

Chapter 5

Timing the Extant Avian Radiation: The Rise of Modern Birds, and the Importance of Modeling Molecular Rate Variation

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ABSTRACT

Unravelling the phylogenetic relationships among the major groups of living birds has been described as the greatest outstanding problem in dinosaur systematics. Recent work has identified portions of the avian tree of life that are particularly challenging to reconstruct, perhaps as a result of rapid cladogenesis early in crown bird evolutionary history (specifically, the interval immediately following the end-Cretaceous mass extinction). At face value this hypothesis enjoys support from the crown bird fossil record, which documents the first appearances of most major crown bird lineages in the early Cenozoic—in line with a model of rapid postextinction niche-filling among surviving avian lineages. However, molecular-clock analyses have yielded strikingly variable estimates for the age of crown birds, and conflicting inferences on the impact of the end-Cretaceous mass extinction on the extant bird radiation. This uncertainty has often been ascribed to a patchy avian fossil record, but the possibility of model misspecification in molecular divergence-time analyses represents an important and relatively underexplored alternative hypothesis. Here, we highlight the necessity of further developing and using models that account for coordinated variation in rates of molecular evolution across a phylogeny (e.g., molecular early burst) as a means of assessing support for a rapid post-Cretaceous radiation of crown birds. We discuss how relationships between life history and substitution rates can mislead divergence-time studies that do not account for directional changes in substitution rates over time, and suggest that these effects might have caused some of the variation in existing molecular date estimates for birds. We suggest multiple paths forward that could help resolve this and similar conflicts within other major eukaryotic clades.

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INTRODUCTION

While the relative contributions of an asteroid impact and severe environmental change from volcanism continue to be debated, there is no doubt the large dinosaurs met their demise at the end-Cretaceous (K-Pg) mass extinction, ~66 million years ago (Brusatte et al., 2015, references therein). The impact of this extinction event on smaller pennaraptoran dinosaurs—the theropod subclade comprising oviraptorosaurs, deinonychosaurs, and the bird lineage, Avialae—has been more difficult to assess, given a relatively sparse fossil record in the latest Cretaceous. However, recent work has indicated that at least five major clades of avialans survived into the terminal Maastrichtian (latest Cretaceous), and thus were likely subject to the K-Pg extinction event (Longrich et al., 2011; Field et al., 2018a; Agnolín et al., 2017). Latest Cretaceous representatives of these clades (Enantiornithes, Palintropiformes, Hesperornithes, Ichthyornithes, and the bird crown clade, Aves) are largely known from isolated, fragmentary fossils (Hope, 2002; Longrich et al., 2011; Dumont et al., 2016; Field et al., 2018a) and, with the exception of crown birds, all are entirely unknown from post-Cretaceous sediments. Assessing whether crownward stem birds (e.g., Enantiornithes) were completely exterminated at the K-Pg boundary is challenging, given the generally meagre Paleocene bird fossil record (Mayr, 2007, 2009, 2016; Field, 2017). Notably, some groups of Cretaceous archosauriforms (e.g., choristoderes) and mammals (e.g., multituberculates) survived the K-Pg mass extinction, only to go extinct later in the Cenozoic (Evans and Hecht, 1993; Wilson, 2014), and it is possible that some representatives of crownward avialans survived the mass extinction event only to succumb later in the early Cenozoic (Mayr, 2007). Nonetheless, no definitively diagnosed stem bird fossils are known from sediments above the K-Pg boundary, and it seems likely that the only major clade of avialans to survive in ecologically significant numbers were crown birds themselves (Longrich et al.,

2011; Mayr, 2016; Field, 2017; Ksepka et al., 2017; Field et al., 2018b, 2020).

Today, crown birds are among the most diverse major groups of tetrapods, with nearly 11,000 living species that occupy virtually every subaerial habitat on Earth (Gill and Donsker, 2018). However, due to their limited Late Cretaceous and early Paleocene fossil record (see Pittman, et al., chapter 2), assessing the timing of the extant avian radiation has been challenging. Fossils representing the earliest known stem-group representatives of many extant avian orders appear throughout the Paleogene, but many derive from a relatively small number of bird-bearing Lagerstätten (e.g., the Messel, Fur, and Green River formations; Mayr, 2009). As a result, the temporal origins of these lineages have been difficult to precisely verify, complicating efforts to assess whether any of them extended into the Cretaceous. To date, only two well-supported crown birds have been described from the Late Cretaceous: *Vegavis iaai* from the terminal Maastrichtian of Antarctica (Noriega and Tambussi, 1995; Clarke et al., 2005; Agnolín et al., 2017), and *Asteriornis maastrichtensis* from the terminal Maastrichtian of Belgium (Field et al., 2020). However, the phylogenetic position of *Vegavis* is unclear (Mayr et al., 2018), with a recent hypothesis finding it to be an early stem group anseriform (Worthy et al., 2017). This position would imply that at least three avian crown group divergences had occurred prior to the K-Pg boundary (i.e., the divergences between Palaeognathae and Neognathae, Galloanserae and Neoaves, and Galliformes and Anseriformes). However, exactly when these divergences would have taken place in the Late Cretaceous is unknown (fig. 1). In light of this uncertainty in the fossil record, molecular divergence-time approaches offer our only means for establishing a timeline for the deepest divergences within the avian crown group.

In general, molecular clock-based estimates of major extant avian clade ages often differ markedly from observed patterns in the fossil record. Early attempts to address the timing of interordinal divergences within crown birds often suggested that many, if not all, diver-

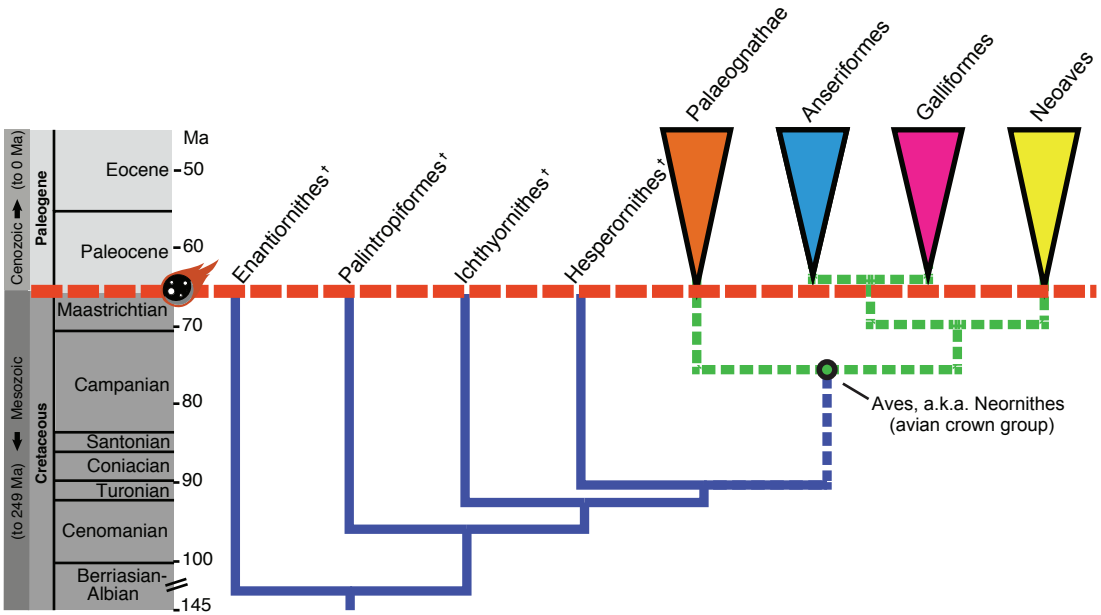


FIG. 1. Schematic phylogeny and approximate divergence times of the major crownward stem bird lineages (blue) and the deepest extant clades within crown birds (green). Most recent common ancestor (MRCA) of crown birds indicated by green node. Dashed lines indicate extant lineages whose time-scaled branch lengths are debated. Divergence times illustrated for crown birds roughly follow those of Prum et al. (2015), and those of stem birds follow (Longrich et al., 2011). Stem bird phylogeny and scale modified from Field et al. (2018a), with stem bird topology following (Field et al., 2018b). K-Pg boundary indicated by dashed red line and asteroid at ~66 Ma.

