1 # Ecological selectivity and the evolution of mammalian substrate

2 # preference across the K–Pg boundary

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27 **Abstract**

28 The Cretaceous-Paleogene (K–Pg) mass extinction 66 million years ago was characterized by a

29 worldwide ecological catastrophe and rapid species turnover. Large-scale devastation of

30 forested environments resulting from the Chicxulub asteroid impact likely influenced the

31 evolutionary trajectories of multiple clades in terrestrial environments, and it has been

32 hypothesized to have biased survivorship of non-arboreal lineages across the K–Pg boundary.

33 Here, we evaluate patterns of substrate preferences across the K–Pg boundary among crown

34 group mammals, a group that underwent rapid diversification following the mass extinction.

35 Using Bayesian, likelihood, and parsimony reconstructions, we identify patterns of mammalian

36 ecological selectivity that are broadly similar to those previously hypothesized for birds. Models

37 based on extant taxa indicate predominant K–Pg survivorship among semi- or non-arboreal

38 taxa, followed by numerous independent transitions to arboreality in the early Cenozoic.

39 However, contrary to the predominant signal, some or all members of total-clade Euarchonta

40 (Primates + Dermoptera + Scandentia) appear to have maintained arboreal habits across the

41 K–Pg boundary, suggesting ecological flexibility during an interval of global habitat instability.

42 We further observe a pronounced shift in character state transitions away from plesiomorphic

43 arboreality associated with the K–Pg transition. Our findings are consistent with the hypothesis

44 that predominantly non-arboreal taxa preferentially survived the end-Cretaceous mass

45 extinction, and emphasize the pivotal influence of the K-Pg transition in shaping the early

46 evolutionary trajectories of extant terrestrial vertebrates.

1. Introduction

47

48 The Cenozoic Era is colloquially known as the "Age of Mammals", and the modern world is

49 populated by over 6,000 extant mammalian species exhibiting an extraordinary diversity of

50 forms and ecologies (Nowak 1999; Burgin et al. 2018). Numerous authors have noted that the

51 evolutionary history of extant mammalian biodiversity may have been shaped by the

52 Cretaceous-Paleogene (K–Pg) transition, an interval that is associated with a complex set of

53 mammalian extinctions, radiations, and shifts in species richness (Clemens 2002; Archibald

54 2011; Wilson et al. 2014; Benevento et al. 2019; Brocklehurst et al. 2021). However, the precise

55 influence of the K–Pg transition on the rate, timing, and nature of mammalian diversification is

56 contentious, and may have varied among major mammalian lineages (Hedges et al. 1996;

57 Springer et al. 2003; Bininda-Emonds et al. 2007; Wible et al. 2007; O'Leary et al. 2013;

58 Halliday et al. 2016; Phillips 2016; Pires et al. 2018; Chen et al. 2019; Grossnickle et al. 2019).

59   Even in the best-sampled North American localities, a comprehensive, direct

60 assessment of global patterns of mammalian ecological changes across the K–Pg boundary is

61 precluded by the relatively sparse mammalian fossil record in the latest Cretaceous and earliest

62 Paleogene (Davies et al. 2017), though strong patterns of ecological selectivity are expected in

63 light of high estimated rates of mammalian extinction (Wilson 2013; Grossnickle and Newham

64 2016; Longrich et al. 2016). Surviving mammalian lineages appear to have undergone rapid

65 morphological diversification from primarily small insectivorous or omnivorous forms, and they

66 colonized a wide range of vacant ecological niches in the aftermath of the mass extinction event

67 (Alroy 1999; Smith et al. 2010; O'Leary et al. 2013; Wilson 2014; Halliday and Goswami 2016a;

68 Grossnickle et al. 2019; Lyson et al. 2019, Shelley et al. 2021). Theoretical studies have

69 predicted that fossorial and semi-aquatic mammals may have had a selective advantage across

70 the K–Pg boundary because their substrate preferences would have shielded them from the

71 severe, short-term effects of the Chicxulub asteroid impact such as a hypothesized heat pulse

72 and associated wildfires (Robertson et al. 2004; DeBey and Wilson 2017). Alongside global fires

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73   and longer-term climatic effects, the asteroid impact resulted in forest devastation on a global

74   scale (Tschudy et al. 1984; Vajda et al. 2001; Nichols and Johnson 2008; Field et al. 2018;

75   Lyson et al. 2019; Carvalho et al. 2021) and substantially altered floral communities for

76   centuries (Wilf and Johnson 2004, Carvalho et al. 2021). Recent work on birds suggested that

77   the collapse of global forests drove arboreal Mesozoic avialans to extinction at the K–Pg

78   boundary, with multiple subsequent originations of arboreal habits arising among crown birds

79   once forests had recovered (Field et al. 2018).

