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1 **Early evolution of modern birds structured by global forest collapse at the end-**
2 **Cretaceous mass extinction**

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24 **Summary**

25 The fossil record and recent molecular phylogenies support an extraordinary early
26 Cenozoic radiation of crown birds (Neornithes) following the Cretaceous-Paleogene (K–
27 Pg) mass extinction [1-3]. However, questions remain regarding the mechanisms
28 underlying the survival of the deepest lineages within crown birds across the K–Pg
29 boundary, particularly since this global catastrophe eliminated even the closest stem
30 group relatives of Neornithes [4]. Here, ancestral state reconstructions of neornithine
31 ecology reveal a strong bias toward taxa exhibiting predominantly non-arboreal lifestyles
32 across the K–Pg, with multiple convergent transitions toward predominantly arboreal
33 ecologies later in the Paleocene and Eocene. By contrast, ecomorphological inferences
34 indicate predominantly arboreal lifestyles among enantiornithines, the most diverse and
35 widespread Mesozoic avialans [5-7]. Global paleobotanical and palynological data show
36 that the K–Pg Chicxulub impact triggered widespread destruction of forests [8, 9]. We
37 suggest that ecological filtering due to the temporary loss of significant plant cover across
38 the K–Pg boundary selected against any flying dinosaurs (Avialae [10]) committed to
39 arboreal ecologies, resulting in a predominantly non-arboreal post-extinction neornithine
40 avifauna composed of total-clade Palaeognathae, Galloanserae, and terrestrial total-clade
41 Neoaves that rapidly diversified into the broad range of avian ecologies familiar today.
42 The explanation proposed here provides a unifying hypothesis for the K–Pg-associated
43 mass extinction of arboreal stem birds, as well as for the post-K–Pg radiation of arboreal
44 crown birds. It also provides a baseline hypothesis to be further refined pending the
45 discovery of additional neornithine fossils from the Latest Cretaceous and earliest
46 Paleogene.

48 **Keywords:** Mass Extinction; K–Pg; Birds; Paleobotany; Ancestral States; Ecological
49 Selectivity

51 **Results**

52 *Neornithine ecological selectivity across the K–Pg*

53 Ancestral ecological reconstructions (AERs) using recent time-scaled avian phylogenies
54 [2, 11] under likelihood, maximum parsimony, and Bayesian stochastic mapping
55 frameworks yielded a clear ecological signal across the K–Pg boundary (Figure 1 and
56 Supplemental Information). The deepest nodes within Neornithes are inferred to be
57 predominantly non-arboreal, both in terms of general lifestyle and nesting substrate,

58 including the most recent common ancestor (MRCA) of Neornithes (the crown bird root
59 node), and the MRCAs of Palaeognathae (ostriches and kin), Neognathae (all non-
60 palaeognath Neornithes), and Neoaves (all neognaths excluding ducks, chickens, and
61 their close relatives). Numerous independent transitions toward predominant arboreality
62 are inferred for deep nodes within Neoaves early in the Cenozoic, including the
63 extremely speciose and largely arboreal Inopinaves (a major clade of ‘core land birds’
64 inferred to have transitioned to predominant arboreality by 64 million years ago) [2].
65 These results are robust to ongoing phylogenetic uncertainty with regard to neoavian
66 interrelationships and divergence times [1, 2, 11, 12].

67

68 *Terrestrial antecedents for numerous modern arboreal bird clades*

69 Our AERs identify several extant clades with inferred transitions to arboreality early in
70 the Cenozoic. Some of these clades, such as Otidimorphae (turacos, cuckoos, and
71 bustards) and Telluraves (all Inopinaves except the Hoatzin), are represented by early
72 diverging crown clade fossils from the early Paleogene. The earliest well-constrained
73 crown neoavian fossil (the stem mousebird *Tsidiyazhi abini*) is inferred by Ksepka and
74 colleagues to be predominantly arboreal [3]. However, that study also suggests that the
75 advanced zygodactyl and semizygodactyl perching specializations of *T. abini* and other
76 arboreal members of Telluraves are the product of multiple independent origins in the
77 Paleocene and Eocene. Additionally, hindlimb proportions among Otidimorphae covary
78 with degrees of arboreality and terrestriality ([13], Figure 2), and indicate that the earliest
79 known crown otidimorph, the stem turaco *Foro panarium*, was most likely ground-
80 dwelling, despite arboreality predominating among extant turacos.

