The tempo of trophic evolution in small-bodied primates

Running title: Trophic evolution in small-bodied primates

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Abstract

Objectives: As a primary trophic strategy, insectivory is uncommon and unevenly distributed across extant primates. This pattern is partly a function of the challenges that insectivory poses for large-bodied primates. In this study, I demonstrate that the uneven distribution is also a consequence of variation in the rate of trophic evolution among small-bodied lineages.

Methods: The sample consisted of 307 species classified by primary trophic strategy and body size, creating an ordered three-state character: small-insectivorous, small-herbivorous, and large-herbivorous. I tested for rate heterogeneity by partitioning major clades from the rest of the primate tree and estimating separate rates of transition between herbivory and insectivory for small-bodied lineages in each partition.

Results: Bayesian analysis of rate estimates indicates that a model with two rates of trophic evolution provides the best fit to the data. According to the model, lorisiforms have a trophic rate that is 4–6 times higher than the rate for other small-bodied lineages.

Conclusions: The rate heterogeneity detected here suggests that lorisiforms are characterized by traits that give them greater trophic flexibility than other primates. Previous discussions of trophic evolution in small-bodied primates focused on the low frequency of insectivory among anthropoids and the possibility that diurnality makes insectivory unlikely to evolve or persist. The present study challenges this idea by showing that a common transition rate can explain the distribution of insectivory in small-bodied anthropoids and nocturnal lemurs and tarsiers. The results of this study offer important clues for reconstructing trophic evolution in early primates.

Keywords   body size, diet, insectivory, herbivory, heterotachy

1 | INTRODUCTION

Primates exhibit an impressive diversity of trophic strategies. Among extant members of the order, frugivory is the most widespread primary strategy, but folivory is also common (Gómez & Verdú, 2012; Kay & Covert, 1984). The clade also includes specialized lineages such as the graminivorous gelada (*Theropithecus gelada*) of the Ethiopian Highlands, the tree-gouging, exudativorous marmosets (genera *Callithrix*, *Mico*, *Callibella*, and *Cebuella*) of Amazonia and the Atlantic Forest, and the exclusively faunivorous tarsiers (family Tarsiidae) of the Malay Archipelago (Fleagle, 2013). Explaining how this diversity arose—and particularly how it has been shaped by other aspects of primate biology—is a major goal of evolutionary primatology.

Body size has been recognized as an important influence on primate trophic evolution since Kay (1975) noted that folivores are mostly large-bodied whereas insectivores are mostly small. The correlation between body size and diet has been attributed to two other size-related trends (Kay, 1975; Kay & Covert, 1984; Kay & Hylander, 1978; Kay & Simons, 1980). First, because insects are small, dispersed, and often elusive, acquiring enough of them to meet metabolic requirements becomes more challenging as body size increases and is probably physiologically impossible above a certain threshold without specializing on social insects (McNab, 1984). Second, as body size decreases, digestive retention time becomes shorter and metabolic rate per unit mass increases, making it difficult for small-bodied primates to extract sufficient nutrition from leaves, which are resistant to chemical digestion and must be slowly fermented in the gut (Lambert, 1998). These arguments have also been invoked to explain why large-bodied frugivorous primates rely on leaves as their main source of dietary protein whereas small-bodied frugivores are dependent on insects (Kay & Simons, 1980; Kay & Covert, 1984). Size differentiation between herbivores and faunivores is pervasive across mammals (Price &

67   Hopkins, 2015; Grossnickle, 2020), indicating that the pattern found in primates is a general

68   feature of mammalian biology.

69   The distribution of trophic strategies within small-bodied primates has generated

70   additional hypotheses of constraint on the evolution of insectivory. Although insects are an

71   important resource for many diurnal primates (e.g., Digby, Ferrari, & Saltzman, 2007; Kinzey,

72   1992; Souza-Alves, Fontes, Chagas, & Ferrari, 2011; Zimbler-DeLorenzo & Stone, 2011),

73   insectivory as a primary trophic strategy (i.e., at least 50% a species' diet) is found mainly in

74   nocturnal lineages (Figure 1). The reason for the rarity of insectivory in small-bodied diurnal

75   lineages is unclear, but one hypothesis that has been proposed is that competition with diurnal

76   birds has limited the ability of primates to become established in the diurnal arboreal insectivore

77   niche (Cartmill, 1980; Charles-Dominique, 1975; Ross, 1996). This idea is difficult to test, but

78   direct interactions between the two clades certainly do occur (Heymann & Hsia, 2015), and there

79   is evidence that such interactions have had an influence on the distribution of species in each

80   clade (Beaudrot et al., 2013a, 2013b).

81   A long history of adaptation to herbivory has also been identified as a possible constraint.

82   In his discussion of primate origins, Rosenberger (2013) advocated for the idea that frugivory

83   was the formative trophic influence on early primate evolution, responsible for many of the

84   apomorphies that distinguish primates from other mammals (Sussman, 1991; Sussman,

85   Rasmussen, & Raven, 2013; Szalay, 1968). As a consequence, he argued, a primarily

86   insectivorous diet presents primates with "intense selective challenges" (Rosenberger, 2013, p.

87   886), making it difficult for them to switch from herbivory to insectivory. Studies of acidic

88   mammalian chitinase genes (*CHIA*s) provide support for the idea that some primate lineages

89   have experienced changes to their digestive biology that may decrease the likelihood of

90   insectivory evolving or persisting (Emerling, Delsuc, & Nachman, 2018; Janiak, Chaney, &

91   Tosi, 2018). However, in contrast to the global constraint proposed by Rosenberger, the

92   distribution of *CHIA* pseudogenes and deletions among extant species indicates that gene

93   functionality has been maintained by selection in some primate lineages and lost multiple times

94   in others (Emerling et al., 2018; Janiak et al., 2018). As noted by the authors of the *CHIA* studies,

95   this pattern of evolution is consistent with the hypothesis that insectivory was important for early

96   primates (Cartmill, 1974, 1992, 2012), with various clades becoming more specialized for

97   herbivory over time, perhaps resulting in variation across the primate tree in the ability to exploit

98   insects as a primary dietary resource.

99   If these constraints, or others, are operating in primates, then they should manifest at the

100   macroevolutionary level as heterogeneity among lineages in the rate of trophic evolution. For

101   example, the hypothesis that diurnality limits the evolution of insectivory predicts that small-

102   bodied anthropoids, which are mostly diurnal, will have a lower rate of transition between

103   trophic states than other small-bodied primate lineages, which are mostly nocturnal.

104   Evolutionary rates have been used to test hypotheses of constraint or to make a posteriori

105   inferences of constraint in a diverse set of organismal traits, including flower size in plants

106   (Barkman et al., 2008), forelimb morphology in marsupials (Cooper & Steppan, 2010), niche

107   evolution in damselfishes (Litsios et al., 2012), growth form in angiosperms (Beaulieu, O'Meara,

108   & Donoghue, 2013), and habitat shifts in diatoms (Nakov, Beaulieu, & Alverson, 2019). The

109   goal of the present study is to evaluate the idea that trophic evolution is constrained in some

110   small-bodied primate lineages by testing for variation in transition rates between insectivory and

111   herbivory against the null hypothesis that a single rate can explain the distribution of insectivory

112   and herbivory across the primate tree.

113

2 | MATERIALS AND METHODS

2.1 | Tree and sample

116 The analyses reported here were conducted using the phylogenetic topology estimated by

117 Springer et al. (2012) for 367 extant primate taxa. This tree was pruned so that only species-level

118 taxa recognized by Groves (2005) were included, resulting in a tree with 307 tips. Springer et al.

119 provided four sets of divergence dates for the tree based on different assumptions about variation

120 in rates of molecular evolution among lineages and the certainty of fossil calibrations. Two of the

121 timetrees were used for the present study: one that assumed autocorrelated rates of molecular

122 evolution with soft-bounded constraints on fossil calibrations, and one that assumed

123 autocorrelated rates but with hard-bounded constraints. These two trees were preferred over the

124 two that assumed independent rates of molecular evolution because autocorrelated rates provide

125 a much better fit to the primate molecular data and appear to be more biologically realistic (dos

126 Reis et al., 2018). The trees are available in the Supporting Information (Text S1 and Text S2).

127 Species were classified as insectivorous or herbivorous using primary field reports or

128 recent reviews that compiled information on dietary composition from such reports. A species

129 was considered insectivorous when insects and other small fauna constituted at least 50% of its

130 diet. For some species, dietary percentages were not available. In those cases, assignments were

131 made using qualitative descriptions from experts as long as the characterizations were

132 compatible with quantitative data for the species' closest living relatives. A total of 26 species

133 were identified as insectivorous (Table 1). The remaining taxa were categorized as herbivorous,

134 which subsumes frugivory, seed predation, folivory, exudativory, and graminivory (see Table S1

135 in the Supporting Information for the full list of taxa and character coding).

136   Species were further divided into small-bodied and large-bodied using literature

137   compilations of body mass (Smith and Jungers, 1997; Jones et al., 2009; Fleagle, 2013). Two

138   sets of analyses were performed using different size thresholds to evaluate whether the value

139   used to dichotomize body size affects interpretations: 800 g and 1 kg. All species were assigned

140   to a size category based on female body mass, given that females are considered more sensitive

141   to energetic constraints than males (e.g., Gordon, Johnson, & Louis, 2013). Taxa without data on

142   body mass were assigned to a size category when their position relative to the threshold could be

143   assumed with high confidence (e.g., all callitrichines are smaller than 800 g).