80   Here, we investigate patterns of substrate preference evolution across crown group

81   mammals—another major K–Pg boundary-crossing terrestrial vertebrate clade. First, we

82   assessed the evidence for whether mammals were subject to comparable habitat-related

83   selectivity across the K–Pg boundary. We performed ancestral state reconstructions (ASRs) of

84   substrate preferences on alternative phylogenetic hypotheses for extant mammals (Meredith et

85   al. 2011; Upham et al. 2019). Though not definitive, when interpreted within the context of

86   available fossil evidence we consider the results suggestive of a pattern of predominant K–Pg

87   survivorship among semi-arboreal or non-arboreal mammals, with extant mammalian clades

88   characterized by obligately arboreal ecologies generally arising in the early Cenozoic. Second,

89   we examined the relative clade-wide frequencies of particularly evolutionary transitions

90   throughout the evolutionary history of Mammalia using a model-based approach. Our analyses

91   identify an interval early in placental mammal evolutionary history marked by a striking increase

92   in inferred transitions toward non-arboreality. Notably, this interval of apparent clade-wide

93   directional selectivity towards non-arboreality aligns with plausibly K–Pg-associated

94   cladogenesis among crown placentals, although we note that the divergence times of early

95   placental clades remain contentious. Acknowledging these lingering divergence time

96   uncertainties, we contend that our analyses help illuminate the hidden influence of the K–Pg

97   transition on major ecological patterns early in the evolutionary history of placental mammals.

98   **2. Material and methods**

99   **Character State Assignment**

100   All 164 mammalian lineages from the time-scaled phylogenetic hypothesis of Meredith et

101   al. (2011), representing most extant family-level phylogenetic diversity, were assigned an

102   ecological character state of arboreal, semi-arboreal, or non-arboreal (electronic supplementary

103   material). Character states reflect where mammals form nests or otherwise reside. More

104   explicitly, we characterize a "nest" as a construct used for: rearing young, resting, or sleeping

105   (examples include the leaf nests of gorillas or the dreys of squirrels). Alternatively, a mammal

106   may reside in a tree without construction of a nest, where its "residence" is primarily used for

107   sleeping or resting, and may involve rearing young but does not involve any structural

108   modifications to the tree (sloths, for example, often find a leafy area in a tree to sleep in but do

109   not modify the tree or its foliage). An arboreal mammal is therefore one that, in the wild, will

110   virtually always reside or nest in a living tree, be it amongst the branches or in an existing tree

111   cavity. To be classed as semi-arboreal, the mammal in question will often reside or nest in a

112   living tree in the wild but does not do so exclusively. In general, for a semi-arboreal mammal,

113   trees are convenient but not essential, and another substrate (e.g., a rock face) may provide a

114   suitable alternative. All species that fall outside these definitions are classed as non-arboreal,

115   such that the mammal in question does not nest or reside in trees at all, or only does so

116   incidentally in a small number of documented cases. We believe this coding strategy is

117   conservative with respect to mammals that exhibit an obligately arboreal ecology for nesting and

118   residence, and it allows us to discriminate among lineages with obligately arboreal habits from

119   those that occupy trees facultatively or opportunistically.

120   **Alternative phylogenetic frameworks**

121   In order to assess the influence of phylogenetic uncertainty on our ancestral ecological

122   reconstructions, we evaluated them with respect to well-supported phylogenetic hypotheses

123   from Meredith et al. (2011) as well as the node-dated maximum clade credibility consensus tree

124   from Upham et al. (2019) and its associated posterior distribution of tree topologies. Both

125   phylogenetic hypotheses are derived from a supermatrix inference approach, with Upham et al.

126   (2019) using sequences for 31 genes (building on the 26 from Meredith et al. 2011). Meredith et

127   al. (2011) used a family-level approach to build a time-calibrated tree of 164 mammalian

128   lineages, of which 142 were single species, 16 were congeneric chimaerics, and six were

129   chimaerics above the genus level. Upham et al. (2019) employed a method that separated

130   phylogenetic inference into divergences between major lineages ("backbone") and clades at the

131   species level ("patch") (Mishler 1994; Jetz et al. 2012) to generate a phylogeny uniting ~4,100

132   species. Our analysis scores the subset of taxa in the Upham et al. (2019) dataset that matched

133   the taxon set from the Meredith et al. (2011) analysis. This yielded two complementary

134   phylogenetic consensus topologies with the same taxon set, on which we estimated character

135   evolution. In the 12 cases where the Upham et al. (2019) dataset did not contain the same

136   species as in Meredith et al. (2011), we replaced the missing species with its closest relative

137   with the same character state (Supporting Information, Table S1). By considering these

138   alternative hypotheses, we specifically assess how robust our inferences are to areas of conflict

139   between the two consensus topologies, such as the monophyly of Euarchonta (Primates +

140   Scandentia + Dermoptera; Upham et al. 2019) and the placement of Scandentia as the sister

141   group to Glires (Rodentia + Lagomorpha; Meredith et al. 2011). Upham et al. (2019) cite

142   posterior probabilities of 0.96 for the monophyly of Euarchonta and 0.78 for Dermoptera +

143   Scandentia. Meredith et al. (2011) found that DNA and amino acid trees agree on the

144   monophyly of Scandentia + Glires but with bootstrap support of <90%.