81

82 *Assessing the extent and timeline of K–Pg forest collapse*

83 Palynological data from K–Pg boundary sections worldwide reveal a vegetation response
84 with a fern spike and floral turnover [14], which together indicate forest destruction on a
85 global scale and a protracted (~1,000-year) onset of the recovery of climax vegetation
86 [15]. We assessed the response of forest communities to the Chicxulub impact in the
87 western interior of North America by conducting high-resolution relative abundance
88 palynological analyses (down to 1 cm sampling intervals immediately above and below
89 the boundary) of the John’s Nose K–Pg boundary section in southwestern North Dakota
90 (Figure 3). The North American K–Pg boundary sections constitute the best high-
91 resolution record of the K–Pg transition in terrestrial ecosystems [16], and John’s Nose is
92 one of two sections in southwestern North Dakota that preserve the boundary clay and
93 impact spherules, providing direct evidence of the Chicxulub impact. The palynological
94 record shows the K–Pg boundary fern spike (*Cyathidites* sp. and *Laevigatosporites* sp., >
95 70 %) 2-7 cm above the boundary, and floral turnover from 7 cm above the boundary as
96 indicated by the disappearance of typical Cretaceous pollens (K-taxa) and the dominance
97 of new pollen types in the earliest Paleocene (*Ulmipollenites krempii*, *Kurtzipites*
98 *circularis*, *K. trispissatus*, *Taxodiaceapollenites* sp., and bisaccate pollen grains; Table
99 S1).

100

101 **Discussion**

102 Synthesis of recent results from palaeontological studies and molecular divergence time
103 analyses supports a major influence of the end-Cretaceous asteroid impact on near-crown

104 and early crown bird evolution [1, 2, 4, 17, 18]. Fossil evidence suggests that the entirety
105 of the neornithine stem group—including pterosaurs and all non-neornithine dinosaurs—
106 perished in the aftermath of the impact [19], 66.02Ma [15]. This includes even the
107 crownward-most Mesozoic avialans outside of living bird diversity, such as
108 Ichthyornithes (*Ichthyornis* and kin), Hesperornithes (*Hesperornis* and kin),
109 Palintropiformes (relatives of *Palintropus retusus* and *Apsaravis ukhaana*), and the
110 diverse and globally widespread Enantiornithes (“opposite birds”), which persisted into
111 the terminal Cretaceous (Maastrichtian) [4] (Figure 4). Although the very deepest
112 phylogenetic divergences within Neornithes likely took place during the Mesozoic, such
113 as the divergence between Palaeognathae and Neognathae (the neornithine root node),
114 and that between Galloanserae and Neoaves (the deepest divergence within Neognathae),
115 virtually the entirety of the avian crown group fossil record is restricted to sediments of
116 Cenozoic age, and the earliest well-supported crown bird fossil is scarcely older than the
117 end-Cretaceous, at approximately 67Ma [3, 20].

118

119 *Factors influencing the post-Cretaceous survival of crown birds*

120 Despite accumulating evidence for the dramatic influence of the Chicxulub asteroid
121 impact on the evolutionary history of the neornithine total clade, little is known about
122 either the factors that drove crownward stem birds such as enantiornithines to extinction,
123 or the biological attributes of early crown birds that survived the mass extinction and
124 radiated in its wake. Recently, selection for the toothless bill which characterizes crown
125 birds was posited as a potential factor favoring crown bird survivorship over other
126 contemporaneous small theropods [21]. This argument suggests that the bill would have

127 facilitated feeding on the hardy seeds and grains that may have been available as a food
128 source in the immediate aftermath of the asteroid impact. While this may be true, such a
129 scenario ignores the fact that teeth do not preclude granivory (some toothed avialans are
130 known to have fed on seeds [22]), and that a toothless bill was acquired multiple times
131 among Mesozoic Avialae, including among derived enantiornithines [23]. Additionally,
132 work incorporating fossil body size estimates, ancestral state reconstructions, and rates of
133 molecular evolution suggests that birds surviving the K–Pg mass extinction underwent
134 transient selection and filtering for reduced body size (a Lilliput Effect) [18], which may
135 have facilitated avian survival by transiently reducing their total energetic requirements.
136 Research on the evolution of neornithine breeding habits [24] suggests that, relative to
137 Enantiornithes, ancestral crown birds may have acquired proportionally larger eggs and
138 alternative nesting substrates. Moreover, evolution of a crown-grade alimentary system
139 has additionally been posited as a factor that may have influenced the post-K–Pg survival
140 of Neornithes [25]; both of these latter hypotheses are tantalizing, and warrant additional
141 research.