144   The size and diet classifications were combined to create a three-state character: small-

145   insectivorous, small-herbivorous, and large-herbivorous. This character was treated as ordered,

146   with direct transitions between small-insectivorous and large-herbivorous prohibited (i.e.,

147   SI↔SH↔LH). This coding scheme allowed transitions between trophic states within small-

148   bodied lineages to be isolated in the analysis without compromising phylogenetic sampling by

149   excluding large-bodied lineages.

150

151   **2.2 | Models of trait evolution**

152   Transition rates between character states were estimated using the multistate speciation and

153   extinction model (MuSSE) in the package diversitree (FitzJohn, 2012) for R (R Core Team,

154   2019). The hypothesis of variation in rates of trophic evolution was tested using diversitree's

155   make.musse.split function, which splits subclades (foreground clades) from the rest of the tree

156   (paraphyletic background) and allows each partition to have separate rate classes. The locations

157   of the splits are selected prior to analysis. Three foreground clades were used for this study:

158   Anthropoidea, Lemuriformes, and Lorisiformes. Initially, models with one split—one foreground

159   clade and the background—were examined. Depending on the results of those analyses, the

160   model set was expanded to include models with two foreground clades.

161   For each character state, MuSSE estimates up to three parameters: the transition rate out

162   of the state (q), the speciation rate for lineages in the state (λ), and the extinction rate for lineages

163   in the state (μ). Thus, a MuSSE model for an ordered three-state character and no splits will have

164   as many as $k = 10$ estimated parameters. Adding a single split will double that number to $k = 20$,

165   which is almost certainly too many for the size of the primate tree. To reduce the parameter set to

166   a more appropriate size, the following constraints were imposed. First, speciation and extinction

167   rates were not allowed to vary by character state or across partitions. Second, transition rates

168   between insectivory and herbivory in small-bodied lineages were set equal to each other within

169   partitions (i.e., $q_{IH} = q_{HI}$, where q_{IH} is the rate from insectivory to herbivory, and q_{HI} is the rate

170   from herbivory to insectivory). Previous analysis of this data set using an unpartitioned tree

171   found that the symmetric-rates model for transitions between trophic states provides a better fit

172   to the data than a model that allows rate asymmetry (i.e., $q_{IH} \neq q_{HI}$) (Scott, 2019). Preliminary

173   model comparisons using Akaike's information criterion indicated that the symmetric-rates

174   assumption is also justified within the partitions examined here. For transitions between size

175   classes among herbivores, there is strong support for rate asymmetry, with the rate into the large-

176   bodied state being several times higher than the rate into the small-bodied state across the

177   primate tree (Scott, 2019). Thus, size transition rates were allowed to vary within partitions.

178   These constraints resulted in two-partition models with $k = 8$ parameters: one trophic transition

179   rate for each partition, two size transition rates for each partition, and one speciation rate and one

180   extinction rate for the entire tree. A three-partition model (two foreground clades and the

181   paraphyletic background) has at least one more parameter ($k = 9$) for the second foreground

182   clade's trophic transition rate and, depending on the results, two additional parameters for that

183   clade's size transitions ($k = 11$).

184

185   **2.3 | Bayesian analysis of rate estimates**

186   Uncertainty in the maximum-likelihood estimate for each transition rate was examined

187   using a Bayesian approach to approximate each parameter's posterior distribution. This part of

188   the analysis was conducted with Markov chain Monte Carlo (MCMC) using diversitree's mcmc

189   function (FitzJohn, 2012). Markov chains were generated following the procedures outlined in

190   Johnson, FitzJohn, Smith, Rausher, & Otto (2011) and FitzJohn (2012), including their use of an

191   exponential prior distribution with a mean of twice the net diversification rate (i.e., speciation

192   rate minus extinction rate) for the entire tree. The chains were run for 120,000 generations, with

193   the first 20,000 being discarded as burn-in. The remaining generations were thinned by sampling

194   every tenth generation, resulting in a final sample of 10,000 generations for further analysis. The

195   R package coda (Plummer, Best, Cowles, & Vines, 2006) was used to examine MCMC

196   diagnostics on the thinned chains. Effective sample sizes for transition rates were high ($n > 8200$,

197   typically $n > 9000$), autocorrelation among generations for each parameter was low ($r < 0.07$,

198   typically $r < 0.03$), and trace plots indicated convergence.

199   The posterior distributions for the parameter estimates were used to compute posterior

200   probabilities for differences between transition rates. The posterior probability that q_i is greater

201   than q_j is simply the proportion of MCMC samples for which that statement is true (Goldberg et

202   al., 2010). Such comparisons were made across partitions (e.g., Anthropoidea versus the

203   background) and within partitions in the case of size transitions (e.g., the rate of transition into

204   the large-bodied state versus the rate into the small-bodied state in Anthropoidea). Because the

205   posterior distributions for Lorisiformes were strongly right-skewed, rates were log-transformed

206   (base *e*) for visual presentation, but all quantitative comparisons were made using the

207   untransformed rates.

208

209   **3 | RESULTS**

210   **3.1 | Two-partition models**

211   With Anthropoidea split from the rest of the tree, there is moderate support for two rates of

212   transition between insectivory and herbivory in small-bodied lineages. Anthropoids have a lower

213   rate than other primates (Figure 2A): the maximum-likelihood estimate for the background rate

214   is approximately 5–7 times higher than the estimate for anthropoids (Table S2). The posterior

215   probabilities for rate heterogeneity in this partitioning scheme range from *PP* = 0.906 to 0.959,

216   depending on the tree and size threshold (Table 2). Support is highest when using a size

217   threshold of 1 kg and the tree with soft-bounded constraints on fossil calibrations.

218   There is strong support for asymmetry in size transition rates among anthropoids, where

219   transitions from small to large occur at a much higher rate than transitions in the reverse

220   direction (*PP* > 0.99; Figure 2B). In other primates, there is no evidence for such rate asymmetry

221   (*PP* < 0.70; Figure 2C). This difference in the pattern of size evolution is driven by the very low

222   transition rate out of the large-bodied state in anthropoids. This rate differs from the other size

223   transition rates with high posterior probability (*PP* > 0.98), whereas the other three rates cannot

224   be statistically distinguished from each other (*PP* < 0.85; compare Figure 2B and 2C).

225   Given the strong support for these contrasting patterns of size evolution, the remaining

226   two-partition models were modified to allow anthropoids to have their own set of size transition

227   rates while constraining the rest of the tree to have a second set of size transition rates, regardless

228   of how the tree was partitioned for the analysis of trophic transition rates. Thus, these models

229   have two partitions for trophic transition rates and two partitions for size transition rates. The

230   model that allowed Lorisiformes to have a distinct trophic rate produced the strongest support for

231   trophic rate heterogeneity among the two-partition models (Figure 3). In this case, lorisiforms

232   have a rate of trophic evolution that is approximately 4–6 times higher than the background rate

233   with high posterior probability ($PP > 0.98$; Table S3). The results from the model that allowed

234   Lemuriformes to have a distinct trophic rate indicate no support for trophic rate heterogeneity

235   ($PP < 0.70$; Figure 4; Table S4).

236

237   **3.2 | Three-partition model**

238   The two-partition analyses suggest three possibilities: (1) that anthropoids have a lower trophic

239   transition rate than other primates, (2) that lorisiforms have a higher rate than other primates, or

240   (3) that the two-partition models do not adequately describe the degree of rate heterogeneity in

241   primates. To distinguish among these alternatives, a three-partition model with anthropoids and

242   lorisiforms both foregrounded was constructed. This model allowed each partition to have its

243   own rate of trophic evolution, with size transition rates partitioned as above (i.e., anthropoids

244   versus all other primates, including lorisiforms; Table S5). Analysis of this model indicates that

245   the anthropoid trophic rate cannot be clearly distinguished from the background rate ($PP < 0.90$),

246   that there is moderate support for lorisiforms having a higher trophic rate than the background

247   ($0.90 < PP < 0.96$), and that anthropoids and lorisiforms are very unlikely to be characterized by

248   a common trophic rate ($PP > 0.98$) (Table 3; Figure 5). These results suggest that, of the models

249   considered here, the two-partition model with Lorisiformes as the foreground clade provides the

250   best description of primate trophic evolution.

251

4 | DISCUSSION

4.1 | Activity pattern and trophic evolution

254 The rate heterogeneity detected here supports the idea that trophic evolution has been more labile

255 in some small-bodied primate lineages than in others. The rarity of primarily insectivorous

256 anthropoids has focused attention on this clade and the possibility that some aspect of diurnal

257 ecology is a constraint on trophic evolution in primates (Cartmill, 1980; Charles-Dominique,

258 1975; Ross, 1996; Scott, 2019). The results of the present study challenge this idea by showing

259 that a single rate of transition between insectivory and herbivory can explain the distribution of

260 trophic strategies among small-bodied lineages of mostly diurnal anthropoids and nocturnal

261 lemurs and tarsiers. Insectivorous anthropoids and lemurs are nested deeply among herbivorous

262 lineages, indicating that insectivory is an evolutionarily recent phenomenon in these two clades

263 (Figure 1). Thus, despite differences in activity pattern, extant anthropoids and lemurs appear to

264 be characterized by similar trophic evolutionary histories where herbivory has predominated and

265 shifts to insectivory have been infrequent.