145   **Model selection**

146   We assessed the relative fit of three alternative time-homogeneous transition models

147   with maximum likelihood in the ape (Paradis et al. 2004) and phytools (Revell 2012) *R* packages

148 (R Core Team 2014) on each consensus tree. Following Field et al. (2018), one model

149 comprised two rates, such that transitions among all three character states (arboreal, semi-

150 arboreal, and non-arboreal) were permitted, but transitions to and from semi-arboreality were

151 allowed a different rate from transitions that bypass this intermediate stage. A second model

152 comprised four rates such that transitions from non-arboreal to arboreal were required to pass

153 through semi-arboreality, with separate forward and reverse rates for each pair of state

154 transitions. These models reflect the presumed biological reality that transitioning from non-

155 arboreality to arboreality or vice versa through an intermediate state likely occurs at a different

156 rate than transitions lacking an intermediate state. We also tested a third maximally

157 parameterized (six-rate) model ("ARD" - all rates different) in which forward and reverse rates

158 were allowed to vary across all states.

159 Hidden Markov Models (HMMs) have emerged as a powerful tool for assessing the

160 possibility that unobserved rate heterogeneity can have an outsized influence on reconstructing

161 the evolutionary history of discrete characters (Beaulieu et al. 2013; Beaulieu and O'Meara

162 2016; Boyko and Beaulieu 2021). In comparison to time-homogeneous models, which assume

163 that specified character transition rates do not evolve, HMMs provide an elegant solution for

164 evaluating the hypothesis that the mode of character evolution has evolved throughout a clade's

165 evolutionary history. To assess this possibility in our data, we generated three HMMs using the

166 corHMM *R* package (Beaulieu et al. 2013). Our initial analysis of time-homogeneous models

167 revealed that the six-rate ARD and four-rate intermediate model were preferred (Table 1).

168 Therefore, we elected to compare three HMMs based on those models. The first of these

169 consisted of a model that included two rate classes; one with an ARD model and one with the

170 four-rate model. The second and third HMMs reflected ARD models with two or three rate

171 classes, respectively. In all cases, we assumed symmetric transition rates among rate classes.

172 As time-homogeneous models are a special case of HMMs (reflecting one rate class), we

173 compared all evaluated models with the Akaike Information Criterion (AIC).

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174   **Reconstructing the evolution of mammalian arboreality**

175   We performed likelihood-based Ancestral State Reconstructions (ASRs) in *R* (R Core

176   Team 2014). We used the ace() likelihood function in ape (Paradis et al. 2004) and a

177   customized implementation of Bayesian stochastic mapping, described below (Bollback 2006;

178   Revell 2012). We also performed maximum parsimony reconstructions using the

179   ancestral.pars() function in the *R* package phangorn (Schliep 2011).

180   As part of the VertLife initiative (http://vertlife.org/data/mammals/) Upham et al. (2019)

181   provided a set of 10,000 credible phylogenetic trees sampled from the Bayesian posterior

182   distribution estimated in that study. Therefore, for analyses based on the Upham et al. (2019)

183   consensus tree, we leveraged this resource to account for stochastic uncertainty in branch

184   lengths and tree topology. For each of the time-homogeneous models we evaluated, we

185   performed a Bayesian stochastic character mapping analysis across 1,000 sampled trees from

186   the Upham et al. (2019) posterior distribution, and we estimated 500 stochastic character maps

187   on each. These results were then summarized with respect to the Upham et al. (2019)

188   consensus tree. For analyses directly using the consensus trees, we estimated 5,000 stochastic

189   maps.

190   To make this task computationally tractable, we generated new *R* code to perform these

191   analyses in parallel across multiple CPUs using the "parallel" (R Core Team 2014), "doSNOW"

192   (Wallig et al. 2020a), and "doParallel" (Wallig et al. 2020b) *R* libraries. Our approach (see

193   simmap_parallel.R; https://github.com/jakeberv/mammal_arboreality) operates on "phylo" or

194   "multiPhylo" tree objects, accelerating several aspects of this analysis. The wrapper function

195   simmap.parallel(), takes minimally as arguments a tree or set of trees, a discrete character

196   dataset, a time-homogeneous model, and a specified assumption about the distribution of

197   character states at the root (optionally equal or following the FitzJohn et al. (2009) root state

198   prior). Briefly, the function first estimates a Q matrix for each of the trees that are passed to it,

199 using fitMK() (Revell 2012), or alternatively accepts an external Q matrix estimate. Then,

200 depending on the options selected, simmap.parallel() generates stochastic character maps on

201 each of the provided trees using fastSimmap() from the *R* package ratematrix (Caetano and

202 Harmon 2017), the estimated Q matrix for each tree, and the stated root prior. Lastly, a final

203 combined multiSimmap object is generated. This output can be parsed by

204 phytools::describe.simmap() with the argument ref.tree set to the target consensus tree on

205 which to summarize the results. We provide additional code to accelerate aspects of this

206 summation in a modified function describe.simmap.alt(), which can otherwise be very time

207 consuming for large numbers of trees (Eliot Miller, *personal communication*, March 2021).