gences between the ~40 extant avian orders (Gill and Donsker, 2018) took place during the Cretaceous (e.g., Cooper and Penny, 1997), substantiating arguments for a limited influence of the end-Cretaceous mass extinction on crown bird evolution. This interpretation stands in stark contrast to patterns in the crown bird fossil record, whereby virtually all of the earliest evidence for extant avian orders—with the exception of the deeply diverging Galloanserae (see mention of *Vegavis* and *Asteriornis* above)—is restricted to Cenozoic sediments (Mayr, 2009). What accounts for these dichotomous interpretations of avian evolutionary history? Have paleontologists simply failed to recover—or consistently failed to identify—a diverse range of neoavian remains from the Cretaceous (summarized by Brown et al., 2008)? Or have molecular-clock estimates of divergence times

somehow failed to account for unrecognized patterns of genomic rate variation (Benton, 1999; Berv and Field, 2018)? These hypotheses are not mutually exclusive, but our ability to address the latter question is currently limited. Clarifying the extent to which these alternatives have affected our understanding of avian evolution is critical for accurately assessing the age of the extant avian radiation, and therefore our ability to correctly interpret how various events in Earth history—asteroid impacts, periods of climatic change, and major tectonic events among them—have influenced the evolution of birds. Moreover, this will allow us to understand whether extant bird orders arose slowly throughout the Late Cretaceous or whether they radiated rapidly in the early Cenozoic, which has important implications for how we understand the nature of major evolutionary radiations.

DISCREPANCIES BETWEEN MOLECULAR
DIVERGENCE TIMES
AND THE BIRD FOSSIL RECORD

Since the earliest attempts to date the age of the avian crown group using molecular divergence times (e.g., Cooper and Penny, 1997), the hypothesis of numerous ordinal-level divergences within Neoaves taking place in the Mesozoic has generally been supported in molecular clock studies (e.g., Brown et al., 2008; Pacheco et al., 2011; Haddrath and Baker, 2012; Crouch et al., 2018). This hypothesis has not been corroborated by the Cretaceous fossil record. All putative neoavian fossils thus far reported from the Mesozoic (Stidham, 1998; Hope, 2002) have instead been identified as stem group birds upon reevaluation (Dyke and Mayr, 1999; Longrich et al., 2011; Mayr et al., 2018). The elusiveness of Cretaceous neoavian fossils is consistent with the hypothesis of a largely post-Cretaceous diversification of crown Neoaves—perhaps no Cretaceous neoavians have been found because they simply had not yet originated at that point in Earth history. As Benton (1999) notes, this hypothesis is eminently testable, since the recovery of Cretaceous crown neoavian fossils would force a reevaluation of a model of explosive order-level neoavian divergences in the wake of the K-Pg. It is probably fair to say, however, that the current consensus among paleornithologists is that such discoveries are unlikely. The probability of crown neoavian fossil discoveries deep in the Cretaceous is presumably low, given the abundant preservation of noncrown avialans that have been recovered from Cretaceous sites around the world (see Pittman et al., chapter 2). Although conclusively “demonstrating” the absence of birds from deeper Mesozoic sediments presents a difficult epistemological problem (Sober, 2009), it appears more likely that the first appearances of major neoavian subclades in the early Cenozoic fossil record are simply a reflection of their early

Cenozoic origins (Mayr, 2009, 2016; Longrich et al., 2011; Feduccia, 2014; Field, 2017; Ksepka et al., 2017).

In contrast to earlier molecular divergence-time analyses, the majority of large-scale phylogenomic divergence-time studies of birds in the last five years have inferred a post-Cretaceous radiation for the majority of the deep divergences within the avian crown group (i.e., divergences within crown Palaeognathae, crown Galloanserae, and crown Neoaves), with variable estimates of the age of the most recent common ancestor of crown birds, hereafter the avian MRCA (Jarvis et al., 2014; Claramunt and Cracraft, 2015; Prum et al., 2015). At first glance, these results—which are consistent with the Late Cretaceous avian fossil record—would appear to reflect more sophisticated analyses with better-justified fossil calibrations yielding more accurate divergence-time estimates. While this is undoubtedly true in part, the reality in its entirety is much less satisfying. As lingering discrepancies between the fossil record (indicating a largely post-Cretaceous radiation of birds) and loosely constrained molecular divergence-time estimates (largely advocating a Cretaceous radiation) have come into better focus, many divergence-time analyses have conditioned soft and hard maxima for internal fossil calibrations on the K-Pg boundary itself (Ericson et al., 2006; Jarvis et al., 2014; Prum et al., 2015). This approach largely precludes divergence-time estimates from exceeding the age of the K-Pg boundary, because explicit prior beliefs are used to constrain the outcome of these analyses (Warnock et al., 2015). While the resultant age estimates from such strongly constrained analyses may well be more accurate than those employing older soft maxima for deep neoavian divergences (and, based on their agreement with evidence from the bird fossil record, we would argue that they *are* indeed more accurate), this approach introduces problematic circularity into the process of inferring divergence times for the deepest nodes in the avian tree of life.

