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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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Summary

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

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

Results

Neornithine ecological selectivity across the K–Pg

Ancestral ecological reconstructions (AERs) using recent time-scaled avian phylogenies [2, 11] under likelihood, maximum parsimony, and Bayesian stochastic mapping frameworks yielded a clear ecological signal across the K–Pg boundary (Figure 1 and Supplemental Information). The deepest nodes within Neornithes are inferred to be 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 *Tsidiiyazhi 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*, *Taxodiaceaepollenites* 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

4

and early crown bird evolution [1, 2, 4, 17, 18]. Fossil evidence suggests that the entirety

of the neornithine stem group—including pterosaurs and all non-neornithine dinosaurs—

perished in the aftermath of the impact [19], 66.02Ma [15]. This includes even the

crownward-most Mesozoic avialans outside of living bird diversity, such as

Ichthyornithes (*Ichthyornis* and kin), Hesperornithes (*Hesperornis* and kin),

Palintropiformes (relatives of *Palintropus retusus* and *Apsaravis ukhaana*), and the

diverse and globally widespread Enantiornithes ("opposite birds"), which persisted into

the terminal Cretaceous (Maastrichtian) [4] (Figure 4). Although the very deepest

phylogenetic divergences within Neornithes likely took place during the Mesozoic, such

as the divergence between Palaeognathae and Neognathae (the neornithine root node),

and that between Galloanserae and Neoaves (the deepest divergence within Neognathae),

virtually the entirety of the avian crown group fossil record is restricted to sediments of

Cenozoic age, and the earliest well-supported crown bird fossil is scarcely older than the

end-Cretaceous, at approximately 67Ma [3, 20].

Factors influencing the post-Cretaceous survival of crown birds

Despite accumulating evidence for the dramatic influence of the Chicxulub asteroid

impact on the evolutionary history of the neornithine total clade, little is known about

either the factors that drove crownward stem birds such as enantiornithines to extinction,

or the biological attributes of early crown birds that survived the mass extinction and

radiated in its wake. Recently, selection for the toothless bill which characterizes crown

birds was posited as a potential factor favoring crown bird survivorship over other

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

11

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, *Tsidiiyazhi 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.

303

Declaration of Interests

315 The authors declare no competing interests.

316

References

318 1.   Jarvis, E.D., Mirarab, S., Aberer, A.J., Li, B., Houde, P., Li, C., Ho, S.Y.W.,
319   Faircloth, B.C., Nabholz, B., Howard, J.T., et al. (2014). Whole-genome
320   analyses resolve early branches in the tree of life of modern birds. Science
321   *346*, 1320-1331.
322 2.   Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Lemmon, E.M.,
323   and Lemmon, A.R. (2015). A comprehensive phylogeny of birds (Aves) using
324   targeted next-generation DNA sequencing. Nature *526*, 569-573.
325 3.   Ksepka, D.T., Stidham, T., and Williamson, T. (2017). Early Paleocene
326   landbird supports rapid phylogenetic and morphological diversification of
327   crown birds after the K-Pg mass extinction. Proceedings of the National
328   Academy of Sciences *114*, 8047-8052.
329 4.   Longrich, N.R., Tokaryk, T., and Field, D.J. (2011). Mass extinction of birds at
330   the Cretaceous-Paleogene (K-Pg) boundary. Proceedings of the National
331   Academy of Sciences *108*, 15253-15257.
332 5.   Chiappe, L.M., and Qingjin, M. (2016). Birds of Stone: Chinese Avian Fossils
333   from the Age of Dinosaurs, (JHU Press).
334 6.   Hopson, J.A. (2001). Ecomorphology of avian and nonavian theropod
335   phalangeal proportions: Implications for the arboreal versus terrestrial
336   origin of bird flight. New Perspectives on the Origin and Early Evolution of
337   Birds, 211-235.
338 7.   O'Connor, J.K., Chiappe, L.M., Gao, C., and Zhao, B. (2011). Anatomy of the
339   Early Cretaceous enantiornithine bird Rapaxavis pani. Acta Palaeontologica
340   Polonica *56*, 463-475.
341 8.   Tschudy, R., Pillmore, C., Orth, C., Gilmore, J., and Knight, J. (1984). Disruption
342   of the terrestrial plant ecosystem at the Cretaceous-Tertiary boundary,
343   Western Interior. Science *225*, 1030-1033.