208 **Investigating clade-wide temporal patterns in character transition rates**

209 　　In addition to individual node and branch reconstructions, we examined the relative

210 frequencies of particular transition types through time across the two consensus trees as well as

211 the posterior tree distribution from Upham et al. (2019). For example, in a two-rate bidirectional

212 model with two states, forward and reverse transition rates can be time-homogeneous while the

213 total counts of particular transition types across all branches vary through time and depend on

214 the structure of the underlying phylogeny. Revell (2017) outlined an approach for visualizing the

215 history of clade-wide changes in character transitions for a discrete character model under

216 stochastic mapping. This approach first takes a stochastic character mapping simulation and

217 partitions the underlying tree into a specified number of time bins. The average number of

218 character transitions across branches and simulations is calculated within each time bin, and

219 then this value is normalized for patterns of cladogenesis by dividing by the total branch length

220 within a time bin. Revell's (2017) example provides a pragmatic solution for visualizing the

221 behavior of a discrete character model through time in the context of stochastic character

222 mapping.

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223   Here, we refine this approach to allow examination of temporal patterns in the relative

224   frequencies of each transition type from a given model (see rate_through_time.R;

225   https://github.com/jakeberv/mammal_arboreality). We generate visualizations for stochastic

226   character mapping under the optimal models for the Meredith et al. (2011) and Upham et al.

227   (2019) consensus topologies, as well as for a sample of 1,000 posterior trees from Upham et al.

228   (2019). These visualizations allow us to further examine the hypothesis that patterns of clade-

229   wide trends in transitions toward and away from arboreality may have been influenced by the K–

230   Pg transition.

231   **3. Results**

232   **Node reconstructions**

233   Under the preferred four-rate model (Table 1), stochastic mapping supports a pattern whereby

234   arboreality emerged repeatedly and independently among several different clades following the

235   K–Pg mass extinction. We detect at least 10 instances of post-K–Pg transitions to arboreality

236   under the Meredith et al. (2011) framework (Fig. 1) and 11 cases across the Upham et al.

237   (2019) dataset (Fig. 2). These general patterns hold across both alternative topologies and

238   under parsimony and likelihood optimality criteria (Supporting information, Figs. S1-18).

239   Bayesian stochastic mapping under the flexible ARD model suggests that state

240   transitions that pass through a semi-arboreal intermediate are detected more frequently than

241   direct-transitions from arboreality to non-arboreality or vice versa (Supporting information, Figs.

242   S6, S9, S12). Additionally, the ARD model detects no direct transitions from non-arboreality to

243   arboreality. By contrast, in the two-rate model, direct transitions from non-arboreality to

244   arboreality are detected at a higher frequency than the reverse, while transitions away from

245   semi-arboreality occur at an intermediate frequency (Supporting information, Figs. S2, S8, S11).

246   We interpret these results to suggest that the transitions inferred under the ARD model are

247   more biologically plausible than those under the two-rate model.

248   Under both the Meredith et al. (2011) and the Upham et al. (2019) consensus

249 topologies, the preferred four-rate and ARD models reconstructed more nodes near the K–Pg

250 boundary as semi-arboreal than did the two-rate model, especially on the Meredith et al.

251 topology (Supporting information, Figs. S5-6, S15-16). Incorporating a sample of 1,000 tree

252 topologies from the posterior distribution of Upham et al. (2019) made little difference in

253 stochastic mapping reconstructions under the two-rate or ARD models (Supporting information,

254 Figs. S15-18). However, for the optimal four-rate model, consideration of posterior topological

255 uncertainty leads to a marked increase in circum K–Pg nodes being recovered as non-arboreal

256 rather than semi-arboreal (compare Fig. 2 to Supporting information, Fig. S14). We suggest this

257 is a consequence of more pronounced changes in the average estimated Q matrix (inset in Fig.

258 2) observed for the four-rate model when compared to the two-rate or ARD models,

259 summarized across the posterior tree sample. Although both sets of reconstructions are

260 generally consistent with the hypothesis of K–Pg-associated selectivity against arboreality, it is

261 clear that considering information from the Upham et al. (2019) posterior tree set as opposed to

262 relying solely on simplified consensus topologies impacts the interpretation of our node state

263 reconstructions.