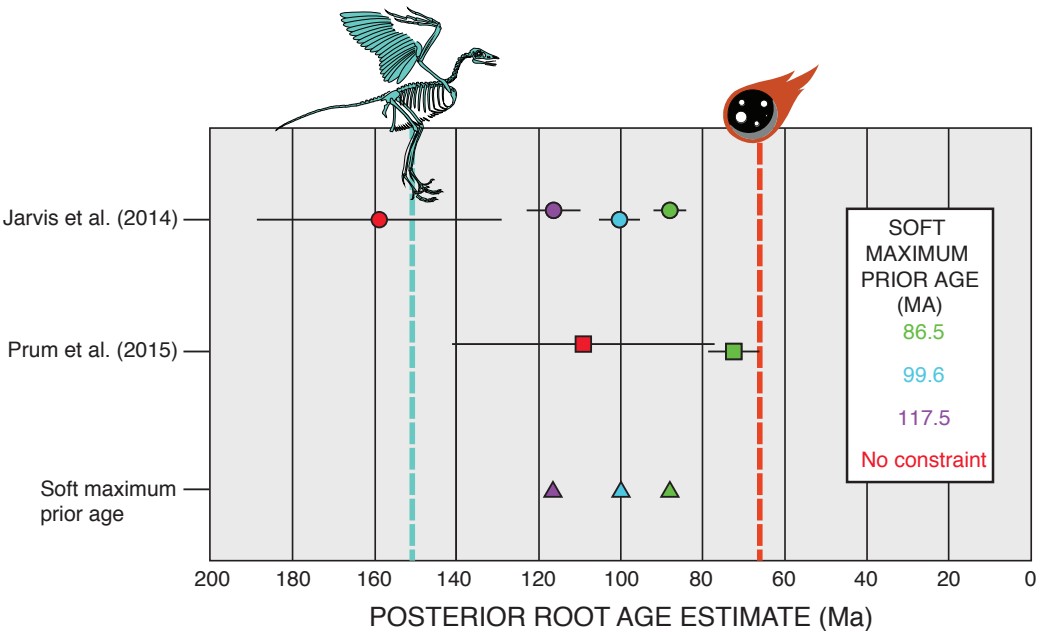


FIG. 2. Mean estimated ages of the crown bird MRCA (circles and squares $\pm$ 95% HPD intervals) are highly dependent on specified soft maximum prior age (triangles). Red circle and square indicate analyses run with no soft maximum age specified. Jarvis et al. (2014) results modified from Cracraft et al. (2015). Prum et al. (2015) results from the “top ten” nucleotide dataset (Berv and Field, 2018). Ages of *Archaeopteryx lithographica* (~155 Ma) and K-Pg boundary (~66 Ma) illustrated.

VARIABILITY AND CIRCULARITY OF CROWN BIRD ROOT AGE ESTIMATES

Estimated ages for the deepest nodes within the avian crown group, including the most recent common ancestor (MRCA) of living birds, have proven extremely sensitive to prior assumptions made about the maximum age of the MRCA. For example, Cracraft et al. (2015) applied 97.5% prior maximum age constraints of 86.5 Ma (following Benton and Donoghue, 2007), 99.6 Ma (following Jarvis et al., 2014), and 117.5 Ma (following Mitchell et al., 2015) to the Jarvis et al., (2014) molecular dataset. These analyses illustrated marked variability in the estimated number of pre-K-Pg order-level neoavian divergences (from a minimum of 1 under the 86.5 Ma constraint, to a maximum of 15 under the 117.5 Ma constraint). Such variability is to be expected, as the increased density of older ages within the prior age distribution elevates the probability of estimating older ages for clades throughout the

tree (Dornburg et al., 2011; Warnock et al., 2012). Additional analyses by Cracraft et al. (2015), removing a specific soft maximum age for the MRCA and otherwise applying the same suite of parameters, resulted in age estimates for the crown bird MRCA in excess of 155 million years. Notably, this estimate is older than the oldest known and most stemward avialan, *Archaeopteryx lithographica* (fig. 2). This sensitivity underscores the sobering conclusion that, in the absence of informative priors, currently available molecular and fossil data, combined with our best model of their evolution, can shed very little light on the influence of the K-Pg mass extinction on avian evolution (fig. 3).

Given the almost complete absence of a Mesozoic crown bird fossil record (and, at the time of writing, the complete absence of any convincing Mesozoic neoavians), there is no strong evidence that can form the basis of a soft maximum age for the avian MRCA (Berv and Field, 2018; Pittman et al., on the fossil record,

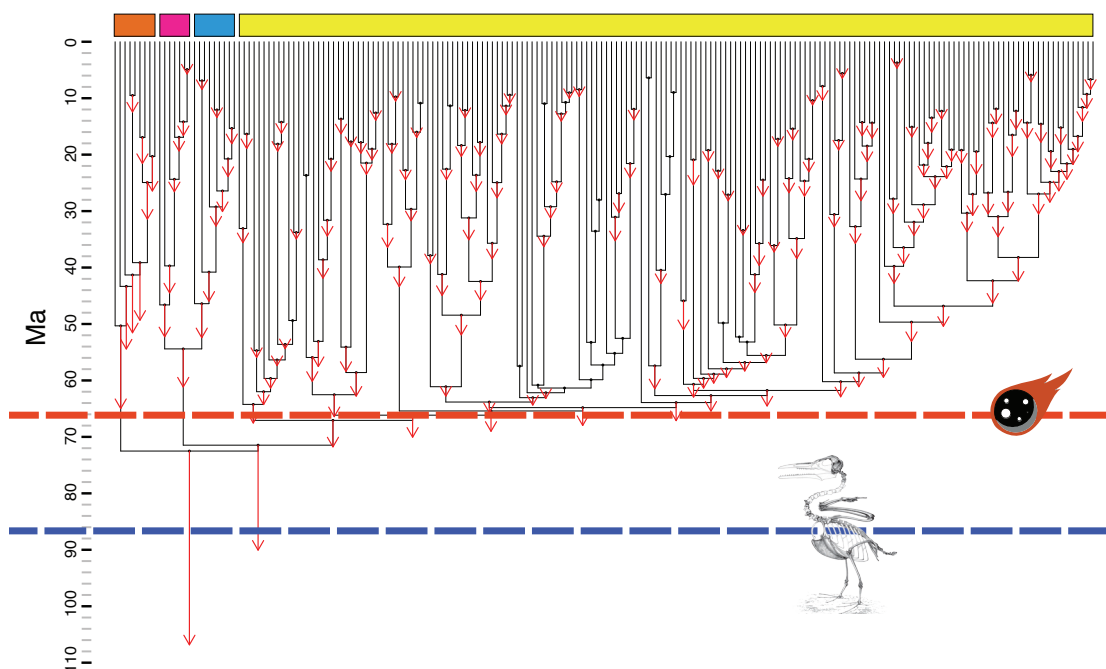


FIG. 3: Analytical influence of soft maximum prior selection on the avian evolutionary timescale (modified from Berv and Field, 2018). Colored boxes represent the major crown bird subclades and correspond to the color scheme from figure 1. Underlying black phylogeny represents the preferred time tree from Prum et al. (2015), applying a soft maximum age of 86.5 Ma for the crown bird MRCA. Red arrows illustrate shifts in estimated clade ages induced by removing this soft maximum prior, with other analytical parameters kept the same. The most severe branch length extensions occur on the deepest lineages of the tree (the lineages most likely to have crossed the K-Pg boundary). However, an important caveat is that the Paleogene calibrations in this analysis have soft maxima informed directly by the K-Pg boundary itself. K-Pg boundary denoted by red line and asteroid; age of the fossil avialan-rich Niobrara Formation “Niobrara Prior” indicated by blue dashed line. *Ichthyornis* reconstruction modified from Marsh (1880).

chapter 2). Nonetheless, we would argue that, because (1) the Cretaceous (144–66 Ma) avialan fossil record is relatively rich, (2) the oldest convincing crown bird, *Asteriornis*, derives from the extreme terminal Cretaceous ~66.7 Ma (Field et al., 2020), and (3) the earliest diverse crown-grade bird fossil assemblage is scarcely older than the K-Pg boundary (within 300,000 years of the boundary; Longrich et al., 2011), specifying soft maxima for the basal divergence within crown birds deep in the Cretaceous is likely unsound. For example, the 117.5 Ma soft maximum age constraint advocated by Mitchell et al. (2015) is 50 million years older than *Asteriornis*

and *Vegavis*—a vast time span equivalent to 75% of the entire Cenozoic. Setting such a large prior age distribution has the intuitive consequence of widening the sampling of molecular divergences into deeper timescales (Dornburg et al., 2011; Warnock et al., 2012). Since soft maxima for the crown bird MRCA are extremely influential—even circular—in divergence-time analyses (figs. 2,3), we argue that assigning such ancient priors is extremely likely to yield inaccurately ancient divergence times for the MRCA of the avian crown group and its major subclades (a similar argument was made for mammals by Phillips, 2016).

