 bird taxa, and is based on the most comprehensive phylogenetic study of Mesozoic birds (O'Connor and Zhou 2012). It has been expanded with the addition of some extra characters and several Paleogene and extant taxa, namely *Gallinuloides, Lithornis, Waimanu, Columba*, and *Crypturellus*. Stratigraphic dates for each fossil taxon were obtained from the literature, mostly from recent primary sources. See SI_1 for stratigraphic dates and sources, SI_2 for additions and modifications to the original matrix, and SI_3 for new matrix. The tree was rooted on the branch between dromaeosaurs and birds, as the most recent studies tend to support the traditional assumption of the monophyly of all birds (including *Archaeopteryx*: see Lee and Worthy 2011; Godefroit et al. 2013).

Morphological Clock Analyses

MrBayes 3.2 (Ronquist et al. 2012b) can simultaneously infer phylogenetic relationships and divergence dates for data sets consisting of fossil and living taxa, using morphological data. Unlike other likelihood or Bayesian programs (e.g., RaxML, BEAST), it can readily correct for an ascertainment bias common in morphological data sets: omission of "parsimony uninformative" characters (those which are either invariant or unique to a single terminal taxon). Such corrections are also possible in principle with BEAST, but require specifying all unrecorded (invariant and autapomorphic patterns), which will be very numerous for multistate data (Gray et al. 2011). In the present analyses, all characters were treated as ordered or unordered as per O'Connor and Zhou (2012); the exception was character 64 (number of ankylosed sacral vertebrae), which was originally ordered but possessed >6 states and thus had to be left unordered due to constraints in MrBayes. There was

significant variation in evolutionary rates across traits, and across branches, according to Bayes Factors *sensu* Kass and Raftery (1995), that is twice the difference in marginal $\log_n$-likelihoods (hereafter abbreviated BF_{KR}). BF_{KR} was calculated using stepping stone analyses (Ronquist et al. 2012b). Use of the gamma parameter for modeling rate variation across traits was favored over assuming all characters evolved at the same rate ($BF_{KR} \sim 110$), and an uncorrelated (igr) relaxed clock for modeling rate variation across branches was favored over both an autocorrelated (tk02) relaxed clock ($BF_{KR} \sim 120$) and a strict clock ($BF_{KR} \sim 220$). However, analyses were performed with optimal (igr) and suboptimal (tk02) relaxed-clock models to investigate the influence of different clock models.

Three alternative maximum age constraints for root (Paraves) were employed, each broadly consistent with the fossil evidence. Paraves is almost certainly no older than 200 Ma, as this exceeds the age of the oldest potential representatives of a much more inclusive clade Tetanurae (e.g., *Cryolophosaurus* (Benson 2010) and *Eshanosaurus* (Barrett 2009)). Some questionable paravian footprints exist at 168.3 Ma (Murdoch et al. 2011), but the earliest unequivocal paravian fossils include forms such as *Anchiornis, Aurornis*, and *Xiaotingia* at ~159 Ma (e.g., Xu et al. 2011; Godefroit et al. 2013). Accordingly, we employ a "loose" hard constraint at 200 Ma (which allows for the age of Paraves to substantially pre-date their earliest fossils), a "tight" hard constraint at 168.3 Ma (which assumes the age of Paraves is close to the age of their earliest fossils), and a soft constraint which places decreasing but nonzero probability on successively older ages (offset exponential with 5% of distribution between 168.3 Ma and infinity). All these differing root assumptions returned similar results.

Because this data set did not focus on modern (crown) birds, it might not have adequately sampled character changes on branches leading to, and within, extant birds. To evaluate whether increased sampling of characters variable within modern birds might affect the results, both analyses were repeated with 20 and with 50 "dummy" synapomorphies added for each of the three (nested) clades of extant birds (*Crypturellus*(*Columba*(*Gallus, Anas*))). Extinct birds that are likely or potentially within some of these clades (*Lithornis, Gallinuloides, Waimanu* and *Vegavis*) were coded as ? for these characters, to prevent them from being excluded from the relevant clade(s). Ideally, future studies should more thoroughly sample these characters empirically. Adding "dummy" autapomorphies for modern bird taxa (or any terminals) would not be meaningful, as MrBayes excludes all autapomorphic characters when correcting for the ascertainment bias found in most in morphological data sets (see above).