264   The overall signal we detect is consistent with the hypothesis of predominant

265 survivorship of non-arboreal or semi-arboreal mammals across the K–Pg boundary: few

266 lineages reconstructed as predominantly arboreal are inferred to have survived the K–Pg mass

267 extinction. However, our analyses also highlight two possible exceptions: euarchontans and

268 marsupials. On the Meredith et al. (2011) topology under all models, early members of total-

269 clade Primatomorpha (Primates + Dermoptera) are inferred to have either retained arboreal

270 habits across the K–Pg boundary (Fig. 1; Supporting information, Fig. S4-6) or acquired

271 arboreality shortly thereafter (see below). On the Upham et al. (2019) consensus topology, in

272 which Euarchonta (Primates + Dermoptera + Scandentia) is inferred to be monophyletic,

273 arboreality is reconstructed as having arisen along the euarchontan stem lineage in all models

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274   (Supporting information, Figs. S13-16). Considering posterior topological uncertainty also leads

275   to Euarchonta being reconstructed as arboreal at the time of the K–Pg transition, whereas the

276   majority of other lineages are reconstructed as non-arboreal under the four-rate model and

277   semi-arboreal otherwise (Fig. 2; Supporting information, Figs. S17-18). Although not supported

278   by Meredith et al. (2011), a monophyletic Euarchonta has frequently been supported by other

279   phylogenetic analyses (Springer et al. 2003; Springer 2004; O'Leary et al. 2013; Chester et al.

280   2015, 2017). Under parsimony and two likelihood models (four-rate and ARD), most marsupials

281   are additionally reconstructed as having retained arboreal habits across the K–Pg boundary, or

282   acquired them shortly thereafter (Fig. 1; Supporting information, Figs. S4-6, S13-16). However,

283   this signal is diminished when considering the Upham et al. (2019) distribution of topologies

284   (Fig. 2).

285   **Clade-wide temporal patterns in character transition rates**

286   For both the Meredith et al. (2011) and Upham et al. (2019) consensus topologies, the

287   highest frequency of character transitions detected by the optimal four-rate model falls within the

288   range of divergence time uncertainty for many clades whose originations have been proposed

289   to be associated with the K–Pg boundary (see Discussion). Moreover, the temporal sequence of

290   peaks in the relative frequencies of particular character transition types appears to be consistent

291   with the hypothesis of selection against obligate arboreality leading up to and through the K–Pg

292   boundary (i.e. transitions away from arboreality, followed by transitions toward arboreality, at

293   least as indicated by analyses on the Upham et al. (2019) consensus topology). These patterns

294   are similar for analyses performed on the Meredith et al. (2011) (Figure 3A) and Upham et al.

295   (2019) (Figure 3B) consensus topologies, as well as the Upham et al. (2019) posterior tree

296   sample (Figure 3C). Tracking fluctuations in the relative frequencies of mammalian ecological

297   transitions approaching the K–Pg boundary (Figure 3), the four-rate model first detects a slight

298   uptick and subsequent reduction in clade-wide transitions from arboreal to semi-arboreal

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299   character states, which remains low to the present. This initial pulse is followed by (or is

300   perhaps concurrent with) a large peak in transitions from semi-arboreal to non-arboreal

301   character states, which declines gradually to the present. This peak of character transitions

302   toward non-arboreality appears stronger in the analyses employing the Upham et al. (2019)

303   topologies than in the analyses using the Meredith et al. (2011) consensus topology.

304   Subsequently, a peak in clade-wide transitions from semi-arboreal to arboreal character states

305   is detectable in both analyses, which returns to pre K–Pg levels. Temporal patterns of character

306   state changes from non-arboreal to semi-arboreal appear relatively flat in the Meredith et al.

307   (2011) topology, with a stronger uptick associated with other peaks in the Upham et al. (2019)

308   topologies. When interpreting these results, it should be noted that only one type of character

309   transition can occur at a given time on a given branch on a given stochastic map. Therefore, an

310   apparent increase in one type of character state transition may necessarily be associated with a

311   decline in the frequency of a different type of character state transition.

312   These patterns emphasize that the most dramatic clade-wide mode changes appear to

313   be associated with the interval encompassing many clade originations hypothesized to be

314   related to the K–Pg transition. These results suggest that the early diversification of placental

315   mammals was associated with clade-wide shifts in the relative rates of character transitions

316   toward and away from particular ecological strategies, and that the sequence of these shifts is

317   consistent with the hypothesis that the transient loss of available arboreal habitats at the K–Pg

318   boundary may have driven those changes. Although the presently wide uncertainty in

319   divergence times precludes a definitive statement, it is important to note that if our documented

320   peaks in evolutionary transitions did occur during the Cretaceous, they could be consistent with

321   the "Early Rise Hypothesis." In that scenario, an ecological radiation of mammals began prior to

322   the Cretaceous-Palaeogene transition, potentially associated with concomitant diversification

323   events among angiosperms and selected groups of insects (Grossnickle et al. 2019a).

4. Discussion

Inference from the fossil record

Our ancestral state reconstructions consistently support survivorship patterns favoring

predominantly non-arboreal or semi-arboreal substrate use across the K–Pg boundary, under

likelihood, Bayesian, and parsimony models. This is consistent with previous ASR approaches

that recover early mammalian nodes as mostly non-arboreal until just after the K-Pg boundary

(Wu et al. 2017). With few exceptions (Lyson et al. 2019), well-preserved mammalian fossils

from close to the K–Pg boundary and the first ca. one million years of the extinction's aftermath

are exceedingly rare (Williamson 1996; Hartman 2002; Lofgren et al. 2004; Wilson et al. 2014).