RAPID POST-CRETACEOUS RADIATION AS AN EXPLANATION FOR THE 'NEOAVIAN COMB'

The phylogenetic interrelationships of the major neoavian subclades have been notoriously challenging to disentangle, and a consensus regarding the higher order topology of Neoaves has yet to be reached (Pittman, et al., on systematics, chapter 1). Virtually all independent phylogenomic studies to date have supported differing neoavian topologies (Ericson et al., 2006; Hackett et al., 2008; McCormack et al., 2013; Jarvis et al., 2014; Prum et al., 2015; Reddy et al., 2017), although the most recent studies all tend to agree on roughly 10 major constituent subclades: Mirandornithes, Aequornithes, Charadriiformes, Gruiformes, Otidimorphae, Columbimorphae, Strisores, Phaethontimorphae, Telluraves, and the perpetually challenging-to-place, monotypic *Opisthocomus* (Reddy et al., 2017; Kimball et al., 2019). The lingering recalcitrance of neoavian relationships makes it a classic example of a difficult phylogenetic problem (the “neoavian comb,” sensu Cracraft et al., 2004), and this recalcitrance has been hypothetically linked to rapid cladogenesis for some time (Ericson et al., 2006; Feduccia, 2014; Jarvis et al., 2014; Ksepka and Phillips, 2015; Prum et al., 2015; Suh, 2016; Musser et al., 2019; Kimball et al., 2019; Houde et al., 2020).

A scenario of rapid cladogenesis—such as that hypothesized to have occurred during post-K-Pg extinction recovery—provides a logical explanation for the distinctive combination of extremely short phylogenetic internodes and incomplete lineage sorting that may be responsible for the lack of a clear branching pattern for this portion of the bird tree of life. The combination of a deep timescale and short times between phylogenetic divergences render this scenario among the most challenging of phylogenetic problems for molecular evidence to disentangle (Degnan and Rosenberg, 2009; Townsend et al., 2012; Dornburg et al., 2017a, 2017b, 2018). Additionally, expectations based on other rapid evolutionary radiations suggest the possibility of high levels of gene flow

among early diverging lineages (Meier et al., 2017). Indeed, if it is the case that early divergences among birds were associated with rampant incomplete lineage sorting and gene flow during a rapid early Cenozoic radiation (Suh, 2016), a clear bifurcating pattern may not exist in the first place (Hahn and Nakhleh, 2015). Regardless, the challenges of resolving the deepest avian divergences are consistent with what we should theoretically expect in a scenario of rapid postextinction avian cladogenesis in the earliest Cenozoic. Further, these challenges have profound implications for our ability to accurately estimate molecular divergence times using existing approaches.

MODELING RATE VARIATION: AMONG-LINEAGE RATE VARIATION VERSUS FAST EARLY RATES

It has long been known that failing to properly account for substitution rate variation among lineages can fundamentally limit the accuracy of molecular dating analyses (Jukes and Holmquist, 1972; Radinsky, 1978; Vawter and Brown, 1986). Early studies of molecular divergence times relied on the assumption that the rate of evolution of a gene or locus can be characterized by a single rate, such as a mean rate, of character change (Bromham and Penny, 2003). However, it quickly became clear that substitution rates often vary substantially, even among closely related lineages (Li et al., 1987; Dornburg et al., 2014; Ho, 2014; Beaulieu et al., 2015; Moorjani et al., 2016). At the level of a gene or locus, site rate variation may be correlated with codon position, transition/transversion biases, or compositional biases toward certain bases (Kumar, 1996). As lineages shift their life histories in response to new ecological opportunities, this can further result in dramatic shifts in the substitution rates of entire loci (Martin and Palumbi, 1993; Bromham, 2002; Smith and Donoghue, 2008). It is not uncommon for clades to exhibit substitution rates varying by up to an order of magnitude for the same locus (Smith and

Donoghue, 2008; Dornburg et al., 2012); Berv and Field (2018) report a 20-fold difference between the fastest and slowest-evolving avian lineages. The consequences of failing to accurately model rates of character change—both across sites and across lineages—are intuitive. Overestimating substitution rates can lead to tree compression, biasing divergence times toward the present (Phillips, 2009; Ksepka and Phillips, 2015; Dornburg et al., 2017b). Conversely, underestimating molecular rates will drive tree expansion, in the worst-case scenario creating an artificial signature of an ancient pulse of diversification (Duchêne et al., 2017a). Developing models to correctly account for variation in substitution rates is an ongoing challenge in molecular dating (Drummond et al., 2006; Duchêne et al., 2014). However, further development of these models is made more challenging by the enormous number of factors that can influence substitution rates, including but not limited to aspects of molecular biology, physiology, life history, and population variation (Mooers and Harvey, 1994; Welch et al., 2008; Bromham, 2009; Lanfear et al., 2010a, 2014; Hodgkinson and Eyre-Walker, 2011).

Perhaps because of this complexity, most approaches to modeling substitution rate variation among lineages use sophisticated statistical models that largely ignore the biological causes and correlates of substitution rate variation, although there are notable exceptions (Lartillot and Poujol, 2010; Lartillot et al., 2016). If we are to time-calibrate the evolutionary history of birds, let alone all life, it will be important to consider instances where the most widely used models of substitution rate variation may be misleading. In particular, largely absent from current approaches to molecular divergence-time estimation are ways to account for another equally important, but less often appreciated, source of substitution rate variation: convergent, directional changes in lineage life history over time.

MODELING RATE VARIATION: LIFE-HISTORY EVOLUTION AND MASS EXTINCTIONS

The fossil record is rich in examples of rapid shifts in organismal size and form (Finarelli and Flynn, 2006; Evans et al., 2012; Bellwood et al., 2014; Huttenlocker, 2014; Near et al., 2014; Berv and Field, 2018). For major groups these shifts are particularly pervasive in the aftermath of mass extinction events (Twitchett, 2007; Friedman, 2010; Sibert et al., 2018). In these cases, the most recent common ancestors of survivors are often hypothesized to be relatively small bodied (Cardillo et al., 2005; He et al., 2010; Huttenlocker, 2014). Small-bodied organisms tend to have larger effective population sizes, shorter generation times, and lower absolute metabolic requirements relative to larger bodied relatives, all of which are predicted to buffer against the effects of the rapid environmental changes that are the hallmarks of mass extinctions (McKinney and Lockwood, 1999). These factors, as well as other life-history characters (below), are strongly correlated with rates of molecular evolution (Lynch and Walsh, 2007; Berv and Field, 2018).