Because many clades were weakly supported, both in modern birds and throughout the tree in general (see Results section), additional analyses were performed with (i) relationships within modern birds constrained to conform to accepted topologies (Dyke and Kaiser

TABLE 1. Divergence dates for birds (Avialae *sensu* Gauthier 1986) and modern birds (crown Aves), inferred from analyses of morphological and stratigraphic data from fossil and living birds, using two different (uncorrelated igr/autocorrelated tk02) clock models and various soft and hard root age constraints

Clock mode	Analysis	Birds (*Archaeopteryx* node)	Modern birds (Crown Aves)
Uncorrelated clock (independent gamma rates)	Root: soft upper bound[a]	177.81 (157.66–204.35)	110.24 (87.10–137.58)
	Root: hard upper bound 168.3Ma	165.28 (159.21–168.22)	103.90 (85.93–124.77)
	Root: hard upper bound 200Ma*	191.61 (176.29–199.84)	115.93 (91.68–141.88)
	" - apomorphies 20[b]	191.65 (176.23–199.81)	116.22 (90.51–143.16)
	" - apomorphies 50[b]	190.88 (174.43–199.80)	118.17 (87.48–150.45)
	" - modern birds constrained[c]	191.97 (177.26–199.92)	116.59 (92.93–141.37)
	" - unstable taxa deleted[d]	190.82 (175.22–199.90)	116.82 (93.43–142.22)
	" - no Paleogene fossils[e]	185.21 (167.50–199.58)	61.13 (29.08–94.50)
Autocorrelated clock (Thorne-Kishino 2002)	Root: soft upper bound[a]	155.07 (150.01–166.53)	99.97 (89.1–110.56)
	Root: hard upper bound 168.3Ma	158.51 (150.94–167.19)	99.75 (88.9–110.48)
	Root: hard upper bound 200Ma	164.82 (150.49–192.56)	94.77 (82.73–107.23)
	" - apomorphies 20[b]	154.87 (150.01–165.82)	91.70 (79.12–106.83)
	" - apomorphies 50[b,f]	152.32 (150.01–156.71)	83.76 (73.08–99.13)
	" - modern birds constrained[c]	158.20 (150.02–175.56)	98.59 (88.57–107.56)
	" - unstable taxa deleted[d]	157.32 (150.00–177.83)	99.03 (87.80–109.03)
	" - no Paleogene fossils[e,g]	178.83 (157.50–199.23)	60.99 (34.40–84.62)

Notes: Median age estimate (and 95% HPD) are presented. Additional sensitivity analyses performed on the analyses with a hard 200 Ma root were (simulated) inclusion of additional synapomorphies within crown Aves, constraining modern birds to conform to broadly accepted relationships, deletion of unstable wildcard taxa, and exclusion of Paleogene crown Aves.
*Indicates analysis depicted in Figure 1.
[a]Exponential (lower bound = 150.1 Ma, mean = 156.17 Ma, 5% of distribution >168.3 Ma).
[b]Matrix modified by adding 20 or 50 dummy apomorphies along each clade of extant birds. (to simulate increased sampling of characters in this clade).
[c](*Crypturellus*, *Lithornis*)((*Columba*, *Waimanu*)(*Anas*, *Gallus*, *Gallinuloides*, *Vegavis*)).
[d]Excluded taxa: *Vorona*, *Hollanda*, *Shenqiornis*, *Liaoningornis*, *Chaoyangia* and *Zhongjianornis*.
[e]Excluded taxa: *Gallinuloides* ∼55 Ma, *Waimanu* ∼59 Ma, *Lithornis* ∼55.8 Ma.
[f]Burn-in extended to 0.4 (from standard 0.25).
[g]Burn-in extended to 0.3 (from standard 0.25).

2011; Ksepka and Boyd 2012; Naish 2012; see Table 1, footnote c), and (ii) exclusion of unstable, wildcard taxa identified using RogueNaRok (Aberer et al. 2012; see Table 1, footnote d). To test the impact of Paleogene crown birds (*Lithornis, Waimanu, Gallinuloides*), analyses were also performed with these taxa excluded. Finally, to investigate whether the tree topologies retrieved were sensitive to clock models and stratigraphic dates, standard undated Bayesian analyses (without any age data or clock models) were also performed.

One major assumption of clock models and "total evidence dating" that needs to be tested is that younger taxa should have undergone more evolutionary change, or anagenesis (Ho et al. 2011). For each taxon, the stratigraphic age, and amount of anagenesis (root-to-tip pathlength in undated Bayesian analysis) was determined; the relationship between these two variables was then assessed using phylogenetically uncorrected and corrected comparisons.