Most fossils known from this interval are too fragmentary to robustly inform reconstructions of

substrate preferences. Indeed, even in cases where strong inferences about the predominant

substrate use of a fossil taxon can be drawn, uncertainty regarding parameters such as nesting

behaviors is unavoidable. Uncertainty surrounding the phylogenetic position of such fossils

presents further challenges with respect to interpreting their implications for early ecological

transitions among crown placentals (Halliday et al. 2017). Accepting these limitations, our

reconstructions are consistent with the preferential survivorship of non-arboreal mammals

across the K–Pg mass extinction. In contrast to evolutionary patterns among crown birds, in

which strong selection for non-arboreal ecologies appears to be unambiguously supported by

both phylogenetic and fossil evidence (Field et al. 2018, Field et al. 2020a), definitive

assessments of selective patterns among K–Pg boundary-crossing mammals will remain

elusive in the absence of additional fossil evidence. Until that time, we interpret our results in the

context of the currently known circum-K–Pg mammalian fossil record, as well as the more

complete records from earlier and later in mammalian evolutionary history.

Based on postcranial morphology, some early (ca.125 Ma) therians including *Eomaia* (Ji

et al. 2002), *Ambolestes* (Bi et al. 2018), and *Sinodelphys* (Luo et al. 2003), have been

interpreted as arboreal or scansorial, as has the oldest known therian, the ca. 160 Ma *Juramaia*

350 (Luo et al. 2011). Mammalian arboreality may have been common in the Mesozoic, concurrent

351 with increasing mammalian locomotor diversity (Chen and Wilson 2015; Grossnickle et al.

352 2019). In contrast, later pre-K–Pg lineages for which locomotor reconstructions are possible,

353 such as the metatherian *Asiatherium* (Trofimov and Szalay 1994) and the eutherians

354 *Barunlestes* and *Zalambdalestes* (Kielan-Jaworowska 1978; Chester et al. 2010, 2012) are not

355 interpreted to have been arboreal (Chen and Wilson 2015). Inclusion of Mesozoic fossil taxa in

356 our reconstructions would likely inflate posterior estimates for early arboreality among

357 mammals. However, given our focus on the K–Pg transition and not the ancestral condition of

358 the earliest crown mammals, we elected to restrict our analyses to taxa whose nesting and

359 residence ecology can be scored consistently and systematically.

360 Compared to other major crown mammalian subclades, we infer early arboreal substrate

361 use in Primatomorpha (Meredith et al. 2011) and Euarchonta (Upham et al. 2019), implying

362 either a rapid adoption of arboreality as forests recovered following the K–Pg transition, or

363 retention of at least facultative arboreality across the extinction event. Although relevant fossil

364 data are limited, we can evaluate the primatomorphan and euarchontan fossil record in order to

365 draw inferences about the relative likelihood of these alternative scenarios. The oldest total

366 group primates known from the fossil record (Chester and Sargis 2020), including the stem

367 primates *Purgatorius* and *Torrejonia* and the crown primate *Teilhardina,* date to within

368 approximately 10 million years following the K–Pg transition (Chester et al. 2015, 2019; Morse

369 et al. 2019). These fossils provide insight into ancestral primate habits in the aftermath of the

370 end-Cretaceous mass extinction. From studies of postcranial morphology, *Purgatorius* and other

371 stem primates like *Torrejonia* are reconstructed as having been specialized for arboreal habits

372 (Chester et al. 2015, 2019). As stem primates, this hypothesis is consistent with our inference

373 that primatomorphans (Meredith et al. 2011) or euarchontans (Upham et al. 2019) may have

374 retained a capacity for arboreality through the K–Pg. The inferred arboreal habits of this lineage

375 across the K–Pg boundary is intriguing in light of an apparently strong selective filter against

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376 arboreal birds at this same time (Field et al. 2018), as well as theoretical and paleobotanical

377 evidence suggesting forest devastation on a global scale following the Chicxulub asteroid

378 impact (Tschudy et al. 1984; Vajda et al. 2001). Although primatomorphans or euarchontans

379 may have retained arboreal habits in hypothetical forested refugia throughout the K–Pg

380 transition, behavioral flexibility and facultative non-arboreality may also have facilitated the

381 survival of arboreally adapted early primatomorphans across the K–Pg. Though extant colugos

382 are specialized gliders and strict herbivores, extant primates have been hypothesized to be

383 resilient in the face of rapid environmental change on account of their sociality, cognition, and

384 dietary and locomotor flexibility (Morris et al. 2011; Mekonnen et al. 2018), and at least some of

385 these and other traits (e.g., omnivory and small body size in the oldest known stem and crown

386 primates; (Szalay and Delson 1979)) may have contributed to the survival of representatives of

387 the primate total group when facing the devastation of forests at the end-Cretaceous.