142 While all of the scenarios described above are plausible and not mutually
143 exclusive, none fully explain the differential survivorship of early crown birds relative to
144 crownward stem birds such as enantiornithines (which, despite differences in biological
145 attributes such as skeletal pneumaticity and growth rates, were likely biologically similar
146 to Neornithes, and probably more diverse and widespread in the terminal Cretaceous) [4].
147 Alone, these scenarios reveal an incomplete picture of broad-scale ecological selectivity
148 among the crown birds that survived the K–Pg mass extinction.

149 We propose a new hypothesis regarding the extinction of stem birds and the
150 survival of crown birds across the K–Pg boundary; namely, that global deforestation
151 caused by the Chicxulub impact induced a selective filter against the survival of arboreal
152 birds. Given compelling evidence for transient asteroid impact-induced deforestation
153 coincident with the end-Cretaceous mass extinction (Figure 3), the selective
154 consequences of widespread forest destruction on i) the extinction of non-neornithine
155 Avialae and ii) survival patterns among Neornithes must be investigated. While this
156 hypothesis likely does not constitute the sole factor influencing end-Cretaceous avian
157 survivorship (indeed, it is unlikely that any single hypothesis completely explains global
158 avian survival patterns), the strength of our results, and their compatibility with other
159 studies (e.g. [18, 21]) suggest that selection against avian arboreality across the K–Pg is
160 likely to have played a major role in structuring the early evolutionary history of
161 Neornithes.

162

163 *Evidence for global deforestation at the K–Pg boundary*

164 The plant fossil record and models of the effects of the Chicxulub impact provide strong
165 evidence for the devastation of forest communities at the K–Pg boundary. Initial
166 disruption came from energy dissipated by the impact blast, leveling trees within a radius
167 of ~1500 km, and as intense radiated heat, which may have ignited wildfires on a global
168 scale [26-28]. This was likely followed by acid rain resulting from the emission of
169 sulfate-rich vapour [29], and ejection of a large quantity of soot into the atmosphere [30],
170 potentially blocking photosynthetic activity for several years and likely inducing limited
171 global climate cooling [31-34]. This phase of suppressed sunlight, notoriously difficult to

172 reconstruct, is supported by the proliferation of saprotrophs thriving on decomposing
173 organic matter [35].

174 The post-impact recovery of terrestrial plant communities occurred in two phases.
175 The first is marked by the dominance of fern spores in a ~1 cm-thick interval [36] (Figure
176 3). Ferns are pioneer re-colonizers of devastated landscapes, and their proliferation
177 represents a classic example of a ‘disaster flora’ composed of taxa capable of rapidly
178 germinating from spores and rhizomes/roots. Recent examples of fern spikes have been
179 recorded in the recolonization of rapidly denuded landscapes, such as freshly deposited
180 lava flows in Hawaii, slopes left barren by massive landslides induced by the 1980
181 eruption of Mount St. Helens, and the short-lived dominance of ferns in the Krakatau
182 floras following its 1883 eruption [8]. The K–Pg fern spike has been identified worldwide
183 and is an indicator of global canopy loss ([14] and references therein). Sedimentation
184 rates based on recent high resolution radiometric dating of K–Pg bentonites from
185 Montana [37] and the Denver Basin [15] show that establishment of the fern spike
186 occurred within a century following the Chicxulub impact, and that the fern spike disaster
187 flora persisted on the order of 1,000 years. This general timescale is corroborated by
188 estimated sedimentation rates from New Zealand (Figure S1). Terrestrial floras were
189 likely devoid of extensive closed-canopy forests during this phase.

190 The second phase is marked by the re-establishment of canopy vegetation: The
191 earliest Paleocene marks a change in forest community structure compared to the
192 Cretaceous. Typical earliest Paleocene plant assemblages are characterized by low
193 taxonomic diversity [38-40] and by a shift of dominance toward new angiosperms and
194 conifers (disappearance of diverse Cretaceous taxa [K-taxa], and proliferation of

195 *Ulmipollenites krempii*, *Kurtzipites* spp., palms [*Arecipites* spp.], *Taxodiaceae* and
196 *Pinaceae*; Figure 3), long-lived plants that are indicative of modern climax communities
197 [14, 41]. This low-diversity flora persists until the appearance of diversity hot-spots ~1.4
198 Myrs after the K–Pg [42].