Analyses used the parallel version of MrBayes (Ronquist et al. 2012b) installed on the e-Research SA HPC computer grid (www.eresearchsa.edu.au/hpc_guides). Each analysis used four replicate runs of 40 million generations, with sampling every 4000 generations; each run consisted of one unheated and three incrementally heated chains. A burn-in of 25% was sufficient for most analyses, but some runs required slightly longer burn-ins (Table 1, footnote f). Within each analysis, all replicate runs converged on

virtually identical tree topologies (standard deviation of clade frequencies across runs <0.02) and parameters (essentially identical traces, with PRSF close to 1.0). The majority-rule consensus tree was generated from combined postburn-in samples of all four replicate runs. Exact parameter settings in MrBayes commands are included in the data matrix (SI_3).

RESULTS AND DISCUSSION

All analyses of the full taxon set gave highly concordant dates for the diversification of modern birds (crown Aves) centered on the Albian, middle Cretaceous (Table 1; Figs. 1 and 2). The median dates range between 94.77 and 115.93 Ma, and the younger limit of the 95% highest posterior density (HPD) is always well within the Mesozoic (73.08–91.68 Ma), thus excluding a Paleogene (<66 Ma) age for modern birds. The deep inferred age of crown Aves is robust to clock models, root age assumptions, and character sampling (Table 1). The (optimal) uncorrelated igr and (suboptimal) autocorrelated tk02 clock models yielded similar dates for crown birds, though the igr clock typically gave wider HPDs (38.84–62.97 Ma) than the tk02 clock (21.46–27.71 Ma). The 95% HPDs for deeper nodes bracketed largely or entirely by fossil taxa are not wider than for nodes near or within crown Aves: although missing data might be expected to generate
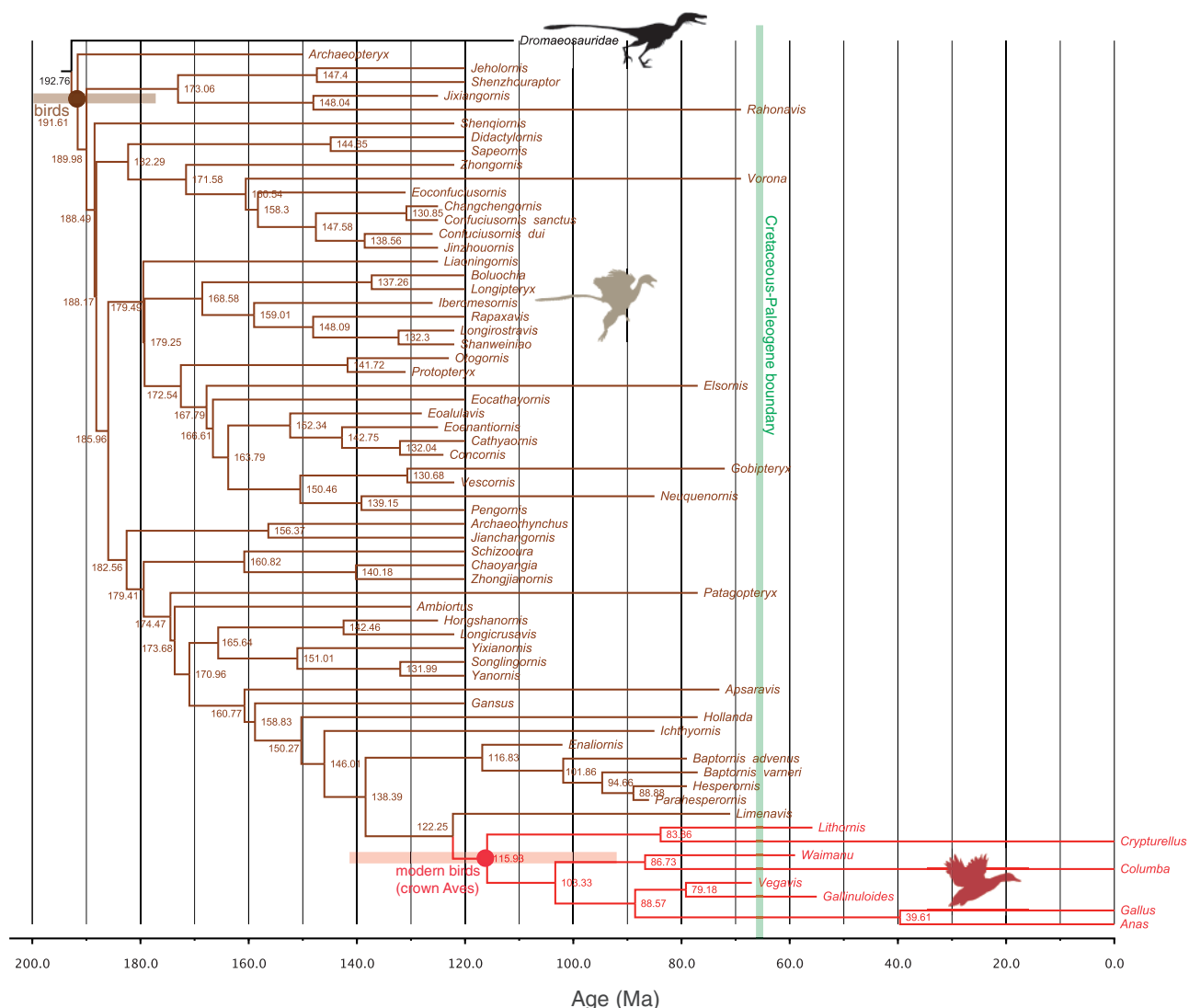
FIGURE 1.   Dated evolutionary tree of birds, from a Bayesian relaxed-clock phylogenetic analysis of fossil and living birds (expanded from O'Connor and Zhou 2012), with an independent gamma clock and root age (Paraves) constrained to <200 Ma (see * in Table 1). Numbers at nodes refer to median ages, and shaded bars indicate the 95% HPD interval for birds (Avialae *sensu* Gauthier 1986) and modern birds (crown Aves). Color codings (pdf version): black = out-group, brown = birds excluding crown Aves, red = crown Aves.