388   There is evidence under some of our models that the early evolutionary history of crown

389 marsupials may have also occurred in an arboreal ecological context (Fig. 1; Supporting

390 information, Figs. S4, S6, S13-14, S16, S18). Our ARD model and in some cases the similar

391 four-rate model yield an arboreal reconstruction for the most recent common ancestor of crown

392 marsupials (Fig. 1; Supporting information, Figs. S6, S14, S16, S18). This inference implies

393 repeated losses of arboreality among marsupials, which would be consistent with the

394 hypothesized retention of plesiomorphic arboreal features in their hands and feet (Bensley

395 1901; Haines 1958; Szalay 1984). Marsupials suffered some of the greatest diversity loss and

396 longest recovery times in the wake of the K–Pg compared with other boundary-crossing

397 mammalian groups (Pires et al. 2018), and we infer a signal of consistent arboreality among

398 several marsupial lineages near the K–Pg boundary. This is congruent with the earliest known

399 post-K–Pg metatherian skeletons from the early Paleocene of Bolivia, which have been

400 reconstructed as scansorial, with *Mayulestes* inferred to be more specialized for arboreality than

401 *Pucadelphys* (Argot 2003).

16

402   Notably, although the fossil record of stem-group bats (Chiroptera) is sparse, the

403 ancestors of crown bats may have been arboreal before they acquired a capacity for powered

404 flight (Gunnell and Simmons 2005; Bishop 2008). However, our results reconstruct much of the

405 chiropteran total-group as predominantly non-arboreal through most of the Paleocene and

406 extending back into the Cretaceous (Fig. 2) (or, in the case of the ARD and four-rate models,

407 potentially semi-arboreal). This is probably a result of the strict application of our character state

408 definitions, where most extant bats were classified as non-arboreal. Many bat species are cave-

409 roosting—thus, they are classified as non-arboreal or semi-arboreal in our analyses, highlighting

410 the fact that our classification of "non-arboreality" does not necessarily imply a predominantly

411 ground-dwelling ecology.

412   A number of major clades whose extant representatives exhibit arboreality across

413 multiple family-level subclades (e.g., primatomorphans or euarchontans, marsupials, and

414 xenarthrans) may have retained a capacity for arboreal habits across the K-Pg boundary and

415 may have already been adapted to exploit arboreal niches relatively quickly as these habitats

416 recovered. By contrast, arboreal latecomers (e.g., dormice, tree squirrels, bats) independently

417 acquired arboreal habits well into the Cenozoic (Figs. 1, 2). In the case of Xenarthra, the earliest

418 known fossil representatives of this group were likely adapted for fossoriality (Gaudin and Croft

419 2015), with arboreality in sloths evolving repeatedly and independently throughout the

420 Cenozoic, presumably in response to factors such as diet specialization and predator evasion

421 (Delsuc et al. 2018, 2019). This pattern appears to be reflected in our ASRs: across the majority

422 of our analyses, we infer non-arboreal ecologies for Xenarthra until very shortly after the K–Pg

423 boundary.

424   As in birds (Mayr 2016; Field et al. 2018), we hypothesize that non-arboreal habits were

425 associated with increased rates of survivorship among mammals across the K–Pg boundary,

426 consistent with earlier qualitative proposals for enhanced survivorship among burrowing/semi-

427 aquatic mammals (Robertson et al. 2004; DeBey and Wilson 2017). Alongside selection against

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428   strict arboreality, many mammalian lineages that passed through the K–Pg mass extinction may

429   have been characterized by reduced body size relative to their pre-extinction antecedents

430   (Lyson et al. 2019); perhaps related to the relationship between body size and total metabolic

431   requirements (McNab 2012; Berv and Field 2018), as well as enhanced survivorship among

432   insectivores and omnivores compared with strict carnivores and herbivores (Sheehan and

433   Hansen 1986; Aberhan et al. 2007). Large-bodied mammals and dietary specialists appear to

434   have been heavily selected against in the immediate wake of the Chicxulub impact (Wilson

435   2013; Grossnickle and Newham 2016; Lyson et al. 2019), with therians only acquiring their

436   greatest body size range well after the mass extinction when niches previously occupied by

437   large dinosaurs opened (Smith et al. 2010). Multituberculates show a similar increase in the

438   disparity of their body sizes and dental complexity following the K–Pg transition, though their

439   mean body size was apparently unaffected (Wilson et al. 2012; Weaver and Wilson 2020).

440   **Analytical assumptions**

441   The evolutionary scenarios proposed here are conditional on the accuracy of the

442   timescale of the extant mammalian radiation estimated in both the Meredith et al. (2011) and

443   Upham et al. (2019) phylogenies. Divergence times estimated with molecular clock models

444   (Wray 2002; Meredith et al. 2011; Bininda-Emonds et al. 2012) may greatly exceed estimates of

445   clade ages derived from fossil evidence (Wible et al. 2007; Forest 2009; O'Leary et al. 2013),

446   and our understanding of the factors underlying this incongruence is improving (Hillis 1987;

447   Patterson 1987; Novacek 1993; Larson 1998; Springer et al. 2003, 2013; Brochu et al. 2004;

448   Springer 2004; O'Leary et al. 2013; Phillips 2016; Field et al. 2020b). In Xenarthra, divergence

449   time analyses from molecular clock models have yielded estimates for the age of the crown

450   clade exceeding 70 Ma (Bininda-Emonds et al. 2007), whereas the oldest crown group

451   xenarthran fossils are approximately 59 Ma (O'Leary et al. 2013; Wilson Mantilla et al. 2021).