344 9. Vajda, V., Raine, J.I., and Hollis, C.J. (2001). Indication of global deforestation
345 at the Cretaceous-Tertiary boundary by New Zealand fern spike. Science *294*,
346 1700-1702.
347 10. Gauthier, J. (1986). Saurischian monophyly and the origin of birds. Memoirs
348 of the California Academy of Sciences *8*.
349 11. Claramunt, S., and Cracraft, J. (2015). A new time tree reveals Earth history's
350 imprint on the evolution of modern birds. Science Advances *1*.
351 12. Reddy, S., Kimball, R.T., Pandey, A., Hosner, P.A., Braun, M.J., Hackett, S.J., Han,
352 K.-L., Harshman, J., Huddleston, C.J., and Kingston, S. (2017). Why do
353 phylogenomic data sets yield conflicting trees? Data type influences the avian
354 tree of life more than taxon sampling. Systematic biology *66*, 857-879.
355 13. Field, D.J., and Hsiang, A.Y. (In press). A North American stem turaco, and the
356 complex biogeographic history of modern birds. BMC Evolutionary Biology.
357 14. Vajda, V., and Bercovici, A. (2014). The global vegetation pattern across the
358 Cretaceous–Paleogene mass extinction interval: A template for other
359 extinction events. Global and Planetary Change *122*, 29-49.
360 15. Clyde, W.C., Ramezani, J., Johnson, K.R., Bowring, S.A., and Jones, M.M. (2016).
361 Direct high-precision U–Pb geochronology of the end-Cretaceous extinction
362 and calibration of Paleocene astronomical timescales. Earth and Planetary
363 Science Letters *452*, 272-280.
364 16. Fastovsky, D.E., and Bercovici, A. (2016). The Hell Creek Formation and its
365 contribution to the Cretaceous–Paleogene extinction: A short primer.
366 Cretaceous Research *57*, 368-390.
367 17. Feduccia, A. (1995). Explosive evolution in Tertiary birds and mammals.
368 Science *267*, 637-638.
369 18. Berv, J.S., and Field, D.J. (2018). Genomic Signature of an Avian Lilliput Effect
370 across the K-Pg Extinction. Systematic Biology *67*, 1-13.
371 19. Brusatte, S.L., Butler, R.J., Barrett, P.M., Carrano, M.T., Evans, D.C., Lloyd, G.T.,
372 Mannion, P.D., Norell, M.A., Peppe, D.J., and Upchurch, P. (2015). The
373 extinction of the dinosaurs. Biological Reviews *90*, 628-642.
374 20. Mayr, G. (2009). Paleogene Fossil Birds, (Berlin: Springer).
375 21. Larson, D.W., Brown, C.M., and Evans, D.C. (2016). Dental disparity and
376 ecological stability in bird-like dinosaurs prior to the end-Cretaceous mass
377 extinction. Current Biology *26*, 1325-1333.
378 22. Zhou, Z., and Zhang, F. (2002). A long-tailed, seed-eating bird from the Early
379 Cretaceous of China. Nature *418*, 405-409.
380 23. Louchart, A., and Viriot, L. (2011). From snout to beak: the loss of teeth in
381 birds. TRENDS in Ecology and Evolution *26*, 663-673.
382 24. Varricchio, D.J., and Jackson, F.D. (2016). Reproduction in Mesozoic birds and
383 evolution of the modern avian reproductive mode. The Auk *133*, 654-684.
384 25. O'Connor, J., Wang, X., Sullivan, C., Wang, Y., Zheng, X., Hu, H., Zhang, X., and
385 Zhou, Z. (2018). First report of gastroliths in the Early Cretaceous basal bird
386 Jeholornis. Cretaceous Research *84*, 200-208.
387 26. Wolbach, W.S., Gilmour, I., Anders, E., Orth, C.J., and Brooks, R.R. (1988).
388 Global fire at the Cretaceous–Tertiary boundary. Nature *334*, 665-669.