266 What distinguishes anthropoids in this analysis is their pattern of size evolution. In

267 contrast to other primates, which are characterized by symmetric rates of transition into and out

268 of the large-bodied state, anthropoids exhibit high rate asymmetry favoring shifts into the large-

269 bodied state. This result is not surprising in light of the well-known differences in the distribution

270 of body size among primate clades (e.g., Charles-Dominique, 1975; Fleagle, 1978, 2013;

271 Jungers, 1984). The prevalence of large body size (>1 kg) in anthropoids is thought to be one of

272 the solutions to the problem of trophic competition with diurnal birds, allowing anthropoids to

273 specialize on herbivorous resources that birds cannot typically access (e.g., leaves and

274   mechanically protected fruits; Charles-Dominique, 1975; Ross, 1996). The results of this study

275   are consistent with this idea, but they do not constitute additional evidence beyond the

276   observation that anthropoids tend to be larger than diurnal birds. Diurnality can be considered an

277   indirect influence on the distribution of insectivory across the primate tree to the extent that it

278   increases the likelihood that large body size will evolve and persist. This effect is magnified by

279   the tendency of diurnal lineages to diversify and accumulate at a higher rate than nocturnal

280   lineages (Magnuson-Ford & Otto, 2012; Santini, Rojas, & Donati, 2015; Scott, 2018, 2019).

281   However, the results of this study suggest that activity pattern does not have an effect on the rate

282   of transition between herbivory and insectivory among small-bodied primates.

283   Because the broad-scale phylogenetic approach adopted here does not address the

284   possibility that lineage-specific factors have produced similar patterns of trophic evolution in

285   diurnal anthropoids and nocturnal lemurs, these results should not be viewed as a decisive

286   rejection of the idea that diurnality is a constraint on primate trophic evolution. Studies

287   conducted at a much finer scale of resolution may reveal different processes operating in each

288   clade and establish equifinality. However, given the current state of knowledge, the low

289   frequency of insectivory among small-bodied diurnal anthropoids does not appear to be unusual

290   and therefore in need of explanation. Instead, it is the lorises and galagos that stand out relative

291   to other small-bodied primates in having a greater tendency to shift between trophic states.

292

293   **4.2 | Commitment to herbivory as a constraint on the evolution of insectivory**

294   The pattern of rate heterogeneity found in primates is consistent with the idea that

295   adaptive commitment to herbivory has reduced the likelihood that insectivory will evolve or

296   persist in some lineages. There are two ways to interpret the pattern of rate heterogeneity in this

297   context. The first posits that the low rate of transition between trophic states found in most of the

298   primate tree is plesiomorphic, meaning that trophic evolution has been conservative for much of

299   the clade's history. This inference, combined with the prevalence of herbivory among extant

300   lineages, aligns with the view that many of the apomorphies that unite primates originated as

301   adaptations for acquiring angiosperm products, and that this aspect of the clade's evolutionary

302   history has biased primates against adopting insectivory as a primary trophic strategy

303   (Rosenberger, 2013; Sussman et al., 2013). It follows that the higher rate of trophic evolution

304   found in lorisiforms represents a derived acceleration, suggesting that lineages in this group

305   evolved traits that allowed them to shift between trophic states more easily than other primates in

306   response to ecological conditions. The evolutionary importance of insects as a primary or

307   secondary dietary resource among lorisiforms was emphasized by Rasmussen & Nekaris (1998),

308   who argued that adaptive divergence between Lorisidae and Galagidae in aspects of locomotor

309   behavior, sensory systems, and life history was driven, in part, by specialization on insects with

310   different properties: cryptic or toxic prey in the case of lorisids versus active and elusive prey in

311   the case of galagids. Notably, the ability to exploit insects has not necessarily channeled

312   lorisiform lineages toward obligate insectivory, as in tarsiers. The present-day expression of this

313   evolutionary history is the gradient of trophic strategies exhibited by galagids and the presence of

314   herbivorous and insectivorous lorisid sister lineages found in both Africa and Asia (Nekaris and

315   Bearder, 2007).

316   The second scenario posits that the transition rate found in lorisiforms is plesiomorphic

317   and that other primate clades evolved slower rates in parallel as they became more committed to

318   a particular trophic strategy: herbivory in Anthropoidea and Lemuriformes, and insectivory in

319   tarsiers. This scenario is less parsimonious than the first, but there are two lines of evidence that

320   suggest convergent, herbivory-driven rate slowdowns in anthropoids and lemurs. First, as noted

321   above, studies of chitinase genes indicate pervasive homoplasy in loss of function in these genes

322   across primates (Emerling et al., 2018; Janiak et al., 2018). Emerling et al. (2018) inferred that

323   the plesiomorphic number of *CHIA*s for placental mammals is five functional genes, and that

324   tarsiers retain this condition, implying that the last common ancestors of Primates and Haplorhini

325   also had five. The anthropoids and lemurs that have been characterized so far, including small-

326   bodied species, have two or fewer functional *CHIA*s, and some large-bodied species in both

327   clades have lost function in all five genes, indicating separate histories of increasing commitment

328   to herbivory (Emerling et al., 2018; Janiak et al., 2018). This conclusion is further reinforced by

329   the observation that the lorisiform *Otolemur garnettii* has three functional *CHIA*s (Emerling et

330   al., 2018; Janiak et al., 2018).

331   The second line of evidence suggesting convergent rate slowdowns in Anthropoidea and

332   Lemuriformes is the history of body-size evolution in each clade's smallest-bodied lineages. The

333   smallest anthropoids are the Callitrichinae, which have long been regarded as phyletic dwarfs

334   (e.g., Ford, 1980; Leutenegger, 1980; Rosenberger, 1992), descended from a common ancestor

335   shared with other platyrrhines that weighed approximately 1–2 kg (Ford & Davis, 1992;

336   Montgomery & Mundy, 2013; Silvestro et al., 2019). The closely related and slightly larger

337   squirrel monkeys (genus *Saimiri*) may also be dwarfed (Ford & Davis, 1992; Rosenberger, 1992;

338   Silvestro et al., 2019). Recent studies of size evolution in lemurs have concluded that the

339   smallest members of this clade—species of the family Cheirogaleidae—have experienced

340   episodes of size reduction similar to those reconstructed for callitrichines (Masters, Génin,

341   Silvestro, Lister, & DelPero, 2014; Montgomery & Mundy, 2013). If these inferences of phyletic

342   dwarfism are correct, then the evolutionary histories of small-bodied anthropoids and lemurs

343   may include long periods of relaxed selection on traits involved in extracting nutrition from

344   insects (e.g., chitinase genes) owing to the lesser importance of insects as a dietary resource at

345   large body size.

346   That most small-bodied anthropoids and lemurs have apparently entered their current size

347   range via phyletic dwarfism contrasts with the pattern evident in lorisiforms and tarsiers, where

348   small size appears to have prevailed throughout their histories (Beard, 1998; Beard, Qi, Dawson,

349   Wang, & Li, 1994; Jaeger et al., 2010; Rossie, Ni, & Beard, 2006; Steiper & Seiffert, 2012;

350   Seiffert, Simons, & Attia, 2003; Seiffert, Simons, Ryan, & Attia, 2005). The observation that

351   tarsiers and at least some lorisiforms retain more functional *CHIA*s than other primates also

352   suggests long histories of small body size with selection to maintain some of the primitive

353   digestive machinery assembled in early insectivorous mammals (Emerling et al., 2018; Janiak et

354   al., 2018). *Otolemur garnettii* is the only lorisiform in which *CHIA*s have been investigated so

355   far (Emerling et al., 2018; Janiak et al., 2018). It is unclear how typical this galagid is of other

356   lorisiforms, but the fact that the number of functional genes retained by *O. garnettii* (three) is

357   intermediate between tarsiers (five) and anthropoids and lemurs (two or fewer) is consistent with

358   the idea that lorisiforms have experienced episodes of adaptation to herbivory without becoming

359   too specialized, resulting in a clade that has been more flexible than crown anthropoids,

360   lemuriforms, and tarsiers with regard to shifting between trophic strategies.

361   Thus, whereas the first scenario outlined above views a slow rate of trophic evolution and

362   commitment to herbivory as evolutionarily ancient and tied to the origin of crown primates, the

363   second scenario raises the possibility that trophic evolution in early crown primates was more

364   labile—similar to lorisiforms—before herbivory came to predominate in the case of crown

365   anthropoids and lemurs, and insectivory in the case of tarsiers. Such trophic flexibility is

366 compatible with a last common ancestor of crown primates that was either primarily herbivorous

367 (Rosenberger, 2013; Sussman et al., 2013) or primarily insectivorous (Cartmill, 1974, 1992,

368 2012), and it implies that the ancestor's feeding adaptations did not necessarily constrain or bias

369 trophic evolution as the crown clade began to diversify in the late Paleocene and early Eocene.

370

371 **4.3 | Evidence for trophic lability in the primate fossil record**

372   The primate fossil record provides some evidence that early small-bodied primates had a

373 greater tendency to shift between trophic states than would be inferred from the distribution of

374 states among extant anthropoids, lemurs, and tarsiers of similar size. Most of the small-bodied

375 primates known from the early and middle Eocene are omomyiforms (e.g., Covert, 1986;

376 Fleagle, 1978, 2013; Gilbert, 2005; Gingerich, 1981). Studies that have examined functional

377 aspects of molar form in this group indicate that it was characterized by a level of trophic

378 diversity similar to that found in extant lorisiforms (Strait, 2001). The evolutionary history of this

379 diversity is difficult to reconstruct with confidence, given uncertainties in the relationships

380 among omomyiform lineages (e.g., Morse et al., 2019; Tornow, 2008; Williams, 1994). Mapping

381 inferred diets onto the phylogenetic tree generated by Seiffert et al. (2018) indicates a minimum

382 of 5–7 shifts between trophic states over the course of approximately 20 million years (Figure 6).