199 Today, avian community diversity is negatively influenced by loss of plant
200 diversity and habitat due to human activity including monospecific agriculture and land-
201 use patterns [43], and the early Paleocene low-diversity floral phase may have similarly
202 affected avian communities at that time.

203

204 *Selective extinction of arboreal stem birds at the K–Pg boundary*

205 As many as five major clades of Mesozoic non-crown avialans are known to have
206 persisted into the final 300,000 years of the Cretaceous [4], and are inferred to have
207 exhibited a diversity of lifestyles (Figure 4). The most diverse and globally widespread of
208 these clades, Enantiornithes, generally exhibit feet with specializations for grasping,
209 including long and opposable hind toes (e.g. [6, 7]). These features have long been used
210 to identify most enantiornithines as tree-dwelling birds [5], although some
211 enantiornithines (e.g. the Late Cretaceous taxa *Elsornis keni* and *Lectavis bretincola*)
212 may have had reduced flight capabilities or wading specializations, suggesting a breadth
213 of ecological habits including predominantly non-arboreal lifestyles [44]. Other
214 crownward avialans known from the terminal Maastrichtian, such as hesperornithines and
215 ichthyornithines [4, 45] exhibit aquatic ecologies, and the extinction of at least their
216 marine representatives is likely related to concomitant extinctions among marine
217 tetrapods at the K–Pg boundary [46]. Little is known regarding the ecological habits of

218 Palintropiformes, another clade of near-crown stem birds thought to have persisted up to
219 the K–Pg boundary [4]. If the generally arboreal habits inferred for most Enantiornithes
220 [5] indicate that they were largely associated with forested environments and dependent
221 upon arboreal habitats, then the widespread destruction of forests coincident with the K–
222 Pg transition would undoubtedly have played a major, if not absolute, role in the demise
223 of this dominant Mesozoic clade. The same should be true for any as-yet undiscovered
224 arboreal specialists among early crown birds and stem group ornithurines in the late
225 Maastrichtian. More generally, a model of deforestation-related ecological selectivity
226 across the K–Pg boundary may help explain broad-scale patterns in the early evolutionary
227 history of other major vertebrate clades (e.g. [47]).

228

229 *Selective survival of non-arboreal crown birds at the K–Pg boundary*

230 Ancestral state reconstructions for the deepest nodes among crown birds yield a clear
231 signal of ecological selectivity across the K–Pg boundary (Figure 1). The deepest nodes
232 within the bird crown (the most recent common ancestor, or MRCA, of Neornithes,
233 Palaeognathae, Neognathae, Galloanserae, and Neoaves) are unambiguously
234 reconstructed as predominantly non-arboreal (Bayesian posterior probabilities and
235 marginal ancestral states all = 100% across both backbone topologies). This
236 reconstruction suggests that no lineages of arboreal crown birds crossed the K–Pg
237 boundary, and that the numerous independent transitions toward arboreality across the
238 neornithine tree of life—including ancient transitions within major clades such as
239 Strisores (hummingbirds, nightjars, and kin), Otidimorphae, Columbimorphae (pigeons

240 and kin), and Inopinaves—took place subsequent to the K–Pg transition, presumably
241 after global forests had rebounded from their devastation following the asteroid impact.

242

243 *Evidence from the early Cenozoic neornithine fossil record*

244 The early crown bird fossil record reveals additional support for a survivorship model
245 whereby lineages surviving the K–Pg mass extinction were predominantly ground
246 dwelling. For example, Otidimorphae (one of the most deeply diverging clades within
247 Neoaves [2]) comprises a disparate group of extant birds across three major subclades:
248 turacos (Musophagidae), cuckoos (Cuculidae), and bustards (Otididae) [2] (Figure 2).
249 Extant turacos are medium-sized, predominantly arboreal frugivores, and bustards are
250 large to very large obligate ground-dwellers. Cuckoos exhibit more varied ecologies,
251 ranging from predominant ground dwelling in the ‘ground cuckoo’ clade Neomorphinae
252 (which includes the Greater Roadrunner, *Geococcyx californianus*) to predominant
253 arboreality in other subclades [48]. Although the early fossil record of Otidimorphae is
254 sparse [20], the earliest known apparent crown otidimorph is the stem group turaco, *Foro*
255 *panarium*, from the early Eocene of Wyoming [13]. Hindlimb proportions covary closely
256 with ecology in Otidimorphae (Figure 2; as they do in many living birds [49]), with
257 arboreal taxa such as turacos and arboreal cuckoos exhibiting relatively short hindlimbs,
258 and predominantly ground-dwelling taxa such as neomorphine ground cuckoos and
259 bustards exhibiting long hindlimbs [13]. The long hindlimb proportions of *F. panarium*,
260 which fall within the range of small bustards, suggest that the arboreal habits of crown
261 turacos arose from ground-dwelling ancestors, consistent with a model in which