389 27. Anders, E., Wolbach, W.S., and Gilmour, I. (1991). Major Wildfires at the
390 Cretaceous-Tertiary Boundary. Global biomass burning atmospheric, climatic
391 and biospheric implications, 485-492.

392 28. Robertson, D.S., Lewis, W.M., Sheehan, P.M., and Toon, O.B. (2013). K‐Pg
393 extinction: Reevaluation of the heat‐fire hypothesis. Journal of Geophysical
394 Research: Biogeosciences *118*, 329-336.

395 29. Ohno, S., Kadono, T., Kurosawa, K., Hamura, T., Sakaiya, T., Shigemori, K.,
396 Hironaka, Y., Sano, T., Watari, T., and Otani, K. (2014). Production of sulphate-
397 rich vapour during the Chicxulub impact and implications for ocean
398 acidification. Nature Geoscience *7*, 279-282.

399 30. Kaiho, K., Oshima, N., Adachi, K., Adachi, Y., Mizukami, T., Fujibayashi, M., and
400 Saito, R. (2016). Global climate change driven by soot at the K-Pg boundary
401 as the cause of the mass extinction. Scientific reports *6*, 28427.

402 31. Vellekoop, J., Esmeray-Senlet, S., Miller, K.G., Browning, J.V., Sluijs, A., van de
403 Schootbrugge, B., Damsté, J.S.S., and Brinkhuis, H. (2016). Evidence for
404 Cretaceous-Paleogene boundary bolide "impact winter" conditions from New
405 Jersey, USA. Geology *44*, 619-622.

406 32. Bardeen, C.G., Garcia, R.R., Toon, O.B., and Conley, A.J. (2017). On transient
407 climate change at the Cretaceous– Paleogene boundary due to atmospheric
408 soot injections. Proceedings of the National Academy of Sciences,
409 201708980.

410 33. Brugger, J., Feulner, G., and Petri, S. (2017). Baby, it's cold outside: Climate
411 model simulations of the effects of the asteroid impact at the end of the
412 Cretaceous. Geophysical Research Letters *44*, 419-427.

413 34. Vajda, V., Ocampo, A., Ferrow, E., and Koch, C.B. (2015). Nano particles as the
414 primary cause for long-term sunlight suppression at high southern latitudes
415 following the Chicxulub impact—evidence from ejecta deposits in Belize and
416 Mexico. Gondwana Research *27*, 1079-1088.

417 35. Vajda, V., and McLoughlin, S. (2004). Fungal proliferation at the Cretaceous-
418 Tertiary boundary. Science *303*, 1489.

419 36. Wolfe, J.A., and Upchurch Jr, G.R. (1986). Vegetation, climatic and floral
420 changes at the Cretaceous-Tertiary boundary. Nature *324*, 148.

421 37. Renne, P.R., Deino, A.L., Hilgen, F.J., Kuiper, K.F., Mark, D.F., Mitchell, W.S.,
422 Morgan, L.E., Mundil, R., and Smit, J. (2013). Time scales of critical events
423 around the Cretaceous-Paleogene boundary. Science *339*, 684-687.

424 38. Johnson, K.R. (1992). Leaf-fossil evidence for extensive floral extinction at the
425 Cretaceous-Tertiary boundary, North Dakota, USA. Cretaceous Research *13*,
426 91-117.

427 39. Johnson, K.R. (2002). Megaflora of the Hell Creek and lower Fort Union
428 Formations in the western Dakotas: Vegetational response to climate change,
429 the Cretaceous-Tertiary boundary event, and rapid marine transgression.
430 Geological Society of America Special Paper *361*, 329-391.

431 40. Bercovici, A., Jacqueline, W., and Pearson, D. (2008). Detailed palaeontologic
432 and taphonomic techniques to reconstruct an earliest Paleocene fossil flora:

433   An example from southwestern North Dakota, USA. Review of Palaeobotany
434   and Palynology *151*, 136-146.

435 41. Vajda, V., and McLoughlin, S. (2007). Extinction and recovery patterns of the
436   vegetation across the Cretaceous–Palaeogene boundary—a tool for
437   unravelling the causes of the end-Permian mass-extinction. Review of
438   Palaeobotany and Palynology *144*, 99-112.