widen HPDs for more basal nodes, their HPDs are truncated at the younger end by the age of included fossils (each node must pre-date the oldest included fossil) and at the older end by the root constraint (each node must postdate the root age).

Changing the maximum constraint on root age (hard 200 Ma, hard 168.3 Ma, or soft exponential) most affected divergence dates near the base of the tree; however, dates higher up the tree (including crown Aves) remained more stable. Finally, (simulated) increased character sampling across modern birds did not substantially increase inferred divergence dates for crown Aves (Table 1).

The morphological and paleontological data, therefore, support molecular inferences that modern birds evolved deep in the Cretaceous. The mid-Cretaceous age for crown Aves inferred here is slightly

younger than the lower Cretaceous age proposed by many (especially earlier) molecular studies, for example ~130 Ma (e.g., Cooper and Penny 1997; Haddrath and Baker 2012), but highly consistent with the most recent and comprehensive dated molecular phylogeny of birds, ~113.2 Ma (Jetz et al. 2012). The current estimate implies a substantial >40 Ma lag between the origin of birds (theropods with forewing-powered flight, first represented by the ~150 Ma *Archaeopteryx*) and the origin of modern birds (Table 1; Figs. 1 and 2). This interval is reasonable given the morphological differences between *Archaeopteryx* and crown Aves (Chiappe and Dyke 2002).