262 representatives of Neoaves in the early Cenozoic retained the ground-dwelling habits of
263 K–Pg survivors.

264 The earliest well-constrained neoavian fossil, *Tsidiyazhi abini*, was recently
265 described from the early Paleocene (~62.5Ma) of New Mexico [3]. *T. abini* was inferred
266 to represent an early stem mousebird (Coliiformes), a clade exhibiting predominantly
267 arboreal habits today. However, ancestral state reconstructions that include *T. abini* and
268 other early Cenozoic fossils suggest that hindlimb modifications for perching may have
269 arisen independently in numerous arboreal clades of Telluraves, including Coliiformes,
270 following the K–Pg mass extinction [3]. This evidence supports a model whereby early
271 ground-dwelling neoavians repeatedly took to the trees relatively early in the
272 Paleocene—potentially filling arboreal niches vacated by Cretaceous enantiornithines and
273 stem ornithurines—following the recovery of global forests after the Chicxulub impact.

274

275 *Conclusions*

276 The sudden onset of the K–Pg extinction event 66.02 Ma poses significant challenges for
277 researchers seeking to unravel its drivers (beyond the asteroid impact itself) and their
278 consequences. These challenges are magnified for taxa with sparse K–Pg fossil records,
279 such as birds, and for scenarios involving phenomena predicted to have taken place over
280 ecological time intervals, such as transient yet widespread impact-related deforestation.
281 Our picture of the contours of this extinction in terms of bird evolutionary history is still
282 incipient; however, consilient evidence from the fossil record [3, 4, 20, 50], molecular
283 divergence time estimates [1, 2, 11], rates of molecular evolution [18], and
284 environmental/ecological reconstructions ([21] and this study), increasingly point to the

285 K–Pg impact and its consequences as playing major roles in the selective filtering of bird
286 survivorship. All available evidence appears congruent with the globally widespread
287 destruction of forests coincident with the K–Pg event imposing a strict filter against the
288 persistence of avialans exhibiting arboreal ecologies.

289 A succession of events implicated in the destruction of global forests would have
290 primarily affected arboreal taxa, including shock waves knocking down trees
291 immediately following the impact, wild fires directly eliminating forest habitats, as well
292 as reduced light levels and associated global cooling delaying forest recovery. Although a
293 multitude of factors undoubtedly influenced avian evolution at the end-Cretaceous mass
294 extinction, including diet [21, 25], body size [18], breeding habits [24], and flight
295 capacity [51], selection for non-arboreal habits appears to have left an indelible mark on
296 the early evolutionary history of crown birds, clearly discernible more than 66-million-
297 years later.

298

299 **Author Contributions:**

300 Conceptualization, D.J.F. and J.A.G.; Methodology, D.J.F., A.B., J.S.B., R.D., T.R.L.
301 and V.V.; Investigation, D.J.F., A.B., J.S.B. and V.V.; Writing – Original Draft, D.J.F.;
302 Writing – Review and Editing, D.J.F., A.B., J.S.B., R.D., D.E.F., T.R.L., V.V. and J.A.G.
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313

314 **Declaration of Interests**

315 The authors declare no competing interests.

316

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- 507

508 **Figure Legends**

509 **Figure 1 Ancestral ecological reconstructions reveal bias toward non-arboreal birds**

510 **across the K–Pg.** Bayesian ancestral ecological reconstructions (AERs) indicate that the

511 most deeply diverging crown bird clades, including Neornithes (all crown birds),

512 Neognathae (Galloanserae + Neoaves), and Neoaves, were ancestrally non-arboreal ($pp >$

513 0.99 for each node), with numerous independent transitions toward arboreality arising in