383 By comparison, the minimum number of shifts required to explain the distribution of states

384 among extant primates is 10 across 60 million years or more of evolution (Scott, 2019),

385 suggesting a relatively high rate of trophic evolution in omomyiforms. This conclusion is also

386 supported by evidence for trophic diversity within two of the earliest genera—*Teilhardina* and

387 *Steinius* (Figure 6; Ni et al., 2004; Strait, 2001; Williams & Covert, 1994).

388   The broader significance of trophic evolution in omomyiforms is unclear owing to a lack

389   of consensus regarding their phylogenetic relationships to the crown clades. Omomyiforms have

390   been interpreted as stem tarsiers, stem haplorhines, or stem primates (see reviews in Fleagle,

391   2013; Martin, 1993; Miller, Gunnell, & Martin, 2005). Rosenberger (2013), adopting the first of

392   these alternatives as a working hypothesis, argued that trophic diversity within omomyiforms

393   reflects different stages in a shift from frugivory to the highly specialized form of insectivory

394   found in extant tarsiers. According to this view, the implications of omomyiform trophic

395   diversity are limited to the tarsier lineage, and the pattern of diversity mostly indicates a

396   directional macroevolutionary trend of increasing insectivory and its attendant morphological

397   adaptations. However, if omomyiforms are stem haplorhines (e.g., Kay, Ross, & Williams, 1997)

398   or representatives of an early radiation of primates not uniquely related to any of the crown

399   clades (e.g., Martin, 1993; Miller et al., 2005), then their pattern of trophic diversity can be

400   plausibly interpreted as consistent with the hypothesis that trophic evolution in early primates

401   was more labile in comparison to crown Anthropoidea, Tarsiidae, and Lemuriformes.

402   Other groups of Eocene primates appear to have been less trophically diverse than

403   omomyiforms and more specialized for herbivory. Adapiformes—the other major radiation of

404   primates known from the early and middle Eocene—are mostly large-bodied and are thought to

405   have filled the ecological niches that are now dominated by extant large-bodied anthropoids and

406   lemurs (i.e., diurnal herbivores) (Covert, 1986; Fleagle, 1978, 2013; Gilbert, 2005).

407   Nevertheless, there is some evidence for trophic diversity among early small-bodied members of

408   this group (e.g., *Donrussellia*, *Asiadapis*, and *Marcgodinotius*; Bajpai et al., 2008; Gilbert,

409   2005). A similar pattern may hold in anthropoids, especially if Eosimiidae are stem anthropoids

410   (Beard, Qi, Dawson, Wang, & Li, 1994; Kay et al., 1997; Williams, Kay, & Kirk, 2010; but see

411   Miller et al., 2005). Small-bodied anthropoids from the late Eocene and early Oligocene have

412   been reconstructed as primarily frugivorous (Kirk & Simons, 2001). In contrast, the molars of

413   middle Eocene eosimiids exhibit morphologies suggesting that these species were more

414   insectivorous than later anthropoids (cf. Heesy & Ross, 2004; Kirk & Simons, 2001) and perhaps

415   comparable to *Saimiri*, the most insectivorous extant anthropoid (Zimbler-DeLorenzo & Stone,

416   2011; Table 1). Thus, although adapiforms and early anthropoids appear to have been largely

417   herbivorous radiations, there are hints of greater trophic diversity in the earliest members of

418   these clades, suggesting that trophic evolution may have been more labile before herbivory

419   became the dominant trophic strategy.

420

421   **5 | CONCLUSIONS**

422   The results of this study indicate that the rate of trophic evolution in small-bodied

423   primates varies among clades. Contrary to expectations, small-bodied anthropoids do not have an

424   unusually low rate in comparison to other lineages. This finding challenges the hypothesis that

425   there is a direct connection between diurnality and the low frequency of insectivorous

426   anthropoids. The main contrast detected here involves lorisiforms, which have a much greater

427   tendency to shift between insectivory and herbivory than other primates. The implications of this

428   pattern of rate heterogeneity are unclear. The most parsimonious interpretation is that the

429   lorisiform rate is apomorphic, implying that primate trophic evolution has been conservative

430   throughout much of the clade's history. However, various lines of evidence suggest the

431   possibility of convergent rate slowdowns in anthropoids, lemuriforms, and tarsiers owing to

432   greater specialization for herbivory in the case of anthropoids and lemurs, and insectivory in the

433   case of tarsiers. These two scenarios can be tested as sampling of the earliest part of the primate

434   fossil record increases, and as our understanding of the Eocene primate phylogeny and trophic

435   adaptations improves.

436

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440

441   **DATA AVAILABILITY STATEMENT**

442   The data used for this study are available in Table S1 in the Supporting Information.

443

444

REFERENCES

445   Bajpai, S., Kay, R. F., Williams, B. A., Das, D. P., Kapur, V. V., & Tiwari, B. N. (2008). The

446   oldest Asian record of Anthropoidea. *Proceedings of the National Academy of Sciences*

447   *of the United States of America*, *105*, 11093–11098.

448   Beard, K. C., Qi, T., Dawson, M. R., Wang, B., & Li, C. (1994). A diverse new primate fauna

449   from middle Eocene fissure-fillings in southeastern China. *Nature*, *368*, 604–609

450   Barkman, T. J., Bendiksby, M., Lim, S.-H., Salleh, K. M., Nais, J., Madulid, D., & Schumacher,

452   T. (2008). Accelerated rates of floral evolution at the upper size limit for flowers. *Current*

453   *Biology*, *18*, 1508–1513.

454   Beard, K. C. (1998). A new genus of Tarsiidae (Mammalia: Primates) from the middle Eocene of

455   Shanxi Province, China, with notes on the historical biogeography of tarsiers. *Bulletin of*

456   *Carnegie Museum of Natural History*, *34*, 260–277.

457   Beard, K. C., Qi, T., Dawson, M. R., Wang, B., & Li, C. (1994). A diverse new primate fauna

458   from middle Eocene fissure-fillings in southeastern China. *Nature*, *368*, 604–609.

459   Beaudrot, L., Struebig, M. J., Meijaard, E., van Balen, S., Husson, S., & Marshall, A. J. (2013a).

460   Co-occurrence patterns of Bornean vertebrates suggest competitive exclusion is strongest

461   among distantly related species. *Oecologia*, *173*, 1053–1062.

462   Beaudrot, L., Struebig, M. J., Meijaard, E., van Balen, S., Husson, S., Young, C. F., & Marshall,

463   A. J. (2013b). Interspecific interactions between primates, birds, bats, and squirrels may

464   affect community composition on Borneo. *American Journal of Primatology*, *75*, 170–

465   185.

466   Beaulieu, J. M., O'Meara, B. C., & Donoghue, M. J. (2013). Identifying hidden rate changes in

467   the evolution of a binary morphological character: the evolution of plant habit in

468   campanulid angiosperms. *Systematic Biology*, *62*, 725–737.

469   Biebouw, K. (2013). Preliminary results on the behavioral ecology of the hairy-eared dwarf

470   lemur (*Allocebus trochotis*) in Andasibe, eastern Madagascar. In J. Masters, M. Gamba,

471   & F. Génin (Eds.), *Leaping ahead: advances in prosimian biology* (pp. 113–120). New

472   York, NY: Springer.

473   Burrows, A. M., & Nash, L. T. (2010). Searching for dental signals of exudativory in galagos. In

474   A. M. Burrows & L. T. Nash (Eds.), *The evolution of exudativory in primates* (pp. 211–

475   233). New York, NY: Springer.

476   Butynski, T. M., & de Jong, Y. A. (2004). Natural history of the Somali lesser galago (*Galago*

477   *gallarum*). *Journal of East African Natural History*, *93*, 23–38.

478   Cartmill, M. (1974). Rethinking primate origins. *Science*, *184*, 436–443.

479   Cartmill, M. (1980). Morphology, function, and evolution of the anthropoid postorbital septum.

480   In R. L. Chiochon & A. B. Chiarelli (Eds.), *Evolution biology of the New World monkeys*

481   *and continental drift* (pp. 243–274). New York, NY: Plenum Press.

482   Cartmill, M. (1992). New views on primate origins. *Evolutionary Anthropology*, *1*, 105–111.

483   Cartmill, M. (2012). Primate origins, human origins, and the end of higher taxa. *Evolutionary*

484   *Anthropology*, *21*, 208–220.

485   Charles-Dominique, P. (1975). Nocturnality and diurnality: an ecological interpretation of these

486   two modes of life by an analysis of the higher vertebrate fauna in tropic forest

487   ecosystems. In W. P. Luckett & F. S. Szalay (Eds.), *Phylogeny of the primates: a*

488   *multidisciplinary approach* (pp. 69–88). New York, NY: Plenum Press.

489   Cooper, W. J, & Steppan, S. J. (2010). Developmental constraint on the evolution of marsupial

490   forelimb morphology. *Australian Journal of Zoology*, *58*, 1–15.

491   Covert, H. H. (1986). Biology of early Cenozoic primates. In D. R. Swindler & J. Erwin (Eds.),

492   *Comparative primate biology: Vol. 1. Systematics, evolution, and anatomy* (pp. 335–

493   359). New York: Alan R. Liss.

494   Digby, L. J., Ferrari, S. F., & Saltzman, W. (2007). Callitrichines: the role of competition in

495   cooperatively breeding species. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M.

496   Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 85–105). Oxford: Oxford

497   University Press.

498   dos Reis, M., Gunnell, G. F., Barba-Montoya, J., Wilkins, A., Yang, Z., & Yoder, A.D. (2018).

499   Using phylogenomic data to explore the effects of relaxed clocks and calibration

500   strategies on divergence time estimation: primates as a test case. *Systematic Biology*, *67*,

501   594–615.