Topologies retrieved across Mesozoic birds are largely congruent with earlier parsimony analyses (O'Connor and Zhou 2012) and undated Bayesian analyses (Fig. 2). In all cases, extensive missing data and the limited
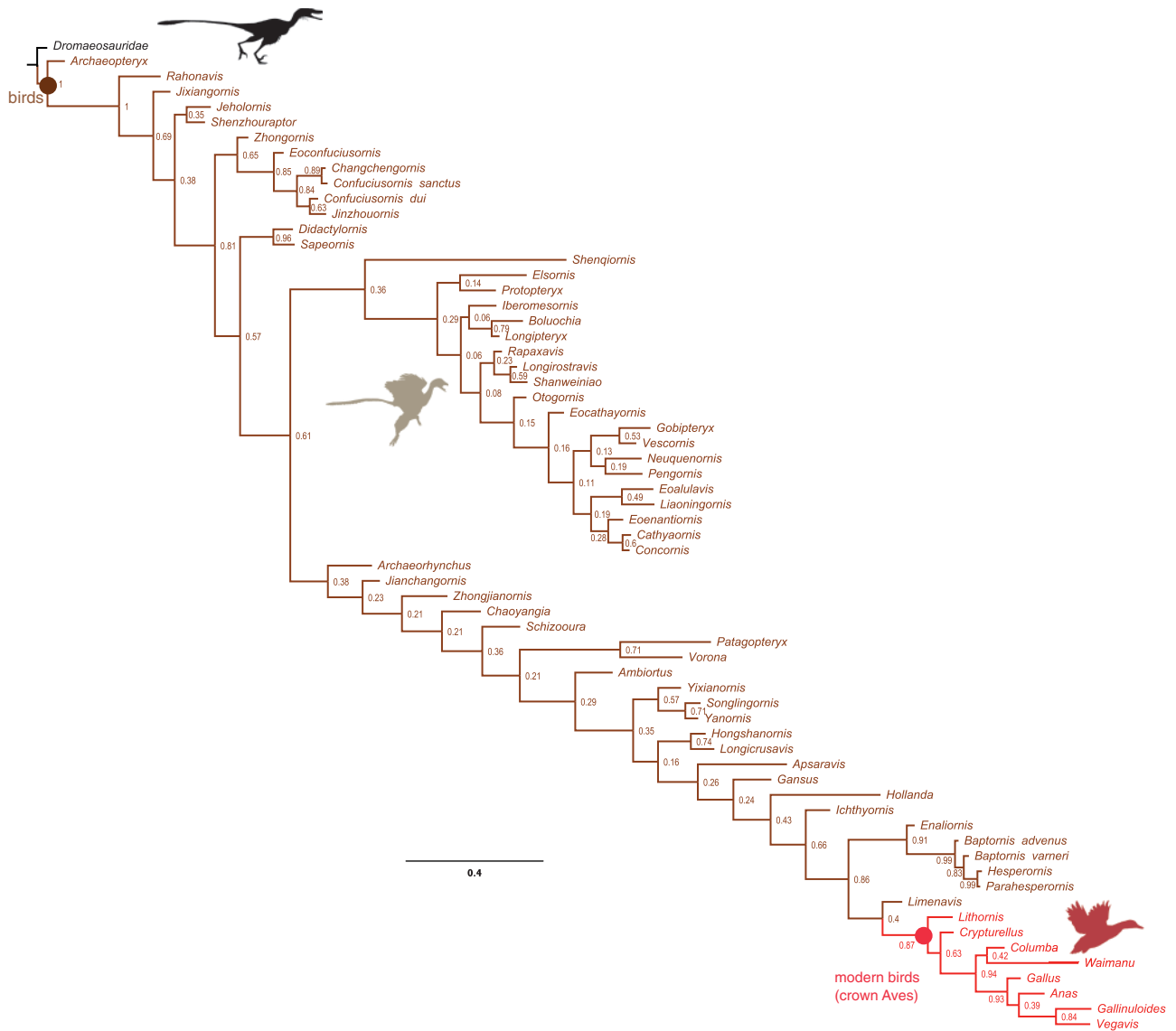
FIGURE 2.   Undated evolutionary tree of birds, from a Bayesian phylogenetic analysis of fossil and living birds (expanded from O'Connor and Zhou 2012) with no clock enforced. Note that geologically more recent taxa (see Fig. 1) generally have longer root-to-tip pathlengths and have thus undergone more anagenesis. Color codings (pdf version): black = out-group, brown = birds excluding crown Aves, red = crown Aves. Numbers at nodes refer to posterior probabilities.

suite of fossilized traits means many clades are poorly supported (see SI 4); in addition, relationships between crown birds vary between analyses, presumably due to taxon and/or character sampling (e.g., different consensus topologies in Figs. 1 and 2). However, the Bayesian approach accommodates this uncertainty by integrating over all sampled tree topologies when inferring divergence dates. Furthermore, the retrieved dates are not an artifact caused by unusual relationships within crown birds, nor by low resolution in general. Constraining relationships between crown birds to conform to accepted relationships did not qualitatively change the results (Table 1). Similarly, repeating the analysis after exclusion of "wildcard" taxa substantially improves support across the tree (e.g., in the analyses with a hard 200 Ma root, the number of in-group nodes

with PP > 0.9 increased from 5 to 12 and from 8 to 16 in the igr and tk clock analyses respectively); however, this improved resolution barely affected divergence date estimates (Table 1).