452   Such discrepancies, which span the K–Pg boundary (ca. 66.02 Ma; Clyde et al. 2016), indicate

18

453   uncertainty regarding the "true" age of important nodes across the mammalian tree of life. This

454   uncertainty is especially relevant to our reconstructions of crown Primatomorpha, for which

455   molecular divergence time analyses frequently estimate a Late Cretaceous origin (Bininda-

456   Emonds et al. 2007; Janečka et al. 2007; Meredith et al. 2011), and likewise for Euarchonta

457   (Janečka et al. 2007; Upham et al. 2019). At present, the oldest known total-clade

458   euarchontan—the arboreal stem primate *Purgatorius*—appears shortly after the K–Pg

459   boundary, ca. 65.9 MYA (Wilson Mantilla et al. 2021). Thus, direct fossil evidence bearing on

460   whether arboreality was retained across the K–Pg boundary in euarchontans or

461   primatomorphans is lacking. If the "true" node age is younger than the K-Pg boundary, it would

462   imply that arboreality may have emerged post-extinction in Euarchonta or Primatomorpha,

463   rather than arising beforehand and being maintained across the extinction horizon. Lastly, we

464   note that the taxon sample in the present analysis, which is mostly restricted to mammalian

465   family-level clades, could also have introduced some bias into our analysis, though it is difficult

466   to quantify how this might affect our results *a priori* (primarily, we expect transition rates to be

467   under-estimated under the present taxon sampling strategy). Mammalian families that exhibit a

468   range of substrate preferences across extant species-level diversity are necessarily represented

469   in our consensus trees by only a single taxon; 36% of such families were scored as arboreal.

470   Therefore, further exploration of these questions in the context of an expanded taxon sample

471   would provide a fruitful direction for future research.

472   **5. Conclusions**

473   The short-term ecological ramifications of the K–Pg mass extinction are difficult to fully

474   assess from our vantage point 66 million years later, but it is increasingly clear that the

475   evolutionary trajectories of arboreal lineages across the vertebrate tree of life were deeply

476   impacted by this mass extinction event (Vajda et al. 2001; Feng et al. 2017; Field et al. 2018).

477   Direct fossil evidence of mammalian ecological habits from the latest Cretaceous and

478   Paleocene will be needed to further test the patterns of mammalian ecological selectivity

479   inferred here. The Late Cretaceous *Deccanolestes* has been interpreted as arboreal, as have its

480   close relatives (the Paleocene adapisoriculids), providing a compelling example of continuous

481   arboreality among non-euarchontan mammals that survived across the K–Pg boundary

482   (Goswami et al. 2011). Although some Late Cretaceous multituberculates have also been

483   proposed to have been arboreal based on isolated fragmentary humeri (DeBey and Wilson

484   2017), inferences based on the most complete skeletal material support Late Cretaceous forms

485   as predominantly ground dwelling or fossorial (Kielan-Jaworowska 1989; Kielan-Jaworowska

486   and Gambaryan 1994; Weaver et al. 2021), and some Paleocene taxa as arboreal (Krause and

487   Jenkins 1983), suggesting survival of predominantly non-arboreal multituberculates across the

488   K–Pg with post-extinction transitions to arboreality.

489   Inferences of mammalian ecological evolution will continue to be refined in light of

490   ongoing improvements in our understanding of mammalian phylogeny, divergence times, and

491   the fossil record (Meredith et al. 2011; O'Leary et al. 2013; Halliday and Goswami 2016b;

492   Phillips 2016; Grossnickle et al. 2019; Upham et al. 2019). Nevertheless, our new results and

493   simulations are consistent with the hypothesis that the K–Pg transition was a fundamental agent

494   driving ecological shifts in the evolutionary history of Mammalia. The phylogeny of crown group

495   mammals appears to retain the selective signature of end-Cretaceous forest devastation over

496   66 million years ago, emphasizing the profound degree to which the evolutionary trajectories of

497   extant terrestrial vertebrates were influenced by the K–Pg catastrophe.

AUTHOR CONTRIBUTIONS

507 J.J.H., J.S.B. and D.J.F. conceived the study. J.J.H. assigned character states and drafted the

508 manuscript. J.S.B. performed ancestral state reconstructions and generated analytical R code.

509 All authors (J.J.H., J.S.B, S.G.B.C., E.J.S., and D.J.F.) contributed to writing and revising the

510 manuscript, and all approved the manuscript for publication.

DATA ACCESSIBILITY

512 R code will be archived at Zenodo with static DOI pending publication but is currently available

513 at https://github.com/jakeberv/mammal_arboreality during review.

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