502   Emerling, C. A., Delsuc, F., & Nachman, M. W. (2018). Chitinase genes (*CHIA*s) provide

503   genomic footprints of a post-Cretaceous dietary radiation in placental mammals. *Science*

504   *Advances*, 4: eaar6478. DOI: 10.1126/sciadv.aar6478.

505   FitzJohn, R. G. (2012). Diversitree: comparative phylogenetic analyses of diversification in R.

506   *Methods in Ecology and Evolution*, *3*, 1084–1092.

507   Fleagle, J. G., (1978). Size distributions of living and fossil primate faunas. *Paleobiology*, *4*, 67–

508   76.

509   Fleagle, J. G. (2013). *Primate adaptation & evolution* (3rd ed.). San Diego, CA: Academic Press.

510   Ford, S. M. (1980). Callitrichids as phyletic dwarfs, and the place of the Callitrichidae in

511   Platyrrhini. *Primates*, *21*, 31–43.

512   Ford, S. M., & Davis, L. C. (1992). Systematics and body size: implications for feeding

513   adaptations in New World monkeys. *American Journal of Physical Anthropology*, *88*,

514   415–468.

515   Génin, F., Yokwana, A., Kom, N., Couette, S., Dieuleveut, T., Nash, S. D., & Masters, J. C.

516   (2016). A new galago species for South Africa (Primates: Strepsirhini: Galagidae).

517   *African Zoology*, *51*, 135–143.

518   Gilbert, C. C. (2005). Dietary ecospace and the diversity of euprimates during the early and

519   middle Eocene. *American Journal of Physical Anthropology*, *126*, 237–249.

520   Gingerich, P. D. (1981). Early Cenozoic Omomyidae and the evolutionary history of tarsiiform

521   primates. *Journal of Human Evolution*, *10*, 345–374.

522   Goldberg, E. E., Kohn, J. R., Lande, R., Robertson, K. A., Smith, S. A., Igić, B. (2010). Species

523   selection maintains self-incompatibility. *Science*, *330*, 493–495.

524   Gómez, J. M., & Verdú, M. (2012). Mutualism with plants drives primate diversification.

525   *Systematic Biology*, *61*, 567–577.

526   Gordon, A. D., Johnson, S. E., & Louis, E. E., Jr. (2013). Females are the ecological sex: sex-

527   specific body mass ecogeography in wild sifaka populations (*Propithecus* spp.).

528   *American Journal of Physical Anthropology*, *151*, 77–87.

529   Grossnickle, D. M. (2020). Feeding ecology has a stronger evolutionary influence on functional

530   morphology than on body mass in mammals. *Evolution*, *74*, 610–628.

531   Groves, C. P. (2005). Order Primates. In D. E. Wilson & D. M. Reeder (Eds.), *Mammal species*

532   *of the world: a taxonomic and geographic reference* (3rd ed., pp. 111–184). Baltimore,

533   MD: Johns Hopkins University Press.

534   Harcourt, C. S., & Nash, L. T. (1986). Species differences in substrate use and diet between

535   sympatric galagos in two Kenyan coastal forests. *Primates*, *27*, 41–52.

536   Heesy, C. P., & Ross, C. F. (2004). Mosaic evolution of activity pattern, diet, and color vision in

537   haplorhine primates. In C. F. Ross & R. F. Kay (Eds.), *Anthropoid origins: new visions*

538   (pp. 665–698). New York, NY: Kluwer Academic/Plenum Press.

539   Heymann, E. W., & Hsia, S. S. (2015). Unlike fellows—a review of primate–non-primate

540   associations. *Biological Reviews*, *90*, 142–156.

541   Hladik, C. M., Charles-Dominique, P., & Petter, J. J. (1980). Feeding strategies of five nocturnal

542   prosimians in the dry forest of the west coast of Madagascar. In P. Charles-Dominique,

543   H. M. Cooper, A. Hladik, C. M. Hladik, E. Pages, G. F. Pariente, A. Petter-Rousseaux, J.

544   J. Petter, & A. Schilling (Eds.), *Nocturnal Malagasy primates: ecology, physiology, and*

545   *behavior* (pp. 41–73). New York, NY: Academic Press.

546   Jaeger, J.-J., Beard, K. C., Chaimanee, Y., Salem, M., Benammi, M., Hlal, O., … Brunet, M.

547   (2010). Late middle Eocene epoch of Libya yields earliest known radiation of African

548   anthropoids. *Nature*, *467*, 1095–1098).

549   Janiak, M. C., Chaney, M. E., & Tosi, A. J. (2018). Evolution of acidic mammalian chitinase

550   genes (*CHIA*) is related to body mass and insectivory in primates. *Molecular Biology &*

551   *Evolution*, *35*, 607–622.

552   Johnson, M. T. J., FitzJohn, R. G., Smith, S. D., Rausher, M. D., & Otto, S. P. (2011). Loss of

553   sexual recombination and segregation is associated with increased diversification in

554   evening primroses. *Evolution*, *65*, 3230–3240.

555   Jones, K. E., Bielby, J., Cadillo, M., Fritz, S. A., O'Dell, J., Orme, C. D. L., … Purvis, A. (2009).

556   PanTHERIA: a species-level database of life history, ecology, and geography of extant

557   and recently extinct mammals. *Ecology*, *90*, 2648.

558   Jungers, W. L. (1984). Aspects of size and scaling in primate biology with special reference to

559   the locomotor skeleton. *Yearbook of Physical Anthropology*, *27*, 73–97.

560   Kay, R. F. (1975). The functional adaptations of primate molar teeth. *American Journal of*

561   *Physical Anthropology*, *43*, 195–216.

562   Kay, R. F., & Covert, H. H. (1984). Anatomy and behavior of extinct primates. In D. J. Chivers,

563   B. A. Wood, & A. Bilsborough (Eds.), *Food acquisition and processing in primates* (pp.

564   467–508. New York, NY: Plenum Press.

565   Kay, R. F., & Hylander, W. L. (1978). The dental structure of mammalian folivores with special

566   reference to Primates and Phalangeroidea. In G. G. Montgomery (Ed.), *The ecology of*

567   *arboreal folivores* (pp. 173–191). Washington, DC: Smithsonian Institution Press.

568   Kay, R. F., Ross, C., & Williams, B. A. (1997). Anthropoid origins. *Science*, *275*, 797–804.

569   Kay, R. F., & Simons, E. L. (1980). The ecology of Oligocene African Anthropoidea.

570   *International Journal of Primatology*, *1*, 21–37.

571   Kinzey, W. G. (1992). Dietary and dental adaptations in the Pitheciinae. *American Journal of*

572   *Physical Anthropology*, *88*, 499–514.

573   Kirk, E. C., & Simons, E. L. (2001). Diets of fossil primates from the Fayum Depression of

574   Egypt: a quantitative analysis of molar shearing. *Journal of Human Evolution*, *40*, 203–

575   229.

576   Lambert, J. E. (1998). Primate digestion: interactions among anatomy, physiology, and feeding

577   ecology. *Evolutionary Anthropology*, *7*, 8–20.

578   Leutenegger, W. (1980). Monogamy in callitrichids: a consequence of phyletic dwarfism?

579   *International Journal of Primatology*, *1*, 95–98.

580   Litsios, G., Pellissier, L., Forest, F., Lexer, C., Pearman, P. B., Zimmerman, N. E., & Salamin,

581   N. (2012). Trophic specialization influences the rate of environmental niche evolution in

582   damselfishes (Pomacentridae). *Proceedings of the Royal Society B*, *279*, 3662–3669.

583   Maddison, W. P., & Maddison, D. R. (2019). Mesquite: a modular system for evolutionary

584   analysis (version 3.61). Available from http://www.mesquiteproject.org.

585   Magnuson-Ford, K., & Otto, S. P. (2012). Linking the investigations of character evolution and

586   species diversification. *American Naturalist*, *180*, 225–245.

587   Martin, R. D. (1993). Primate origins: plugging the gaps. *Nature*, *363*, 223–234.

588   Masters, J. C., Génin, F., Silvestro, D., Lister, A. M., & DelPero, M. (2014). The red island and

589   the seven dwarfs: body size reduction in Cheirogaleidae. *Journal of Biogeography*, *41*,

590   1833–1847.

591   McNab, B. K. (1984). Physiological convergence amongst ant-eating and termite-eating

592   mammals. *Journal of Zoology, London*, *203*, 485–510.

593   Miller, E. R., Gunnell, G. F., & Martin, R. D. (2005). Deep time and the search for anthropoid

594   origins. *Yearbook of Physical Anthropology*, *48*, 60–95.

595   Montgomery, S. H., & Mundy, N. I. (2013). Parallel episodes of phyletic dwarfism in callitrichid

596   and cheirogaleid primates. *Journal of Evolutionary Biology*, *26*, 810–819.

597   Morse, P. E., Chester, S. G. B., Boyer, D. M., Smith, T., Smith, R., Gigase, P., & Bloch, J. I.

598   (2019). New fossils, systematics, and biogeography of the oldest known crown primate

599   *Teilhardina* from the earliest Eocene of Asia, Europe, and North America. *Journal of*

600   *Human Evolution*, *128*, 103–131.

601   Nakov, T., Beaulieu, J. M., & Alverson, A. J. (2019). Diatoms diversify and turn over faster in

602   freshwater than marine environments. *Evolution*, *73*, 2497–2511.

603   Nash, L. T., Bearder, S. K., & Olson, T.R. (1989). Synopsis of *Galago* species characteristics.

604   *International Journal of Primatology*, *10*, 57–80.

605   Nekaris, K. A. I., & Bearder, S. K. (2007). The lorisiform primates of Asia and mainland Africa.

606   In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. K. Bearder (Eds.),

607   *Primates in perspective* (pp. 24–45). Oxford: Oxford University Press.