439 42. Johnson, K.R., and Ellis, B. (2002). A tropical rainforest in Colorado 1.4
440   million years after the Cretaceous-Tertiary boundary. Science *296*, 2379-
441   2383.

442 43. Lee, M.-B., and Martin, J.A. (2017). Avian Species and Functional Diversity in
443   Agricultural Landscapes: Does Landscape Heterogeneity Matter? PloS one *12*,
444   e0170540.

445 44. Chiappe, L.M., and Walker, C.A. (2002). Skeletal morphology and systematics
446   of the Cretaceous Euenantiornithes (Ornithothoraces: Enantiornithes).
447   Mesozoic Birds: Above the Heads of Dinosaurs, 240-267.

448 45. Dumont, M., Tafforeau, P., Bertin, T., Bhullar, B.-A., Field, D., Schulp, A.,
449   Strilisky, B., Thivichon-Prince, B., Viriot, L., and Louchart, A. (2016).
450   Synchrotron imaging of dentition provides insights into the biology of
451   Hesperornis and Ichthyornis, the "last" toothed birds. BMC evolutionary
452   biology *16*, 178.

453 46. Schulte, P., Alegret, L., Arenillas, I., Arz, J.A., Barton, P.J., Bown, P.R., Bralower,
454   T.J., Christeson, G.L., Claeys, P., Cockell, C.S., et al. (2010). The Chicxulub
455   Asteroid Impact and Mass Extinction at the Cretaceous-Paleogene Boundary.
456   Science *327*, 1214-1218.

457 47. Feng, Y.-J., Blackburn, D.C., Liang, D., Hillis, D.M., Wake, D.B., Cannatella, D.C.,
458   and Zhang, P. (2017). Phylogenomics reveals rapid, simultaneous
459   diversification of three major clades of Gondwanan frogs at the Cretaceous–
460   Paleogene boundary. Proceedings of the National Academy of Sciences *114*,
461   E5864-E5870.

462 48. Payne, R.B. (1997). Family Cuculidae (cuckoos). In Handbook of the Birds of
463   the World, vol. 4. Sandgrouse to Cuckoos, J. del Hoyo, A. Elliott and J. Sargatal,
464   eds. (Barcelona: Lynx Edicions), pp. 508-607.

465 49. Norberg, U.M. (1979). Morphology of the wings, legs and tail of three
466   coniferous forest tits, the goldcrest, and the treecreeper in relation to
467   locomotor pattern and feeding station selection. Philosophical Transactions
468   of the Royal Society of London B: Biological Sciences *287*, 131-165.

469 50. Field, D.J. (2017). Big-time insights from a tiny bird fossil. Proceedings of the
470   National Academy of Sciences *114*, 7750-7752.

471 51. Feo, T.J., Field, D.J., and Prum, R.O. (2015). Barb geometry of asymmetrical
472   feathers reveals a transitional morphology in the evolution of avian flight.
473   Proceedings of the Royal Society B *282*, 20142864.

474 52. Bercovici, A., Vajda, V., Pearson, D., Villanueva-Amadoz, U., and Kline, D.
475   (2012). Palynostratigraphy of John's Nose, a New Cretaceous—Paleogene
476   Boundary Section in Southwestern North Dakota, USA. Palynology *36*, 36-47.