The dates retrieved here are notably sensitive to inclusion or exclusion of the Paleogene forms. Excluding *Gallinuloides* (∼55 Ma), *Lithornis* (∼55.8 Ma) and *Waimanu* (∼59 Ma) produces much younger inferred dates for crown Aves (∼60 Ma) which postdate the K-Pg boundary. In these analyses, the uppermost Cretaceous *Vegavis* is retrieved as a stem rather than crown bird. The three Paleogene crown Aves are therefore critical to retrieving the mid-Cretaceous divergence date: the derived morphologies of these fossils are most consistent with a relatively lengthy evolutionary history of crown Aves that extends deep into the
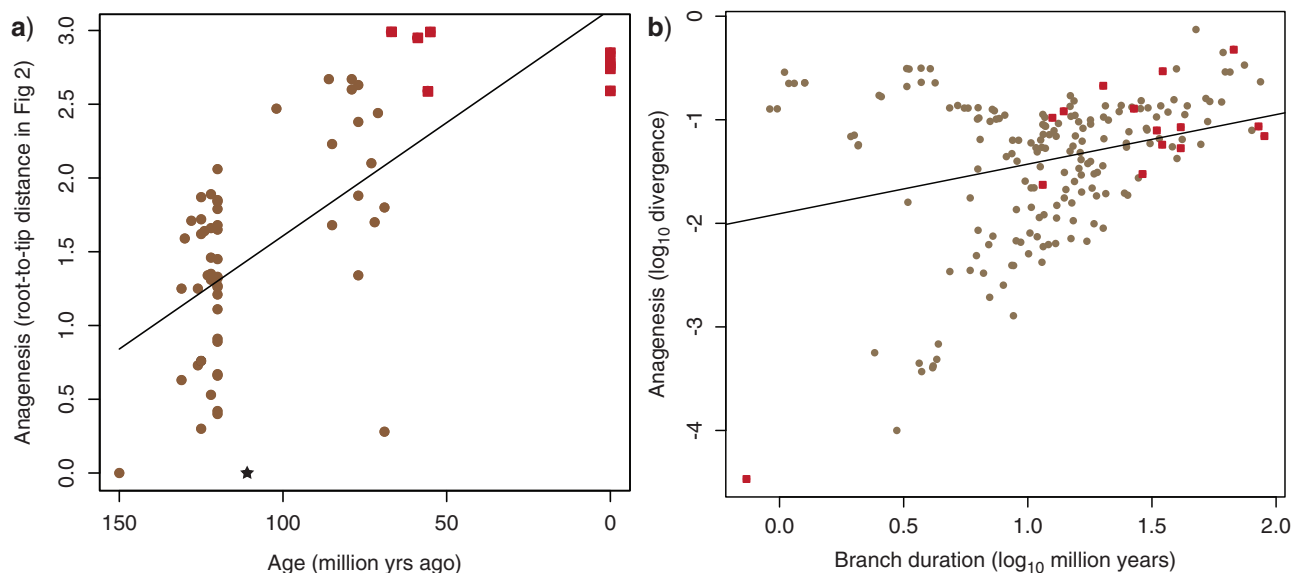
FIGURE 3. The association in birds between (a), age of terminal taxon (stratigraphic position) and anagenesis (total root-to-tip distance in undated analysis: Fig. 2), and (b), branch duration and anagensis (branch length in undated analysis: Fig. 2). Both regressions are significant ($P < 0.001$; see text for details), but points in Figure 3a are phylogenetically uncorrected. Symbols: star (black in pdf) = out-group, circle (brown in pdf) = birds excluding crown Aves, square (red in pdf) = crown Aves.

Cretaceous. However, one major potential complication is poorly accommodated by common clock models used in divergence dating: rate heterogeneity across time (Crandall et al. 2012; Bielejec et al. 2013). If, for instance, morphological (and molecular) rates were elevated across all bird lineages during an explosive early Paleogene diversification, divergence dates estimated by morphological (and molecular) clock methods would be biased toward older values. The large resultant morphological (and molecular) differences between modern bird lineages would be incorrectly attributed to a lengthy period of "normal paced" divergence, instead of a shorter period of more rapid evolution.

The branch lengths in the parsimony and undated Bayesian analyses also reveal that younger taxa (Fig. 1) have consistently undergone more evolutionary change (longer root-to-tip pathlengths: Fig. 2), consistent with expectations of clock models and total evidence dating that stratigraphically younger taxa should (on average) exhibit more anagenesis. This association between age and anagenesis is significant whether one uses phylogenetically uncorrected or corrected comparisons. For instance, there is a highly significant association ($P << 0.001$; Fig. 3a) between the stratigraphic age of terminal taxa and their total anagenesis as reflected in root-to-tip pathlength, but these comparisons are confounded by phylogenetic nonindependence. Standard comparative methods are inapplicable for this data, because neither "stratigraphic age" nor "total anagenesis" satisfy the evolutionary models in such methods, for example these cumulative traits do not evolve by Brownian motion. Phylogenetically independent comparisons are possible if one compares the duration of each branch (in dated analysis: Fig. 1) with inferred amount of evolution (in undated analysis:

Fig. 2), and this results in a significant association ($P << 0.001$; Fig. 3b).