608   Ni, X., Wang, Y., Hu, Y., & Li, C. (2004). A euprimate skull from the early Eocene of China.

609   *Nature*, *427*, 65–68.

610   Niemitz, C. (1984). Synecological relationships and feeding behaviour of the genus *Tarsius*. In

611   C. Niemitz (Ed.), *Biology of tarsiers* (pp. 59–75). Stuttgart: Gustav Fischer Verlag.

612   Plummer, M., Best, N., Cowles, K., & Vines, K. (2006). CODA: convergence diagnosis and

613   output analysis for MCMC. *R News*, *6*, 7–11.

614   Price, S. A., & Hopkins, S. S. B. (2015). The macroevolutionary relationship between diet and

615   body mass across mammals. *Biological Journal of the Linnean Society*, *115*, 173–184.

616   Rasmussen, D. T., & Nekaris, K. A. (1998). Evolutionary history of lorisiform primates. *Folia

617   Primatologica*, *69*(*Suppl.* 1), 250–285.

618   R Core Team (2019). R: a language and environment for statistical computing. Vienna, Austria:

619   R Foundation for Statistical Computing. https://www.R-project.org/.

620   Rosenberger, A. L. (1992). Evolution of feeding niches in New World monkeys. *American

621   Journal of Physical Anthropology*, *88*, 525–562.

622   Rosenberger, A. L. (2013). Fallback foods, preferred foods, adaptive zones, and primate origins.

623   *American Journal of Primatology*, *75*, 883–890.

624 Ross, C. (1996). Adaptive explanation for the origins of the Anthropoidea (Primates). *American*

625 *Journal of Primatology*, *40*, 205–230.

626 Rossie, J. B., Ni, X., Beard, K. C. (2006). Cranial remains of an Eocene tarsier. *Proceedings of*

627 *the National Academy of Sciences of the United States of America*, *103*, 4381–4385.

628 Rovero, F., Marshall, A. R., Jones, T., & Perkin, A. (2009). The primates of Udzungwa

629 Mountains: diversity, ecology and conservation. *Journal of Anthropological Sciences*, *87*,

630 93–126.

631 Santini, L., Rojas, D., & Donati, G. (2015). Evolving through day and night: origin and

632 diversification of activity pattern in modern primates. *Behavioral Ecology*, *26*, 789–796.

633 Scott, J. E. (2018). Reevaluating cases of trait-dependent diversification in primates. *American*

634 *Journal of Physical Anthropology*, *167*, 244–256.

635 Scott, J. E. (2019). Macroevolutionary effects on primate trophic evolution and their implications

636 for reconstructing primate origins. *Journal of Human Evolution*, *133*, 1–12.

637 Seiffert, E. R., Simons, E. L., & Attia, Y. (2003). Fossil evidence for ancient divergence of

638 lorises and galagos. *Nature*, *422*, 421–424.

639 Seiffert, E. R., Boyer, D. M., Fleagle, J. G., Gunnell, G. F., Heesy, C. P., Perry, J. M. G., &

640 Sallam, H. M. (2018). New adapiform primate fossil from the late Eocene of Egypt.

641 *Historical Biology*, *30*, 204–226.

642 Seiffert, E. R., Simons, E. L., Ryan, T. M., & Attia, Y. (2005). Additional remains of *Wadilemur*

643 *elegans*, a primitive stem galagid from the late Eocene of Egypt. *Proceedings of the*

644 *National Academy of Sciences of the United States of America*, *102*, 11396–11401.

645   Silvestro, D., Tejedor, M. F., Serrano-Serrano, M. L., Loiseau, O., Rossier, V., Rolland, J., …

646   Salamin, N. (2019). Early arrival and climatically-linked geographic expansion of New

647   World monkeys from tiny African ancestors. *Systematic Biology*, *68*, 78–92.

648   Smith, R. J., & Jungers, W. L. (1997). Body mass in comparative primatology. *Journal of*

649   *Human Evolution*, *32*, 523–559.

650   Souza-Alves, J. P., Fontes, I. P., Chagas, R. R. D., & Ferrari, S. F. (2011). Seasonal versatility in

651   the feeding ecology of a group of titis (*Callicebus coimbrai*) in the northern Brazilian

652   Atlantic Forest. *American Journal of Primatology*, *73*, 1199–1209.

653   Springer, M. S., Meredith, R. W., Gatesy, J., Emerling, C. A., Park, J., Rabosky, D. L., …

654   Murphy, W. J. (2012). Macroevolutionary dynamics and historical biogeography of

655   primate diversification inferred from a species supermatrix. *PLoS ONE*, *7*, e49521. DOI:

656   10.1371/journal.pone.0049521.

657   Steiper, M. E., & Seiffert, E. R. (2012). Evidence for a convergent slowdown in primate

658   molecular rates and its implications for the timing of early primate evolution.

659   *Proceedings of the National Academy of Sciences of the United States of America*, *109*,

660   6006–6011.

661   Strait, S. G. (2001). Dietary reconstruction of small-bodied omomyoid primates. *Journal of*

662   *Vertebrate Paleontology*, *21*, 322–334.

663   Sussman, R. W. (1991). Primate origins and the evolution of angiosperms. *American Journal of*

664   *Primatology*, *23*, 209–223.

665   Sussman, R. W., Rasmussen, D. T., & Raven, P. H. (2013). Rethinking primate origins again.

666   *American Journal of Primatology*, *75*, 95–106.

667   Szalay, F. S. (1968). The beginnings of primates. *Evolution*, *22*, 19–36.

668   Tornow, M. A. (2008). Systematic analysis of the Eocene primate Omomyidae using gnathic and

669   postcranial data. *Bulletin of the Peabody Museum of Natural History*, *49*, 43–129.

670   Williams, B. A. (1994). *Phylogeny of the Omomyidae and implications for anthropoid origins*

671   (Unpublished doctoral dissertation). University of Colorado, Boulder.

672   Williams, B. A., & Covert, H. H. (1994). New early Eocene anaptomorphine primate

673   (Omomyidae) from the Washakie Basin, Wyoming, with comments on the phylogeny

674   and paleobiology of anaptomorphines. *American Journal of Physical Anthropology*, *93*,

675   323–340.

676   Williams, B. A., Kay, R. F., & Kirk, E. C. (2010). New perspectives on anthropoid origins.

677   *Proceedings of the National Academy of Sciences of the United States of America*, *107*,

678   4797–4804.

679   Zimbler-DeLorenzo, H. S., & Stone, A. I. (2011). Integration of field and captive studies for

680   understanding the behavioral ecology of the squirrel monkey (*Saimiri* sp.). *American*

681   *Journal of Primatology*, *73*, 607–622.

682

683

684 **FIGURE CAPTIONS**

685 **FIGURE 1.** Primate phylogenetic tree from Springer et al. (2012) showing the distribution of

686 trophic states by activity pattern among small-bodied species (<1 kg) at the tips (Scott, 2019).

687 Cathemeral species are grouped with diurnal species. Large-bodied species, which are uniformly

688 herbivorous and mostly diurnal, are not labeled. The relative frequency of insectivorous species

689 is much greater among nocturnal lineages (41.5%) than among diurnal lineages (9.5%).

690

691 **FIGURE 2.** Posterior distributions of trophic transition rates (A) and size transition rates (B, C)

692 for the model with Anthropoidea split from the rest of the tree and a size threshold of 800 g. The

693 results shown here were generated using the timetree that assumed autocorrelated rates and soft-

694 bounded constraints. Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor =

695 Lorisiformes, q = transition rate, SL = small to large, LS = large to small.

696

697 **FIGURE 3.** Posterior distributions of trophic transition rates for the model with Lorisiformes

698 split from the rest of the tree and a size threshold of 800 g. The results shown here were

699 generated using the timetree that assumed autocorrelated rates and soft-bounded constraints.

700 Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor = Lorisiformes, q =

701 transition rate.

702

703 **FIGURE 4.** Posterior distributions of trophic transition rates for the model with Lemuriformes

704 split from the rest of the tree and a size threshold of 800 g. The results shown here were

705 generated using the timetree that assumed autocorrelated rates and soft-bounded constraints.

706   Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor = Lorisiformes, q =

707   transition rate.