477   53.   Field, D.J., Hanson, M., Burnham, D.A., Wilson, L.E., Super, K., Ehret, D.J.,
478   Ebersole, J.A., and Bhullar, B.A.S. (In press). Complete *Ichthyornis* skull
479   illuminates mosaic assembly of the avian head. Nature.
480   54.   Bell, A., and Chiappe, L.M. (2016). A species-level phylogeny of the
481   Cretaceous Hesperornithiformes (Aves: Ornithuromorpha): implications for
482   body size evolution amongst the earliest diving birds. Journal of Systematic
483   Palaeontology *14*, 239-251.
484   55.   Ocampo, A., Vajda, V., and Buffetaut, E. (2006). Unravelling the Cretaceous-
485   Paleogene (KT) catastrophe: Evidence from flora fauna and geology. Impact
486   Series, 203-227.
487   56.   Del Hoyo, J., Elliot, A., and Sargatal, J. (1992). Handbook of the Birds of the
488   World. Barcelona: Lynx Editions.
489   57.   Hsiang, A.Y., Field, D.J., Webster, T.H., Behlke, A.D.B., Davis, M.B., Racicot, R.A.,
490   and Gauthier, J.A. (2015). The origin of snakes: revealing the ecology,
491   behavior, and evolutionary history of early snakes using genomics,
492   phenomics, and the fossil record. BMC Evolutionary Biology *15*, 1-22.
493   58.   Olson, S.L. (1992). A new family of primitive landbirds from the Lower
494   Eocene Green River Formation of Wyoming. In Papers in avian paleontology
495   honoring Pierce Brodkorb, Volume 36, K.E. Campbell, ed. (Natural History
496   Museum of Los Angeles County Science Series), pp. 137-160.
497   59.   Team, R.D.C. (2003). R: a language and environment for statistical computing.
498   R Foundation for Statistical Computing, Vienna, Austria.
499   60.   Paradis, E., Claude, J., and Strimmer, K. (2004). APE: analyses of
500   phylogenetics and evolution in R language. Bioinformatics *20*, 289 - 290.
501   61.   Revell, L.J. (2012). Phytools: An R package for phylogenetic comparative
502   biology (and other things). Methods in Ecology and Evolution *3*, 217-223.
503   62.   Bollback, J.P. (2006). SIMMAP: stochastic character mapping of discrete traits
504   on phylogenies. BMC bioinformatics *7*, 88.
505   63.   Schliep, K.P. (2011). PHANGORN: Phylogenetic analysis using R.
506   Bioinformatics *27*, 592 - 593.
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

18

impact. Concentric background rings demarcate geologic periods: inner grey circle at the

centre is Late Cretaceous, with K–Pg boundary (66.02 Ma) shown by the red dashed line;

white ring is the Paleogene (66.02-23.03Ma), separated from the Neogene (23.03-

2.58Ma) by the dashed blue line. Tips extend to the present. Piecharts at nodes indicate

SIMMAP posterior probabilities for ancestral ecology, under our model. Branch colors

represent a single randomly sampled stochastic character map from a posterior sample of

1,000 maps. Underlying phylogeny and taxonomy follow [2]; qualitatively identical

patterns are inferred using an alternative phylogenetic hypothesis [11]. See also Figures

S2-S4, and doi.org/10.5281/zenodo.1204464 for alternative reconstructions.

Figure 2 Hindlimb ecomorphology suggests delayed transitions toward arboreality

among Cenozoic crown birds. Early Cenozoic fossils of some modern lineages

exhibiting largely arboreal habits suggest that their early antecedents were likely ground

dwelling [3, 50]. Hindlimb indices ((tarsometatarsus length + tibiotarsus length)/ femur

length) are plotted for the major clades within crown Otidimorphae: turacos (A; strictly

arboreal), cuckoos (B; exhibiting arboreal, non-arboreal, and mixed members), and

bustards (C; strictly ground-dwelling), as well as the early Eocene stem turaco *Foro*

panarium (D). *F. panarium* exhibits elongated hindlimb proportions greatly exceeding

the range of extant turacos and arboreal cuckoos, suggesting non-arboreal habits.

Predominantly arboreal taxa are green, predominantly non-arboreal are brown, and

'mixed' are grey. See also Table S2.

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   <u>Determining the approximate timeframe of K–Pg forest recovery</u>

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   <u>Neornithine ancestral ecological reconstructions</u>

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 quadribrachys*), 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 <u>Fossil bird ecomorphology</u>

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 <u>Ancestral ecological reconstructions</u>

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 <u>Fossil bird ecomorphology</u>

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