514 the early Cenozoic, presumably after global forests had recovered from the Chicxulub

515 impact. Concentric background rings demarcate geologic periods: inner grey circle at the
516 centre is Late Cretaceous, with K–Pg boundary (66.02 Ma) shown by the red dashed line;
517 white ring is the Paleogene (66.02-23.03Ma), separated from the Neogene (23.03-
518 2.58Ma) by the dashed blue line. Tips extend to the present. Piecharts at nodes indicate
519 SIMMAP posterior probabilities for ancestral ecology, under our model. Branch colors
520 represent a single randomly sampled stochastic character map from a posterior sample of
521 1,000 maps. Underlying phylogeny and taxonomy follow [2]; qualitatively identical
522 patterns are inferred using an alternative phylogenetic hypothesis [11]. See also Figures
523 S2-S4, and doi.org/10.5281/zenodo.1204464 for alternative reconstructions.

524

525 **Figure 2 Hindlimb ecomorphology suggests delayed transitions toward arboreality**
526 **among Cenozoic crown birds.** Early Cenozoic fossils of some modern lineages
527 exhibiting largely arboreal habits suggest that their early antecedents were likely ground
528 dwelling [3, 50]. Hindlimb indices ((tarsometatarsus length + tibiotarsus length)/ femur
529 length) are plotted for the major clades within crown Otidimorphae: turacos (A; strictly
530 arboreal), cuckoos (B; exhibiting arboreal, non-arboreal, and mixed members), and
531 bustards (C; strictly ground-dwelling), as well as the early Eocene stem turaco *Foro*
532 *panarium* (D). *F. panarium* exhibits elongated hindlimb proportions greatly exceeding
533 the range of extant turacos and arboreal cuckoos, suggesting non-arboreal habits.
534 Predominantly arboreal taxa are green, predominantly non-arboreal are brown, and
535 ‘mixed’ are grey. See also Table S2.

536

537 **Figure 3: Palynological record of the John’s Nose section in North Dakota.**

538 Extinction (disappearance of K-taxa) and floral turnover are evidenced by changes in
539 relative abundance of common pollen taxa across the K–Pg boundary (modified from
540 [52]). BC = K–Pg boundary clay. See also Figure S1 and Table S1.

541

542 **Figure 4: Avialan diversity at the end-Cretaceous.** At least four major clades of near-
543 crown stem neornithines persisted into the latest Maastrichtian [4], including
544 Enantiornithes, the most widespread and diverse clade of Mesozoic Avialae. Figure
545 follows stratigraphic ranges from [4], with topology following recent work (e.g. [53, 54]).

546

547 **STAR Methods**

548 CONTACT FOR REAGENT AND RESOURCE SHARING

549 Further information and requests for resources and reagents should be directed to and will
550 be fulfilled by the Lead Contact, Daniel J. Field (d.j.field@bath.ac.uk).

551

552 METHOD DETAILS

553 Examining the extent of end-Cretaceous deforestation

554 Floral changes were characterized by analyzing relative abundance data of palynomorphs
555 (pollen, spores, algae) from twelve samples spanning the K–Pg boundary from the John’s
556 Nose section, southwest North Dakota [52]. Stages of recovery were categorized based
557 on Euclidean Distance of the relative abundance data for the 12 palynological
558 assemblages. Raw abundance data and stratigraphic sampling resolution are presented in
559 Table S1.

560

561 Determining the approximate timeframe of K–Pg forest recovery

562 The onset of fern recovery is estimated based on Iridium content in the sediments hosting
563 the fern-spore spike based on the fall-out time calculated in Ocampo et al. [55]. The
564 duration of fern spore dominance is based on combined calculations of sedimentation
565 rates from K-Pg boundary successions in New Zealand [9] and the USA [15].