708

709   **FIGURE 5.** Posterior distributions of trophic transition rates for the model with Anthropoidea

710   and Lorisiformes each split from the rest of the tree and a size threshold of 800 g. The results

711   shown here were generated using the timetree that assumed autocorrelated rates and soft-

712   bounded constraints. Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor =

713   Lorisiformes, q = transition rate.

714

715   **FIGURE 6.** Phylogenetic distribution of trophic strategies among early and middle Eocene

716   omomyiform genera. Dietary reconstructions for each genus are based mainly on the work of

717   Strait (2001), with additional information from Ni, Wang, Hu, & Li (2004) and Williams &

718   Covert (1994). Parsimony reconstructions of diet, obtained using Mesquite (v. 3.61; Maddison &

719   Maddison, 2019), indicate a minimum of 5–7 shifts between trophic states, depending on how

720   ambiguous taxa are coded. The reconstructions shown here are based on the data set where

721   *Bownomomys* and *Dyseolemur* were coded as ambiguous (see Strait, 2001). The tree was taken

722   from the Bayesian tip-dating phylogenetic analysis conducted by Seiffert et al. (2018; see their

723   figure 17). Branch lengths are proportional to time; the tree spans approximately 20 million years

724   from root to most recent tip (*Necrolemur*). *Teilhardina* includes *T. asiatica* and *T. belgica*;

725   *Steinius* includes *S. vespertinus* and *S. annectens*; the use of *Bownomomys* here follows Morse et

726   al. (2019) and is equivalent to *Teilhardina americana* in previous studies. See Strait (2001) and

727   Seiffert et al. (2018) for the complete lists of species-level taxa.

728

TABLE 1   Primates classified as insectivorous for this study

Species	% Faunivory	Source
Galagoides thomasi	70	Nekaris & Bearder, 2007
Galagoides demidoff	70	Nekaris & Bearder, 2007
Galago matschiei	qualitative[†]	Nash, Bearder, & Olson, 1989
Galago moholi	52	Nekaris & Bearder, 2007
Galago gallarum	qualitative[†]	Butynski & de Jong, 2004
Galago senegalensis	50	Burrows & Nash, 2010
Paragalago orinus	qualitative[†]	Rovero, Marshall, Jones, & Perkin, 2009
Paragalago granti	qualitative[†]	Génin et al., 2016
Paragalago zanzibaricus	70	Harcourt & Nash, 1986
Otolemur garnettii	50	Harcourt & Nash, 1986
Loris lydekkerianus	96	Nekaris & Bearder, 2007
Loris tardigradus	100	Nekaris & Bearder, 2007
Arctocebus calabarensis	85	Rothman et al., 2014
Arctocebus aureus	85	Rothman et al., 2014
Allocebus trichotis	70	Biebouw, 2013
Mirza coquereli	>50	Hladik, Charles-Dominique, & Petter, 1980
Microcebus rufus	54	Rothman et al., 2014
Tarsius dentatus	100	Niemitz, 1984
Tarsius tarsier	100	Niemitz, 1984
Tarsius sangirensis	100	Niemitz, 1984
Cephalopachus bancanus	100	Niemitz, 1984
Carlito syrichta	100	Niemitz, 1984
Saimiri sciureus	79–97	Zimbler-DeLorenzo & Stone, 2011
Saimiri oerstedii	90	Zimbler-DeLorenzo & Stone, 2011
Saimiri boliviensis	75	Zimbler-DeLorenzo & Stone, 2011
Saimiri ustus	as for other *Saimiri*	Zimbler-DeLorenzo & Stone, 2011

[†] For some species, dietary percentages were not available. In such cases, I used qualitative accounts from experts as long as the description was consistent with quantitative data for the species' closest living relatives. See Table S1 in the Supporting Information for the full sample.

TABLE 2 Support for trophic-rate differences in two-partition models

| | Posterior probability | | | |
| | AUTOsoft tree | | AUTOhard tree | |
Model comparison	t.800	t.1000	t.800	t.1000
Anthropoidea < background	0.917	0.959	0.906	0.946
Lorisiformes > background	0.985	0.992	0.983	0.989
Lemuriformes > background	0.622	0.676	0.614	0.647

Notation: AUTOsoft = autocorrelated rates of molecular evolution and soft-bounded constraints; AUTOhard = autocorrelated rates of molecular evolution and hard-bounded constraints; t.800 = size threshold of 800 g; t.1000 = size threshold of 1 kg.

TABLE 3 Support for trophic-rate differences in the three-partition model

| | Posterior probability | | | |
| | AUTOsoft tree | | AUTOhard tree | |
Model comparison	t.800	t.1000	t.800	t.1000
Anthropoidea < background	0.791	0.861	0.787	0.838
Loriformes > background	0.939	0.951	0.933	0.950
Lorisformes > Anthropoidea	0.986	0.995	0.984	0.991

Notation: AUTOsoft = autocorrelated rates of molecular evolution and soft-bounded constraints; AUTOhard = autocorrelated rates of molecular evolution and hard-bounded constraints; t.800 = size threshold of 800 g; t.1000 = size threshold of 1 kg.
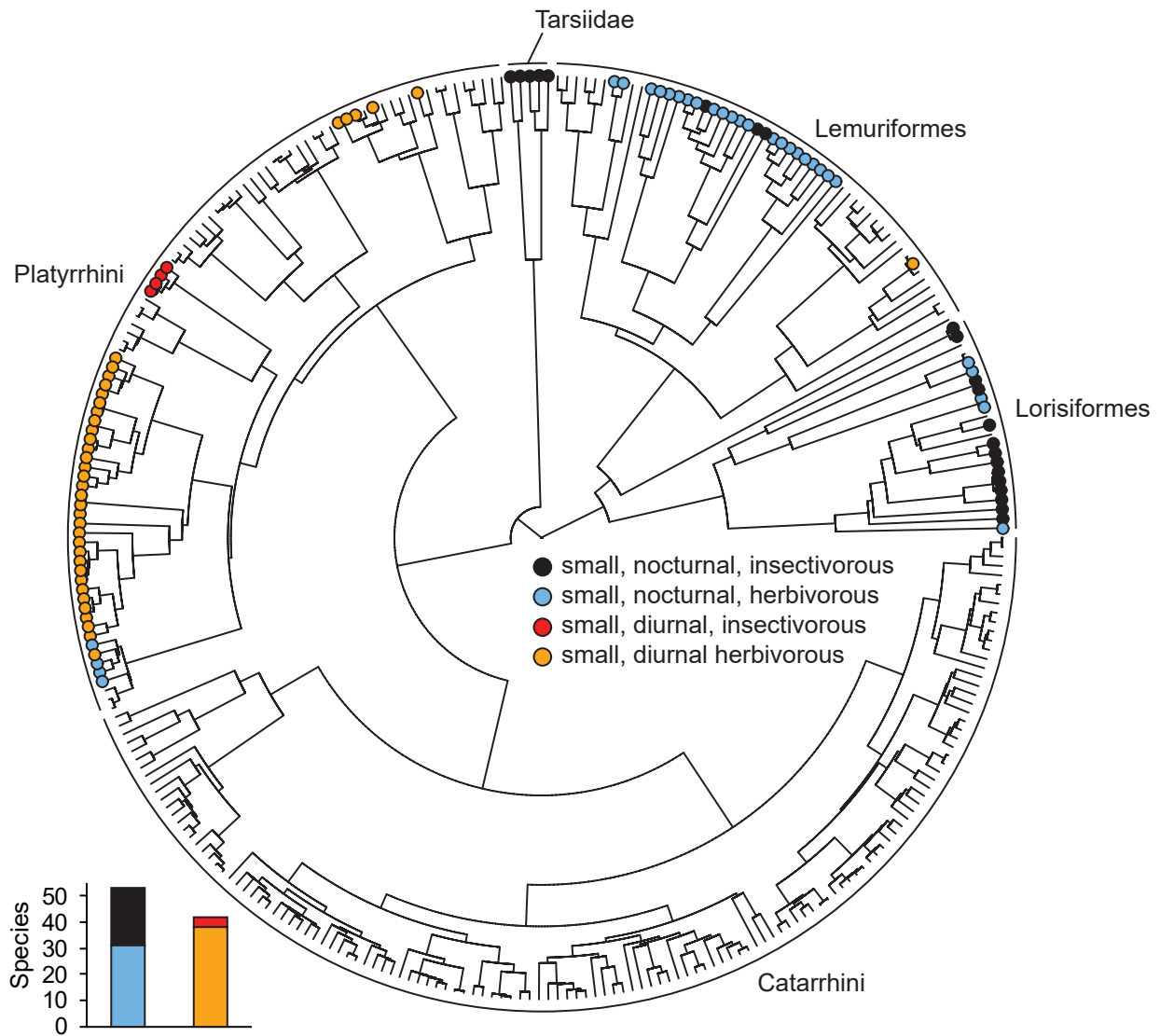
FIGURE 1. Primate phylogenetic tree from Springer et al. (2012) showing the distribution of trophic states by activity pattern among small-bodied species (<1 kg) at the tips (Scott, 2019). Cathemeral species are grouped with diurnal species. Large-bodied species, which are uniformly herbivorous and mostly diurnal, are not labeled. The relative frequency of insectivorous species is much greater among nocturnal lineages (41.5%) than among diurnal lineages (9.5%).
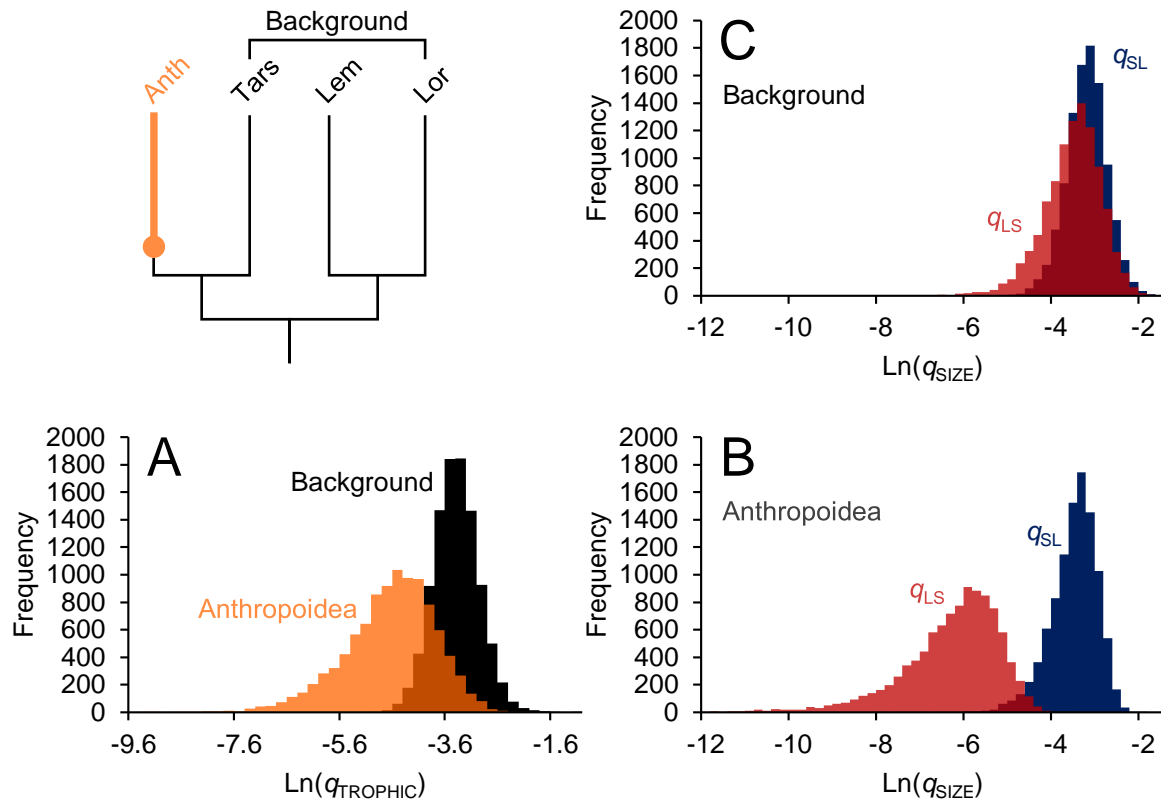
FIGURE 2. Posterior distributions of trophic transition rates (A) and size transition rates (B, C) for the model with Anthropoidea split from the rest of the tree and a size threshold of 800 g. The results shown here were generated using the timetree that assumed autocorrelated rates and soft-bounded constraints. Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor = Lorisiformes, q = transition rate, SL = small to large, LS = large to small.
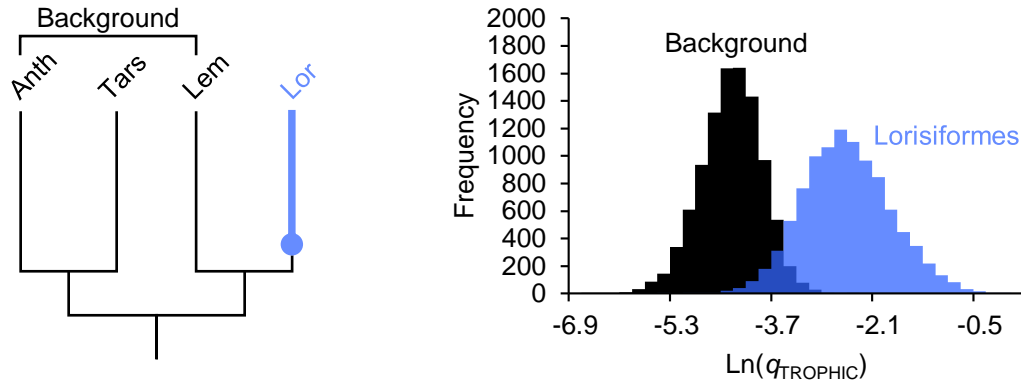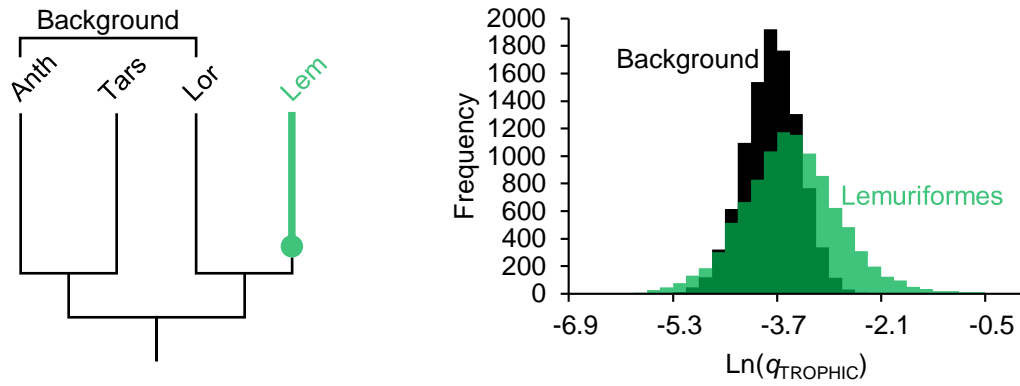
FIGURE 3. Posterior distributions of trophic transition rates for the model with Lorisiformes split from the rest of the tree and a size threshold of 800 g. The results shown here were generated using the timetree that assumed autocorrelated rates and soft-bounded constraints. Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor = Lorisiformes, q = transition rate.
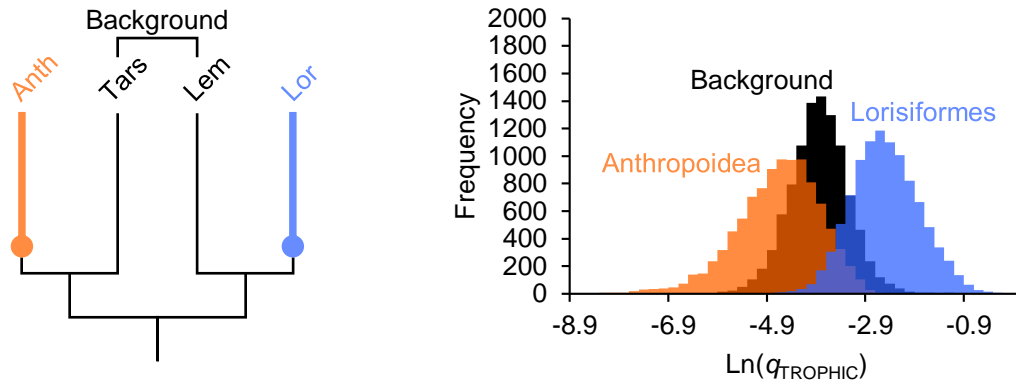
FIGURE 4. Posterior distributions of trophic transition rates for the model with Lemuriformes split from the rest of the tree and a size threshold of 800 g. The results shown here were generated using the timetree that assumed autocorrelated rates and soft-bounded constraints. Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor = Lorisiformes, q = transition rate.