The hypothesis of a “fast-running” molecular clock across mass extinction events was raised by Benton (1999); however, plausible drivers of such an acceleration have largely gone uninvestigated, and the hypothesis has not gained considerable traction (but see Lee et al., 2013; Berv and Field, 2018). This is unfortunate, as a growing body of literature examining correlations between molecular rates and life history offers a number of plausible and nonmutually exclusive macroevolutionary drivers that could have instigated a pulse of molecular evolution in the wake of the K-Pg mass extinction. In particular, for several major clades of vertebrates such as birds and mammals, numerous authors have confirmed a strong negative correlation between nucleotide substitution rate and body size, due to numerous size-linked biological and demographic factors that correlate with substitution rate (Martin and Palumbi, 1993; Dornburg et al., 2012; Nabholz et al., 2016; Berv and Field, 2018).

Birds may have exhibited elevated substitution rates in the wake of the K-Pg mass extinction for a number of reasons. First, and likely most importantly, smaller birds have shorter generation times on average, resulting in more genome copying events and thus more mutations and more substitutions per unit of time (Mooers and Harvey, 1994; Baer et al., 2007; Lehtonen and Lanfear, 2014). Generation time has been consistently shown to be strongly linked to substitution rates in taxa across the Tree of Life (Martin and Palumbi, 1993). Second, smaller birds have higher mass-specific metabolic rates on average, which may cause higher rates of DNA damage and thus higher mutation rates and higher substitution rates per unit of time (Mindell et al., 1996), although this hypothesis remains controversial because the mechanism linking metabolic rate to germline DNA damage remains unclear (Lanfear et al., 2007). Therefore, if K-Pg-surviving birds were relatively small bodied, relatively short generation times and higher mass specific metabolic rates would both be expected to result in high substitution rates in the wake of the K-Pg. Additionally, regardless of correlations between substitution rates and life history, lineages that survive mass extinction events are expected to have smaller effective population sizes in the early stages of postextinction recovery, which may itself cause a transient pulse of substitutions (Lanfear et al., 2014).

Following Berv and Field (2018), we suggest that a burst of rapid molecular evolution may have taken place early in the evolutionary history of crown birds. We refer to this phenomenon as an “epoch effect” (Lee and Ho, 2016), and suggest that such a cladewide substitution rate acceleration may be partially responsible for the enduring uncertainty in avian crown group age estimates as well as those for major crown bird subclades. It may be that the fast, early rates of crown birds were induced by selective extinction of larger species and/or size reduction among surviving lineages at the K-Pg extinction event (Twitchett, 2007), and suggest that this extinction-induced acceleration in the rate of molecu-

lar evolution may provide a plausible means of reconciling the incongruence between loosely constrained molecular divergence-time analyses and fossil-based estimates of divergence times in birds and other organisms.

PLAUSIBILITY OF AN ‘ACCELERATED’ MOLECULAR CLOCK EARLY IN CROWN BIRD HISTORY

BODY SIZE: Body size selectivity among K-Pg survivors may have accelerated the avian molecular clock. The evidence linking small body size to increased rates of molecular evolution raises a key question: How likely was the K-Pg to have acted as a filter on avian body size? Reductions in body size among survivors across mass extinction horizons, though often difficult to observe in clades lacking extensive pre- and postextinction fossil records, have been termed the “Lilliput effect” (Urbanek, 1993). Preliminary attempts to discern evidence for an avian Lilliput effect across the K-Pg based on fossil body size estimates (Field et al., 2013) and fossil calibrated ancestral body size reconstructions (Berv and Field, 2018) have yielded results consistent with transient body-size reduction across this mass extinction horizon (fig. 4). A Lilliput effect among avian survivors would, at least theoretically, have limited their total metabolic requirements in the early aftermath of the K-Pg, a calamitous interval during which the prospect of avian survival in itself may have been tenuous at best (Robertson et al., 2004, 2013; Longrich et al., 2011; Feduccia, 2014; Larson et al., 2016; Field et al., 2018b). Thus, if an avian Lilliput effect did take place, we would predict it to have induced a pulse of elevated substitution rates in the early Paleocene. This acceleration could cause currently available molecular-clock methods to dramatically underestimate the true substitution rates at the base of the avian tree of life, resulting in artificially ancient divergence time estimates for deep crown bird nodes as a consequence of tree extension (Berv and Field, 2018; fig. 4).

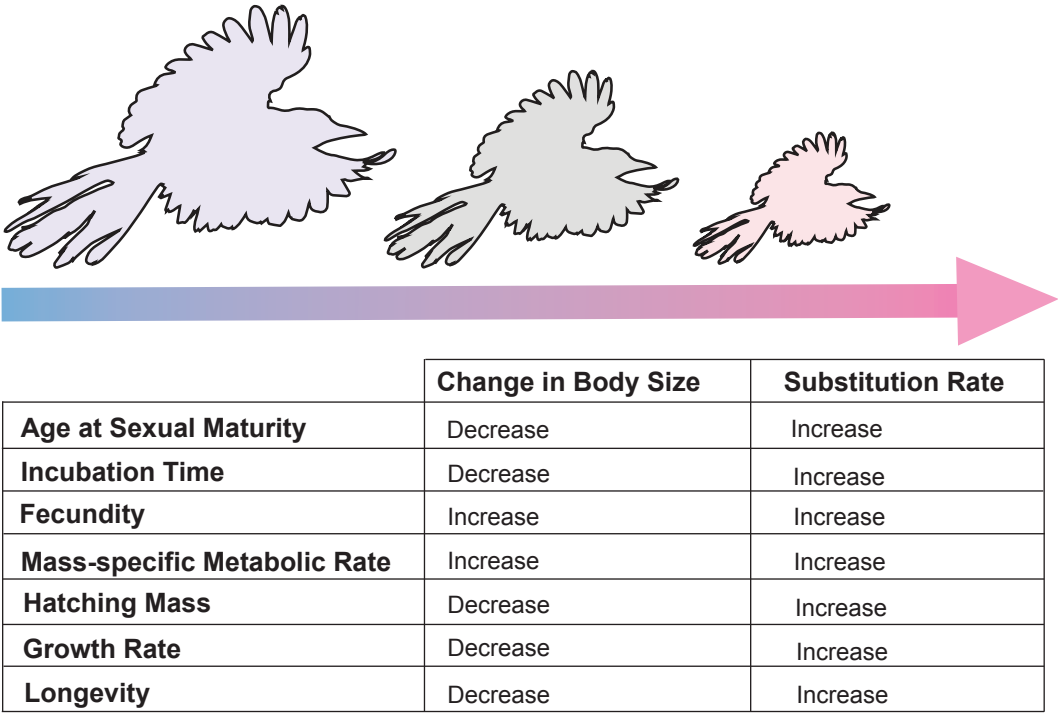


FIG. 4. Expected influence of avian body size decreases on life history variables linked to substitution rate for exon rich data (modified from Berv and Field, 2018). Reductions in avian body size are predicted to result in increased avian substitution rates.