Likelihood and Bayesian approaches to morphological phylogenetics are in relative infancy and many methodological questions remain; for example, the advisability of applying any single likelihood (or parsimony) model across characters with highly heterogenous evolutionary dynamics, whether the correction for ascertainment bias adequately compensates for undersampling of autapomorphies, and whether morphological evolution is too episodic to apply even relaxed-clock models. The present analysis is the first attempt to evaluate morphological–paleontological evidence with quantitative phylogenetic dating methods analogous to those used in molecular studies, and it is hoped will spur further empirical analyses—especially among paleobiologists—which will help answer these questions.

Molecular and morphological approaches using clock models have complementary strengths: the molecular studies can analyze vast numbers of characters using well-tested stochastic models, whereas the morphological studies can sample more widely across intermediate taxa (extinct forms) and across time (stratigraphic ages). These two approaches suggest broadly consistent (mid-Cretaceous) evolutionary timescales for the diversification of modern birds, and imply that many lineages of modern birds existed in the upper Cretaceous and crossed the KPg boundary. If this is true, the generally low fossil fossilization potential of birds is by itself insufficient to explain the absence of modern birds until the uppermost Cretaceous (Ksepka and Boyd 2012), but an additional factor might be the especially patchy upper Cretaceous fossil record on southern continents where they might have arisen

([Brocklehurst et al. 2012](#)). However, there remains the distinct possibility that the morphological and molecular dates are both incorrect, despite being concordant: for instance, greatly elevated rates of morphological and molecular evolution near the KT boundary could lead to overestimates of divergence times from both data sources. The consequences of rate variation across time slices (epochs) have not been studied as extensively as those of rate variation across lineages and across characters (Crandall et al. 2011; Beilejec et al. 2013); however, this factor can potentially impact greatly on estimates of divergence dates. As an example, an hypothesized 5-fold increase in morphological and molecular evolutionary rates in metazoans during the early Cambrian could systematically inflate inferred divergence dates by hundreds of millions of years, from ∼558 Ma to ∼940 Ma ([Lee et al. 2013](#)).

References

Aberer A., Krompass D., Stamatakis A. 2012. Pruning rogue taxa improves phylogenetic accuracy: an efficient algorithm and webservice. Syst. Biol. 62:162–166.

Bapst P. 2012. Paleotree: an R package for paleontological and phylogenetic analyses of evolution. Methods Ecol. Evol. 3:803–807.

Barrett P.M. 2009. The affinities of the enigmatic dinosaur *Eshanosaurus deguchiianus* from the Early Jurassic of Yunnan Province, People's Republic of China. Palaeontology 52:681–688.

Benson R.B.J. 2010. The osteology of *Magnosaurus nethercombensis* (Dinosauria, Theropoda) from the Bajocian (Middle Jurassic) of the United Kingdom and a re-examination of the oldest records of tetanurans. J. Syst. Palaeontol. 8:131–146.

Bielejec F., Lemey P., Baele G., Rambaut A., Suchard M.A. 2013. Inferring heterogeneous evolutionary processes through time: from sequence substitution to phylogeography. arXiv:1309.3075 [accessed 12.11.2013].

Brocklehurst N., Upchurch P., Mannion P.D., O'Connor J. 2012. The completeness of the fossil record of Mesozoic birds: implications for early avian evolution. PLoS One 7:e39056. doi:10.1371/journal.pone.0039056.

Brusatte S.L. 2011. Calculating the tempo of morphological evolution: rates of discrete character change in a phylogenetic context. In: Elewa A.M.T. editor. Computational paleontology. Heidelberg, Germany: Springer. p. 53–74.

Chiappe L.M., Dyke G. 2002. The Mesozoic radiation of birds. Ann. Rev. Ecol. Syst. 3:91–124.

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

Cooper A., Penny D. 1997. Mass survival of birds across the cretaceous-tertiary boundary: molecular evidence. Science 275:1109–1113.

Crandall E.D., Sbrocco E.J., deBoer T.S., Barber P.H., Carpenter K.E. 2012. Expansion dating: calibrating molecular clocks in marine species from expansions onto the Sunda Shelf following the last glacial maximum. Mol. Biol. Evol. 29:707–719.

Dyke G., Kaiser G. (eds.) 2011. Living dinosaurs: the evolutionary history of modern birds. Oxford, UK: John Wiley & Sons.