FIGURE 5. Posterior distributions of trophic transition rates for the model with Anthropoidea and Lorisiformes each split from the rest of the tree and a size threshold of 800 g. The results shown here were generated using the timetree that assumed autocorrelated rates and soft-bounded constraints. Anth = Anthropoidea, Tars = Tarsiiformes, Lem = Lemuriformes, Lor = Lorisiformes, q = transition rate.
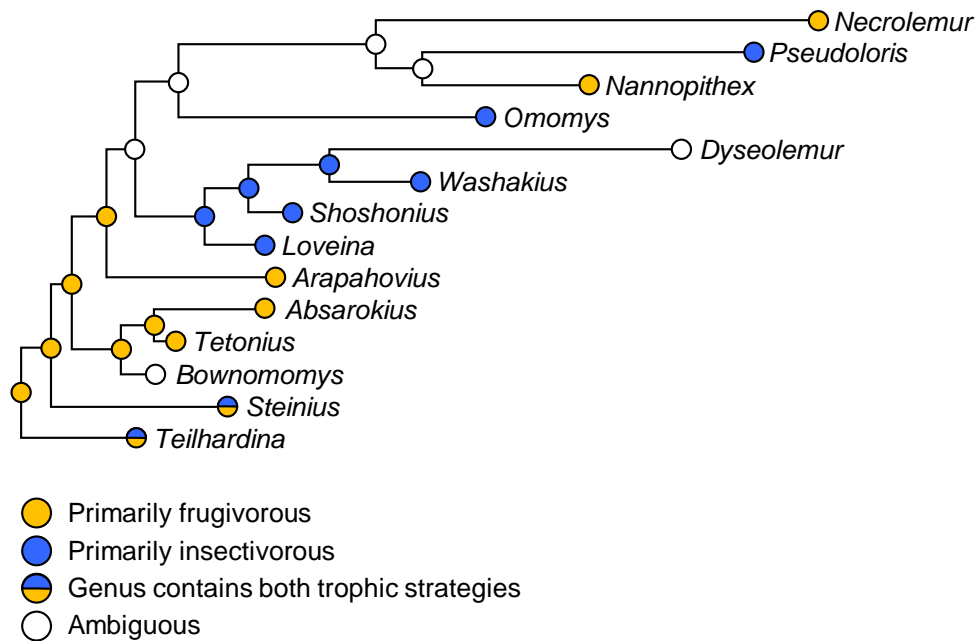
FIGURE 6. Phylogenetic distribution of trophic strategies among early and middle Eocene omomyiform genera. Dietary reconstructions for each genus are based mainly on the work of Strait (2001), with additional information from Ni, Wang, Hu, & Li (2004) and Williams & Covert (1994). Parsimony reconstructions of diet, obtained using Mesquite (v. 3.61; Maddison & Maddison, 2019), indicate a minimum of 5–7 shifts between trophic states, depending on how ambiguous taxa are coded. The reconstructions shown here are based on the data set where *Bownomomys* and *Dyseolemur* were coded as ambiguous (see Strait, 2001). The tree was taken from the Bayesian tip-dating phylogenetic analysis conducted by Seiffert et al. (2018; see their figure 17). Branch lengths are proportional to time; the tree spans approximately 20 million years from root to most recent tip (*Necrolemur*). *Teilhardina* includes *T. asiatica* and *T. belgica*; *Steinius* includes *S. vespertinus* and *S. annectens*; the use of *Bownomomys* here follows Morse et al. (2019) and is equivalent to *Teilhardina americana* in previous studies. See Strait (2001) and Seiffert et al. (2018) for the complete lists of species-level taxa.