Berv and Field (2018) confirmed a strong negative correlation between body size and nucleotide substitution rate across the avian crown group for a sample of exon-rich nucleotide data, consistent with the expectation that transitions toward smaller body size may induce accelerations in substitution rate (Martin and Palumbi, 1993; Nabholz et al., 2016; fig. 4). Ksepka and Phillips (2015) identified similar patterns, although the hypothesis of a Lilliput effect-induced rate acceleration was not investigated in that study. To investigate the potential for coordinated body size fluctuations to influence avian divergence-time estimates, Berv and Field (2018) first divided the avian crown group into seven major subclades. They then ran strict and relaxed clock divergence-time analyses, further subsampling “small,” “median,” and “large” sized species from each of those clades. When the age of the crown bird MRCA was estimated using a dataset

of the smallest representatives from those seven major clades, an avian MRCA age of ~116 Ma was obtained (fig. 5). By contrast, analyses rerun using the largest representatives from the seven major clades resulted in a MRCA age of ~78 Ma (fig. 5). Finally, analyses run using “median-sized” taxa within those major clades yielded an intermediate avian MRCA age of ~95 Ma (fig. 5). These analyses clearly illustrate the potential for evolutionary perturbations in body size to induce branch length extensions and contractions. These results have profound implications for divergence-time analyses if the K-Pg extinction selected for small body size among boundary-crossing lineages.

POST-K-Pg POPULATION SIZE: A collapse in post-K-Pg population sizes may have accelerated the avian molecular clock. The theoretical link between body size and rates of avian genomic substitution is strong, even if directly

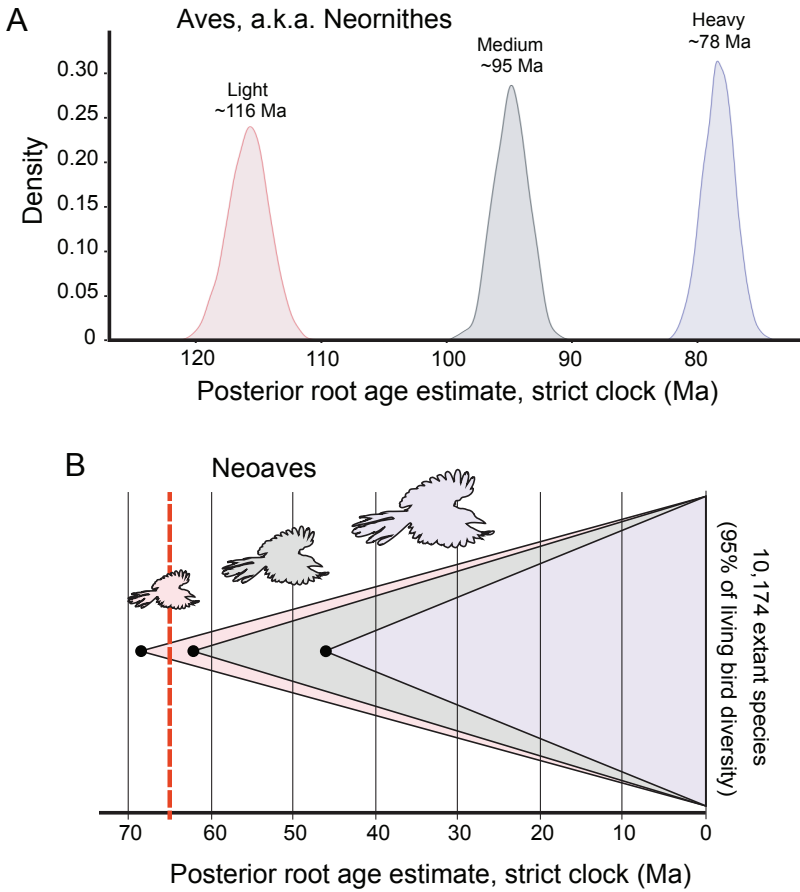


FIG. 5. The influence of body size on estimates of crown bird and neoavian clade ages from strict clock analyses (modified from Berv and Field, 2018). **A**, Results of body size partitioning on estimates of the age of the crown bird MRCA. The “heavy” body size partition (blue) yields a mean crown bird MRCA estimate ~17 million years younger than the “medium” body size partition, and ~38 million years younger than the “light” body size partition (pink). **B**, Results of body size partitioning on estimates of the age of the neoavian MRCA. “Heavy” body size partition yielded a neoavian MRCA estimate of ~46 Ma (blue), “medium” body size partition ~63 Ma (grey), “light” body size partition ~68 Ma (pink). Dashed red line corresponds to the K–Pg boundary.

modeling body size change across the K–Pg boundary is challenging in light of a sparse crown bird fossil record in the latest Cretaceous and earliest Cenozoic. But why is the fossil record during this interval so sparse? First, factors related to fossil preservation and recovery potential may conspire against the discovery of small-bodied fossils (Brown et al., 2013); thus, selectivity for reduced body size in the wake of the K–Pg may be partly responsible for a limited early Cenozoic record. How-

ever, a more important factor may have been the actual ecological rarity of birds triggered by the Chicxulub asteroid impact and its apocalyptic aftereffects (Robertson et al., 2004; Field et al., 2018b), which must have devastated population sizes even among surviving species. Such rarity—which can easily be misinterpreted as absence (Hull et al., 2015)—is likely also to blame for the limited bird fossil record during the first five million years of K–Pg recovery.

Could the devastation of population sizes in the wake of the K-Pg have exacerbated a substitution rate acceleration among birds? Theoretical work has established a negative relationship between population size and substitution rate when most mutations are slightly deleterious (Woolfit, 2009). For slightly deleterious mutations, the strength of drift scales negatively with effective population size (Kimura, 1968), leading to increases in substitution rates across lineages subjected to large reductions in effective population size (Ohta, 1973; Woolfit and Bromham, 2003; Lanfear et al., 2014). This may occur even when reductions in population size lead to a decline of absolute genetic diversity on micro-evolutionary scales within lineages. Depending on the relative interplay of these phenomena, dramatic changes in population sizes throughout Earth history may be associated with transient changes in substitution rates across the Tree of Life. If surviving lineages of birds—and indeed other organisms—across the K-Pg boundary suffered substantial and long-lasting reductions in their population sizes, then the relationship between drift and population size may have transiently increased nucleotide substitution rates in lineages surviving the K-Pg mass extinction. In combination with a probable Lilliput-effect-related acceleration of the molecular clock (Berv and Field, 2018), a population size-related acceleration would have increased the number of nucleotide substitutions in K-Pg boundary-crossing lineages, thereby increasing the lengths of the phylogenetic branches subtending many extant avian orders, and driving inevitable overestimates of the ages of these clades.

TREE PRIORS: MODELING LINEAGE DIVERSIFICATION AND TAXON SAMPLING

While the focus of the present article concerns the potential for underappreciated sources of systematic bias in inferences of substitution rates, the assumption of particular “tree priors” in divergence-time analyses is also germane, and deserves at least a brief discussion. Some avian

divergence-time analyses have applied a Yule process tree prior (e.g., Jetz et al., 2012), which assumes that lineages branch at a constant birth-rate without any chance of extinction (Yule, 1925). The assumptions of such a simple diversification model will clearly not be met for many clades. However, the potential effects of this kind of prior misspecification in divergence-time analyses are only beginning to receive more attention (Condamine et al., 2015). For example, given the assumption of a constant-rate Yule tree prior and a relaxed clock (as described in Drummond and Bouckaert, 2015), the interaction of these priors may result in a situation where the clock model is forced to fit slower or faster rates into branch lengths that are highly conditioned by the assumed tree prior. As such, it is possible that this type of prior misspecification may further confound both avian substitution rate and divergence-time estimates.