Gauthier J. 1986. Saurischian monophyly and the origin of birds. Mem. California Acad. Sci. 8:1–55.

Gray R.R., Tatem A.J., Johnson J.A., Alekseyenko A.V., Pybus O.G., Suchard M.A., Salemi M. 2011. Testing spatiotemporal hypothesis of bacterial evolution using methicillin-resistant *Staphylococcus aureus* ST239 genome-wide data within a Bayesian framework. Mol. Biol. Evol. 28:1593–1603.

Godefroit P., Cau A., Hu D.-H., Escuillié F., Wu W., Dyke G. 2013. A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. Nature 498: 359–362.

Haddrath, O., Baker, A.J. 2012. Multiple nuclear genes and retroposons support vicariance and dispersal of the palaeognaths, and an Early Cretaceous origin of modern birds. Proc. R. Soc. Lond. B. 279:4617–4625.

Ho S.Y.W., Lanfear R., Phillips M.J., Barnes I., Thomas J.A., Kolokotronis S.-O., Shapiro B. 2011. Bayesian estimation of substitution rates from ancient DNA sequences with low information content. Syst. Biol. 60:366–375.

Hunt G., Carrano M.T. 2010. Models and methods for analyzing phenotypic evolution in lineages and clades. In: Alroy J., Hunt G., editors. Short course on quantitative methods in paleobiology. Denver, CO: The Paleontological Society. p. 245–269.

Jetz W., Thomas G.H., Joy J.B., Hartmann K., Mooers A.O. 2012. The global diversity of birds in space and time. Nature 491:444–448.

Kass R.E., Raftery A.E. 1995. Bayes factors. J. Amer. Stat. Assoc. 90:773–795.

Ksepka D. T., Boyd C. A. 2012. Quantifying historical trends in the completeness of the fossil record and the contributing factors: an example using Aves. Paleobiology 38:112–125.

Lee M.S.Y., Worthy T. 2011. Likelihood reinstates *Archaeopteryx* as a primitive bird. Biol. Lett. 8:299–303.

Lee M.S.Y., Soubrier J., Edgecombe G.D. 2013. Rates of phenotypic and genomic evolution during the Cambrian Explosion. Curr. Biol. 23:1889–1895.

Longrich N.R., Tokaryk T.T., Field D. 2011. Mass extinction of birds at the Cretaceous-Paleogene (K-Pg) boundary. Proc. Natl Acad. Sci. USA 108:15253–15257.

Mudroch A., Richter U., Joger U., Kosma R., Ide O., Maga A. 2011. Didactyl tracks of paravian theropods (Maniraptora) from the ?Middle Jurassic of Africa. Plos One 6:e14642. doi:10.1371/journal.pone.0014642.

Naish D. 2012. Birds. In: Brett-Surman M.K., Holtz T.R. Jr., Farlow J.O., editors. The complete dinosaur. Bloomington, IN: Indiana University Press. p. 379–424.

O'Connor J.K., Zhou Z.-H. 2012. A redescription of *Chaoyangia beishanensis* (Aves) and a comprehensive phylogeny of Mesozoic birds. J. Syst. Palaeont. 11: 889–906.

O'Leary M.A., Bloch J.I., Flynn J.J., Gaudin T.J., Giallombardo A., Giannini N.P., Goldberg S.L., Kraatz P., Luo Z.-X., Meng J., Novacek M.J., Perini F.A., Randall Z.S., Rougier G., Sargis E.J., Silcox M.T., Simmons N.B., Spaulding M., Velazco P.M., Weksler M., Wible J.R., Cirranello A.L. 2013. The placental mammal ancestor and the post–K-Pg radiation of placentals. Science 339:662–667.

Pyron R.A. 2011. Divergence time estimation using fossils as terminal taxa and the origins of Lissamphibia. Syst Biol 60:466–481.

Ronquist F., Klopfstein S., Vilhelmsen S., Schulmeister S., Murray D.L., Rasnitsyn A.P. 2012a. A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. Syst. Biol. 61:973–999.

Ronquist F., Teslenko M., van der Mark P., Ayres D.L., Darling A., Höhna S., Larget B., Liu L., Suchard M.A., Huelsenbeck J.P. 2012b. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61:539–542.

van Tuinen M., Stidham T.A., Hadly E.A. 2006. Tempo and mode of modern bird evolution observed with large-scale taxonomic sampling. Hist. Biol. 18:205–221.

Xu X., You H., Du K., Han, F. 2011. An *Archaeopteryx*-like theropod from China and the origin of Avialae. Nature 475:465–470.