566

567 Neornithine ancestral ecological reconstructions

568 Ancestral ecological reconstructions (AERs) were performed using recent time-scaled
569 neornithine phylogenies incorporating nearly every extant avian family-level clade [2,
570 11]. The 198 extant species in the original Prum *et al.* phylogenetic dataset [2], and the
571 229 from Claramunt and Cracraft [11] were scored as either predominantly arboreal,
572 predominantly non-arboreal, or ‘mixed’ (for taxa that spend much of their time in both
573 arboreal and non-arboreal settings). These alternative hypotheses span the present range
574 of uncertainty with regard to neornithine phylogenetic topology and divergence times.
575 Scorings were based on descriptions of general ecology, nest substrate, and foraging
576 substrate from [56]. Discrete codings for general lifestyle and nest substrate categories
577 are presented at doi.org/10.5281/zenodo.1204464, along with annotated R code (to
578 reproduce all analyses) and alternative reconstructions. Categorizing behavior for the
579 purpose of ancestral ecological reconstructions can be subjective (e.g. [57]); however, we
580 consider our criteria for bounding categories to be consistent, and to capture the
581 predominant ecological habits of each included species. For example, while the Greater
582 Roadrunner (*Geococcyx californianus*) is known to nest in low trees and bushes between

583 1-3m above the ground [56], it is generally considered predominantly ground-dwelling (a
584 scoring that well-reflects its general lifestyle and foraging substrate), and we therefore
585 considered ‘non-arboreal’ to be a more suitable category for *G. californianus* than
586 ‘mixed’. We believe that our conclusions are robust to alternative codings in similar
587 borderline cases, such as the Shining-blue Kingfisher (*Alcedo quadibrachys*), which
588 nests in burrows but is otherwise well classified as tree-dwelling and was therefore
589 classified as generally arboreal. Additionally, we performed reconstructions using scores
590 for general nest category (nests in trees vs. nests on ground vs. nests either in trees or on
591 ground), codings that may be less subjective. These reconstructions unambiguously
592 support ground-nesting habits as ancestral for the deepest neornithine nodes. The scenario
593 supported by these results (clear bias toward non-arboreal nesting across the K–Pg) is
594 qualitatively the same as that from our analysis of general lifestyle, and so are presented
595 as supporting data (Figure S2 and doi.org/10.5281/zenodo.1204464).

596

597 Fossil bird ecomorphology

598 An existing morphometric dataset for Otidimorphae [13] was expanded. Digital calipers
599 sensitive to 0.01mm were used to measure the total length of the femur, tibiotarsus, and
600 tarsometatarsus for adult turacos, cuckoos, and bustards (raw data in Table S2). Seven
601 species of Musophagidae were examined, representing every major musophagid
602 subclade. Thirty species of Cuculidae were examined from across the extant diversity of
603 cuckoos, and five species of Otididae were measured. Following [22], measurements
604 from extant taxa were compared to measurements from the fossil stem turaco *Foro*
605 *panarium* [13, 58].

606

607 QUANTIFICATION AND STATISTICAL ANALYSIS

608 Ancestral ecological reconstructions

609 Likelihood-based AERs were performed in R [59] using the `ace()` likelihood function in
610 `ape` [60] and the `make.simmap()` Bayesian stochastic character mapping (SIMMAP)
611 function in `phytools` [61, 62]. For both sets of analyses, we implemented a two-rate
612 transition matrix that defines one rate for forward and reverse transitions between
613 arboreality and non-arboreality, and another rate for forward and reverse transitions
614 between mixed and arboreal states, and mixed and non-arboreal states (in R: `matrix(c(0,`
615 `2, 1, 2, 0, 2, 1, 2, 0), nrow=3)`). This model allows transitions that pass through the mixed
616 phase to be favored, without preventing direct transitions. Under this model, the marginal
617 ancestral states (from `ace`) and Bayesian posterior probabilities from SIMMAP were
618 nearly identical ($R^2 > 0.99$), so we present our Bayesian results in Figure 1, summarized
619 across 1,000 stochastic character maps. Predominant arboreality and predominant non-
620 arboreality dominated inferred reconstructions throughout the tree (41.8% and 50.5% of
621 the tree, respectively), with mixed ecologies reconstructed across only 7.7% of the tree in
622 Figure 1. We also performed maximum parsimony reconstructions of ancestral ecological
623 habits and nesting substrate using the `ancestral.pars()` function with regular MPR
624 optimization implemented in the `phangorn` R package [63] (Figure S3 and
625 doi.org/10.5281/zenodo.1204464), which corroborated the results described above.

626

627 Fossil bird ecomorphology

628 Following [13], hindlimb indices were calculated by summing the lengths of the
629 tarsometatarsus and tibiotarsus, and dividing by the length of the femur.

630

631 DATA AND SOFTWARE AVAILABILITY

632 Scripts for the ancestral ecological reconstructions, as well as the input data for these
633 analyses and all AER results are archived at doi.org/10.5281/zenodo.1204464.

634

635