More complex tree priors (which, for example, allow for constant-rate extinction) are available, and are perhaps reasonable starting points (Nee et al., 1994; Mooers and Heard, 1997; Nee, 2001). However, a recent study (Claramunt and Cracraft, 2015) convincingly showed that the lineage-sampling fraction (i.e., the proportion of sampled taxa relative to the total number of extant lineages) can also have a significant and predictable effect on estimated avian divergence times (Yang and Rannala, 1997). By failing to account for incomplete sampling, the most-often used tree priors (Yule and birth-death) bias deep nodes to be older and young nodes to be younger (see supplemental materials in Claramunt and Cracraft, 2015). Stadler (2009) showed that we cannot empirically estimate both sampling probability together with birthrates and death rates: “One of these has to be known in order to estimate the other two.” Thus, the sampling fraction can have a significant effect if it is small (Stadler, 2009), which is commonly the case for large-scale investigations of avian divergence times (Alfaro et al., 2009; Jarvis et al., 2014; Prum et al., 2015). Not only does the sampling fraction influence divergence-time estimates, but so does the

sampling model. Taxa sampled to date backbone phylogenies are selected in a deliberately nonuniform manner to maximize diversity across the tree, enriching the tree for ancient branching events. Failing to account for diversified taxon sampling will bias birth and death estimates toward low speciation rates and near-zero death rates (Höhna et al., 2011), and thus will skew divergence-time estimates. Given the results of Claramunt and Cracraft (2015), we recommend that the birth-death-sampling tree prior (Stadler, 2009) be incorporated as the “null” tree prior for future investigations of avian divergence times relying on family-level (or similarly incomplete) sampling. Combined consideration of sampling fraction *and* the substitution rate biases discussed here will likely result in increasingly accurate and precise molecular age estimates for the crown bird MRCA. Correspondingly, we predict that more integrative models will shift age estimates for the age of crown birds later in the Cretaceous than have typically been recovered.

BIOGEOGRAPHIC DATING TO BOUND MAXIMUM AGE ESTIMATES

A sparse fossil record limits how reliably we can assign maximum ages for the deepest clades of modern birds in divergence-time analyses. However, maximum ages may be estimated under certain idealized paleogeographic and biogeographic conditions. As an example, a radiation endemic to a volcanic island is generally assumed to be younger than the island itself (Lerner et al., 2011). Biogeographic dating is the practice of time-calibrating trees based on plausible relationships among biogeography, paleogeography, and clade age (Ho et al., 2015; De Baets et al., 2016). Biogeographic dating operates under the premise that paleogeographic events—such as continental rifting or the rising of a mountain range—should influence when and where lineages diversify. If a paleogeographic event and a phylogenetic divergence are both congruent with a biogeographic disjunction and a hypothetical biogeographic scenario, then

using that paleogeographic event's age to date the divergence event represents a means for establishing hypotheses of maximum clade ages.

There is no shortage of paleogeographic events that potentially influenced the diversification of crown bird lineages. Clades endemic to newly habitable islands or mountains have been used to impose hard maximum age constraints as described above, as with the reemergence of New Zealand (Cooper and Cooper, 1995; Landis et al., 2008) or with the uplift of the Andes (Hoorn et al., 2010). Similarly, new interregional dispersal corridors may serve as soft maximum age constraints for radiations within regions, such as the collision of the Sunda and Sahul Shelves (e.g., Lohman et al., 2011) that facilitated the Out-of-Australia oscine passerine radiation (Moyle et al., 2016; Oliveros et al., 2019). Vicariance calibrations are a third type of calibration that depict an ancestrally widespread lineage split into two descendant lineages by a newly formed geographical barrier. The final throes of Gondwanan vicariance during the Paleogene may explain some crown bird biogeographic disjunctions between South America and Australia, two continents that shared an Antarctic connection perhaps as recently as the Eocene (Scher and Martin, 2006; Near et al., 2015). While vicariance calibrations generate strong maximum and minimum age constraints, they are often the most difficult biogeographic scenarios to justify (Goswami and Upchurch, 2010; Kodandaramaiah, 2011). Although few such paleogeographic events are likely to bear directly upon the origins of the deepest crown bird nodes (e.g., Palaeognathae, Galliformes, Anseriformes, Neoaves) during the Early Paleogene, they are still indirectly useful. Maximum age constraints interspersed throughout the phylogeny may serve to limit the maximum age of a crown group—which may otherwise extend to implausibly ancient age estimates in the absence of maximum age constraints (fig. 5; Cracraft et al., 2015)—and thereby bound node age estimation errors.

In practice, there are two principal strategies for time-calibrating phylogenies with biogeography: prior-based node calibration methods and

process-based inference methods. Biogeographic node calibration methods emulate a singular and specific biogeographic scenario (Ho et al., 2015; De Baets et al., 2016) in a manner similar to how fossil node calibrations are applied (Parham et al., 2011). However, an important distinction is that fossil priors are justified by asserting phylogenetic relationships between extant and fossil taxa based on morphological affinities, while biogeographic priors are justified by hypothesizing interactions among paleogeography, biogeography, and diversification that are often quite circumstantial. Correspondingly, in dating analyses for modern birds, biogeographic node calibrations are often critiqued as dubious because they invoke specific scenarios that fail to rule out alternative explanations (Claramunt and Cracraft, 2015; Gibb et al., 2015; Field and Hsiang, 2018). Because we generally do not know the true biogeographic history of any clade, process-based methods absorb this uncertainty into the broader inference problem. Process-based methods estimate not only divergence times, but also the full distribution of plausible biogeographic scenarios and palaeogeographic interactions that are compatible with the observed species ranges under a defined model of range evolution (Landis, 2017; Landis et al., 2018). Where prior-based methods are useful for their efficiency and simplicity, process-based methods are designed to handle the sources of historical uncertainty inherent to characterizing crown bird biogeography and diversification (Mayr, 2009, 2016; Claramunt and Cracraft, 2015; Prum et al., 2015; Berv and Field, 2018; Saupe et al., 2019).

Regardless of which biogeographic dating method is applied, the resultant divergence-time estimates should be viewed cautiously and critically. Lack of data on the ranges of extinct lineages can bias range reconstructions to reflect only present day distributions (Donoghue and Moore, 2003; Crisp et al., 2011; Friedman et al., 2013; Wood et al., 2013; Dornburg et al., 2015; Federman et al., 2015; Field and Hsiang, 2018; Saupe et al., 2019). However, these approaches can be used to provide expectations of what combination of

biogeographic conditions and molecular rates would be necessary under alternative temporal hypotheses of diversification. In the case of birds, such approaches could be particularly useful in testing for congruence between biogeography and different hypotheses of clade age.

THE WAY FORWARD

There is evidently cause for concern that life-history-driven fluctuations in substitution rates can bias molecular-clock-based age estimates of crown bird divergences. The question becomes: where to go from here? One solution is the development of a time-heterogeneous clock model that can explicitly account for the pernicious K-Pg-related divergence-time errors introduced above. This model would be similar in its implementation to node dating—that is, at certain (user-defined) time slices, nodes, or branches, rates of evolution may be calibrated to increase or decrease, either suddenly or slowly, on the basis of independent evidence from the fossil record (e.g., in the case of birds, along the stem lineages of Palaeognathae, Neognathae, Galloanserae, and Neoaves). In practice, this concept may be encoded into an empirical prior that describes the acceleration and deceleration of molecular substitution rates over time, leveraging evidence from the fossil record of periodic trends in directional trait evolution (such as shifts in body size) and the co-evolutionary relationship between life history traits and molecular rates. However, such a model also poses the risk of high circularity depending on what is considered evidence by the investigator. In the case of the avian fossil record, limited information would simply lead to such a model reflecting the community's emerging prior beliefs and be no different than setting time constraints based on limited fossil data. This is not to say that such a model is without value, as even knowingly enforcing prior beliefs would generate expectations of the levels of heterotachy necessary to reconcile conflict between molecular and fossil-based age estimates.

An alternative solution is to develop molecular clock models that can integrate the complex correlational patterns between substitution rate and quantitative traits, like body size or other life history characters. Encouragingly, such models are already being developed (Lartillot and Poujol, 2010), providing a more sophisticated framework from which to account for the issues outlined above. This class of models could be further expanded to guide expectations of rate changes along specific branches of a given tree using advances in divergence dating that incorporate fossils as terminal taxa (Ronquist et al., 2012; Zhang et al., 2015) and mixed clock models that allow the degree of rate autocorrelation to fluctuate (Lartillot et al., 2016). By reconstructing ancestral states using fossil data (potentially incorporating expectations of preservation bias or temporal gaps), this would highlight where on a tree to expect changes in traits that might otherwise be masked by the absence of fossil taxa. Combining the expected distribution of trait states with an expectation of how strongly molecular rates correlate with these traits could guide the distributions of rates and times estimated for a given branch. While such a model is appealing, the computational burden of existing methods with the ability to model life history evolution currently limits their applicability in large-scale phylogenomic datasets (Berv and Field, 2018). In the case of avian phylogeny, this approach is also challenged by apparent body size decreases across the K-Pg influencing multiple lineages (Berv and Field, 2018). If such rapid changes occurred, they could render early small forms largely indiscernible in ancestral state reconstructions. Moreover, clade-wide epoch effects are not likely to be exclusively restricted to periods of extinction recovery: recent investigations of cichlid genomes suggested an acceleration of molecular rates prior to the onset of the adaptive radiation of African rift lake cichlids, suggesting that periods of rapid molecular evolution may represent a precondition of adaptive radiation in some instances (Brawand

et al., 2014). If this is true, then epoch effects could be commonly responsible for inducing large errors in divergence-time estimates. Further developments along these lines will certainly be fruitful for dating the Tree of Life as a whole, and it remains to be seen how such approaches could alter our understanding of early avian evolution.

In contrast to developing increasingly complex models, principles of phylogenetic experimental design offer a third approach: choosing markers that are not correlated with life history. Advocates of this approach have long argued that investigators use predictive frameworks for selecting loci of high utility for specific phylogenetic problems (Townsend, 2007; Townsend et al., 2012; Chen et al., 2015; Prum et al., 2015; Dornburg et al., 2016, 2017b; Bleidorn, 2017; Duchêne et al., 2017b). The use and development of these approaches has largely been restricted to tackling issues that arise when character states converge due to either substitution saturation (Dornburg et al., 2014; Theriot et al., 2015; Gilbert et al., 2018; Near et al., 2018) or biased patterns of nucleotide change (Borowiec et al., 2015; Romiguier et al., 2016; Dornburg et al., 2017a). However, selecting loci that do not depict a signature of directional change in molecular rates as a consequence of life history shifts is also an experimental design problem. For birds, assessing the strength of correlations between substitution rates and body sizes across loci, or among substitution types, could offer an additional criterion for selecting loci for divergence-time estimation (Smith et al., 2018). For example, it is well known that in mammals, substitutions that have occurred in CpG contexts display more clocklike behavior than most other types of substitution (Lanfear et al., 2010b). Further scrutinizing this candidate set of loci or substitutions to test against other major sources of error in divergence-time estimation such as substitution saturation (Phillips, 2009; Dornburg et al., 2014), high variance of site rates (Tinn and Oakley, 2008; Brandley et al., 2011), or clade-specific rate heterogeneity (Soltis et al., 2002; Dornburg et al.,

2012) should in principle lead to refined molecular clock estimates that could mitigate against the potential for “epoch effects” to mislead divergence-time analyses.

Regardless of whether these or other approaches are taken as the path forward for developing a better understanding of avian divergence times, it is important to consider that there is only one true history of paravian evolution. Given the currently wide-ranging estimates for the age of crown bird origins (fig. 2), there is still tremendous opportunity to unmask pathologies in our use of both molecular and paleontological data. It is our view that the evidence for organismal life histories that favored mass extinction survival and recovery, coupled with the strong correlation of these traits with molecular rates in markers commonly used for phylogenetics, suggest an underappreciated source of error for divergence-time estimation (Berv and Field, 2018). If life-history-associated shifts in molecular rates are responsible for systematically biasing age estimates for crown birds, then strategies such as those outlined above should all eventually converge on a similar range of age estimates. It is our hope that this review catalyses work testing this hypothesis.

CONCLUSIONS

An accurate understanding of the antiquity of the deepest crown bird nodes has broad implications for reconstructing the macroevolutionary history of modern birds. Assessing the interplay of the extant paravian radiation with major events in Earth history (e.g., Prum et al., 2015), periods of climatic upheaval (e.g., Claramunt and Cracraft, 2015), and potential episodes of vicariance (e.g., Cracraft, 2001) all fundamentally depend on reliable estimates of the age of the avian crown group and its major subclades. Moreover, estimates of diversification rates similarly depend on confident assessments of phylogenetic branch lengths. However, conflicts between paleontological

evidence and molecular divergence-time estimates cast a long shadow of uncertainty over downstream inferences.

We propose that a driver of this conflict may be a failure to account for epoch effects in substitution rates caused by epoch effects in life history traits. If our hypothesis of elevated nucleotide evolution in the wake of the K-Pg mass extinction is correct, then this presents the exciting possibility that the resultant pulse of molecular evolution provided the genomic substrate for the rapid early Cenozoic diversification of modern avian lineages (Brawand et al., 2014). Lingering debates regarding the timing of deep evolutionary divergences within other major eukaryotic groups—such as major angiosperm subclades (e.g., Koenen et al., 2019), eutherian mammals (e.g., Phillips et al., 2016), acanthomorph fishes (e.g., Alfaro et al., 2018), and even crown Metazoa (e.g., Lee and Ho, 2016)—may additionally be related to similar epoch effects, suggesting that pulses of molecular evolution may often be associated with major evolutionary radiations. The development of divergence-time approaches capable of accommodating epoch effects, and simultaneously accounting for the interplay between molecular evolution and selection on life history parameters, would not only enable testing of this hypothesis but also more generally aid in establishing a more robust understanding of how major events in Earth history have influenced evolutionary patterns across the Tree of Life.

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